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USE IT AND LOSE IT? BEHAVIORAL AND ENERGETIC INFLUENCES ON LIZARD TAIL AUTOTOMY

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ABSTRACT

In many lizard species, the ability to autotomize (lose) the tail allows for immediate survival in the face of predation. However, tails are often used in communication and energy storage, and so tail autotomy can thus decrease an individual's overall fitness. In this study, I examine this tradeoff in species that use the tail differently. I predict less frequent tail autotomy in species that use the tail for social display or energy storage, as a full tail is particularly valuable. In species that primarily display the tail in an anti-predatory context, I predict the frequency of tail loss will be higher, as the tail is made especially vulnerable to autotomization. I studied seven lizard species that vary in tail use: greater earless lizards (*Cophosaurus texanus*) and curly tail lizards (*Leiocephalus carinatus)* use tails frequently in display; Mediterranean house geckos (*Hemidactylus frenatus*) and crested anoles (*Anolis cristatellus*) use tails occasionally; and green anoles (*Anolis carolinensus*), Texas spiny lizards (*Sceloporus olivaceus*), and Texas spotted whiptails (*Aspidoscelis gularis*) almost never include tail movements in display. I observed lizards of each species in the field to quantify the use of the tail in social contexts, and performed predator simulation trials to quantify tail use in anti-predatory contexts. I calculated the energetic content of the tail using bomb calorimetry. I found that the frequency of tail autotomy varies from 20-60 % of individuals across the seven species, and lizards that use their tail in a social context also tend to do so in an anti-predatory context. Finally, I found that total energy content in the tail is positively associated with tail loss frequency across species. By studying lizard tail loss, we can better understand the evolutionary trade-offs

involved in balancing the benefit of predator evasion with the cost of tail loss in social and energetic utility.

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INTRODUCTION

Introduction to Lizard Tail Autotomy

Autotomy is an adaptive defense mechanism by which animals can sacrifice an appendage to escape threats. Autotomy occurs in many different types of animals, from invertebrates like crabs and starfish, to vertebrates like lizards, and even rodents (Zimmer-Faust 1989; Shargal et al. 1999). In many cases, limbs or other appendages are designed to break off easily, so that only minimal physical damage is incurred. To this end, many appendages that can be autotomized have a series of breakage planes. Breakage planes are points along the appendage where the anatomical structures allow autotomy to occur with minimal damage to the organism. In many species breakage planes serve to limit blood loss after the trauma, facilitate quick closure and healing of the wound, and stimulate the regeneration process. In the case of tail autotomy, breakage planes also ensure that the tail breaks off at the point of contact so that the organism retains as much of the appendage as possible (Fleming et al. 2007).

Perhaps the most well-known example of autotomy occurs in lizards, in which the tail may be “dropped” or “broken” in response to the threat of predation (Clause and Capaldi 2006). Along the tails of many lizard species, each vertebra features a breakage plane composed of interwoven muscle fibers that pull apart with minimal damage to the surrounding tissue. The autotomization of the tail is triggered by the contracting of the caudal muscles in the tail along the breakage planes, causing the vertebrae to split and the tail to drop off. This process is semi-voluntary, in that the preparation of the tail for autotomy is instigated by neural mechanisms. In some cases, the tail can even drop off with no physical contact (Clause and Capaldi 2006).

Once the tail is autotomized, it wriggles vigorously to distract the predator from pursuing the lizard. The rate of this thrashing varies across species, but in species with high rates of post-autotomy tail movement, the lizard's ability to escape increases greatly (Dial and Fitzpatrick 1983). In most lizard species, the tail will regenerate after it is lost, but some 23–25 lizard species have independently lost the capacity to autotomize and regenerate the tail (Arnold 1994). In species that exhibit regeneration, the regenerated tail tissue is distinct from the bone and muscle composition of the original tail. Instead, the tail regenerates as a cartilaginous rod. Because the regenerated tail lacks the internal structure of the original tail, including breakage planes, any further autotomy event will occur at the same site or closer to the lizard's body where breakage planes are still intact (Bateman and Fleming 2009).

Costs and Benefits of Tail Autotomy

Studies on tail autotomy often focus on the relationship between predation pressure and tail autotomy in different populations of a species. Interestingly, studies have found that discerning a clear relationship between these two factors is very difficult. Some connection between high predator intensity and high frequency of tail loss has been shown (Cooper et al. 2004). Other studies, however, suggest that this relationship is over-simplified (Fleming et al. 2013). A high frequency of tail loss can indicate that a lizard population is more conspicuous, the predators are more inefficient, or the lizard population's escape tactic relies on autotomy over another method (Medel et al. 1988; Bateman and Fleming 2009; Bateman and Fleming 2011). These studies suggest that the behavior of the predators and the behavior of their lizard prey interact in a community to determine tail loss frequencies (Fleming et al. 2013).

In general, tail autotomy in lizards is often studied in the context of ecological trade-offs, as the benefits of autotomy are countered by a variety of costs. For one, once the tail is autotomized the lizard is at a higher risk for injury or death. Studies repeatedly show that mortality rates are higher for lizards with incomplete tails, due to an increased vulnerability to predators or insufficient energy reserves to survive harsh environmental conditions (Bauwens 1981; Wilson 1992; Fox and McCoy 2000). Tail autotomy also forces lizards to make behavioral changes that limit their access to resources, disadvantaging them compared to lizards with intact tails. This is likely because tailless lizards must take into account their increased likelihood of being captured by predators in a tailless state (Downes and Shine 2001). For example, tailless lizards may spend more time foraging than lizards with intact tails, and may adapt different strategies in foraging to accommodate their increased vulnerability to predators. More time spent foraging means less time to engage in social interactions, but more time to restore energy stores that were lost from autotomy (Martin and Salvador 1993). In the Iberian rock lizard, *Lacerta monticola*, tailless lizards preferred to forage in areas with more stable perches, and avoided areas that would require the lizard to navigate flimsy surfaces (Martin and Salvador 1993). This restriction on foraging habitat and foraging strategies combine to limit both prey availability and foraging success, resulting in an overall low quality diet for tailless lizards in comparison to lizards with intact tails (Martin and Salvador 1993). Tailless *Psammodromus algirus* (large psammodromus) lizards are also at a disadvantage when foraging. During the regeneration period, tailless lizards of this species will spend more time assessing risk and reward trade-offs before attempting to capture prey than tailed lizards (Martin and Avery 1997). This analysis results in tailless lizards maintaining a significantly smaller attack radius compared to lizards with intact tails. A smaller attack radius means that the prey must stray within a smaller distance from tailless lizards in order for them to risk an attack. More time spent assessing prey means that lizards with autotomized tails have decreased foraging success in comparison to lizards with intact tails (Martin and Avery 1997). Tailless lizards also show patterns of preferring to predate on larger prey in an attempt to compensate for missed opportunities when foraging options are limited by tail loss (Martin and Avery 1997). Similarly, in the keeled earless lizard, *Holbrookia propinqua*, tailless lizards stay closer to cover when foraging, limiting their ability to forage effectively compared to their competitors with unbroken tails (Cooper 2003). Overall, it seems the loss of the tail may benefit the lizard by allowing it to escape immediate threats; however, the period following autotomy can greatly increase the lizard's vulnerability to further predation. This forces the individual to devote more time and energy to offsetting the disadvantages that accompany an autotomy event instead of toward furthering their reproductive success.

Additionally, for some species the tail is vital to locomotor performance. The tail helps to stabilize and counterbalance the lizard during jumping and sprinting, two important anti-predator defenses. In arboreal lizards, jumping ability decreases after autotomy. Although jumping *distance* remains unaffected, the stability that the tail usually provides is lacking after autotomy, causing the lizard to lose control of body movement during a jump (Gillis et al. 2009). The effects of autotomy on sprint speed have also been examined in many species. Generally, iguanid lizards tend to suffer a cost in sprint speed from autotomy; gecko species, however, sometimes show an increase in sprint speed after autotomy (Daniels 1983; McElroy and Bergmann 2013). In addition, the distance a lizard can sprint can be significantly lower as a result of tail loss, and tailless lizards take more frequent pauses during sprints (Martin and Avery 2002). However, the decreases in these performance factors may only be observable when lizards have lost more than 51% of the tail, suggesting that autotomy may only be severely limiting to locomotor functioning when lizards lose the majority of their tail (Lin et al. 2006). The decrease in these locomotive capacities when autotomy occurs can directly affect a lizard's chances of survival by limiting its escape abilities when attacked by predators.

Next, for many lizards, the tail plays an important role in communication with conspecifics and/or predators. In some species, tail signaling is an important aspect of male-male aggression and courtship between the sexes that may be severely limited when the tail is lost (Cooper 2001). In the large psammodromus, dominant males that undergo tail loss quickly lose territory and access to females to smaller males with intact tails, and have comparatively lower rates of reproductive success (Salvador et al. 1995, 1996). Tail loss similarly affects the social status of females in the Iberian rock lizard. In this species, males favored females with intact tails over females with regenerated tails (Martin and Salvador 1993). In the common side blotched lizard, *Uta stansburiana*, studies repeatedly find that the loss of the tail results in a drop in dominance. In one study, females preferred males with long intact tails over males with autotomized tails (Fox et al. 1990). Another study on tail loss in this species showed that the proportion of the tail that was lost was associated with a decrease in social status, and lizards with the highest proportion of tail loss were the lowest in dominance (Fox and Rostker 1982). The decrease in social status due to tail loss may actually be the result of decrease in overall body size, a factor that is well known to be associated with dominance (Tokarz 1995). However, when tail length was artificially restored in the common side-blotched lizard, the increase in body size did not yield a return to the individuals' original social status in male-male competition (Fox et al. 1990). This finding has important implications for the social outcomes of tail loss—even though the tail regenerates, the regenerated tail may not restore the lizard's previous social status.

Other species of lizard use tail signaling to deter predation, for example to warn predators that the individual is alert and would not be an easy meal, or to deflect attention from the lizard's vital organs to the tail so that the lizard can escape through autotomy if attacked. Some species, however, use their tail in both social and anti-predatory contexts (Dial 1986; Cooper 2001). This dual use of the tail may be because anti-predator signals tend to be conspicuous and exaggerated, features that also suit a courtship or aggression display with conspecifics (Cooper 2001). This capacity may support its role in both social and anti-predatory contexts.

Further, the tail is often the site of lipid stores that sustain the lizard when food intake is low. For many species, including skinks and geckos, the tail is the primary site of lipid storage in the body. One study examined caudal lipid storage in relation to tail loss in the metallic skink, *Niveoscincus metallicus,* finding that this species stored nearly all of its fat in the section of the tail closest to the lizard's body (Chapple and Swain 2002). When Chapple and Swain analyzed the location of autotomy along the tail, they found that this species, while maintaining a high frequency of tail autotomy, rarely autotomized the tail in the proximal region resulting in a relatively low energetic cost to tail autotomy (Chapple and Swain 2002). The results of this study revealed that caudal energy reserves may be vital enough for survival that lizards have evolved strategies to prevent autotomy from interfering with the fat storage capacities of the tail. However, this is not always the case, as tail autotomy often does diminish lizards' energetic capacities and metabolic functioning.

The process of regeneration is also energetically costly, depleting energy resources that would have otherwise been used in reproductive or developmental processes. For example, in the Texas banded gecko, *Coleonyx brevis*, tail loss can have substantial negative effects on female fecundity. Females with regenerated tails devote less than half of the energy toward egg production than females with intact tails, and females with regenerated tails store much less fat in the tail and have smaller fat stores overall compared to females with intact tails (Dial and

Fitzpatrick 1981). Due to this deficit in energy resources, females with regenerated tails consumed more food than tailed females but did not invest the higher level of consumption to make up the difference in reproductive output, even though there was no difference between the two groups of females in effort toward courtship. This would imply that while females with regenerated tails in this species put in the effort to increase their reproductive output, losing the ability to store fat caudally puts a cap on their reproductive capability. As a result, females with regenerated tails produced smaller and fewer eggs than females with original tails (Dial and Fitzpatrick 1981). Regenerating a limb early in life can also decrease overall growth rate, leading to smaller adult size and delayed onset of sexual maturation, two factors that can directly impact future mating success (Maginnis 2006). Considering these findings on the importance of energetic storage in the tail and autotomy, it is clear the loss of the tail as an energy reservoir can decrease the lizard's chances of survival and reproduction in the long-term.

Hypotheses of the Maintenance of Tail Autotomy

The evolution of tail autotomy in lizards is clearly the result of a complex balance between the costs and benefits of tail loss and regeneration; however, the ways in which these factors differentially influence the variation in the frequency of tail autotomy across species is unknown. Tail autotomy thus results in evolutionary trade-offs similar to many other traits: one form of a trait (here, tail loss) may allow for long-term survival but lesser reproductive success, while the other (tail retention) provides greater reproductive success but higher risk of injury or death

(Aspi & Hoikkala 1995; Schantz et al. 1995; Brooks 2000). The ability to autotomize the tail therefore presents an opportunity to examine an interesting evolutionary question: Do the demonstrated costs of tail autotomy in lizard species that use the tail as a locomotive necessity, social tool, and/or energetic reservoir affect the frequency of tail loss in predatory encounters?

In this thesis, I test the hypothesis that differences among species in tail signaling behaviors and energy storage in the tail are associated with the frequency of tail autotomy. If the benefit of losing the tail in a predator encounter is less than the social or energetic advantages the tail provides, I expect that the rate of tail loss will be lower. I test this hypothesis in seven species that vary in tail use. Two of these species use tails frequently in display. The greater earless lizard (*Cophosaurus texanus*) has a tapered tail with a black and white stripe underside, which it uses to signal to conspecifics and predators by lifting the tail and waving it in a sinusoidal pattern. The curly tailed lizard (*Leiocephalus carinatus)* has a long and muscular tail that it curls into a spiral that varies in intensity depending on the circumstances of interactions (Cooper 2001; Kircher and Johnson 2017). The Mediterranean house geckos (*Hemidactylus turcicus*) and crested anoles (*Anolis cristatellus*) use tails occasionally in display. Gekkonid lizards, including the Mediterranean house gecko included in this study, occasionally display the tail by waving it in sinusoidal patterns or rapidly twitching the distal portion (Marcellini 1977). Crested anole tail display is not well documented in the literature; however, they are occasionally observed displaying the tail by waving it in sinuosoidal patterns in the field (James Stroud and Michele Johnson, *pers. comm.*). Green anoles (*Anolis carolinensus*), Texas spiny lizards (*Sceloporus olivaceus*), and Texas spotted whiptails (*Aspidoscelis gularis*) use tails rarely in display.

In this study, I tested a series of predictions designed to elucidate the relationship between tail use in social, anti-predatory, and energetic contexts and the frequency of tail loss. First, I predict that lizard species that exhibit high social tail use will have lower frequency of tail autotomy, because using the tail in social interactions is one vital component of mating success. Second, species with increased anti-predatory tail signaling will have increased frequency of tail autotomy, because the use of the tail in this context exposes it to a higher risk of targeting for predator attacks. Additionally, post-autotomy tail movement may be associated with the success of the tail autotomy escape strategy. Therefore, species with high levels of post autotomy tail movement may show a greater frequency of tail autotomy. Lastly, species with increased energetic use of the tail will have lower frequency of tail autotomy, because the autotomy would eliminate an important source of energy storage, and affect other functions like growth and reproductive capacities.

METHODS

Study Species and Field Sites

In this study, seven species were examined for patterns in tail loss frequency. All data were collected during the lizard summer breeding season. I studied each species in multiple field sites using data collected from 2012–2018, capturing individuals for tissue analysis and collecting data on the behavioral use of the tail, anti-predator tail use, and tail loss frequencies (Appendix 1). Curly tail lizards were studied in the Bahamas in 2012 and in Florida in 2017 and 2018. Greater earless lizards, house geckos, and green anoles were studied in Texas in 2017 and 2018. Crested anoles were studied in Puerto Rico in 2004 and Miami, Florida during 2017. Texas spiny lizards were captured and anti-predator behavioral data was collected for this study in Texas in 2018, while social behavioral data on Texas spiny lizards was collected in Texas during 2012 and 2013. Texas spotted whiptail lizards were also studied and collected in Texas during 2012 and 2013 and additional behavioral data for this study on whiptails was collected in Texas in 2018.

Behavioral Observations

Behavioral observations for these seven species were conducted in the 2012–2017 summer breeding seasons (Table 1). Individuals were observed for 10–130 min in the field. I observed both male and female adult lizards, which were located by searching in likely habitats for each species. Lizards were located for observation by scanning the ground, vegetation, or other structures in search of undisturbed individuals. Because house geckos are nocturnal, observations of this species were conducted only at night, using red lights to avoid disturbing them. Geckos were located by searching on man-made constructions with light sources, where they are commonly found.

During each focal observation, any social tail display was recorded, and when it was clear, the target of the display was noted. Individuals were often observed displaying clearly at conspecifics, but in these data, there were no predator encounters during any focal observation period. For this reason, I counted tail displays during these observation periods as social displays, and excluded them in my analysis of anti-predator tail display. Data collected during behavioral observations were converted into tail displays per minute. Whenever possible, individuals observed in 2017 and 2018 were captured after observation by hand or with a noose in order to take morphological measurements. I noted each lizard's sex and measured its body mass to the nearest 0.1 g with a Pesola spring scale. I also measured its snout-vent length (SVL), total tail length, and the portion of the tail that was regenerated (if the tail had been autotomized in the past) to the nearest 1 mm, using a clear plastic ruler.

When a lizard was located for observation, I noted the presence of an autotomized or regenerated tail, often easy to distinguish if the tail was missing entirely or marked by a difference in color, shape and length characteristic of regenerated tails. If it was unclear whether the tail was regenerated, I recorded this data after capture and closer inspection. The sex of the individual being observed was also recorded when possible. For green anoles, spiny lizards, and spotted whiptails, sex was determined from a distance by their size and secondary sex characteristics. The sex of adult green and crested anoles is often easy to distinguish, as males are generally substantially larger than females, and males have a significantly larger dewlap. Male and female spiny lizards are also straightforward to identify, as males have bright blue coloration on the lateral parts of their bellies, while females of this species have white belly coloration. If sex could not be identified from a distance for these species, the individual was captured and examined for the presence of hemipenes, which confirmed that an individual was male. Whiptails could be identified as male or female by coloration, as males have blue-black ventral coloration while females possess a white, unmarked belly. Curly tails and geckos do not possess sexually dimorphic traits that make sex identification achievable from a distance. Therefore, after observations of these two species, I recorded the sex after the individual was captured based on the presence or absence of hemipenes.

Crested anole individuals included in the morphological component of this study were taken from lizards housed in Trinity University's Vivarium that were originally intended for a different study on the effects of testosterone manipulation on behavior. Crested anoles in this study had either had their testes removed, received a high testosterone implant, or were left unaltered. Before the initiation of my study, the crested anoles were housed in the Trinity University Vivarium, following standard lizard care guidelines (Sanger et al. 2008). For the other six species, a subset of captured individuals was transported to Trinity University's Vivarium where they were housed and cared for according to the following procedure for up to 14 days before tissues were collected. Each lizard was housed in an individual cage (27x21x14 cm^3) and fed crickets coated in Fluker's calcium powder (Port Allen, LA) ad libitum, and misted with water daily. Each cage contained a R'zilla terrarium liner (Zilla, Franklin, WI), two small PVC pipes as perches, and a wire mesh hammock. For geckos, cages also included a refuge of crumpled paper towels for geckos. The lighting was set to mimic the natural cycle of day and night during the summer, 13 hours of light and 11 hours of dark using 25W full spectrum UV heat lamps (Zoo Med Laboratories, Sacramento, CA). Temperature in the facility ranged from 25–29°C and humidity in the facility ranged from 56–75%. Wooden boards were placed between cages to prevent visual contact between lizards.

Predator Simulation Trials

Predator simulation trials were used to induce the lizard's natural response as it becomes aware of a predation threat, in order to collect data on tail use in an anti-predatory context, following Cooper (2001) and Kircher and Johnson (2017). Predator approaches were conducted when an undisturbed lizard was spotted, or after a focal observation period was concluded. The approach consisted of one researcher walking toward the lizard with a slow, measured gait in a linear path. As the lizard fled the human predator, I observed the lizard tail display during flight, recording the number of tail displays the lizard exhibited. I attempted to capture all individuals after the predator trials were conducted to record additional morphological data, but many lizards would take refuge out of my reach following these trials. The data on tail use in predator trials were converted to a proportion of individuals who exhibited tail use in the trials for each species.

House geckos were most often found on vertical surfaces, such as the walls of human-made structures, and often did not flee until an approaching researcher was extremely close to the lizard. The standard approach described above therefore proved to be an ineffectual way to stimulate a flight response from house geckos. However, geckos are nocturnal and particularly sensitive to light, often fleeing from flashlights shone on them during night observations. For this reason, I modified the approach component of the predator trial for geckos by shining a bright spotlight on an individual for 10 sec to observe its reaction to a perceived threat. I recorded tail display behavior and any movement during this period. To simulate the threat of predation more closely, after 10 seconds of shining the light, a second person struck the surface the gecko was on near the gecko, causing it to flee. I recorded any tail movement in response to the threat.

Post-Autotomy Tail Analysis

Videos were taken of post-autotomy tail movement for analysis of these movement patterns in relation to intact tail use in each species. For each individual, the length of the tail was measured to the nearest 1 mm using a clear plastic ruler, and a mark was placed near the base of the tail at 75% of the total tail length. Lizard tails were then manually autotomized by pinching firmly at the base of the 75% mark. The autotomized tail was then immediately pinned to a laminated cardboard surface covered with graph paper. The post-autotomy tail movement was recorded via a GoPro Hero 3 camera, positioned directly over and about 0.3 m above the tail. After the tail stopped moving, the recording ended and the autotomized tail mass was measured to the nearest 0.0001 g using a Denver Instrument scale. Later, I used these videos to quantify the rate of post-autotomy tail movement. Tail movements were counted during the first 10 seconds after autotomy, and these values were averaged for each species to create a species average for the rate of post-autotomy tail movement. In addition, each video was examined carefully to create a qualitative account of the post-autotomy tail movement across species.

Immediately after tail autotomy was induced, the lizards were sacrificed via rapid decapitation. Using scissors, I also collected a 1 cm portion of the proximal region of the remaining tail for histological analysis. Following videorecording, the remainder of the autotomized tail was retained for use in bomb calorimetry. All tail tissues were stored at -80°C until they were used later in bomb calorimetry. I conducted bomb calorimetry on tail tissue samples to determine the average caloric content of the tail for each species. Autotomized tail tissues for each species were removed from the freezer and desiccated at 90°C until completely dry (approximately 1 day for smaller species, and 2 days for larger species) in a Fisher Scientific Isotemp oven. After dessication, all the tails for a species were ground together to produce a uniform powder. Benzoic acid was added to the tail sample to increase the combustibility of the organic tail mass. Otherwise, the tails would not combust completely and energy calculations would be inaccurate. Pellets composed of 0.1 g of tail sample and 0.4 g of benzoic acid produced the best results. This ratio was determined through a process of trial and error in which I aimed for a pellet composition that yielded consistent energy values, produced the ideal 1°C temperature change, and combusted completely with little soot remaining after combustion.

The approximately 0.5 g pellet was placed in the bomb calorimeter and the initial temperature was recorded until stabilization. After firing the bomb, final temperature values were recorded until a peak value was reached. These data were used to calculate the average caloric content of the tail per g of tissue for each species using two formulas. First, the energy of the heat of combustion of the calorimeter ($Q_{calorimeter}$) was found using the following equation: $Q_{calorimeter}=10.2$ KJ/°C (ΔT). Second, the caloric content of the tail sample (ΔU_{sample}) was found using the following equation that accounts for the addition of benzoic acid (BA): $-Q_{calorimeter}=Q_{rxn}=m_{BA}(\Delta U_{BA})+m_{sample}(\Delta U_{sample})$, where *m* is the mass, *U* is energy content, and *Q* is energy from heat of combustion. This calculation yields the energy in kilojoules per gram of tail tissue. This calculation was made for every pellet, and each calculation for each species was averaged to yield an average energy content per g for each species. Then, these average values for each species were multiplied by the average mass of the tail in grams for each species to produce species averages for the total energy content in the tail.

Statistical Analyses

To determine whether species differed in rates of tail use during social display or anti-predatory trials, in the rates of post-autotomy tail movement, or in the proportion of the tail lost, I used a series of ANOVA, followed by Tukey's HSD post-hoc tests.

To determine the relationship between the frequency of tail autotomy and the social, anti-predatory, and energetic uses of the tail, a series of Phylogenetic Generalized Least Squares (PGLS) linear regressions were performed in R (R Core Team, 2018) using the *pgls* function in the caper package (Orme, 2013). These analyses were performed using the squamate phylogeny presented in Pyron et al. (2013), pruned to include only the species in this study. Curly tail lizards were not included in analyses using the data on the social use of the tail, because the behavioral data on this species was originally collected for a different study, focusing on the intensity of tail display in this species. The available data on tail display describes the degree to which the tail was being displayed, but not the rate of display (Kircher and Johnson 2017). From these data it is clear that the curly tails display the tail near constantly, but I was not able to derive a numerical value for the rate of tail use per min.

RESULTS

Frequency of Observed Tail Autotomy

The seven species examined in this study exhibited a wide range of observed tail autotomy. Curly tail lizards had the highest frequency of observed tail autotomy, with 62.1% of individuals observed or captured having a regenerated tail. Crested anoles were next, with 53.2% of individuals demonstrating tail loss, followed by the house geckos, green anoles, Texas spotted whiptails, earless lizards, and Texas spiny lizards, all ranging 20–30% (Fig.1).

Tail Loss and Social Use of the Tail

Observational data roughly confirmed expected trends in the social use of the tail among the seven species (Fig. 2; ANOVA: $F_{5,327} = 30.530$, $p < 0.001$). The two high display species, the curly tail lizard and the earless lizard, used their tail the most frequently in social contexts. The curly tail lizard displayed its tail near constantly, while the earless lizard displayed its tail in a social context approximately once per minute. The crested anole used its tail more frequently than the house gecko in a social context, but both species had very low rates of tail display. Green anoles, Texas spotted whiptails, and Texas spiny lizards nearly never displayed their tails socially. Post-hoc analyses revealed that the earless lizards' use of the tail in a social context was significantly greater than geckos, crested anoles, green anoles, Texas spiny lizards, and Texas spotted whiptails, but these five species were not significantly different from each other. Curly tails were excluded from this analysis because the data on social tail use for this species reflected the intensity, not the rate, of social tail display.

Across species, there was no relationship between tail loss frequency and rate of tail use in social display (PGLS: $F_{1,3} = 0.11$, $p = 0.76$). Curly tail lizards were again excluded from this analysis.

Tail Loss and Anti-Predatory Use of the Tail

Species differed in their use of tail signaling in an anti-predatory context (ANOVA: $F_{5,207} = 13.9$, $p < 0.001$). Curly tails used their tails when approached 100% of the time, while earless lizards displayed their tails in around half of the predator trials.. The earless lizard displayed its tail in an anti-predatory context significantly more than the gecko, crested anole, green anole, Texas spiny lizard, and Texas spotted whiptail, but these five species were not significantly different from each other in post-hoc analyses (Fig. 3). Curly tails were excluded from this analysis because the data collected during predator trials measured the intensity of tail display rather than the frequency.

There was no relationship between tail loss frequency and the proportion of predator simulation trials in which lizards used their tails to display (PGLS: $F_{1,4} = 1.98$, $p = 0.23$). However, tail display in an anti-predatory context was highly correlated with tail use in a social context across species (PGLS: $F_{1,3} = 150$, $p = 0.001$; Fig. 4.

Post-Autotomy Tail Movement

The frequency of tail loss was not associated with rate of post-autotomy tail movement (PGLS: $F_{1,4} = 1.02$, $p = 0.36$; Fig. 5). Species differed in the rate of post-autotomy tail movement (ANOVA: $F_{6,73} = 6.64$, $p < 0.001$; Fig. 6). Additionally, the species showed qualitative differences in post-autotomy tail movement. Geckos tended to move the tail fluidly and sinusoidally; however, some tails only showed a weak twitching movement toward the tip of the tail. Thus, the overall movement of the gecko tails was erratic and inconsistent across individuals. Similarly, crested anole tails tended toward a sinusoidal movement pattern, however, the movement was consistently choppy compared to the other species. The fluid sinusoidal pattern was often interrupted by twitching, a change in direction, or sudden straightening of the tail. Earless lizards showed a vigorous and fluid sinusoidal movement pattern; however, with only two individuals recorded this description may not be fully representative of the species. Curly tails showed the most vigorous movement out of the seven species. The tail consistently thrashed rapidly back and forth, and the tail curled into a tight spiral at either end of the tail's range. The Texas spotted whiptail showed very rapid tail movement, with the tail curling into a tight spiral on each side, similar to the curly tail lizard. Green anole tails showed less curvature than the other species, moving back and forth while kept nearly straight. The tail movement was highly consistent and slow, and generally kept a regular tempo. In a similar fashion, the Texas spiny lizard kept its tail straight, and it seemed to lift its tail off the ground more than move from side to side.

Tail Loss and Energy Content of the Tail

Average total tail energy per species was positively associated with tail loss frequency when I included logSVL as a covariate, contrary to our predictions (PGLS: $F_{2,3} = 5.589$, $p = 0.045$; Fig. 7).

Tail Loss Frequency and Proportion of the Tail Lost

Species were marginally different in the proportion of the tail that was lost to tail autotomy, when the total length of the tail was included as a covariate (ANOVA: $F_{7,99} = 0.011$, $p = 0.074$; Fig. 8). However, there was no relationship between tail loss frequency, and proportion of the tail lost in autotomy (PGLS: $F_{1,4} = 0.70$, $p = 0.45$).

DISCUSSION

In these seven species, I find no evidence for an association between the frequency of tail autotomy and the use of the tail in social or predatory contexts. However, my results suggest that species that use their tail in a social context also tend to do so in a predatory context, confounding independent tests of their use between these functions. Additionally, the results presented here indicate an association between high tail energy and frequent tail loss. I consider these results in more detail below.

Social Use of the Tail and Tail Loss Frequency

Considering the importance of having a full tail to the reproductive success of lizards, especially lizards that use tail display as part of the courtship ritual, it is interesting that I found no relationship between the importance of tail display and the frequency of autotomy. However, this may be explained in part by potential differences in the force required to remove the tail, as this force has been reported to vary in relation to the social importance of the tail. For example, in *Uta stansburiana,* one study found that females autotomized the tail more readily than males. Males suffer greater social costs than females when the original tail is lost, and these different costs of tail autotomy in this species resulted in the evolution of sexual dimorphism in the ease of autotomy (Fox et al. 1998). Interestingly, females required the same force each time the tail was autotomized, while males autotomized regenerated tails with more ease than the original tail (Fox et al. 1998). This finding shows that the social costs of tail loss can influence the occurrence of autotomy, however, the ease of autotomy may better reflect this pattern than the frequency of autotomy.

The lack of relationship between the social use of the tail and tail loss frequency may also be is attributable to the relatively small sample size of species included in this study. Moreover, I included two “high tail display” species and five species that used tail signaling rarely if at all. The curly tailed lizard was not included in the statistical analysis of social tail use and tail loss frequency despite being the highest tail use species in the study. It is possible that the inclusion of the curly tail lizard may have changed the outcome of the results, although the curly tailed lizard also showed the highest frequency of tail autotomy in the study, making it unlikely that the results including this data would have produced a result in line with my predictions. A larger sample of species that represent a broader range of social tail use would offer a more rigorous test of this hypothesis.

Use of the Tail in Predatory Context and Tail Loss Frequency

The frequency of tail loss was not associated with the use of tail display toward predators in these seven species. However, in these species, tail display in a predatory context was associated with tail display in a social context. This relationship makes it difficult to disentangle the use of the tail in each context and any differential effects on the frequency of tail autotomy. As pointed out by Cooper (2001), the pattern of tail movement in social displays in also useful in signaling to predators, either to deter approach or distract the predator away from the lizards’ vital body parts. Although the tail is important to social species for their reproductive success, the adoption of tail display by these species in predatory contexts may protect them from deadly predator encounters. In order to better understand these different uses of tail display, it may be productive to conduct an ancestral state reconstruction analysis. In this analysis, the use of the tail in either social interactions or predatory encounters would be matched to the phylogenetic histories of these species. This process could help clarify which behavior evolved first—and as a result, which behavior is the primary use of the tail for each species. This information may help explain why species that seem to use the tail the same way, like the curly tailed lizard and the earless lizard, show opposite trends in tail loss frequency.

Overall, descriptions of post-autotomy tail movement seem consistent with what is recorded in the literature. Dial and Fitzpatrick (1983) note that green anoles show lethargic post-autotomy tail movement, and Higham and Russell (2009) discuss the erratic and variable movements of gecko tails, both in alignment with my descriptions. There was no relationship between the rate of post-autotomy tail movement and tail loss frequency (Fig. 5). Thus, even for species that exhibit high frequencies of tail loss, there is no associated increase in post-autotomy tail movement. Factors influencing post-autotomy tail movement may act independently of the factors influencing the dependence on autotomy as an escape strategy. Dial and Fitzpatrick (1983) found that high levels of post-autotomy tail movement could increase a lizard’s escape time by as much as 40%, and Cooper (2004) found that species under low predation pressure showed lower levels of post-autotomy tail movement. These two findings point to predation pressure as an important determinant of post autotomy tail movement. Importantly, I previously noted that predation pressure is not a good measure to use when understanding the frequency of tail autotomy in a lizard population. However, it may be more relevant to questions of post-autotomy tail movement. Originally, I predicted that the degree of post-autotomy tail movement would be influenced by a species' dependence on tail autotomy as an escape strategy. I speculated that an increased reliance on autotomy would be accompanied by high levels of post autotomy tail movement, ensuring that the sacrifice was worthwhile for the lizard. While the dependence on autotomy as a strategy is influenced by the full spectrum of costs and benefits of tail loss, the factors influencing post-autotomy tail movement are confined to the predator encounter. This contextual difference explains why factors like predation pressure and predator behavior in a population may be directly driving the evolution of post-autotomy tail movement, and why it may be unrelated to the frequency of autotomy in a population.

Energy Content and Tail Loss Frequency

Total energy content in the tail was positively associated with tail loss frequency, when I used the logSVL as a covariate to control for differences in body size across the species. This result directly opposes my prediction, that a high energy content in the tail would be associated with a lower frequency of tail autotomy because the loss of this asset would negatively affect the lizard's reproductive success. However, this result may be explained when considering the events that may occur immediately post-autotomization during a predator encounter. In species that have a high energy tail, consuming the tail itself may satisfy the predator and deter further pursuit of the now-tailless lizard. In species with low energy tails, the autotomized tail may fail to tempt the predator, resulting in an overall less successful predator escape strategy for these species. Therefore, the species with high energy tails may receive more benefit from the autotomization strategy than species with low energy tails, leading to increased reliance on autotomization for species with high energy tails. Some support for this speculation exists in the literature. One study found that species with regenerated tails with equal or higher energy content than the original tail had a higher frequency of tail autotomy compared to species with regenerated tails with less energy content than the original tail (Vitt et al. 1977). This result corroborates our findings, and indicates that high energy content in the tail is associated with an increased dependence on tail autotomy as a predator escape strategy.

Given the high costs of tail autotomy, it is puzzling why some species that depend heavily on the tail in a variety of functions, like the curly tailed lizard that uses its high-energy tail constantly in social interactions, anti-predator display, and locomotor performance should have such a high frequency of tail loss. Some studies have noted that the occurrence of partial tail loss may help resolve some of these unintuitive results (Cromie and Chapple 2012; Chapple and Swain 2002). By engaging tail autotomy toward the distal portion of the tail, species could avoid the most severe costs of tail loss by preserving lipid stores near the base of the tail, maintaining the structural integrity of the tail as much as possible, and reducing the regeneration period. However, I found no relationship between the portion of the tail lost and the frequency of tail loss, indicating that even species like the curly tailed lizard suffer the full brunt of the costs of tail autotomy at high frequencies (Fig. 8).

In future investigations on this topic, it may be important to note the age of the individuals collected. Prior to reproduction, young lizards may be more heavily influenced by the costs of tail autotomy compared to older individuals that have already reproduced. This effect is seen in juveniles that will allocate energy resources to increasing body size during growth rather than to regenerating an autotomized tail (Vitt et al. 1977). On the other hand, some species may be more likely to autotomize the tail as a juvenile than as an adult. For example, in the skink species *Eumeces fasciatus* and *E. laticeps,* hatchlings sport a blue tail that serves to distract predators away from the lizard's body and encourage autotomization (Cooper and Vitt 1985). It seems that age might be an important determinant of predator escape strategies across species. Therefore, the age of the lizard may be an important factor to consider when evaluating the influence of the costs of tail loss on its frequency in populations across species.

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TABLES

Table 1. Total number of hours of focal behavioral observation, and number of individuals observed for each species.

	Curly Tail	Earless Lizard	House Gecko	Crested Anole	Green Anole	Texas Spotted Whiptail	Texas Spiny Lizard
N	34	24	85	59	222	43	29
Hours	24.5	24.6	30.0	76.4	127.0	18.7	19.6

FIGURES

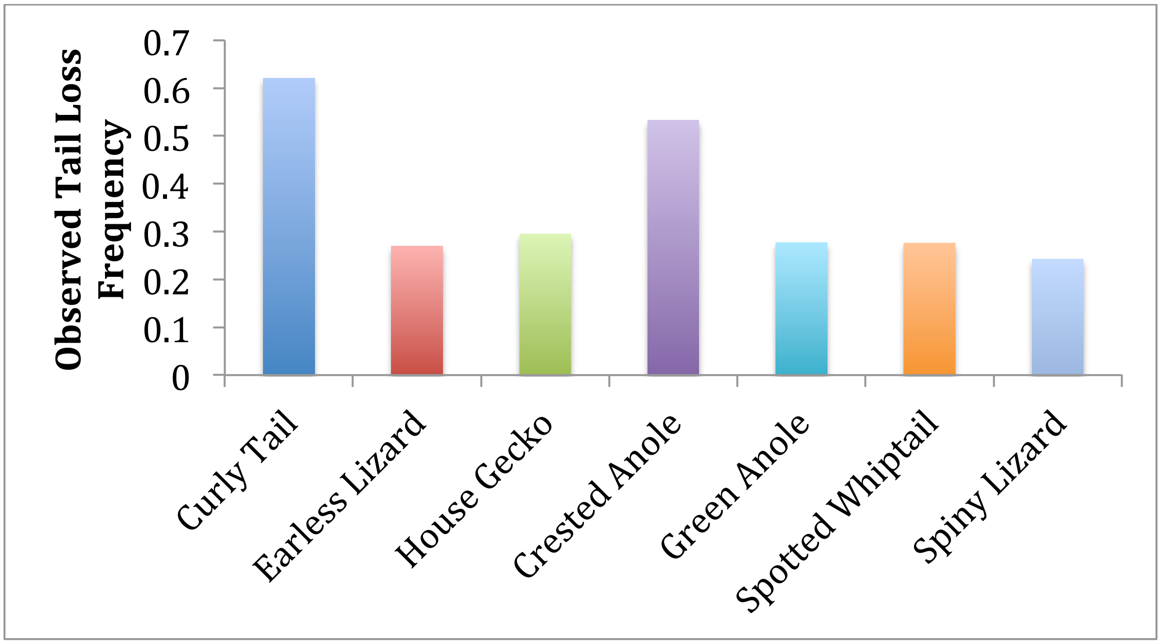

Fig. 1 Frequency of observed tail loss across seven species in natural habitats. Species are ordered by frequency of tail use, with the most frequent tail use occurring by species on the left, to the least frequency tail use by species on the right.

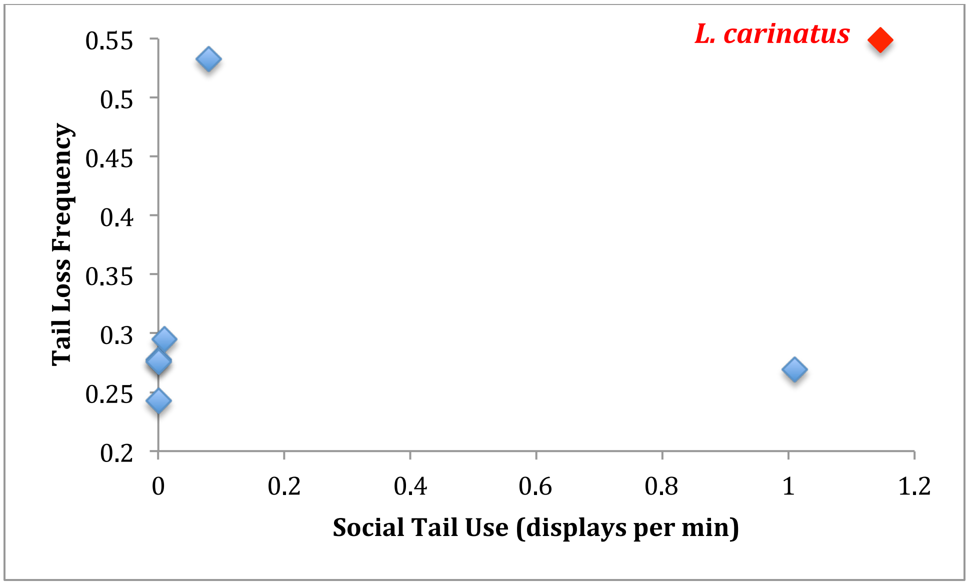

Fig. 2. No relationship exists between the social use of the tail and tail loss frequency (i.e., the proportion of individuals of each species that had autotomized tails) across six species, excluding *L. carinatus (*PGLS: $F_{1,3} = 0.11$, $p = 0.76$*)*. Red marker position reflects the measured *L. carinatus* tail loss frequency and the estimated social tail use as compared to the other species.

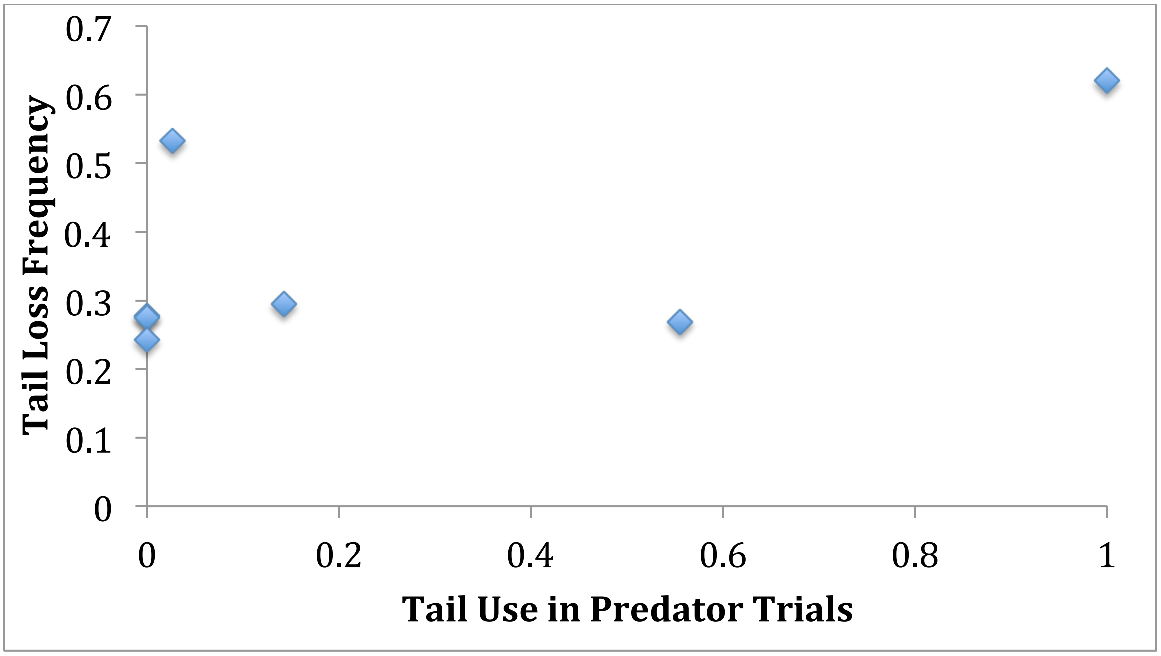

Fig. 3. No relationship exists between tail use in an anti-predatory context (i.e., the proportion of individuals of each species that used their tail during predator escape) and the frequency of tail loss (i.e., the proportion of individuals of each species that had autotomized tails; PGLS: $F_{1,4} = 1.98$, $p = 0.23$).

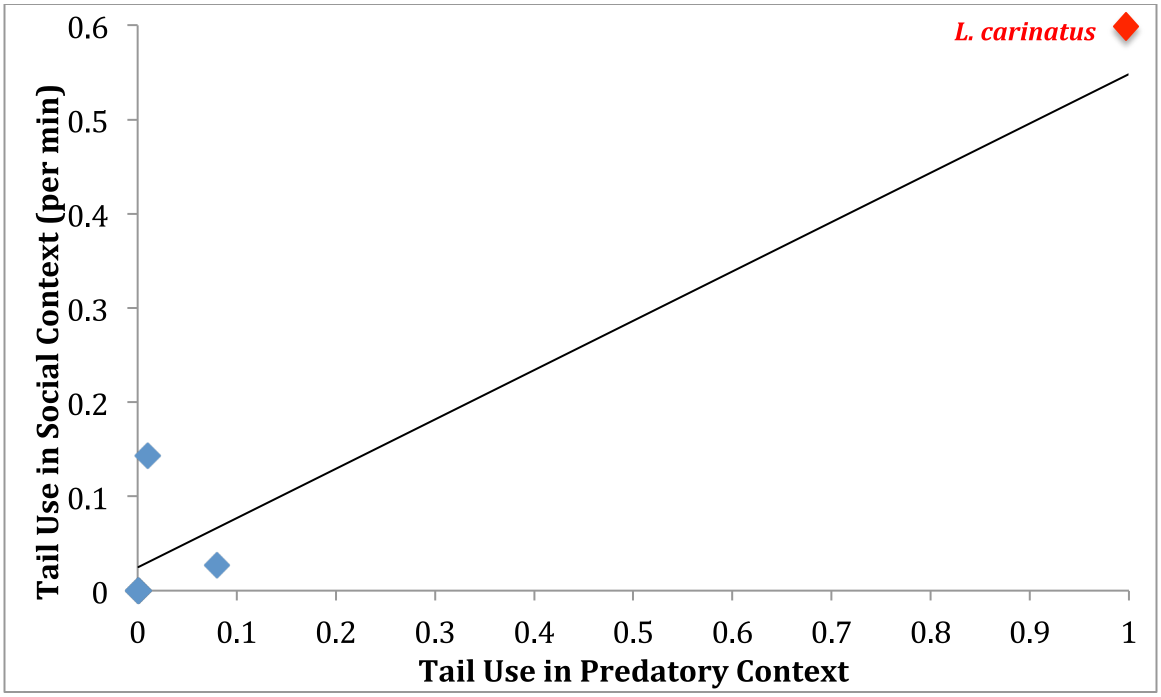

Fig. 4. Tail use in an anti-predatory context (i.e., the proportion of individuals of each species that used their tail during predator escape) is highly associated with tail use in a social context across species, excluding *L. carinatus*(PGLS: $F_{1,3}$ = 150, p = 0.001). Red marker position reflects estimated *L. carinatus* tail use in social context based on observational data, and measured tail use in anti-predatory context.

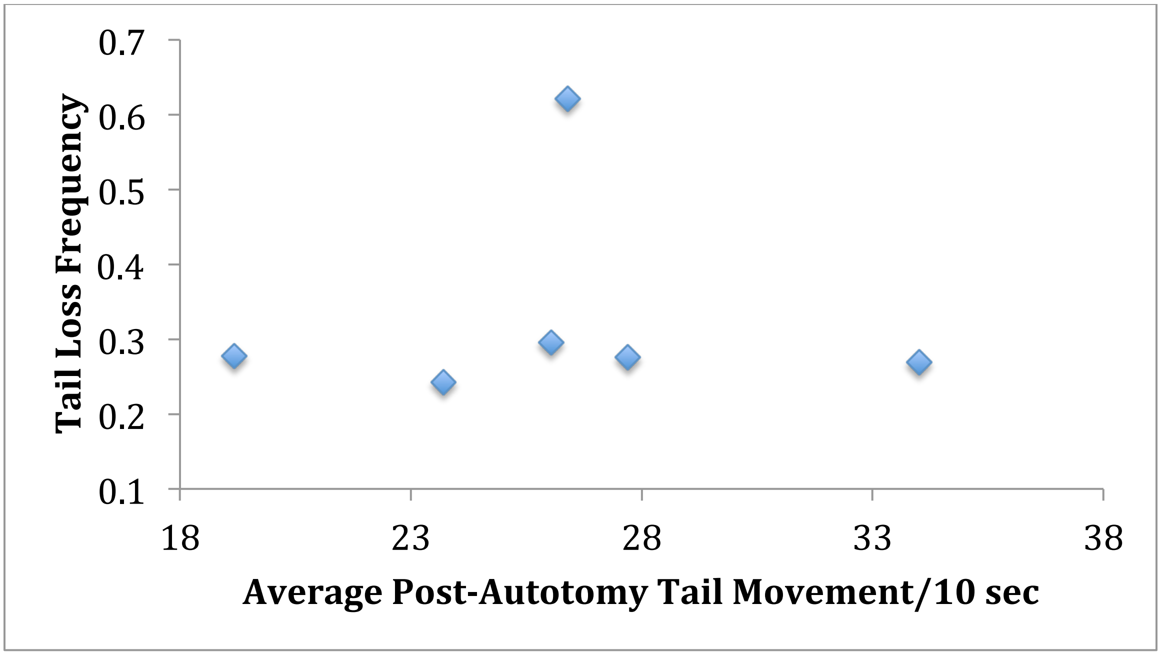

Fig. 5. No relationship between the rate of post-autotomy tail movement and frequency of tail loss (i.e., the proportion of individuals of each species that had autotomized tails) across species (PGLS: $F_{1,4} = 1.02$, $p = 0.36$).

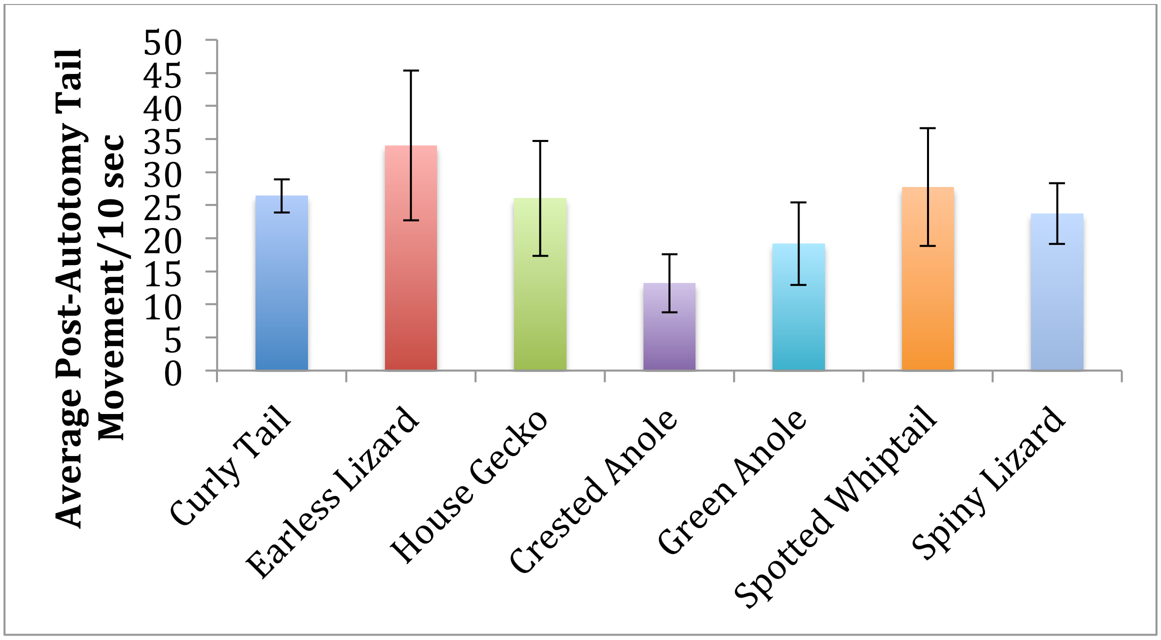

Fig. 6. Species differ in rates of post-autotomy tail movement (± SD within the first 10 seconds immediately following autotomy (ANOVA: $F_{6,73}$= 6.64, p < 0.001).

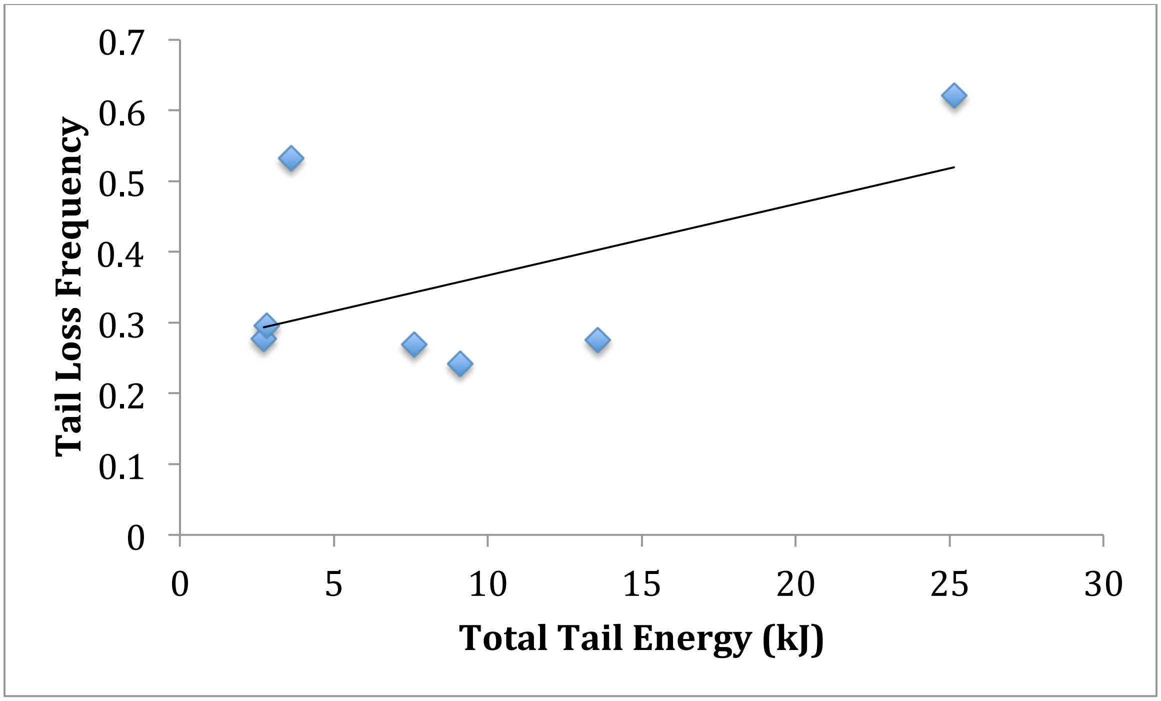

Fig. 7. Total energy content in the tail is positively associated with tail loss frequency (i.e., the proportion of individuals of each species that had autotomized tails), with logSVL included as a covariate (PGLS: $F_{2,3} = 5.589$, $p = 0.045$).

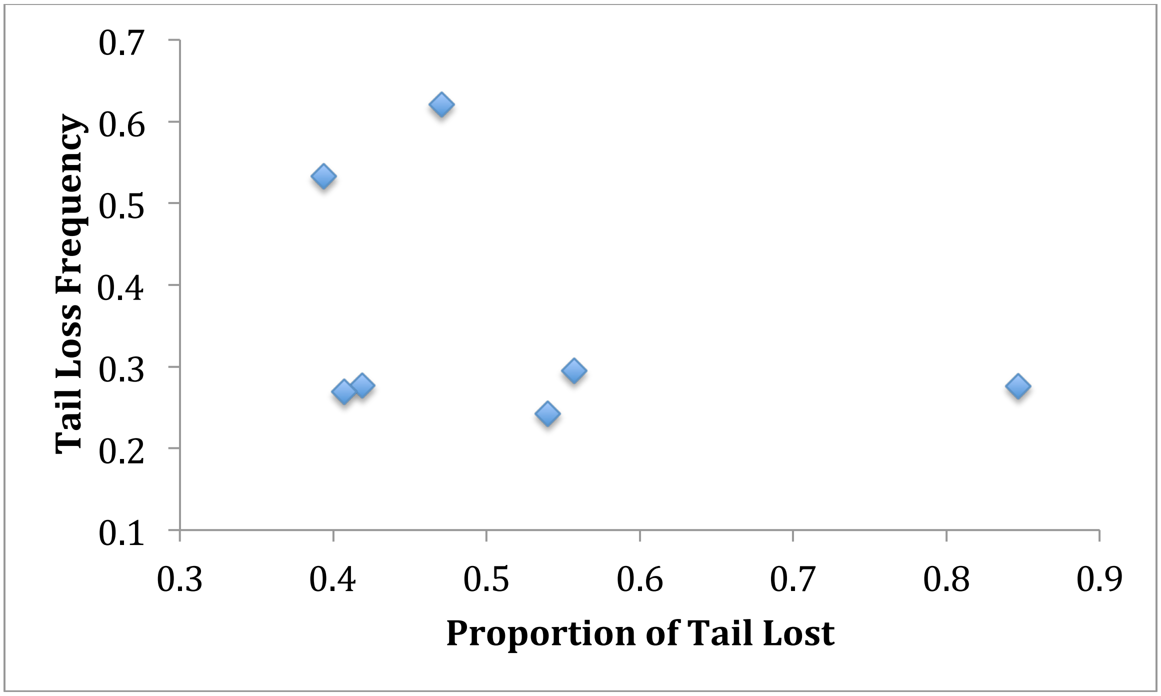

Fig. 8. No relationship exists between the proportion of tail lost and tail loss frequency (i.e., the proportion of individuals of each species that had autotomized tails; PGLS: $F_{1,4}$= 0.70, p = 0.45).

APPENDIX

Appendix 1. Dates and field sites for data collection in seven lizard species.

	Curly Tail	Earless Lizard	House Gecko	Crested Anole	Green Anole	Texas Spotted Whiptail	Texas Spiny Lizard
Behavioral Observation	Bahamas, 2012 Crooked Island	Texas, 2017 Seminole Canyon State Park	Texas, 2017 Palmetto State Park Trinity University	Rio Grande, Puerto Rico, 2004 El Verde Field Station's Stream House	Texas, 2017 Trinity University San Antonio Botanical Gardens Witte Museum Palmetto State Park	Texas, 2012-2013 Lake Bastrop, North Shore Park Bastrop County	Texas, 2012 Bexar County Comal County Hays County Travis County Palmetto State Park Texas, 2013 Headwaters Natural Area
Predator Trials	Bahamas, 2012 Crooked Island	Texas, 2017 Seminole Canyon State Park Texas, 2018 Bexar County	Texas, 2017 Seminole Canyon State Park Palmetto State Park Trinity University	Miami, Florida, 2017 Fairchild Botanical Gardens University of Miami	Texas, 2017 Trinity University San Antonio Botanical Gardens Witte Museum Palmetto State Park	Texas, 2018 Bexar County	Texas, 2018 Bexar County Headwaters Natural Area
Tail Loss Frequency	Florida, 2017 Jupiter Florida, 2018 East coast	Texas, 2017 Seminole Canyon State Park	Texas, 2017-2018 Palmetto State Park Trinity University	Miami, Florida, 2017 Fairchild Botanical Gardens University of Miami	Texas, 2017 Trinity University San Antonio Botanical Gardens Witte Museum Palmetto State Park	Texas, 2018 Bexar County	Texas, 2018 Bexar County Headwaters Natural Area
Capture	Florida, 2017 Jupiter	Texas, 2017 Seminole Canyon State Park Texas, 2018 Bexar County	Texas, 2017-2018 Palmetto State Park Texas, 2018 Trinity University campus	Miami, Florida, 2017 Fairchild Botanical Gardens University of Miami	Texas, 2017 Trinity University San Antonio Botanical Gardens Witte Museum Palmetto State Park	Texas, 2018 Bexar County	Texas, 2018 Bexar County Headwaters Natural Area