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Telling Tails: Selective Pressures Acting on Investment in Lizard Tails*

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ABSTRACT

Caudal autotomy is a common defense mechanism in lizards, where the animal may lose part or all of its tail to escape entrapment. Lizards show an immense variety in the degree of investment in a tail (i.e., length) across species, with tails of some species up to three or four times body length (snout-vent length [SVL]). Additionally, body size and form also vary dramatically, including variation in leg development and robustness and length of the body and tail. Autotomy is therefore likely to have fundamentally different effects on the overall body form and function in different species, which may be reflected directly in the incidence of lost/regenerating tails within populations or, over a longer period, in terms of relative tail length for different species. We recorded data (literature, museum specimens, field data) for relative tail length ($n = 350$ species) and the incidence of lost/regenerating tails ($n = 246$ species). We compared these (taking phylogeny into account) with intrinsic factors that have been proposed to influence selective pressures acting on caudal autotomy, including body form (robustness, body length, leg development, and tail specialization) and ecology (foraging behavior, physical and temporal niches), in an attempt to identify patterns that might reflect adaptive responses to these different factors. More gracile species have relatively longer tails (all 350 spp., $P < 0.001$; also significant for five of the six families tested separately), as do longer (all species, $P < 0.001$; Iguanidae, $P < 0.05$; Lacertidae, $P < 0.001$; Scindidae, $P < 0.001$), climbing (all species, $P < 0.05$), and diurnal (all species, $P < 0.01$; Pygopodidae, $P < 0.01$) species; geckos without specialized tails ($P < 0.05$); or active-foraging skinks ($P < 0.05$). We also found some relationships with the data for caudal autotomy, with more lost/regenerating tails for nocturnal lizards (all 246 spp., $P < 0.01$; Scindidae, $P < 0.05$), larger skinks ($P < 0.05$), climbing geckos ($P < 0.05$), or active-foraging iguanids ($P < 0.05$). The selective advantage of investing in a relatively longer tail may be due to locomotor mechanics, although the patterns observed are also largely consistent with predictions based on predation pressure.

Introduction

Lizard tails are more versatile than one might at first imagine. They contribute to locomotor speed, endurance, and balance (Mushinsky and Gans 1992; Gans and Fusari 1994; Pianka and Vitt 2006; reviewed in Bateman and Fleming 2009); storage of fats (reviewed in Bernardo and Agosta 2005); and signaling and, therefore, social status (e.g., Fox et al. 1990; Langkilde et al. 2005). Lizards can also use their tail to escape a potential predator, either by employing it in active defense (e.g., *Agama agama* can use the tail as a whip and regenerated tails become club-like; Harris 1964; Schall et al. 1989) or by shedding it (caudal autotomy) to escape entrapment (Arnold 1988). Cast-off tails will also move extensively (Higham et al. 2013), detracting attention and further ensuring that the lizard can make its escape. Caudal autotomy can significantly increase survival of a predatory encounter (Congdon et al. 1974; Daniels 1985*a*; Daniels et al. 1986), and therefore it is not surprising that at least 13 of the ~20 families of lizards have retained the ancestral condition of being able to autotomize their tail (Zani 1996; Bateman and Fleming 2009).

Generally, where we would predict a greater reliance on caudal autotomy, we could also argue that we would find species with longer tails. A relatively long tail may act to help direct a predatory attack away from the lizard's body and therefore provide a greater "buffer," positioning vulnerable body parts at a greater distance from a pursuing predator when attack occurs (sensu Vitt 1983). As regenerated lizard tails lack intravertebral autotomy planes (the anatomical adaptation that facilitates autotomy), regenerated tail portions are generally lost less readily than are the original tails (this is evident through

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multiple tail breaks forming only a very small portion of all total tail damage; e.g., Vitt 1983). Long tails are therefore also likely to allow escape from multiple predatory encounters through economy of autotomy, where the tail breaks immediately proximal to the point of entrapment (but see Daniels 1985*a*).

A number of intrinsic factors have been proposed (outlined in table 1) to influence the incidence and selective advantages of tail autotomy across species, including body form (robustness, size, leg development, specialization of the tail) and the degree of exposure to potential predation through the lizard's foraging mode, physical niche, or temporal activity patterns (Pianka and Pianka 1976; Vitt et al. 1977; Pianka and Huey 1978; Jaksić and Fuentes 1980; Vitt 1983; Arnold 1984, 1988; Mushinsky and Gans 1992; Bauer and Russell 1994; Van Sluys et al. 2002; Tanner and Perry 2007; Hare and Miller 2010; Bateman and Fleming 2011). We can use these observations to make predictions about the incidence of lost/regenerating tails and relative tail length of lizard species:

1. *Body size.* Arnold (1984, p. 138; 1988) predicted that caudal autotomy may be more advantageous for "delicate" species, while large lizards "are often capable of active defence against predators by biting, clawing and tail lashing." We therefore predict more caudal autotomy and longer tails for smaller species.

2. *Robustness.* Arnold (1984, p. 138) also suggested that caudal autotomy "will be more important for delicately constructed forms with limited ability to fight back than for more robust species." We therefore predict more caudal autotomy and longer tails in more gracile species.

3. *Leg development.* Arnold (1984) also suggested that elongate (usually legless) lizards (e.g., some anguids, some scincids, pygopodids, and anniellids) that are fossorial or live close to the earth-vegetation interface or under objects (e.g., leaf litter) may incur relatively small locomotor costs as a result of tail loss because they use their whole bodies for serpentine movement or burrowing and when they lose their tail they simply become a shorter version of their former self (their microhabitat also provides protection from potential predators). We therefore predict more caudal autotomy and longer tails for functionally legless species compared with legged species.

4. *Tail specialization.* Although loss of even an unspecialized tail incurs costs for most lizards studied (Bateman and Fleming 2009), if the tail performs a specialized function that significantly increases survivorship (e.g., increases mobility when climbing, jumping, etc.; Brown et al. 1995; Medger et al. 2008; Fleming et al. 2009; Gillis et al. 2009; Fleming and Bateman 2012), then, even if it regenerates to full function, loss of the tail can compromise survival while it is growing back. We therefore predict more caudal autotomy and longer tails for species that have unspecialized tails.

5. *Foraging mode.* An animal being pursued is likely to be attacked from behind on the tail. Consequently, widely ranging active-foraging lizards have been predicted to have longer tails as an antipredator tactic while sit-and-wait species are more likely to rely on crypsis (Huey and Pianka 1981; Vitt 1983). We therefore predict more caudal autotomy and longer tails for active-foraging species compared with sit-and-wait species.

6. *Spatial habit.* Animals that use more exposed environments are more likely to have use for a long, autotomizable tail than cryptic ground-dwelling (or fossorial) species. We therefore predict more caudal autotomy and longer tails for climbing species.

7. *Temporal activity.* A long, autotomizable tail is more likely to be adaptive for surviving encounters with visually hunting predators but would be less effective distraction from the body for olfactory-hunting predators. We therefore predict more caudal autotomy and longer tails for diurnal species compared with nocturnal species.

We tested these predictions using a taxonomically diverse range of 350 lizard species. We took relatedness into account by using Felsenstein's (1985) independent contrasts.

Methods

Data were collected from extensive searches through the literature, museum specimens (Western Australian Museum), and both published field databases (e.g., Brandley et al. 2008; Meiri 2010) and unpublished field databases (app. A, available online, gives a list of species and data used in this study).

Two dependent measures were collected:

a. Relative tail length (residual of log tail length [TL] vs. log snout-vent length [SVL]). Relative tail length was recorded for 350 species representing 19 families. SVL (mm) and TL (mm) for intact specimens were used to calculate relative tail length as the residual of log TL versus log SVL. This measure of relative tail length was not different from a normal distribution (Kolmogorov-Smirnov [K-S] test, $d = 0.06$, $P > 0.20$).

b. Incidence of lost/regenerating tails (arsine–square root [incidence in sampled population]). In most lizard species, when the tail regenerates, in addition to differences in internal structure (the new tail has cartilage, not bone, and lacks intravertebral fissure planes; Gilbert et al. 2013), the external structure may also differ, often showing marked changes in scalation and color. The incidence of regenerating tails in natural populations is therefore a reflection of the incidence of animals successfully escaping entrapment by exercising autotomy (Bateman and Fleming 2011). Data on the incidence of lost/regenerating tails in natural populations were collected for 246 species (where ≥10 individuals for each species were examined) representing 14 families. We also recorded the incidence of lost/regenerating tails for museum specimens (up to ~100 individuals for each species), particularly focusing on pygopodids and skinks (where habit or body form that allowed important contrasts to be made with data for other taxa that were already available). We did not include families where there is no caudal autotomy reported (Chameleonidae, Varanidae); as extremely fast top-order predators, there may be little reason to expect varanids to have retained caudal autotomy as a defense, while chameleons use their prehensile tails extensively for locomotion. We were careful to exclude specimens that had no indication of tail regrowth (evidenced by epithelium over the tail stump) because these

Table 1: Predictions relating morphological, ecological, and behavioral factors to relative tail length (a) and incidence of lost/regenerating tails (b) in lizards

	a. Relative tail length			b. Incidence of lost/regenerating tails		
Prediction	Short-tailed species	Long-tailed species	Support for prediction	Species with fewer lost/ regenerating tails	Species with more lost/ regenerating tails	Support for prediction
1. Body size	Large	Small	No	Large	Small	No
2. Robustness	Robust	Gracile	Yes	Robust	Gracile	...
3. Leg development	Legged	Legless	Yes[a]	Legged	Legless	...
4. Tail specialization	Specialized tail	Tail not specialized	Yes	Specialized tail	Tail not specialized	...
5. Foraging mode	Sit-and-wait	Widely ranging, active foragers	Yes	Sit-and-wait species[b]	Widely ranging, active foragers[b]	Yes
6. Spatial habit	Use protected microhabitat	Use exposed or higher microhabitat	Yes	Use protected microhabitat	Use exposed or higher microhabitat	Yes
7. Temporal activity patterns	Nocturnal	Diurnal	Yes	Nocturnal	Diurnal	No

Note. Generally, we have made similar predictions for the incidence of tail loss and relative tail length (although footnote b indicates the exception). The "Support for prediction" columns summarize whether the evidence of this study either supports (Yes) or refutes (No) these predictions for the data on relative tail length and the incidence of lost/regenerating tails. An ellipsis indicates there is no support either way.

[a] Data for skinks contradict this prediction.

[b] Vitt (1983) predicted that widely ranging foragers would have longer tails but fewer lost/regenerating tails than would sit-and-wait foragers because their predators would remain motionless until the lizard was within striking distance and most attacks would therefore be directed to the body of the lizard (making tail loss an ineffective escape mechanism).

Table 2: Summary of multiple regression analyses examining factors relating to relative tail length$^{\text{FIC}}$ (a) and the incidence of lost/regenerating tails$^{\text{FIC}}$ (b) in lizards

	a. Relative tail length$^{\text{FIC}}$				b. Incidence of lost/regenerating tails$^{\text{FIC}}$			
	Beta	ß	t	P	Beta	ß	t	P
All species:	$R^2 = .377$, $F_{7, 341} = 29.47$ ($N = 349$)			<.001	$R^2 = .064$, $F_{7, 237} = 2.32$ ($N = 245$)			<.05
Robustness$^{\text{FIC}}$	**−.61 ± .05**	**−.30 ± .02**	**−12.74**	<.001	−.06 ± .07	−.05 ± .06	−.96	
Body length (SVL)$^{\text{FIC}}$	**.30 ± .05**	**.28 ± .04**	**6.63**	<.001	.05 ± .06	.07 ± .10	.73	
Leg development$^{\text{FIC}}$	**.23 ± .05**	**.18 ± .04**	**5.02**	<.001	.02 ± .07	.03 ± .09	.36	
Specialized tail$^{\text{FIC}}$	**−.14 ± .05**	**−.09 ± .03**	**−3.00**	<.01	−.11 ± .07	−.10 ± .07	−1.60	
Foraging mode$^{\text{FIC}}$	.05 ± .05	.02 ± .02	1.06		.12 ± .07	.08 ± .04	1.77	
Habit$^{\text{FIC}}$	**.11 ± .04**	**.04 ± .02**	**2.56**	<.05	.07 ± .07	.04 ± .04	1.06	
Activity$^{\text{FIC}}$	**.15 ± .04**	**.10 ± .03**	**3.31**	<.01	**−.22 ± .07**	**−.24 ± .07**	**−3.32**	<.01
Agamidae:	$R^2 = .379$, $F_{4, 24} = 3.65$ ($N = 29$)			<.05	$R^2 = .078$, $F_{4, 16} = .34$ ($N = 21$)			
Robustness$^{\text{FIC}}$	**−.55 ± .16**	**−.17 ± .05**	**−3.39**	<.01	−.20 ± .25	−.17 ± .21	−.79	
Body length (SVL)$^{\text{FIC}}$	.02 ± .17	.01 ± .11	.13		−.03 ± .28	−.06 ± .54	−.10	
Foraging mode$^{\text{FIC}}$	.20 ± .16	.05 ± .04	1.22		.22 ± .25	.16 ± .18	.90	
Habit$^{\text{FIC}}$	.25 ± .17	.06 ± .04	1.47		.06 ± .29	.04 ± .19	.20	
Gekkonidae:	$R^2 = 0.397$, $F_{6, 55} = 6.03$ ($N = 62$)			<.001	$R^2 = .097$, $F_{6, 46} = .81$ ($N = 53$)			
Robustness$^{\text{FIC}}$	**−.59 ± .12**	**−.42 ± .08**	**−4.98**	<.001	−.03 ± .16	−.04 ± .19	−.21	
Body length (SVL)$^{\text{FIC}}$	.22 ± .12	.22 ± .12	1.75		.02 ± .16	.03 ± .28	.12	
Specialized tail$^{\text{FIC}}$	**−.29 ± .12**	**−.12 ± .05**	**−2.55**	<.05	−.23 ± .17	−.17 ± .12	−1.40	
Foraging mode$^{\text{FIC}}$	−.05 ± .11	−.02 ± .04	−.48		−.10 ± .15	−.07 ± .10	−.68	
Habit$^{\text{FIC}}$	.22 ± .12	.08 ± .04	1.94		**.35 ± .17**	**.23 ± .11**	**2.09**	<.05
Activity$^{\text{FIC}}$	−.04 ± .12	−.02 ± .06	−.34		−.14 ± .15	−.12 ± .14	−.89	
Iguanidae:	$R^2 = .323$, $F_{4, 35} = 4.18$ ($N = 40$)			<.01	$R^2 = .430$, $F_{4, 24} = 4.52$ ($N = 29$)			<.01
Robustness$^{\text{FIC}}$	**−.60 ± .16**	**−.31 ± .08**	**−3.84**	<.001	.29 ± .18	.41 ± .26	1.59	
Body length (SVL)$^{\text{FIC}}$	**.42 ± .15**	**.27 ± .10**	**2.72**	<.05	−.22 ± .17	−.49 ± .38	−1.28	
Foraging mode$^{\text{FIC}}$	−.10 ± .14	−.03 ± .03	−.75		**.37 ± .16**	**.24 ± .11**	**2.26**	<.05
Habit$^{\text{FIC}}$	.18 ± .15	.03 ± .02	1.25		.31 ± .17	.17 ± .10	1.81	
Lacertidae:	$R^2 = .654$, $F_{2, 17} = 16.09$ ($N = 20$)			<.001	$R^2 = .292$, $F_{2, 13} = 2.68$ ($N = 16$)			
Robustness$^{\text{FIC}}$	**−.79 ± .16**	**−.36 ± .07**	**−5.10**	<.001	.17 ± .24	.13 ± .17	.72	
Body length (SVL)$^{\text{FIC}}$	**.67 ± .16**	**.51 ± .12**	**4.31**	<.001	.48 ± .24	.53 ± .26	2.03	
Pygopodidae:	$R^2 = .860$, $F_{5, 12} = 14.72$ ($N = 18$)			<.001	$R^2 = .299$, $F_{5, 12} = 1.02$ ($N = 18$)			
Robustness$^{\text{FIC}}$	.01 ± .28	.01 ± .27	.05		.61 ± .39	.63 ± .40	1.56	
Body length (SVL)$^{\text{FIC}}$	−.05 ± .24	−.09 ± .40	−.22		−.14 ± .34	−.24 ± .58	−.41	
Habit$^{\text{FIC}}$	.19 ± .18	.06 ± .06	1.04		−.13 ± .26	−.04 ± .09	−.51	
Activity$^{\text{FIC}}$	**.72 ± .22**	**.28 ± .09**	**3.23**	<.01	.20 ± .31	.08 ± .13	.65	
Scincidae:	$R^2 = .455$, $F_{6, 76} = 10.58$ ($N = 83$)			<.001	$R^2 = .263$, $F_{6, 44} = 2.62$ ($N = 51$)			<.05
Robustness$^{\text{FIC}}$	**−.60 ± .11**	**−.34 ± .06**	**−5.27**	<.001	−.18 ± .16	−.24 ± .22	−1.11	
Body length (SVL)$^{\text{FIC}}$	**.37 ± .10**	**.34 ± .09**	**3.66**	<.001	**.31 ± .15**	**.64 ± .32**	**2.03**	<.05
Leg development$^{\text{FIC}}$	**.29 ± .10**	**.15 ± .05**	**2.92**	<.01	.06 ± .15	.06 ± .16	.40	
Foraging mode$^{\text{FIC}}$	**.26 ± .10**	**.12 ± .05**	**2.54**	<.05	.14 ± .17	.14 ± .17	.84	
Habit$^{\text{FIC}}$	.07 ± .09	.03 ± .04	.85		−.05 ± .14	−.04 ± .11	−.33	
Activity$^{\text{FIC}}$	−.01 ± .09	−.01 ± .05	−.16		**−.35 ± .14**	**−.40 ± .16**	**−2.47**	<.05

Note. All factors were corrected for phylogeny using Felsenstein's independent contrasts (FIC). Values shown are the standardized Beta coefficients (calculated assuming all factors have a mean of 0 and SD of 1) and the ß coefficients for each factor tested; values in bold indicate a significant contribution of that factor to the dependent variable. SVL = snout-vent length.

were likely to represent damage due to capture or postmortem handling. The incidence of lost/regenerating tails was arcsine–square root transformed to accommodate dealing with proportions; this measure was not different from a normal distribution (K-S, $d = 0.08$, $P > 0.20$).

For all species, the following independent factors were also recorded.

Body size. SVL was recorded as average values (or median reported, i.e., avoiding extremes). These data were log transformed to meet the requirements of normal distribution (K-S, $d = 0.06$, $P > 0.20$).

Robustness. We drew extensively from Meiri (2010) for body mass (m_b; g) data, and we support his statement that body mass data are not sufficiently reported in the literature. Ro-

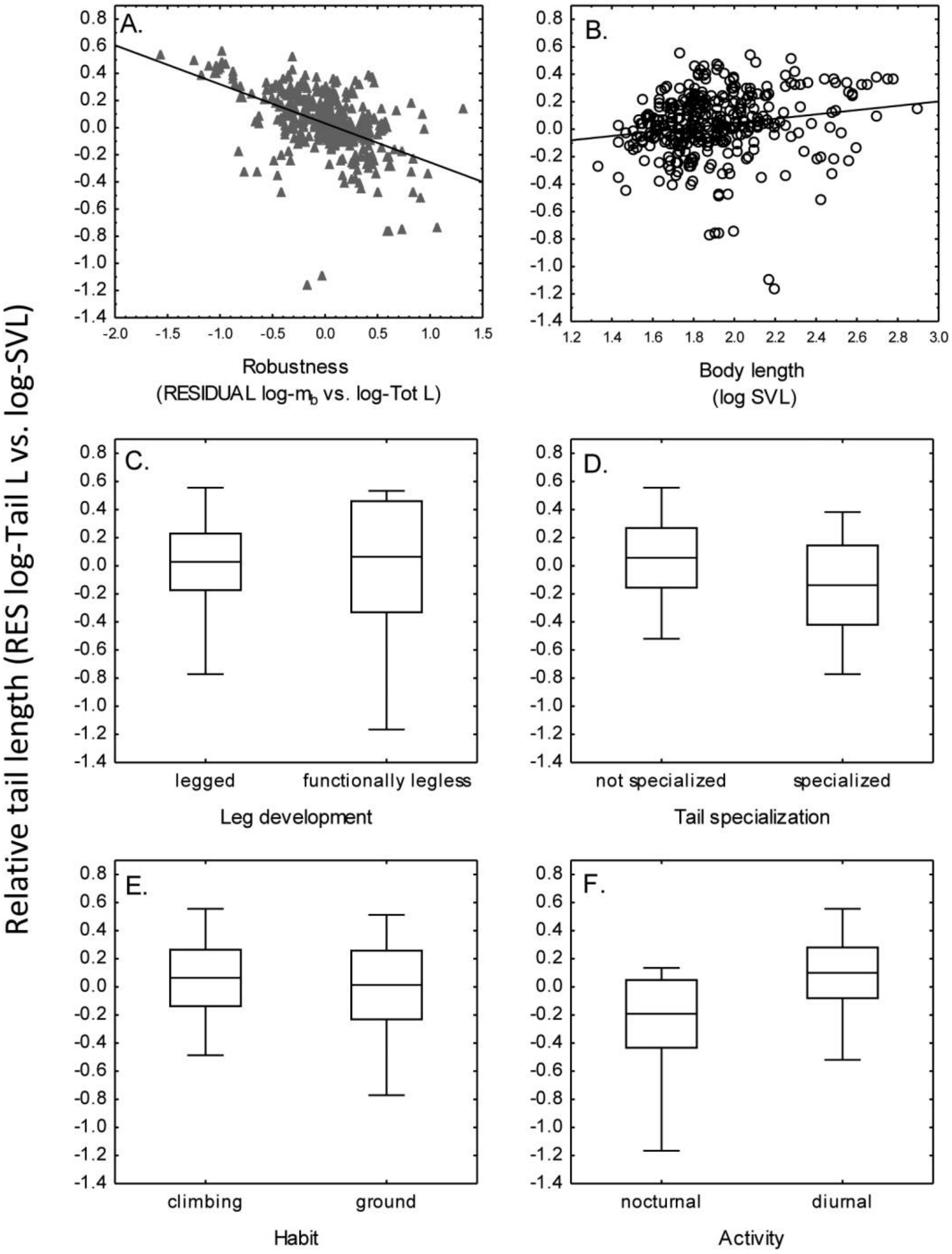

Figure 1. Relative tail length for 350 lizard species compared with body form and behavior factors that showed a significant relationship with this dependent variable. For scatterplots, each point represents a species; for box-and-whisker plots, values are the means ± 1 SD, and whiskers represent the nonoutlier range. m_b = body mass; RES = residual; SVL = snout-vent length; Tot L = total length.

bustness was calculated as the residual of log m_b versus log total length (where total length = SVL + TL). This measure of robustness was not significantly different from a normal distribution (K-S, $d = 0.05$, $P > 0.20$). We included TL in the measure (i.e., used total length rather than just SVL) because robustness of the tail was specifically of interest for this study.

Leg development. This was recorded for each species from literature records, identifying each species as either functionally legless ($=0$; including legs that are reduced and not likely to be able to bear the animal's body mass) or legged ($=1$).

Tail specialization. Given that there are so many potential functions for lizard tails, we applied a fixed set of criteria

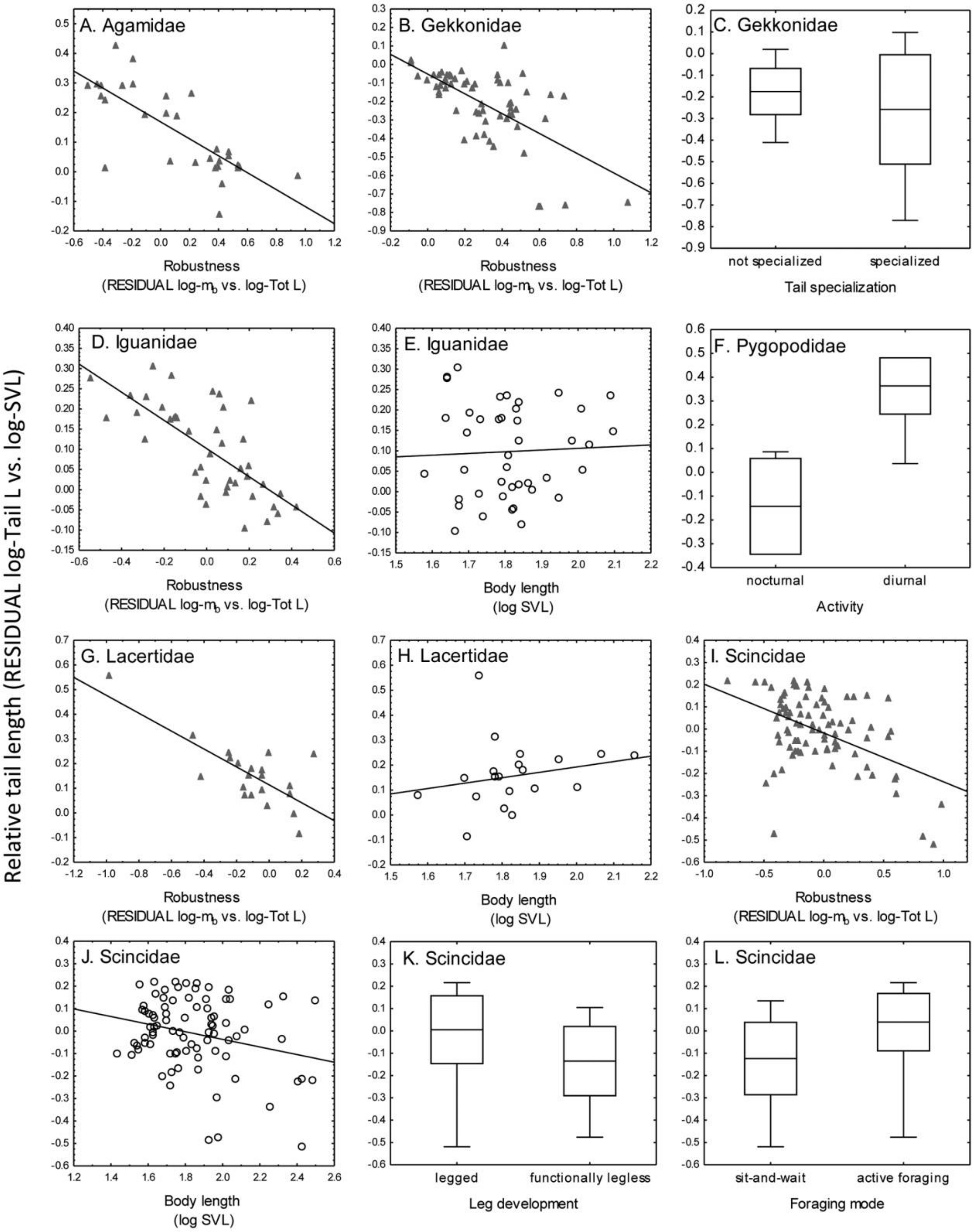

Figure 2. Summary of factors that are significantly correlated with relative tail length (% of snout-vent length [SVL]) of a series of lizards of six families (30 agamids, 63 geckos, 41 iguanids, 21 lacertids, 19 pygopodids, and 84 skinks). For scatterplots, each point represents a species; for box-and-whisker plots, values are the means ± 1 SD, and whiskers represent the nonoutlier range. Although the relationship for skinks appears to be negative on the two-way plot (*I*), the slope (ß) of this factor is positive when considered together with all the other variables in the multiple regression analysis (table 2). m_b = body mass; Tot L = total length.

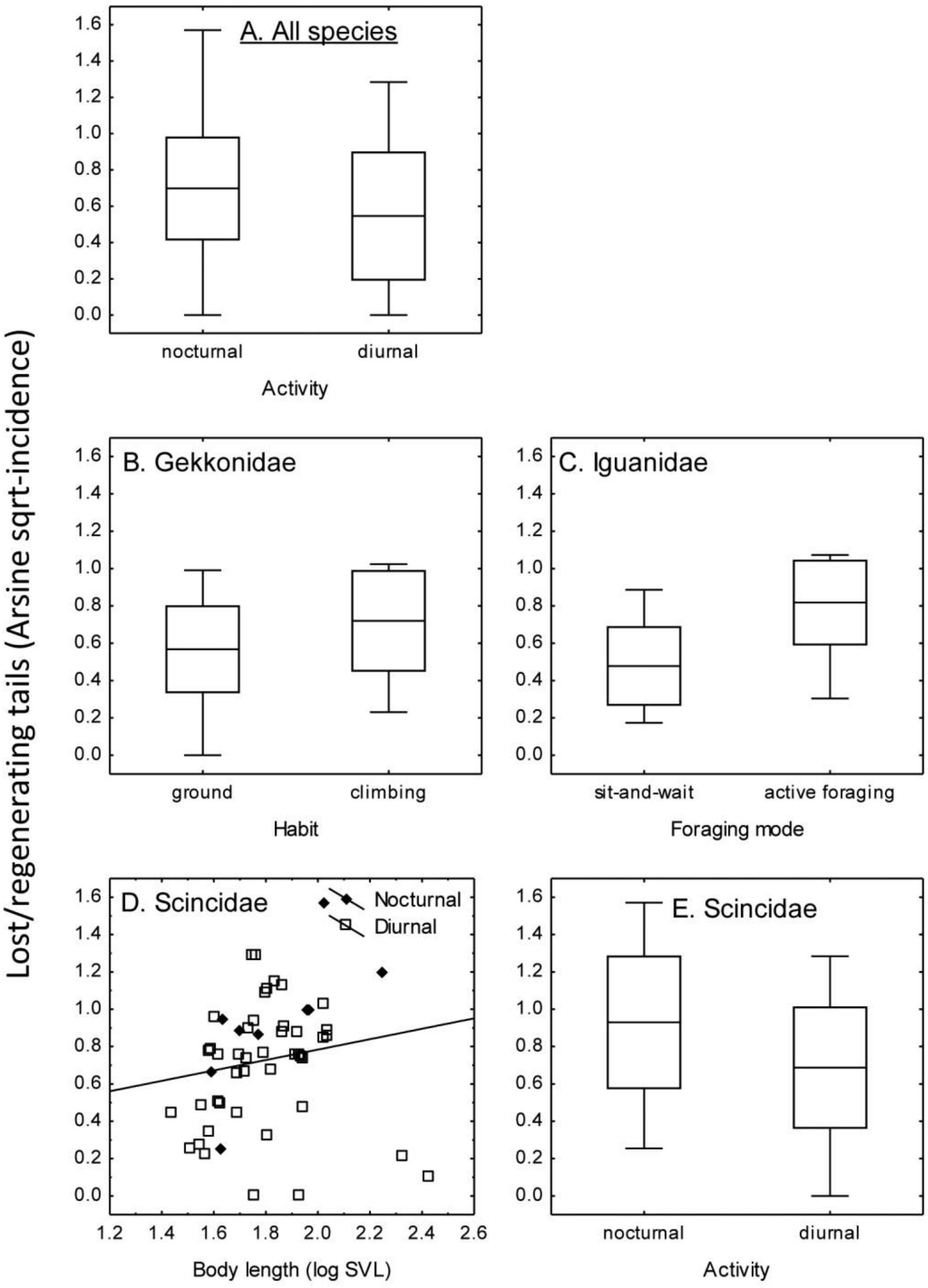

Figure 3. Incidence of lost/regenerating tails for 246 lizard species (*A*) compared against activity and then significant factors for skinks (*B*, *C*) and iguanids (*D*). For scatterplots, each point represents a species; for box-and-whisker plots, values are the means ± 1 SD, and whiskers represent the nonoutlier range. sqrt = square root; SVL = snout-vent length.

(largely following Bauer and Russell 1994) to identify tail specialization and therefore did not include functions such as social display, storage of lipids, propulsion (terrestrial or swimming), or use as a counterbalance. The presence of an actively functional tail (not specialized = 0; specialized = 1) was considered for each species on the basis of behavior/anatomy observations (literature). Species classified as having specialized tails had tails that are prehensile (e.g., chameleons, some varanids, *Corucia zebrata*, *Anguis fragilis*, *Elgaria multicarinatus*, *Hoplodactylus* spp., *Naultinus* spp., *Rhacodactylus* spp.), bear an adhesive pad (e.g., *Lygodactylus* spp., *Eurydactylodes* spp., *Bavayia* spp.), have defensive squirting glands (e.g., *Strophurus* spp.), have specialized anatomy and function (e.g., *Nephrurus* spp.), or are modified (sometimes as part of whole-body modifications) to be able to block tunnels (e.g., *Uromastyx acanthinurus*, *Diplodactylus conspicillatus*, *Egernia depressa*, *Egernia stokesii*).

Foraging mode. This was derived from literature records (e.g., Meiri et al. 2012). Taxa were predominantly classified as either sit-and-wait (=0) or active foraging (=1).

Spatial habit. We recorded the physical niche of each species on the basis of literature records (e.g., Brandley et al. 2008) or field observations, classifying animals as ground dwelling (=0; principally terrestrial but also species noted as semifossorial, fossorial/burrowing) or climbing (=1; arboreal, semiarboreal, and saxicolous).

Temporal activity patterns. We recorded temporal niche for each species (taxon predominantly nocturnal = 0; diurnal = 1).

Statistics

We acknowledge that there is likely to be a phylogenetic signal in this data set. To deal with this, we carried out Felsenstein's (1985) independent contrasts (FIC) method to take into account phylogenetic relationships. The phylogeny developed (app. B, available online) was based on broad taxonomic classifications to distinguish among recognized suborders, families, and subfamilies (NCBI 2013), with resolution of polytomies where possible following the most recent available phylogeny available for each group (29 source trees; app. B). Most source trees were derived from morphological and mtDNA characters, although nuclear DNA sequences and other sources of data were also used. Polytomies were handled by using zero branch lengths; branch lengths were set according to Pagel's method (Garland et al. 1992).

We used the FIC method in the computer program PDAP (Garland et al. 1992, 1993, 1999; Garland and Ives 2000) running through Mesquite (ver. 2.75; Midford et al. 2009). Phylogenetically independent contrasts of each dependent and independent variable (FIC) were calculated. FIC values were standardized using the branch length transformation (square root) that produced the least correlation between the absolute standardized FIC value and its standard deviation (Garland et al. 1992).

The functions of tails are not mutually exclusive, and lizard tails are therefore subject to multiple selective pressures. Selective pressures could work in concert (e.g., selection for tails that are readily autotomized and also show a great deal of movement postautotomy, ensuring that they attract the attention of the potential predator; Higham et al. 2013), or they could counteract each other (e.g., election for thinner, more fragile tails that can be more readily autotomized as an antipredator mechanism competes with selection for stouter tails that could contribute to propulsion during locomotion; Arnold 1984). Because of the multiple layers of selection likely to be acting on lizard tails, we have elected to undertake a multivariate analysis, where all the potential independent factors are considered simultaneously in the analyses.

Data were analyzed by multiple regression separately for the two dependent variables (relative tail length^{FIC} and the incidence of lost/regenerating tails^{FIC}) and FIC values of the independent factors (table 1). Data were analyzed for all species and then separately for six families for which there were sufficient numbers of species ($n \geq 17$) for which data were available (Agamidae, Gekkonidae, Iguanidae, Lacertidae, Pygopodidae, Scincidae). For analyses at the family level, we tested only traits where there were more than five species in each category (e.g., >5 diurnal species but also >5 nocturnal species). Using the FIC values generates (n species − 1) contrasts.

Results

Table 2 summarizes the results of multiple regression analyses investigating relationships between relative tail length^{FIC} and the incidence of lost/regenerating tails^{FIC} with FIC measures of body form and ecology. The FIC data met the expectations of multiple regression analyses (distributions of the residuals did not differ from a normal distribution). The significant relationships for these analyses are illustrated in figures 1–3, where the raw values for individual species (not the FIC values) are presented.

a. Relative Tail Length

Relative tail length^{FIC} (n = 350 species) was influenced by all of the factors tested (table 2, pt. a).

Robustness. Gracile species have relatively longer tails than do robust species. Patterns with robustness were evident for all 350 species considered together (fig. 1*A*) as well as for 30 agamid (fig. 2*A*), 63 gecko (fig. 2*B*), 41 iguanid (fig. 2*D*), 21 lacertid (fig. 2*G*), and 84 skink (fig. 2*I*) species (but not for 19 pygopodid species).

Body Size. There was a positive correlation between relative tail length^{FIC} and body length^{FIC} when all species were analyzed together (fig. 1*B*), as well as for the iguanid (fig. 2*E*), lacertid (fig. 2*H*), and skink (fig. 2*J*) species (but not for the agamid, gecko, or pygopodid species). Although the relationship for skinks appears to be negative on the two-way plot (fig. 2*J*), the slope (ß) of this factor is positive when considered together with all the other variables in the multiple regression analysis.

Leg Development. There was a greater range in relative tail length for functionally legless species compared with legged species when all taxa were analyzed together (fig. 1*C*) and overall longer tails for legged species (positive ß values in table 2). At the family level, leg development^{FIC} could be tested only for skinks (since there are no legless agamids, geckos, iguanids, or lacertids and no legged pygopodids). As for the all-species analysis, legged skinks have longer tails than do functionally legless skinks (fig. 2*K*).

Tail Specialization. Specialized tails are shorter than nonspecialized tails for all species analyzed together (fig. 1*D*) and for the 63 gecko species (27 of which had specialized tails; fig. 2*C*; note the negative values on the *Y*-axis—most geckos have shorter tails than predicted). We had fewer than five species with specialized tails for each of the other families and therefore could not test this trait for other families.

Foraging Mode. There was no significant effect of foraging mode$^{\mathrm{FIC}}$ on relative tail length$^{\mathrm{FIC}}$ when all species were analyzed together; similarly, there was no significant effect for agamids, geckos, or iguanids. For skinks, widely ranging active foragers have longer tails than do sit-and-wait species (fig. 2*I*).

Spatial Habit. For all species analyzed together, climbing species have relatively longer tails than do ground-dwelling species (fig. 1*E*; positive ß in table 2, pt. a). Habit$^{\mathrm{FIC}}$ was not significantly related to relative tail length$^{\mathrm{FIC}}$ for agamids, geckos, iguanids, pygopodids, or skinks.

Temporal Activity Patterns. For all species analyzed together, diurnal species have relatively longer tails than do nocturnal species (fig. 1*F*); the same pattern was evident for pygopodids (fig. 2*F*). Activity$^{\mathrm{FIC}}$ was not significantly related to relative tail length$^{\mathrm{FIC}}$ for geckos or skinks.

b. Incidence of Lost/Regenerating Tails

When all 246 species were analyzed together, the incidence of lost/regenerating tails$^{\mathrm{FIC}}$ was correlated with activity$^{\mathrm{FIC}}$ (table 2, pt. b): nocturnal species have more lost/regenerating tails than do diurnal species (fig. 3*A*). For 54 gecko species, climbing taxa show more lost/regenerating tails than do ground-dwelling species (fig. 3*B*). There is a higher incidence of lost/regenerating tails in active-foraging species than in sit-and-wait iguanid species (30 species; fig. 3*C*). For 52 skink species, there are more lost/regenerating tails in bigger skinks (fig. 3*D*) and more for nocturnal skinks than for diurnal skinks (fig. 3*E*).

Discussion

In this study, we present compelling evidence that body form (robustness, size, leg development, and tail specialization) and ecology (foraging mode, ground dwelling vs. climbing, temporal activity patterns) influence relative tail length for 350 lizard species. Although it is less conclusive, we also found factors that were associated with the incidence of lost/regenerating tails among 246 species. Our findings were largely consistent with our theoretical predictions (table 1). In this discussion, we review the evidence for each factor.

Body Size

Among lizards, there are few published data addressing a relationship between body size and tail autotomy. Dial (1978) recorded that for two sympatric geckos, the larger species (*Coleonyx reticulatus*) had a lower frequency of tail breaks than did the smaller congeneric species (*Coleonyx brevis*), with *C. reticulatus* also noted as more aggressive. Daniels et al. (1985*a*) recorded higher incidence of tail autotomy in juvenile compared to adult *Christinus marmoratus* geckos during escape from a small mammalian predator. Similarly, Fox et al. (1998) found that larger male *Uta stansburiana* were less prepared to lose a tail than were smaller (younger) males. For both the last two studies, an explanation of ontogenetic difference in experience and learning could be invoked. Bateman and Fleming (2008) tested an analogous situation in Orthoptera and recorded an increase in the time taken to autotomize an entrapped limb across a range of species of increasing body size, suggesting that size may be an important determinant of the use of autotomy as an escape mechanism, particularly in association with other defense mechanisms such as armor and chemical defense.

Contrary to Arnold's (1984, 1988) predictions regarding body size, we instead found relatively longer tails in larger lizards and more lost/regenerating tails in larger skinks (e.g., *Oligosoma macgregori*, *Cyclodomorphus* spp.). It is possible that these skinks are some of the longest-lived species (Hare and Miller 2010), which may account for accrued caudal autotomies. Some of the largest lizards are nonautotomizing varanids, which have relatively elongated tails that assist with locomotion and balance (Patanant 2012). Confounding effects of speed of escape may be responsible for these somewhat confusing patterns, but the relationship between escape speed and the incidence of lost/regenerating tails has surprisingly been paid little attention.

Robustness

We found that gracile species have relatively longer tails than do more robust species, consistent with Arnold's (1984) contention that larger and, by extension, proportionally stronger lizards may rely less on autotomy as a defense mechanism because they can fight back. There was, however, no relationship between robustness and the incidence of lost/regenerating tails.

Leg Development

We found a wider range in relative tail length for functionally legless species compared with legged species, which is likely to reflect confounding effects for a fossorial lifestyle as well as locomotory constraints for species moving around in arboreal niches. Although we did not find any significant effects of leg development on the incidence of lost/regenerating tails, we recorded longer tails for legged species (positive ß coefficients when all other factors were taken into account for the all-species analysis as well as for skinks). Legless skinks appear to follow the pattern observed in snakes, with relatively shorter tails and longer bodies (Brandley et al. 2008), which is likely to reflect selection for a fossorial niche. Two-thirds of the 10 legless skink species tested are fossorial. By contrast, among 19 pygopodid species included in these analyses, only three are fossorial; the majority of pygopodids are active aboveground, that is, predominantly terrestrial (e.g., most *Delma* spp.) or semiarboreal (e.g., *Pletholax gracilis*). We noted extremely long tails in these nonfossorial legless species. For example, *Delma* spp. pygopodids have tails averaging 200%–300% of SVL. Losing the majority of the tail (48% ± 10% of individuals across 11 *Delma* spp. show sign of lost/regenerating tails) means that these animals lose two-thirds to three-quarters of their total body length. Such a substantial change in body form must affect locomotion in these animals.

A longer tail may serve to increase the length of body that legless lizards (all legless taxa) can press against the substrate they move through, adding traction and thereby forward propulsion (Pianka and Vitt 2006). Mushinsky and Gans (1992) noted that Florida sand skinks *Neoseps reynoldsi* move across substrates by pushing the anterior part of the trunk forward and away from the posterior portion of the trunk. In tailless individuals, the posterior portion of the trunk slides backward when it is straightened, slowing the animal's forward movement. Shedding their tail therefore markedly changes the mass of the animals, as well as the degree of contact with their substrate and therefore the degree of friction that can be generated with the substrate to use as points of propulsion. Longer tails may therefore have a selective advantage for legless species in terms of facilitating aboveground locomotion and escape from entrapment (autotomy). Although legged species may show greater reliance on their legs for propulsion, studies suggest that the mass of the tail in legged species also enhances traction of the hind feet, playing a significant part in locomotion in legged species (McElroy and Bergmann 2013). We note, however, that data comparing locomotion of legless and legged small lizards (including a range of body forms) are too scarce to draw substantive conclusions at present.

Tail Specialization

Previous studies have not supported the hypothesis that lizards would be less willing to autotomize a specialized tail (e.g., Vitt et al. 1977; Bauer and Russell 1994). When Bauer and Russell (1994) tested this theory, they found that an actively functional tail resulted not in loss of the ability to autotomize or a difference in the prevalence of autotomy in populations but in a change of the position at which the tail is lost; species that use their tail to grip the substrate demonstrate more proximal tail loss (i.e., they no longer have intravertebral fracture planes in the more distal vertebrae). In this study, we found that specialized tails were likely to be shorter than unspecialized tails, but we found no evidence of different incidence of lost/regenerating tails.

Foraging Mode

Huey and Pianka (1981) noted that of six sympatric lacertid species, those that are sit-and-wait foragers, which generally use crypsis to escape detection by predators, had relatively shorter tails than species that escape by running (and that are generally widely foraging). Vitt (1983) found a similar result for 12 sympatric species. However, we found no significant effect of foraging mode on relative tail length for all 350 species considered together or for 30 agamid, 63 gecko, or 41 iguanid species; however, among 84 skink species, active-foraging species have longer tails than do sit-and-wait species. Furthermore, active-foraging iguanids show more lost/regenerating tails (30 species tested).

Spatial Habit

Various authors have recorded higher frequencies of autotomy for species that use more exposed or more raised (e.g., trees or rocks) microhabitats (Pianka and Pianka 1976; Pianka and Huey 1978; Jaksić and Fuentes 1980; Arnold 1984; Tanner and Perry 2007). This pattern also seems to occur intraspecifically, with some cohorts (i.e., males) that make use of higher, more exposed display perches exhibiting a higher frequency of lost/regenerating tails than do females and juveniles (Bateman and Fleming 2011). We found relatively longer tails for climbing species (long tails may be a selective advantage for balance for arboreal and saxicolous species, in addition to being beneficial to autotomize) but also more lost/regenerating tails (geckos only).

Temporal Activity Patterns

We recorded rather ambiguous results for the effects of activity patterns on lizard tails. We found that diurnal lizards had relatively longer tails (evident for all species as well as for 19 pygopodid species), but there was no pattern in terms of relative tail length for geckos or skinks (which may be due to little variability in these data; only 8% of gecko species tested were diurnal, while only 14% of skinks were nocturnal). However, we also found that there was a higher incidence of lost/regenerating tails among the few nocturnal skinks included in the analyses. Hare and Miller (2010) found no effect of activity pattern on the incidence of lost/regenerating tails or the time taken to autotomize the tail for six New Zealand lizard species. However, Downes and Shine (2001) found that tail loss rendered *Lampropholis guichenoti* more susceptible to a diurnal snake predator than was the case for intact lizards, but autotomy did not affect survival in the presence of a nocturnal snake predator. This could reflect the efficiency of nocturnal versus diurnal predators; there may be selection for efficient visually hunting predators to avoid striking at autotomizable tails (e.g., Vervust et al. 2011; but see Bateman et al., forthcoming), whereas the location on the body of a strike from a nonvisual (nocturnal) predator may be random, potentially resulting in higher autotomy rates.

Limitations of the Data for Lost/Regenerating Tails

Although we present data that simply indicate whether an animal has undergone a previous episode of caudal autotomy, there are a number of limitations of these data. First, there were factors that we could not include in our analyses because too few data were available. Despite obvious morphological differences between the sexes of many species (Jaksić and Fuentes 1980; Fobes et al. 1992), the majority of research to date suggests no significant sex difference in tail loss frequency (Vinegar 1975; Chapple and Swain 2002, 2004; Van Sluys et al. 2002; Lin et al. 2006; Hare and Miller 2010); few studies have indicated sex differences (Vitt 1981; Bateman and Fleming 2011). Additionally, tail damage is likely to be cumulative and to accrue through the life of an individual (Hare and Miller 2010). Although various authors have recorded differences in frequency of tail breaks between different age groups (Daniels 1985*a*; Fox et al. 1998), these data should be interpreted with caution. A caveat is that because of the loss of intravertebral autotomy planes in regenerated tails, subsequent autotomies using this mechanism will generally take place more proximally, and even if it has undergone multiple autotomy events, an animal will often still appear to have suffered a single caudal autotomy event (but see Vitt 1983). Therefore, although autotomy events will intuitively accumulate over time (older individuals are more likely to have undergone multiple autotomy events), it may not be possible to determine age differences in susceptibility at a single point in time or to reliably assess multiple bouts of tail loss.

Second, some species show a high incidence of lost/regenerating tails but only at the distal-most tip (e.g., the pygopodid *Pletholax gracilis*). The incidence of lost/regenerating tails may therefore not reliably reflect the selective pressures acting on these animals, and recording the position of tail breaks is likely to be just as important as recording the total incidence (Cromie and Chapple 2012). We note, however, that Vitt (1983) found no support for his predictions that a greater proportion of tail breaks should occur distal to the tail base in widely foraging species compared to sit-and-wait species.

Third, some generally nonautotomizing taxa (e.g., iguanids, some skinks) demonstrate an ontogenetic loss of vestigial fracture planes (Arnold 1984). The developmental loss of intravertebral autotomy in these groups could reflect differences in susceptibility to predation for small (young) compared with larger (old) individuals, especially for large species. The potential link with ontogenetic dietary shifts (e.g., Chapple 2003) also warrants further investigation. In some of these species (e.g., *Tiliqua* spp. skinks), juveniles can autotomize tails but apparently do not regenerate them (P. A. Fleming and P. W. Bateman, personal observations; Arnold 1984; Fenner et al. 2006). Ontogenetic differences in susceptibility to predation and changes in body size and form are worth considering in more detailed studies.

Can We Use the Incidence of Lost/Regenerating Tails to Reveal Predation Pressure?

Because caudal autotomy is an antipredator defense, it is usually, and reasonably, assumed that the incidence of lost or regenerating tails in natural populations is likely to reflect the different predation pressures that populations are subject to (Medel et al. 1988; Diego-Rasilla 2003; Chapple and Swain 2004; Cooper et al. 2004). For example, locations that harbor a high diversity of saurophagous predators may be associated with species displaying high incidence of tail loss and therefore regeneration. However, there are two major caveats pertinent to this assumption.

First, it presumes that caudal autotomy is reflected in the incidence of lost/regenerating tails, when, in fact, this reflects only attempted predation by inefficient predators (which are successfully avoided or are distracted by the shed tail; Arnold 1988). Efficient predators would leave no sign of predation on members of the population in terms of an increase in the incidence of lost/regenerating tails because the entire animal would be removed (Arnold 1988; Fox et al. 1994; Bateman and Fleming 2011). The behavior of predators may therefore be more important than predator density, but for most predators, we have little information regarding their foraging and feeding behavior (i.e., efficiency).

Second, using the incidence of lost/regenerating tails as a marker of predation does not take into account intrinsic factors that would otherwise influence the incidence of tail damage (Arnold 1988; Pafilis et al. 2009; but see Hare and Miller 2010). Making simple presumptions about predation effects on tail damage in natural populations by comparing across species largely ignores these innate factors and therefore undermines the validity of the link between the incidence of lost/regenerating tails and predation pressure.

Furthermore, examining the incidence of lost/regenerating tails provides only a snapshot in time, revealing patterns of tail damage in individual populations that may vary with sampling methods (e.g., the use of museum specimens may underestimate the incidence of tail damage as a result of collection criteria) and according to the populations sampled (e.g., Medel et al. 1988; Chapple and Swain 2004; Cooper et al. 2004). Relative tail length may provide a more robust measure of longer-term selective pressures acting on lizard tails than the incidence of lost/regenerating tails alone.

Summary and Conclusions: An "Expendable Tail" Hypothesis

For some invertebrates, such as spiders and harvestmen, it appears that the costs of losing one or two appendages are negligible (Guffey 1999; Johnson and Jakob 1999; Brueseke et al. 2001; Brautigam and Persons 2003; but see Bateman and Fleming 2006). This has led researchers to suggest that these animals effectively have "spare legs" (sensu Guffey 1999) that can be forfeited to potential predators. Could the same "spare appendage" hypothesis apply to some lizards? It is hard to imagine that lizards such as *Takydromus sexlineatus* (tail ~4.5 × SVL) and some of the *Delma* spp. (tails ~3.4–3.7 × SVL) would become substantially slower if they lost 10% of the length of their tails. What about 20%? Or 30%? Lin and Ji (2005) indicate that locomotor performance of *Takydromus septentrionalis* (tail 2.5 × SVL) is almost unaffected by tail loss until more than 71% of the tail (in length) was lost. Cromie and Chapple (2012) recently suggested that researchers have failed to consider the effects of variation in the amount of tail shed when reviewing costs associated with caudal autotomy. These very long-tailed lizard species may be extremely informative in this regard.

In conclusion, our findings may be important when we review the data related to field studies. While many studies have reported significant costs of caudal autotomy, many others have reported that there are no significant effects of caudal autotomy on locomotion (Daniels 1983, 1985*b*; Huey et al. 1990; Brown et al. 1995; McConnachie and Whiting 2003; Lin and Ji 2005), growth rate (Vitt and Cooper 1986; Martín and Salvador 1993; Althoff and Thompson 1994; Fox and McCoy 2000; Webb 2006), female fecundity (Fox and McCoy 2000), or changes in behavior (Kaiser and Mushinsky 1994; Kelt et al. 2002; Cooper 2003; McConnachie and Whiting 2003; Langkilde et al. 2005; Capizzi et al. 2007). If we are to direct studies toward assessing the costs of autotomy, perhaps we should not expect every taxon to show a significant cost of losing its tail. The present data suggest that the greatest costs of caudal autotomy are borne by larger nocturnal sit-and-wait species that rely on crypsis rather than escape by dropping their tail. We predict that these species are therefore more likely to reveal costs of autotomy when studied in the field or laboratory.

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Literature Cited

Althoff D.M. and J.N. Thompson. 1994. The effects of tail autotomy on survivorship and body growth of *Uta stansburiana* under conditions of high mortality. Oecologia 100: 250–255.

Arnold E.N. 1984. Evolutionary aspects of tail shedding in lizards and their relatives. J Nat Hist 18:127–169.

———. 1988. Caudal autotomy as a defence. Pp. 235–273 in C. Gans and R. Huey, eds. Biology of the Reptilia. Liss, New York.

Bateman P.W. and P.A. Fleming. 2006. Increased susceptibility to predation for autotomized house crickets (*Acheta domestica*). Ethology 112:670–677.

———. 2008. An intra- and inter-specific study of body size and autotomy as a defense in Orthoptera. J Orthop Res 17: 315–320.

———. 2009. To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last twenty years. J Zool (Lond) 277:1–14.

———. 2011. Frequency of tail loss reflects variation in predation levels, predator efficiency, and the behaviour of three populations of brown anoles. Biol J Linn Soc 103:648–656.

Bateman P.W., P.A. Fleming, and B. Rolek. Forthcoming. Bite me: blue tails as a "risky-decoy" defense tactic for lizards. Curr Zool.

Bauer A.M. and A.P. Russell. 1994. Is autotomy frequency reduced in geckos with "actively functional" tails? Herpetol Nat Hist 2:1–15.

Bernardo J. and S.J. Agosta. 2005. Evolutionary implications of hierarchical impacts of nonlethal injury on reproduction, including maternal effects. Biol J Linn Soc 86:309–331.

Brandley M.C., J.P. Huelsenbeck, and J.J. Wiens. 2008. Rates and patterns in the evolution of snake-like body form in squamate reptiles: evidence for repeated re-evolution of lost digits and long-term persistence of intermediate body forms. Evolution 62:2042–2064.

Brautigam S.E. and M.H. Persons. 2003. The effect of limb loss on the courtship and mating behavior of the wolf spider *Pardosa milvina* (Araneae: Lycosidae). J Insect Behav 16:571–587.

Brown R.M., D.H. Taylor, and D.H. Gist. 1995. Effect of caudal autotomy on locomotor performance of wall lizards (*Podarcis muralis*). J Herpetol 29:98–105.

Brueseke M., A. Rypstra, S. Walker, and M. Persons. 2001. Leg autotomy in the wolf spider *Pardosa milvina:* a common phenomenon with few apparent costs. Am Midl Nat 146: 153–160.

Capizzi D., L. Luiselli, and L. Vignoli. 2007. Flight initiation distance in relation to substratum type, sex, reproductive status and tail condition in two lacertids with contrasting habits. Amphibia-Reptilia 28:403–407.

Chapple D.G. 2003. Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. Herpetol Monogr 17: 145–180.

Chapple D.G. and R. Swain. 2002. Distribution of energy reserves in a viviparous skink: does tail autotomy involve the loss of lipid stores? Aust Ecol 27:565–572.

———. 2004. Inter-populational variation in the cost of autotomy in the metallic skink (*Niveoscincus metallicus*). J Zool (Lond) 264:411–418.

Congdon J.D., L.J. Vitt, and W.W. King. 1974. Geckos: adaptive significance and energetics of tail autotomy. Science 184: 1379–1380.

Cooper W.E.J. 2003. Shifted balance of risk and cost after autotomy affects use of cover, escape, activity, and foraging in the keeled earless lizard (*Holbrookia propinqua*). Behav Ecol Sociobiol 54:179–187.

Cooper W.E.J., V. Pérez-Mellado, and L.J. Vitt. 2004. Ease and effectiveness of costly autotomy vary with predation intensity among lizard populations. J Zool (Lond) 262:243–255.

Cromie G.L. and D.G. Chapple. 2012. Is partial tail loss the key to a complete understanding of caudal autotomy? Aust Ecol 38:452–455.

Daniels C.B. 1983. Running: an escape strategy enhanced by autotomy. Herpetologica 39:162–165.

———. 1985*a*. Economy of autotomy as a lipid conserving mechanism: an hypothesis rejected for the gecko *Phyllodactylus marmoratus*. Copeia 1985:468–472.

———. 1985*b*. The effect of tail autotomy on the exercise capacity of the water skink, *Sphenomorphus quoyii*. Copeia 1985:1074–1077.

Daniels C.B., S.P. Flaherty, and M.P. Simbotwe. 1986. Tail size and effectiveness of autotomy in a lizard. J Herpetol 20:93–96.

Dial B.E. 1978. Aspects of the behavioral ecology of two Chihuahuan desert geckos (Reptilia, Lacertilia, Gekkonidae). J Herpetol 12:209–216.

Diego-Rasilla F.J. 2003. Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards. Behav Proc 63: 1–7.

Downes S.J. and R. Shine. 2001. Why does tail loss increase a lizard's later vulnerability to snake predators? Ecology 82: 1293–1303.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Fenner A.L., M.N. Hutchinson, and C.M. Bull. 2006. Unique tail regeneration in a pygmy bluetongue lizard, *Tiliqua adelaidensis*. Herpetofauna 36:68–69.

Fleming P.A. and P.W. Bateman. 2012. Autotomy, tail regeneration and jumping ability in Cape dwarf geckos (*Lygodactylus capensis*; Gekkonidae). Afr Zool 47:55–59.

Fleming P.A., L. Verburgt, M. Scantlebury, K. Medger, and P.W. Bateman. 2009. Jettisoning fuel? caudal autotomy and locomotory energetics of the Cape dwarf gecko *Lygodactylus capensis* (Gekkonidae). Physiol Biochem Zool 82:756–765.

Fobes T.M., R. Powell, J.S.J. Parmerlee, A. Lathrop, and D.D. Smith. 1992. Natural history of *Anolis cybotes* (Sauria: Polychridae) from an altered habitat in Barahona, Dominican Republic. Caribb J Sci 28:200–207.

Fox S.F., J.M. Conder, and A.E. Smith. 1998. Sexual dimorphism in the ease of tail autotomy: *Uta stansburiana* with and without previous tail loss. Copeia 1998:376–382.

Fox S.F., N.A. Heger, and L.S. Delay. 1990. Social cost of tail loss in *Uta stansburiana*: lizard tails as status-signalling badges. Anim Behav 39:549–554.

Fox S.F. and J.K. McCoy. 2000. The effects of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana* in the field. Oecologia 122:327–334.

Fox S.F., S. Perea-Fox, and R. Castro Franco. 1994. Development of the tail autotomy adaptation in lizards under disparate levels of predation at high and low elevations in Mexico. Southwest Nat 39:311–322.

Gans C. and M. Fusari. 1994. Locomotor analysis of surface propulsion by three species of reduced-limbed fossorial lizards (Lerista: Scincidae) from Western Australia. J Morphol 222:309–326.

Garland T., Jr., A.W. Dickerman, C.M. Janis, and J.A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Syst Biol 42:265–292.

Garland T., Jr., P.J. Harvey, and A.R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst Biol 41:18–32.

Garland T., Jr., and A.R. Ives. 2000. Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. Am Nat 155:346–364.

Garland T., Jr., P.E. Midford, and A.R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. Am Zool 39:374–388.

Gilbert E.A.B., S.L. Payne, and M.K. Vickaryous. 2013. The anatomy and histology of caudal autotomy and regeneration in lizards. Physiol Biochem Zool 86:631–644.

Gillis G.B., L.A. Bonvini, and D.J. Irschick. 2009. Losing stability: tail loss and jumping in the arboreal lizard *Anolis carolinensis*. J Exp Biol 212:604–609.

Guffey C. 1999. Costs associated with leg autotomy in the harvestmen *Leiobunum nigripes* and *Leiobunum vittatum* (Arachnida: Opiliones). Can J Zool 77:824–830.

Hare K.M. and K.A. Miller. 2010. Frequency of tail loss does not reflect innate predisposition in temperate New Zealand lizards. Naturwissenschaften 97:197–203.

Harris V. 1964. The life of the rainbow lizard. Hutchison, London.

Higham T.E., K.R. Lipsett, D.A. Syme, and A.P. Russell. 2013. Controlled chaos: three-dimensional kinematics, fiber histochemistry, and muscle contractile dynamics of autotomized lizard tails. Physiol Biochem Zool 86:611–630.

Huey R.B., A.E. Dunham, K.L. Overall, and R.A. Newman. 1990. Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. Physiol Zool 63:845–872.

Huey R.B. and E.R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.

Jaksić F.M. and E.R. Fuentes. 1980. Correlates of tail losses in twelve species of *Liolaemus* lizards. J Herpetol 14:137–141.

Johnson S. and E. Jakob. 1999. Leg autotomy in a spider has minimal costs in competitive ability and development. Anim Behav 57:957–965.

Kaiser B.W. and H.R. Mushinsky. 1994. Tail loss and dominance in captive adult male *Anolis sagrei*. J Herpetol 28:342–346.

Kelt D.A., L.K. Nabors, and M.L. Forister. 2002. Size-specific differences in tail loss and escape behavior in *Liolaemus nigromaculatus*. J Herpetol 36:322–325.

Langkilde T., R.A. Alford, and L. Schwarzkopf. 2005. No behavioural compensation for fitness costs of autotomy in a lizard. Aust Ecol 30:713–718.

Lin Z.-H. and X. Ji. 2005. Partial tail loss has no severe effects on energy stores and locomotor performance in a lacertid lizard, *Takydromus septentrionalis*. J Comp Physiol B 175: 567–573.

Lin Z.-H., Y.-F. Qu, and X. Ji. 2006. Energetic and locomotor costs of tail loss in the Chinese skink, *Eumeces chinensis*. Comp Biochem Physiol A 143:508–513.

Martín J. and A. Salvador. 1993. Tail loss reduces mating success in the Iberian rock-lizard, *Lacerta monticola*. Behav Ecol Sociobiol 32:185–189.

McConnachie S. and M. Whiting. 2003. Costs associated with tail autotomy in an ambush foraging lizard, *Cordylus melanotus melanotus*. Afr Zool 38:57–65.

McElroy E.J. and P.J. Bergmann. 2013. Tail autotomy, tail size, and locomotor performance in lizards. Physiol Biochem Zool 86:669–679.

Medel R.G., J.E. Jiménez, S.F. Fox, and F.M. Jaksíc. 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. Oikos 53: 321–324.

Medger K., L. Verburgt, and P.W. Bateman. 2008. The influence of tail autotomy on the escape response of the Cape dwarf gecko, *Lygodactylus capensis*. Ethology 114:42–52.

Meiri S. 2010. Length-weight allometries in lizards. J Zool (Lond) 281:218–226.

Meiri S., J.H. Brown, and R.M. Sibly. 2012. The ecology of lizard reproductive output. Glob Ecol Biogeogr 21:592–602.

Midford P.E., T. Garland Jr., and W. Maddison. 2009. PDAP: PDTREE package for Mesquite, version 1.15. http://mesquiteproject.org/pdap_mesquite/.

Mushinsky H.R. and C. Gans. 1992. The role of the tail in channel passage by the sand skink, *Neoseps reynoldsi*. Amphibia-Reptilia 13:393–403.

National Center for Biotechnology Information (NCBI). 2013. Taxonomy browser. NCBI, Bethesda, MD.

Pafilis P., J. Foufopoulos, N. Poulakakis, P. Lymberakis, and E.D. Valakos. 2009. Tail shedding in island lizards (Lacertidae, Reptilia): decline of antipredator defenses in relaxed predation environments. Evolution 63:1262–1278.

Patanant K.C. 2012. Heads you lose, tails you win: notes on a tail-assisted foraging behavior in *Varanus* (*Odatria*) *kingorum*. Biawak 6:74–77.

Pianka E.R. and R.B. Huey. 1978. Comparative ecology, resource utilisation and niche segregation among gekkonid lizards in the southern Kalahari. Copeia 1978:691–701.

Pianka E.R. and H.D. Pianka. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. Copeia 1976:125–142.

Pianka E.R. and L.J. Vitt. 2006. Lizards: windows to the evolution of diversity. University of California Press, Berkeley.

Schall J.J., C.R. Bromwich, Y.L. Werner, and J. Midlege. 1989. Clubbed regenerated tails in *Agama agama* and their possible use in social interactions. J Herpetol 23:303–305.

Tanner D. and J. Perry. 2007. Road effects on abundance and fitness of Galapagos lava lizards (*Microlophus albemarlensis*). J Environ Manag 85:270–278.

Van Sluys M., D. Vrcibradic, and C.F.D. Rocha. 2002. Tail loss in the syntopic lizards *Tropidurus itambere* (Tropiduridae) and *Mabuya frenata* (Scincidae) in southeastern Brazil. Stud Neotrop Fauna Environ 37:227–231.

Vervust B., H. Van Loy, and R. Van Damme. 2011. Seeing through the lizards trick: do avian predators avoid autotomous tails? Cent Eur J Biol 6:293–299.

Vinegar M.B. 1975. Comparative aggression in *Sceloporus virgatus*, *S. undulatus consobrinus* and *S. u. tristichus* (Sauria: Iguanidae). Anim Behav 23:279–286.

Vitt L.J. 1981. Tail autotomy and regeneration in the tropical skink, *Mabuya heathi*. J Herpetol 15:454–457.

———. 1983. Tail loss in lizards: the significance of foraging and predator escape modes. Herpetologica 39:151–162.

Vitt L.J., J.D. Congdon, and N.A. Dickson. 1977. Adaptive strategies and energetics of tail autotomy in lizards. Ecology 58: 326–337.

Vitt L.J. and W.E.J. Cooper. 1986. Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): age-specific differences in costs and benefits. Can J Zool 64:583–592.

Webb J.K. 2006. Effects of tail autotomy on survival, growth and territory occupation in free-ranging juvenile geckos (*Oedura lesueurii*). Aust Ecol 31:432–440.

Zani P.A. 1996. Patterns of caudal autotomy evolution in lizards. J Zool (Lond) 240:210–220.