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ABSTRACT—We investigated the importance of size, loss of tail, and running speed of banded geckos (*Coleonyx variegatus*) in encounters with a predatory snake (*Hypsiglena chlorophaea*) in experimental arenas. We discovered, contrary to previously reported results and our own hypotheses based on observations in the field, that none of these factors influenced risk of predation, and that autotomy was not used commonly as a tactic to escape predators. Based on these results and observed behavior during predation trials, we question whether tail autotomy in this species is an effective anti-predator adaptation.

RESUMEN—Investigamos la relevancia del tamaño corporal, desprendimiento de la cola, y velocidad de escape de la lagartija (*Coleonyx variegatus*) en encuentros con el depredador ofidio (*Hypsiglena chlorophaea*) en arenas experimentales. Descubrimos, contrario a resultados aportados previamente y a nuestras propias hipótesis fundamentadas en observaciones del campo, que ninguno de estos factores influyó en el riesgo de la depredación, y que la autotomía no fue empleada como táctica habitual para escapar de los depredadores. Basándonos en estos resultados y en el comportamiento observado durante las pruebas de la depredación, cuestionamos si la autotomía caudal en esta especie es una adaptación efectiva frente a los depredadores.

Predators can exert strong selective pressures on prey organisms, and squamates employ a variety of behaviors that appear to have evolved to aid in avoidance of predators (Greene, 1988). The nocturnal terrestrial geckos *Coleonyx variegatus* and *C. brevis* have been useful subjects for studies of some of these behaviors (e.g., Congdon et al., 1974; Johnson and Brodie, 1974; Dial et al., 1989). This is in part because they respond quickly and dramatically to presence of a potential predator, even in a laboratory setting. The typical response includes standing rigidly with legs extended so that the body is elevated off the substrate and slowly undulating the autotomous tail over the back. By drawing the attention (and strike) of a predator to the autotomous tail, the lizard may be able to escape with its life. A strike to another part of the body affords no such opportunity. *Coleonyx variegatus* has many characteristics typical of autotomous lizards (Arnold, 1984); it is small, delicate, and has no obvious means of physical defense. The tails are banded, which probably renders it conspicuous under low lighting. Some individuals readily drop their tails when captured by humans, and by the time they reach full size, 55% (males) to 74% (females) of *C. variegatus* have lost their tails at least once (Parker, 1972).

In addition to these natural-history observations, experiments in laboratory settings have demonstrated the escape value of caudal autotomy in a variety of species (Bateman and Fleming, 2009), including *C. variegatus* and C. *brevis* (Congdon et al., 1974; Dial, 1978). The latter two studies have became part of standard material for teaching animal behavior to undergraduate students, making their way into introductory textbooks (e.g., Alcock, 1993). Based on this evidence, we hypothesized that, in general, *Coleonyx* with tails should have an advantage over tailless geckos in escaping from predators.

Interestingly, size of body may affect use of tail autotomy as a tactic to avoid predators by *C. variegatus.* In nature, we observed that large and small *C. variegatus* tended to respond differently to disturbance by humans. When their diurnal cover was lifted, large geckos usually exhibited the typical response described above. However, small geckos tended to flee while squeaking loudly. We hypothesized that smaller geckos may be less successful at escaping predation through use of tail autotomy because their tails are smaller and, therefore, may be less effective as visual lures. Thus, perhaps they are more likely to survive an encounter with a predator by fleeing than by attempting to use a relatively inconspicuous caudal lure. Bateman and Fleming (2009) reviewed several instances of lizards in which young and adults differed in predator-defense strategies, including differences in caudal-autotomy behavior. Meanwhile, why would a large gecko remain in the presence of a predator if flight was an option likely to be successful? If both tactics might be

TABLE 1—Summary of hypotheses tested in this study of the importance of size, loss of tail, and running speed of banded geckos (*Coleonyx variegatus*) in encounters with a predatory snake (*Hypsiglena chlorophaea*) and corresponding results.

Hypothesis	Experiment	Result
Large geckos are more likely than small geckos to use tail autotomy in escaping from predators.	1, 2	Tail autotomy was rare; size did not affect probability of capture.
Geckos with tails have a survival advantage over tailless geckos in encounters with predators.	2	Tail autotomy was rare; size and tail treatment did not affect probability of capture.
Being tailless is more disadvantageous for large geckos than for small geckos in escaping from predators.		
Large geckos have slower speeds during escapes than small geckos.	3	Burst speed was not strongly correlated with size; burst speed did not increase after tail autotomy.
Geckos have higher burst speeds afte tail autotomy.		
Geckos with higher burst speeds have an advantage in escaping from predators.	4	Burst speed did not affect probability of capture.

equally likely to result in escape, certainly autotomy is more costly than flight. We hypothesized that larger geckos chose autotomy because they have relatively slow speeds during escapes; perhaps, due to their pendulous tails. Tails of smaller geckos are thinner and appear less likely to interfere with locomotion.

We performed four sets of experiments to test our hypotheses (Table 1). First, we compared risks of predation for pairs of tailed geckos, one large and one small, in a relatively small arena with a predatory snake (*Hypsiglena chlorophaea*). Second, we performed a similar test but with four geckos at a time, two large and two small, where we had autotomized the tail of one gecko in each size-class. Next, we measured burst speed of a group of geckos across a wide range in size, both before and after inducing tail autotomy. Finally, we compared risk of predation for pairs of geckos matched in size and presence of tail but differing in burst speed.

MATERIALS AND METHODS—Geckos used in this study were collected from Maricopa County, Arizona, in March 1992, and had been kept in captivity <6 months. All were feeding well and were maintained under similar conditions. In experiments where tails were autotomized, we grasped the tail close to the base with forceps and pulled gently until intravertebral breakage. In some instances, geckos that survived a trial were re-used in subsequent trials, but, in those instances, geckos were matched for number of experiences in trials, as well as any other relevant factors dictated by experimental protocol.

Areas of tails were measured using an adaptation of the technique described by Wise and Buchanan (1992); geckos were placed on a sheet of clear plastic, immobilized by gently pressing down with a piece of soft foam rubber, and the outlines from a dorsal aspect was traced onto paper. These outlines were cut out and areas of the tail were measured using a portable leaf-area meter. Data on snout-vent lengths and areas of tail from all geckos used in these experiments were analyzed so that the overall relationship between size of body and tail could be determined.

Snakes (*Hypsiglena chlorophaea*) were collected in the same area as the geckos, and all were adults large enough to subdue and swallow prey throughout the range in size of geckos presented. Snakes were not fed for ≥14 days prior to each trial. Geckos and snakes were maintained in the same room where trials were conducted, at 26°C. Striking sites and other behavioral observations were recorded where possible, but sometimes interactions took place under a shelter that obscured observation. To reduce any possible influence due to presence of an observer, movements of observers were minimized and the least possible aspect was presented that still allowed observation. In addition, most trials were videotaped, observers were not in the room during the trial, and more detailed review was possible.

Experiment 1: Risk of Predation and Size—Fifteen pairs of geckos were chosen such that the larger member of each pair was ≥1.4 times the mass of the smaller. The smallest absolute difference between members of any pair was 1.15 g. For each trial, a pair was placed into an arena (0.192 m^2 floor area) with a gravel floor and allowed to acclimate. The arena contained one shelter large enough for both geckos to hide. A *H. chlorophaea* was placed in the arena where it remained until it had captured and eaten one gecko.

Experiment 2: Risk of Predation, Size, and Autotomy—Twenty sets of geckos were chosen that differed in size and presence of a tail. Each set consisted of a pair of large geckos, similar in mass, and a pair of small geckos, also similar in mass. In each set, the difference between the smallest large gecko and the largest small gecko was always ≥1.0 g. For each trial, one of the large and one of the small geckos was chosen randomly to have its tail removed as described above. The four geckos were then placed in an arena (1.76 m^2 floor area) and allowed 15 min to acclimate to surroundings. The arena contained several pieces of bark and artificial plants that could be used for hiding. A *H. chlorophaea* was placed in the arena and remained until it had captured and eaten one gecko.

Experiment 3: Burst Speed, Size, and Autotomy—We defined maximum burst speed as the maximum speed each gecko attained over 100 mm, beginning from a standing position. This is about the distance that geckos usually fled from snakes that approached them in previous experiments. We also recorded speed of each gecko running a distance of 250 mm, because measurements of these longer distances tended to be less variable and may more accurately reflect abilities of an animal (D. B. Miles, pers. comm.).

Burst speeds of 18 geckos with mass of 0.5-5.7 g (snout-vent length, range 37.2–66.7 mm) were measured on a standard racetrack (Miles and Smith, 1987) at 23°C. Geckos were allowed to acclimate to laboratory conditions for 3 days; during this time, they were each raced several times to familiarize them with the procedure. The floor of the racetrack was covered with sand, which gave geckos good traction for movement and is their natural substrate. Geckos were tested by holding them quietly directly behind a photocell, and on release, timing their movement from the first photocell to additional photocells 100 and 250 mm away. Some geckos did not run immediately upon being released; these were prodded gently on the tail. Geckos were allowed 20–30 min between trials, and the minimum time for 2–3 trials was used as the best estimate of burst speed for each individual. Immediately after this initial set of trials, tails were removed from all 18 geckos and their burst speeds were re-measured. Procedures for this second set of trials were otherwise as described above.

Experiment 4: Risk of Predation and Burst Speed—Geckos used in burst-speed trials were paired by mass and burst speed such that differences in mass were minimized and differences in burst speed were maximized (largest difference in mass between two members of a pair was 0.7 g; in the pair with the most similar burst speeds, the faster gecko was 3.6 times the speed of the slower). These pairs were tested for differences in risk of predation as described above for Experiment 1, but the test setting was the arena used in Experiment 2.

Statistical Analysis—All tests were one-tailed unless otherwise noted. We used model 1 regressions under the assumption that, in each case, dependent variables were random, that measurement errors were independent, and that they came from the same random, normal distribution with constant variance. We tested these assumptions by visual examination of probability plots of residuals and plots of Studentized residuals against estimated values. We also examined normality of residuals using skewness and kurtosis coefficients and the Lilliefors test. We found no serious violation of the assumptions.

Results—Slope of a least-squares regression line through a log-log scatter plot of data for snout-vent length and size of tail did not significantly differ from 2.0 ($n = 70$, one-tailed *t*-test $P < 0.001$); thus, positive allometry is not indicated. Larger geckos had absolutely but not relatively larger tails.

Between the time when geckos were placed into arenas and a snake was introduced, geckos in all predation experiments typically explored the arena slowly while holding their tails over their backs. When they detected a snake, most geckos lowered their tails and stopped moving. If the snake moved closer, geckos usually fled a short distance. Successful captures occurred while geckos were not moving and often were ca. 10–15 cm from the snake. In these instances, it appeared that geckos were unaware of snakes. In no instance was a gecko observed orienting toward an approaching snake, raising its tail when a snake was near, or otherwise moving in the near presence of a snake, except to flee.

In Experiment 1, the larger of the two geckos was taken in 10 of 15 trials; this difference is not significant ($\chi^2 = 1.67$, $df = 1$, one-tailed *t*-test $P > 0.100$). In Experiment 2, large tailed, large tailless, small tailed, and small tailless geckos were each taken 5 times in 20 trials ($\chi^2 = 0.0$, $df = 4$, *t*-test $P = 1.0$; Table 1).

Slopes of regression lines comparing snout-vent length and burst speed (Experiment 3) were not significantly different from zero for either tailed or tailless geckos (two-tailed *t*-tests, $n = 18$ for both, both *P*-values > 0.10). Correlation analysis also demonstrated that snout-vent length had only a weak relationship with burst speed (r for tailed $= 0.318$, r for tailless $= 0.406$). Although many geckos ran slightly faster after removal of their tail, a one-tailed paired *t*-test revealed that this difference was not significant ($t = 0.11$, $df = 17$, $P > 0.10$). In Experiment 4, geckos with higher burst speeds were taken in 6 of 10 trials. This difference is not significant ($\chi^2 = 0.40$, $df = 1$, one-tailed *t*-test $P > 0.100$; Table 1).

Overall, 23 strikes on tailed geckos were observed in their entirety. Of these, 14 (61%) were to the head or neck, 6 (26%) to the legs, 1 (4%) to the body, 1 (4%) to the base of the tail, and 1 (4%) to the tail. Thus, strikes to the head and neck were 1.6 times as common as strikes to other parts of the body. The single strike to the tail resulted in the only case of autotomy in the 35 trials that included tailed geckos.

Discussion—Behavioral differences observed in the field that prompted this study were similar to those that have been noted in other squamates (Greene, 1988). For example, Pough (1978) reported that juvenile *Nerodia sipedon* did not attempt to defend themselves against threats, but instead fled a short distance and hid. In contrast, conspecific adults confronted predators and vigorously defended themselves by striking. Pough (1978) demonstrated that these behavioral differences corresponded to increased aerobic endurance in the large snakes, making an extended and vigorous physical exertion possible. Smaller size of juvenile snakes also made physical defense less likely to succeed against any larger potential predator.

In addition to having different physical capabilities, smaller individuals might be expected to have different predation-avoidance behaviors for a host of reasons. Smaller individuals may be vulnerable to smaller predators or a different set of predators entirely (Werner and Gilliam, 1984). Size also is likely to be strongly correlated with age, and probably experience as well. Experience with predators may be useful in making the appropriate response to a predator for several reasons. For example, inexperienced individuals may be less likely to rapidly and correctly identify a potential predator, and may be less familiar with available refuges (Arnold, 1984). Finally, the energetic value of the tail may depend on size. Young lizards that autotomize their tails may lose resources important to somatic growth at a critical time, and thus, regeneration may be especially costly.

We initially assumed that an ontogenetic increase in relative size of tail might make the tail-autotomy defense less effective for smaller individuals. However, our data demonstrated that tails of smaller *C. variegatus* were absolutely, but not relatively, smaller than those of larger geckos. This is unlike the situation reported for another gecko, *Phyllodactylus marmoratus* (Daniels et al., 1986), in which tails of juveniles are both absolutely and relatively smaller than those of adults. Our research, therefore, does not support our adaptive hypothesis for different behaviors performed by small and large geckos in the field.

In our laboratory experiments, geckos of all sizes reacted similarly to presence of snakes; they lowered their tails and froze. Thus, differences in behavior that we observed in the field in response to disturbance by humans were not replicated in laboratory trials with snakes. These results are particularly puzzling because we deliberately attempted to replicate experimental conditions used by Congdon et al. (1974), especially in our Experiment 2. Other authors (e.g., Johnson and Brodie, 1974) also have described this stereotyped behavior, although not always specifically relating it to presence of snakes that naturally prey on *C. variegatus* (e.g., Johnson and Brodie, 1974; Parker and Pianka, 1974). Interestingly, we did see the same behaviors in the field as in the laboratory when geckos were disturbed for maintenance or feeding, suggesting that additional tests with a more aggressive snake, such as *Masticophis flagellum*, might be informative. Because there is so little known about conditions and settings of natural predator-prey interactions between these species, it is difficult to speculate meaningfully about the many other ways in which field and laboratory conditions differ. However, it is possible that tail-waving behavior is not used exclusively or even primarily in the context of predator-prey encounters with snakes like *H. chlorophaea*.

We also did not detect that previous loss of tail increased risk of predation. These results stand in contrast to those of Congdon et al. (1974), who reported that tailed *C. variegatus* escaped from attacks by *H. chlorophaea* more often than did tailless geckos, presumably through autotomy. Unfortunately, direct comparison of our results with those of Congdon et al. (1974) is difficult because they did not report how many times tailless geckos were attacked, where they were attacked, or if they escaped. Because we were concerned that our samples may have been too small to reveal real differences that may exist, we performed a power test (Brown et al., 1990) using results from Congdon et al. (1974) and sizes of our samples. They reported that in 30 trials all attacked tailless geckos were captured, while only 63% of attacked tailed geckos were captured. Using size of our sample (20 trials) and a one-tailed binomial test, the probability that we missed a true difference of this magnitude is 0.04. Thus, it is unlikely that we failed to detect a significant result simply due to smaller samples. Additional replication of these experiments should be performed to explore these differences.

A variety of potential explanations exist to account for the observation that tailless geckos were not more vulnerable to the predator than tailed geckos. Given that the snake in our trials was nocturnal; perhaps, loss of tail did not affect its primary mechanism for detection of prey. Downes and Shine (2001) invoked this possibility to help explain why tailless individuals of a diurnal skink were not more vulnerable to a nocturnal snake, although they were more vulnerable to a diurnal snake. It also is possible that lizards that lost their tails changed their antipredator behavior, such as reducing their flight-initiation distance, as compensation (Bateman and Fleming, 2009).

Finally, our hypothesis that larger geckos with tails would have slower burst speeds than smaller geckos with tails was not supported; neither presence of tail nor size of body influenced burst speed. In studies of another species of gecko with a pendulous tail (but using smaller samples and only adults), Daniels (1983) reported that loss of tail nearly doubled running speed. It is not clear whether Daniels (1983) measured burst speed, i.e., starting from a stationary position or from some point after motion had begun. Other studies of locomotion in lizards with and without tails have reported increases in some measure of speed, decreases, or no effect as we found (Arnold, 1988; Bateman and Fleming, 2009). Our observations made during predation events suggest that most geckos that were aware of a nearby snake, and all those that fled from the snake, ran fast enough to escape. Interpretation of the small sample in Experiment 4 is difficult, but those results plus our additional qualitative observations suggest that differences in burst speed did not influence likelihood of being captured.

Our results lead us to question the importance of tail autotomy as a predator-defense behavior in this species, at least against *Hypsiglena*. Examination of stomach contents of *Hypsiglena* from California and Arizona revealed that *Coleonyx* is only a minor part of their diets (Rodríguez-Robles et al. 1999), and in every instance where geckos occur, their tails were still attached (P. Thule and H. W. Greene, pers. comm.; J. T. Vanderyt and R. L. Burke, pers. comm.). In our experiments, we observed only one instance in which the tail was struck by a snake; strikes to the head and other parts of the body were more common. Similar locations of strikes were reported by Dickson (1976) for these two species. Thus, predation by *H. chlorophaea* may not result in significant selective pressures favoring tail autotomy.

In addition, we observed that captive adult *C. variegatus* raise and undulate their tails under a variety of conditions not associated with potential attack by snakes, such as in the presence of food, conspecifics, and when placed in unfamiliar surroundings. Tail waving appears to be a general stress response and may have been misinterpreted as a response to a predatory snake.

It also is unlikely that caudal coloration is an adaptation to enhance effectiveness of autotomy, because while tails of *C. variegatus* are banded conspicuously, so are the entire bodies and heads of juveniles, as are many adults. Further, tail waving and caudal autotomy occur throughout all members of the genus and sister taxa (L. L. Grismer, pers. comm.), as well as in most Gekkonidae (Arnold, 1984). Its presence in *C. variegatus* may reflect persistence of a primitive condition, rather than an adaptation to recent pressures of predation. Finally, Arnold (1988) and Bateman and Fleming (2009) pointed out that there are many potential causes of loss of tails in lizards, and that data for loss of tails alone are not necessarily good indications of predator-escape events.

We suggest that the tail-waving behavior of *Coleonyx*, commonly explained as a behavior to avoid predation by snakes, may be an artifact of disturbance by humans. We doubt that tail autotomy is important in reducing predation by the snake *Hypsiglena*, and consider the evidence that *Hypsiglena* is even an important predator to be unconvincing for the following reasons. First, tail autotomy failed to reduce predation by *H. chlorophaea* in both our experiments and those of Dickson (1976). Second, *Coleonyx* is only rarely detected in stomachs of wild-captured *Hypsiglena*, and in all of these instances, the geckos had their tails intact. Finally, we were unable to explain why juvenile and adult *Coleonyx* differed in their reaction to disturbance by humans, but note that this difference in behavior was not repeated in the presence of a more natural predator.

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