


# Behavioral patterns in the early-stage antipredator response change after tail autotomy in adult wall lizards

Irene Fernández-Rodríguez<sup>1,2</sup>  | Florentino Braña<sup>1</sup>

<sup>1</sup>Department of Organisms and Systems Biology (Zoology), University of Oviedo, Oviedo, Spain

<sup>2</sup>Research Unit of Biodiversity (UMIB, UO/CSIC/PA), University of Oviedo, Mieres, Spain

## Correspondence

Irene Fernández-Rodríguez, Department of Organisms and Systems Biology (Zoology), University of Oviedo, Oviedo 33071, Spain.  
Email: [irefdezrguez@hotmail.com](mailto:irefdezrguez@hotmail.com)

## Abstract

Autotomy is a drastic antipredator defense consisting of the voluntary shedding of a body part to escape from the predators. The loss of a body part may impair locomotion, feeding or mating, so animals may face a higher predation risk shortly after autotomy. Thus, until regeneration is completed, prey may adjust their behavior to reduce predation risk, and this could involve secondary costs. We assessed the effect of tail loss on the antipredator behavior of wall lizards (*Podarcis muralis*), comparing the behavior of tailed and tailless individuals exposed to a predatory snake (*Coronella austriaca*) scent, under controlled experimental conditions. Tailless lizards spent significantly more time performing behaviors with antipredatory significance (e.g., moving slowly), whereas tailed individuals performed exploratory walking for significantly more time. Moreover, tailless lizards spent more time basking, which probably increases the effectiveness of their cryptic design and decreases detection by predators. Lizards intensified the tongue flick rates when exposed to a pungent control or snake scents, as compared to their response to a neutral control. Besides, both tailed and tailless lizards intensified some aspects of their antipredator behavior (walking slowly and avoiding refuge use) when exposed to snake scent, which indicates discrimination of the smell of predatory snakes. Lizards decreased refuge use when exposed to predator scents, probably because the refuges are evaluated as unsafe due to a high concentration of snake scents. To conclude, our experiments showed that, after losing their tails, wall lizards modify their behavior in a way that likely minimizes predation risk.

## KEYWORDS

*Coronella austriaca*, olfactory cues, *Podarcis muralis*, predator avoidance, predator recognition

## 1 | INTRODUCTION

The evolution of animal morphology and behavior is partially driven by predation, which implies a strong selecting pressure, so that prey have evolved diverse antipredator strategies to avoid being killed

(Abrams, 2000; Johnson & Belk, 2020). Prey's defensive strategies can be categorized into primary and secondary defenses (Greene, 1988; Langerhans, 2007; Lind & Cresswell, 2005). Primary defenses reduce the probability of detection and identification by a predator (e.g., cryptic designs, immobility or anachoresis; Caro, 2005;

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* published by Wiley Periodicals LLC

Michelangeli & Wong, 2014), while secondary defenses diminish the probability of capture and death once the attack has been initiated (e.g., armours, spines, toxins, mimicry or elusiveness signaling; Ruxton et al., 2018). Among the secondary defenses, aimed at disrupting attacks and allowing the escape from the predator, autotomy is a particularly drastic one, as the threatened animal suffers the voluntary detachment of a body part to wriggle out of the predator, and to provide a distraction that enables the escape success (Maginnis, 2006). Autotomy is relatively common among vertebrates and can affect different peripheral expendable parts of the body, such as the limbs, the skin or the tail (Higham et al., 2013). In particular, caudal autotomy to avoid predation is very common and taxonomically widespread in lizards (Bateman & Fleming, 2009; Bellairs & Bryant, 1985; Greene, 1988), to such an extent that in many natural populations more than 50% of adult animals have mutilated or re-generated tails (Chapple et al., 2002; Downes & Shine, 2001; Fernández-Rodríguez & Braña, 2020, for the herein studied population of *Podarcis muralis*).

Despite the benefits of autotomy to avoid predation, the loss of a body part can entail several immediate consequences, such as decreased locomotor performance, degradation of social status, or restriction in communication between conspecifics, which may negatively affect daily activities, like habitat selection, foraging, moving, mating, or facing new predator encounters (see the reviews of Bateman & Fleming, 2009; Emberts et al., 2019; Lawrence, 2010; Maginnis, 2006). Because of these major drawbacks, autotomy is frequently followed by regeneration of the lost parts, which restores partially or completely their functionality (Fernández-Rodríguez & Braña, 2020; Lin et al., 2017). However, regeneration takes time and, until it is complete, animals suffer from locomotor impairment and lack the possibility of using the lost parts as a distraction in new encounters with predators, so they might face an increased risk of predation (Fox & McCoy, 2000; Lin et al., 2017). Thus, to cope with these costs and reduce predation risk after autotomy, animals have frequently evolved the ability to adopt behavioral adjustments, such as changes in activity time, space use, foraging, or escape tactics (Bateman & Fleming, 2011; Fox et al., 1981; Ramsay et al., 2001). Some of the behavioral modifications may, in turn, imply secondary costs, so there could be a trade-off between avoiding predation and performing other fitness-related activities. For instance, increasing foraging time to fulfill the extra energetic requirements for regeneration may increase predation risk (Dial & Fitzpatrick, 1981; Fox, 1978), and increasing anachoresis (i.e., staying longer in shelters) may imply a decrease on activity time, mating and feeding opportunities, even leading to a decrease in body condition (Martín, 2001).

The adaptive value of autotomy relies on the balance between its costs and benefits (Arnold, 1988), so it is necessary to identify the behavioral changes associated with the loss of a part of the body, and to evaluate the potential costs derived from such injury. The functional costs of tail loss have been widely studied in lizards (for a review, see Bateman & Fleming, 2009), which are very suitable models to study the behavioral adjustments undergone to reduce the risk of predation after autotomy (Martín & Salvador, 1993;

Michelangeli et al., 2020; Salvador et al., 1995; Wilson, 1992). Within this framework, the aims of this study are to assess the effect of tail loss on the antipredator behavior of wall lizards (*P. muralis*), comparing the activity and behavior of tailed and tailless individuals in the laboratory when exposed to olfactory cues from the smooth snake (*Coronella austriaca*), a specialized predator whose diet is mainly composed of small reptiles. Most squamate reptiles strongly rely on chemical cues to develop social, reproductive, exploratory, predatory, and antipredator behaviors, for which they have evolved complex vomeronasal chemoreception systems (Cooper, 1997; Schwenk, 1995). Specifically, several studies have shown that lacertid lizards are able to detect predators from their chemical cues and deposits (Thoen et al., 1986; Van Damme & Quick, 2001; see, for *P. muralis*, Amo et al., 2004a, 2005), so we have carried out laboratory tests to assess the possible differences in behavior and activity of tailed and tailless lizards exposed to olfactory signals from predators.

## 2 | MATERIAL AND METHODS

### 2.1 | Laboratory experiments

The common wall lizard *P. muralis* (Laurenti, 1768) is a small lacertid lizard (Reptilia: Lacertidae) of 4.8–6.9 cm snout-vent-length (SVL) which is widely distributed throughout central and southern Europe, inhabiting rocky environments of natural and anthropic areas from 0 to 2400 m of elevation (Salvador, 2014). The smooth snake (*C. austriaca* Laurenti, 1768) is a small constrictor snake (Reptilia: Colubridae) of 50–60 cm length that inhabits rocky and shrubland areas of south Europe, from 0 to 1700 m of elevation (Galán, 2014). The smooth snake feeds mostly on lacertid lizards, like *P. muralis*, although it incorporates an increasing number of small mammals into its diet as it grows (Reading & Jofré, 2013; Rugiero et al., 1995).

Thirty-three adult wall lizards ( $N_{\text{females}} = 17$ ;  $N_{\text{males}} = 16$ ) were captured by noose in rural areas of central Asturias (northern Spain) with presence of smooth snakes, so the lizards included in our experiment likely have had some previous contact with this specialist predator in its natural environment. The experiments were carried out in September 2018, once the reproductive period is over, thus reducing behavioral biases due to sex and the reproductive condition of the individuals. The animals were transported to the laboratory of Zoology (University of Oviedo), housed in terraria (50 L × 37 W × 25 cm H) exposed to a natural photoperiod (approximately 12 h light and 12 h darkness) and provided with water and food ad libitum (crickets, mealworms, and cockroaches). Animals were randomly housed in groups of three lizards each, composed of either two females and one male, or two males and one female. Lamps of 35 W suspended 20 cm above the cages allowed lizards to thermoregulate within their thermal preferred range. Both males and females were measured for SVL and divided into a control ( $N_{\text{females}} = 8$ ;  $N_{\text{males}} = 8$ ; mean ± SD SVL: 5.95 ± 0.41 cm) and an experimental group ( $N_{\text{females}} = 9$ ;  $N_{\text{males}} = 8$ ; mean ± SD SVL: 6.08 ± 0.47 cm). Tail autotomy was induced to the experimental group by holding the animals firmly from the base of the

tail for 2–5 s, until they released it autonomously, leaving a tail stub of  $0.96 \pm 0.17$  cm (mean  $\pm$  SD). To minimize behavioral biases due to handling when inducing autotomy, lizards of the control group were manipulated in a similar way to the experimental individuals but avoiding tail detachment. Animals were allowed to rest for 2 days after manipulation, so that tailless lizards could recover from the physical trauma and acclimate to moving and performing their routine activities in their new tailless condition. Each lizard was subjected on three consecutive days to behavioral tests conducted in three structurally homogeneous environments, only differing in olfactory cues, namely: one environment impregnated with a neutral odor (distilled water), another with a predator odor (*C. austriaca*) and a third with an intense odor with no specific biological significance (cologne); each individual did only one trial per day and the order of the trials for each individual was randomized. The trials consisted in leaving the lizards in an open opaque-walled terrarium (62 L  $\times$  43 W  $\times$  40 cm H), with a 100 W lamp suspended in the middle of the arena to give them the opportunity to thermoregulate, and the floor covered with absorbent paper impregnated with the specific odors. A hollow brick was placed in the middle of the terrarium under the heat source, which could be used either as a substrate for thermoregulation or as a shelter. Lizards were allowed to move freely in the test arena for 15 min and, during that time, behaviors with possible meaning in antipredator defense were recorded and timed. Before starting the trials, lizards were placed in an incubator at 25°C for 30 min, so that they could reach a body temperature close to the lower limit measured in active animals in the field. This was aimed to guarantee that they were active from the beginning of the trial, but close to the lower limit of the preferred thermal range of the species, which is near 32°C (Bauwens et al., 1995; Braña, 1991, 1993), so that lizards will probably have the urge to thermoregulate.

For the neutral control trial, the bottom of the terrarium (brick and paper) was sprayed with distilled water. The trial with smooth snake scent aimed to simulate the presence of a specific predator to evaluate the possible differences between tailed and tailless lizards in their response to specific predator cues. To impregnate the brick and the substrate of the terrarium with the snake's scent, an adult smooth snake was placed in the terrarium, letting it move freely for 20 h and removing it just before starting the trial. For this procedure, we used two adult smooth snakes (female's total length: 64 cm; male's total length: 55 cm) that were housed in a terrarium (116 L  $\times$  52 W  $\times$  41 H, cm) located in a different area than the terraria of lizards, so that lizards were visually and olfactory isolated from the snakes. During the experiment, the snakes were fed approximately once per week with fresh or thawed detached lizard tails. To determine if lizards recognize the scent of the snake or just react to an intense odor, we tested, as an additional control, the behavior of the lizards when exposed to a pungent odor without a specific biological meaning (cologne), according to the usual experimental protocol for olfactory recognition tests in reptiles (e.g., Dial & Schwenk, 1996; Van Damme & Quick, 2001). For the pungency control we used the commercial cologne Deliplus "Brisa", from Maverick laboratories S.L.U. After each trial the terraria and the bricks were cleaned and disinfected with

alcohol and diluted bleach, and then rinsed with water to reduce all scents.

All the trials were recorded with a videocamera (Sony HDR-CX210E) mounted above the experimental terrarium and, based on previous studies on lizard behavior (Amo et al., 2004a; Ortega et al., 2018; Thoen et al., 1986; Van Damme et al., 1990), six types of behavioral responses were recognized and timed in the videorecordings (played back with the software Windows Media Player), with a total time of 15 min for each lizard in each of the three trials. We have considered the following behavioral responses:

- **Slow moving:** slow and intermittent motion, with frequent stops of 1–2 s and scattered or jerky movements (Avery, 1993; Braña, 2003), likely aiming to evaluate the surrounding area or trying to minimize detectability by possible predators (Kramer & McLaughlin, 2001).
- **Normal moving:** rather fast and continuous movement, often with some changes in pace and direction, interpreted as mainly exploratory.
- **Motionless:** the lizard does not perform any displacement for at least 5 s and neither adopts the typical thermoregulatory postures (see "basking").
- **Hide in the refuge:** enter and remain inside the refuge (hollow brick) for at least 5 s.
- **Basking:** the lizard is located under the heat source, immobile and adopting the characteristic postures of thigmothermic and/or heliothermic thermoregulation (see, e.g., Bradshaw & Main, 1968; Muth, 1977).
- **Tongue flick:** number of times that the lizard protruded and rapidly retracted the tongue, as a measure of exploratory activity supposedly aimed at capturing chemosensory information.

Other behavioral patterns that have been described as part of the lizard's antipredatory repertoire, such as "foot shake" or "tail waving" (e.g., Font et al., 2012), have been infrequent or unclear in our recordings and have not been considered.

## 2.2 | Statistical analyses

All the variables met the assumptions of normality and homogeneity of variances (Kolmogorov-Smirnov and Levene tests,  $p > 0.05$  in all cases), except for the variables "refuge" in the trials with snake scent (Kolmogorov-Smirnov test:  $Z = 1.935$ ,  $p = 0.001$ ) and "motionless" in the control trials (Kolmogorov-Smirnov test:  $Z = 1.444$ ,  $p = 0.030$ ). Thus, the variables "refuge" and "motionless" were  $\log_{10}$  transformed to achieve normality. A one-way analysis of variance (ANOVA) with SVL as the dependent variable and tail group as factor was done to check that the control and the experimental groups were homogeneous in terms of size (SVL). To test possible differences in the behavior of tailed and tailless individuals in the three trials (neutral control, cologne scent, and snake scent), a two-way repeated measures multivariate analysis of variance (MANOVA) was done with all

the behavioral variables measured (i.e., total time moving slowly, walking normally, motionless, hiding in the refuge and basking) as the dependent variables, and type of trial, tail group and sex as factors; posthoc comparisons between the pairs of trials were done with Tukey tests.

The frequency of tongue movements was analysed independently, as it was measured as a rate (number per unit of time), while the other variables express the time spent on certain behaviors which are mutually exclusive, unlike the movements of the tongue, which were always performed simultaneously with some other behavioral pattern. Therefore, possible differences in the rate of tongue flicks between tailed and tailless lizards and between the different olfactory stimuli were tested by a repeated measures ANOVA with tail group and sex as inter-subject factors. The assumption of sphericity was checked with a Mauchly's test. Posthoc comparisons to identify particular between-pair differences among the three trials types were done with Tukey tests when the overall analyses indicated significant differences. Significant level was set at 0.05 for all the analyses done in this study. Statistical analyses were performed in SPSS (version 20).

### 3 | RESULTS

Tailed and tailless lizards did not differ in SVL (one-way ANOVA:  $F_{1,31} = 0.807$ ,  $p = 0.376$ ). Results of the two-way repeated measures MANOVA carried out on variables that indicate the time spent in developing characteristic behaviors are summarized in Table 1 and Figure 1. There are several behavioral changes associated with tail condition: tailless individuals spent more time performing stereotyped slow moving and basking than tailed lizards, whereas tailed lizards spent more time walking normally than tailless ones. No differences were found between tailed and tailless lizards in the time spent performing other behaviors, and sex was not a significant factor for any of the variables included in the analysis.

Regarding the behavioral patterns in the three different trials (neutral control, pungent control, snake scent), lizards spent significantly more time walking slowly during the trial with snake odor than during the neutral and cologne control tests (posthoc comparisons, neutral control vs. cologne:  $p = 0.323$ , neutral control vs. snake:  $p < 0.001$ , cologne vs. snake:  $p < 0.001$ ). Besides, lizards spent significantly less time inside the refuge during the trial with snake scent than in the neutral and pungent control trials (posthoc comparisons: neutral control vs. cologne:  $p = 0.250$ , neutral control vs. snake:  $p = 0.034$ , cologne vs. snake:  $p = 0.001$ ). No differences were found between the different types of trials with respect to the time spent performing any other behavior (Table 1;  $p > 0.05$  in all cases). No significant interactions were found between type of trial and sex or tail group in any of the behavioral variables (Table 1).

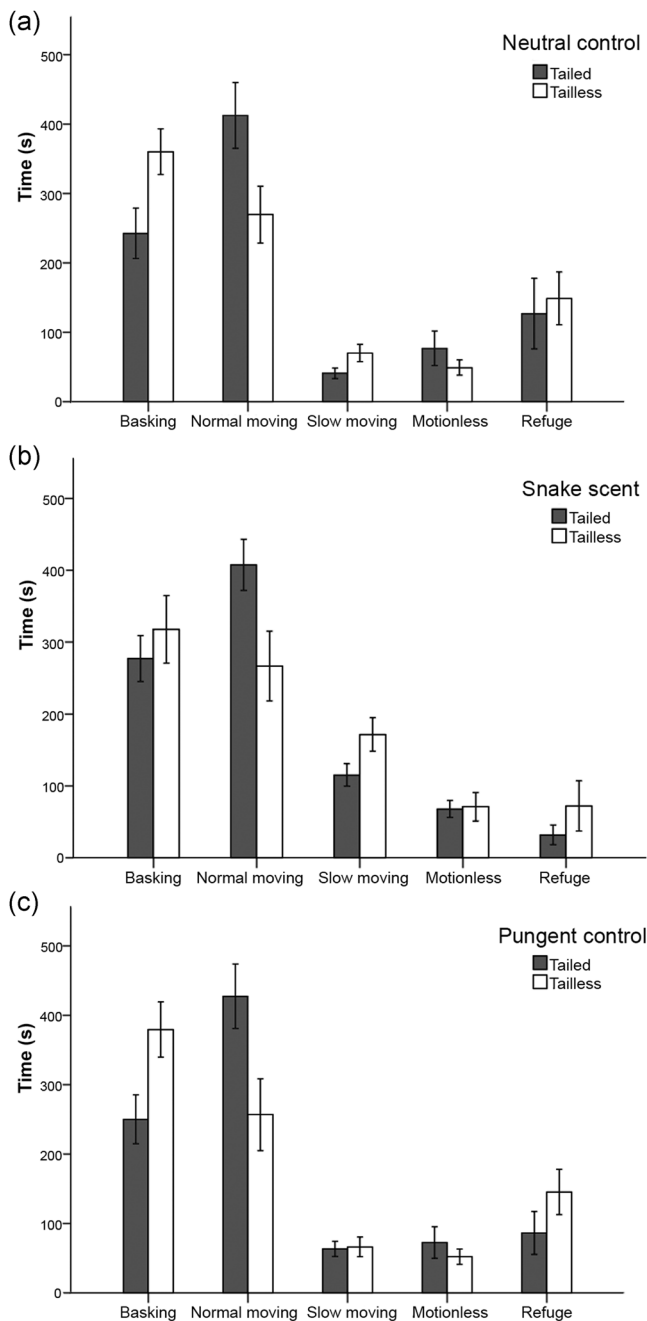
The assumption of sphericity was met in the repeated measures ANOVA with tongue flicks as dependent variable (Mauchly's test:  $W = 0.899$ ,  $p = 0.224$ ). Lizards did not exhibit differences in tongue

**TABLE 1** Statistical results of the two-way repeated measures MANOVA carried out with the time spent by lizards performing five characteristic behaviors

	Behavioral variables	F value	p value
Trial	Basking	0.101	0.888
	Normal moving	0.024	0.964
	Slow moving	29.530	<b>&lt;0.001</b>
	Motionless	0.122	0.873
	Refuge	7.024	<b>0.005</b>
Tail group	Basking	5.921	<b>0.021</b>
	Normal moving	8.223	<b>0.008</b>
	Slow moving	5.022	<b>0.033</b>
	Motionless	0.299	0.589
	Refuge	3.236	0.082
Sex	Basking	0.493	0.488
	Normal moving	1.364	0.252
	Slow moving	0.661	0.423
	Motionless	3.690	0.065
	Refuge	0.781	0.384
Trial × Tail group	Basking	1.280	0.286
	Normal moving	0.321	0.696
	Slow moving	2.508	0.110
	Motionless	0.070	0.923
	Refuge	0.093	0.859
Trial × Sex	Basking	0.211	0.791
	Normal moving	1.915	0.163
	Slow moving	1.227	0.291
	Motionless	0.643	0.520
	Refuge	0.929	0.390
Tail group × Sex	Basking	0.183	0.672
	Normal moving	1.565	0.221
	Slow moving	1.920	0.176
	Motionless	0.268	0.609
	Refuge	0.520	0.448

Note: Type of trial (neutral control, pungent control and snake scent), tail group (tailed or tailless), and sex (male or female) were included as categorical inter-subject factors. Significant values are highlighted in bold.

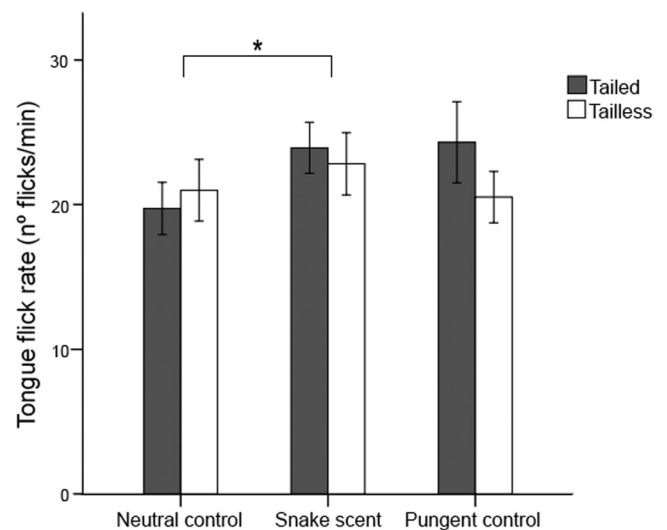
flick rate according to their tail group (tailed/tailless) or their sex (repeated measures ANOVA,  $p > 0.05$  in both cases; Figure 2) but performed significantly more flicks per minute when confronted with snake than in the neutral control trial (repeated measures ANOVA:  $F_{2,28} = 3.753$ ,  $p = 0.036$ ; posthoc comparisons: neutral control vs. cologne:  $p = 0.159$ , neutral control vs. snake:  $p = 0.010$ , cologne vs. snake:  $p = 0.509$ ).



**FIGURE 1** Behavioral responses of tailed (gray) and tailless (white) lizards, in three trials conducted using different olfactory stimuli: (a) a neutral control (distilled water); (b) a predator snake (*Coronella austriaca*) scent; (c) a pungent odor (cologne). Values are mean ( $\pm$ SE) total time spent by the lizards in each activity during the trial

## 4 | DISCUSSION

Tail autotomy in lizards is an effective, yet drastic antipredator response once the predator has initiated a pursuit (Arnold, 1988; Ruxton et al., 2018). But lacking the tail often constrains locomotor performance (Fernández-Rodríguez & Braña, 2020; Medger et al., 2008), which is essential for a number of ecologically relevant tasks that are closely related to fitness, such as feeding, territory patrolling or mating (Braña,



**FIGURE 2** Tongue flick per minute of tailed (gray) and tailless (white) lizards in the three trials in which the environment is impregnated with different smells: a neutral control (distilled water), a predator snake (*Coronella austriaca*) scent and a pungent control (cologne). Values are means  $\pm$  SE; \* $p < 0.05$

2003; Garland & Losos, 1994; Husak, 2006). In addition, the probability of avoiding predation, either by fleeing or by shedding again the tail, decreases after autotomy (Fox & McCoy, 2000), so lizards are expected to exhibit some behavioral adjustments to minimize the costs of lacking the tail, at least until regeneration is completed. According to this prediction, and regardless of the presence of predator scents, tailless lizards in our experiment spent significantly more time than tailed ones performing behaviors with probable antipredator significance, such as stereotyped slow moving, and tended to minimize behaviors that imply greater exposure and increase detectability, such as exploratory walking. Previous studies showed that walking slowly and performing slow and jerky movements, together with tail waving and foot shaking, are general antipredator behaviors in lacertid lizards (Mencía et al., 2016; Ortega et al., 2018; Thoen et al., 1986; see Font et al., 2012 for *P. muralis*), and probably reduce the likelihood of detection by predators or favor the ability to respond to their attacks (Labra & Niemeyer, 2004). Besides, remaining motionless while basking surely enhances the cryptic value of the dorsal design, thus reducing the probability of detection and, on the other hand, decreases the stimulus for attack by predators, which are frequently triggered by sudden movements of the prey (see, for predatory snakes, Shine & Sun, 2003). Moreover, the greater tendency of tailless lizards to remain immobile is consistent with the pattern observed in wall lizards in other situations of locomotor impairment, such as the burden of pregnancy (Braña, 1993). On the other hand, basking is known to be costly in terms of exposure to visual predators (Alford & Lutterschmidt, 2012), especially depending on the microhabitats selected for thermoregulation, which may change after tail loss (Martín & Salvador, 1993), but these potential shifts in microhabitat use after tail loss and its relation to thermoregulation, are beyond the aims and design of this study. Another explanation for the higher time devoted by tailless lizards to thermoregulation would be to

optimize their physiological functions to accelerate healing and regeneration.

The present study shows antipredatory behavioral changes in tailless wall lizards, a species on which we had shown in a previous study that suffers a significant decrease in locomotor ability after the loss of the tail (Fernández-Rodríguez & Braña, 2020). Other lizards, like the iguanian *Sceloporus virgatus*, the lizard *Psammotomus algirus* and the skinks *Lampropholis delicata*, *L. guichenoti* and *Scincella lateralis*, also present alterations in their antipredator behavior and a locomotor impairment after tail loss (Cromie & Chapple, 2012; Downes & Shine, 2001; Formanowicz et al., 1990; Martín & Avery, 1998; Michelangeli et al., 2020). On the other hand, the geckos *Amalosa lesueurii* and *Teraroscincus scincus*, and the skink *Pseudocordylus melanotus*, do not suffer from locomotor impairment after tail loss and neither do alter their antipredator behavior after tail loss (Kelehear & Webb, 2006; Lu et al., 2010; McConnachie & Whiting, 2003). This supports the idea that such behavioral adjustments are adopted to minimize vulnerability after tail loss, at least partially because of the consecutive reduction in locomotor capacity, but further studies would be necessary to specifically address this issue.

Lizards use information mediated by chemical signals for feeding, social and sexual communication or predator detection, and tongue flicking contributes to the chemosensory perception mechanism associated to the vomeronasal organ (Cooper, 1994), so that the frequency of tongue movements outside the mouth can be reliably interpreted as an indicator of variations in exploratory and information gathering behaviors (Cooper & Burghardt, 1990; Gove, 1979). In our experimental tests, the behavioral responses related to chemoreception were not affected by tail loss, since both tailed and tailless lizards exhibited similar patterns of tongue flicking during the three trials. Regardless of their tail condition, wall lizards increased tongue flick rates in environments impregnated with intense olfactory signals (either colony or snake scent), thus indicating an intensification of the exploratory pattern, but this does not provide evidence that they specifically recognize the predator. However, although the tongue movements are almost equally intensified by the exposure to the smell of snakes and to a pungent odor, which is not significant from the perspective of the set of lizards' ecological interactions, other behavioral responses observed in our trials indicate that lizards were able to discriminate the smell of predatory snakes. For example, both tailed and tailless lizards intensified certain patterns of antipredator behavior (e.g., moving slowly) when exposed to snake scent, as compared to the patterns shown in the neutral and the pungent control trials. Indeed, the differentiated response to snake chemical cues does not imply the recognition of *C. austriaca* as a lizard-specific predator, but some studies conducted on the antipredatory responses of lacertid lizards frequently showed that lizards are able to discriminate between the chemical cues of lizard-predatory snakes and those of non-sauropogous snakes (e.g., Mencia et al., 2016; Ortega et al., 2018; Van Damme & Quick, 2001; see, for *P. muralis*, Amo et al., 2004a; Durand et al., 2012). Therefore, given that the lizards used in our experiment were adults collected in the field in a locality where they coexist with smooth snakes, it is plausible to propose that their recognition of the snake's scent may have been species-specific.

Wall lizards in our experiments spent significantly less time inside the refuge in the predator-scented environment, which indicates that they did not resort to anachoresis when exposed to predator chemical cues. The avoidance of shelters could occur for two different reasons: one immediate, based on the olfactory information provided by the refuge itself; and the other general, based on an a priori consideration of the safety of a shelter as protection against a specific type of predator. Regarding the first aspect, we have verified that the smooth snakes placed in the terrarium often spent a long time sheltering inside the holes of the bricks, so those shelters surely had a high concentration of snake chemical cues, and this is a possible reason why they were generally avoided by the lizards. Secondly, since the smooth snake is an ambush foraging predator that frequently lurks from crevices and holes between stones (Amo et al., 2004c), the brick holes could be evaluated as unsafe shelters by lizards (Amo et al., 2004b, 2005; Durand et al., 2012), especially when the environment is saturated with the snake scent, indicating a nearby presence of the predator. It is worth remembering that the lizards used in this study were adults caught in the field, so that they had possibly had previous contact with predatory snakes, which makes it difficult to conclude whether these behaviors are innate or learned, although some previous studies have suggested a limited role of experience in the expression of antisnake behavior in wall lizards (Durand et al., 2012).

To conclude, our study gives evidence of how lizards resort to behavioral modifications after tail loss, which likely minimizes the higher risk of predation until the lost capacities are restored after the completion of regeneration. Increasing wariness may contribute to minimize detection by the predators and diminish predation risk, which lizards achieve by decreasing activity levels (Downes & Shine, 2001; Martín & Salvador, 1995; Michelangeli et al., 2020), changing the microhabitat use (Fox et al., 1981) or modifying the escape tactics (Cooper, 2003, 2007; Dial & Fitzpatrick, 1981; Fleming et al., 2007). According to Brodie et al. (1991), defensive mechanisms can be divided into predator-avoidance (reducing the probability of detection and encounter with the predator) and antipredator strategies (reducing the probability of capture and death after detection). Lizards' tail autotomy is clearly an antipredator mechanism that occurs once the attack has been triggered, while the behavioral modifications displayed in the presence of olfactory signals are early-stage predator-avoidance mechanisms. Tailless lizards not only have reduced locomotor capacities (Fernández-Rodríguez & Braña, 2020), but nor can they resort again to autotomy to avoid predation, so their antipredator defenses are diminished until regeneration is completed. Our study gives evidence of an exacerbation of lizards' predator-avoidance mechanisms when their antipredator mechanisms are diminished as a consequence of tail loss. These kinds of behavioral changes have also been observed in other animal taxa that undergo autotomy, such as starfishes, crabs, damselflies, or grasshoppers (see the reviews of Emberts et al., 2019; Fleming et al., 2007; Maginnis, 2006). However, these antipredatory responses come at a cost, since they imply an allocation of time and energy and thus may incur trade-offs with other functions directly related to self-maintenance and fitness (Lind & Cresswell, 2005). Even so, we show that animals modify their behavior after autotomy.

## ACKNOWLEDGEMENTS

This study was conducted with permission from the Ministry of Infrastructures, Land Use and Environment of the Principality of Asturias Regional Government, for the capture and maintenance of the animals (2018/009359; PROAE 16/2019). Irene Fernández-Rodríguez was supported by a Severo Ochoa fellowship from the Principality of Asturias (BP16192). We would like to thank the anonymous reviewers whose comments helped to improve and clarify this manuscript.

## CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, Irene Fernández-Rodríguez, upon reasonable request.

## ORCID

Irene Fernández-Rodríguez  <http://orcid.org/0000-0001-5944-5731>

## REFERENCES

- Abrams, P. A. (2000). The evolution of predator-prey interactions: Theory and evidence. *Annual Review of Ecology and Systematics*, 31, 79–105.
- Alford, J. G., & Lutterschmidt, W. I. (2012). Modelling energetic and theoretical costs of thermoregulatory strategy. *Journal of Biological Dynamics*, 6, 63–79.
- Amo, L., López, P., & Martín, J. (2004a). Chemosensory recognition and behavioral responses of wall lizards, *Podarcis muralis*, to scents of snakes that pose different risks of predation. *Copeia*, 2004(3), 691–696.
- Amo, L., López, P., & Martín, J. (2004b). Wall Lizards combine chemical and visual cues of ambush snake predators to avoid overestimating risk inside refuges. *Animal Behaviour*, 67, 647–653.
- Amo, L., López, P., & Martín, J. (2004c). Chemosensory recognition of its lizard prey by the ambush smooth snake, *Coronella austriaca*. *Journal of Herpetology*, 38, 451–454.
- Amo, L., López, P., & Martín, J. (2005). Chemical assessment of predation risk in the wall lizard, *Podarcis muralis*, is influenced by time exposed to chemical cues of ambush snakes. *Herpetological Journal*, 15, 21–25.
- Arnold, E. N. (1988). Caudal autotomy as a defense. In C. Gans, & R. B. Huey (Eds.), *Biology of the reptilia: Ecology B: Defense and life history* (Vol. 16, pp. 237–273). Alan R. Liss, Inc.
- Avery, R. A. (1993). Experimental analysis of lizard pause-travel movement: Pause increases probability of prey capture. *Amphibia-Reptilia*, 14, 423–427.
- Bateman, P. W., & Fleming, P. A. (2009). To cut a long tail short: A review of lizard caudal autotomy studies carried out over the last 20 years. *Journal of Zoology*, 277, 1–14.
- Bateman, P. W., & Fleming, P. A. (2011). Failure to launch? The influence of limb autotomy on the escape behavior of a semiaquatic grasshopper *Paroxya atlantica* (Acrididae). *Behavioral Ecology*, 22(4), 763–768.
- Bauwens, D., Garland, T., Castilla, A. M., & van Damme, R. (1995). Evolution of sprint speed in lacertid lizards: Morphological, physiological, and behavioral covariation. *Evolution*, 49(5), 848–863.
- Bellairs, A., & Bryant, S. V. (1985). Autotomy and regeneration in reptiles. In C. Gans, F. Billett, & P. F. A. Maderson (Eds.), *Biology of the reptilia: Development B* (Vol. 15, pp. 301–410). John Wiley and Sons.
- Bradshaw, S. D., & Main, A. R. (1968). Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. *Journal of Zoology*, 154, 193–221.
- Braña, F. (1991). Summer activity patterns and thermoregulation in the wall lizard, *Podarcis muralis*. *The Herpetological Journal*, 1, 544–549.
- Braña, F. (1993). Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos*, 66(2), 216–222.
- Braña, F. (2003). Morphological correlates of burst speed and field movement patterns: The behavioral adjustment of locomotion in wall lizards (*Podarcis muralis*). *Biological Journal of the Linnean Society*, 80(1), 135–146.
- Brodie, E. D. Jr., Formanowicz, D. R. Jr. & Brodie, E. D. III (1991). Predator avoidance and antipredator mechanisms: Distinct pathways to survival. *Ethology, Ecology and Evolution*, 3, 73–77.
- Caro, T. M. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press.
- Chapple, D. G., McCoull, C. J., & Swain, R. (2002). Changes in reproductive investment following caudal autotomy in viviparous skinks (*Niveoscincus metallicus*): Lipid depletion or energetic diversion? *Journal of Herpetology*, 36, 480–486.
- Cooper, W. E. (1994). Chemical discrimination by tongue-flicking in lizards: A review with hypotheses on its origin and its ecological and phylogenetic relationships. *Journal of Chemical Ecology*, 20, 439–487.
- Cooper, W. E. (1997). Correlated evolution of prey chemical discrimination with foraging, lingual morphology and vomeronasal chemoreceptor abundance in lizards. *Behavioral Ecology and Sociobiology*, 41, 257–265.
- Cooper, W. E. (2003). Shifted balance of risk and cost after autotomy affects use of cover, escape, activity, and foraging in the keeled earless lizard (*Holbrookia propinqua*). *Behavioral Ecology and Sociobiology*, 54, 179–187.
- Cooper, W. E. Jr. (2007). Compensatory changes in escape and refuge use following autotomy in the lizard *Sceloporus virgatus*. *Canadian Journal of Zoology*, 85, 99–107.
- Cooper, W. E. Jr., & Burghardt, G. M. (1990). A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. *Journal of Chemical Ecology*, 16, 45–65.
- Cromie, G. L., & Chapple, D. G. (2012). Impact of tail loss on the behaviour and locomotor performance of two sympatric *Lampropholis* skink species. *PLOS One*, 7(4), e34732.
- Van Damme, R., Bauwens, D., Vanderstighelen, D., & Verheyen, R. F. (1990). Responses of the lizard *Lacerta vivipara* to predator chemical cues: The effects of temperature. *Animal Behavior*, 40, 298–305.
- Van Damme, R., & Quick, K. (2001). Use of predator chemical cues by three species of lacertid lizards (*Lacerta bedriagae*, *Podarcis tiliguerta*, *Podarcis sicula*). *Journal of Herpetology*, 35, 27–36.
- Dial, B. E., & Fitzpatrick, L. C. (1981). The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia*, 51, 310–317.
- Dial, B. E., & Schwenk, K. (1996). Olfaction and predator detection in *Coleonyx brevis* (Squamata: Eublepharidae), with comments on the functional significance of buccal pulsing in geckos. *Journal of Experimental Zoology*, 276, 415–424.
- Downes, S., & Shine, R. (2001). Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology*, 82, 1293–1303.
- Durand, J., Legrand, A., Tort, M., Thiney, A., Michniewicz, R. J., Coulon, A., & Aubret, F. (2012). Effects of geographic isolation on anti-snakes responses in the wall lizard, *Podarcis muralis*. *Amphibia-Reptilia*, 33, 199–206.
- Embets, Z., Escalante, I., & Bateman, P. W. (2019). The ecology and evolution of autotomy. *Biological Reviews*, 94, 1881–1896.
- Fernández-Rodríguez, I., & Braña, F. (2020). The movement dynamics of autotomized lizards and their tails reveal functional costs of caudal autotomy. *Integrative Zoology*, 15, 511–521.
- Fleming, P. A., Muller, D. L., & Bateman, P. W. (2007). Leave it all behind: An evolutionary and taxonomic perspective of autotomy in invertebrates. *Biological Reviews*, 82, 481–510.

- Font, E., Carazo, P., Pérez de Lanuza, G., & Kramer, M. (2012). Predator-elicited foot shakes in wall lizards (*Podarcis muralis*): Evidence for a pursuit-deterrent function. *Journal of Comparative Psychology*, *126*, 87–96.
- Formanowicz, D. R., Brodie, E. D., & Bradley, P. J. (1990). Behavioural compensation for tail loss in the ground skink, *Scincella lateralis*. *Animal Behaviour*, *40*, 782–784.
- Fox, S. F. (1978). Natural selection on behavioral phenotypes of the lizard *Uta stansburiana*. *Ecology*, *59*, 834–847.
- Fox, S. F., & McCoy, K. J. (2000). The effects of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana*. *Oecologia*, *122*, 327–334.
- Fox, S. F., Rose, E., & Myers, R. (1981). Dominance and the acquisition of superior home ranges in the lizard *Uta stansburiana*. *Ecology*, *62*, 888–893.
- Galán, P. (2014). *Coronella austriaca*. In A. Salvador (Ed.), *Fauna Ibérica: Reptiles* (Vol. 10, 2nd ed., pp. 681–706). Museo Nacional de Ciencias Naturales CSIC.
- Garland, T., & Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In P. C. Wainwright, & S. M. Reilly (Eds.), *Ecological morphology* (pp. 240–302). University of Chicago Press.
- Gove, D. (1979). A comparative study of snake and lizard tongue-flicking with an evolutionary hypothesis. *Zeitschrift für Tierpsychologie*, *51*, 58–76.
- Greene, H. W. (1988). Antipredator mechanisms in reptiles. In C. Gans, & R. B. Huey (Eds.), *Biology of the reptilia: Ecology B: Defense and life history* (Vol. 16, pp. 1–152). Alan R. Liss, Inc.
- Higham, T. E., Russell, A. P., & Zani, P. A. (2013). Integrative biology of tail autotomy in lizards. *Physiological and Biochemical Zoology*, *86*, 603–610.
- Husak, J. F. (2006). Does speed help you survive? A test with collared lizards of different ages. *Functional Ecology*, *20*, 174–179.
- Johnson, J. B., & Belk, M. C. (2020). Predators as agents of selection and diversification. *Diversity*, *12*, 415.
- Kelehear, C., & Webb, J. K. (2006). Effects of tail autotomy on anti-predator behavior and locomotor performance in a nocturnal gecko. *Copeia*, *2006*, 803–809.
- Kramer, D. L., & McLaughlin, R. L. (2001). The behavioral ecology of intermittent locomotion. *American Zoologist*, *41*, 137–153.
- Labra, A., & Niemeyer, H. M. (2004). Variability in the assessment of snake predation risk by *Liolaemus* lizards. *Ethology*, *110*, 649–662.
- Langerhans, R. B. (2007). Evolutionary consequences of predation: Avoidance, escape, reproduction, and diversification. In A. M. T. Elewa (Ed.), *Predation in organisms* (pp. 177–220). Springer.
- Lawrence, J. M. (2010). Energetic costs of loss and regeneration of arms in stellate Echinoderms. *Integrative and Comparative Biology*, *50*(4), 506–514.
- Lin, J.-W., Chen, Y.-R., Wang, Y.-H., Hung, K.-C., & Lin, S.-M. (2017). Tail regeneration after autotomy revives survival: A case from a long-term monitored lizard population under avian predation. *Proceedings Royal Society B*, *284*, 20162538.
- Lind, J., & Cresswell, W. (2005). Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, *16*, 945–956.
- Lu, H., Ding, G., Ding, P., & Ji, X. (2010). Tail autotomy plays no important role in influencing locomotor performance and anti-predator behavior in a cursorial gecko. *Ethology*, *116*, 627–634.
- Maginnis, T. L. (2006). The costs of autotomy and regeneration in animals: A review and framework for future research. *Behavioral Ecology*, *17*(5), 857–872.
- Martín, J. (2001). When hiding from predators is costly: Optimization of refuge use in lizards. *Etología*, *9*, 9–13.
- Martín, J., & Avery, R. A. (1998). Effects of tail loss on the movement patterns of the lizard, *Psammotromus algirus*. *Functional Ecology*, *12*, 794–802.
- Martín, J., & Salvador, A. (1993). Thermoregulatory behaviour of rock lizards in response to tail loss. *Behaviour*, *124*, 123–126.
- Martín, J., & Salvador, A. (1995). Effects of tail loss on activity patterns of rock-lizards, *Lacerta monticola*. *Copeia*, *1995*(4), 984–988.
- McConnachie, S., & Whiting, M. J. (2003). Costs associated with tail autotomy in an ambush foraging lizard, *Cordylus melanotus melanotus*. *African Zoology*, *38*(1), 57–65.
- Medger, K., Verburt, L., & Bateman, P. W. (2008). The influence of tail autotomy on the escape response of the Cape Dwarf Gecko, *Lygodactylus capensis*. *Ethology*, *114*, 42–52.
- Mencia, A., Ortega, Z., & Pérez-Mellado, V. (2016). Chemical discrimination of sympatric snakes by the mountain lizard *Iberolacerta galani* (Squamata: Lacertidae). *The Herpetological Journal*, *26*, 149–155.
- Michelangeli, M., Melki-Wegner, B., Laskowski, K., Wong, B. B. M., & Chapple, D. G. (2020). Impacts of caudal autotomy on personality. *Animal Behaviour*, *162*, 67–78.
- Michelangeli, M., & Wong, B. B. M. (2014). A recent predatory encounter influences subsequent male signalling behaviour in a desert-dwelling fish. *Behavioral Ecology*, *25*, 928–932.
- Muth, A. (1977). Body temperature and associated postures of the zebra-tailed lizard, *Calisaurus draconoides*. *Copeia*, *1977*, 122–125.
- Ortega, Z., Mencia, A., & Pérez-Mellado, V. (2018). Antipredatory behaviour of a mountain lizard towards the chemical cues of its predatory snakes. *Behaviour*, *155*(10–12), 817–840.
- Ramsay, K., Kaiser, M. J., & Richardson, C. A. (2001). Invest in arms: Behavioural and energetic implications of multiple autotomy in starfish (*Asterias rubens*). *Behavioral Ecology and Sociobiology*, *50*, 360–365.
- Reading, C. J., & Jofré, G. M. (2013). Diet composition changes correlated with body size in the Smooth snake, *Coronella austriaca*, inhabiting lowland heath in southern England. *Amphibia-Reptilia*, *34*, 463–470.
- Rugiero, L., Capula, M., Filippi, E., & Luiselli, L. (1995). Food habits of Mediterranean populations of the smooth snake (*Coronella austriaca*). *Herpetological Journal*, *5*, 316–318.
- Ruxton, G. D., Allen, W. L., Sherratt, T. N., & Speed, M. P. (2018). *Avoiding attack: The evolutionary ecology of crypsis, aposematism and mimicry* (2nd ed.). Oxford University Press.
- Salvador, A. (2014). *Podarcis muralis*. In A. Salvador (Ed.), *Fauna Ibérica: Reptiles* (Vol. 10, 2nd ed., pp. 576–589). Museo Nacional de Ciencias Naturales CSIC.
- Salvador, A., Martín, J., & López, P. (1995). Tail loss reduces home range size and access to females in male lizards, *Psammotromus algirus*. *Behavioral Ecology*, *6*, 382–387.
- Schwenk, K. (1995). Of tongues and noses: Chemoreception in lizards and snakes. *Trends in Ecology and Evolution*, *10*, 7–12.
- Shine, R., & Sun, L.-X. (2003). Attack strategy of an ambush predator: Which attributes of the prey trigger a pit-viper's strike? *Functional Ecology*, *17*, 340–348.
- Thoen, C., Bauwens, D., & Verheyen, R. F. (1986). Chemoreceptive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. *Animal Behaviour*, *34*, 1805–1813.
- Wilson, B. S. (1992). Tail injuries increase the risk of mortality in free-living lizards (*Uta stansburiana*). *Oecologia*, *92*, 145–152.

**How to cite this article:** Fernández-Rodríguez, I., Braña, F. (2022). Behavioural patterns in the early-stage antipredator response change after tail autotomy in adult wall lizards. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *337*, 250–257. <https://doi.org/10.1002/jez.2562>