Intrapopulation variation in injury frequencies in the sand lizard, *Lacerta agilis* (Squamata, Lacertidae)

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Injury rates (broken tails and missing toes) were studied in a population of Lacerta agilis in the Czech Republic. The frequency of regenerated tails increased continuously with snout-vent length (SVL) and did not differ between males and females. This suggests that the probability of tail breakage does not differ between age classes and sexes in this population. In lizards with regenerated tails, similar lengths of the remaining portion of the original tail were found in males and females. Because males had longer intact tails, they thus detached longer portions of the tail than females. The length of the regenerated portion of the tail did not differ between the sexes. Thus, autotomy removed sexual dimorphism in tail length. Incidence of missing toes was relatively low (3.6%) and occurred only in males, which suggests that it was a result of agonistic encounters rather than of predation.

Key words: tail autonomy, regenerated tails, toe loss, sex differences, morphometry.

Introduction

Lizards, like other animals, suffer injuries due to accidents, diseases, predation encounters and fights with conspecifics during their life. The most frequent types of injuries in lizards are broken tails and missing toes. Tail autotomy, besides the obvious benefit of facilitating escape during a predatory attack, also has substantial costs (ARNOLD, 1984, 1988) which may decrease survival and fitness after autotomy (MARTÍN & SALVADOR, 1993; SALVADOR et al., 1995; WILSON, 1992, but see NIEWIAROWSKI et al., 1997 for contrasting results). Thus, tail loss can have an important effect on lizard life histories.

As a part of a wider study (GVOŽDÍK, unpubl. data) on ecology and morphometry of the

sand lizard, Lacerta agilis Linnaeus, 1758, I analyzed within-population variation in injury rates to determine possible sex and age differences in frequency of regenerated tails and missing toes. Furthermore, I gathered information about morphometry of intact and regenerated tails in both sexes.

Material and methods

Lacerta agilis is a small (total length about 200 mm in C Europe), diurnal, insectivorous lizard occurring in a substantial part of Europe and temperate Asia (BISCHOFF, 1984). Females lay 6–12 eggs in June (RYKENA, 1988). The lizards reach maturity in the third activity season (STRIJBOSCH & CREEMERS, 1988).

Data were gathered during one season - in 1994. The study area was a 1.9 ha sand pit situated 3.5 km NW from the town of Opava (17°53'E, 49°08'N, 280 m altitude). The bottom of the sand pit was enclosed by 8-10 m high walls, except for a 4 m wide drive. Approximately one third of the area was covered by bare sand with little vegetation, the second third was well vegetated by grass (Calamagrostis epigeios), various ruderal herbs (e.g. Plantago sp., Equisetum sp., Urtica sp.) and scattered birches (Betula pendula) and the last third consisted of birch forest. During field work I walked through the area from sunrise to the end of lizard activity, i.e. 60 min after not having seen any lizard. A total of 159 lizards were captured and recaptured by hand or by noosing. Every lizard caught was individually marked by toe clipping (WAICHMAN, 1992) and the following information was recorded: date of capture, sex (in subadults and adults only), tail status (intact, broken or regenerated), occurrence of naturally missing toes, snout-vent length (SVL), tail length (TL) for intact tails, original tail base length (TBL) and length of regenerated portion (RTL) for broken and regenerated tails, and body mass (BM). All measurements were taken using dial callipers (0.1 mm resolution) and Pesola scales (0.1 g resolution).

I have classified first captured lizards by their SVL and BM into three age groups, which were defined using size data of age-known individuals from a previous capture-recapture study (Gvoždíκ, unpubl. data): (i) juveniles (1st calendar year of life; size range: 24.1–34.5 mm), (ii) subadults (2nd calendar year of life; size range: 26.5–66.4 mm) and (iii) adults (3rd calendar year of life and older; size range: 54.8–83.9 mm). Juveniles and subadults were combined as immature individuals for further analysis.

Because of sexual dimorphism in TL (BORCEA, 1979), I have applied a linear regression model for relationships of TL to SVL (log transformed) separately for males and females. From these regression models I have calculated theoretical or predicted TLs (PTL) for lizards with broken tails (VITT & COOPER, 1986). Using PTL, I have further determined (i) the portion of the remaining original tail (TBL/PTL), (ii) the broken portion of the tail (ATL = PTL - TBL), (iii) the broken portion of the tail relative to PTL ([PTL - TBL]/PTL) and (iv) the already regenerated portion of the tail (RTL/[PTL - TBL]).

I have ignored recaptures for statistical analyses. Because the probability of being autotomized usually increases with age (Schoener & Schoener, 1980; Vitt, 1983), I have applied a log-linear model (Sokal & Rohlf, 1995) to test the effect of sex, age, natural logarithm of SVL (In SVL) and their interaction on the probability of having a regenerated tail. The In SVL seems to be a more reliable estimate of age than untransformed values, because the relationship between age and SVL is exponential rather than linear (Olsson & Shine, 1996). The relationship between regenerated tail frequency and In SVL was modelled by logistic regression. The remaining categorical data were compared using a G-test and Fisher's exact test. Distri-

butions of continuous variables were compared using a Kolmogorov-Smirnov two-sample test. For comparison of continuous characters between the sexes, and between injured and uninjured individuals, I used Student's t-test, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) with \ln SVL as the covariate. All data showing deviations from normality or homogeneity of variances were transformed (Box-Cox transformation; SOKAL & ROHLF, 1995) before statistical analysis. A significance level of P < 0.05 was used for all tests. Statistical tests were performed using the JMP statistical program (SAS Institute, 1995).

Results

Only four adult and four juvenile lizards caught during the whole season had freshly broken tails. Regenerated tails occurred in 39% of all captured lizards. Frequency of regenerated tails was three times lower in juveniles than in adults (Tab. 1; G-test, G = 14.49, df = 2, P < 0.001). The probability of having a regenerated tail increased with SVL (logistic regression, df = 1, χ^2 = 17.38, P < 0.0001). Adult males had a similar probability of having regenerated tails as females of the same size (log-linear model, df = 1, χ^2 = 0.31, P = 0.57). Thus, their data could be lumped for further analysis. The probability of occurrence of a regenerated tail did not differ between immatures and adults after removing the effect of SVL (df = 1, $\chi^2 = 0.78$, P = 0.38).

Table 1. Frequency of regenerated tails and missing toes in males, females and immatures of *Lacerta agilis*.

Category	n	Broken tail	Toe loss
Males	68	33 (48.5%)	6 (8.8%)
Females	56	26~(46.4%)	0
Immatures	42	6 (14.3%)	0
Total	166	65 (39.2%)	6(3.6%)

Summary statistics of SVL and tail length of injured and non-injured individuals are presented in Table 2. Males had longer original tails than females of the same SVL. In autotomized individuals tail length (TBL + RTL) did not differ significantly between the sexes and it was not dependent on SVL (ANCOVA, effect of sex: $F_{1,55} = 0.008$, P = 0.93; effect of SVL: $F_{1,55} = 0.0002$, P = 0.99). Males had similar TBL and RTL as females (Tab. 2). The predicted length of the detached portion of the tail was longer in males than in females. The distribution of TBL relative to PTL showed

Table 2. Summary statistics (mean \pm standard error, minimum – maximum) of snout-vent lengths and tail lengths in males and females of *Lacerta agilis* with intact and broken (regenerated) tails. All measurements are in mm.

Trait	Whol	P	
	n=35	Females $n = 30$	
SVL	67.9 ± 1.0 54.8-77	70.5 ± 1.3 56.1-81.1	0.13ª
TL	$110.5 \pm 1.1 \\ 81.1-130.6$	$102.1 \pm 1.2 \\ 83.8 - 118.7$	< 0.0001 ^b

Broken	and	regenerated	tails
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	n = 33	Females $n = 26$	
SVL	69.9 ± 1.2	72.6 ± 1.8	0.04^{a}
	56.3 - 81.2	60.5 - 83.9	
PTL	112.6 ± 2.0	108.2 ± 2.0	$< 0.0001^{\rm b}$
	89.3-132.1	90.2 - 122.1	
TBL	34.4 ± 3.9	34.8 ± 4.5	0.94^{a}
	11.2-89.8	9.4 - 85.6	
ATL	78.3 ± 4.9	73.4 ± 5.3	0.51^{a}
	9.3 - 115.4	12.8 - 106.0	
RTL	36.0 ± 3.2	36.1 ± 4.7	0.99^{a}
	0-98	0 - 62.9	

SVL – snout-vent length; TL – original tail length; PTL –predicted original tail length; TBL – original tail base length; ATL – autotomized tail length; RTL – regenerated tail length. *aStudent's t-test; *bANCOVA with SVL as the covariate; P – values refer to comparisons between the respective values of males and females.

no differences between the sexes (Kolmogorov-Smirnov two-sample test, P>0.5; Fig. 1). The frequency of minimal TBL (0–10% PTL) was similar between the sexes (Fisher's exact test, P=0.32). On average, TBL consisted 33% of PTL in both sexes (Tab. 2). RTL reached to 100% of the detached portion (PTL – TBL; Fig. 2). Distribution of RTL relative to ATL showed no differences between the sexes (Kolmogorov-Smirnov two-sample test, P>0.5).

Toe loss occurred only in males (G-test, G = 5.28, df = 1, P < 0.05; Tab. 1). SVL's of injured males ranged from 54.8 to 79.0 mm. From two to seven toes were missing on one to three feet in injured lizards. Frequencies of missing toes did not differ between fore and hind feet (G = 0.40, df = 3, P = 0.94).

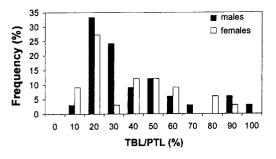


Fig. 1. Distribution of remaining portions of original tails as percentages of the length of original tail in males and females of *Lacerta agilis*.

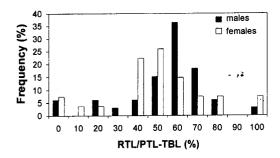


Fig. 2. Distribution of regenerated portions as percentages of original broken portion of tail (RTL/PTL – TBL) in males and females of *Lacerta agilis*.

Discussion

Males had similar relative frequencies of regenerated tails to females. Previous studies have shown that males of L. agilis have a higher frequency of regenerated tails than females (TERTYSHNIKOV, 1976) whereas in other populations regenerated tails were more frequent in females (RAHMEL & MEYER, 1987). Because the probability of having a regenerated tail increases with SVL (Ter-TYSHNIKOV, 1976; RAHMEL & MEYER, 1988; this study), the higher frequency of regenerated tails in females could be a result of size differences between males and females instead of higher injury rates (see Fig. 6 in RAHMEL & MEYER, 1987). This example clearly shows the importance of using log-linear models instead of chi-square tests for comparisons of regenerated tail frequencies between sex or age categories. Using this approach I showed that the probability of having a regenerated tail was a passive function of length of life with no effect of reproductive activity after maturity.

The results of this study show no difference in TBL between the sexes. These findings indicated little constraints of the supposed longer nonautotomized portion of the tail for the position of tail breaks in males (BARBADILLO et al., 1995). However, because I have not used TBL's of freshly autotomized lizards, results could be biased due to possible sex differences in growth rates of TBL (VITT et al., 1977). Nevertheless, growth of the original portion of the tail is substantially slower than of the regenerated one (VITT & COOPER, 1986) and growth of TBL, if sex differences exist, is slower in females than in males (VITT et al., 1977). If this is the case in L. agilis, males had even more tail breaks at the closest point to the tail base than females, which is consistent with my previous statement.

Tail breaks occurred at the same proportions of the original tails in both sexes. Males thus detached a longer portion of their tails than females. This means that autotomy should be on average more materially and energetically costly for males than for females (see Arnold, 1984 for a review of costs of autotomy). However, without any additional data, it is questionable whether these differences are biologically significant. Despite longer portions of autotomized tails, injured males had similar lengths of their regenerated portions as females. Thus autotomy and subsequent regeneration removed differences in tail length between the sexes. It follows that if any advantage of longer tails for males exists, autotomized males did not possess it.

Missing toes occurred only in adult males which suggests they were more likely a result of aggressive encounters between males than predation or other possible causes, e.g., ant infestations (TINKLE, 1967) or necrosis following by dysecdysis of toes (HAZELL et al., 1985; HUDSON, 1996). In comparison with other lizard populations (TIN-KLE, 1967; SCHOENER & SCHOENER, 1980; MID-DELBURG & STRIJBOSCH, 1988; HUDSON, 1996) frequency of missing toes was relatively low. Low incidence of toe loss in a population may indicate that (i) it is rare or (ii) it is common but the damaged animals suffer higher mortality (HUDSON, 1996). If toe loss affects survival, then a sex ratio biased in favour of females should be observed. However, the sex ratio (0.8:1) showed no significant difference from 1:1 (P = 0.57) in this study. Toe loss was a relatively rare injury in this population (but see Olsson, 1992) nevertheless it can cause difficulties with possible misidentification of individuals marked by toe-clipping. This may be overcome, however, by comparing other characteristics (sex, size, regenerated tail) with previous capture records (HUDSON, 1996), and by amputation of only the terminal toe digit using an appropriate marking scheme i.e., no more than one clipped digit on every foot.

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FAUNISTICAL NOTES

First records of Blasticotomidae, Tenthredinidae, Pamphiliidae (Hymenoptera) from Slovakia

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Blasticotomidae

Blasticotoma filiceti Klug, 1834 Material examined: C Slovakia, Kremnické vrchy Mts, Králické sedlo – búda Dobrá jama (7279) (= grid reference number of the Databank of Slovak fauna), 1050 m a.s.l., 4 July, 2000, 3 larvae on *Dryopteris carthusiana*, leg. L. Roller. Distribution: N and C Europe and Far East (Zhelokhovtsev, 1988). The species has been rarely collected in Europe. Larva is a stem borer of ferns. Known food plants are *Athyrium filix-femina*, *Polystichum*, *Dryopteris*, *Matteuccia struthiopteris*