

## WHY DOES TAIL LOSS INCREASE A LIZARD'S LATER VULNERABILITY TO SNAKE PREDATORS?

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**Abstract.** We examined how autotomy-induced shifts in behavior of a diurnal lizard (*Lampropholis guichenoti*) and two natural snake predators influence the outcome of predatory interactions. During staged encounters in seminatural enclosures, we estimated the consumption order of lizards with recently autotomised tails ("tailless") and intact tails ("tailed"). Tail loss increased a lizard's chances of being consumed first by a diurnal snake (*Demansia psammophis*), but not by a nocturnal species (*Rhinoplocephalus nigrescens*). We presented snakes with an inert tailed lizard vs. tailless lizard, scoring which was consumed first. Neither predator actively selected tailless prey. We quantified variation in the behavior of tailed and tailless lizards that determines the outcome of predator-prey interactions. Tailless lizards were not easier to detect visually or via chemoreception than were tailed lizards. Instead, the higher consumption rate of tailless lizards by the diurnal snake probably reflects reduced locomotor performance, and their tendency to flee sooner from approaching predators (thereby eliciting attack by this snake). In contrast, tail presence or absence did not determine a lizard's chances of detection by the nocturnal snake. Thus, tail loss can induce shifts in behavior of lizards, affecting their later chances of being consumed by some predators, but not by others.

**Key words:** antipredator behavior; caudal autotomy; *Demansia psammophis*; foraging mode; *Lampropholis guichenoti*; lizard; locomotor performance; microhabitat selection; nonrandom predation; prey selection; prey vulnerability; *Rhinoplocephalus nigrescens*; snake.

### INTRODUCTION

Autotomy of body parts is a defense mechanism employed by many organisms (e.g., lizards, snakes, reviewed in Arnold [1988]; salamanders, reviewed in Ducey et al. [1993]; crustaceans, cnidarians, spiders, insects, reviewed in Klawinski and Formanowicz [1994]). Such nonlethal injury usually facilitates release by a predator, and the shed portion of the body is often used as a distraction, engaging the attention of the predator during the lizard's escape (Arnold 1988). However, although autotomy yields an immediate benefit in terms of survival, an individual's subsequent fitness may be reduced by ensuing costs. For instance, losing body parts can slow growth rate, hinder foraging ability, decrease reproductive output, and diminish social status (reviewed in Smith 1995).

Autotomy may also reduce an individual's subsequent ability to evade predators, at least until the lost part of the body is regenerated (Arnold 1988, Robinson et al. 1991, Smith 1995). This depends on at least two factors: (1) how the loss of body parts influences the later behavior of prey and their predators (Allan and Flecker 1988, Arnold 1988), and (2) the species-specific foraging tactics employed by possible hunters (Greene and Landry 1985). Predators might actively

select (or reject) autotomised prey (Pastorok 1981, Greene and Landry 1985), but these tendencies could be masked if behavioral differences among damaged and nondamaged prey influence their chances of encountering or escaping potential hunters (Abrams 1986, Onkonburi and Formanowicz 1997). Alternatively, differential predation may result from shifts in the perceptible capacities of predators and the behavior of prey, rather than active prey selection per se (Pastorok 1981, Williamson 1993). Losing body parts can alter behavior that is a key component of predator-prey interactions, such as an individual's defensive capacity (Bildstein et al. 1989), locomotor performance (Semlitsch 1990, Robinson et al. 1991), levels of activity (Formanowicz et al. 1990, Martin and Salvador 1992), chemoreceptive responses (J. Hucko and P. Cupp, *personal communication*), and escape effectiveness (Congdon et al. 1974, Dial and Fitzpatrick 1983, Robinson et al. 1991). Additionally, autotomy-induced behavioral modifications are likely to affect an individual's chances of being consumed by some predators but not others (see Medel et al. 1988, Dial and Fitzpatrick 1983). For instance, shifts in levels of activity are probably crucial when prey are faced with active hunters, but largely irrelevant against predators that are sequestered under retreat sites when prey are moving about (Skelly 1994).

Tail autotomy is a major predator escape tactic in 13 of the ~20 lizard families, and can substantially influence behavior that may determine a lizard's chances of being consumed by predators. Running speed increases

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after tail loss in some lizards, but is substantially reduced or not affected in others (Arnold 1988). Tailless lizards may also restrict their general use of microhabitats, decrease distances to refuges during active periods, flee sooner from approaching predators, and lessen their time spent moving as well as general activity levels (reviewed in Martin and Salvador 1997). The reduced ability of tailless lizards to avoid predators has been demonstrated by staging direct encounters in laboratory environments (e.g., Congdon et al. 1974, Dial and Fitzpatrick 1984, Vitt and Cooper 1986), and inferred from indirect evidence obtained from comparisons of natural populations (reviewed in Wilson 1992, Niewiarowski et al. 1997).

Despite an abundant literature on this topic, no single study has examined how autotomy-induced shifts in the behavior of lizards and their predators interact to influence the outcome of predatory encounters. Most previous research has been conducted from a prey's perspective. It has either been purely correlative, or laboratory encounters were staged to directly examine escape success rather than the detailed interplay of behavior that affected the outcomes (reviewed in Arnold 1988, Niewiarowski et al. 1997). Two complimentary studies on *Scincella lateralis* (ground skink) provided important information on how tail loss modified levels of activity, flight distance, escape speed, and flight success from a snake predator (Dial and Fitzpatrick 1984, Formanowicz et al. 1990). However, no investigators have explored the ramifications of tail loss from a predator's perspective. Similarly, we are not aware of any researchers who have used various predators differing in foraging tactics to investigate how tailless lizards best cope with the selection pressures of multiple predators. In this study, we staged replicate encounters between unrestrained lizards and snakes in seminatural enclosures to examine differential consumption of lizards with recently autotomized tails vs. those with intact tails. These predation encounters were repeated with two snake species that differed in foraging mode. We then performed a series of manipulative experiments to examine behavioral processes that underlie the patterns of prey consumption by snakes in these predation encounters. By integrating the findings from these procedures, we were able to isolate the behavioral mechanisms of predation that affected the chances that tailed lizards and tailless lizards would be consumed by the two species of snakes.

## MATERIALS AND METHODS

### *The study system*

We used *Lampropholis guichenoti* (common garden skink) as our model prey. These small, heliothermic skinks, which have an adult snout-vent length (SVL) of 40 mm, are widely distributed in southeastern Australia, locally abundant, and a major item of prey for many elapid snakes (Shine 1991, Cogger 1994). When

faced with an approaching snake predator, these lizards first remain motionless, and then flee short distances to hiding places (S. Downes, *personal observation*). High frequencies of tail breaks followed by rapid regeneration in natural populations of this species (67% of adults from our study population,  $n = 485$ ; S. Downes, *unpublished data*) suggest that caudal autotomy may be a common tactic for escaping predators (Vitt et al. 1977). Our predators were *Demansia psammophis* (yellow-faced whip snake) and *Rhinoplocephalus nigrescens* (eastern small-eyed snake [*Cryptophis nigrescens* in earlier literature]). We selected these elapid snakes because they are small (maximum adult SVL of 650 mm in our study populations), occur sympatrically with garden skinks over most of their range, and scincid lizards are an important part of their diets. Both of these snakes search actively for prey. However, whip snakes are diurnal and pursue active lizards (Shine 1980, Scanlon 1998), whereas small-eyed snakes are nocturnal and search for sleeping (diurnally active) lizards (Shine 1984). Both snakes usually seek shelter under rocks or logs (Cogger 1994).

### *Animals and their maintenance*

The study consisted of a series of experiments conducted during November and December in 1996, 1997, and 1998. Whip snakes and small-eyed snakes were captured by hand at least four weeks prior to these times from areas along coastal New South Wales, Australia. We only used each snake once per experiment, but the same individuals were used in different experiments throughout the study. At least 20 days before use in our experiments, adult garden skinks were collected by hand or using sticky traps (Downes and Borges 1998) from areas near Sydney, New South Wales. Aggressive encounters in captive garden skinks are rare, especially among females (Torr and Shine 1996). Nonetheless, to reduce the potentially confounding effects of aggressive interactions among prey, we used only nongravid female lizards in our studies (Kaiser and Mushinsky 1985). Additionally, because it was not possible to obtain large numbers of animals with original tails, we used only animals that had completely regrown tails. The lizards ranged from 30 to 42 mm in SVL (mean  $\pm 1$  SE =  $36.1 \pm 0.14$ ) and up to 72 mm in tail length (mean  $\pm 1$  SE =  $51.0 \pm 0.70$ ). With every second lizard, we used forceps to induce tail loss 10 mm posterior to the base (hereafter referred to as tailless skinks), and removed the distal 5 mm from the tails of the remaining skinks (hereafter referred to as tailed skinks). We did not anaesthetize our subjects prior to inducing autotomy, as this process is neurologically controlled, and shown only by live, conscious animals. This adaptation serves to minimize blood loss and trauma. None of our lizards showed ill effects from our procedures. Unless otherwise stated, we performed experiments 10 days after tail manipulation, and lizards were not used in more than one experiment.

We housed the skinks and snakes at the University of Sydney, in separate rooms at 18°C. The light cycle was the natural cycle of the surrounding area. Lizards were maintained in plastic cages (220 × 130 × 70 mm) covered with soil (10 mm in depth) and containing wooden shelters, and fed mealworms and crickets every third day. Lizards used in the predation encounters were kept in groups of six individuals (three tailed lizards and three tailless lizards of the same SVL ± 0.5 mm), but skinks were housed individually in all other cases. Snakes were maintained individually in plastic cages (220 × 260 × 70 mm) lined with paper and containing a rock shelter, and fed one adult garden skink every 7–10 days. However, in all experiments involving snakes, we used individuals that were deprived of food for eight days. Heating was provided by an underfloor element that maintained a thermal gradient from ambient to 38°C for 8 h/d, falling to ambient temperatures overnight. All of the animals were supplied with water ad libitum.

*Estimates of nonrandom consumption of tailed vs. tailless lizards*

To examine nonrandom predation of tailed vs. tailless lizards we staged encounters between one snake and one prey group (three tailed skinks and three tailless skinks of the same SVL) in outdoor enclosures (1.8 × 1.8 m, with metal walls 1.6 m high). Hereafter these trials are termed “predation encounters”. The enclosures were located in a compound covered with plastic mesh to exclude large predators. Grasses and weeds in each enclosure were regularly pruned to ~50 mm in height. Two sandstone retreat sites (280 × 280 × 15 mm) and two pine blocks (200 × 100 mm<sup>2</sup>, 10 holes [18 × 60 mm] in one face) were supplied such that the same shelter type was available in diagonally opposing corners.

To determine the order in which snakes consumed the six prey in each group, we used wire microtags (0.25 mm in diameter; Northwest Marine Technology, Olympia, Washington, USA) to uniquely code skinks, and a hand-held X-ray scope (Lixi, Downers Grove, Illinois, USA) to read the tags from within the digestive tracts of snakes (see Downes 2000 for a detailed account of this procedure). The wire tags were injected under the skin of the lizard’s ventral surface, between the forearms. Individuals one to three were inserted with one, two, or three 0.5 mm long tags, and individuals four to six were injected with one, two or three 1 mm long tags. Upon injection, individual codes were checked using the X-ray scope. Extensive trials suggest that these methods have little, if any, influence on the behavior and well-being of skinks (Downes 2000).

We introduced one prey group into an enclosure and allowed them to acclimate undisturbed for three days. We began our predation encounters on the morning of the fourth day by introducing a small-eyed snake to the enclosure, or on the evening of the fourth day by in-

roducing a whip snake to the enclosure. This procedure was adopted to enable snakes to explore the new environment for up to 12 h before foraging commenced. Shortly after dawn on every day during the encounter, each snake was captured and its body cavity was scanned with an X-ray scope to identify which prey had been eaten and the order in which they had been consumed (see Downes 2000 for more information on these procedures). Snakes were returned to their points of capture immediately after scanning. An encounter was terminated when at least three of the lizards were eaten (~4–6 days), but all of the lizards were usually consumed. We performed this experiment over two years (1996–1997) with 25 whip snakes (mean SVL ± 1 SE = 524 ± 53 mm) and 24 small-eyed snakes (mean SVL ± 1 SE = 502 ± 47 mm). During each trial, a maximum of 14 enclosures was used, and equal numbers of each snake species were predators. All encounters began on sunny days with the forecast of similar weather for at least the next three days.

*Foraging patterns of snakes*

Before examining processes that may underlie nonrandom predation on skinks, it was necessary to verify the foraging patterns of the different snake predators. We determined whether snakes consumed lizards during the day or night by scoring when individual snakes ( $n = 10$  whip snakes, 10 small-eyed snakes) and garden skinks ( $n = 20$ ) were moving in an enclosure at hourly intervals over a 24-h period. Observations after dark were made with an Apple Nigteagle Vision Scope (Apple, Sydney, New South Wales, Australia). Following this, we estimated whether whip snakes searched for lizards that were in shelters or lizards that were actively moving about, by noting the times at which the whip snakes and garden skinks emerged from their overnight retreat sites during the first morning of each predation encounter. Garden skinks were considered to be active before snakes if three or more skinks (of any type) were observed out of their retreat site for at least 20 min before their potential predator.

*Estimates of active selection of tailed vs. tailless lizards by snakes*

To examine whether snakes actively selected among prey, we presented individual predators in outdoor enclosures with an inert tailed skink vs. an inert tailless skink, and scored which prey was consumed first. This procedure controlled for potential variation in the behavior of tailed and tailless lizards that may have prevented snakes from obtaining their preferred prey. All data are expressed as means ± 1 SE. For the trials with whip snakes ( $n = 15$ , SVL = 584 ± 33 mm), euthanasia was performed on a tailed skink and tailless skink (using carbon dioxide). The lizards were then immediately placed onto separate thin wooden carriages (30 × 4 mm, the body of the skink entirely covered the wood) that were both attached by fishing line to the end of a

rod (1 m long). These carriages (and skinks) were lowered onto an area devoid of vegetation, ~150 mm in front of the head of an actively searching whip snake, and were simultaneously slightly moved vertically by raising and lowering the horizontal rod. We recorded the first prey seized.

For the trials with small-eyed snakes ( $n = 14$ , SVL =  $434 \pm 43$  mm), we placed both a live tailed and tailless skink (individually tagged) in the same hole of one of the wooden retreat sites shortly before dusk, and covered the hole with cardboard until the snake became active. We then removed the cover and allowed the snake to select one or other prey. A pilot study on 10 lizard pairs indicated that skinks remained within the same hole of the retreat site at least until 0700 the next day. We scanned the body cavity of a snake before 0700 the following morning using the same procedure outlined above. Opportunistic observations ( $n = 3$ ) with the night vision scope suggested that a lizard is unable to escape from the retreat site upon being discovered by a foraging snake. On three occasions a snake did not select either skink; however, these experiments were successfully repeated on the following night.

*Estimates of differential vulnerability of tailed vs. tailless lizards*

*Discrimination of prey chemical cues by snakes.*—The responses of snakes to chemical cues of potential prey items may indicate the differential detection of certain prey (reviewed in Ford and Burghardt 1993). We recorded the chemoreceptive responses of snakes toward control and lizard scents immediately, and 10 days after manipulating the tail lengths of lizards. Four chemical stimuli were presented on the cotton swabs of 300-mm wooden applicators. (1) Swabs were dipped into distilled water (neutral control). (2) Swabs were dipped into a 1:1 solution of a commercial cologne and distilled water (pungency control). (3 and 4) Integumentary chemicals were obtained from tailed garden skinks and tailless garden skinks. Swabs were dipped into distilled water and blotted dry before they were rolled across the dorsal, lateral, and ventral surfaces of the lizard's tail (or the base). The snakes were tested one or two days prior to a predation encounter. Trials were conducted in a preset, fixed order whereby each treatment was presented first, to a randomly selected sample of six or seven individuals of the same species. The next treatment of the trial followed in this order: control, cologne, small garden skink, and large garden skink. To begin a trial, we slowly approached the snake's home cage and placed the swab 10–20 mm anterior to its snout. We then recorded the number of tongue flicks for a 60-s period beginning with the first tongue extrusion. We allowed at least two hours before presenting animals with another swab. Whip snakes ( $n = 25$ ) were tested between 0800 and 1630, and trials with small-eyed snakes ( $n = 24$ ) were carried out be-

tween 1800 and 2330 with the aid of a dim red light. The room temperature was  $25^\circ \pm 0.5^\circ\text{C}$ , snakes were always alert and stationary, and never attacked the swabs.

*Discrimination of predator chemical cues by lizards.*—Chemoreception is a common mechanism by which lizards can detect (and subsequently respond to) the presence of potential snake predators (reviewed in Schwenk 1995). We used the same procedures described above for snakes, to determine the responses of tailed lizards and tailless lizards to snake chemical cues ( $n = 21$  in both cases) two and nine days post-manipulation. In addition to the control and cologne swabs, the skinks were presented with scents from (3) whip snakes, and (4) small-eyed snakes. The trials were conducted in a preset, fixed order whereby each treatment was presented first, to a randomly selected sample of five or six tailed skinks and five or six tailless skinks. The next treatment of the trial followed this order: control, cologne, whip snake, small-eyed snake. Our scoring system was based on the assumption that fleeing from the swab during the trial was a stronger response than any number of tongue flicks (see Burghardt 1969, Cooper and Burghardt 1990 for a detailed justification of this procedure). Each trial was scored as the total number of tongue flicks in 60 s if the lizard did not run away from the swab. If the reptile fled from the swab, we used a base unit (the greatest number of tongue flicks given by any lizard in response to any stimulus) plus (60 minus the latency to run, measured in seconds). These trials were performed between 0800 and 1630 at  $25^\circ \pm 0.5^\circ\text{C}$ .

*Activity and movement patterns of lizards.*—A lizard's activity and movement patterns may influence its chances of being detected by visually oriented predators like whip snakes (e.g., Formanowicz et al. 1990). We observed the behavior of skinks within each enclosure prior to releasing the snake in the predation encounters. To simulate conditions where a lizard perceives a potential risk of predation, we covered each enclosure with the scents of predators by allowing a snake to move over the grass. At 0800 on the third day after introducing the skinks to each enclosure, we began observations that continued until 1700. Each enclosure was scanned for exactly two minutes, approximately each hour, and we noted the number of tailed and tailless lizards that were active (i.e., not under shelter) and whether they were stationary (this included basking) or moving.

*Retreat site selection by lizards and snakes.*—A diurnal lizard's choice of overnight retreat site may affect its chances of being detected by nocturnal predators such as small-eyed snakes. After the snakes were introduced to enclosures during the predation encounters, we waited for skinks to become inactive (~1700) and recorded the retreat site selected by each individual (lizards were returned to their retreat after identification). On the first morning of each predation encounter,

we recorded the overnight retreat site of snakes before they were captured for scanning. We also scored whether a lizard's choice of overnight retreat site affected its chances of being the first prey item for small-eyed snakes in the predation encounters.

*Flight responses of lizards.*—Garden skinks often become motionless upon detecting danger, but flee towards hiding places when approached by a predator (S. Downes, *personal observation*). We scored whether tail loss affected a lizard's tendency to flee from an approaching predator (flight response; Ydenberg and Dill 1986) immediately after tail breakage and 10 days later ( $n = 21$  for tailed and tailless lizards in both cases). The body sizes of lizards in each treatment group were similar. The predator was a model plastic snake (400 mm long), and our trials were performed at  $25^\circ \pm 0.5^\circ\text{C}$  in a large wooden arena ( $600 \times 650 \times 1800$  mm). We attached fishing line to the snake's neck and fed the other end through a small hole in the floor at the opposite end of the arena, passing it to one side. A transparent holding container ( $50 \times 170 \times 250$  mm) was placed immediately behind the hole, and the entire arena base was lined with sand. A lizard was allowed to acclimate inside the chamber for 10 min. We then commenced the trial if the lizard was at the front of the chamber and facing the snake. Otherwise, we herded the lizard into this position but did not disturb it for another 5 min. We then raised a partition located in front of the model and swung open the front end of the holding chamber. The model was left stationary for 5 s. We then moved the model 50 mm closer to the skink and left it stationary for 5 s. This procedure was repeated until the skink fled to the back of the container or the snake touched the skink.

*Locomotor performance of lizards.*—Speed is important for a fleeing lizard. We tested the immediate and persistent effects of tail removal on a lizard's locomotor performance using the 21 tailed lizards and 21 tailless lizards that were used in chemical detection trials. We sprinted these lizards one and eight days post-manipulation, and every 10 days thereafter (and measured their tail length) for 60 days; by this time, most tailless lizards had regrown at least 70% of their original tail length. Tests were performed over a range of body temperatures ( $16^\circ$ ,  $21.5^\circ$ ,  $27^\circ$ , and  $32.5^\circ\text{C}$ ), in a randomized order, for every lizard at each time interval. To begin a trial, a lizard was transferred directly from its container to the holding area of a raceway (40 mm wide), whereupon it was released and allowed to run a 1-m distance. If necessary, the lizard was chased with an artist's paintbrush. Photocells located at 250-mm intervals along the runway recorded the cumulative time taken for lizards to cross each successive infrared beam. Readings were corrected and expressed as meters per second. Each lizard was run twice with at least 30 min separating runs. From these data, we calculated the mean sprint speed over 1 m (mean of the runs),

and mean burst speed (mean of the fastest speed over any 250-mm segment).

*Frequency of tail loss in tailed lizards.*—Snakes may more easily capture tailless lizards because they can no longer employ tail loss (Congdon et al. 1974, Dial and Fitzpatrick 1984). The X-ray scope used to identify individual prey inside snakes also produced an image of the outline of a skink, indicating the presence or absence of a tail (Downes 2000). We determined the number of consumed tailed lizards that were tailless inside the stomachs of snakes during the predation encounters. We also noted how many uneaten tailed lizards were tailless at the termination of the predation encounters.

*Time to handle lizards.*—An attack is successful only if the predator can kill and consume the captured prey. We recorded staged laboratory encounters on videotape, to measure the time that it took whip snakes and small-eyed snakes ( $n = 25$  and  $24$  respectively) to kill and consume tailed and tailless lizards. These experiments were performed at  $25^\circ \pm 0.5^\circ\text{C}$  in glass terraria ( $400 \times 250 \times 100$  mm), that were devoid of shelter to permit the rapid capture of prey. Skinks were introduced to terraria containing snake predators. Half of the snakes of each species were presented with tailed individuals in the first instance. From the videotapes, we timed the period between the first seizure of the skink and the swallowing of this prey to the base of its tail (handling time). Both species of snake maintained a firm bite during envenomation.

#### Data analysis

The data were checked for all relevant assumptions before statistical analysis. Some variables were log-transformed to normalize variances. Goodness-of-fit tests were used to compare observed and expected (random) frequencies of categorical data. We used log-linear models (LLM) to test for significant interactions between three or more categorical variables. We fitted models with interaction effects of uniform order to the data. In each case, the model of complete independence fitted the data well (i.e.,  $P > 0.05$  for the likelihood ratio), thus we concluded that this was the "best" model (Lee 1978). Analysis of variance (ANOVA) was used to examine the relative contribution of different factors to the total amount of the variability in continuous dependent variables. We used repeated-measures ANOVA for repeated measures of similar variables on the same animal (i.e., the response to scent stimuli, and time to handle lizards) or the same variable over time or at different temperatures (i.e., running speed). The factors and repeated measures used in each ANOVA model are reported with the summaries of results. We included "first lizard type" as a factor in ANOVA on data from the handling times of snakes, because half of the subjects were first presented with either tailed or tailless lizards. There was no significant interaction between the type of lizard presented first to a snake

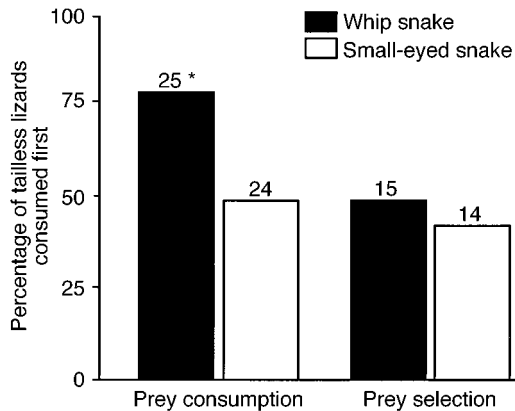


FIG. 1. The proportion of tailless lizards that were the first prey for whip snakes (*Demansia psammophis*) and small-eyed snakes (*Rinoplocephalus nigrescens*) during the experiments examining differential prey consumption and prey selection. See *Materials and Methods* for definitions. The number of snakes used in each experiment is shown above each bar. An asterisk above the histogram indicates a significant bias ( $P < 0.05$ ) as indicated by goodness-of-fit tests.

and the other factors considered in the ANOVA model. All analyses were tested for statistical significance at the  $P < 0.05$  level.

## RESULTS

### *Estimates of nonrandom consumption of tailed vs. tailless lizards*

We scored the type of prey consumed first in each predation encounter and used these data to examine nonrandom consumption of tailed vs. tailless lizards by snakes. A larger than expected proportion of tailless lizards was captured first by whip snakes ( $\chi^2$  test:  $df = 1$ ,  $P < 0.001$ ), but tail length did not influence the chances that a lizard would be the first prey item for small-eyed snakes ( $\chi^2$  test:  $df = 1$ ,  $P = 1.00$ ; Fig. 1).

### *Foraging patterns of snakes*

Our 24-h observation of the activity of snakes and lizards confirmed that whip snakes and garden skinks are strictly diurnal (no individuals were active during the night) and small-eyed snakes are strictly nocturnal (no snakes were active during daylight). In the mornings, skinks were usually moving about before the whip snake in the same enclosure (this was the case in 23 vs. 2 enclosures;  $\chi^2$  test:  $df = 1$ ,  $P < 0.001$ ). Late in the afternoons, whip snakes usually became inactive before skinks in the same enclosure (this was the case in 21 vs. 4 enclosures;  $\chi^2$  test:  $df = 1$ ,  $P < 0.001$ ). Thus, during the predation encounters whip snakes probably interacted with lizards that were active, whereas small-eyed snakes always interacted with lizards that were sequestered within their overnight retreat site.

### *Estimates of active selection of tailed vs. tailless lizards by snakes*

Both snake species randomly selected their first prey when we presented them with an inert tailed lizard and an inert tailless lizard at the same time ( $\chi^2$  test:  $df = 1$ ;  $P = 0.285$ ,  $0.796$  for small-eyed snakes and whip snakes respectively; Fig. 1). Thus, these predators did not actively select among lizards based on the presence or absence of a tail.

### *Estimates of differential vulnerability of tailed vs. tailless lizards*

*Discrimination of prey chemical cues by snakes.*—The responses of snakes and lizards to control scents (as measured via tongue flicking) were extremely weak (mean number of flicks per minute  $\leq 4.80$  in all cases); thus, we performed our analyses without these data. Because we were interested in a reptile's capacity to respond to biologically meaningful chemical cues rather than the ability to simply detect a novel stimulus, our response variable was the difference between the number of tongue flicks toward reptile scent and the number of tongue flicks toward cologne scent.

Whip snakes responded more strongly to the odors of tailless lizards soon after tail removal than they did 10 days later (ANOVA with snake species as a factor and scent and time as repeated measures: time  $\times$  scent:  $df = 1$ ,  $47$ ;  $P = 0.001$ ; Fig. 2a). However, separate analyses on data from these two time periods showed no significant variation in the responses of snake predators to the scents of lizards with and without tails (ANOVAs with snake species as a factor and scent as a repeated measure:  $df = 1$ ,  $47$ ;  $P = 0.359$ ,  $0.234$  immediately and 10 days later respectively; Fig. 2a).

*Discrimination of predator chemical cues by lizards.*—Tail loss affected the responses of lizards to snake chemical cues, but the magnitude of these trends varied with time since tail removal (ANOVA with tail condition as a factor and scent and time as repeated measures: time  $\times$  scent:  $df = 1$ ,  $36$ ;  $P = 0.026$ ; Fig. 2b). We therefore performed separate analyses on data from the two time periods. Immediately after tail manipulation, tailless lizards responded significantly more strongly to the scents of both snake species than did lizards with tails (ANOVA with tail condition as a factor and scent as a repeated measure:  $df = 1$ ,  $36$ ;  $P = 0.039$ ; Fig. 2b). However, there was no such result 10 days after tail removal (using the same ANOVA model:  $df = 1$ ,  $36$ ;  $P = 0.559$ ; Fig. 2b). There was no significant variation in the number of tailed vs. tailless lizards that fled from the scent stimuli during the trials (immediately: 23 tailless vs. 17 tailed; 10 d later: 26 tailless vs. 18 tailed;  $\chi^2$  test:  $df = 1$ ,  $P = 0.343$ ,  $0.228$  respectively).

*Activity and movement patterns of lizards.*—All data are expressed as mean  $\pm 1$  SE. Tailless lizards were less likely to be out of their retreat sites during the day

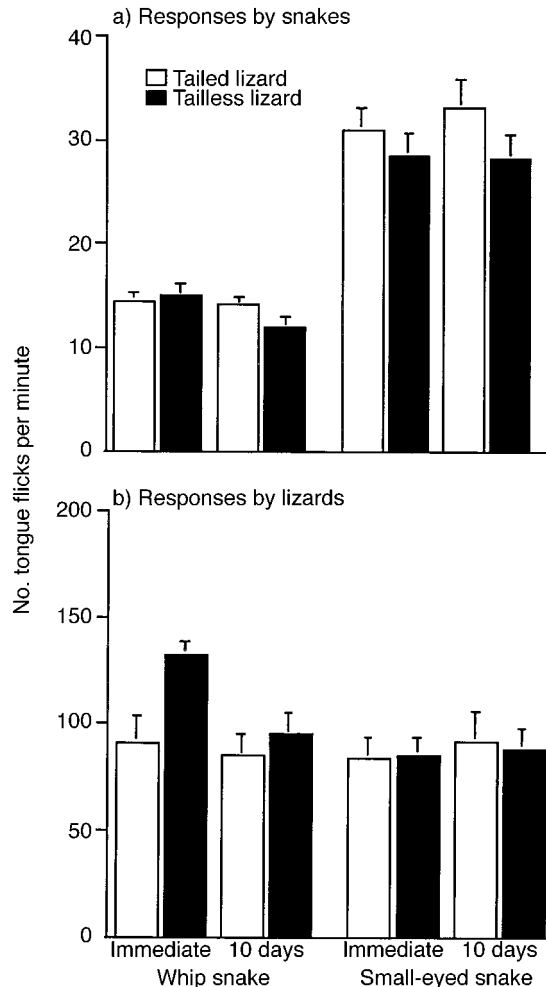


FIG. 2. Mean + 1 SE frequency of tongue flicks per minute by (a) whip snakes (*Demansia psammophis*) and small-eyed snakes (*Rinoplocephalus nigrescens*) in response to cotton swabs treated with the scents of tailed garden skinks and tailless garden skinks (*Lampropholis guichenoti*), and (b) by tailed garden skinks and tailless garden skinks in response to cotton swabs treated with the scents of whip snakes and small-eyed snakes. In both cases, the response variable is the number of tongue flicks toward snake or lizard scent minus the number of tongue flicks toward cologne (see *Materials and Methods* for a justification of this procedure). Trials were conducted as soon as we manipulated the tails of the lizards (immediate), as well as just prior to our staged encounters (10 days later).

than were lizards with tails (number of active tailless vs. tailed lizards/enclosure/hour:  $1.05 \pm 0.06$  vs.  $1.38 \pm 0.07$ ; ANOVA with snake scent and tail condition as factors:  $df = 1, 54$ ;  $P = 0.005$ ). Relative to tailed lizards, a significantly greater proportion of skinks without tails remained stationary while they were away from their retreat site (percentage of stationary tailless vs. tailed skinks:  $90 \pm 2\%$  vs.  $58 \pm 4\%$ ; using the same ANOVA model:  $df = 1, 54$ ,  $P < 0.001$ ).

*Retreat site selection by lizards and snakes.*—The overnight retreat site selection behavior of lizards was

not significantly influenced by the presence or absence of a tail (log-linear model of independence between tail condition, snake scent, and retreat site:  $df = 7$ ,  $P = 0.997$ ). In most cases, lizards selected wooden blocks as overnight shelters (number of skinks/enclosure:  $0.7 \pm 0.3$  rock vs.  $4.0 \pm 0.3$  wood vs.  $1.7 \pm 0.3$  grass). Whip snakes preferred rocks as overnight shelters (22 rock vs. 1 wood vs. 2 grass;  $\chi^2$  test:  $df = 2$ ,  $P < 0.001$ ), whereas small-eyed snakes preferred grass as a diurnal retreat site (2 rock vs. 3 wood vs. 19 grass;  $\chi^2$  test: 2  $df$ ,  $P < 0.001$ ). Snakes and lizards never shared the same retreat site.

Skinks that sheltered in grass were significantly more likely to be the first prey for small-eyed snakes than were those that spent the night in wooden or rock retreat sites (percentage of lizards in each retreat site consumed first = 26% wooden, 50% grass, 0% rock;  $\chi^2$  test:  $df = 2$ ,  $P < 0.001$ ).

*Flight responses of lizards.*—The flight responses of tailless skinks and tailed skinks differed immediately after tail manipulation and also 10 days later. In both cases, tailless lizards were significantly more likely to flee from the model snake predator than were tailed lizards (number of tailed vs. tailless lizards that fled: immediately, 13 vs. 20; 10 d later, 12 vs. 19;  $\chi^2$  test:  $df = 1$ ;  $P = 0.018, 0.021$  respectively).

*Locomotor performance of lizards.*—Tail loss influenced a lizard's subsequent running performance, but the magnitude of these trends depended on test temperatures and time since breakage (ANOVA with tail condition as a factor and temperature and time as repeated measures: tail condition  $\times$  temperature  $\times$  time:  $df = 18, 756$ ;  $P < 0.001$  over 1 m and 0.25 m; Fig. 3). We therefore used the same ANOVA model but performed separate analyses on data from two time periods and without data at the coldest temperature ( $16^\circ\text{C}$ ). At the three warmest temperatures ( $20.5^\circ$ ,  $27^\circ$ , and  $32.5^\circ\text{C}$ ), tailless lizards were significantly slower than lizards with tails for up to 40 d postautotomy ( $df = 1, 336$ ;  $P < 0.001$  over 1 m and 0.25 m), representing a mean reduction in speed of between 12% and 15%. However, there was no significant difference in the running speeds of tailed and tailless lizards between 40 days and 60 days postautotomy at these warm temperatures ( $df = 1, 84$ ;  $P = 0.761, 0.484$  over 1 m and 0.25 m respectively; Fig. 3). Tail loss did not significantly affect a lizard's running speed at the coldest test temperature (ANOVA with tail condition as a factor and time as a repeated measure:  $df = 1, 252$ ;  $P = 0.528, 0.485$  over 1 m and 0.25 m respectively; Fig. 3). Most tailless lizards had regrown ~50% of their original tail length by 40 days after tail removal.

We used partial correlation techniques to examine (separately for each temperature) the strength of the relationship between tail growth and locomotor performance with the effects of time since tail loss removed. For each time period ( $n = 7$ ) we used data from three different tailless lizards that were randomly se-

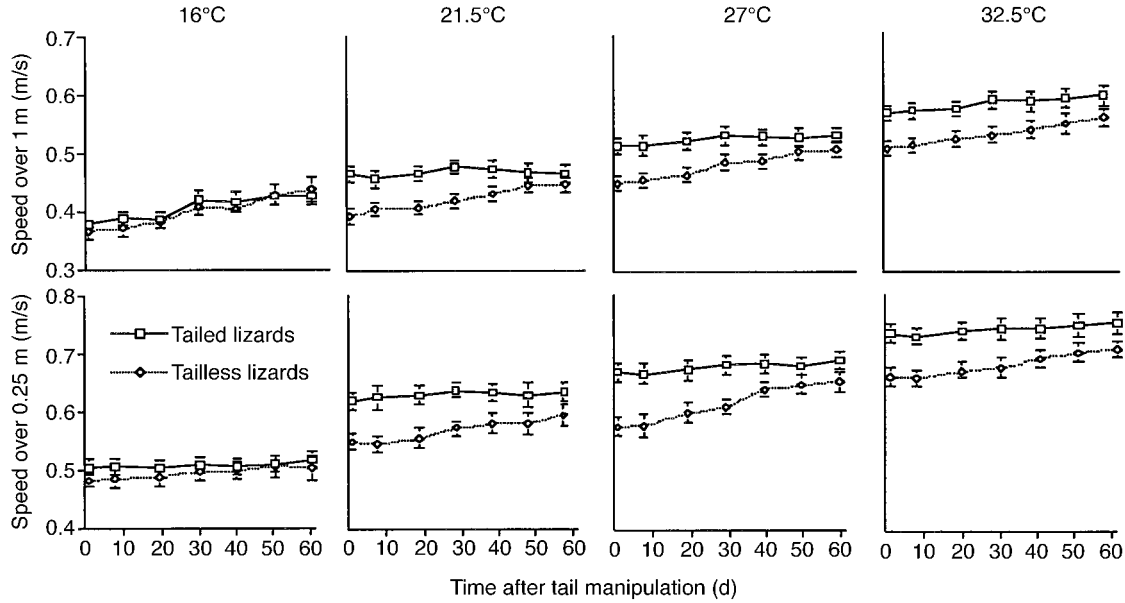


FIG. 3. Mean  $\pm$  1 SE locomotor performance (meters per second) of tailed garden skinks and tailless garden skinks (*Lampropholis guichenoti*,  $n = 21$  in both cases). Sprint speeds were measured one and eight days after we manipulated their tails, and every 10 days thereafter for 60 days. At each time interval, we repeated the trials at four different body temperatures: 16°, 21.5°, 27°, and 32.5°C. Upper and lower graphs display speeds over 1 m and 0.25 m respectively.

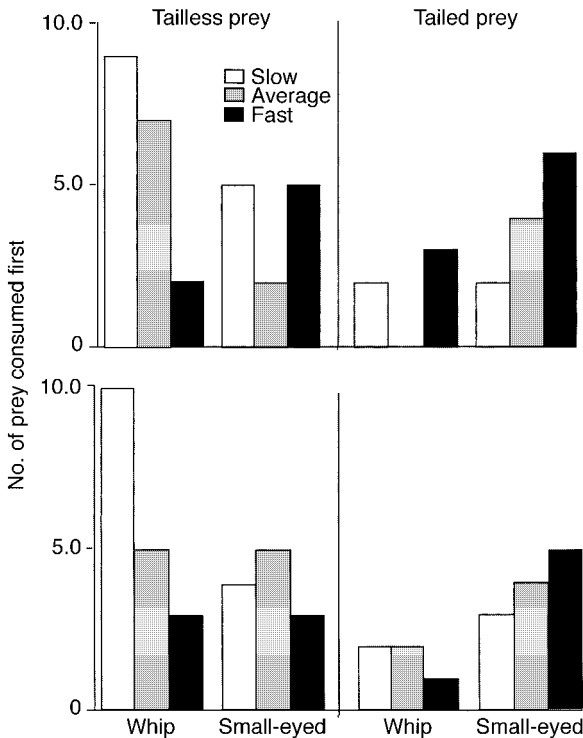


FIG. 4. The summed number of “slow,” “average,” and “fast” sprinting lizards that were the first prey taken by whip snakes (*Demansia psammophis*) and small-eyed snakes (*Rinoplocephalus nigrescens*) during the predation encounters. The upper and lower graphs use locomotor performance over 1 m and 0.25 m, respectively, to categorize lizards into the three sprinting classes.

lected from the 21 tailless individuals used in the experiment. There was no relationship between the running speeds of tailless lizards and tail regrowth at the coldest test temperature ( $r = -0.022, 0.120$  for 1 m and 0.25 m respectively), but there were strong positive relationships between the speeds of tailless lizards and tail regrowth under the warmer conditions ( $r > 0.502$  in all cases).

We classified the prey within each enclosure as “fast” (ranked 1 against the other two lizards of the same type), “average” (ranked 2), or “slow” (ranked 3), and scored the status of the first individual consumed by each snake during the predation trials. The fastest tailless individuals were generally less vulnerable to whip snakes than were slow sprinters of the same prey type (Fig. 4) but this trend fell short of statistical significance ( $\chi^2$  test:  $df = 2, P = 0.114$  over 0.25 m and 1 m). No such trend was evident for either type of prey during encounters with small-eyed snakes ( $\chi^2$  test:  $df = 2, P > 0.368$  for both tests over 0.25 m and 1 m; Fig. 4).

*Frequency of tail loss in tailed lizards.*—During the predation encounters with small-eyed snakes, we never found a recently autotomised tailed lizard within a predator, and none of the uneaten tailed lizards were tailless. However, during predation encounters with whip snakes, 14% of the consumed tailed lizards ( $n = 66$ ) employed tail loss prior to being eaten and 56% of the uneaten tailed lizards ( $n = 9$ ) were tailless. We could not assess at what point during the predation encounters the tailed lizards employed caudal autotomy.

*Time to handle lizards.*—Tail presence or absence did not significantly affect the time that it took snakes to kill and consume captured skinks (mean  $\pm$  1 SE time to handle tailed vs. tailless:  $65.1 \pm 4.9$  s vs.  $65.8 \pm 8.4$  s; ANOVA with snake species and first lizard type as factors and tail condition as a repeated measure:  $df = 1, 47$ ;  $P = 0.874$ ).

#### DISCUSSION

Most predation events can be divided into five main phases: encounter, detection, pursuit, subjugation and consumption (after Endler 1986). Opportunistic observations during our predation trials indicate that the snakes and lizards within our enclosures were always in an encounter situation. That is, the distances separating snakes and lizards were at all times less than their detection radii (e.g., Lima and Dill 1990). Since tail presence or absence in lizards did not affect how long it took snakes to consume prey, we also assume that this phase was not of major consequence. Whip snakes actively pursued moving lizards and at least some of their attempts to subdue skinks were unsuccessful; thus, the detection, pursuit and subjugation phases of predation were important in encounters with this species. In contrast, detection was the only phase in which there was likely to be sufficient variation in the predation efficiency of small-eyed snakes, because our lizards were inactive while this species was hunting. We have restricted our discussion to those phases of predation that may have influenced prey consumption.

Our predation experiments were designed to mimic an encounter between a snake and a group of skinks in their natural habitat. Our trials were performed under conditions that mimicked those in the field. We used large numbers of individual predators to avoid pseudoreplication (Hurlbert 1984), only female lizards were used to minimize aggressive interactions among prey (Kaiser and Mushinsky 1985), and tailed skinks had the tips of their tails removed to control for possible stress associated with tail manipulation (Wise and Jaeger 1998). Hence, our findings are likely to accurately demonstrate how tail loss affects a garden skink's later chances of being consumed by our nocturnal and diurnal snake predators. Our results for the diurnally foraging snakes are consistent with those of other investigators in that tailless lizards are more likely to be consumed by predators in laboratory experiments (e.g., Congdon et al. 1974, Daniels et al. 1986, Dial and Fitzpatrick 1984). However, we are not aware of another study that staged encounters between diurnal tailed and tailless lizards and nocturnal predators (but for examples of differential utility of tail autotomy as an escape tactic against different kinds of predators see Dial and Fitzpatrick 1983, Medel 1988). We found that tail loss did not affect a lizard's subsequent chances of being consumed by the nocturnal small-eyed snake.

The patterns in our predation data were not deter-

mined by active choice behavior of whip snakes (see also Menge 1972, Downes 2000). Instead, nonrandom predation by these snakes reflects the differential vulnerability of tailed and tailless lizards (Pastorok 1981, Williamson 1993). Thus, tail loss altered some behavioral components of the predator-prey interaction between snakes and lizards, and the dire consequences of these shifts depended on the species-specific foraging strategies employed by potential predators. We are aware of only one other study that may have coincidentally tested for active selection of tailed vs. tailless lizards by predators. Before staging encounters between spotted night snakes (*Hypsiglena achrorhyncha*) and geckos (*Coleonyx variegatus*), Congdon et al. (1974) tested for differences in predator attack and prey behavior related to the presence or absence of tails on lizards. They found no such differences.

Several lines of evidence suggest that the reduced escape speed of tailless lizards may have increased their chances of being consumed by whip snakes (see also Christian and Tracy 1981, Watkins 1996). Whip snakes are swift, visually oriented predators that pursue active prey (Scanlon 1998), and garden skinks rely heavily on running to escape predators (Qualls and Shine 1998). Tail loss reduced the running speed of skinks by between 12% and 15% for several weeks after breakage (depending on the test temperature; Fig. 3), and slower tailless lizards were more likely to be captured by whip snakes than were faster tailless lizards (note however, that this result fell short of statistical significance; Fig. 4). Additionally, tail loss resulted in few persistent modifications to other aspects of the behavior of garden skinks and whip snakes that might have increased the chances of tailless lizards being captured. However, prey movement typically elicits predatory attack by whip snakes (Scanlon 1998; S. Downes, *unpublished data*). Thus, the tendency of tailless lizards to flee from approaching predators may have increased their chances of being pursued by this snake species (Kanou and Shimozawa 1983, Skelly 1994). Tailless lizards were also temporarily unable to employ tail loss as a last-ditch defense against whips snakes (Wilson 1992), and our results indicate that this may have enhanced their chances of being captured by an attacking snake (see also Congdon et al. 1974, Dial and Fitzpatrick 1984).

In contrast, selection of overnight microhabitats by garden skinks (rather than tail presence or absence) was an important determinant of their probability of being consumed by small-eyed snakes (see Martin and Salvador 1992, Jones and Paszkowski 1997). Lizards sheltering within grass were eaten most often. This trend likely reflects how frequently snakes detected lizards in the different retreat sites (Pastorok 1981, Schwarzkopf and Shine 1992). Small-eyed snakes may have concentrated their search within grass microhabitats, since they usually selected these areas as diurnal retreat sites. Our behavioral assays suggest that chemorecep-

tion is an important mechanism for prey detection by small-eyed snakes (Fig. 2a). This capacity probably affected the detection rates of skinks by small-eyed snakes (Schwenk 1995, Downes 1999), but we do not know how this might have varied among retreat sites. We cannot assess why most lizards avoided grass retreat sites, because our experiments focused on behavioral differences between tailed vs. tailless lizards, rather than on variation in the behavior of lizards under different risks of predation (Lima and Dill 1990). Tailed and tailless lizards were not differentially vulnerable to small-eyed snakes, because tail loss did not influence either the chemosensory responses of these predators, or a lizard's selection of overnight retreat site.

Our results show that autotomy-induced shifts in behavior can vary significantly over small temporal scales. For instance, recently autotomised lizards responded more strongly to the scents of snakes than did tailed lizards, but there was no such trend upon staging our encounters 10 days later (Fig. 2b). In many cases, there is probably a high chance of subsequent attack immediately after an unsuccessful predation attempt. Thus, a heightened ability to detect snake scent may enhance instantaneous predator avoidance by tailless lizards that have a reduced ability to escape by fleeing (Thoen et al. 1986, Schwenk 1995). Another explanation is that we may not have adequately simulated an autotomic event on our tailed skinks (by removing only the tip of their tail), and the stronger responses of tailless lizards might reflect stress associated with tail removal (Wise and Jaeger 1998). Regardless of the mechanism(s), the outcomes of our predation encounters might have been different if they had been conducted sooner after tail removal (see also Martin and Salvador 1992).

We examined how tail loss affected behavioral components of predator-prey interactions, because natural selection may act more directly on these whole-organism performance abilities than on lower-level morphological and physiological traits (e.g., Arnold 1983, Garland and Losos 1994). Our experiments did not address whether caudal autotomy influences the probability of an encounter situation between a lizard and a snake. However, we have shown that tail loss modifies behavior that directly impacts on predation encounters, increasing the chances that garden skinks will be consumed by (some) snake predators. Tail loss also induces shifts in behavior that are not directly related to predation. These modifications may indirectly affect a lizard's probability of being eaten (e.g., Fox and Rostker 1982, Martin and Salvador 1993, 1997). Studies comparing predation by snakes that do not actively select among prey can isolate mechanisms that underlie the differential vulnerability of tailless vs. tailed prey. That is, underlying behavioral processes can be examined in a stepwise fashion by selecting a suite of predators whose species-specific foraging modes operate on a different phase (or phases) of predation. This approach

offers additional information on how tailless lizards best cope with the selection pressures of multiple predators. Many snake-lizard systems may prove to be good predator-prey models for future research in this area, as well as for studies of differential prey consumption in general.

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