



# Tail autotomy is associated with boldness in male but not female water anoles

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Received: 6 October 2020 / Revised: 13 January 2021 / Accepted: 19 January 2021 / Published online: 2 February 2021  
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## Abstract

Sex differences in personality traits, such as boldness, are often driven by differences in life history strategies. Specifically, in a polygynous mating system where males defend territories to acquire mates, it may be beneficial for males to exhibit higher levels of boldness compared to females. However, males may also suffer a higher cost due to their bold behavior. Yet, few studies have documented evidence of the differential costs of boldness between the sexes. We examined these relationships in water anoles (*Anolis aquaticus*), using tail autotomy as a proxy for predation risk and/or injury from intraspecific competition. We measured boldness as latency to emerge from a refuge into a novel environment. We predicted that (1) males would exhibit bolder behavior than females, (2) boldness would be positively associated with tail autotomy (i.e., lizards with evidence of autotomized tails would be bolder than lizards without evidence of tail autotomy), and (3) a higher proportion of males would exhibit evidence of tail autotomy than females. We found that in our behavioral test, (1) boldness did not differ between the sexes, but that (2) there were sex differences in the costs of boldness, such that boldness was positively associated with tail autotomy in males but not in females, and (3) males tended to be more likely to exhibit evidence of tail autotomy. Together, these results suggest that males may suffer a higher cost of boldness due to sex differences in reproductive strategies.

## Significance statement

The sexes often differ in behavior because males and females use different tactics to fulfill reproductive success. Boldness is a personality trait that benefits both sexes in terms of acquiring resources. However, boldness should benefit males more when they defend territories and compete for mates. Though what is the cost of bold behavior and does this differ between the sexes? Here, we found that boldness is associated with risk-induced injuries (tail loss) in male water anoles, but not in females. The loss of the tail has been shown to have serious fitness consequences in lizards. Thus, male water anoles suffer a higher cost of bold behavior than females. Our results provide insight on the ecological relevance of boldness, and how selection may have led to differences in personality between the sexes.

**Keywords** *Anolis aquaticus* · Personality · Predation · Sex differences

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Communicated by T. Madsen

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## Introduction

Personality (including boldness, exploration, activity, sociability, and aggressiveness) is the consistent among-individual differences in behavior across time and/or contexts (Réale et al. 2007; Stamps and Groothuis 2010). Personality is shaped via social environments and ecological factors (Dall et al. 2004; Smith and Blumstein 2008; Wolf and Weissing 2012) and is linked to inherent trade-offs that could affect an individual's growth, reproductive success, and mortality (Carere and Eens 2005; Bergmüller and Taborsky 2010). For example, in juvenile cichlids (*Amatitlania nigrofasciata*), individuals that are fast to explore novel environments are

slower to respond to predators (Jones and Godin 2010), and in great tits (*Parus major*), individuals that were more willing to explore a novel environment were more likely to return to forage quicker after being startled, thus allowing them to acquire more resources (van Oers et al. 2004).

Sex differences in personality are common and can arise and be maintained via sexual selection (Schuett and Dall 2009; Munson et al. 2020) due to differences in male and female life history strategies, such as investment in gamete production, parental care, or intrasexual competition (Trivers 1972). Certain behavioral types could be associated with sex-specific reproductive behaviors (Biro and Stamps 2008; Swierk et al. 2014). Dingemanse and de Goede (2004) found that great tit (*Parus major*) males that explore more are better at outcompeting other males to find mates, but females do not experience the same fitness benefit of exploration. Sex differences in the costs and benefits of exhibiting certain behavioral types may largely depend on the type of mating system and the operational sex ratio of the population as these are associated with the intensity at which individuals compete for mates (Mitani et al. 1996; Smith and Sandell 1998). Particularly in polygynous systems, males increase their reproductive success by investing in aggression to defend resources, females, and/or establishing a dominance rank (Emlen and Oring 1977). In the white-bellied ant bird (*Myrmeciza longipes*), males are more aggressive than females, as aggressive males control and protect territories and mates, which overall can increase their fitness (Fedy and Stutchbury 2005).

Boldness (i.e., risk-taking) is one such personality trait that is likely to differ between the sexes (Clark 1994; Piyapong et al. 2010; Niemelä et al. 2012; King et al. 2013). Particularly in a polygynous mating system, the benefits and costs of boldness may differ between the sexes. Bolder individuals tend to have greater access to resources (including mates) in species as diverse as rodents (Fuxjager et al. 2010), fishes (Ward et al. 2004), and lizards (Short and Petren 2008). Yet, boldness is assumed to incur higher predation rates. In the common roach (*Rutilus rutilus*), bolder individuals have a greater susceptibility to cormorant (*Phalacrocorax carbo*) predation compared to less bold individuals (Hulthén et al. 2017). In systems where males defend territories to acquire mates, it may be beneficial for males to exhibit high levels of boldness. In females, boldness may be relatively less important to their reproductive success, other than for access to food resources (e.g., Ariyomo and Watt 2012; Videler et al. 2015). The costs of bold behavior are likely to differ between the sexes as well. However, most studies typically only show direct evidence of the benefits of boldness (e.g., resource and mate acquisition), but evidence for relevant ecological costs (e.g., predation risk) is rarely reported (but see Biro and Post 2008; Hulthén et al. 2017; Moiron et al. 2020).

The costs of boldness include a higher likelihood of predation, but this is hard to quantify in animals without observing

natural predator-prey interactions or monitoring survival of individuals in a population over time. Breakage of the tail, also known as tail autotomy, is consistently used as a measure of predation risk in lizards (Turner et al. 1982; Gifford et al. 2008), snakes (Pleguezuelos et al. 2010), and salamanders (Shaffer 1978; Labanick 1984). Tail autotomy has significant fitness consequences to the individual and therefore is a useful indicator of the cost of boldness (Fox and Rostker 1982; Martin and Salvador 1993; Althoff and Thompson 1994; Niewiarowski et al. 1997; Wilson and Booth 1998; Fox and McCoy 2000; Maginnis 2006; Bateman and Fleming 2009). Many lizards exhibit tail autotomy to increase their chances of survival during a predator encounter (Arnold 1988). In most lizards, tail autotomy is the controlled voluntary shedding of the tail that occurs along a breakage plane within vertebrae (Clause and Capaldi 2006). Following autotomy, many species of lizards exhibit tail regrowth; however, tail autotomy “scars” remain for the lifetime of the lizard, and regrown tail portions lack new vertebrae and are visually distinct from the original tail. As such, an individual’s history of tail autotomy can be determined by simple visual inspection. Tail autotomy is very costly because it includes the loss of caudal fat reserves, impaired locomotory function, and decreased reproductive capacity (Brown et al. 1995; Ritzman et al. 2012). Though most studies show that predation is most commonly related to tail autotomy (e.g., Turner et al. 1982; Medel et al. 1988; Fox et al. 1994), intraspecific interactions (e.g., male competition) can likewise induce autotomy (Bateman and Fleming 2009). Because of the strong links among tail autotomy, risk (either through predators or competitors), and individual fitness, evidence of tail autotomy can be used to quantify a cost of boldness. Alternatively, tail autotomy may alter personality/boldness, as demonstrated by Michelangeli (2020), in which individuals that recently suffered tail loss became less bold, and by Wise et al. (2004) wherein tailless individuals were more aggressive as intruders compared to tailed individuals. Regardless, sex differences would likely still be apparent, especially if males are more likely to suffer tail autotomy than females.

Here, we tested the relationships among sex, boldness, and tail autotomy to determine whether the costs of boldness differ between male and female water anoles (*Anolis aquaticus*). The literature is divided regarding whether there are (Vinegar 1975; Brown and Ruby 1977; Vitt 1981; Smith 1996) or are not (Van Sluys et al. 2002; Chapple and Swain 2002, 2004; Lin et al. 2006; Brock et al. 2015) sex differences in tail autotomy rates. Importantly, one piece of information lacking from the literature is the relationship of tail autotomy and sex differences in boldness, as boldness and predation studies in squamate reptiles typically only focus on males (Carter et al. 2010; Kuo et al. 2015). Males and females have different life histories, which affect behavior and rates of injury from competition and/or predation (Jennions and Telford

2002). The water anole is a species amenable to explore these questions because, like many lizards, they exhibit a polygynous mating system wherein males engage in male-male competition to defend territories and resources required by females for mating (Meyers et al. 2006; Márquez and Márquez 2019; Keogh et al. 2012). Furthermore, because populations are densely distributed in Neotropical streams (Savage 2005) with a variety of predator species, water anoles are exposed daily to high levels of competition and predation risk. Anoles are squamate reptiles that use tail autotomy as a morphological defense mechanism to avoid predation (Etheridge 1967; Russell and Bauer 1992). Therefore, frequency of tail loss is a reliable measure of competition and/or predation (Arnold 1988; Bateman and Fleming 2011; Higham et al. 2013). Importantly, water anoles also exhibit sexual dimorphism in morphology and behavior. Males are larger than females and have a conspicuous reddish-orange dewlap (colorful flap of skin on the throat) (Savage 2005) that is used as sexual signal to defend territories and attract mates (Jenssen 1977; Williams and Rand 1977). Females lack dewlaps and are generally less conspicuous than males. The size of the dewlap in this species is positively correlated with boldness (Putman et al. 2018), suggesting that bolder males may benefit from enhanced territories and/or reproductive success. However, a cost of boldness may be a higher probability of tail autotomy due to being more exposed to predators and/or being involved in more territorial interactions.

To test the relationships among boldness, tail autotomy, and sex, we conducted a survey of water anoles in Costa Rica over two summers, in which we quantified the presence/absence of tail autotomy scars. For a subset of adults, we conducted behavioral assays for boldness in a testing arena: Individuals that had shorter latencies to emerge from a refuge were considered bolder (Putman et al. 2018; Réale et al. 2007). We predicted that (1) males would exhibit bolder behavior than females, (2) boldness would be positively associated with tail autotomy (i.e., lizards with autotomized tails would be bolder than lizards without tail autotomy), and (3) a higher proportion of males would exhibit evidence of tail autotomy than females.

## Methods

### Study site and species

We conducted our study at Las Cruces Biological Station, near San Vito, Costa Rica, over two summer field seasons (June and July) in 2018 and 2019. Las Cruces Biological Station is comprised of premontane tropical forest, ranging from 1100 to 1500 m in elevation (Santos Barrera et al. 2014). Water anoles are found in streamside habitats, and

adults are 52–77-mm snout-vent length (SVL) (Márquez and Márquez 2019).

### Quantifying tail autotomy

As part of a larger mark and recapture study, each day from 9:00 to 14:00, we would slowly walk within the study area to search for anoles. We looked inside of crevices and under rocks to ensure that we were spotting all lizards, and not just those out in the open. If an unmarked anole was sighted, we captured it and took morphological measurements. Morphological data included snout-vent length (SVL), tail length, evidence of tail autotomy (yes or no), and the length of the original tail remaining if autotomy was present (we refer to this as the break distance). We considered evidence of tail autotomy if an individual had the distal part of its tail missing or if its tail has been regrown, thus exhibiting a visible tail scar (Jacyniak et al. 2017). We determined anole sex by the presence (male) or absence (female) of a dewlap. Prior to being released at their place of capture, each anole was marked with a specific color code using non-toxic nail polish and/or unique bead tags for individual identification from a distance (Galdino et al. 2014).

### Boldness trials

We performed boldness trials for all captured adult anoles. We quantified boldness as the latency to emerge from a refuge into a novel environment (Seda et al. 2012; Putman et al. 2018). We used a white foldable plastic storage enclosure (33.0 cm in length  $\times$  25.4 cm in width  $\times$  48.3 in height) to serve as the novel environment. We cut the removable top of the enclosure so that the outer frame was left and replaced the inner portion with a mesh see-through material for clear visibility into the enclosure. We lined the enclosure walls with white paper (in 2018) replaced after each trial, or lined the outside of the enclosure with an opaque plastic sheet (in 2019) to prevent the anole from being distracted by the outside environment. Anoles were placed headfirst into a refuge which was then placed at one end of the enclosure. The refuge consisted of a dark green, circular, plastic container (10.9 cm diameter  $\times$  6.1 cm, with a 6.25-cm<sup>2</sup> opening). Once the refuge (which contained the anole) was placed into the enclosure, we allowed the trial to run undisturbed for 20 min. We recorded trials using action cameras attached to a tripod overlooking the enclosure (Akaso EK7000 or GoPro Hero 3). After the trial, we took the temperature of the anole using a non-contact infrared temperature gun (Etekcity Lasergrasp 774). To prevent an individual's scent from influencing another anole's behavior, we cleaned the enclosure and refuge thoroughly between trials with antibacterial wipes or dishwashing soap. Although we did not provide anoles with ample time to acclimate to the novel enclosure prior to the start of behavioral trials, our

methods are in line with similar studies that have conducted trials shortly after capture (e.g., Carter et al. 2012; Hedrick and Kortet 2012; Carazo et al. 2014; Kuo et al. 2015; Horváth et al. 2020).

We conducted two trials on every individual on separate days in random order. We conducted trials in the laboratory in 2018 and in the field in 2019, but all other trial parameters remained the same between years. In 2018, anoles were housed in individual plastic enclosures ( $12 \times 19 \times 13.5$  cm) in a temperature-controlled room ( $20\text{--}23$  °C) with a 12:12 light:dark photoperiod, which approximated anole habitat conditions in nature. Boldness trials were randomized and occurred on the day of capture in the afternoon (in the same temperature-controlled room) and the following morning in 2018, and anoles were released to their place of capture no more than 48 h later. In 2019, we tested anoles once at the start of the field season and once at the end (average of 12 days apart), for a total of two trials per individual. Trials were randomized and took place in the morning until the afternoon (9:00 to 14:00). Temperature of the testing enclosure ranged from  $17.8$  to  $24.2$  °C with mean  $\pm$  SD =  $21.7 \pm 1.4$  °C. None of the lizards tested had broken their tail between trials. If unmarked, we marked anoles for individual identification as above to prevent retesting individuals.

We coded behaviors from the video recordings of the trials using JWatcher (v 1.0). It was not possible to record data blind because our only treatment was tail autotomy, and that was clearly visible on the lizards in the video recordings. We quantified boldness as time to head, the latency of the anole to expose its head out of the refuge and into the novel arena. Because most anoles did not fully emerge from refuge during the 20-min trial, time to head was used as our measure of boldness instead of full body emergence. Time to head is a behavior that is widely used as a proxy of boldness (e.g., Herczeg et al. 2009; Scharnweber et al. 2011; Edelaar et al. 2012; Niemelä et al. 2012; Herde and Eccard 2013; Clary et al. 2014; Mayer et al. 2016; Stanley et al. 2017; Petróczki et al. 2019). We also verified that the latencies to head and to full body emergence were highly positively correlated (using data from trials in which anoles fully emerged:  $N = 40$ , Pearson's  $r = 0.755$ ,  $p < 0.001$ ).

## Statistical analyses

All analyses were conducted in R (v. 3.6.1) (R Development Core Team 2019), with alpha set to 0.05.

## Analysis on tail autotomy

Across two field seasons, we caught 135 adult water anoles (95 in 2018 and 40 in 2019): 57 females and 78 males. We used a Pearson's Chi-square test to assess population-level

differences in tail autotomy (yes/no) among adult females and adult males.

## Analyses on boldness

In all, we performed two boldness trials on 48 individuals (2018, 18 females and 20 males; 2019, 5 females and 5 males). Because time to head contained right censored time-to-event data (i.e., time to expose head from the refuge, right censored at 20 min), we used a Cox proportional hazard regression (survival package in R; Therneau 2015) with paired data (i.e., individuals were tested twice) to determine whether boldness differs between the sexes and associates with tail autotomy in anoles. We included SVL as a factor because previous studies have shown important effects of body size on boldness (Harris et al. 2010; Hedrick and Kortet 2012; Carazo and Noble 2014). We included year to account for the different testing conditions used between 2018 and 2019. Finally, we included temperature to account for temperature effects on behavior (which preliminary analyses revealed as important). Even though we tested 48 individuals, our sample size for this final survival model was reduced to 80 observations on 40 individuals (2018, 15 females and 15 males; 2019, 5 females and 5 males) as we did not have temperature data for every trial. We looked for interactions between each of the model factors and only found a significant sex\*tail break interaction (see “Results” section and Table 1). Because of this, we also performed two additional Cox proportional hazard regression analyses on males and females separately. We included the same factors as above in these models (except for sex).

To evaluate whether the extent or severity of tail autotomy influences behavior, we performed a second Cox proportional hazard regression model on time to head with data restricted to anoles that had experienced a tail break. In this model, we included the same factors as above, except tail break (yes/no) that was replaced with the break ratio, which is the length of the original tail remaining divided by SVL. The break ratio

**Table 1** Results of the Cox proportional hazard regression model for time to head

|                | HR    | 95% CI     | Z      | p      |
|----------------|-------|------------|--------|--------|
| Tail break     | 1.25  | 0.589–2.67 | 0.586  | 0.558  |
| Sex            | 1.13  | 0.519–2.46 | 0.308  | 0.758  |
| SVL            | 0.980 | 0.928–1.04 | -0.723 | 0.470  |
| Temperature    | 1.05  | 0.879–1.25 | 0.505  | 0.613  |
| Year           | 1.74  | 1.00–3.02  | 1.96   | 0.050* |
| Tail break*sex | 2.90  | 1.06–7.906 | 2.08   | 0.038* |

HR hazard ratio, CI confidence intervals, Z Z-score, SVL snout-vent length. Asterisks indicate statistical significance at 0.05



is indicative of the number of tail autotomy events experienced in a lizard's lifetime because subsequent tail breaks must occur anterior to the current break site. Lower break ratios indicate that more of the original tail had been lost through autotomy compared to higher break ratios. In this model, we had 24 observations on 12 individuals (2018, 4 females and 5 males; 2019, 2 females and 1 male).

Cox proportional hazard regression models are not able to determine whether anoles exhibit consistent among-individual variability in behavior. We previously demonstrated that water anoles exhibit significant repeatability in refuge emergence (Putman et al. 2018). Here, we report the intraclass correlation coefficient (ICC) from a linear mixed model using the same fixed effects as above (in the full model) and anole identity as a random factor. The ICC estimates how strongly responses of the same group (i.e., within individual anole) are correlated. We used a likelihood ratio test to determine whether inclusion of anole identity is significant in the mixed model. We report the full results of this model in Online Resource as further support for our findings. However, we primarily focus on the results from the Cox proportional hazard regression below because it is the most appropriate model for censored data.

## Results

### Rates of tail autotomy

We caught 135 adult water anoles (95 in 2018 and 40 in 2019)—57 females and 78 males. We found that 42 anoles had experienced tail autotomy (~ 31% of all anoles captured)—24.6% of females and 35.9% of males. These differences between the sexes were marginally non-significant ( $X^2 = 3.267$ ,  $df = 1$ ,  $p = 0.071$ ).

### Boldness, sex, and tail autotomy

For our analyses, we included two trials for each of 20 males and 20 females across two field seasons. We found that although the sexes did not differ in time to head ( $p = 0.758$ ; Table 1), there was a significant sex\*tail break interaction ( $p = 0.038$ ; Table 1) on time to head in the Cox proportional hazard regression model, and the rate of head emergence was 1.74 times higher in our second field season compared to the first (effect of year:  $p = 0.050$ , Table 1). The global (overall) significance of this model was  $p = 0.005$  (Wald test = 18.65,  $df = 6$ ). Separate Cox proportional hazard regression models showed having an autotomized tail significantly related to time to head in male anoles ( $p = 0.025$ ; Figs. 1b and 2a), whereas there was no such relationship in females ( $p = 0.394$ ; Figs. 1a and 2b). The rate of head emergence was 3.13 times higher for males with tail autotomy compared to males without tail autotomy (Fig. 2a).

For anoles that had experienced a tail break, we found no effect of break ratio (the amount of the original tail remaining) on time to head ( $p = 0.147$ , Online Resource 1). In this model, we found that males with tail autotomy were more bold (more likely to emerge sooner) than females with tail autotomy ( $p = 0.008$ ), and we retain the significant effect of year ( $p < 0.001$ ), but caution that only three individuals in this dataset came from year two. The full results of this model can be found in Online Resource.

The ICC for anole identity was 0.243, and inclusion of this random factor into a mixed model was significant ( $X^2 = 17.14$ ,  $p < 0.001$ ). The linear mixed model qualitatively supports the survival analysis results above with a significant sex\*tail break interaction ( $N = 40$  anoles,  $p = 0.021$ ; full results in Online Resource 1 and Online Resource 2).

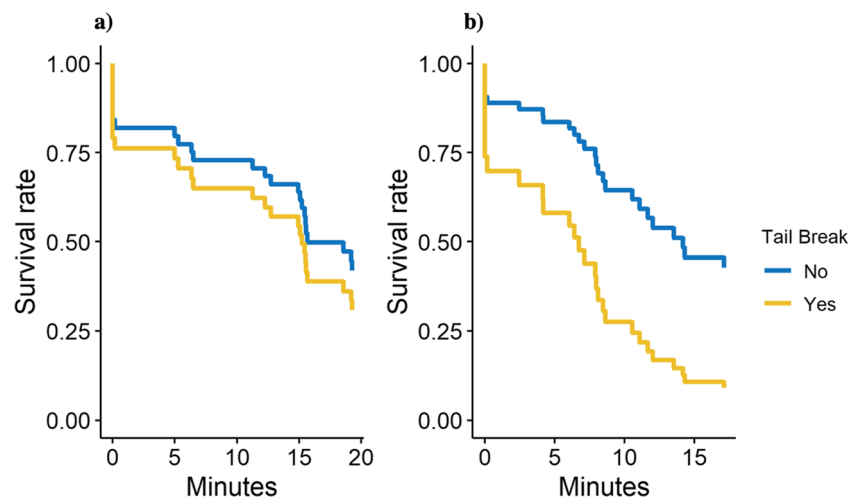
## Discussion

In our study, water anoles did not exhibit sex differences in levels of boldness, but rather in the costs of boldness. We found marginally significant results for our first prediction that males are more likely to exhibit evidence of tail autotomy than females. Though our results show weak support, it still shows that males may experience higher predation risk and/or more attacks from competitors than females. We did not find support for our second prediction that males would be bolder than females. However, boldness was associated with tail autotomy in males and not in females: Males that had experienced tail autotomy were bolder than males that had not, and males with evidence of tail autotomy were bolder than females with evidence of tail autotomy. This suggests that males may suffer a higher cost of bold behavior, likely due to differences in their reproductive behaviors associated with territory defense. Overall, our study suggests that boldness differentially affects tail autotomy patterns across the sexes and that these differences may arise and be maintained via sexual differences in life history strategies.

### Tail autotomy and boldness

Overall, male and female water anoles did not differ in levels of boldness, but rather in the relationship between boldness and tail autotomy. Males that had experienced tail autotomy were bolder (shorter time to head) compared to males without tail autotomy, a relationship that was not apparent in females. In brown anoles (*A. sagrei*), bolder males are also more likely to have autotomized tails (Kuo et al. 2015), and in Namibian rock agamas (*Agama planiceps*), bolder males have greater access to resources but suffer higher tail loss (Carter et al. 2010). Both these studies support our results in which boldness associates with tail autotomy; however, these studies only tested males and not females. We also looked at whether the

**Fig. 1** Adjusted survival curves showing how tail break (yes or no) affected time to head estimated from the Cox proportional hazard model in **a** female and **b** male water anoles. Survival rate is the proportion of individuals still in the refuge

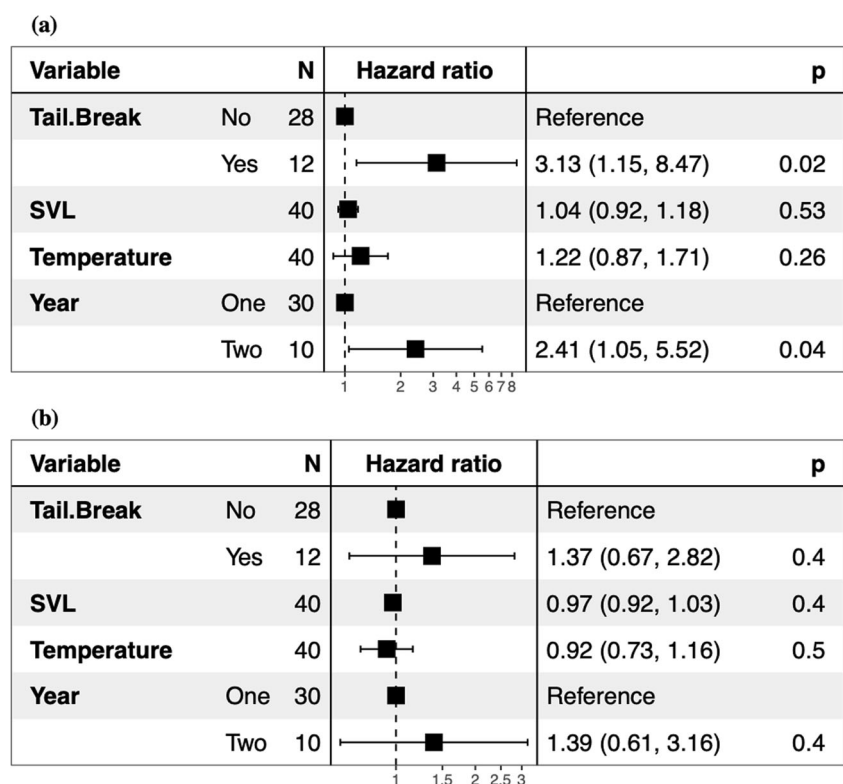


extent of tail loss influenced behavior by examining the relationship between the break ratio (amount of original tail remaining) and time to head. We did not find a significant relationship between these two traits. If bolder individuals, and especially males, are more likely to experience tail autotomy, we should expect that these individuals would have lower break ratios as they suffer multiple tail loss events throughout their life. However, our sample size for this analysis was low; therefore, more studies would be needed to fully evaluate this relationship. Finally, we found a significant effect of year, wherein lizards from 2019 had a quicker time to head (bolder) than lizards from 2018. This could be due to the fact

that these lizards were tested in their natural conditions (i.e., in the field) and they could have been less stressed than lizards brought back to the lab.

Our study is the first, to our knowledge, to find such sex differences in the costs of boldness. Male-biased tail autotomy in relation to boldness may be due to sex differences in reproductive behaviors (e.g., territorial defense, male-male competition, and mate acquisition). An individual's dominance rank can influence reproductive success, and boldness is often positively correlated with dominance (Dahlbom et al. 2011). In water anoles, dewlap size is positively correlated with male boldness (Putman et al. 2018), and dewlap size has been

**Fig. 2** Results of the Cox proportional hazards model on time to head (TTH) in **a** male and **b** female water anoles. Forest plot shows the hazard ratios along with their 95% confidence intervals, which are also displayed numerically to the right. A hazard ratio of 1 means no risk, a hazard ratio greater than 1 suggests an increased risk (more likely to stick head out), and a hazard ratio below 1 suggests a smaller risk (less likely to stick head out). SVL = snout-vent length



shown to correlate with male dominance in anoles (*A. carolinensis*) (Bush et al. 2016). Therefore, anoles with larger dewlaps would be expected to have a larger fitness benefit (e.g., success in attaining mates, resources, and in competition) as they are bolder and have a higher dominance rank compared to individuals with smaller dewlaps. Male anoles not only use their dewlaps for mating displays but also for territorial displays during male-male interactions (Cooper 1977; Steffen and Guyer 2014), and bolder males are more likely to be involved in competitive interactions. Therefore, tail autotomy in bolder male anoles may also be due, in part, to intraspecific competition. For example, in Kotschy's gecko (*Cyrtopodion kotschyi*) and the Mediterranean house gecko (*Hemidactylus turcicus*) intraspecific competition led to tail autotomy in lizards more than predation did (Itescu et al. 2017). Though this study focused on aggression and not boldness, it does highlight how sex differences in behavior could drive male-biased injuries.

It is also important to recognize that tail autotomy may influence boldness as opposed to it being a consequence of bold behavior. Michelangeli et al. (2020) found that tail autotomy in delicate skinks (*Lampropholis delicata*) impacted personality as individuals minimized activity to reduce exposure from potential predators. Similarly, in northern zigzag salamanders (*Plethodon dorsalis*), tail autotomy altered antipredator behaviors as autotomized individuals fled further from a touch stimulus and explored novel enclosures more (Bliss and Cecala 2017). However, our results do not support this hypothesis as we would expect anoles with autotomized tails to exhibit longer latencies to emerge, which was not what we found. It is possible that tail autotomy may temporarily reduce activity and boldness in the short term (i.e., immediately after experiencing a tail break), but bolder individuals could still be more likely to have tail autotomy scars than less bold individuals over the long term. A further study would need to test this as we only had a single anole with a recent tail break based on 0% regenerated tissue at the break site.

It is likely that other personality traits such as aggressiveness, exploration, activity, or sociability may correlate with boldness (forming a behavioral syndrome) and also affect tail autotomy in water anoles. Behavioral syndromes have been found in a diversity of organisms such as stickleback fish (*Gasterosteus aculeatus*) (Bell and Stamps 2004), field crickets (*Gryllus integer*) (Kortet and Hedrick 2007), and fishing spiders (*Dolomedes triton*) (Johnson and Sih 2005). We only focused on boldness, but future work could test how other personality types and/or behavioral syndromes affect tail autotomy in water anoles between both sexes.

### Sex differences in tail autotomy

Though we found marginally significant results in sex differences in tail autotomy, our results are still indicative that males

tended to be more likely to exhibit evidence of tail autotomy than females. Sex differences in tail autotomy could be due to the fact that males are more susceptible to predation attacks particularly during the reproductive season. Males could be more susceptible to predation attacks because of their conspicuous morphology (i.e., body size, sexual ornaments) and/or behavior resulting in males being more conspicuous and exposed (Magnhagen 1991). Male *Anolis* lizards extend their dewlap and head-bob to females in mating displays (Crews 1975; Tokarz 1995; Jenssen et al. 2000). Though these visual signals are favored by sexual selection, they can also draw the attention of predators (Endler 1992; Fleishman 1992). For example, in brown anoles (*A. sagrei*), the rate of dewlap extensions decreased in the presence of a simulated predator (Simon 2007).

Other studies conducted across a broad range of taxa have also shown patterns of males being more susceptible to predator attacks. For example, in crickets (*Gryllus integer* and *G. lineaticeps*), males produce a calling song in order to attract females, but gravid female parasitoid flies (*Ormia ochracea*) are also attracted to the calling song and use it to locate male crickets as their victims to lay their eggs (Gray and Cade 1999; Gray et al. 2007; Dobbs et al. 2020). This pattern is also seen in mammals (Sommer 2000; Kraus et al. 2008), fish (Magurran and Seghers 1994; Tobler et al. 2008), and frogs (Lodé et al. 2004; Bernal et al. 2007). In all these studies, males were more susceptible to predator attacks due to conspicuous male reproductive behaviors.

### Conclusions

This study contributes to our understanding of sex differences in behavior within an ecological context. We found that (1) a higher proportion of males have evidence of tail autotomy, though only marginally significant; (2) males are not bolder than females; but (3) boldness associates with history of tail autotomy in males but not in females. Future studies should explore how other sexually distinct personality types and/or behavioral syndromes affect tail autotomy between the sexes. In all, our study suggests that the sexes may experience different selective pressures (e.g., trade-offs and costs of bold behavior) on personality traits (Wolf et al. 2007; Schuett et al. 2010).

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00265-021-02982-w>.

**Acknowledgments** We thank Andrea Fondren, Diana Lopera, Maegan Delfin, Michael-Luca Natt, Denise Ortega, Mykel Lizama, Johniah Gomez, and Scott Walter for assistance with data collection. We would also like to thank Rodolfo Quirós for his logistical support. We thank two anonymous reviewers for their helpful comments.

**Funding** Our research was supported by the National Science Foundation Louis Stokes Alliances for Minority Participation (LSAMP) Program through the Organization for Tropical Studies Research Experience for Undergraduates (REU) for the U.S. Underrepresented Minority Students Summer Program (grant # HRD1712757).

**Data availability** The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request. Data analyzed in this paper are presented in Online Resource 1 and Online Resource 2 (Tables 1 and 2).

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest

**Ethics approval** This research was conducted under the Scientific Research Permit numbers R-SINACPNI-ACLAP-043–2018 and R-SINACPNI-ACLAP-022–2019, and all methods were approved by the UCLA Animal Research Committee (ARC-2016–051–03C) and Binghamton University (IACUC Protocol #817–19). All applicable institutional guidelines for the use of animals were followed.

**Informed consent** Not applicable.

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