# Social Cost of Tail Loss in *Uta stansburiana*

Abstract. *Tail removal from dominant juvenile* Uta stansburiana *resulted in a decrease in social status in dyadic encounters. Most lizards were affected after removal of two-thirds of their tails. In some pairs, dominant lizards lost status after removal of one-third of their tails but regained dominance after the other member of the pair lost two-thirds of its tail. Tail loss in nature may impose a social handicap to successful home range acquisition and thereby increase risk of death.*

Lizards' tails are sometimes adapted for specialized functions in swimming, fighting, climbing, and running (*1*), or often for generalized functions such as fat storage (*2*). Taxa in which tails have more generalized functions tend to exhibit a suite of characters that promote easy tail loss, or tail autotomy (*2*). The benefit of autotomy is that the tail may be lost to a predator while the lizard escapes (*2, 3*). A lizard that has lost its tail is more susceptible to predation (*3*), although in some species tails regenerate (*2*). Even among lizards (and salamanders) without specialized tail functions, loss of a tail may mean loss of stored energy, which can reduce somatic growth (*2, 4*) and reproductive output (*5*). Some lizards even return to the site of the predatory attack to recoup some of the lost energy by ingesting their severed tails if not eaten by the predator (*6*). We report another consequence of tail loss in the desert lizard *Uta stansburiana*: a decline in social status after removal of the tail. In the field, tail breakage is a frequent occurrence in these lizards (*7*).

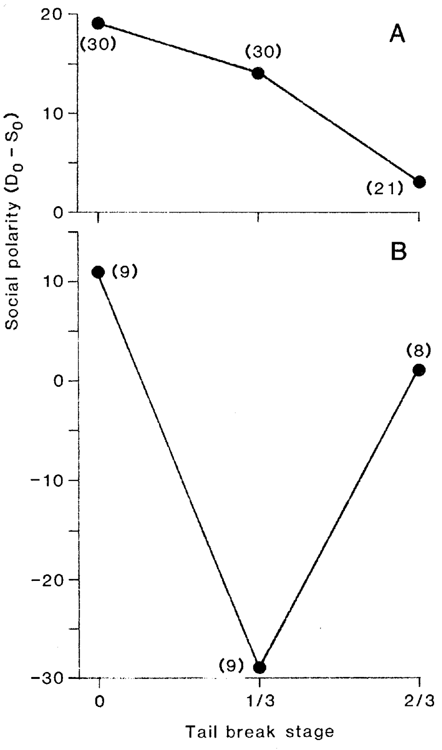

Fig. 1. Social polarity in *Uta stansburiana*: aggressive scores of original dominants ($D_o$) minus original subordinates ($S_o$) of lizard pairs for 0, 1/3, and 2/3 of tails removed from dominant lizards. (A) Removal of 1/3 and 2/3 of the tail from same lizard. (B) Removal of 1/3 of the tail from initial dominant and 2/3 from the new dominant after status reversal. Number in parentheses are the numbers of pairs; points are group means.

Large lizards dominate small conspecies in both laboratory (*8*) and field encounters (*9*). This sometimes results in the large lizards having more territory and, for males, access to more females (*10*). Dominant juvenile *U. stansburiana* can also select better habitats than subordinates, enjoy increased survival (*11*), and ultimately enhance individual fitness.

In many lizards, including *U. stansburiana*, the tail is a substantial portion of total body size, and loss of it may diminish a lizard's ability to dominate conspecies even if (as in *U. stansburiana*) the tail is not used actively in agonism. Berry (*12*) observed three dominant male chuckwallas fall in social rank after they lost their tails in the field. One regained his position after his tail regenerated. We observed a similar alteration in the social status of 30 pairs of juvenile *U. stansburiana*, matched by sex and size (*13*), after their tails were removed in the laboratory.

The lizards were caged alone, and then matched pairs were introduced into a neutral arena (0.75 m by 1.00 m) lined with sand, and were observed for 1 hour. All agonistic behavior patterns were tallied, and the lizard with the higher score was considered dominant (*14*). The score of the subordinate lizard was subtracted from that of the dominant, and this difference was called social polarity. Subsequent encounters were scored in the same way (original dominant less subordinate), so that the sign of the difference indicates relative agonistic polarity of the retested pair with reference to the first encounter; magnitude reflects the degree of agonistic disparity between them.

The first experiment had three stages: initially no part of the tails was removed (0 stage). Immediately after the first encounter, the distal one-third of the tail of each dominant was broken off (*15*) and the lizards were returned to solitary housing for 2 weeks. When the same pairs interacted again (1/3 stage), no statistically significant change in social polarity occurred [Wilcoxon matched-pairs signed-rank test (MPSRT): $T = 203$, $N = 30$ pairs, $P > .10$] (Fig. 1A). In nine of these encounters, however, there was a reversal in polarity, and the lizards in these pairs were removed for another type of experiment, which is described below. The distal halves of the tails (2/3 of original lengths) were broken off from the 21 dominant lizards for which a reversal in social status was not observed. After 2 more weeks of solitary housing these 21 pairs interacted a third time (2/3 stage), and a significant decline in social polarity from both the first and second stages to the third stage was observed (Wilcoxon MPSRT: 0 to 2/3, $T = 26$, $N = 21$ pairs, $P < .001$; 1/3 to 2/3, $T = 21$, $N = 21$ pairs, $P < .001$) (Fig. 1A). Loss of one-third of the tail had no appreciable effect on social relationships of juvenile *U. stansburiana*. Loss of two-thirds of the tail appreciably decreased a juvenile's ability to dominate a conspecies of the same snout-vent size.

After the 1/3-stage encounter the distal two-thirds of the tails were broken off from the new dominants (subordinates at 0 stage) in the nine pairs in which there was a reversal in polarity. After 2 weeks of solitary housing eight pairs (one of the original nine pairs was excluded because a lizard died) interacted again (2/3 stage). In this experiment dominants from the first encounter were missing one-third of their tails and subordinates from the first encounter were missing two-thirds of their tails. There was a significant increase in social polarity from the 1/3 to

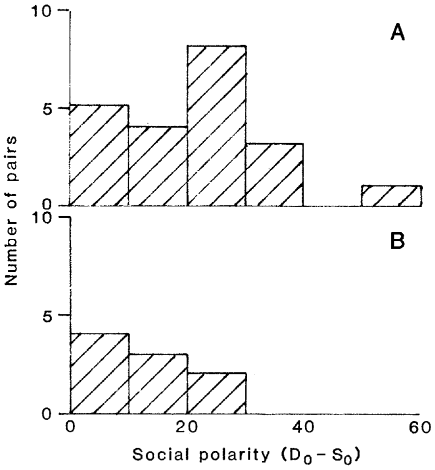

Fig. 2. Frequency distributions of original social polarity among (A) 21 pairs that did not reverse social status after losing 1/3 of the tail and (B) 9 pairs that did reverse social status after losing 1/3 of the tail.

2/3 stage (Wilcoxon MPSRT: $T = 1$, $N = 8$ pairs, $P < .02$; (Fig. 1B). Among this set of lizards dominants lost their social advantage after loss of one-third of their tails but regained their status after the other pair members (new dominants) lost two-thirds of their tails. In fact, social polarity of these pairs at the 2/3 stage was not significantly different from the 0 stage (Wilcoxon MPSRT: $T = 7$, $N = 8$ pairs, $P > .10$) (Fig. 1B).

In nature, nutrition, age, past social experience, site of encounter, endocrine environment, and so on, can affect social status. By controlling many of these factors, we were able to observe the effect of tail loss on social relationships (*16*). A juvenile *U. stansburiana* that loses its tail and becomes subordinate to nearby conspecifics, may be unable to secure a high-quality home range (*11*) and in turn be subject to an increased risk of death (*17*). Tail autotomy is probably a predator defense of last resort.

The nine pairs of lizards for which a reversal in social polarity was observed at the 1/3 stage had initially (0 stage) been closer to social parity than the other 21 pairs (Mann-Whitney $U$ test: $z = 2.29$, $N = 21,9$, $P < .05$) (Fig. 2). This difference alone, however, does not account for their reversal in status. The decrease in social polarity from the 0 to the 1/3 stage for these pairs was also significantly greater than that for the others (Mann-Whitney $U$ test, $z = 4.01$, $N = 21, 9$, $P < .001$).

Why these nine pairs were initially closer to social parity is not related to sex or body size. The original dominants (0 stage) were slightly heavier than the original subordinates (Wilcoxon MPSRT: $T = 88$, $N = 28$ pairs, $P < .01$), but the weight disparity was similar for all 30 pairs. Total tail lengths and tail-body ratios of the nine pairs were not different from the others. In short, we could find no morphological differences to explain why some pairs reversed status at the 1/3 stage, and some did not.

It was only when two-thirds of the tail was lost that the lizards in the first experiment showed a social effect (Fig. 1A). Tail replacement (stump growth plus regeneration) is fastest for tails broken most proximally (*7*). Although this fast basal regeneration is a proximate physiological response (*18*), an ultimate benefit is the rapid return of the tail to a length sufficient to restore the social status of the lizard after significant loss of its tail.

These experiments were not designed to separate the effect of loss of total body length from the complete syndrome of tail loss (that is, major body wound, loss of organ of balance, loss of stored energy, and so on). The deficiencies other than loss of length may also contribute to loss of social status.

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13. First-year lizards were collected from Winkler County, Texas, in early September 1980. Fifteen pairs of each sex were matched in size by snout-vent length (within 2.0 mm) and by total length (within 3.0 mm).
14. Both sexes show aggression and equivalent agonistic behavior patterns (*11*). Lateral displays, supplants, bites and licks, and superimpositions were weighted 1.0. Push-ups, because of their high rate of delivery, apparently low energetic cost, and frequent nondirected delivery (that is, assertion bobs), were weighted 0.5. The single submissive pattern observed, ventral flattening (*17*), was weighted −1.0. The agonistic score for each lizard was computed as the sum of weighted frequencies of agonistic behavior patterns.
15. The tails were autotomized by the lizards when pinched firmly between the experimenter's fingers, simulating the bite of a predator. *U. stansburiana* does not drop its tail without such stimulus.
16. Body growth during tail regeneration is often slowed in lizards (*2, 4*). Under the conditions of captivity and short timespan of these experiments, however, growth in snout-vent length within pairs was equivalent; differences in snout-vent length within pairs did not significantly change over the experimental interval (Wilcoxon MPSRT: 0 to 2/3 stage, $T = 56$, $N = 16$ nonzero pairs, $P > .05$; 1/3 to 2/3 stage, $T = 6$, $N = 7$ nonzero pairs, $P > .05$).
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19. We thank S. Bontrager, C. Bloom, and E. Shoemaker for logistical aid. Supported in part by NSF grant DEB-78-07156 to S.F.F.

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# Cotransmitters in the Motor Nerves of the Guinea Pig Vas Deferens: Electrophysiological Evidence

Abstract. *The contractile response of the guinea pig vas deferens to motor nerve stimulation is biphasic. The first phase is antagonized by the specific adenosine triphosphate–receptor antagonist arylazido aminoproprionyl adenosine triphosphate (ANAPP$_3$), and the second by the α-receptor antagonist prazosin. The underlying electrical event, the excitatory junction potential, is also blocked by ANAPP$_3$, but not by prazosin.*

The contractile response of the guinea pig vas deferens to a single pulse, or to short trains of stimuli, is biphasic; the second phase (phase II) is blocked by $\alpha_1$-receptor antagonists and is therefore assumed to be adrenergic, while the initial twitch response (phase I) is resistant to adrenergic antagonists (*1, 2*). Our laboratory recently showed that phase I is specifically antagonized by arylazido aminoproprionyl adenosine triphosphate (ANAPP$_3$), a photoaffinity label and structural analog of adenosine triphosphate (ATP) which has been shown to be a specific antagonist of the $P_2$ class of purine receptors in this tissue (*3, 4*). On the basis of these findings, it has been proposed that the biphasic nature of the contractile response is a result of the action of cotransmitters: ATP or a related purine mediating phase I through $P_2$-receptors and norepinephrine mediating phase II through $\alpha_1$-receptors.

Blakeley *et al.* (*5*) recently demonstrated in the guinea pig vas deferens that the action potential and phase I of the contractile response to motor nerve stimulation are blocked by the calcium channel blocker nifedipine, while phase II is largely unaffected. This implies that phase I is dependent on the summation of excitatory junction potentials (EJP's) to threshold and the firing of action potentials producing the initial switch. Since ANAPP$_3$ is able to antagonize phase I specifically, and since phase I is dependent on the summation of EJP's, we investigated the effect of ANAPP$_3$ on EJP's in this muscle.

Intracellular microelectrodes filled