Sex does not affect tail autotomy in lacertid lizards

Panayiotis Pafilis[1],*, Kostas Sagonas[2], Grigoris Kapsalas[1], Johannes Foufopoulos[3], Efstratios D. Valakos[4]

[1] *Department of Zoology and Marine Biology, School of Biology, National and Kapodistrian University of Athens, Panepistimioupolis, Ilissia 15784, Greece. *Corresponding author.* E-mail: ppafil@biol.uoa.gr*

[2] *School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, United Kingdom*

[3] *School of Natural Resources and Environment, Dana Building, 430 East University, University of Michigan, Ann Arbor, MI 48109-1115, USA*

[4] *Department of Animal and Human Physiology, School of Biology, National and Kapodistrian University of Athens, Panepistimioupolis, Ilissia 15784, Greece*

Abstract. Caudal autotomy is one of the most effective and widespread defensive mechanisms among lizards. When predators grasp the tail, lizards are able to shed it from the point of the attack and further. Numerous factors have been reported to affect tail-shedding performance such as temperature, age, predation pressure, intraspecific competition etc. Interestingly, the impact of sex on tail loss remains greatly understudied. Here, we analyzed tail autotomy performance, simulated in the lab, in 12 species of lacertid lizards belonging to five genera (*Algyroides*, *Anatololacerta*, *Hellenolacerta*, *Ophisops*, *Podarcis*). Our aim was to investigate whether sex affects caudal autotomy and/or the duration of post-autotomic tail movement. We failed to detect any effect of sex on tail loss in the species examined. Also, we did not find any sexual impact on the duration of tail movement after autotomy, with a single exception. Our findings suggest that autotomy serves as a defensive tactic equally in both sexes and is used in the same extent.

Keywords. Predation, intraspecific competition, defense, Greece.

INTRODUCTION

Autotomy, the self-amputation of a body limb, is rather rare among vertebrates: the behavior is restricted to reptiles (Cooper and Alfieri, 1993; Hoare et al., 2006), salamanders (Marvin, 2010; Romano et al., 2010) and very few mice (Seifert et al., 2012). Undoubtedly, lizards are the champions of autotomy (Arnold, 1984; Bellairs and Bryant, 1985). Most families of the suborder shed their tail in response to mechanical stimuli exerted by a predator's attack (Arnold, 1987; Downes and Shine, 2001; Bateman and Fleming, 2009). The identity of the predator may vary. It could be any occasional or specialized saurophagous predator (e.g., snakes, birds, mammals) as traditional theory predicts (Pianka, 1970; Turner et al., 1982; Cooper et al., 2004), or a conspecific, triggered by intraspecific competition, as recent literature suggests (Pafilis et al., 2009b; Donihue et al., 2016; Itescu et al., 2017). In either case the result remains the same: the shed tail trashes vigorously, fuelled by anaerobic metabolism, to distract the predator while the tailless lizard escapes (Dial and Fitzpatrick, 1983; Pafilis et al., 2005).

Many factors are known to affect caudal autotomy such as temperature, age and body shape (Arnold, 1984; Daniels, 1984; Pafilis and Valakos, 2008; Fleming et al., 2013). Previous studies on other aspects of autotomy did not report sexual effects on the trait, without though focusing on this particular issue (Chapple and Swain, 2004; Pafilis et al., 2005; Brock et al., 2015, but see Itescu et al., 2017). However there are several clues indicat-

ing that tail autotomy could be sexually biased (Pérez-Mellado et al., 1997; Bateman and Fleming, 2009). Male lizards, particularly those belonging to territorial species, expose themselves in their effort to defend their territory (Kaiser and Mushinsky, 1994; Salvador and Veiga, 2001). Thus, typical 'alien' predators (non conspecifics) have better chances to prey on the more conspicuous males that patrol or oversee their territory, a fact that could lead to higher autotomy rates (Bateman and Flemming, 2011; Marshall et al., 2016). Also, intramale competition may increase tail loss. Male lizards are much more aggressive against their peers compared to females (Kwiatkowski and Sullivan, 2002; Lailvaux and Irschick, 2007; McEvoy et al., 2013). Ergo, agonistic encounters between males are more common and may end up to tail loss (Cooper and Vitt, 1987; Bateman and Fleming, 2009; Cooper et al., 2015). Nonetheless, a byproduct of this increased intraspecific competition could be a higher propensity of males to hold on to tails more strongly.

On the other hand, females are expected to lessen their ability to autotomize because of the high energetic demands of vitellogenesis and offspring production (Dial and Fitzpatrick, 1981; Hare and Miller, 2010). Species with high reproductive output (massive clutches) restrict or even completely lose autotomic abilities to offset the high costs of caudal autotomy (Pafilis and Valakos, 2008). Also, intrafemale competition is minimal since females do not defend territories (Braña, 1996; Moreira et al., 2006). Moreover, in some lizard families where males maintain harems, females interact frequently and do not compete (Zamudio and Sinervo, 2000). Hence females do not attack each other and incidents of tail loss are rare (Cooper et al., 2015).

Tail autotomy comes with many disadvantages, such as degradation of social status (Fox et al., 1990; Salvador et al., 1995), loss of caudal fat that many species store in their tail (Roig et al., 2000; Chapple and Swain, 2002a; Cencetti et al., 2011), alterations in locomotion (Chapple and Swain, 2002b; Cromie and Chapple, 2012; Savvides et al., 2017, but see Kelehear and Webb, 2006), reduction of the immune function (Slos et al., 2009) and impaired reproduction (Fox and McCoy, 2000; Chapple et al., 2002). Nonetheless, in the case of intraspecific predation there is a clear advantage for the conspecific predator. By shedding and consuming a conspecific tail, males kill two birds with one stone: they may reduce their rival's ability to mate (Fox and Rostker, 1982; Martín and Salvador, 1993) and gain an energetically rich meal (McConnachie and Whiting, 2003; Cooper et al., 2015). Hence, intraspecific predation comes with a strong advantage, particularly favorable beneficial for males.

In this study we aimed to clarify whether sex influences caudal autotomy performance. To this end we simulated tail shedding in the lab in 12 species of lacertid lizards. First, we hypothesized that since males are more exposed to predation (inter- or intraspecific) due to their particular social role, they would demonstrate higher rates of tail loss. In the case of insular species though, conditions are more complicated. Predation is more relaxed on the islands (MacArthur and Wilson, 1967; Whittaker and Fernández-Palacios, 2007) and this drives to higher lizard densities (Rodda and Dean-Bradley, 2002; Buckley and Jetz, 2007) that trigger more intense intraspecific competition (Knell, 2009; Raia et al., 2010). Relaxed predation advocates lower autotomy rates (traditional theory) whereas intraspecific competition suggests higher ones (recent approach), which would be even higher among males due to more frequent intraspecific agonistic encounters (Mougeot et al., 2003; Kokko and Rankin, 2006; Cooper et al., 2015). Second, we expected that post-autotomy duration of tail movement between males and females would not differ, as this feature appears to be conservative among species (Pafilis et al., 2005; Pafilis et al., 2008).

MATERIAL AND METHODS

Study species

We examined the rates of caudal autotomy in 12 lacertid lizards assigned in five genera: *Algyroides* (*A. moreoticus* and *A. nigropunctatus*), *Hellenolacerta* (*H. graeca*), *Ophisops* (*O. elegans*) and *Podarcis* (*P. cretensis, P. peloponnesiacus, P. erhardii, P. gaigeae, P. milensis, P. muralis* and *P. tauricus*) (Table 1 for sample sizes - 914 individuals in total). The focal species are distributed in different locations and habitats in mainland and insular Greece (Fig. 1). All of them are small, diurnal insectivorous predators, with snout vent length (SVL) varying from 55 up to 85 mm (Valakos et al.; 2008). For each individual we recorded SVL, sex and the condition of the tail (intact or regenerated). For the purposes of this study we worked exclusively with adult individuals with intact tails.

Captured lizards were transferred to the laboratory facilities of the Department of Biology at the University of Athens. All animals were housed individually in vitreous terraria (18 × 32 × 15 cm) with sand and artificial shelters and were held at 30 °C under a controlled photoperiod with fluorescent tube lighting (12 h light: 12 h dark). An incandescent heat lamp (60 Watts) above each terrarium allowed lizards to thermoregulate for eight hours per day. Lizards were fed every other day with mealworms coated with supplementary vitamins and minerals and had access to water *ad libitum*.

Predation simulation and postautotomy tail movement

Prior to the experimental procedure food was withheld from lizards for two days (Pafilis et al., 2009a). We simulated predation using the method proposed by Pérez-Mellado et al.

Fig. 1. Map of the collecting sites in mainland and insular Greece, NE Mediterranean Basin.

(1997). Since body temperature may affect caudal autotomy (Bustard, 1968; Daniels, 1984), lizards were allowed to thermoregulate for two hours in a specially designed terrarium (100 × 25 × 25 cm) with two ice bags at one end and two heating lamps (100 W and 60 W) at the other end that provided a thermal gradient ranging from 10 to 50 ºC (Van Damme et al., 1986). After achieving its preferred body temperature, each lizard was placed in a terrarium with cork substrate in order to maintain good traction during predation simulation. We used a pair of calipers to simulate the bite of a preda-tor and grasped the tail 20 mm behind the cloaca for 15 sec. To standardize pressure, the calipers were closed to half the original diameter of the tail (Pérez-Mellado et al. 1997). Lizards were free to react and were not restrained. If autotomy occurred, we recorded the duration of movement of the shed, thrashing tail from the moment of autotomy to complete cessation of movement (no continuous twitches for 20 sec) using a digital timekeeper.

Table 1. Values for snout-vent length (SVL; mm) in males and females for all species and t-test results (P > 0.05, ns; P ≤ 0.05, *; P ≤ 0.01, **; P ≤ 0.001, ***). Means ± standard deviation; sample size in parenthesis.

Species	Males	Females	t-test
Algyroides moreoticus	48.07 ± 1.25 (22)	44.43 ± 1.85 (15)	***
Algyroides nigropunctatus	62.08 ± 3.13 (26)	58.29 ± 2.44 (18)	***
Anatololacerta oertzeni	65.18 ± 1.91 (26)	60.10 ± 2.10 (20)	***
Hellenolacerta graeca	80.16 ± 2.24 (23)	77.47 ± 2.31 (17)	***
Ophisops elegans	55.33 ± 2.18 (24)	51.18 ± 1.78 (17)	***
Podarcis cretensis	64.65 ± 2.11 (17)	58.34 ± 2.14 (14)	***
Podarcis peloponnesiacus	85.01 ± 2.23 (46)	80.49 ± 2.04 (42)	***
Podarcis erhardii	66.90 ± 4.69 (40)	63.89 ± 5.05 (29)	*
Podarcis gaigeae	61.02 ± 3.44 (19)	55.74 ± 4.36 (18)	***
Podarcis milensis	65.22 ± 2.09 (24)	60.04 ± 2.24 (16)	***
Podarcis muralis	68.15 ± 2.22 (28)	70.35 ± 1.92 (13)	**
Podarcis tauricus	79.59 ± 2.89 (18)	75.08 ± 2.41 (14)	***

Statistics

We examined the normality of our data using the Kolmogorov-Smirnov and Lilliefors normality tests. Whenever parametric assumption was not met, data were log-transformed. T-test was used to compare the SVL between two sexes. Chi-square test followed by Fischer exact test was used to compare autotomy performance between the two sexes in each species.

We used analysis of variance (ANOVA) to compare the duration of tail movement between the two sexes in each species. In order to eliminate the influence of SVL on the duration of tail movement we repeated the above-mentioned analysis using the SVL as covariate (ANCOVA). All comparisons were conducted independently for each species. All statistical analyses were conducted in R 3.2.5 (R Development Core Team, 2015).

RESULTS

The comparison of body length revealed significant sexual dimorphism for all species (Table 1), with males being larger than females (the opposite pattern was revealed only in one species, *Podarcis muralis*). Chi-square test showed that rates of caudal shedding (all P > 0.05; Table 2) did not differ between sexes within each species (Fig. 2). The same lack of sexual differences was detected regarding the post-autotomy duration of tail movement (all P > 0.05; Table 3).

DISCUSSION

Caudal autotomy is quite common among lizards and a growing body of literature continuously provides new insights. However, the impact of sex on tail loss remains rather obscure. Here, we examined the possible

Table 2. Differences in tail autotomy rates between males and females for all species and Chi-square (χ^2) test results (df = degree of freedom).

Species	χ^2	df	P
Algyroides moreoticus	0.099	1	0.753
Algyroides nigropunctatus	0.076	1	0.783
Anatololacerta oertzeni	0.172	1	0.687
Hellenolacerta graeca	0.360	1	0.549
Ophisops elegans	0.022	1	0.881
Podarcis cretensis	0.121	1	0.728
Podarcis peloponnesiacus	0.022	1	0.883
Podarcis erhardii	0.216	1	0.642
Podarcis gaigeae	0.067	1	0.795
Podarcis milensis	0.286	1	0.593
Podarcis muralis	0.134	1	0.715
Podarcis tauricus	0.168	1	0.682

sexual effect by investigating aspects of tail autotomy. Our results clearly refuted our first working hypothesis. We found no sexual differences in the rates of tail shedding in the 12 focal species. Our analyses revealed that insular species also conformed to this pattern. In line with our second prediction, we found no difference in the duration of the post-autotomic movement between sexes.

Sex had no effect on caudal loss. Though several differences arose from the rates of tail shedding among species unveiling striking differences (e.g., 80% in *A. nigropunctatus* compared to 32% in *P. gaigeae*), intraspecies analyses yield a uniform pattern in tail autotomy performance between males and females. Contrary to our initial prediction, the higher exposure to predators and the
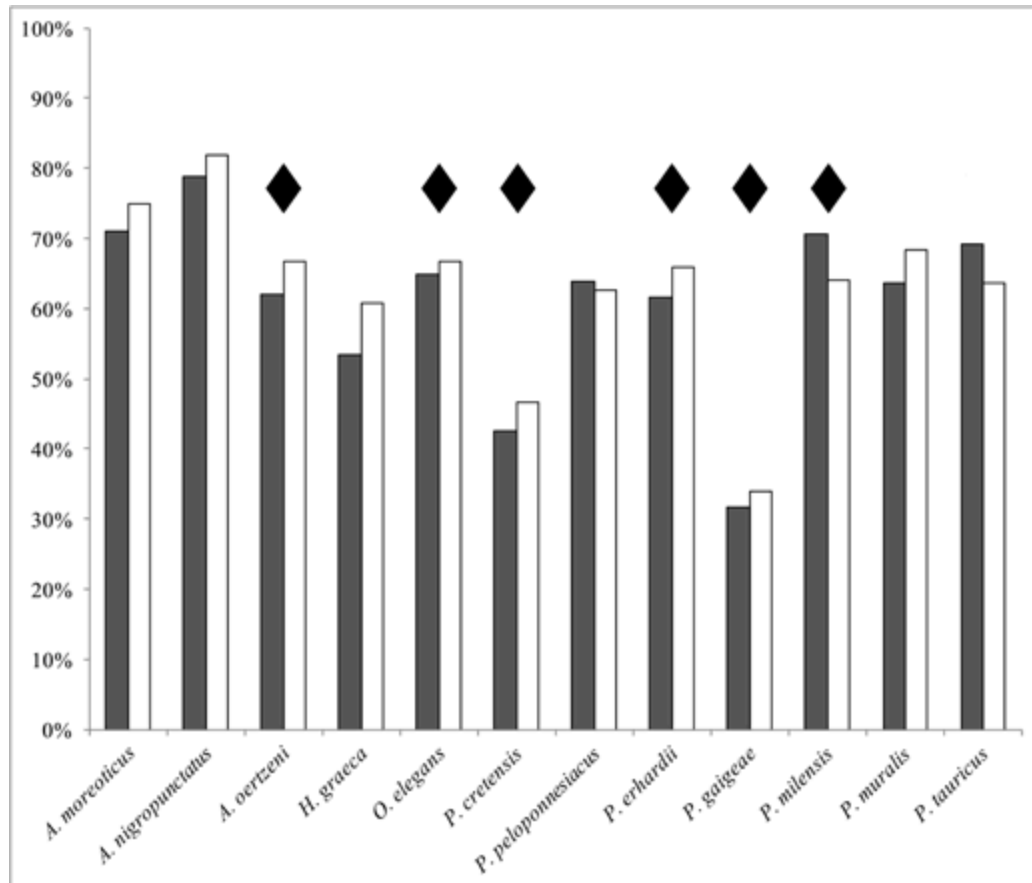
Fig. 2. Rates of laboratory autotomy (dark bars for males and light bars for females). Black diamonds denote island species.

Table 3. Values for the duration of post-autotomy tail movement (min) in males and females for all species and ANOVA and ANCOVA results (P values in parenthesis): Means ± standard deviation; sample sizes are the same reported in Table 1.

Species	Males	Females	ANOVAs	ANCOVAs
Algyroides moreoticus	5.19 ± 0.25	5.34 ± 0.31	$F_{1,35} = 2.88$ (0.099)	$F_{1,34} = 0.035$ (0.851)
Algyroides nigropunctatus	5.29 ± 0.31	5.15 ± 2.44	$F_{1,42} = 4.04$ (0.051)	$F_{1,41} = 3.68$ (0.062)
Anatololacerta oertzeni	6.15 ± 0.27	6.31 ± 0.29	$F_{1,44} = 3.89$ (0.055)	$F_{1,43} = 0.09$ (0.762)
Hellenolacerta graeca	6.55 ± 0.22	6.69 ± 0.23	$F_{1,38} = 3.72$ (0.061)	$F_{1,37} = 2.78$ (0.104)
Ophisops elegans	4.95 ± 0.23	5.09 ± 0.23	$F_{1,39} = 3.43$ (0.072)	$F_{1,38} = 1.1$, (0.292)
Podarcis cretensis	5.54 ± 0.27	5.71 ± 0.27	$F_{1,29} = 2.86$ (0.101)	$F_{1,28} = 3.09$ (0.089)
Podarcis peloponnesiacus	6.48 ± 0.35	6.34 ± 0.34	$F_{1,86} = 3.63$ (0.060)	$F_{1,85} = 1.95$ (0.167)
Podarcis erhardii	6.14 ± 0.30	6.31 ± 0.05	$F_{1,67} = 3.09$ (0.083)	$F_{1,66} = 2.76$ (0.101)
Podarcis gaigeae	5.71 ± 0.30	5.55 ± 0.23	$F_{1,35} = 3.44$ (0.076)	$F_{1,34} = 3.51$ (0.069)
Podarcis milensis	6.46 ± 0.24	6.61 ± 0.25	$F_{1,38} = 3.76$ (0.060)	$F_{1,37} = 3.81$ (0.060)
Podarcis muralis	6.23 ± 0.31	6.14 ± 0.29	$F_{1,39} = 0.86$ (0.360)	$F_{1,38} = 1.23$ (0.273)
Podarcis tauricus	5.45 ± 0.22	5.59 ± 0.21	$F_{1,30} = 3.32$ (0.079)	$F_{1,42} = 0.56$ (0.459)

different levels of intrasexual aggressiveness were not transformed into higher autotomy rates for males (Fig. 2). Our findings suggest that both sexes employ caudal autotomy at the same extent, at least among lacer-

tids. The few studies that have assessed the impact of sex on tail autotomy provide contradictory results. On the one hand, Itescu et al. (2017) reported that male geckos (*Mediodactylus kotshyi*) had higher autotomy frequencies

than females in 31 different populations. These authors attributed the higher male autotomic rates to the more intense intraspecific competition. On the other hand, Fox et al. (1998) found that males of the phrynosomatid lizard *Uta stansburiana* shed their tail less easily compared to females and retain it more strongly as they approach sexual maturity. The latter researchers ascribed the tendency of males to avoid autotomy to the significance of the tail in reproductive success (Fox et al., 1998). The above indicate that phylogeny might have a distinct role on the sexual differentiation of autotomy. Coming to lacertids, although aggressive interactions with conspecific are well known (Castilla and Van Damme, 1996; Salvador and Veiga, 2001; Cooper et al., 2015), they do not seem to account for sexual differences in tail shedding performance according to our results.

At this point we have to stress out an important caveat in our study: both sampling in the field and experimental procedure in the lab took place during the non-reproductive period. Reproduction triggers major shifts in lizards (Bauwens and Thoen, 1981; Brodie, 1989). Future mothers avoid exposing themselves to open areas so as to avoid predation, and adopt a more cryptic behavior (Shine, 1980; Karasov and Anderson, 1984; Braña, 1993). On the contrary, males are much more active and aggressive during the same period as they protect their territory and fight against rivals for access to females (Martín and Forsman, 1999; Salvador and Veiga, 2001; Troncoso-Palacios and Labra, 2012). Most probably, inter- and intraspecific predation pressure during the reproductive period would differ because of the dramatic behavioral shifts that both sexes undergo. Reassessment of tail autotomy performance during this period would shed further light on the impact of reproduction (e.g., Cooper et al., 2009).

Despite the two contradicting drivers of tail autotomy prevailing on islands (low predation and high intraspecific competition), islanders followed the same pattern with mainland species and showed no sexual differences in tail autotomy performance (Fig. 2). However, island size might play a role. Lizard densities are higher on islands thanks to ecological release (Buckley and Jetz, 2007; Novosolov et al., 2016) and this applies to Mediterranean lacertids as well (Chondropoulos and Lykakis, 1983; Adamopoulou, 1999; Scalera et al., 2004). The highest densities, though, have been reported from very small islets (Castilla and Bauwens, 1991; Pérez-Mellado et al., 2008; Pafilis et al., 2013). Intraspecific competition peaks on these islets and very often includes consumption of conspecific limbs such as tails (Raia et al., 2010; Donihue et al., 2016; Lymberakis et al., 2016). Cannibalism on these islets may be as common that lizards may

change their physiology and morphology to cope with this extreme intraspecific competition (Pafilis et al., 2016). Such antagonistic encounters are much more common and intense among males (Brock et al., 2015; Cooper et al., 2015). Our study was carried out on large islands that might host abundant populations (varying from 76 to 396 individuals per hectare) but certainly not as dense as those on the small Mediterranean islets. Also, we have to clarify that these large islands had considerably many predators, fewer though compared to the mainland (Pafilis et al., 2009a). Repeating the experiment on predator-free islet populations might yield useful new insights.

The duration of post-autotomy movement did not differ between sexes, in accordance with our second prediction. At this point, we have to stress out that though there was marginal significance in the duration of tail thrashing post autotomy between the sexes, this difference was eliminated by taking into account body size. Shed tails thrashed between five and seven minutes (Table 3), receiving values that fall within the same range with other Greek lacertids (Pafilis et al., 2005; Pafilis et al., 2009a). Our findings come to corroborate previous reports on *Podarcis* lizards (Pafilis et al., 2005; Pafilis et al., 2008). Duration of movement after tail shedding is very important for the successful escape from predators (Dial and Fitzpatrick, 1983; Cooper et al., 2004). We believe that this importance is reflected in the lack of sexual differentiation in post-autotomy movement.

We report that tail shedding performance and post-autotomic duration are not affected by sex. Future research that would repeat the experiment during the reproductive period and include gravid females would provide further interesting results. Also, experimental work on small islets would shed light on the impact of intense intramale competition on autotomy rates.

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