Tail Autotomy, Tail Size, and Locomotor Performance in Lizards*

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ABSTRACT

The effect of tail autotomy on locomotor performance has been studied in a number of lizard species. Most of these studies (65%) show that tail autotomy has a negative effect on sprint speed, some studies (26%) show no effect of autotomy on sprint speed, and a few (9%) show a positive effect of autotomy on sprint speed. A variety of hypotheses have been proposed to explain the variation across these studies, but none has been tested. We synthesize these data using meta-analysis and then test whether any of four variables explain the variation in how tail autotomy impacts sprint speed: (1) differences in methodology in previous studies, (2) phylogeny, (3) relative tail size, and (4) habitat use. We find little evidence that methodology or habitat use influences how sprint speed changes following tail autotomy. Although the sampling is phylogenetically sparse, phylogeny appears to play a role, with skinks and iguanids showing fairly consistent decreases in speeds after autotomy and with lacertids and geckos showing large variation in how autotomy impacts speed. After removing two outlying species with unusually large and long tails (*Takydromus* sp.), we find a positive relationship between relative tail size and sprint speed change after autotomy. Lizards with larger tails exhibit a greater change in speed after tail loss. This finding suggests that future studies of tail autotomy and locomotor performance might profitably incorporate variation in tail size and that species-specific responses to autotomy need to be considered.

Introduction

Autotomy is a widespread phenomenon in which an animal voluntarily sheds an appendage, as defined by Fredericq (1892) and reviewed by Maginnis (2006). Perhaps the most conspicuous form of autotomy involves the loss of the tail, as exhibited by many species of lizards and salamanders (Wake and Dresner 1967; Arnold 1984, 1988). Tail autotomy is most often associated with attempted predation, with the animal sacrificing its tail to a predator in order to escape. The most obvious benefit to this behavior is that the animal survives the predation attempt (Daniels et al. 1986), with the potential for future reproductive output.

Whereas the benefits of tail autotomy are simple and obvious, the costs associated with this behavior are more diverse and obscure (recently reviewed in Clause and Capaldi 2006; Bateman and Fleming 2009). Several decades of research have shown that autotomy can result in the loss of fat reserves (Dial and Fitzpatrick 1981; Wilson and Booth 1998); reduced time spent foraging (Cooper 2003); reduced social status (Fox and Rostker 1982); a shift in energy allocation to tail regeneration, resulting in reduced growth (Congdon et al. 1974); and reduced reproductive output, including lower egg mass (Dial and Fitzpatrick 1981) and fecundity (Wilson and Booth 1998). In sum, tail autotomy can result in lower future fitness because these costs have a negative impact on future survivorship and reproductive output but less so than immediate death as a result of predation.

Animals use locomotion in a variety of ecologically relevant contexts, including foraging, territory defense, mate guarding, and predator escape, and thus locomotor performance is expected to be an important predictor of fitness (Arnold 1983; Garland and Losos 1994). Several studies have shown that tail autotomy has a negative impact on locomotor performance via a reduction in sprint speed (e.g., Ballinger et al. 1979; Punzo 1982). However, a handful of studies have shown the opposite effect, that tail autotomy increases locomotor performance (e.g., Daniels 1983; Brown et al. 1995), and still others have shown that autotomy has no effect on locomotor performance (e.g., Huey et al. 1990). The reason for this lack of consensus is unclear. One possibility is that these studies have used disparate methodologies, resulting in different findings. Another possibility is that species- or clade-specific responses to autotomy are present and that no general trends exist among lizards. Finally, it could be that some aspect of tail morphology (e.g., size or shape) or species ecology (i.e., habitat use) could explain the variation in these studies' results. These possibilities have not been previously explored because all of the available data have not been combined into a single analysis.

A number of hypotheses have been proposed to help explain the mechanisms by which the tail might affect maximum sprint

speed and how tail loss might affect locomotor performance. First, in many tailed ectotherms the tail generates a large frictional force in the opposite direction to the accelerative force used to propel the animal forward, because the tail is dragged along the substrate during locomotion (Arnold 1997; Willey et al. 2004). Thus, one would hypothesize that tail loss would result in enhanced locomotor performance as a result of the loss of this impairing frictional force (Daniels 1983). Second, having a long and heavy tail is thought to position the animal's center of mass posteriorly, close to the hind limbs, so that the hind limbs can apply a greater force to the substrate (Snyder 1949; Arnold 1984). In this scenario, loss of the tail would shift the center of mass anteriorly, decreasing hind limb propulsive force and resulting in reduced sprint speed (Ballinger et al. 1979; Punzo 1982). Third, the tail may play an important role as a counterbalance in the mechanics of the lateral undulatory movements that occur during locomotion, and loss of the tail may alter kinematic parameters, such as stride length and frequency (Hamley 1990; Martin and Avery 1998; Cromie and Chapple 2012). In this case, tail loss would also likely result in decreased locomotor performance. For all three hypotheses, one might predict that a relatively larger tail would have a greater influence on running mechanics and that losing a relatively larger tail would result in a greater change in locomotor performance after autotomy.

Here we take a multifaceted approach to addressing how tail autotomy influences locomotor performance in lizards. First, we present new data on the maximum sprint velocity and acceleration of four new species before and after autotomy. Second, we conduct a meta-analysis using the published data (including our new data) on the impact of tail autotomy on maximum sprint speed in lizards. We use these data to address four variables expected to explain sprint speed change after autotomy. First, we examine the influence of three sources of methodological variation: the technique of sprint speed measurement, the time after autotomy that performance was remeasured, and the experimental design. We expect studies that used video to record speed will show the greatest difference in speed, followed by electronic racetracks and then stopwatches, because video is the most accurate and the stopwatch is the least accurate means of recording time-based data. We expect that studies that waited longer after autotomy to remeasure performance will show a smaller change in speed, because it is thought that high levels of stress hormones immediately following autotomy may temporarily increase performance (Landkilde and Shine 2006). We expect that a repeated-measures design will show greater changes in performance compared to an experimental-control design because repeated-measures design is a more powerful experimental design strategy (Quinn and Keough 2002). Second, given the variation in body shape and natural history observed across lizards, we expect clade-specific differences (e.g., skinks vs. geckos) in the effect of autotomy on performance. Third, we test the hypothesis that relatively larger tails result in a larger change in performance after autotomy, because the size of the tail may be indicative of function during locomotion. Fourth, we expect that habitat use will explain the magnitude of change in performance change after autotomy. In particular, we expect arboreal species to show the greatest change in performance after autotomy, because these species may possess the most actively functional tails (Ballinger 1979; Arnold 1997; Jusufi et al. 2008; Gillis et al. 2009). Our goal is to identify factors that explain variation in the change in performance as a result of autotomy and to suggest future directions for studies of the effect of tail autotomy on locomotor performance.

Methods

Tail Autotomy and Sprint Speed in Four Species of Lizard

Animals. We purchased six adult male *Takydromus sexlineatus* from a commercial supplier (California Zoological Supply) and captured six adult *Anolis carolinensis* on the College of Charleston campus. We captured 19 adult *Holbrookia maculata* to the north of the Santa Rita Mountains, south of Tucson, Arizona, and we captured 24 adult *Aspidoscelis sonorae* on the University of Arizona campus, Tucson. We housed *T. sexlineatus* in groups of three in 116-L plastic tubs with a loose, sandy peat moss substrate and ample climbing surfaces. We housed *A. carolinensis* individually in 19-L aquaria with a similar substrate and climbing surfaces. We fed both species vitamin-dusted crickets three times weekly and misted them with water daily for the duration of the experiment. *Anolis carolinensis* were released at their site of capture; *T. sexlineatus* were euthanized using carbon dioxide and preserved for future anatomical studies. We conducted all trials with *H. maculata* and *A. sonorae* within 36 h of capture, during which time we housed these animals in inflated plastic bags in a dark cooler and immediately after which we released these animals at site of capture. All animals that we used in locomotor trials were healthy.

Prior to all experiments, we painted a small dot at the base of the skull on the dorsum of each lizard with nontoxic white paint. We used this marker to digitize each video frame of each trial to record the animal's instantaneous position and calculate the instantaneous velocity and acceleration.

Locomotion Trials. Prior to all trials, we placed *T. sexlineatus* in an incubator set at 35°C for 1 h and allowed them to rest in the incubator for 1 h between trials on the same day. We ran *A. carolinensis* in an environmentally controlled room set to 30°C. Lizards ran along a racetrack toward a dark hide box. The racetrack was 3 m long and 0.35 m wide, with wooden sidewalls 0.4 m tall. The surface of the track was covered with cork bark, which provided excellent traction. We ran *A. carolinensis* on a 30° incline, as many species of *Anolis* are known to jump and not run on horizontal surfaces (Losos 1990). We ran *A. sonorae* and *H. maculata* in the field on a 1.5-m-long, 10-cm-wide racetrack at ambient temperatures of 35°–40°C, after being allowed 1 h to come to optimal body temperature.

For each trial, we positioned lizards in a resting, motionless posture at the beginning of the racetrack, with the entire body in the camera's field of view. We used hand clapping and waving and gentle tapping on the base of the tail to induce a rapid locomotor burst. We continued to clap and wave to encourage lizards to run along the length of the track. We ran each individual along the raceway three to four times with and without the tail. We used a Casio EXLIM EX-F1 or a Fastec Troubleshooter 250 camera to record the trials, positioning the camera with its lens perpendicular to the surface of the raceway so as to record video from the dorsal side over the initial 1 m of the racetrack. We collected video at 240–300 frames per second, depending on species, as suggested by Walker (1998) and following previous studies (Vanhooydonck et al. 2006; Bergmann and Irschick 2010; McElroy and McBrayer 2010).

Video Analysis. We imported digital videos to a personal computer and manually trimmed them using Adobe Premier Elements to begin 10–20 frames before the lizard began moving, until the lizard was completely out of camera view. We used the program DLTdv3 (Hedrick 2008) to digitize the white marker at the base of the skull to obtain position coordinates for each frame of video. Then we fitted a quintic spline function to the position versus time data using the Spline Toolbox in MatLab. We fitted the spline function so that its residuals were less than 1 mm, which was reasonable given the size of the lizard and the size of the white marker (2–3 mm). We then used a custom MatLab script to calculate the first and second derivatives from the spline coefficients fitted to the position data, which provided us with instantaneous velocity and acceleration data, respectively, for each frame of each video. We retained the trial(s) with the greatest maximum velocity and acceleration values for each individual in each treatment for further analysis; sometimes this was the same trial, and at other times it was different trials for the same individual.

Tail Autotomy. After we collected performance data on lizards with intact tails, we manually autotomized their tails by grasping them at the base of the tail (slightly posterior to the cloaca) between thumb and index finger to initiate maximal tail autotomy. We allowed lizards to struggle while grasped until they autotomized their tail (this typically took 5–30 s). We gently blotted each lizard's tail stump with a clean towel to wick away the minimal amount of blood lost. We allowed lizards to recover after autotomy (times are found in table 1) to allow the tail wound to dry.

Statistical Analysis. We compared maximum sprint speed and acceleration before and after autotomy using paired-sample *t*-tests for each species separately, using JMP 8.0.1 (SAS Institute, Cary, NC). We tested the assumption of homoscedasticity using an F_{max} test and the assumption of normality using a Kolmogorov-Smirnov test (Sokal and Rohlf 1995).

Meta-Analysis of the Effects of Autotomy on Sprint Speed

Data Collection. We compiled all published studies of the effect of tail autotomy on horizontal sprint speed, resulting in a data set for 23 species. Studies consisted of both repeated-measures designs, in which each individual was tested before and after autotomy, and two-sample designs, in which one group of animals served as a control and a second group had autotomized tails. Speed was measured using (1) photocells placed at 0.25 or 0.5 m along a racetrack, (2) a stopwatch to time a standard distance run, or (3) a video camera. Tailless trials were conducted from a few hours to several weeks postautotomy. For each study, we extracted the mean and standard deviation for sprint speed for lizards running with and without their tail and the sample size for each group of lizards (in repeated-measures designs, the sample size would be equal for the two groups). We then calculated the effect size, *d*, the correction for small sample sizes, *J*, and the pooled variance, s_{ij}, for each study, following Gurevitch and Hedges (2001). Table 1 summarizes the compiled data.

To obtain measures of relative tail size, we measured snout-vent length (SVL), tail length, body width (at the widest point), and tail base width (at the level of the cloaca) of two to 10 adult museum specimens of each species. We then estimated relative tail size in two ways. First, we defined relative tail length as the ratio of tail length to SVL. Second, we defined relative tail volume as the ratio of tail volume to body volume. We estimated tail volume as the volume of a cone,

$$\text{tail volume} = \frac{1}{3}\pi r^2 h, \tag{1}$$

where *r* is half of tail base width and *h* is tail length, and body volume as the volume of a prolate ellipsoid,

$$\text{body volume} = \frac{4}{3}\pi a^2 b, \tag{2}$$

where *a* is half of body width and *b* is half of SVL.

Statistical Analyses. We conducted all analyses of the data using JMP v8 (SAS Institute), SAS v9.22 (SAS Institute), R v2.15.1 (R Core Development Team 2012), and Mesquite v2.73 (Maddison and Maddison 2010). Since species values are not independent because of shared evolutionary history, traditional statistical analyses cannot be used. To address this issue we pruned the lizard supertree from Bergmann and Irschick (2012) to include only species for which we had data and used phylogenetically informed analyses (see below for details). Five species in our data set were not present in the supertree, so we recoded these with a congener and then pruned the tree (*Hemidactylus bowringii* was replaced with *Hemidactylus frenatus*, *Cordylus melanotus* with *Cordylus cordylus*, *Lygodactylus capensis* with *Lygodactylus bernardi*, *Sceloporus virgatus* with *Sceloporus magister*, and *Aspidoscelis sonorae* with *Aspidoscelis flagellicaudus*). The result was a phylogeny for all species in our data set with branch lengths (fig. 1). To conform to the assumptions

Table 1: Summary of attributes of studies included in meta-analysis, including data we collected on tail size

Species	Experiment design	Speed measure	Time (d)	Speed$_{tail}$ (ms^{-1})	Speed$_{aut}$ (ms^{-1})	Effect size	RTL	RTV	Habitat	Clade	References
Cophosaurus texanus	RM	SW	1–2	1.40 ± .20	.95 ± .14	−2.49	1.19	.20	T	Iguanidae	Punzo 1982
Holbrookia maculata	RM	V	1	1.32 ± .26	1.41 ± .34	.30	.91	.10	T	Iguanidae	Jones and Lovich 2009; this study
Uma notata	RM	SW	1–2	1.38 ± .12	.80 ± .07	−5.78	1.09	.15	T	Iguanidae	Punzo 1982
Sceloporus virgatus	E	SW	NR	.73 ± .21	.51 ± .33	−.77	1.25	.14	T	Iguanidae	Cooper et al. 2009; Jones and Lovich 2009
Anolis carolinensis	RM	V	14	1.46 ± .19	1.30 ± .13	−.91	1.79	NR	A	Iguanidae	Irschick et al. 2005; this study
Aspidoscelis sexlineatus	RM	SW	1–3	1.95 ± .33	1.29 ± .23	−2.20	2.33	.45	T	Teiidae	Ballinger et al. 1979
Aspidoscelis sonorae	RM	V	1	1.84 ± .09	1.76 ± .08	−.92	2.21	NR	T	Teiidae	Jones and Lovich 2009; this study
Takydromus septentrionalis	RM	V	3	1.02 ± .33	.58 ± .49	−1.03	3.30	.70	G	Lacertidae	Arnold 1998; Lin and Ji 2005
Takydromus sexlineatus	RM	V	60	1.44 ± .41	1.40 ± .54	−.08	4.92	.93	G	Lacertidae	Arnold 1998; this study
Podarcis muralis	RM	V	2	.77 ± .06	1.22 ± .12	4.70	2.00	.42	R	Lacertidae	Brown et al. 1995
Podarcis lilfordi	RM	SW	<1	1.61 ± .56	1.16 ± .38	−.91	1.42	.17	SA	Lacertidae	Arnold 1998; Cooper et al. 2004
Psammodromus algirus	E	V	14	1.59 ± .18	1.02 ± .18	−2.84	2.59	.47	SA	Lacertidae	Arnold 1998; Martin and Avery 1998
Plestiodon fasciatus	E	V	1	.71 ± .16	.55 ± .18	−.92	1.59	.24	T	Scincidae	R. M. Goodman 2006; Jones and Lovich 2009
Plestiodon chinensis	RM	V	3	.93 ± .34	.71 ± .13	−.86	1.53	.25	SA	Scincidae	Lin et al. 2006
Lampropholis guichenoti	RM	ER	1	.46 ± .07	.39 ± .07	−1.07	1.40	NR	T	Scincidae	Downes and Shine 2001
Niveoscincus metallicus	RM	ER	3	.35 ± .10	.24 ± .05	−1.43	1.39	.21	T	Scincidae	Chapple and Swain 2002
Trachylepis maculilabris	E	SW	<1	.77 ± .25	.54 ± .15	−1.01	1.32	.22	SA	Scincidae	Cooper and Smith 2009
Lampropholis delicata	E	ER	2–7	.50 ± .21	.38 ± .21	−.55	1.70	.23	T	Scincidae	Chromie and Chapple 2012
Cordylus m. melanotus	E	ER	>1	2.21 ± .38	1.94 ± .63	−.47	1.11	.14	R	Cordylidae	McConnachie and Whiting 2003
Oedura lesueurii	RM	ER	7	.45 ± .13	.44 ± .21	−.05	.75	.16	R	Gekkonidae	Kelehear and Webb 2006
Lygodactylus capensis	RM	V	2	.81 ± .13	.82 ± .15	.06	1.10	NR	A	Gekkonidae	Medger et al. 2008
Christinus marmoratus	RM	V	4	1.45 ± .22	3.49 ± .58	4.56	1.25	NR	A	Gekkonidae	Daniels 1983
Hemidactylus bowringii	E	V	2	1.21 ± .19	1.06 ± .20	−.75	1.18	.16	R	Gekkonidae	Ding et al. 2012
Teratoscincus scincus	RM	V	7	.83 ± .16	.89 ± .14	.38	.71	NR	T	Gekkonidae	Lu et al. 2010

Note. Speeds are shown as mean ± SD. A = arboreal; E = experimental-control; ER = electronic racetrack; G = grass-specialist; NR = not recorded; RM = repeated measures; R = rock; RTL = relative tail length; RTV = relative tail volume; SA = semiarboreal; SW = stopwatch; T = terrestrial; V = video.
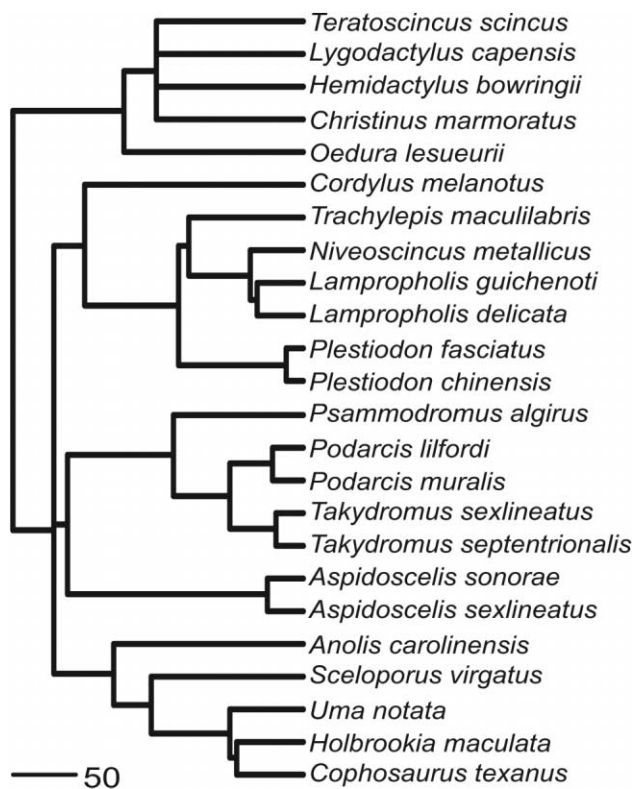
Figure 1. Phylogeny for the species included in the meta-analysis of the effect of tail autotomy on sprint speed, pruned from the supertree of Bergmann and Irschick (2012). Scale bar represents 50 million years, and branches are proportional to their lengths.

of regression and ANOVA, we transformed relative tail length and effect size using the equation

$$\frac{1}{1 + e^{-x}},$$

where x was relative tail length, because relative tail length was severely right skewed (skewness = 2.35) on account of the extremely long tails of the two *Takydromus* spp. We $\log_{10}$ transformed relative tail volume and the absolute value of effect size. All of the transformed variables conformed to a normal distribution (Shapiro-Wilk test, $W > 0.921$, $P > 0.071$), except effect size, which was slightly nonnormal (Shapiro-Wilk, $W = 0.884$, $P = 0.012$). We considered this acceptable, given that regression and ANOVA are robust to slight deviations from normality (Sokal and Rohlf 1995).

We used the data to address three questions: (1) Do methodological differences affect results of how sprint speed is affected by tail autotomy? (2) Does relative tail size influence the degree of effect of tail autotomy on sprint speed? (3) Does a species' habitat or clade membership influence the effect of tail autotomy on sprint speed?

Do methodological differences affect results?   We used one-way phylogenetic ANOVAs (Garland et al. 1993) to test the hypotheses that effect size differs by (1) experimental design

or (2) method of sprint speed measurement. We used the Phytools package (Revell 2012) in R to perform these analyses. To conduct the phylogenetic ANOVA, we ran 1,000 simulations to create a null F distribution to test the F value computed from the observed data. To test the relationship between effect size and number of days after autotomy that speed was remeasured, we used reduced major axis regression (RMA; McArdle 1988) of phylogenetically independent contrasts (PICs; Felsenstein 1985), and we ran the regressions through the origin (Garland et al. 1992). We used the maximum recovery time when a range was given (table 1). We computed PICs in Mesquite using the PDAP package (Midford et al. 2010). We checked for adequate standardization of the PICs by plotting the absolute value of standardized contrasts against standard deviations (Garland et al. 1992), and no significant trends were detected. We adjusted the degrees of freedom for hypothesis testing downward by 2 to control Type I error rates due to the two soft polytomies in the Gekkota (see Garland and Diaz-Uriarte 1999). We also reran this analysis without *T. sexlineatus*, because the number of days after autotomy was much greater than it was for other species (60 d; table 1).

Does relative tail size influence the effect of autotomy on sprint speed?   We used RMA regression of PICs to test the hypothesis that larger relative tail size results in a larger magnitude of change (absolute effect size) in locomotor performance after autotomy. We used absolute effect size because our hypothesis was focused not on whether speed increased or decreased but rather on the magnitude of performance change after tail loss. We first computed PICs for absolute effect size, relative tail length, and volume. These PICs were not properly standardized; therefore, we applied Grafen's rho transformation ($\rho = 0.5$) to achieve proper standardization (Grafen 1989). We then computed two RMA regressions, forced through the origin with degrees of freedom adjusted downward by 2, using the PICs for (1) relative tail length versus absolute effect size and (2) relative tail volume versus absolute effect size. We examined the residuals from the RMA regressions and found that two PICs were outliers: for the node at the base of the two *Takydromus* species and for the node at the base of the *Takydromus-Podarcis* clade (fig. 2). We repeated our analysis without the two *Takydromus* species. We chose to delete these two species for three reasons: because their relative tail lengths and volumes are outliers (table 1), even when one considers a much broader sample of relative tail lengths (Losos 1990; Irschick et al. 1997; Vitt et al. 2000; Kohlsdorf et al. 2001; Wiens and Slingluff 2001; Bickel and Losos 2002; Losos et al. 2002; Schulte et al. 2004; B. Goodman 2006; Wiens et al. 2006; Stuart-Fox and Moussalli 2007; Verwaijen and Van Damme 2007; Mahler et al. 2010; B. Vanhooydonck and A. Herrel, unpublished data); they are grass swimmers, which likely exerts a unique selective pressure on tail function (Arnold 1997, 1998; Wiens et al. 2006); and they impact both nodes that had the largest residuals.

Does a species' habitat use or clade influence the effect of autotomy on sprint speed?   We used one-way phylogenetic ANOVAs (Garland et al. 1993) to test the hypotheses that effect size differs by habitat use or clade membership. We used the
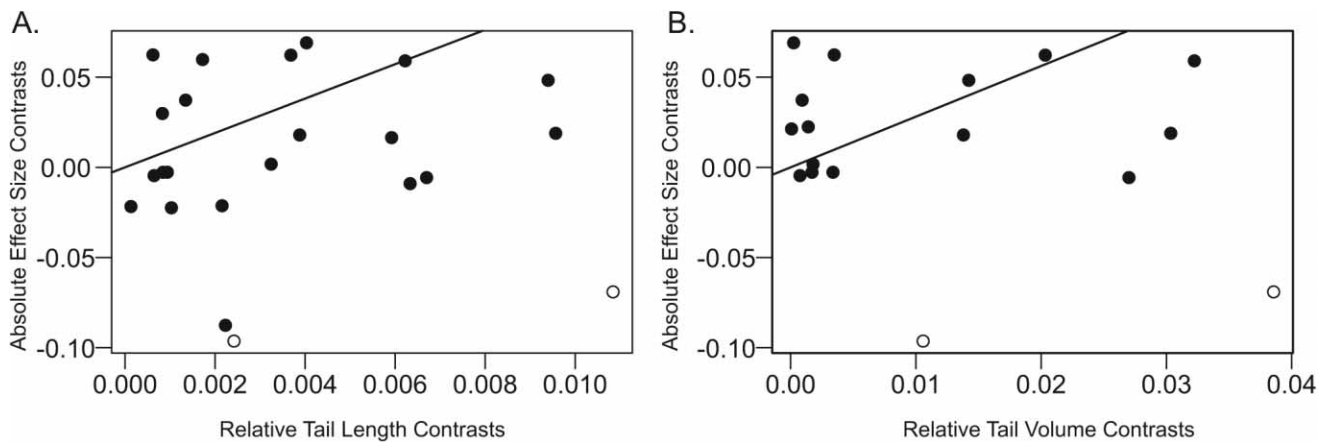
Figure 2. *A*, Relative tail length phylogenetic independent contrasts (PICs) versus absolute effect size PICs. *B*, Relative tail volume PICs versus absolute effect size PICs. Lines are reduced major axis regressions forced through the origin based on the analyses excluding the two *Takydromus* species. The two open circles correspond to nodes that were considered outliers and excluded from some analyses (see text).

Phytools package (Revell 2012) in R to conduct the phylogenetic ANOVA with 1,000 simulations.

Results

The Effect of Autotomy on Running Performance in Four Species of Lizard

Table 2 summarizes performance before and after autotomy. For *Takydromus sexlineatus*, neither maximum sprint speed ($t_5 = 0.267$, $P = 0.800$) nor maximum acceleration ($t_5 = 0.709$, $P = 0.510$) was significantly different before and after autotomy. For *Anolis carolinensis*, maximum sprint speed was significantly reduced following autotomy ($t_4 = -3.00$, $P = 0.040$), but maximum acceleration was not ($t_4 = -0.36$, $P = 0.736$). For *Holbrookia maculata*, neither maximum sprint speed ($t_{18} = -1.12$, $P = 0.278$) nor maximum acceleration ($t_{18} = 1.036$, $P = 0.314$) was significantly different before and after autotomy. Finally, for *Aspidoscelis sonorae*, neither maximum sprint speed ($t_{23} = 0.677$, $P = 0.505$) nor maximum acceleration ($t_{23} = 0.118$, $P = 0.907$) was significantly different before and after autotomy.

Meta-Analysis of the Effects of Autotomy on Sprint Speed

Do methodological differences affect results?   Effect size did not differ based on experimental design (phylogenetic ANOVA: $F_{1,22} = 0.940$, $P_{sim} = 0.341$) or speed measurement technique (phylogenetic ANOVA: $F_{2,21} = 3.20$, $P_{sim} = 0.139$). The PICs for effect size were not correlated with PICs for the number of days after autotomy that speed was remeasured ($r = 0.174$, $F_{1,20} = 0.687$, $P = 0.416$). Removing *T. sexlineatus* had no effect on this lack of relationship ($r = -0.060$, $F_{1,19} = 0.076$, $P = 0.786$).

Does relative tail size influence the effect of autotomy on sprint speed?   The RMA regressions of absolute effect size PICs on relative tail length PICs ($r^2 = 0.011$, $F_{1,20} = 0.256$, $P = 0.619$,

slope = 9.51) and absolute effect size PICs on relative tail volume PICs ($r^2 = 0.018$, $F_{1,14} = 0.298$, $P = 0.594$, slope = 2.74) were not significant and had exceedingly low r^2 values. In contrast, we did find significant relationships between effect size PICs and relative tail length PICs ($r^2 = 0.203$, $F_{1,18} = 5.10$, $P = 0.037$, slope = 9.53) and between effect size PICs and relative tail volume PICs ($r^2 = 0.440$, $F_{1,12} = 11.0$, $P = 0.006$, slope = 2.81) when the *Takydromus* species were removed, suggesting that the loss of a relatively larger tail (in terms of both length and volume) has a larger effect on change in sprint speed following autotomy (fig. 2).

Does a species' habitat use or clade influence the effect of autotomy on sprint speed?   The effect size for change in sprint speed due to tail autotomy did not differ between habitat use categories (phylogenetic ANOVA: $F_{4,19} = 2.26$, $P_{sim} = 0.250$) or clade membership (phylogenetic ANOVA: $F_{5,18} = 1.52$, $P_{sim} = 0.928$).

Discussion

Methodological Impacts on Sprint Speed–Tail Autotomy Studies

Given the range of studies undertaken on the effect of autotomy on sprint speed (table 1), it is not surprising that different experimental designs and methods of measuring speed have been used. In general, these differences appear to have little bearing on the estimation of the change in speed after autotomy. Experimenters have waited anywhere from several hours to several weeks to remeasure sprint speed following autotomy, when presumably the effects of stress hormones would be different (Landkilde and Shine 2006), and yet this variation also has no effect on sprint speed changes after autotomy. This could be explained by different hormonal responses and hormone effects in different species, suggesting that Landkilde and Shine (2006) studied a species of skink that may not be representative of how other lizards respond to autotomy. Another possibility

Table 2: Locomotor performance before and after tail autotomy for four new species presented in this study

Species	Sample size	Preautotomy speed (m/s)	Postautotomy speed (m/s)	Preautotomy acceleration (m/s^2)	Postautotomy acceleration (m/s^2)
Takydromus sexlineatus	6	1.40 ± .22	1.44 ± .17	21.6 ± 4.54	25.5 ± 2.93
Anolis carolinensis	5	1.46 ± .08	1.30 ± .06	29.4 ± 2.89	27.6 ± 3.03
Holbrookia maculata	19	1.32 ± .06	1.41 ± .08	17.3 ± 1.80	15.1 ± 1.82
Aspidoscelis sonorae	24	1.84 ± .09	1.76 ± .08	42.6 ± 3.01	42.0 ± 3.52

Note. Values are presented as means ± 1 SEM.

is that the 23 published records are so different in other aspects of methodology that one would not be able to detect an effect of time elapsed since autotomy on performance.

Although we focused on three obvious aspects of experimental methodology, other aspects certainly exist. For example, there almost certainly were differences between studies with respect to how animals were handled and cared for, how temperature was regulated, the racetrack dimensions, and the stimulus used to elicit the escape response. If we wish to gain a clear picture of the effect of autotomy on performance in lizards, we suggest that investigators adopt the following standardized and repeatable methodology: all lizards should be subjected to autotomy and rerun within 3–5 d of autotomy. This amount of time is long enough to allow for wound healing and to ameliorate any potential effects of stress hormones but short enough to avoid long-term animal care and health issues and to avoid the potential of the animal learning how to compensate for running without a tail. Electronic racetracks with photosensors or a video camera should be used to record speed, which will avoid human errors inherent in operating a stopwatch. We note that a video camera could record a lizard running across a surface marked every 25 cm (McElroy et al. 2008), such that the time that the lizard crosses each line could be recorded. Using cameras (even those that record at 30 frames per second) would alleviate the need for expensive and technically complex electronic racetracks. Repeated-measures designs are preferable because of their greater statistical power (Quinn and Keough 2002). Aside from standardizing methodology, it would be useful to conduct studies that explicitly manipulate conditions such as recovery time postautotomy and handling procedures and that measure several aspects of the physiological response (e.g., performance, hormone levels) across a multispecies sample.

The Effect of Tail Autotomy on Sprint Speed

Previous studies have presented evidence indicating each of the three possible effects of tail autotomy on sprint speed in lizards (increased, decreased, or no effect; table 1). The most prevalent finding (15/23 studies, or 65%) is a significant decrease in sprint speed after autotomy. Six studies (26%) found no effect following autotomy, and only two studies (9%) recorded an increase in sprint speed following autotomy. Interestingly, these studies are not evenly distributed across the clades that have

been examined. All skinks (six species) and four of five iguanid species show a decrease in sprint speed. Geckos and lacertids show mixed results. One gecko shows an increase, one gecko shows a decrease, and the other three species show no effect. One lacertid shows an increase, three show a decrease, and one species shows no effect. Although we are limited to only a sparse sampling of species in each clade, a generality that can be drawn from these observations is that some lizard clades exhibit a consistent effect of autotomy (e.g., scincids and iguanids) whereas others are more labile in how autotomy affects performance (e.g., geckos and lacertids).

Why these clade-level differences exist is unclear, but one possibility resides in differences in the biomechanics of locomotion among clades. For example, these groups show clear differences in body shape (Miles et al. 2007; Bergmann and Irschick 2012), which could impact locomotor mechanics during sprinting (Bergmann and Irschick 2010) and result in differential effects of autotomy on performance. Another possibility is that the function of the tail or limbs during sprinting is variable among lizard clades (e.g., skinks and iguanids vs. lacertids and geckos) and even within lizard families. If this is the case, then tail loss will incur different effects in these clades. Another possibility is that changes in stress hormone levels following autotomy could play a role in increasing or decreasing sprint speed, although this seems unlikely given that most studies wait a few days before testing resumes and this would presumably allow stress hormones to return to baseline values (Landkilde and Shine 2006). A final possibility is that the differences observed are due to variation in behavioral motivation before and after autotomy. In this case, the increase in speed observed in *Podacis muralis* may be the result of altered antipredator strategies following autotomy and associated increased behavioral motivation to sprint quickly (Brown et al. 1995). This possibility would suggest that some lizard species with intact tails either do not sprint at near-maximal speeds (by choice) and ramp up to maximum speeds only when triggered by autotomy or sprint maximally when the tail is present and then are induced to slow down after autotomy as a means of enhancing predator avoidance or decreasing detection probability. In fact, slower locomotion is associated with crypsis in many lizard species (Pianka 1986; Bickel and Losos 2002; Pianka and Vitt 2003).

Overall, this data set supports the notion that tails play a

functional role during locomotion (Vitt et al. 1977; Daniels 1985; Gillis et al. 2009; Libby et al. 2012) because 74% of the published studies show a significant change in sprint speed after autotomy. In most species, the tail seems to play a functional role in enhancing locomotor performance such that losing the tail compromises sprint speed. Several mechanisms have been proposed to explain such a finding, including the tail (1) serving as a counterbalance that positions the center of mass closer to the hind limbs (Ballinger 1979; Punzo 1982), (2) enabling greater stride length due to the inertia of the tail and its connection with the hind limb via the mm. caudofemoralis longus and brevis (Hamley 1990; Martin and Avery 1998), or (3) providing enhanced stability during fast locomotion (Cromie and Chapple 2012). Only two species sped up after autotomy, suggesting that their tail is a mechanical impairment (Daniels 1983), although behavioral issues could also be involved (Brown et al. 1995).

Perhaps the single biggest issue facing studies of the effects of autotomy on locomotor performance has been the lack of biomechanical techniques employed. We lack experiments that use force plates, electromyography, and kinematic analysis as tools to describe how body dynamics and muscle function change following tail autotomy. These issues are starting to be explored (Medger et al. 2008; Libby et al. 2012), and so the near future may reveal much about tail function, autotomy, and locomotor performance in lizards.

Explaining Variation in Sprint Speed after Tail Autotomy

We tested the hypothesis that tail size (relative length and volume) explains variation in how tail autotomy affects sprint speed. Our results provide moderate corroboration of this hypothesis. If we remove two outlying species, there is a significant positive relationship between relative tail size and the magnitude of sprint speed change after autotomy, so the loss of a relatively larger tail leads to a greater change in speed (fig. 2). This would further support the notion that tails play a functional role during locomotion (Vitt et al. 1977; Daniels 1985; Gillis et al. 2009; Libby et al. 2012) because relatively bigger tails presumably could have greater functional impact. However, we note the species with the largest tails (*Takydromus* sp.) show very small changes in performance (table 1), suggesting that a functional role of the tail in sprint performance is not ubiquitous among lizards.

Although relative tail size explains a significant amount of the variation in performance change after autotomy, the amount of variation explained was 20% for relative tail length and 44% for relative tail volume, suggesting that a large amount of the variation in performance is not explained by tail size (80% and 56%, respectively). We explored two other factors that could explain this variation, habitat use and clade membership, but neither of these explained a significant amount of variation in performance change after autotomy. We note that our categories for habitat use are quite coarse and generally are based on observational studies from the literature. Perhaps a more detailed treatment of habitat use would offer greater ex-

planatory power. Another factor that could explain this variation is species-specific responses that would be difficult to detect statistically (i.e., species are responding to autotomy in different ways).

There is some support for the species-specific response idea. Our analyses indicated that *Takydromus* species were highly influential on the ability to detect a positive correlation between relative tail size and magnitude of change in speed (fig. 1). These species may be outliers because of some aspect of their specific biology or natural history that causes them to respond differently to autotomy based on their tail size. For example, they are grass swimmers, and this habitat type is known to have coevolved with several morphological variables, including an elongate and narrow body and tail (Wiens et al. 2006). In order to better control for variation in how species respond to tail autotomy, it may be useful to examine a single clade of lizards (e.g., several *Takydromus* species or phrynosomatines, etc.) and to include much more detailed information on each species' tail function, anatomy, and natural history. Such a well-designed and integrative study would help better identify clade- or species-specific responses to tail autotomy and should go a long way toward helping us understand which factors influence the ways autotomy affects locomotor performance.

We have focused solely on sprint speed because of the relatively large amount of available published data. However, perhaps the most obvious gap in our understanding of how autotomy affects locomotor performance is for aspects other than sprint speed. A handful of studies have examined the impact of tail autotomy on climbing (Chapple and Swain 2002; Jusufi et al. 2008; Medger et al. 2008), falling (Jusufi et al. 2008), jumping (Gillis et al. 2009; Libby et al. 2012), branch running/ perching (Ballinger 1973; Vitt and Ohmart 1975; Brown et al. 1995), swimming (Daniels 1985), and endurance capacity (Martin and Avery 1995; Chapple and Swain 2002; Fleming et al. 2009). However, we lack a general consensus about how autotomy affects such performance traits across species, because only one or a few species have been studied for each aspect of performance. This is especially important because recent studies reveal an active functional role of the tail in climbing (Jusufi et al. 2008), jumping (Gillis et al. 2009; Libby et al. 2012), and walking (Boistel et al. 2010), suggesting that actively functional tails are common among lizards and that very few (if any) species have truly passive tails that are used only for autotomy (Vitt et al. 1977). Future studies should consider multiple aspects of performance across multiple species and focus on testing hypotheses regarding tail function using a standardized approach to generate a more complete understanding of how tail autotomy impacts locomotor performance.

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