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Tail autotomy effects on the escape behavior of the lizard *Gonatodes albogularis* (Squamata: Sphaerodactylidae), from Córdoba, Colombia

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Abstract

Background: Caudal autotomy appears to be an adaptation strategy to reduce the risk of being preyed upon. In an encounter with a predator, the prey must reduce the risk of being preyed upon, and one of the strategies that has exerted a strong pressure on selection has been tail loss. In lizards, it has been demonstrated that tail loss reduces the probability of survival in the event of a second attack; therefore, they must resort to new escape strategies to reduce the risk of falling prey. In order to evaluate the effect of tail loss on the escape behavior of *Gonatodes albogularis* in natural conditions, we took samples from a forest interior population. We expected that individuals that had not lost their tails would allow the predator to get closer than those that had lost it. For each sample, we recorded the following: (1) escape behavior, measured through three distances (e.g., approach distance, escape distance, and final distance); (2) distance to shelter; and (3) length of tail. We included only males in the study since we did not record any females without a tail and far fewer with a regenerated tail.

Results: We found that tail loss does have an effect on the escape behavior of *G. albogularis*. Males that have their tails intact allow the predator to come closer, and we found a negative correlation between the approach distance and the length of the tail.

Conclusion: Our results support the escape behavior theory, in which *G. albogularis* males drop their tails when the risk of predation is much higher than the cost of fleeing.

Keywords: Caudal autotomy; Escape behavior; Predation; *G. albogularis*

Background

In lizards, caudal autotomy is considered an anti-predation strategy, the main aim of which is to increase survival of the individual when other escape behavior has been ineffective (Maginnis 2006; Bateman and Fleming 2009; Lovely et al. 2010). However, tail loss has associated costs during the regeneration period in terms of reproduction and survival (Shine 1980; Fox and McCoy 2000; Webb 2006). For example, the absence of the tail in the first instance affects balance and all processes associated with locomotive performance (Vitt and Ohmart 1975; Ballinger et al. 1979; Arnold 1988; Martín and Avery, 1998), stockpiling resources (Vitt et al. 1977; McConnachie and Whiting 2003; Clause and Capaldi 2006), and social status (Martin

and Salvador 1993; Salvador et al. 1995; Niewiarowski et al. 1997; Fox and McCoy 2000). In addition, caudal autotomy makes individuals more vulnerable to predation (Dial and Fitzpatrick 1984; Daniels et al. 1986; Downes and Shine 2001; Cooper et al. 2004; Medger et al. 2008). In addition, tail regeneration requires a large amount of energy, and individuals must undergo periods of nutritional deficiency, such that adults stop reproducing, while younger groups stop growing while the tail regenerates (Arnold 1988; Andersson 1994; Webb 2006; Doughty et al. 2003; Lin et al. 2006).

In tree-dwelling lizards, running and jumping are the locomotive methods most commonly employed for moving through the habitat, capturing prey, and evading predation (Moermond 1979; Pounds 1988; Losos and Irschick 1996; Irschick and Losos 1998). However, few studies on caudal autotomy have examined the costs of tail loss with regard to escape behavior, since the tail is

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used for gripping the substrate or for propelling the body during movement as well as for speed and resilience (Toro et al. 2003, 2004; Lailvaux and Irschick 2007; Fleming and Bateman 2011). In the *Anolis* genus of lizard, patterns of movement and the position of the tail can affect its ability to jump and consequently its escape agility (Higham et al. 2001; Gillis et al. 2009). In some species of geckos, it has been demonstrated that the tail determines the direction of the body when moving from one place to another, which helps it to avoid predation (Jusufi et al. 2008; Sun et al. 2009; Ding et al. 2012). Thus, lizards develop early escape behaviors in order to minimize the negative consequences of caudal autotomy (Cooper 2003, 2007), as well as implementing search behaviors for anti-predation shelters (Formanowicz et al. 1990; Langkilde et al. 2005; Zhao et al. 2008). Ultimately, however, any post-caudal autotomy behavior potentially reduces the individual's adaptation capacity (Maginnis 2006; Gillis et al. 2009; Fleming and Bateman 2011).

Within this context, we used the *Gonatodes albogularis* lizard as a model, and we examined the effects that caudal autotomy has on escape behavior. Specifically, we concentrated on answering the following questions: (i) Are there significant differences in the approach distances of a potential predator between individuals with their tails intact and those without tails or with partially regenerated tails?; (ii) Does the length of the tail have a significant relationship with the approach distance, the final distance, and the escape distance?; and (iii) Are there significant differences in the shelter distances between individuals with their tails intact and those without tails or with partially regenerated tails? For this exercise, we concentrated on males, since no females with caudal autotomy were found while the study was being carried out.

Methods

Study area

Fieldwork was conducted in a tropical dry forest relict (Tr-DF) to the south of the Department of Córdoba, Columbia. The study site is located at a height of 12 m above sea level, between 08°34'48.7"N and 75°42'28.4"W. The median annual temperature is 28°C with 1,300 mm of annual rainfall distributed in a unimodal-biseasonal pattern (e.g., dry season and rainy season). Notably, the study site belongs to one of the last wooded outposts in the Department of Córdoba and in the Caribbean region, in the biogeographical province of Choco-Magdalena (Hernández-Camacho et al. 1992).

Study model

The yellow-headed gecko *Gonatodes albogularis* (Duméril & Bibron, 1836) is a relatively small (up to 51.0 mm in rostrum-cloacal length), diurnal, tree-dwelling

lizard of the Sphaerodactylidae family, and native to the lowlands of Chiapas, México on the Pacific watershed and Guatemala on the Atlantic watershed, extending to the south down to the northwest of Columbia and western Venezuela (Savage 2002) and also found on islands such as Aruba, Curacao, Tortuga, La Orchila, Gorgona, La Española, Jamaica, The Cayman Islands, and Cuba (Krysko 2005). It lives in dry and wet tropical forests, both in primary and secondary forests, and in open areas, from sea level up to a maximum altitude of 1,500 m (Rivero-Blanco 1979; Köhler 2003; Schargel 2008). They are generally found in proximity to tree trunks, but they can also be observed in cracks in rocks and rarely on fallen leaves. They present with marked sexual dimorphism: male adults have a black body, a whitish stomach, an orange-colored or dark yellow head, a black retina, and white distal end of the tail; while females present with a coffee-colored base upon which there are many light spots, from white to cream, across the whole body, but without the white tail tip. They do not have movable eyelids; the body and the head are covered with granular scales, and the fingers are cylindrical with non-retractable claws (Ellingson 1994). The natural predators of this species are larger lizards and some species of snakes, birds, and mammals (Fitch 1973; Bello 2000).

Fieldwork

The samples were taken between March and April of 2012. During sample collection, we used the free search method without restrictions between 0900 and 1700 hours. For the escape behaviors, a potential predator was simulated by a person, always the same individual, who always approached at a constant speed (1 m s^{-1}). Once each individual was located, we recorded the first reaction that it demonstrated (e.g., movement of the head, of the tail, or any other reaction) as an indication that the 'prey' had detected the 'predator'. The escape behavior was measured in the following way: (i) the 'predator' placed himself at a distance of 5.0 m and began the approach towards each individual directly and in a straight line, at a constant speed; (ii) once the lizard began its escape behavior, the 'predator' stopped. Immediately afterwards, the approach distance, the escape distance, and the final distance were measured. All distances were taken in a straight line using a tape measure. The approach distance was defined as the distance between the 'predator' and the lizard at the moment in which the latter began its escape. The escape distance was the distance between the lizard's initial resting place and the point at which it stopped after its escape; and the final distance was the distance between the 'predator' and the point at which the lizard stopped after its escape (Bauwens and Thoen 1981; Bulova 1994; Vanhooydonck et al. 2007). If the lizard ran and hid (e.g., in a crack and underneath fallen leaves), the

escape distance was measured between the initial position of the individual and the entrance to the hiding place. To reduce the possibility of repeatedly observing the same individual, the excursions were made on parallel transects that were marked and separated from each other by 10 m.

In addition to these distances, the distance to the nearest place of shelter was also measured. This was the distance between the initial position of the individual and the place that it disappeared from view (e.g., crack, hollow, and tree bark).

Once the observations had been taken, all of the individuals were captured and measured (rostrum-cloacal length (RCL); tail length (TL)) with an analog Vernier caliper (precision 0.1 mm). The state of the tail was also recorded (e.g., tail intact, missing tail, and with regenerated tail). Only those individuals with a RCL higher than the minimum for sexual maturity (30.1 mm for males and 31.7 for females; Serrano-Cardozo et al. 2007) were included in the sample.

Statistical analysis

All of the variables were transformed (Log10) before carrying out the analysis. In order to see whether escape behavior differs depending on the state of the tail, a multivariate analysis of variance (MANOVA) and an analysis of variance (ANOVA) were applied using STATISTICA 2001 Version 8.0, with the state of the tail as a factor and the approach distance, escape distance, final distance, and the distance to shelter as dependent variables. Subsequently, with a *post hoc* analysis (Tukey), we identified which comparisons accounted for significant differences (Dytham 1999). Finally, we used a Pearson correlation to examine if there was any relationship between tail size and escape behavior.

Results

We recorded a total of 79 male adults and found individuals with tails in different states (e.g., intact, absent, and regenerated). We found that tail loss does have an effect on escape behavior. The multivariate analysis of variance allowed us to observe that the state of the tail has an effect on escape behavior ($F_{2,76} = 67.765, P = 0.0001$). The analysis of variance showed that the approach distance differed significantly between tail states ($F_{2,76} = 52.898, P = 0.00001$; Figure 1). However, with regard to the escape distance and the final difference there, were no significant differences ($F_{2,76} = 2.5680, P = 0.08333$; $F_{2,76} = 0.36929, P = 0.69246$; Figure 2 and 3, respectively). Tukey's *post hoc* analysis revealed differences in the approach distance between individuals with an intact tail and the other groups (e.g., absent tail and regenerated tail; Table 1).

We also observed that individuals with tails in different states of regeneration were found in different places

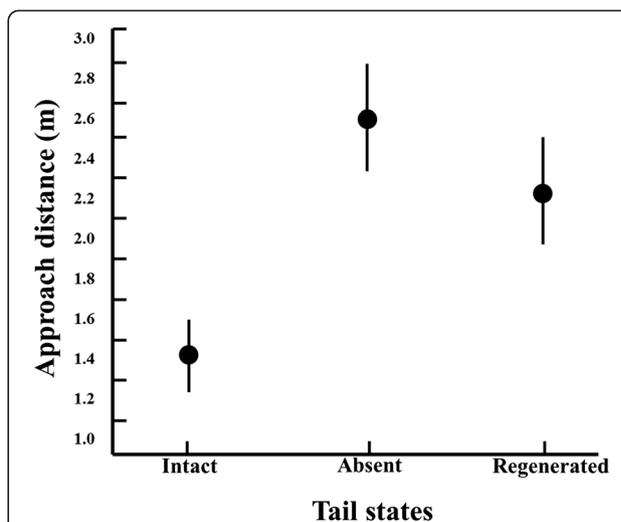


Figure 1 Approach distance vs. tail states. Approach distance (m) that male *Gonatodes albogularis* exhibit when confronted with a potential predator in relation to three tail states (average \pm IC).

within the microhabitat with regard to the closeness to, or distance from, places of safety. The analysis of variance showed differences in the distance to shelter between individuals with different tail states ($F_{2,76} = 12.956, P = 0.00001$; Figure 4). The *post hoc* analysis revealed differences between individuals with an intact tail and the other groups (e.g., absent tail and regenerated tail; Table 1).

Tail length seems to be related to escape behavior to a large degree. The correlation analysis showed that there is a significant negative correlation between the approach distance and the length of the tail ($r = -0.71, P > 0.05$; Figure 5). In other words, when individuals have a longer tail, they allow the predator to come closer, while escape

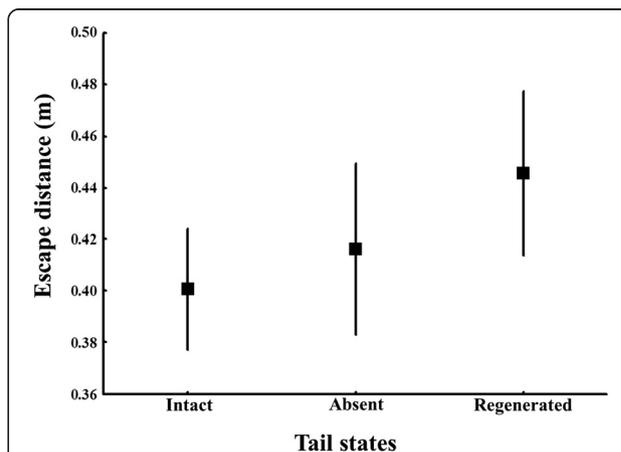


Figure 2 Escape distance vs. tail states. Escape distance (m) that male *Gonatodes albogularis* exhibit when confronted with a potential predator in relation to three tail states (average \pm IC).

Table 1 Tukey's a posteriori analysis

Tail	Intact	Absent
Intact		
Absent	0.000109; 0.000119	
Regenerated	0.000109; 0.024502	0.265345; 0.094200

This analysis shows the comparisons between individuals with intact, absent, or regenerated tail regarding approach distance (first values) and refuge distance (second values).

distances and final distances were not related to tail length ($r = -0.15, P > 0.05; r = -0.08, P > 0.05$, respectively).

Discussion

Our results demonstrate that tail loss does have an effect on the escape behavior of the lizard *G. albogularis*. The individuals we found with different tail states (e.g., intact, absent, and regenerated) were males only. This pattern could be explained by various factors: it is possible that it is much more costly for females to lose their tails, since they would expend a great deal of energy during the time that it is regenerating, energy that could be used for other activities. *G. albogularis* females have a continuous reproductive cycle, which indicates that they are always investing energy in the production of ovules (Serrano-Cardozo et al. 2007). Therefore, regenerating their tails would imply an additional energy expenditure. Bohórquez et al. (2010) found that this lizard uses a tail-waving display in the presence of conspecifics and potential predators and that males use this type of behavior with a significantly higher frequency than females, finding that the differences were significant.

It is known that ovule production implies greater energy expenditure than the production of spermatozooids (Krebs and Davies 1993; Andersson 1994), and this

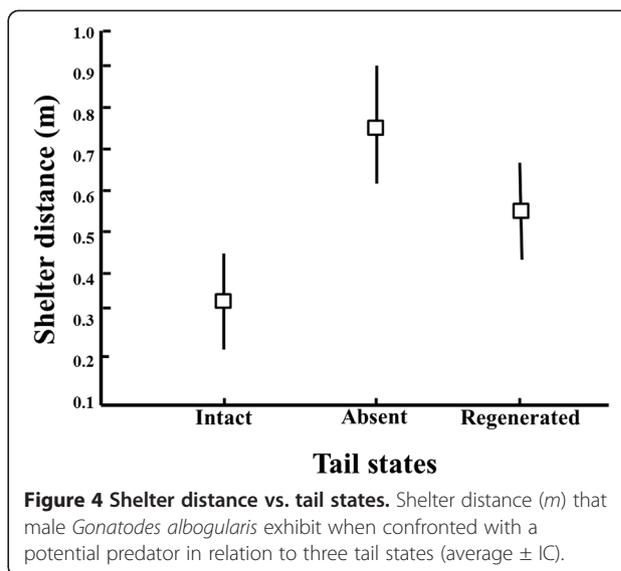


Figure 4 Shelter distance vs. tail states. Shelter distance (m) that male *Gonatodes albogularis* exhibit when confronted with a potential predator in relation to three tail states (average \pm IC).

applies equally to reptiles (Congdon et al. 1982). In addition, it is the females of this species of lizard that take care of the nest (MD-L, personal observation), which is to say that they have an additional expenditure compared with males. For all of the above reasons, it is much easier for males to drop their tails, and this is why they use the tail-waving display more frequently. If a predator seizes them by the tail, they drop it and can successfully evade a predatory event. Females cannot take such risks since they must distribute their energy to other activities such as ovule production and parental care, which is undertaken by the females in this species of lizard (MD-L, personal observation). Besides this, it is very possible that females do not need to carry out this kind of behavior since they are much more reticent and reclusive than males (Ellingson 1994).

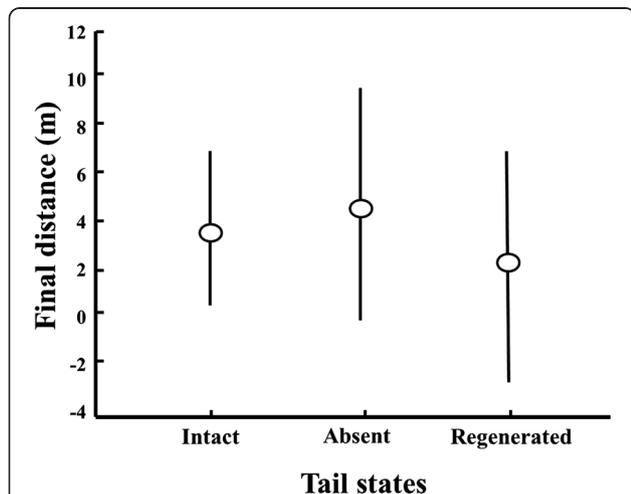


Figure 3 Final distance vs. tail states. Final distance (m) that male *Gonatodes albogularis* exhibit when confronted with a potential predator in relation to three tail states (average \pm IC).

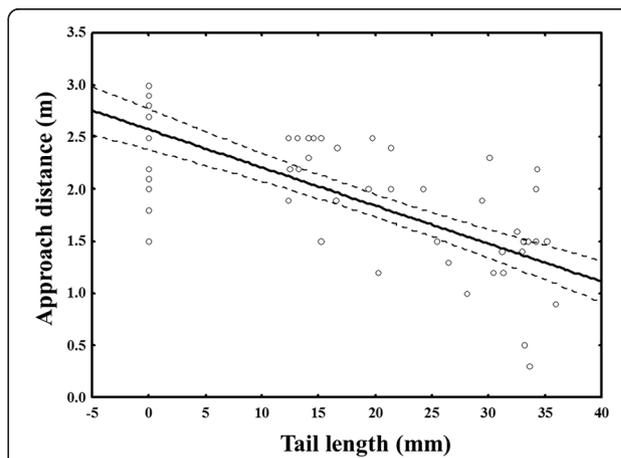


Figure 5 Correlation between approach distance and tail length. Correlation between the approach distance of a potential predator (m) and the tail length of the prey (mm).

It has been demonstrated that tail loss brings about a loss of running speed, which could constitute a significant disadvantage for lizards (Ballinger et al. 1979; Punzo 1982; Dial and Fitzpatrick 1984), thus increasing the risk of predation. It has been suggested therefore that the reduction in the distance that the prey allow to the predator, after the loss of the tail, as has been seen in some ground lizards, could be combined with a change in strategy for avoiding predators. Becoming more reticent or keeping to habitats with larger objects for protection is one example of a change in strategy (Formanowicz et al. 1990; Smith 1996).

Our results reflect the fact that the approach distances were smaller in males with intact tails, indicating that individuals that have the opportunity to execute caudal autotomy allow the predator to come closer. This affirms the escape behaviors theory put forward by Ydenberg and Dill (1976), in which an animal decides to escape when the risk of predation is greater than the cost of escape; ultimately, *G. albogularis* males drop their tails, since it is otherwise much more likely that they would fall prey.

Our data do not show if caudal autotomy has an influence on the probability that the lizard *G. albogularis* would survive an encounter with potential predators (e.g., snakes, birds, and mammals; Fitch 1973; Bello 2000). However, we have demonstrated that tail loss modifies escape behavior and has direct repercussions on encounters with a potential predator, which increases the possibility that these lizards are preyed upon more easily. In addition, tail loss also induces changes in behavior that are not directly related to predation, and these modifications can indirectly affect the probability that a lizard will be captured (Fox and Rostker 1982; Martin and Salvador 1993, 1997).

We found a strong negative correlation between the approach distance and the length of the tail. In other words, when individuals have a longer tail, they allow the predator to come closer. It has been demonstrated that the tail is used to maintain balance during movement in ground habitats (Vitt and Ohmart 1975; Ballinger et al. 1979), and it has also been demonstrated that *G. albogularis* uses some movements that are known as tail-waving display, which act as a behavior to evade and dissuade predators (Bohorquez et al. 2010). We believe that when individuals have a longer tail, they are more agile and allow the predator to come closer. In addition, we can say that when the tail is longer, the tail-waving display is much more effective and dissuades predators more easily.

With regard to the use of space, we found that individuals with intact tails tend to be found in areas close to shelter, while individuals with absent tails move much further away from shelter. This scenario suggests that while tail loss reduces locomotive abilities in some

lizards (Ballinger et al. 1979), it increases them in others (Daniels 1983). Therefore, it is probable that tail loss does not decrease running speed in this species of lizard. However, this may contradict the negative correlation between the approach distance and tail length, since the length of the tail would be more associated with evasion and dissuasion (tail-waving display) than with running distance.

Conclusions

Individuals who have lost the tail become more vulnerable to predation, is why you should take the race long before individuals with tail intact, *G. albogularis* not only uses its tail to detach, but has developed a deterrence strategy and evasion which also uses the queue. So by not having it is more exposed to predation.

There may be an effect on many variables set on escape behavior in the lizard *G. albogularis*, however caudal autotomy seems to be a strategy that allows individuals successfully overcome a meeting with a potential predator.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MD-L Participated in all article; AO-L participated in the design of the study and performed the statistical analysis and JZ-O participated in the discussion and conclusions.

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