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Sexual Dimorphism in the Ease of Tail Autotomy: *Uta stansburiana* with and without Previous Tail Loss

STANLEY F. FOX, JASON M. CONDER, AND ALLIE E. SMITH

Tail autotomy is used by many lizard species to escape predation, but in those species that have the adaptation, the degree to which it is developed depends on relative costs and benefits. The same may be true for the development of tail autotomy in the two sexes of the same species. We examined the ease of tail autotomy of male and female *Uta stansburiana*. Correcting for tail thickness, males lose their tail significantly less easily than females and retain it even more strongly as they grow larger from sexual maturity on. Although both sexes lose social status after tail loss, females may have available an alternative, subordinate, social role in which they can retain some reproductive success. Males do not have such an alternative strategy, and since they need both a complete tail and high social status for reproductive success, they require more stimulus to autotomize their tail (i.e., the cost of tail autotomy is higher in males than in females). For both males and females, lizards with incomplete tails from a previous autotomy have reduced antipredator defense via tail autotomy. We predicted that second-time autotomy would occur more readily, as compensation. But females did not show this compensation and autotomized the tail with equal ease the first and second times. Males autotomized more easily the second time, but we do not interpret this change as compensation for a shorter tail. For males, the cost of tail loss is much reduced after a prior tail autotomy; they have already lost their social status following autotomy, and further tail loss is less consequential. At the second autotomy, males reduced their ease of tail autotomy to equal that of females, and females did not show facilitated second-time autotomy. Therefore, males, like females, did not show easier tail autotomy as compensation for an incomplete tail.

TAIL autotomy, the self-induced separation of the tail from the body practiced by many lizard species to escape predation (Bellairs and Bryant, 1985; Arnold, 1988), has costs and benefits that may differ among species (Vitt et al., 1977; Fox et al., 1994) or among years for the same species (Niewiarowski et al., 1997). The benefit of the adaptation is escape from predation; a lizard, when grasped by the tail by a predator, can autotomize the tail and escape running while the predator is left behind with the expendable member (Dial and Fitzpatrick, 1983; Medel et al., 1988). Tailed lizards can save themselves in this manner whereas those with incomplete tails do so less frequently (Congdon et al., 1974; Dial and Fitzpatrick, 1984; Vitt and Cooper, 1986). However, there are costs to tail autotomy. Compared with their tailed counterparts, tailless lizards may run more slowly (Ballinger et al., 1979; Punzo, 1982; Formanowicz et al., 1990; but see Daniels, 1983; Brown et al., 1995), suffer decreased somatic growth (Ballinger and Tinkle, 1979; Smith, 1996; Niewiarowski et al., 1997; but see Vitt and Cooper, 1986; Althoff and Thompson, 1994), and decreased reproductive output (Smyth, 1974; Dial and Fitzpatrick, 1981) and can fall in social status (Fox

and Rostker, 1982; Fox et al., 1990) with the consequence of a reduced home-range size and/or (for males) access to fewer females (Martín and Salvador, 1993; Salvador et al., 1996). Large tailless males may sometimes retain their dominance but restrict their activity and decrease the size of their home range such that their reproductive success suffers (Salvador et al., 1995).

The tail autotomy adaptation has evolved and reevolved more than once in the Squamata (Arnold, 1988) and is expressed to different degrees among species that have it. Even within the same species, the ease of tail autotomy (not necessarily its frequency) can be influenced by temperature (Werner, 1964; Brattstrom, 1965; Bustard, 1968), age (Daniels, 1984), body condition (Daniels, 1984), and habituation to captivity (Bellairs and Bryant, 1985; Arnold, 1988). How a prey is grasped by a predator can even affect the ease of tail autotomy (Arnold, 1988; Beneski, 1989). Within the same species, and between species when phylogenetic effects are considered, the expression of the tail autotomy adaptation is the net selective effect of costs and benefits. We hypothesize the same for the case of the two sexes within a species.

We conducted experiments on the ease with which the two sexes of the lizard *Uta stansburiana* autotomize their tails. Previous work has shown that both sexes of this species lose social status after tail loss (Fox and Rostker, 1982) and that the tail is used as a badge of high social status, especially in females (Fox et al., 1990). Females may have available an alternate, subordinate, social role that can be adopted subsequent to tail loss and that may salvage some reproductive success, albeit less than that of tailed females that fill dominant roles and occupy high-quality home ranges (Fox et al., 1981). Males apparently have no such alternate strategy available and need both their tail and high status for reproductive success. Consequently, we predicted that males, compared with females, would autotomize their tails less easily.

Moreover, once the tail (usually a portion thereof) is autotomized, the efficacy of tail autotomy as a predation defense is diminished until it can regenerate. *Uta stansburiana* with incomplete tails suffer higher mortality than those with complete tails (Wilson, 1992; S. F. Fox and J. K. McCoy, unpubl.). Nevertheless, many *U. stansburiana* survivors autotomize the tail more than once (Tinkle, 1967). We also conducted experiments on the ease of tail autotomy after a previous autotomy. We predicted that both sexes would autotomize the tail more easily the second time as a way to compensate for the reduced defense of an incomplete tail, but if there were a difference between the sexes in facilitated second-time autotomy, it would be related to differences in relative costs and benefits.

MATERIALS AND METHODS

Over 2–4 September 1995, using the methods of Fox (1978), we captured specimens of *U. stansburiana* from Winkler County, Texas, where previous studies of the ecology and behavior of this species have been conducted (Tinkle, 1967; Fox, 1983; Fox et al., 1981). Only individuals with completely intact tails were retained for experiments. Subjects were taken to Oklahoma State University where they were maintained in the laboratory in individual 3-L plastic cages (each lined with sand, outfitted with a plastic plant for cover, and capped with a hardware cloth top) under a photoperiod and thermal regime as per natural fall conditions at their collection locality. Both 150-W incandescent bulbs and 40-W fluorescent lights were used for illumination and heat. Electric timers turned on (and off) the fluorescent lights 30 min before (and after) the incandescent lights. Lizards

were fed live crickets dusted with vitamin powder and given water every other day. Calcium, in the form of crushed, ground, chicken eggshells mixed with sand, was available at all times. We followed animal care guidelines of Oklahoma State University and the National Institutes of Health.

After three weeks in captivity, we measured the force necessary to elicit tail autotomy. The lizards were used also in another study designed to test whether exposure to a simulated predation encounter would heighten the ease of tail autotomy (unpubl.). Since this other study found no indication of a difference in ease of tail autotomy related to this exposure, we pooled the results from treatment and control lizards from this experiment and compared the sexes for a dimorphism of the facility of tail autotomy. Briefly, lizards were handled as follows. First, we placed each lizard (inside its cage) in a lighted incubator for 15 min, warming it to a temperature of 38 C, normal body temperature for this lizard under natural field conditions (Tinkle, 1967). Half of the subjects in each sex group were exposed to a simulated attack by a predator. For these, we introduced each lizard individually into a 0.80 × 0.55 m sand-substrate arena and kept it running by prodding it repeatedly and vigorously with a soft, 5-cm wide paintbrush as necessary. After 45 sec, we took the lizard from the arena and immediately measured the force necessary to elicit tail autotomy at a point near the tail midlength. Directly after the tail autotomized, we measured the cloacal temperature of the lizard. During pilot runs, we discovered that the body temperature of the lizards fell slightly during the simulated predator exposure. Because temperature can influence the ease of tail autotomy, we wanted to keep the body temperature of treatment and control lizards the same. Consequently, control lizards (the other half of each sex group) were removed from the incubator, held in a cool ice chest (still in their home cages) for about 1 min to allow their body temperature to fall the same as the treatment lizards, and, without exposure to a simulated encounter with a predator, were subjected to the same measurement of force inducing tail autotomy.

For some subjects, we also measured the force necessary to elicit autotomy of the tail a second time, four to seven weeks after the first autotomy. By this time some minimal regeneration had occurred, 4–20 mm, but the tail was still incomplete in all subjects. The second autotomy was induced always proximal to the first break, in the original, unregenerated portion of the tail. Lizards were maintained in the laboratory

under the conditions described above until the second measurement.

We measured force required to elicit tail autotomy as per Fox et al. (1994). The lizard was held firmly upside down underneath a fixed $19.0 \times 5.2 \times 0.6$ cm rectangular plexiglass plate (venter against the plate) with its tail positioned below an oval hole (1.0×0.4 cm) cut perpendicular to the length of the plate. A 3.2×0.8 cm wire hook attached to a spring scale was passed through the oval hole and around the tail at approximately the midpoint of its length. While one person held the lizard to the plate, the other slowly pulled the spring scale upward, which caused a pinching force to be exerted on the tail, much like the pressure applied by the mouth or beak of a real predator. At the moment the tail autotomized, the force (in grams, later converted to Newtons) registering on the spring scale was read.

The wire hook did not cut through the tail. Instead, the lizard was stimulated by the applied pressure of the hook to autotomize its tail. *Uta stansburiana* is a species with a well-developed tail autotomy adaptation (Bellairs and Bryant, 1985) and thus possesses various fracture planes within most caudal vertebrae where autotomy can occur (Arnold, 1988). In almost every instance, our placement of the wire hook coincided closely enough to a fracture plane so as to stimulate autotomy, signaled visibly by a quivering of the tail just prior to release. In the few cases where its placement did not elicit autotomy, we repositioned it slightly and reapplied pressure. Tail autotomy is an active process of the differential contraction of various caudal muscles that is neurologically controlled and is shown only by live, conscious animals (Arnold, 1988). We did not, therefore, anesthetize our subjects prior to measuring ease of autotomy. Tail loss is common among species that possess the autotomy adaptation, and details of the adaptation serve to minimize blood loss and trauma. The tail regenerates after autotomy. None of our subjects showed ill effects from our procedure.

Two days after tail autotomy, we measured the height and width of the remaining tail base with dial calipers at the site of autotomy. Using the standard formula for an ellipse, we calculated the cross-sectional tail area at the site of the break.

RESULTS

Autotomy of intact tails.—The force necessary to elicit tail autotomy depends on tail thickness (Fox et al., 1994), so we conducted regression

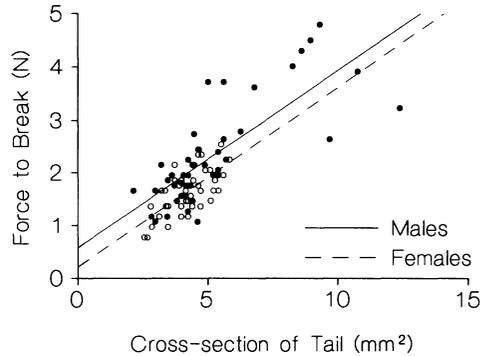


Fig. 1. Force necessary to elicit first tail autotomy versus tail thickness for males (filled circles) and females (open circles).

analysis of force versus tail thickness and compared the slopes of the lines for the two sexes and found them not to be significantly different (ANOVA: $F_{1,79} = 0.002$, $P = 0.96$). However, the regression line (or y-intercept) was significantly higher for males than for females (ANCOVA: $F_{1,80} = 9.036$, $P = 0.004$; Fig. 1). Accounting for tail thickness, males require more force applied to the tail than do females to stimulate tail autotomy.

The residuals from the common regression of force versus tail thickness (pooling data from both sexes) give the thickness-corrected variation of the observed force for each subject from the force predicted from the regression line. Lizards that lose their tails more readily (independent of tail thickness) will have negative residuals, and those losing their tails less readily will have positive residuals. We pooled data from both sexes and performed this regression (significant nonzero slope: $F_{1,81} = 124.390$, $P < 0.001$). We then plotted the resultant residuals against SVL and found a significant positive relationship ($F_{1,81} = 50.643$, $P < 0.001$; Fig. 2). As lizards grow larger in body size, their ease of tail autotomy decreases, independent of tail thickness.

It was also possible to compare the slopes of the separate regression lines of the two sexes. Males had a significantly steeper slope than did females (ANOVA: $F_{1,79} = 5.657$, $P = 0.02$; Fig. 2). As both sexes grow, the ease of tail autotomy decreases faster in males than in females—males require more and more force than do females to induce autotomy. Furthermore, the body size at which the sex-specific lines notably diverge beyond their intersection point of equal retention is roughly 45–46 mm SVL, or the minimal size of sexual maturation in males (Tinkle, 1967).

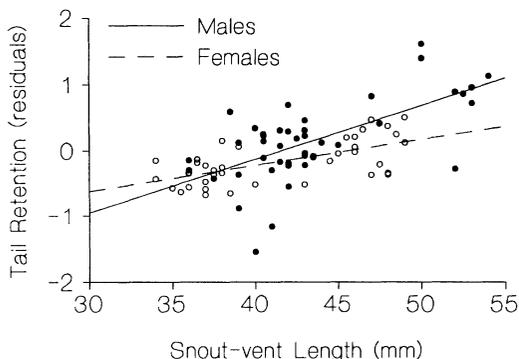


Fig. 2. Tail retention (residuals of pooled points of Fig. 1) versus snout-vent length (SVL) for males (filled circles) and females (open circles).

Despite our attempts to maintain subjects at equivalent temperatures, males averaged slightly cooler (0.4 C) than did females (t -test adjusted for unequal variances: $t = 2.65$, $df = 76.1$, $P = 0.01$). This slight temperature difference possibly could have confounded the observed sexual dimorphism of ease of tail autotomy. However, when we plotted the above residuals against body temperature, we found no significant regression ($F_{1,81} = 0.366$, $P = 0.547$). Correcting for tail thickness, ease of tail autotomy was independent of temperature across the limited range of temperatures in our experiment.

Autotomy of once-broken tails.—We used the same type of analysis for the data collected from lizards that were induced to autotomize their tail a second time. In this case, the separate regression lines for each sex had both equivalent slopes (ANOVA: $F_{1,59} = 0.155$, $P = 0.70$) and equivalent heights (or y-intercepts; ANCOVA: $F_{1,60} = 0.295$, $P = 0.59$; Fig. 3). Males and females lost their tails the second time with about equal facility. Compared with the first experiment in which lizards had intact tails, at the second autotomy, either the females had changed to lose the tail less easily or the males had changed to lose it more easily. Therefore, we compared the ease of autotomy the first and second time for each lizard, but to do this we first had to adjust for the fact that the tail was thicker the second time in all instances because the second break was induced proximal to the first break. Because the relationship between force necessary to induce autotomy and tail thickness is linear, we divided the force by tail thickness to derive force per unit tail cross-sectional area. Separately for the sexes, we then compared this thickness-corrected force at the two episodes of tail autotomy. Females required

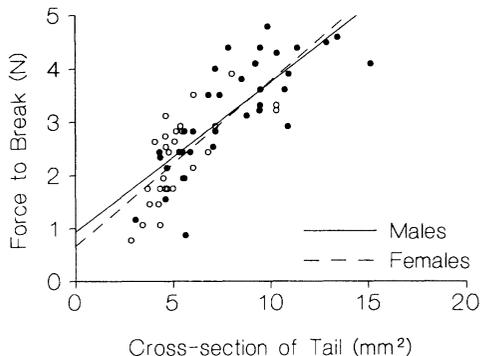


Fig. 3. Force necessary to elicit second tail autotomy versus tail thickness for males (filled circles) and females (open circles).

the same force to elicit autotomy both times (paired t -test: $t = 1.295$, $df = 26$, $P = 0.21$), whereas males required significantly less force the second time (paired t -test: $t = 2.343$, $df = 34$, $P = 0.025$).

Although we tried to standardize our methods to keep subjects at the same temperature, at the time of the second autotomy, there was again a significant difference of body temperature between the sexes (t -test: $t = 3.410$, $df = 60$, $P = 0.001$), although this time the males averaged slightly warmer (0.7 C) than did the females. Nevertheless, we found no relationship between the residuals derived from the second-time force versus tail thickness and temperature ($F_{1,61} = 0.095$, $P = 0.759$). Again, over the small range of temperatures observed in our experiment, there was no statistical relationship between the ease of autotomy and temperature. Thus, there is no evidence that the small temperature difference between the sexes played a role in the ease of tail autotomy after prior tail loss.

DISCUSSION

Our study is the first to show sexual dimorphism of ease of tail autotomy: male *U. stansburiana* autotomize their tail less readily than do females and retain it even more strongly once they attain sexual maturity. Once the tail is lost, however, males surrender their tendency to retain the tail and lose it with a facility equal to that of females. Females show the same ease of tail autotomy regardless of whether it is their first or second autotomy.

For both sexes, tail loss can lead to decreased social status in *U. stansburiana* (Fox and Rostker, 1982) and, with it, decreased ability to retain a high-quality home range (Fox et al., 1981; Fox,

1983), which, in turn, can negatively affect survival (Fox, 1978). Females may adopt an alternate, subordinate, social role following tail autotomy and use the absence of the tail to signal that role (Fox et al., 1990). Without superior social status, tailless females may accept lower-quality home ranges and avoid agonistic encounters with conspecifics. In any case, they will probably find mates, and any saved energy can be channeled into producing larger offspring (S. F. Fox and J. K. McCoy, unpubl.). No alternative strategy seems available to males. Males must have large, high-quality territories to gain mating opportunities and accrue superior reproductive success. With decreased social dominance, tailless males face reduced opportunities to secure superior territories (Fox et al., 1981) and, consequently, reduced opportunities to attract mates. In other lizard species, too, tailless individuals lose social status and fight less (Martín and Salvador, 1993, 1995); tailless males lose territory and access to females (Salvador et al., 1995, 1996) and copulate less frequently (Martín and Salvador, 1993).

Because females may have an alternate social role to accept following tail loss and males may not, it is reasonable that males will practice tail autotomy less readily than females. Tail autotomy is socially more costly to males compared with females. Before the tail assumes an importance in mate acquisition for males, it is autotomized with equivalent facility by juveniles of both sexes. But with sexual maturity and competition for mates, the tail and its association with dominance becomes more important for males than for females; males become more reluctant than females to lose the tail and especially so from the minimal size of reproduction.

Nevertheless, female lizards that have autotomized their tails can suffer costs, especially reproductive ones. For lizard species whose tails are rich in stored lipids (Daniels, 1984; Vitt and Cooper, 1986), females who have lost their tails show inferior reproduction (Smyth, 1974; Dial and Fitzpatrick, 1981). Vitt et al. (1977) predicted that short-lived species that rely heavily on tail autotomy as a predation defense (such as *U. stansburiana*) should allocate considerable energy toward tail regeneration and consequently show compromised reproduction. But *U. stansburiana* does not store much lipid in the tail (Althoff and Thompson, 1994), and a recent field study of the effect of tail loss on female reproduction in *U. stansburiana* discovered that female reproduction in this species suffers little following tail autotomy (S. F. Fox and J. K. McCoy, unpubl.). Clutch size, egg size, and

hatchling size of tailless mothers, compared with tailed ones, were not smaller.

An alternative explanation for the sexual difference in ease of tail autotomy that we observed relates to sexual dimorphism in the non-autotomous proximal section of the tail as seen in some lacertid lizards (Barbadillo et al., 1995). In four species, males had slightly longer series of nonautotomous caudal vertebrae than did females, presumably to protect the hemipenes and associated musculature from damage by preventing deep autotomy. Indeed, in a wild population of *Lacerta vivipara*, males showed significantly fewer autotomies than did females at very short distances from the tail base (Barbadillo et al., 1995). However, our induced autotomies were far removed distally from this proximal series of nonautotomous vertebrae and even from pelvic muscles that insert into the tail (Russell and Bauer, 1992; Arnold, 1994). Thus, the sexual difference in ease of tail autotomy that we observed in our experiment is not likely to be a consequence of any sexual dimorphism of the proximal segment of the tail that may be related to the site where male hemipenes are housed.

Females autotomized the tail with equal ease whether or not they had a prior autotomy. We did not observe easier tail autotomy in females when the tail was incomplete and supposedly offering less of a defense against predators. With an alternate social strategy, incompletely tailed females that lose even more of their tail will still obtain reproductive success, although most likely less than fully or more completely tailed ones (Martín and Salvador, 1993; S. F. Fox and J. K. McCoy, unpubl.). Under a strong predation regime with the benefits of tail autotomy high, and the costs moderated by an alternate social strategy available following tail loss, females have likely evolved the ability to autotomize their tails readily and with a minimal requisite force. This minimal force to elicit autotomy is the same for first- or second-time autotomy. On the other hand, males autotomized the tail more readily the second time, with the same minimal force that females require. Males that have autotomized the tail previously, however reluctantly, have likely fallen in social status and face poor chances to mate; they have little to lose by autotomizing even more of their tail. Males at the second autotomy, compared with their first one, have less of a cost associated with tail loss and thus autotomize more readily. Nevertheless, males did not show easier tail autotomy than did females at the second autotomy, and females autotomized the tail with equal facility regardless of whether they had a prior au-

totomy. Consequently, in males (as in females), we found no evidence that tail autotomy occurred more easily for lizards with incomplete tails, as compensation for a shorter tail that is a compromised defense against predation.

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