

Effects of Caudal Autotomy on Postnatal Growth Rates of Hatchling *Psammodromus algirus*

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ABSTRACT.—Tail autotomy has clear advantages regarding predator escape, but it also has several associated costs (i.e., impaired locomotion, loss of social status, and reduced growth and reproductive output). We examined the costs of severe autotomy on growth rates of hatchlings of the lacertid lizard *Psammodromus algirus* during the first weeks of postnatal development. Hatchlings from two populations in central Spain were autotomized on the fifth day after hatching and kept in common garden conditions for 35 days when they were measured again. Hatchlings from both populations, independently of the autotomy treatment, did not differ in the mass gained during the experiment. However, there were differences in body growth between tailless and tailed hatchlings; tailless hatchlings grew at a slower rate than tailed ones, after controlling for the effects of body condition at the onset of the experiment and the resources assimilated. Moreover, independently of their population of origin, hatchlings that invested more in body growth also invested more in regenerating their tails, and no trade-offs were apparent. Because hatchlings were housed in common garden conditions, this result could be attributable to differences in individual capacity to obtain and assimilate resources.

In reptiles, growth is indeterminate, but it is subject to proximate environmental effects (Dunham, 1978). This is especially true for species inhabiting temperate climatic zones, where seasonal variations in food availability determine the periods when individuals are able to grow (Boyce, 1979; Adolph and Porter, 1993). For hatchlings, activity prior to hibernation may be crucial because the body size attained prior to hibernation can determine winter survival (Civantos et al., 1999; Iraeta et al., 2008). Thus, hatchlings should grow as much as possible before the onset of the winter.

On the other hand, if hatchlings are foraging actively to obtain food to grow, they are simultaneously exposing themselves to increased predation risk. An intact tail is especially important for hatchlings because for many lizard species the tail serves as storage of fat reserves (Bernardo and Agosta, 2005) that are decisive for winter survival (Avery, 1970; Bauwens, 1981), and also because caudal autotomy, which is considered a predator defense mechanism and is widespread in lizards (Bellairs and Bryant, 1985), is essential in hatchlings, because other antipredatory mechanisms, such as locomotor performance, are not yet at their maximal capacity. Compared to adults, hatchlings allow a closer approach by predators, take longer to find a refuge, and are more likely to remain visible (Whiting et al., 2003). The antipredatory mechanism of attracting attention to an autotomizable part of the body either by having it more colorful (Castilla et al., 1999) or by moving it to focus predator attention (Cooper, 1998) has proven to be advantageous because it increases the chances of escape in case of attack (Congdon et al., 1974).

Thus, although tail autotomy has clear benefits, it also has serious immediate and long-term costs, both for hatchlings and adults: it may impair locomotor performance (Martin and Avery, 1998; Chapple and Swain, 2002a), reduce reproductive investment (Dial and Fitzpatrick, 1981; Bernardo and Agosta, 2005), diminish social status or mating success (Martin and Salvador, 1993; Salvador et al., 1995), and reduce survival (Wilson, 1992; Fox and McCoy, 2000; but see Niewiarowski et al., 1997). In addition, tail regeneration may be energetically expensive (Bellairs and Bryant, 1985); therefore, it may require

the diversion of energetic resources from growth (or reproduction) to tail regeneration (Vitt et al., 1977; Smith, 1996).

Here, we experimentally examine the effects of a severe autotomy a few days after hatching on the postnatal growth rates of hatchling *Psammodromus algirus* lizards from two populations in central Spain separated by an altitudinal gradient of approximately 600 m. Although consequences of tail autotomy in *P. algirus* have been addressed in several papers (Salvador et al., 1996; Martin and Avery, 1998; Salvador and Veiga, 2005), all of them have dealt with adults and not with hatchlings. We hypothesize that tail autotomy should decrease the growth rate in body size; tail and body growth should be correlated negatively given the limited availability of time and resources prior to the first hibernation period; and tail regeneration might differ between populations subject to different environmental selection pressures.

MATERIAL AND METHODS

Study Species and Study Areas.—*Psammodromus algirus* is a medium-sized (adult snout–vent length 60–90 mm; mass 6–16 g) lacertid lizard that inhabits shrubland and forest habitats of the western Mediterranean basin. Our low-elevation study area was located at El Pardo (Madrid, central Spain: 40°31'N, 03°47'W; 650 m elevation), a cleared holm oak (*Quercus ilex*) broad-leaved, perennial forest. The high-elevation site was a deciduous Pyrenean oak (*Quercus pyrenaica*) forest located at Navacerrada (Cerro de la Golondrina, Sierra de Guadarrama, central Spain: 40°44' N, 4°00' W; 1,300 m elevation), at 32 km by air from the lowland site. According to field observations done in the early spring of 2006 at both study sites, the frequency of natural autotomy is higher at the low-elevation site (17 of 38 autotomized juveniles, 44.7%) than at the high-elevation site (17 of 66 autotomized juveniles, 25.8%; $\chi^2 = 3.95$, $df = 1$, $P = 0.047$).

Husbandry of Hatchlings and Autotomy Experiment.—For this study, we used 18 hatchlings of *P. algirus* that were raised in our laboratory (Universidad Complutense de Madrid) during the 2009 breeding season. Hatchlings were obtained from wild-caught lizards from both populations that were bred in the laboratory. Eggs were incubated at a constant temperature of 28°C reared as described in Iraeta et al. (2006).

After hatching, hatchlings were measured (snout–vent length [SVL] and tail length), and mass was determined with a

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precision balance (± 0.01 g). They were then placed in individual terraria with standard accommodation (light, water). Lizards were fed crickets (*Acheta domesticus*) ad libitum that had been dusted with a commercial vitamin and calcium supplement. On the fifth day after hatching, a subset of hatchlings ($N = 9$) were forced to autotomize their tails. To achieve this, juveniles were held by the proximal portion of the tail with a pair of tweezers until they released the tail. These hatchlings were measured (SVL and tail length) and weighed both prior to and immediately after autotomy. The degree of autotomy was on average $79.5 \pm 0.01\%$ of total tail length, with no differences between sites ($F_{1,7} = 0.02$, $P = 0.892$). Hatchlings that were not forced to release their tails were also measured (SVL and tail length) and weighed on the fifth day after birth. All hatchlings were measured again at an age of 40 ± 1 days (mean \pm SD; range = 38–43), that is, 35.3 ± 1.2 days after tail loss (range = 34–40) in the case of autotomized lizards. Thus, autotomized hatchlings were measured a total of four times (at hatching, prior to and after autotomy at an age of 5 days, and at an age of 40 ± 1 days), whereas controls were measured only three times (at hatching, at an age of 5 days, and at an age of 40 ± 1 days).

Growth Rate Estimates and Data Analysis.—We calculated size-specific growth rate (i.e., growth in length) and tail-specific growth rate (i.e., tail length increase) using the formula: $\ln(\text{length}_2 / \text{length}_1) / (\text{date}_2 - \text{date}_1)$, where date_2 and date_1 are the dates at the end and the beginning of the experiment, respectively. A similar rate was calculated for the increase in body mass (i.e., mass-specific growth rate) during the experiment. These rates reflect the instantaneous proportionate increase in body size, tail length, or body mass on a per-day basis (Sinervo, 1990). The body condition of hatchlings prior to autotomy was estimated using the residuals of the regression of log-body mass on log-SVL.

Maternal effects are common in reptiles, and they may confound the comparison between hatchling lizards exposed to different treatments. Accordingly, we controlled for possible maternal effects using clutch as a random factor in Mixed Model ANCOVAs of the effects of autotomy on growth rates prior to hibernation. All analyses were performed using the General Linear Models (GLM) and Variance Components and Mixed-Model ANOVA/ANCOVA modules of the statistical package Statistica 6.1. The Mixed Model, used for testing the significance of the effects of clutch (random factor), autotomy, and site of origin (fixed factors) on hatchling growth rates, requires leaving the random effects independent of the fixed effects (Searle et al., 1992) by constructing appropriate error terms. Statistica 6.1 uses Satterthwaite's method of denominator synthesis to find the linear combinations of sources of random variation that serve as error terms for each effect. Thus, the degrees of freedom for the denominator mean-square can be fractional rather than integer values, meaning fractions of sources of variation were used in synthesizing error terms for significance testing.

RESULTS

Hatchlings did not differ in SVL or body mass at hatching between experimental autotomy treatments, but there were clear differences between sites in both SVL (two-way ANOVA, treatment: $F_{1,14} = 0.98$, $P = 0.340$; site: $F_{1,14} = 13.13$, $P = 0.002$; interaction: $F_{1,14} = 1.74$, $P = 0.208$) and body mass at hatching (two-way ANOVA, autotomy treatment: $F_{1,14} = 2.04$, $P = 0.175$; site: $F_{1,14} = 9.36$, $P = 0.008$; interaction: $F_{1,14} = 1.70$, $P = 0.213$). Hatchlings from low-elevation (SVL, mean \pm SD = 29.89 ± 0.65

mm; body mass: 0.560 ± 0.04 g) were larger than high-elevation ones (SVL: 28.89 ± 0.33 mm; body mass: 0.513 ± 0.01 g). Hatchlings did not differ between sites or treatments in tail length at hatching (two-way ANOVA, autotomy treatment: $F_{1,14} = 0.02$, $P = 0.893$; site: $F_{1,14} = 1.52$, $P = 0.238$; interaction: $F_{1,14} = 0.00$, $P = 1.00$). Moreover, there were no differences between sites or autotomy treatments in hatchlings' body condition on the fifth day after hatching (two-way ANOVA, autotomy treatment: $F_{1,13} = 0.50$, $P = 0.493$; site: $F_{1,13} = 0.27$, $P = 0.611$; interaction: $F_{1,13} = 0.03$, $P = 0.868$).

To determine whether there were differences between populations or autotomy treatments in the resources ingested that produced an increase in body mass during the experiment, we analyzed mass-specific growth rate, which did not differ between autotomy treatments or populations (Mixed-Model ANOVA; autotomy treatment: $F_{1,2.22} = 0.001$, $P = 0.973$; site: $F_{1,2.87} = 6.57$, $P = 0.087$; clutch: $F_{3,0.95} = 7.57$, $P = 0.270$; autotomy \times site interaction: $F_{1,1.07} = 6.11$, $P = 0.232$; autotomy \times clutch interaction: $F_{2,9} = 0.52$, $P = 0.613$).

We analyzed the effects of tail loss on size-specific growth rate while controlling for possible individual differences in assimilation of resources by using both body condition prior to autotomy and mass-specific growth rate during the experiment as covariates. A Mixed-Model ANCOVA with size-specific growth rate as the dependent variable, clutch as a random factor, site and treatment as fixed factors, and mass-specific growth rate and body condition at autotomy as covariates, showed that nonautotomized hatchlings and those in better condition at autotomy increased their size faster than juveniles in poorer condition or that suffered autotomy, independently of their clutch and site of origin (body condition: $F_{1,7.97} = 17.00$, $P = 0.003$; mass-specific growth rate: $F_{1,2.64} = 7.96$, $P = 0.08$; autotomy treatment $F_{1,3.38} = 9.99$, $P = 0.043$; site: $F_{1,3.24} = 0.54$, $P = 0.511$; clutch: $F_{3,1.73} = 3.81$, $P = 0.242$; autotomy \times site interaction: $F_{1,2.49} = 0.41$, $P = 0.578$; autotomy \times clutch interaction: $F_{2,6} = 1.66$, $P = 0.267$, see Fig. 1).

There was no trade-off between size-specific growth rate and tail regeneration in autotomized lizards. Instead, these variables were correlated positively ($r = 0.755$; $P = 0.019$; see Fig. 2). Such positive correlation was not confounded by body condition at autotomy or site of origin, as shown by stepwise multiple

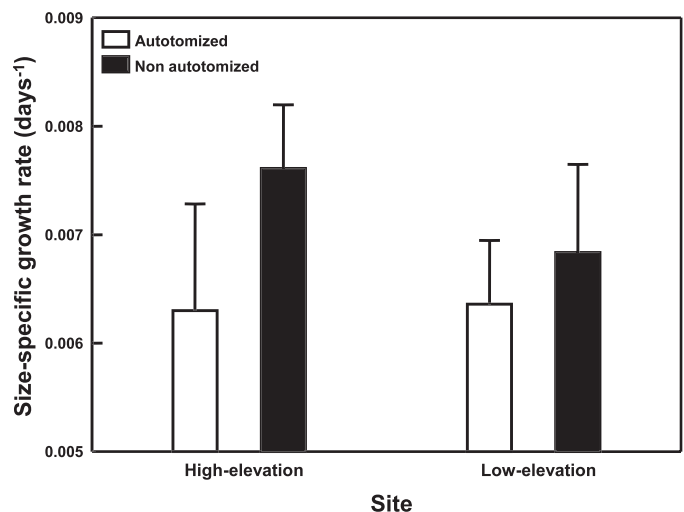


FIG. 1. Size-specific growth rates (mean \pm SE), adjusted for initial body condition and mass-specific growth rate during the experiment, of autotomized and intact hatchlings from high- and low-elevation sites.

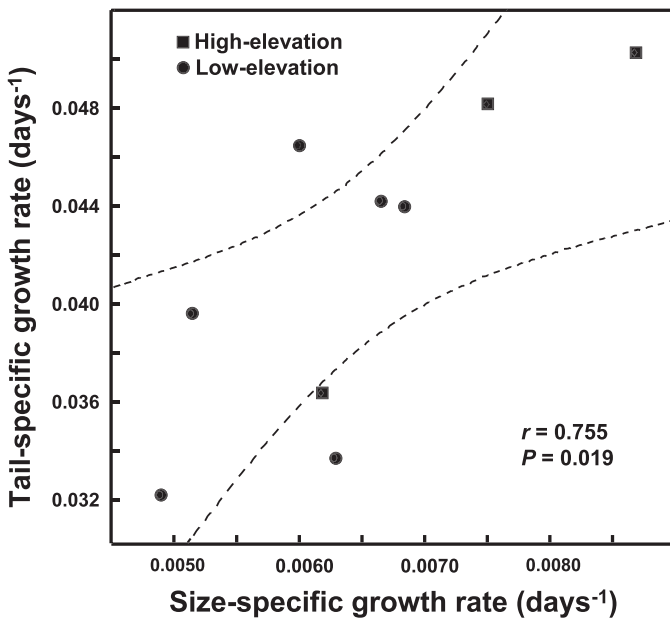


FIG. 2. Correlation between tail regeneration rates and size-specific growth rates for autotomized hatchlings from high- and low-elevation sites. Dashed lines represent 95% confidence intervals.

regressions (both forward and backward, and independently of which growth rate, i.e., tail or SVL, was used as the dependent variable) in which the models obtained included either size-specific growth rate or tail-specific growth rate as the only predictor variable.

DISCUSSION

The results of our study support the hypothesis that tail autotomy has distinct effects on growth rate during the early postnatal period. Hatchlings from both populations, independently of the autotomy treatment, did not differ in their body mass gain during the experiment. However, there were differences in the way they allocated those resources: for a given body condition and mass-specific growth rate, autotomized hatchlings grew at slower rates than those that were not forced to autotomize.

On the other hand, we found no differences between populations in the allocation of resources to tail regeneration. This was an unpredicted result because we expected that hatchlings from the low-elevation population, where higher frequencies of natural autotomy suggest higher predation risk, perhaps attributable to lower refuge availability (Iraeta et al., 2010), would have invested more in regenerating their tail to overcome further predator attacks (Tsasi et al., 2009). The absence of between-sites differences might reflect low statistical power resulting from small sample sizes, but it might also be attributable to a threshold in the amount of resources that can be allocated to regenerate the tail without compromising winter survival, taking into account that there are selective pressures to reach a minimum body size prior to the winter (Iraeta et al., 2008). Selective pressures induced by higher predation risk at the low-elevation site could also be buffered if hatchlings modified their behavior after autotomy, as it has been suggested for *Uta stansburiana* hatchlings (Niewiarowski et al., 1997). A similar behavioral response has been found in gravid females from this population (Iraeta et al., 2010).

Extensive tail loss involves loss of caudal fat stores that may be important for winter survival (Avery, 1970). Moreover, tail regeneration entails energetic costs (Bellairs and Bryant, 1985). Thus, autotomized hatchlings might be expected to have poorer winter survival than their tailed conspecifics. These costs may aggravate the negative effects on winter survival of their reduced size-specific growth rate caused by autotomy (Civantos et al., 1999; Iraeta et al., 2008). However, individuals from both populations allocated a significant amount of resources to tail regeneration and were able to regenerate approximately 88% of the initial tail length during the approximately 45-day experiment. Because the majority of the caudal fat reserves in lizards are stored in the proximal third of the tail (Chapple and Swain, 2002b), which has a smaller probability of being autotomized, individuals that lose their tails early in life are likely to be able to store sufficient fat in their shortened tail to survive over winter (Avery, 1970).

Although tail autotomy significantly reduced the size-specific growth rate of hatchlings, when we analyzed the relationship between tail regeneration and body growth in autotomized hatchlings, we did not find a trade-off between these two fitness-related variables. Similar results have also been reported for adult *U. stansburiana* (Fox and McCoy, 2000). Surprisingly, our results showed that, whatever their population of origin, autotomized hatchlings that invested more in body growth were also able to invest more in tail regeneration (Fig. 2). A possible explanation for this unexpected result is that all lizards were housed in a common garden set-up and were provided with food ad libitum, which probably allowed them to obtain sufficient energy for both tail regeneration and body growth, thus masking any potential allocation trade-off. However, this explanation is not consistent with the positive relationship depicted in Figure 2, which could be more simply explained by the hypothesis that some individuals are better in obtaining resources from captured prey; therefore, they can invest more in both traits than others. This is consistent with the positive effect of body condition prior to autotomy on the subsequent size-specific growth rate of hatchlings (see Results). A similar reasoning was proposed by Van Noordwijk and de Jong (1986) to explain the absence of trade-offs, or even the positive relationship, between apparently conflicting life-history traits in wild populations.

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