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ORIGINAL RESEARCH

Autotomy in Achala copper lizard: do sex and body size traits influence tail loss and regeneration?

F. Cabezas-Cartes[1], M. M. Torres[2], L.J. Viladrich[3], G. Lopez Juri[4,5] & S. Naretto[4,5,6]

[1]Laboratorio de Ecofisiología e Historia de vida de Reptiles, Instituto de Investigaciones en Biodiversidad y Medio Ambiente (INIBIOMA), Universidad Nacional del Comahue, CONICET, San Carlos de Bariloche, Argentina
[2]Grupo de Investigaciones de Ecología en Ambientes Antropizados (IdEAS), INIBIOMA, Universidad Nacional del Comahue, CONICET, San Carlos de Bariloche, Argentina
[3]Laboratorio de Investigación y Conservación de la Biodiversidad (InCoBIO), Centro de Investigaciones y Transferencia de Río Negro (CONICET-UNRN), Viedma, Argentina
[4]Laboratorio de Biología del Comportamiento, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Cordoba, Argentina
[5]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto de Diversidad y Ecología Animal (IDEA), Cordoba, Argentina
[6]School of Natural Sciences, Macquarie University, Sydney, NSW, Australia

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Correspondence
Sergio Naretto, Laboratorio de Biología del Comportamiento, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299, Cordoba 5000, Argentina.
Email: narettosergio@gmail.com

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Abstract

Autotomy in animals, the voluntary loss of a body part at a specific location, is a widespread behaviour observed across various groups. This mechanism provides several advantages, such as predator evasion, escape from entrapments, and even reduced injury costs from agonistic interactions. Lizards display tail autotomy in response to predation and intraspecific aggression. Moreover, it is common for these reptiles to have sexually dimorphic traits, such as colouration and body size, which may influence predation risk and consequently their antipredatory strategies. This study focuses on the Achala copper lizard (*Pristidactylus achalensis*) which inhabits an isolated highland ecosystem in central Argentina. This species is an ideal study model due to its territorial and aggressive behaviour, high intraspecific competition and sexual dichromatism. The aims of this study were to determine the influence of sex and body size on the occurrence of tail autotomy in *P. achalensis*. Additionally, we assessed the cost of autotomy by analysing the distance between the vent and the tail cut. Furthermore, we investigated the possibility of repeated tail autotomy by a single individual. Our results showed that in *P. achalensis*, sex and body size interacted significantly resulting in different patterns of tail autotomy. In females, the frequency of autotomy increased gradually with body size, whereas in males it increased more abruptly and reached its maximum frequency at smaller body sizes than in females. Males presented higher autotomy frequencies than females, likely because they are more likely to be perceived by avian predators than cryptic females. The findings of this study contribute to broadening the knowledge of lizard behaviour, shedding light on the complex interplay between predation, intraspecific competition and reproductive dynamics in this unique species.

Introduction

Autotomy can be defined as the voluntary loss of a body part at a specific location, which involves one or more breakage planes (Emberts et al., 2019). The benefits of this behaviour range from some well-known aspects, such as escape from predators, to less-known advantages, like getting out from non-predatory entrapments (Hodgkin et al., 2014; Maginnis, 2008). Such benefits also help reduce the costs associated with retaining an injured limb (e.g. infection; Emberts et al., 2017) and have even been observed to increase reproductive success in spiders that lose appendages (Snow et al., 2006). This behaviour is a widespread strategy present in several groups of animals, including invertebrates such as crustaceans, echinoderms (Fleming et al., 2007) and cephalopods (Bush, 2012), as well as vertebrates like rodents (Shargal et al., 1999), salamanders (Wake & Dresner, 1967) and lizards (Bateman & Fleming, 2009). Specifically, lizards are the group

in which autotomy, especially tail autotomy, has been extensively studied considering its presence in 13 of the 20 Saurian families (Downes & Shine, 2001).

Several factors have been pointed out as determinants of tail autotomy in lizards, such as predation pressure (Cooper Jr et al., 2004; Diego-Rasilla, 2003), habitat (Arnold, 1984; Tanner & Perry, 2007), sex (Vitt, 1981), levels of intraspecific aggression (Jennings & Thompson, 1999; Matuschka & Bannert, 1987; Vitt & Zani, 1997) and ontogeny (Brandl & Völkl, 1988; Vitt et al., 1977). Among these factors, predation intensity emerges as the most evident and influential variable affecting the incidence of autotomy. A higher predation pressure has been associated with a higher incidence of autotomy in certain lizard species (Cooper Jr et al., 2004; Diego-Rasilla, 2003). Additionally, it has been demonstrated that species inhabiting microhabitats with greater exposure or higher-elevation locations (trees or rocks) tend to exhibit higher autotomy frequencies (Jaksić & Fuentes, 1980; Pianka & Huey, 1978; Pianka & Pianka, 1976). Although there is limited evidence regarding differences in tail loss frequency between females and males (Barbadillo & Bauwens, 1997; Bateman & Fleming, 2009), dichromatic species may expose the sexes to different predation risks due to variations in their camouflage. Furthermore, intraspecific competition has been identified as an important variable influencing autotomy in lizard species experiencing high population densities (Itescu et al., 2017; Pafilis et al., 2009). Another factor to consider is the flexibility of antipredatory strategies (Baxter-Gilbert et al., 2018). For instance, as a lizard grows, its increased size may reduce predation risk, allowing the use of less costly strategies (e.g. biting and clawing) as the primary defences. In antipredatory strategies with limited applicability (usable once or a few times), the timing of implementation during ontogeny becomes crucial. Moreover, the tail performs fundamental functions in the biology of lizards, from locomotion and sexual behaviours to the accumulation of energy reserves (Bateman & Fleming, 2009). Therefore, the location of the breakage line and, consequently, the size of the tail post-autotomy may be influenced by intrinsic characteristics of the individual, such as body size, sex and reproductive condition.

The Achala copper lizard (*Pristidactylus achalensis*), a member of the Leiosauridae family, exhibits a restricted distribution within an isolated highland ecosystem covering the highest area of the mountains in central Argentina (Minoli & Avila, 2017). This species hibernates during the cold season and has a brief reproductive season during the warm months (Blengini et al., 2020). Furthermore, *P. achalensis* is territorial and aggressive (Naretto & Chiaraviglio, 2023; Torres et al., 2019) and individuals showcase bite scars with distinct distributions between sexes: males predominantly possess more scars in the anterior region, whereas females exhibit scars primarily on the tail (Naretto & Chiaraviglio, 2020). These bite scars serve as evidence of intraspecific interactions (Naretto et al., 2022). Interestingly, bite scars are more frequent during the reproductive season, underscoring the importance of biting in mating competition and copulation (Naretto & Chiaraviglio, 2020). In addition to intraspecific competition, an event of cannibalism has been observed, suggesting intense intraspecific aggressiveness (Torres et al., 2019). Other noteworthy aspects of this species are its sexual dimorphism in body size and sexual dichromatism, with males displaying green dorsal colorations and females having brown and yellow dorsal colorations. This difference in coloration influences their camouflage against avian predators, such as the American kestrel (*Falco sparverius* Linnaeus, 1758), the variable hawk (*Geranoaetus polyosoma* Quoy & Gaimard, 1824) as well as passerines like the black-billed shrike-tyrant (*Agriornis montana* D'Orbigny & Lafresnaye, 1837). Torres et al. (2021) have determined that raptors can perceive the difference in coloration between sexes, whereby males are more conspicuous than females to this type of predator.

Our hypothesis postulates that intrinsic traits of species, such as sex and body size, play a crucial role in influencing tail autotomy. We predict differences in the frequency of autotomy between sexes and body sizes due to their exposure to different predation risks and agonistic behaviours. The aims of this study are as follows: (1) to ascertain the presence of autotomy in *P. achalensis* and analyse whether sex and body size influence the occurrence of this behaviour; (2) to estimate the extent of sacrifice made by these lizards through tail autotomy by examining the distance between the vent and the point where the tail is severed and the efforts made to regenerate the tail by measuring the length of regenerated tails and (3) to assess the occurrence of multiple instances of autotomy in individuals.

Materials and methods

Data collection

Pristidactylus achalensis individuals were caught from wild populations in the Pampa de Achala region, Argentina (31.50° S, 64.92° W to 31.63° S, 64.82° W) during their active season between October and March from 2014 to 2021, using a pole with a loop of string. Subsequent to capture, we recorded the following data: ID number, Snout-Vent Length (SVL), Sex, Sexual Maturity (Adult or Juvenile), Autotomy (Yes or No), and Regenerated tail for individuals with autotomy (Yes or No). We distinguished regenerated tails from tails without autotomy based on their morphology, considering coloration, pattern and size of scales. For lizards with autotomy, we measured the distance from the vent to the cut line and for lizards with regenerated tails, from the cut line to the end of the regenerated tail. Morphological measurements were obtained using a digital calliper (digital gauge CA-01, Lee Tools, Guangzhou, China; ±0.02 mm). To determine whether individuals were adults or juveniles, we employed a threshold based on the minimum reproductive SVL as reported by Naretto and Chiaraviglio (2020, noting the smallest gravid female with an SVL of 90.1 mm, and the smallest male with sperm measuring 92.55 mm SVL). We captured 273 lizards (120 females and 153 males). We recaptured 51 of the 273 individuals (24 females and 26 males) to assess the occurrence of multiple instances of autotomy in individuals. Some of the recaptures occurred within weeks, whereas others spanned several years. Previously captured individuals were identified by comparing photographs taken of the shape and size of a black spot in the neck region. To enhance the reliability of gular spot identification,

we implemented an additional step by marking the ID number on the belly with permanent paint (mark retained until the lizards shed their skin). Moreover, territorial behaviour played a significant role in recaptures, since the majority of the recaptured individuals were found on the same rock, facilitating their identification. To validate our identification method, we cross-referenced the gular spots with unique morphological characteristics, such as tail malformations or missing toes. We classified the lizards based on their SVL into six body size categories: minimum to 90 mm (including juveniles) (14 females, 7 males), 90–95 mm (30 females, 10 males), 95–100 mm (43 females, 26 males), 100–105 mm (27 females, 49 males), 105–110 mm (4 females, 40 males) and more than 110 mm (including only 14 males). Nine lizards were excluded from this categorisation because we lacked data about their body size.

Statistical analyses

We only used the data from the first capture in the analyses in order to avoid pseudo-replication due to recaptures. We performed Contingency Tables and chi-square tests to compare the frequency of autotomy between sexes. Additionally, a generalized linear model (Zuur et al., 2009) with a binomial error distribution and a logit link function was employed to explore the factors determining the autotomy frequency. The presence or absence of autotomy was considered the response variable, whereas sex (two levels: females and males), SVL and their interaction were treated as predictor variables. To fit this model, we used the function 'glm' from R, and we checked the dispersion by performing a quantile regression with the standardized residuals and predicted values with the package 'DHARMa' (Hartig, 2022). In order to compare the distance between the vent and the cut line between sexes and the length of regenerated tails, we employed analysis of covariance (ANCOVA) with SVL as a covariate, incorporating interaction term between the predictor variables 'sex' and 'SVL'. In cases where the interaction was not significant, it was subsequently removed from the model. For each individual, we calculated the percentage of SVL that represents the cut line. Linear regression models were also used to explore relationships between variables. For linear models, we verified residual normality with the Shapiro–Wilk test and homogeneity variance with the Bartlett test. All analyses were executed using R v.4.3.0 (R Core Team, 2024) with a significance threshold for the tests of 0.05.

Results

We observed autotomy in 35% of the population with 95 lizards showing evidence of autotomy and 178 lizards lacking such evidence. Specifically, 28% of the females experienced autotomy, whereas 40% of males experienced autotomy. When not accounting for body size, the frequency of autotomy was similar between sexes ($\chi^2 = 3.4525$, d.f. = 1, $P = 0.0631$).

In the examination of autotomy factors, while considering both body size (SVL) and sex, the interaction between both factors influenced the frequency of autotomy. The model indicated a significant interaction between sex and SVL ($\chi^2 = 7.0625$, d.f. = 1, $P = 0.0079$). Moreover, the individual factors of sex ($\chi^2 = 7.0908$, d.f. = 1, $P = 0.0078$) and SVL ($\chi^2 = 13.6247$, d.f. = 1, $P = 0.0002$) were also significant. The proportion of individuals with autotomy increases with body size in both sexes but in different forms (Fig. 1). In females, the increase in autotomy was more linear and gradual, whereas in males, the increase was more abrupt with more autotomy frequency in smaller body sizes (less than 95 mm SVL) compared to females. Additionally, juvenile individuals exhibited autotomy evidence with the smallest female experiencing autotomy having an SVL of 86.15 mm and the smallest male having an SVL of 86.25 mm.

The average distance from the vent to the cut line was 6.34 ± 2.49 cm (mean ± SD; Q1–Q3 = 4.43–8.17; minimal = 1.59 cm and maximal distance = 12.14 cm), representing 63% of the SVL (mean calculated based on the percentage of each individual). Males and females displayed differences in the distance from the vent to the cut line (Fig. 2; ANCOVA with SVL as covariate, sex effect term $F_{2,88} = 27.361$, $P < 0.0001$; SVL effect term covariate $F_{2,88} = 0.062$, $P = 0.9374$). The distance from the vent to the cut line represented 75.77% of the SVL of males, whereas in females, it represented a mean of 50.81%.

We observed that 76% of individuals who experienced autotomy possessed regenerated tails (72 out of 95 individuals), and there were no differences between sexes (82% in females and 75% in males; $\chi^2 = 0.2433$, d.f. = 1, $P = 0.6218$). The mean length of regenerated tails was 1.99 ± 1.48 cm (Q1–Q3 = 0.89–2.95 and a maximum of 9.39 cm), and this length was similar between sexes (males mean = 1.86 ± 1.62 cm and females mean = 2.21 ± 1.22 cm; ANCOVA with SVL as covariate, sex effect term $F_{3,70} = 1.104$, $P = 0.2971$; SVL effect term covariate $F_{3,70} = 3.749$, $P = 0.0569$). The length of the regenerated tail was found to be related to the line of autotomy ($F_{1,70} = 40.14$, $P < 0.0001$) with regenerated tails being longer when the line was closer to the vent.

We recaptured 51 lizards with 27 showing no signs of autotomy in any capture (time range spanning from a few weeks and over 2 years). Among the 24 recaptured individuals with autotomy evidence, 16 displayed autotomy from the first capture, whereas 8 did not exhibit autotomy in the initial capture but experienced it between captures.

It is interesting to note that for 4 recaptured individuals with prior autotomy the line of autotomy differed by an average of 2.84 cm between captures. The autotomy line was closer to the vent in subsequent captures, indicating that autotomy occurred more than once (Fig. 3). Another evidence of multiple autotomy per individual is the tail absence in recaptures of the same individual who had regenerated tail, hence experienced previous autotomy.

Discussion

Autotomy, as voluntary release of the tail, can represent the difference between survival and death in lizards, and our study confirms that *Pristidactylus achalensis* possesses the capacity to employ this mechanism. Interestingly, our findings reveal a distinct pattern when considering sex and body size. A

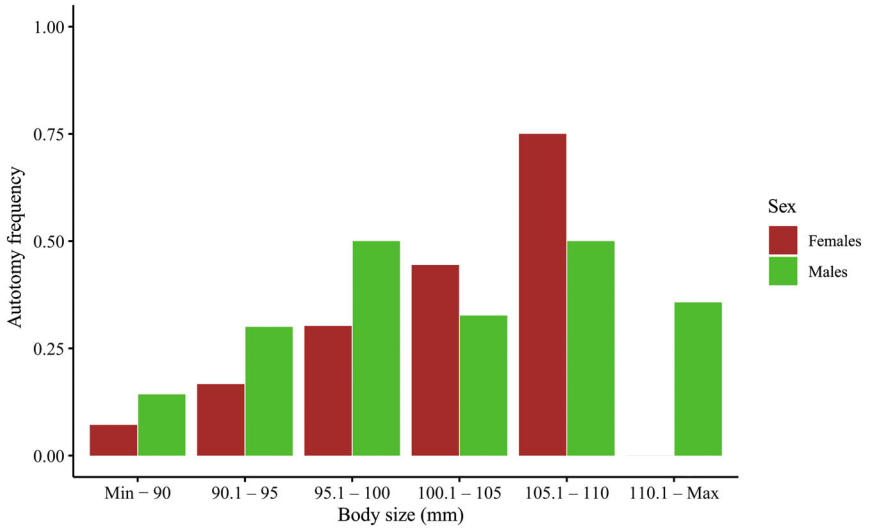

Figure 1 Autotomy frequency per sex and body size (measured in mm) category in *Pristidactylus achalensis*. *N* by categories: minimum to 90 mm: 14 females and 7 males, 90.1–95 mm: 30 females and 10 males, 95.1–100 mm: 43 females and 26 males, 100.1–105 mm: 27 females and 49 males, 105.1–110 mm: 4 females and 40 males, 110.1 mm to maximum: 0 females and 14 males.

previous study on this species confirmed that males of *P. achalensis* are brighter and more conspicuous against their backgrounds than cryptic females and juveniles (the coloration pattern of which resemble that of females) and that avian predators can perceive this difference in coloration (Torres et al., 2021). As a consequence, it could be expected that males present a higher frequency of autotomy. However, considering only sex, the frequency of autotomy was similar between females and males and similar to those reported for other lizards (Pafilis et al., 2017; Sousa et al., 2016; Vidal et al., 2022). Additionally, juveniles also exhibit autotomy, which means that their cryptic coloration and smaller size are not enough to avoid being perceived by predators and that they also must use autotomy as a way to survive predation. Another possible explanation is that tail loss in juveniles could be due to intraspecific competition or aggression from adults. Nevertheless, the differences between males and females are marginally non-significant and may indicate a pattern of lower autotomy frequency in females than males.

Environmental conditions and predator types likely influence the occurrence of autotomy and its limitations within sexes in *Pristidactylus* species, as has been shown in *Anolis* lizards (Vidal et al., 2022). Moreover, population traits such as density play a crucial role in determining the intensity of intraspecific interactions such as aggressiveness. *Pristidactylus* species inhabit diverse environments featuring a variety of potential predators (Labra & Rosenmann, 1992) and ecological conditions. For instance, some *Pristidactylus* species inhabit similar environmental conditions (top areas of mountains), such as *P. achalensis* and *P. casuhatiensis*, but the latter exhibits much lower population densities (Lujan Ogeda et al., 2023) than *P. achalensis*. In certain species, intraspecific aggression may

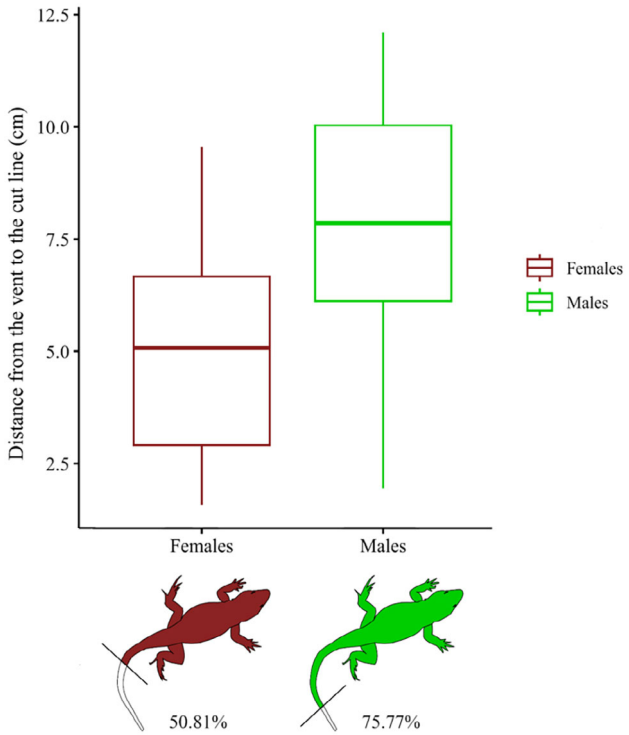

Figure 2 Boxplot showing the distances from the vent to the cut line in females and males illustrating the minimum (lower whisker), median, maximum (upper whisker) and interquartile range represented by the box height. Additionally, a schematic representation of the mean percentage of retained tail relative to SVL (snout-vent length) is provided for each sex.

outweigh predation as a driving force. Considering that male lizards are considerably more aggressive towards other males than towards females (Cooper Jr et al., 2015), a higher frequency of autotomy in males would be more plausible. However, the interaction of factors such as sex and size may complicate the analysis, since different size classes are subject to different intensities of aggressiveness. In addition, a higher population density may pressure individuals to expose themselves to greater predation risk due to the need for longer exposure times while competing for shelters and mates. On the other hand, other *Pristidactylus* species inhabit different habitat conditions, like the forest-dwelling *P. torquatus* (Labra & Rosenmann, 1992), providing diverse scenarios for comparative studies. The autotomy pattern seems common in rock-dwelling species (Arnold, 1984), whereas it is plausible that climbing trees may require greater tail support, leading individuals to avoid sacrificing their tails. Furthermore, *P. achalensis* lives in rocky areas with abundant caves and narrow crevices where lizards find refuge and interact with conspecific and predators. Therefore, this habitat structure with crevices of small dimensions can lead to entrapments, making autotomy a useful solution to such situations. Therefore, studying the differences in the pattern of autotomy between species of this genus may provide interesting insights into the evolution of this mechanism. Given the traits of *P. achalensis*, we expect it to be the species with the highest rates of autotomy in the genus.

Another crucial aspect of the tail is its role in copulation behaviour (Fox & McCoy, 2000; Martin & Salvador, 1993). In some species of the genus *Pristidactylus*, males and females cross their tails during copulation (Naretto *per. obs.*; Lujan Ogeda et al., 2023). The fact that tail muscles play an important role in copulation behaviour could explain the lower autotomy frequency in larger males compared to females and their cuts being more distant from the vent. In this way, males might avoid autotomy as an anti-predatory defence and opt for less costly defences, such as biting and clawing, in order to maintain reproductive success.

The evaluation of the frequency of autotomy according to different body sizes could be biased because we do not have data on survival rates in different body sizes. However, we noted an increase in autotomy frequency with body size, which may be attributed to various causes. For example, large lizards are old and so likely to have experienced more exposure to predators, or increased intraspecific competition, as body size increases. Another explanation could be the delaying of or avoiding autotomy in smaller sizes. Females seemed to exhibit a pattern where the occurrence of autotomy is greater at larger sizes, while males seemed to initiate autotomy at smaller sizes. A noteworthy trend was observed, with larger females displaying a higher frequency of autotomy compared to smaller females, and lower autotomy frequency in smaller females compared to males. This pattern could suggest the idea of autotomy as a strategy to avoid copulation in *P. achalensis*. In this species, Naretto and Chiaraviglio (2020) showed variations between sexes in the location of lizard bites. As bite scars may evidence differences in intraspecific interactions, autotomy could also represent distinctions in the intrasexual and intersexual behaviour. As scars on females were predominantly on the tail, while scars on males concentrated in the anterior region such as the head, this pattern shows the tail of females as a target for bites, and repetitive bites may stimulate autotomy. New studies should be conducted to explore autotomy in a sexual context, both in intrasexual competition such as agonistic encounters and in intersexual interactions.

The percentage of retained tail after autotomy was lower in females than in males. A possible explanation for this could be that females captured in this study may have undergone autotomy on more than one occasion, thereby reducing the observed value. The non-autotomous base of the tail is longer in males than females, and as hypothesised by Barbadillo et al. (1995) the hemipenes and the associated musculature could be the reason for the sexual difference in the cut line. The vertebra structure could constrain the minimum autotomy line because it is where the hemipenes muscles insert. Although there are species in which the costs of losing the tail do not impact performance, for example, the cordylid lizard *Cordylus melanotus melanotus* (McConnachie & Whiting, 2003), such losses could still represent depletion of energy reserves that are especially crucial for reproduction in females (Doughty et al., 2003).

Finally, we confirmed that autotomy could occur more than once. Recapturing individuals with changes in the autotomy line between captures suggests the occurrence of multiple autotomy events. Furthermore, the absence of regenerated tails in subsequent recaptures of autotomized individuals provides additional evidence for repeated autotomy events.

In conclusion, our study confirms the occurrence of autotomy in different classes of individuals and reveals variations in

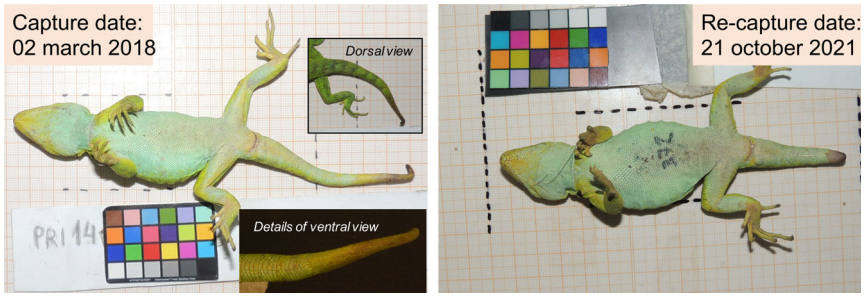

Figure 3 Evidence of multiple autotomy of the same individual.

patterns that may correspond to diverse intraspecific interactions or predation risk. Planning experimental or focal studies to understand the causes of tail cuts is challenging due to the associated costs to individuals and their ethical concerns. Nevertheless, comparing the patterns found here across different species or populations subject to varying densities could provide valuable insights. In addition to tail cutting, lizards have the capacity to regenerate their tails and undergo multiple autotomy events. While these results align with expectations for lizards with autotomy, reporting them contributes to increasing data and beginning to dissect intra-specific variability in the autotomy mechanism.

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Author contributions

All authors share the first authorship of the manuscript. All authors conceived the ideas and designed the methodology; SN and GLJ collected the data and all authors analysed the data; all authors contributed to interpreting results, contributed critically to the drafts, and gave final approval for publication.

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Conflicts of interest

The authors declare that they have no conflicts of interest.

Data availability statement

The data can be found at https://osf.io/cfvpn/?view_only=6042f4d8d0934a79b4d20afdc9178ff6.

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