

Tales of lizard tails: effects of tail autotomy on subsequent survival and growth of free-ranging hatchling *Uta stansburiana*

P.H. Niewiarowski, J.D. Congdon, A.E. Dunham, L.J. Vitt, and D.W. Tinkle

Abstract: Potential costs and benefits of tail autotomy in lizards have been inferred almost exclusively from experimental study in semi-natural enclosures and from indirect comparative evidence from natural populations. We present complementary evidence of the costs of tail autotomy to the lizard *Uta stansburiana* from detailed demographic study of a natural population. On initial capture, we broke the tails of a large sample of free-ranging hatchlings (560) and left the tails of another large sample (455) intact, and then followed subsequent hatchling growth and survival over a 3-year period. Surprisingly, in 1 out of the 3 years of study, survival of female hatchlings with broken tails exceeded that of female hatchlings with intact tails. Furthermore, no effects of tail loss on survivorship were detected for male hatchlings. However, in 2 years when recaptures were very frequent (1961, 1962), growth rates of hatchlings with broken tails were significantly slower than those of their counterparts with intact tails. We discuss our results in the broader context of estimating the relative costs and benefits of tail autotomy in natural populations, and suggest that long-term demographic studies will provide the best opportunity to assess realized fitness costs and benefits with minimum bias. We also describe how experimentally induced tail autotomy can be used as a technique to complement experimental manipulation of reproductive investment in the study of life-history trade-offs.

Résumé : Les coûts et bénéfices potentiels de l'autotomie de la queue chez les lézards ont presque toujours été évalués au cours d'études expérimentales dans des enceintes semi-naturelles ou par des preuves comparatives indirectes chez des populations naturelles. Nous présentons ici des données complémentaires sur les coûts de l'autotomie chez le lézard *Uta stansburiana*, données obtenues par l'étude démographique détaillée d'une population naturelle. Au moment de la capture initiale, nous avons brisé la queue des lézards néonates en liberté d'un grand échantillon (560) et laissé intacte la queue des lézards d'une autre échantillon (455) et nous avons par la suite observé la croissance et la survie de ces lézards au cours d'une période de 3 ans. Étonnamment, au cours de l'une de ces 3 années, les petits lézards femelles à queue coupée ont eu une survie meilleure que les petites femelles à queue intacte. Chez les jeunes mâles, la perte de la queue n'a pas eu d'effet sur la survie. Cependant, au cours des 2 années où les recaptures ont été très fréquentes (1961, 1962), les taux de croissance des petits lézards à queue coupée se sont avérés significativement plus lents que ceux des lézards à queue intacte. Nous examinons nos résultats en vue de l'estimation des coûts et bénéfices relatifs de l'autotomie de la queue chez les populations naturelles et nous croyons que ce sont des études démographiques à long terme qui permettront le mieux d'évaluer les coûts et bénéfices réels du fitness avec un minimum d'erreur. Nous décrivons aussi de quelle façon l'autotomie expérimentale de la queue peut servir de technique complémentaire à la manipulation expérimentale de l'investissement reproducteur dans l'étude des compromis démographiques.

[Traduit par la Rédaction]

Introduction

Many organisms exhibit morphological or behavioral traits that are associated with predator avoidance. A conspicuous

example is tail autotomy, a trait widespread in lizards and typically interpreted as an adaptation for escape from predators (Arnold 1988). Observations of natural encounters between lizards and their predators are rare, so evidence to support the hypothesis that autotomy enhances an individual's probability of surviving a predator's attack is either indirect (e.g., recovery of tails from stomach contents of predators) or obtained from observation of staged experimental encounters between lizards and predators in semi-natural enclosures (e.g., Vitt et al. 1977; Congdon et al. 1974; Dial and Fitzpatrick 1984; Daniels et al. 1986). Although direct evidence from natural populations of the benefits of tail autotomy is lacking, the potential benefit is obvious: a reduced probability of death during a given encounter with a predator.

The potential costs of autotomy are ultimately realized as decrements to subsequent survival, reproduction, or both, but very few studies have elaborated the actual mechanisms

Received May 30, 1996. Accepted October 15, 1996.

P.H. Niewiarowski. University of Akron, Department of Biology, Akron, OH 44325-3908, U.S.A.

J.D. Congdon. University of Georgia, Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, U.S.A.

A.E. Dunham. Department of Biology, Leidy Laboratories, University of Pennsylvania, Philadelphia, PA 19104-6018, U.S.A.

L.J. Vitt. Oklahoma Museum of Natural History, University of Oklahoma, 1335 Asp Avenue, Norman, OK 73019-0606, U.S.A.

D.W. Tinkle.¹ Museum of Zoology, University of Michigan, Ann Arbor, MI 48109, U.S.A.

¹ Deceased.

linking autotomy to decreased survival and reproduction in natural populations (for a review see Arnold 1988 and for a summary see Wilson 1992). Costs, like benefits, have therefore largely been inferred from staged encounters with predators or from experimental manipulations that demonstrate effects on traits presumably related to mortality or reproduction (e.g., social status; Fox and Rostker 1982; Fox et al. 1990; Kaiser and Mushinsky 1994; Brown et al. 1995). Although the potential costs of autotomy seem obvious, demonstrating their relative importance in natural populations has been problematical because the underlying mechanisms are often indirect. For example, it is possible that tail loss in one encounter with a predator may reduce an individual's probability of escape in subsequent encounters (e.g., Congdon et al. 1974). But a reduction in the probability of escape may be ameliorated by behavioral changes subsequent to tail loss that compensate by reducing an individual's probability of encountering predators (e.g., Martin and Salvador 1992, 1993). An interaction between a reduced escape probability due to tail loss and changes in behavior affecting the probability of encountering a predator is just one way in which simple estimates of the "costs" of autotomy (e.g., reduced escape probability) may not reveal the true fitness costs in the population(s) of interest. Overall, relevant estimates of realized costs of autotomy (in terms of fitness), and elucidation of the mechanisms by which they are expressed, may be difficult to obtain from experiments testing a single component (e.g., experimentally staged encounters between tailless lizards and predators) of a set of potentially interacting components. Although the realized costs of autotomy in natural populations may be difficult to identify, evolutionary and ecological analyses seeking to explain variation in tail autotomy will ultimately depend on such data (Arnold 1988; Wilson 1992).

Long-term demographic studies of natural populations, where individual lizards are marked and followed from birth to death, provide one of the best opportunities to estimate the costs of autotomy in free-ranging populations, for two reasons. First, it is at least possible to evaluate the realized costs of autotomy completely (e.g., the overall effect on mortality, given a reduced probability of escape *and* a reduced probability of predator encounter in the example given above). Second, correlates of mortality, like age and social status, can be accounted for in analyses of costs and benefits. One significant potential hindrance to studying autotomy in conjunction with demographic study is that experimental manipulation of individuals (e.g., breaking the tail) is usually not concordant with the goals of demographic study. Nevertheless, some populations that are observed to have high tail-loss rates (e.g., Tinkle 1967; Schoener and Schoener 1980) can supply adequate sample sizes for estimating the consequences of autotomy for growth and survival.

We analyzed the relationship between tail loss and subsequent growth and survival rates in a population of *Uta stansburiana* that was the subject of intensive demographic study (Tinkle 1967). Our study complements a recent study by Wilson (1992), who compared survival rates of *U. stansburiana* as a function of tail completeness in seven geographically separated populations of the same species. In contrast to Wilson (1992), who analyzed the effects of natural tail loss of juveniles and adults, we analyzed the

effects of tail loss on 560 hatchlings whose tails we broke on initial capture. Frequent recapture of individual hatchlings allowed us to compare, in addition to survival probabilities, the effect of tail loss on subsequent growth rates. Our goal was to evaluate the strength and expression of two potential costs of tail autotomy (reduced growth and survival) in a natural population of lizards. Where sample sizes permitted, we tested whether there were seasonal, annual, or sex-based differences in either growth rate or survival as a function of autotomy.

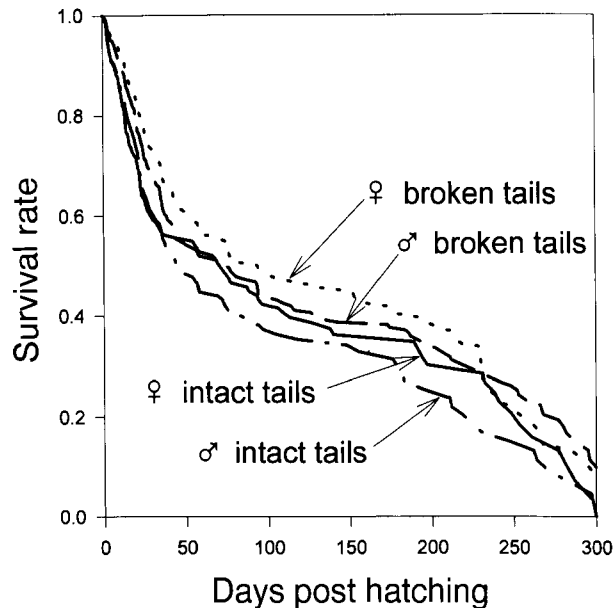
Materials and methods

Data presented here were collected as part of a long-term demographic project conducted between 1957 and 1966 near Kermit, Winkler County, Texas (Tinkle 1967). *Uta stansburiana* in this population are active year-round, but with substantially reduced frequency of activity between October and March (Tinkle 1967). Females reach maturity at 125 ± 34.5 days of age and their probability of survival to 308 days of age is 0.086 (Tinkle 1967). Tail-regeneration rates in juveniles depend on a variety of factors, but regeneration can be completed in as little as 32 days in the case of newly emerged hatchlings losing up to two-thirds of their tails (for details see Tinkle 1967). During the field seasons 1961–1963, we compared growth and survivorship of three cohorts of hatchlings whose tails we broke during first capture with data for hatchlings whose tails we left intact. Tails were broken haphazardly and there was no indication of any bias in tail breaking. Censusing in this project was frequent, with searches for unmarked animals being made, on average, every 7.38 ± 2.33 days year-round. Recapture of all juveniles was attempted at roughly 2-week intervals, but we did not compare growth rates and probabilities of survival over these relatively short, distinct intervals (e.g., Wilson 1992) because it did not appear that complete census was accomplished. Consequently, we analyzed growth rates in one of two ways, dictated by the distribution and extent of capture data. In 1961, recaptures of different individuals were sufficient to allow linear growth rates (change in snout–vent length (SVL)/change in time) to be analyzed without having to use a repeated measures analysis (e.g., Niewiarowski and Roosenburg 1993). Sample sizes were not large enough for further comparison of growth rates of males and females with and without broken tails, but Tinkle (1967) showed that male and female hatchlings with intact tails grow at similar rates.

In contrast to the recapture data from 1961, few recaptures on a given day during the 1962 field season provided a sample too small for a linear analysis of growth. Overall, however, a large number of individuals were recaptured 5 or more times over the course of the year, enabling us to use a nonlinear growth model to estimate growth parameters (characteristic rate and asymptotic body size). We fit a logistic-by-length model because it provided the best fit to the data (for a comparison of growth models see Dunham 1978), and then judged the differences between growth parameters to be significant if the 95% confidence intervals did not overlap. Recaptures of males and females were sufficient to allow the effects of tail break to be analyzed separately for males and females. Finally, growth data from 1963 were too limited for growth rates to be compared using either linear or nonlinear techniques, so they are not included here.

As a result of using two different analytical techniques to characterize growth of hatchlings in 1961 and 1962, direct comparison of growth rates between years was not possible. However, the main difference between linear analysis and nonlinear models of growth is in the type of data each method is best suited to analyze (for a review see Andrews 1982). In the present study, our main aim was to compare the growth of hatchlings with intact versus broken tails within years, therefore we chose analytical methods most appropriate for the data.

Fig. 1. Log-linear estimates of survival of hatchling *Uta stansburiana* with intact versus broken tails, 1961–1964. Survival rates over the interval 1961–1963 were significantly higher for hatchlings with broken tails. The shapes of survival functions were similar between years, and separate analyses by year, sex, and tail condition are reported in Table 1.



Survival analysis in natural populations is frequently complicated by an inability to assign an exact date of death to individuals. When complete censuses are made, survival differences can be estimated by comparing the relative numbers of individuals remaining at the end of the interval (e.g., Wilson 1992). Technically, such data are censored (Cox and Oakes 1984) because the death of each individual is only known to occur within the census interval rather than on a specific date. Recapture data from the frequent but incomplete censuses used in this study present similar but more extreme difficulties, because without complete census it is never certain that a particular individual died during a given interval. To compare survival probabilities between hatchlings with broken and intact tails, we first estimated the date of death for each individual. We defined the interval during which an individual died as starting with the date of last capture and ending with the date of the next census. Mortality risk as a function of time was then calculated for each group (i.e., with broken or intact tails) and sex within group, using a nonlinear log-rank survival function with interval censoring (Proc LIFETEST; SAS Institute Inc. 1990). Mortality risk data were compared for the entire interval (1961–1963), separately for each year in which there were sufficient data (1961, 1962) and for animals that were marked at any point in 1961 and last captured in 1962. Even though *U. stansburiana* are still active during the winter, activity levels are much reduced compared with those in other seasons (Tinkle 1967), so the last comparison provides a crude evaluation of differences in over-winter survival between hatchlings with and without tails.

Assigning a date of death to an individual in the way we did could result in biased estimates of mortality risk because we assumed that all living individuals were censused on each date, an assumption that is probably false. Nevertheless, we see no reason why potential bias in estimating mortality risk would necessarily differ between hatchlings with and without tails. However, it is possible that such a bias could arise if the daily probability of capture for hatchlings with intact tails was different from the probability of capture for those with broken tails. To evaluate if the probability

of capture (total number of captures/total interval length) was different for hatchlings with intact versus broken tails, we used a Kolmogorov–Smirnov two-sample test to compare distributions of the probability of capture as a function of number of captures for each group. An inability to reject the hypothesis that the distribution of capture probabilities differed suggests that our method of comparing the estimates of mortality risk between the two groups of hatchlings is reasonable.

Estimates of survival in open populations always assume that individuals not recaptured have died and not merely emigrated from the study site. Substantial effort was made in our mark–recapture study to determine if individual lizards were emigrating out of the study population (for details see Tinkle 1967). While emigration rates in this population of *U. stansburiana* appeared to be very low (approximately 4%), we cannot unambiguously discount the possibility that emigration rates differed between hatchlings with intact and broken tails. However, we are not aware of any published data documenting differences in migratory behavior associated with tail autotomy.

Results

During the field seasons of 1961–1963, a total of 1015 hatchlings were captured and marked, of which 455 had intact tails (153, 258, 44 in 1961, 1962, and 1963, respectively) and 560 (270, 262, 28 in 1961, 1962, and 1963, respectively) had broken tails as a result of initial capture. We did not record the length of the autotomized portion of tails. Subsequent to their initial capture, hatchlings were recaptured 1–9 times (3.5 ± 0.14 and 2.85 ± 0.12 (average ± 2 SE) recaptures per individual with broken and unbroken tails, respectively) over all three field seasons. Daily probability of recapture was not related to number of recaptures for hatchlings either with or without broken tails (linear regression, $R^2 = 0.0003$, $P = 0.81$, and $R^2 = 0.002$, $P = 0.27$ for intact and broken tails, respectively). Hatchlings with broken tails were recaptured more often than those with intact tails (Kolmogorov–Smirnov two-sample test, $KSa = 2.33$, $P = 0.0001$), but daily recapture probabilities were not significantly different ($KSa = 1.31$, $P = 0.07$).

For both male and female hatchlings with broken and intact tails, survival over the entire study period declined rapidly during the first 50 days of life, somewhat more slowly between 50 and 200 days, and then rapidly between 200 and 300 days (Fig. 1). Somewhat unexpectedly, survival was greater for hatchlings that suffered a tail break on initial capture relative to those that did not (Fig. 1). For both males and females, the survival probability was significantly higher for lizards with broken tails. Average age at death was 86.07 ± 5.83 and 67.93 ± 7.63 days for hatchlings with broken and intact tails, respectively.

Separate analyses by year (Table 1) revealed that in 1961 there were no differences in survival between females or males with broken versus intact tails. However, in 1962, female hatchlings with broken tails experienced significantly higher survival than their counterparts with intact tails (Table 1). Interestingly, there were no differences in survival between males with intact versus broken tails in 1962 (Table 1). Finally, there were no differences in survival (for males or females) between hatchlings with intact versus broken tails while overwintering between 1961 and 1962 (Table 1).

Table 1. Log-rank test of equal mortality risk between hatchlings with intact versus broken tails as a function of survival interval and sex.

Survival interval	Sex	χ^2	<i>P</i>
1961–1963	Both	9.9888	0.0016
	Female	4.3310	0.0374
	Male	5.1845	0.0228
1961	Both	1.7797	0.1822
	Female	0.9524	0.3291
	Male	1.1354	0.2866
1962	Both	7.1690	0.0074
	Female	4.3137	0.0378
	Male	2.5703	0.1089
1961–1962	Both	0.0114	0.9148

Note: In all cases where there were significant differences between hatchlings with broken and intact tails, survivorship of the former was higher.

Table 2. Comparison of fitted parameters from nonlinear logistic-by-weight growth analysis of data from 1962.

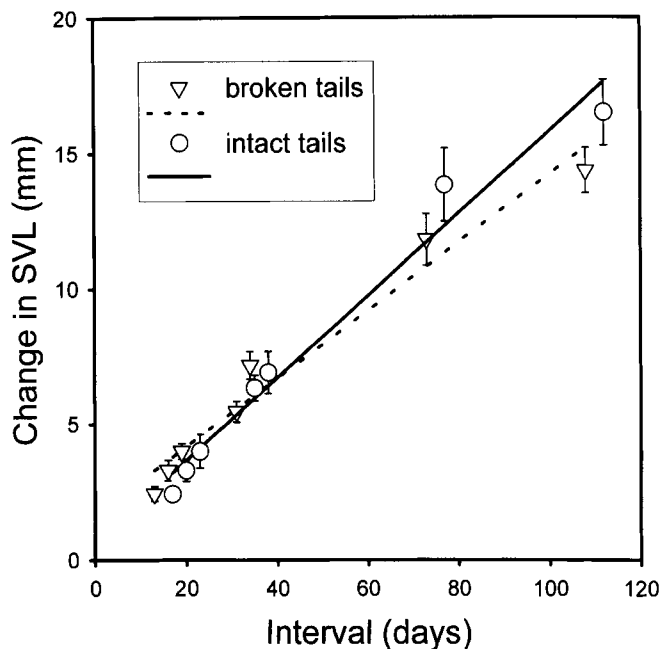
A1	Sex	<i>r</i>	<i>n</i>	Tail
49.80 ± 1.56	Male	0.018 ± 0.003	26	Broken
51.51 ± 1.39	Male	0.022 ± 0.003	6	Intact
45.36 ± 0.94	Female	0.015 ± 0.001	27	Broken
43.90 ± 1.21	Female	0.027 ± 0.005	5	Intact

Note: A1 is predicted asymptotic body size, *r* is growth rate, and *n* is sample size. Values are given as means and 95% CI. Values with overlapping CIs are judged to be not significantly different (see Methods).

In 1961, the linear growth rate of hatchlings with intact tails was greater than that for hatchlings with broken tails (Fig. 2; heterogeneous slopes, ANCOVA, $F_{[1,183]} = 5.86$, $P = 0.02$). Average initial hatchling SVLs did not differ between the two groups (ANOVA, $F_{[1,183]} = 1.66$, $P = 0.20$), so differences in growth rate were not a consequence of differences in initial size. In 1962, the growth rate (*r*) was significantly higher for females with intact tails than for females with broken tails (Table 2, Fig. 3). In contrast, autotomy did not significantly affect the growth rates of male hatchlings (Table 2, Fig. 3). Similarly, autotomy did not significantly affect asymptotic body sizes of either male or female hatchlings (Table 2, Fig. 3). Unfortunately, substantially different distributions of recapture data in 1961 and 1962 precluded using a single method across years to compare growth rates between hatchlings with and without broken tails.

Discussion

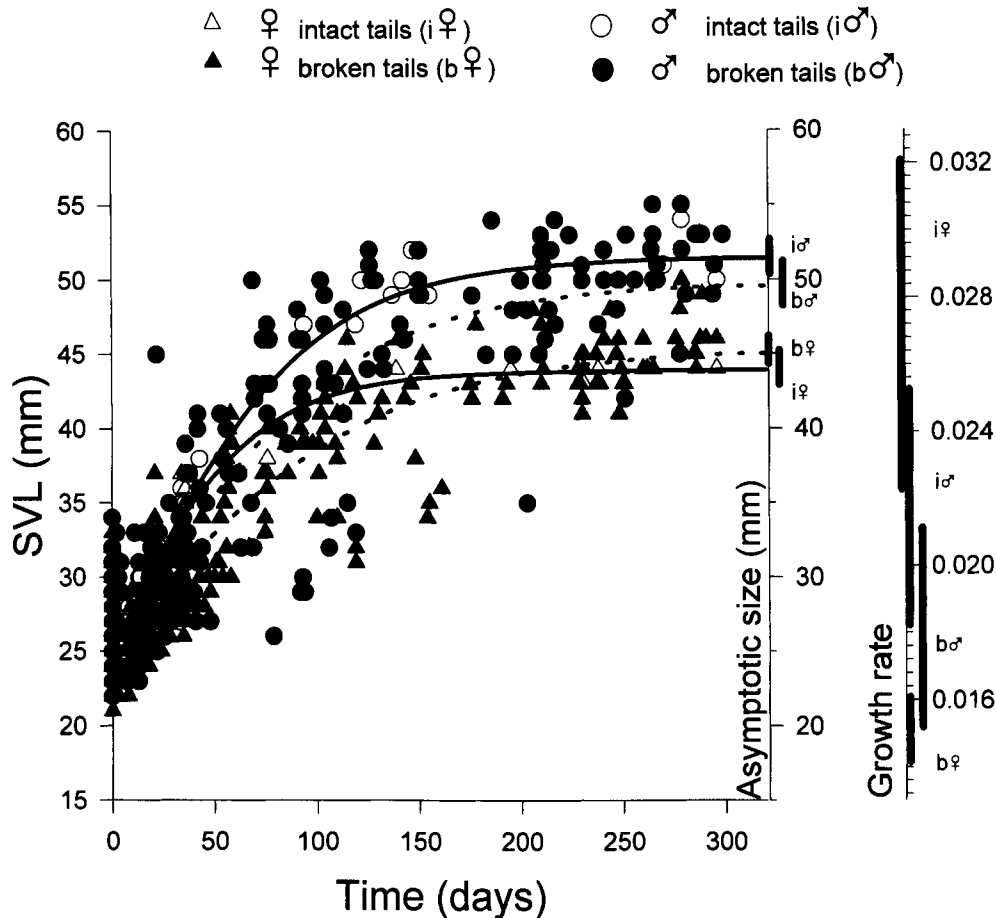
The results of our examination of the effects of tail loss on growth suggest that in both 1961 and 1962, the main effect of tail loss was to reduce growth rates. In 1961, the growth rates of hatchlings with intact tails were significantly greater than those of hatchlings with broken tails. In 1962, there were enough data to further compare the effects of autotomy on males and females separately. Nonlinear analysis revealed an interaction between sex and tail loss, with tail loss signifi-

Fig. 2. Linear growth rates (activity season 1961) of hatchlings with intact ($n = 63$) versus broken ($n = 121$) tails. Initial SVLs did not differ between groups, but slopes were heterogeneous; hatchlings with intact tails grew significantly faster than hatchlings with broken tails. Symbols are offset for clarity.

cantly reducing the growth rates of females but not of males. Tail loss did not affect asymptotic body size in either sex. *Uta stansburiana* can suffer high rates of tail loss, but juveniles typically regenerate their tails rapidly (Tinkle 1967; Wilson 1992), leading to the expectation that under resource limitation, growth rates of hatchlings with damaged tails should be lower than those of hatchlings with intact tails. It is noteworthy that a growth rate effect was detected in 2 years in which resource availability may have differed widely. Although we do not have direct estimates of resources available to the hatchlings in our study, we do know that hatchling densities in 1962 were 52–78% of those in 1961 (Tinkle 1967). If total resource availability was similar between years, then per capita resource availability may have been higher in 1962. In other studies, there is evidence that resource availability may mediate the growth rate effects of tail loss. For example, ad libitum food in the laboratory appeared to ameliorate differences in growth rates between free-ranging tailed and tailless hatchling *Sceloporus jarrovi*, whereas growth rates of free-ranging tailed and tailless hatchling *Sceloporus scalaris* were significantly different when food was abundant but not when food was scarce (Ballinger and Tinkle 1979). Clearly, predicting the consequences of tail loss for growth rates will require knowledge about the resource environment, at least for some species.

Comparison of data on mortality risk produced unexpected results: survival was actually greater for tailless hatchlings than for hatchlings with intact tails. We are not the first to report increased survival of lizards with autotomized tails. Althoff and Thompson (1994) found that in Nevada, survivorship was higher in adult *U. stansburiana* with autotomized tails than in those with intact tails. In contrast, they found that both adults and juveniles with broken tails had

Fig. 3. SVL as a function of time since initial capture (activity season 1962) of hatchlings with intact versus broken tails. Regression lines (broken lines for broken tails, solid lines for intact tails) are growth curves predicted from a logistic-by-length nonlinear model of growth of hatchlings starting at 25 mm SVL. Heavy lines on axes indicate 95% confidence intervals about the respective means. Asymptotic sizes did not differ between groups, but the growth rate of female hatchlings with intact tails was significantly faster than that of females with broken tails. Growth rate differences between males with intact and broken tails were not significant.



lower survival rates than lizards with intact tails in a population in Washington. The cause of the higher survival rates of hatchlings with broken tails in our study is unclear, but we can suggest a mechanism. It is possible that the behavior of hatchling *U. stansburiana* changes as a result of tail loss, so that the risk of death due to predation or other causes is decreased. Whether a lizard's tail is intact or not can be associated with social status in *U. stansburiana* (Fox and Rostker 1982; Fox et al. 1990) and *Anolis sagrei* (Kaiser and Mushinsky 1994). Furthermore, in at least one population of *U. stansburiana*, dominance is positively associated with home-range quality (Fox et al. 1981) and therefore with pre-reproductive survivorship (Fox 1978). Our results do not seem consistent with these mechanisms because hatchlings with injured tails had a lower mortality risk. However, if elevated social status requires high rates of "risky" behaviors (sensu Marler and Moore 1988, 1991), tail loss and the concomitant decrease in social status and frequency of associated behaviors could actually enhance survival (Formanowicz et al. 1990). Changes in frequency of behaviors other than those directly related to social status (e.g., displays, agonistic encounters, territorial defense) may also compensate for the expected increase in mortality risk associated with tail loss. For example, tailless *Lacerta*

monticola changed foraging tactics and utilization of foraging microhabitats relative to the foraging behavior of *L. monticola* with intact tails, so the predation risk may have been reduced (Martin and Salvador 1993).

Alternatively, the effects of tail loss on survivorship may vary from year to year depending on many factors, including the predation environment (e.g., type and abundance of predators). It is clear that mortality levels in squamate populations can vary considerably, both spatially and temporally (e.g., Tinkle 1967; Dunham 1978, 1982; Parker and Brown 1980; Brown and Parker 1984; McLaughlin and Roughgarden 1989; Andrews and Nichols 1990), and it would not be surprising if mechanisms linking tail loss to mortality risk also varied spatially and temporally. In the case of the *U. stansburiana* population we studied, it would be especially interesting to know if the reduced hatchling density in 1962 (the year when hatchlings with broken tails had higher survivorship than hatchlings with intact tails) compared with 1961 resulted from increased mortality due to predation in 1962. There was a trend towards reduced adult survivorship in adults in 1962 compared with 1961 (Tinkle 1967).

Complications involved in interpreting the overall consequences of tail loss in our study illustrate the importance of measuring both the costs and benefits of tail loss in units of

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