

The rate and pattern of tail autotomy in five species of Puerto Rican anoles

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ABSTRACT

Background: In lizards, tail autotomy is used in defence against predators.

Question: Can we infer predation regime from the frequency and pattern of tail autotomy in five lizard species?

Organisms: Five species of common Puerto Rican anoles: *Anolis cristatellus*, *A. evermanni*, *A. gundlachi*, *A. krugi*, and *A. pulchellus*.

Methods: Monte Carlo simulations. Our Monte Carlo models incorporated the probability of tail loss (as opposed to mortality) during a predatory attack, the strength of the tail over its length (tail strength modelled as a heterogeneous probability of breakage among caudal vertebrae in the tail), and age-biased sampling (young lizards are more likely to have intact tails, but less likely to be included in our sample).

Results: Our models exhibited good fit to the data, with the best fitting model showing a significant lack of fit in only one species. Our parameter estimates had biologically reasonable values. Our estimated rate of mortality from predatory attacks resulting in either mortality or tail injury was quite high (> 0.4 in the best fitting model) for all species. In three of the five species, the best fitting model included heterogeneity in the strength (probability of breakage) of the tail over its length, with the tail much more likely to break towards the tip than towards the base. The remaining two species (*A. krugi* and *A. pulchellus*), for which heterogeneous tail strength was not part of the best fitting model, are known from other studies to be ecologically and morphologically similar. These two also had the most similar estimated mortality rates.

Keywords: *Anolis*, caudal, maximum likelihood, predation, regeneration, simulation.

INTRODUCTION

Tail autotomy and regeneration are morphological features common among squamate reptiles (Etheridge, 1967; Arnold, 1984, 1988; Bellairs and Bryant, 1985; Clause and Capaldi, 2006). Autotomy is the process whereby an organism sheds a body part, typically to avoid capture (Maginnis, 2006). In most families of lizards, the tail can be dropped via breakage of the epidermis, dermis,

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and a caudal vertebra at a predetermined intra-vertebral fracture point (Etheridge, 1959, 1967; Cox, 1969; Bellairs and Bryant, 1985). Following autotomy, the tail typically regenerates but does not return to its original condition. Rather, the regenerated tail is supported by the growth of a rod of cartilage in place of the vertebrae that supported the original tail (Etheridge, 1967; Bellairs and Bryant, 1985). For this reason, regenerated tails can be easily distinguished from intact tails in radiographs, even when they very closely resemble the original tail externally.

There is abundant evidence of a defensive role for autotomy (Congdon *et al.*, 1974; Vitt *et al.*, 1977; Arnold, 1984). By shedding the tail, a lizard may occupy or distract a potential predator, facilitating escape. However, species and populations vary widely in their tendencies to autotomize, and there is also variation in the causes and consequences of autotomy among lizards. As a result, the role of autotomy in the ecology and biology of lizards has been the subject of considerable study. Many studies of tail autotomy have focused on the cost–benefit analysis of tail loss with reference to its effects on locomotor performance, social status, reproductive success, growth, and energetics (e.g. Ballinger, 1973; Vitt *et al.*, 1977; Fox and Rostker, 1982; Fox and McCoy, 2000; Gillis *et al.*, 2009; see reviews in Arnold, 1984, 1988; Bateman and Fleming, 2009). In the present study, we use the frequency and pattern of tail autotomy in five species of lizard to draw inferences about the predatory environment for these species. By ‘pattern’, we specifically mean the frequency distribution of the number of caudal vertebrae in intact and regenerated tails in this study. We are particularly interested in estimating the probability with which an injury-producing predation event results in mortality versus tail loss [we call this probability ‘predator efficiency’, following Schoener (1979)]; however, we also estimate the values of other parameters likely to influence the distribution of caudal vertebrae number in original and regenerated tails in a population of lizards, and of interest in the study of reptilian tail autotomy.

The inference of predation from tail autotomy in lizards has a long history. Classically, the raw frequency of autotomy was used as an index of predation pressure (Rand, 1954; Pianka, 1970; Tinkle and Ballinger, 1972; Vitt *et al.*, 1977; Vermeij, 1982; Van Sluys *et al.*, 2002; Cooper *et al.*, 2004). Rand (1954) was perhaps the first to infer predation pressure from the frequency of regenerated tails, suggesting that if there is a constant ratio between lizards escaping capture and those killed, then the frequency of damaged tails observed in a population increases with the level of predation pressure. Studying populations of *Cnemidophorus lemniscatus* on Honduras and its offshore islands, Rand estimated that mainland lizards suffer predation pressures eight times greater than the island lizards from corresponding differences in autotomy frequency (Rand, 1954). Subsequently, Pianka (1970) adopted these methods in a study of *Cnemidophorus tigris*, similarly assuming that differences in the frequency of broken tails between populations reflected differences in predation intensity. This method has since been widely applied to infer and compare the intensity of predation within and between populations or species (e.g. Pianka, 1967; Seligmann *et al.*, 2003; Clause and Capaldi, 2006).

However, theory challenges the simple interpretation in which autotomy frequency directly reflects predation intensity. In an influential paper, Schoener (1979) demonstrated that under a simple model where (1) predation mortality is constant over time, (2) the probability of predation injury (autotomy) is constant over time, and (3) predators are the only source of injury or death, contrary to the assumption of many prior empirical studies one does not expect higher predation intensity to produce a higher population frequency of autotomy. In fact, only predator efficiency (and not predation intensity) will influence the population frequency of autotomy in Schoener’s (1979) simple model. In particular, decreased predator efficiency is expected to increase the population frequency of autotomy

(due to less efficient predators leaving behind more survivors with regenerated tails), and vice versa. Schoener (1979) also relaxed the assumptions listed above, and although the relationship between predation intensity, predator efficiency, and the rate of tail autotomy becomes more complex for more complicated models, predator efficiency and the frequency of regenerated tails in the population are expected to be negatively correlated under most circumstances. This showed that increasing predation intensity does not necessarily increase tail autotomy frequency.

In this study, we investigated autotomy in populations of five species of *Anolis* lizards from Puerto Rico to determine whether the frequency and pattern of autotomy vary as a function of species, ecology or environment. We obtained unique data in the form of the caudal vertebrae counts for each individual in several large series of Puerto Rican lizards. These data provide information about tail autotomy because, as noted above, anoles and other lizards do not replace lost caudal vertebrae during tail regeneration.

We also used a unique method to characterize the ecological processes underlying autotomy. First, we developed alternative biological models for predation and tail loss in the lizard species of our study. Our biological models contained realistic features such as a parameter representing the relative probability that a lizard would die or survive during an injury-producing predatory attack, and another parameter describing heterogeneity in tensile strength over the length of the tail (lizard tails tend to break most easily towards the tip).

To optimize these models, we would ideally like analytic expressions for the probability distribution of caudal vertebrae number (our data) at equilibrium, as a function of our model parameters. Unfortunately, the complexity of the ecological process of tail autotomy in lizards made these models difficult to derive analytically. So instead of explicitly analysing the probability distributions of caudal vertebrae number, we used individual-based computer simulations to estimate them. We did this under several models for autotomy, as well as under a wide range of parameter conditions, finely varied among simulations. This enabled us to optimize alternative models for predation and tail autotomy by evaluating the approximate probability of our data for different model and parameter conditions (the model likelihood), all without an explicit analytic derivation of the expected probability distribution of our model. We then compared our models using standard criteria (e.g. Burnham and Anderson, 2002). Because this technique is based on numerical simulation, we call it simulation-based model estimation (and the procedure for obtaining our model estimates, simulation-based maximum likelihood, because of its similarity to standard procedures of maximum likelihood estimation). Although very computationally intensive, this unusual model estimation method has the potential to yield interesting insights into a wide variety of ecological and evolutionary problems. This is because it frees us from fitting only mathematically tractable models to sometimes idiosyncratic biological data.

As previously mentioned, our data consisted of caudal vertebrae counts and tail autotomy frequencies from five species of Puerto Rican anoles. Anoles, lizards in the genus *Anolis*, constitute the most species-rich amniote genus (Losos, 2009). The group contains an estimated 400 species distributed throughout the neotropics. The Caribbean anoles are best known for the repeated evolution of similar forms, called 'ecomorphs' for their convergent similarity in ecology and morphology, across different Greater Antillean isles (Williams, 1983; Losos, 2009). In this study, we examined the frequency and pattern of tail autotomy in five common Puerto Rican anole species: *Anolis cristatellus*, *A. gundlachi*, *A. krugi*, *A. pulchellus*,

and *A. evermanni*. Figure 1 shows the phylogenetic relationships of the species in the study (pruned from Nicholson *et al.*, 2005). According to the ecomorph categorizations of Williams (1972, 1983), *A. cristatellus* and *A. gundlachi* are both trunk-ground anoles, favouring life on trunk surfaces and foraging both there and on the ground. *Anolis krugi* and *A. pulchellus* are grass-bush species, found typically on slender blades of grass and in low-lying bushes. Finally, *A. evermanni* is the solitary representative of the trunk-crown anoles examined herein. It is an arboreal habitat specialist, utilizing the trunks and crowns of trees, as its ecomorph designation would suggest (Schoener and Schoener, 1971) (Fig. 1). Relevant to this study, grass-bush anoles in general, and *A. krugi* and *A. pulchellus* in particular, possess slender, elongate tails – sometimes nearly three times as long as their bodies. Conversely, the trunk-ground anoles, *A. cristatellus* and *A. gundlachi*, are much more robust with considerably shorter tails.

We chose the species in this study for several reasons. All five are closely related within the *Anolis* phylogeny and are from a single region, the Puerto Rican bank of Caribbean islands. A similar pool of predators exists across this region. Furthermore, these five species are all within the ‘*cristatellus* group’, a clade of anoles with similar expected ontogeny (Brandley and de Quieroz, 2004; Nicholson *et al.*, 2005) (Fig. 1). Because of their close relations, we expect these species to be similar in many of the traits that could bias inferences from autotomy frequency.

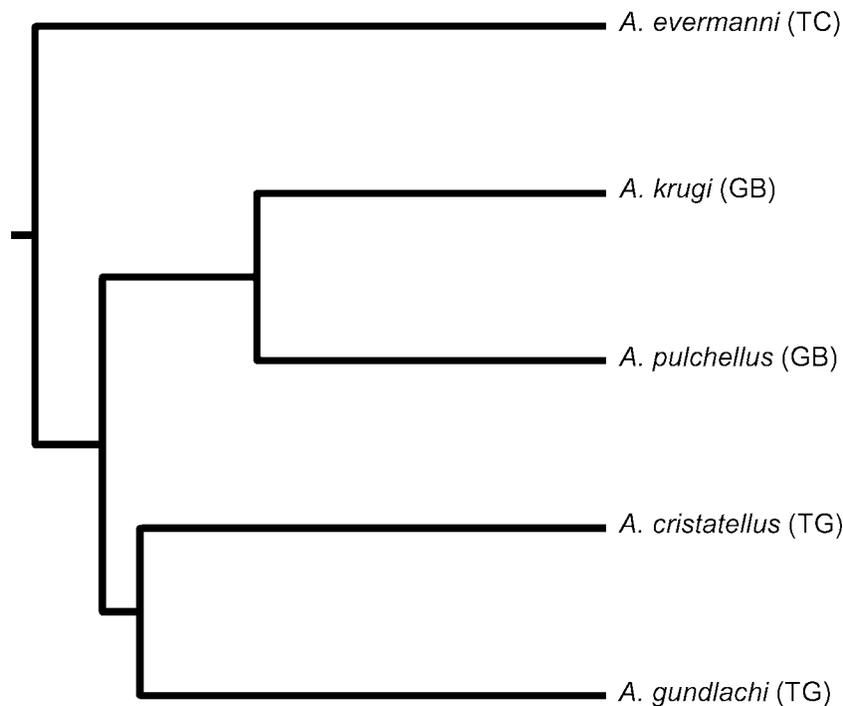


Fig. 1. Phylogenetic tree for the five species in the present study. The tree was obtained by pruning the phylogeny of Nicholson *et al.* (2005). Ecomorph categories are provided using the same coding as in Table 1.

METHODS

In the present study, we collected data for tail autotomy from five species of anoles, and then fit and compared four alternative models for tail autotomy to the data of each species. Our data consisted of caudal vertebrae counts for each individual in every sample, as well as whether each tail was original or broken and regenerated; and we fit our alternative models using a unique simulation method to estimate biologically relevant aspects of tail autotomy for the species in this study. In the following sections, we describe our procedures for data collection, our four autotomy models, and finally, our method for model estimation and comparisons.

Data collection

We sampled 1366 adult male anoles collected from 12 different localities on the main island of Puerto Rico and the small neighbouring island of Vieques. Sample sizes, reported in Table 1, were extremely heterogeneous among species for a variety of reasons unrelated to the present study. For all species aside from *A. cristatellus*, all specimens originated from one site or from a small number of nearby sites. We sampled the largest fraction of the specimens of *A. cristatellus* (712 of 924) from one locality (Cayo de Tierra, on the Puerto Rican offshore island of Vieques), whereas we collected most of the remainder of the sample for this species at Playa Lucía, near Yabucoa on the main island. In the Results, we address whether variability among *A. cristatellus* populations is likely to have influenced any of our inferences in the present study. Once collected, we preserved the specimens whole and stored them in 75% ethanol. One collector (L.J.R.) was present during the collection of all specimens used in our analyses, and all collecting was performed without bias with regard to the condition of the tail.

To score autotomy we used Varian Image View and Acquisition, and Kevex X-ray Source Interface 4.1.3 software to obtain digital radiographs of each specimen. We then used the morphometrics software tpsDig2 (Rohlf, 2008) to diagnose autotomy and obtain counts of the number of caudal vertebrae. A tail was complete in its original form if the caudal vertebrae were present from the most proximal to the most distal portion of the tail. A tail was regenerated if the distal end of the tail appeared as cartilage only, lacking ossified vertebrae. If the X-ray image was difficult to read, we re-X-rayed the tail tip to obtain a high-resolution image of the most distal vertebrae. Invariably, high-resolution X-ray images

Table 1. Descriptive statistics for each species

Species	Ecomorph	<i>N</i>	SVL (mm)	Relative TL	Frequency	Vertebrae
<i>A. cristatellus</i>	TG	924	62.1 (0.168)	1.86 (0.005)	0.712 (0.015)	39.5 (0.009)
<i>A. evermanni</i>	TC	94	61.2 (0.491)	1.86 (0.014)	0.723 (0.046)	44.0 (0.002)
<i>A. gundlachi</i>	TG	108	68.6 (0.388)	1.93 (0.010)	0.537 (0.048)	44.7 (0.015)
<i>A. krugi</i>	GB	115	47.4 (0.449)	2.63 (0.013)	0.574 (0.046)	44.9 (0.018)
<i>A. pulchellus</i>	GB	73	44.0 (0.268)	2.53 (0.015)	0.589 (0.058)	45.4 (0.047)

Note: Ecomorphs (from Williams, 1983) are as follows: TG = trunk-ground, TC = trunk-crown, GB = grass-bush. SVL is snout-to-vent length; Relative TL is the tail length calculated as a ratio over SVL, for unbroken tails only. Frequency is the injury frequency (i.e. the frequency of lizards with broken or regenerated tails). Finally, Vertebrae is the number of caudal vertebrae in intact tails. Standard errors of each mean are also provided (in parentheses).

clearly showed if the caudal vertebrae tapered and formed the original tail-tip, or if the tip of the tail had fractured and lost the most distal vertebrae.

Using the X-ray images, we counted caudal vertebrae number beginning at the most proximal vertebra with distally facing transverse processes and ending at the most posterior caudal vertebra. In cases where the tail had fractured, the final vertebra included in the count was the final intact vertebra – the fractured bone was not included in the numerical count. We also measured snout-to-vent length (SVL) and tail length from each specimen (although for all calculations involving quantitative tail length described herein, we use only original tails).

Autotomy models

We fit four different tail autotomy models using simulation-based maximum likelihood estimation and model selection. As briefly described previously, our model estimation involved simulating the biological processes of predation, tail autotomy, and mortality under a variety of models and model conditions, then comparing the equilibrium distribution for caudal vertebrae number obtained in simulations to the distributions we observed empirically. This procedure will be elaborated in a subsequent section. Our specific biological models for predation, tail autotomy, and mortality are as follows:

1. *Simple mortality model*

The simplest model used in this study was a one-parameter model. In this model, the population begins with lizards possessing tails with numbers of caudal vertebrae drawn randomly from the relative frequency distribution of unbroken tails observed in our sample for the species in question. In each time-step, a randomly chosen lizard is subject to a predation event with probability $1/N$ for a population consisting of N lizards. For all simulations of this model (and those described below), we set $N = 1000$, and the number of time-steps to 10,000. The specific value of N used for simulation is unimportant because the equilibrium relative frequency distribution of caudal vertebrae number turns out to be independent of N . We found that the time to equilibrium varied as a direct function of N , although 10,000 time-steps seemed to result in a stable equilibrium relative frequency distribution of caudal vertebrae number under all simulation conditions explored in this study.

In model (1), predation events result in mortality with a probability of m and tail autotomy with a probability of $1 - m$. Only predation (or predation attempts) with an outcome of mortality or autotomy can affect the distribution of tail lengths in the population, so no other type of attempted predation (for example, a predator attack resulting in neither mortality nor tail autotomy) is considered. Since such predation events are successful with probability m , the estimated parameter m corresponds to the efficiency of predatory attacks (Schoener, 1979).

If the outcome of predation is mortality, then the lizard is assumed to be instantly replaced by a new lizard possessing a complete tail. This assumption is fairly reasonable for species with constant population size. If the outcome of predation is autotomy, and the lizard was initially in possession of a complete tail, then the tail length of the lizard is shortened to a number of pre-break caudal vertebrae drawn from a uniform probability distribution with limits determined by the smallest observed number of pre-break caudal vertebrae and the total number of vertebrae in the original tail of the lizard:

i.e. $t_b \sim U(\min(\text{obs}), \text{original})$, where t_b is the post-autotomy number of pre-break caudal vertebrae. The uniform distribution may not be realistic in all lizards, but is a simplifying assumption of this first model.

If, by contrast, the autotomizing lizard has previously lost a portion of its tail, it is assumed that tail regeneration was effectively instantaneous and that the lizard now has a complete tail consisting of a portion that is original, t_b , and a portion that is regenerated, t_r , where $t_b + t_r$ equals the original tail length of the lizard. The assumption of instantaneous regeneration is obviously somewhat unrealistic, although certain species do regenerate tails very close to their original length and external appearance (Arnold, 1984; Bellairs and Bryant, 1985; personal observation). After a second unsuccessful predation attempt, the new tail length (in pre-break caudal vertebrae), t_b' , will be an integer drawn from the uniform distribution $\sim U(\min(\text{obs}), \text{original})$. However, if this new length is not shorter than the number of pre-break caudal vertebrae already remaining in the tail, then the lizard's tail length is unshortened (again, in terms of caudal vertebrae number) by autotomy. This is equivalent to autotomy of only cartilage-supported regenerated tail, which will obviously have no impact on the remaining number of caudal vertebrae.

There is no limit to the number of non-fatal attacks a lizard can potentially suffer (where $(1 - m)^{b-1}m$ is the probability of suffering $b - 1$ such attacks, before dying on the b th attack). However, the tail can only lose vertebrae (or stay equal in length) in each such attack, since caudal vertebrae are not regenerated after they are lost.

2. Mortality plus sampling model

One simplifying assumption of model (1) is that all lizards have an equal probability of being found in our sample, regardless of their age. Since young lizards are more likely to have complete tails, age-biased sampling will tend to skew the estimated probability distributions of the simplest model (1), above. Sampling in our study was decidedly and intentionally biased. In fact, as previously noted, we only collected adult male lizards in this study. Furthermore, our samples from different species probably contained different age biases. We have no specific *a priori* hypothesis of how these age biases might affect the distribution of caudal vertebrae number observed in our empirical samples; however, age bias will clearly influence the expected distribution of caudal vertebrae number at equilibrium.

Thus, to estimate and accommodate age bias, in so far as it affected the likelihood of our model, we introduced a new parameter, a , which represents the cut-off 'age' (measured in terms of the mean number of predation events per individual in the population) below which individuals will be excluded from the sample. In all other respects, this model is the same as model (1). In fact, if $a = 0.0$, this model reduces to model (1).

The parameter a has a second possible interpretation. If we were to make the assumptions that the age bias in sampling was similar among the different species in this study, and that m has the same value in juveniles and adults, then the parameter a should indicate the expected number of predation events from hatching to 'adulthood' (defined only by the criterion that adulthood allows inclusion in the study). Thus, high a might also indicate a higher overall rate of predation in the population. Combining a with the predator efficiency, the probability of survival to adulthood (inclusion in our study) then becomes $(1 - m)^a$. Note that a cannot be interpreted this way if m varies among different life stages. For example, if m is very high on young lizards (meaning that a predator attack is much more likely to result in mortality than autotomy), then our estimate of a will tend towards

zero (even though the probability of survival to adulthood in this case is probably nowhere near 1.0). This is because as m goes to 1.0 for juveniles, all lizards surviving to adulthood will have intact tails, even if their cohort suffered intense predation pressure.

Sampling bias and the average number of predation events prior to adulthood are two very different interpretations of the parameter a . This is because these two factors cannot be effectively disentangled in our data. Thus, it might be better to consider a to be a ‘nuisance’ parameter in the present models (with several possible biological interpretations, which we will address again in the Discussion).

3. Mortality plus tail strength model

Another simplifying assumption of model (1) is that the strength of the tail is invariant along its length. To incorporate heterogeneity in the tensile strength of the tail along its length, we introduced a new parameter, s , as a scaling parameter of the location of tail autotomy. We modelled variation in tail strength across its length as heterogeneity in the probability of autotomy from the base of the tail to its tip. To do this, we drew autotomized tails randomly from a β -distribution with shape parameters $\alpha = 1.0$ and $\beta = 1/s$. The probability of tail autotomy as a function of caudal vertebra number, x , is thus given by the modified β probability density function:

$$f(x) = \left(\frac{1}{x_I - x_{\min}} \right) \left(\frac{\Gamma(1 + 1/s)}{\Gamma(1/s)} \right) \left(\frac{x - x_{\min}}{x_I - x_{\min}} \right)^{\frac{1}{s} - 1}. \quad (1)$$

In this equation, x_I and x_{\min} are the intact tail length and the smallest numbers of caudal vertebrae found in the sample, respectively, and $\Gamma(z)$ represents the Γ function evaluated at z .

We chose the modified β -distribution, given above, because the probability of tail autotomy increases monotonically towards the tip of the tail when $0.0 < s < 1.0$, and decreases monotonically with tail length when $s > 1.0$. (Monotonically increasing tail strength towards the tip of the tail seems very biologically unrealistic in anoles. Unsurprisingly, no data set suggested an optimal value of $s > 1.0$; see Results.) When $s = 1.0$, the probability of tail autotomy is uniform across the length of the tail. Figure 2 shows the expected probability distributions of tail post-autotomy caudal vertebrae numbers for several values of s estimated in this study (see Results). In all other respects, model (3) is the same as model (1) – and reduces to model (1) if $s = 1.0$, as noted above. (This is also evident in equation 1 because it reduces to the uniform probability density function if $s = 1.0$.)

4. Full model

We also evaluated a full model in which we simultaneously estimated: the probability of mortality during a predation event resulting in either mortality or tail autotomy, m (vs. the probability of tail autotomy during a predation event, $1 - m$); the sampling threshold, a , in terms of mean predation events per individual in the population; and, finally, a scaling parameter for the strength of the tail over its length, s . If s is fixed at 1.0 and a is fixed at 0.0, then this model also reduces to model (1).

Monte Carlo simulation-based model identification

As briefly noted earlier, we used Monte Carlo simulation-based likelihood estimation to fit our four alternative models of tail autotomy to the pattern of tail loss in five species of

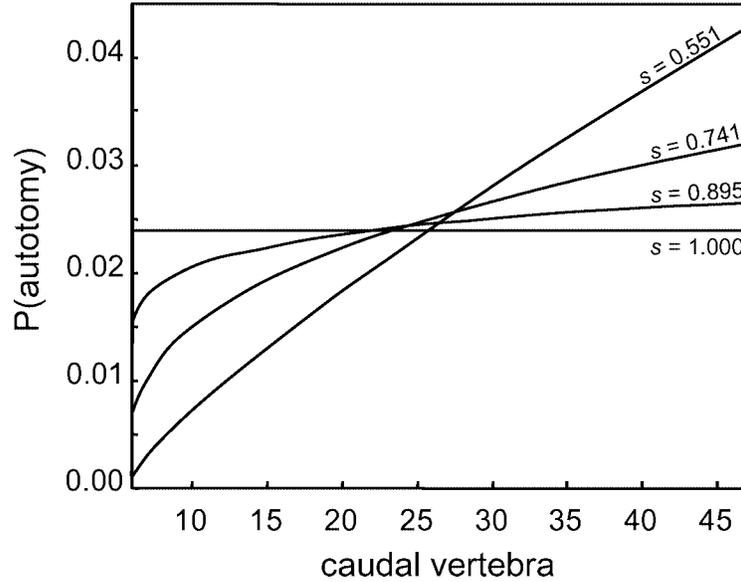


Fig. 2. Probability functions for the location of tail autotomy in caudal vertebrae rank for various values of the tail strength parameter, s , estimated in this study. When the autotomy event is the first that an individual experiences, the break position is also the number of remaining caudal vertebrae after the predation attempt. $s = 1.0$ indicates no variation in the strength of the tail along its length, whereas $s < 1.0$ indicates that the tail is more likely to break near the tip than near the base. Since *Anolis* tails are generally thickest at their base, we might expect $\hat{s} < 1.0$, and indeed no instance of $\hat{s} > 1.0$ was found in this study (see Results; Table 3).

Anolis lizards. We used a simulation-based approach for estimation because the predicted equilibrium distributions of caudal vertebrae for different models of tail loss are not available. Rather than attempt to derive these complicated distributions analytically, we performed Monte Carlo simulations to obtain mean equilibrium relative frequency distributions for each model and set of parameter conditions.

Under the assumption that the true unknown equilibrium probability distribution for each model and set of parameter conditions would be approximated by the large sample average relative frequency distribution across simulations, i.e.

$$p(x) \approx \frac{1}{r} \sum_{i=1}^r f_{\text{sim}(i)}(x), \quad (2)$$

we used simulation-obtained mean relative frequency distributions as a proxy for the probability distribution for parameter optimization. The approximation of the unknown probability distribution by the mean relative frequency distribution should be increasingly exact for an increasing number of replicate simulations, r .

In equation (2), $p(x)$ is the true unknown probability of x pre-break caudal vertebrae for a given set of conditions, r is the number of replicate simulations, as previously noted, and $f_{\text{sim}(i)}(x)$ is the relative frequency of pre-break caudal vertebrae at equilibrium in the i th simulation. The mean relative frequency of a given value for x , $\overline{f_{\text{sim}(i)}(x)}$, should converge to

the true unknown probability of x as the number of replicates, r , becomes large (i.e. as $r \rightarrow \infty$). In our analyses, we set r to 5000 for each model and set of parameter conditions.

Because in each of our models the model parameters had natural bounds (see below), we performed a grid search of parameter space. For each model and set of parameter conditions, we first obtained the estimated probability distribution, equation (2), via 5000 numerical simulations to equilibrium. We then evaluated the approximate likelihood of the model and its parameters (θ) by computing:

$$L(\theta | \mathbf{x}, g) = \prod_{i=1}^n p(x_i) \approx \prod_{i=1}^n \frac{1}{r} \sum_{j=1}^r f_{\text{sim}(j)}(x_i). \quad (3)$$

Although this is technically an approximation of the likelihood, it should be nearly exact for large r . Indeed, we found that the likelihood, L , of a given set of simulation conditions was highly reproducible across replicated sets of simulations.

In equation (3), \mathbf{x} is a $n \times 1$ vector containing the number of caudal vertebrae in each of n lizards in the sample and g is our biological model for tail autotomy. As $p(x)$ is a probability distribution (not density function), and thus, necessarily, $0 \leq p(x) \leq 1.0$ for all values of x , (3) is expected to evaluate to a very small number for large n . For computational convenience (i.e. to avoid the need to manipulate very small numbers), we can alternatively express (3) as a log-likelihood:

$$\log(L) = \sum_{i=1}^n \log(p(x_i | g, \theta)). \quad (4)$$

After evaluating the log likelihoods of each model and parameter conditions, we can compare them using likelihood ratio tests if the models are nested. In this case, we first compute the log ratio $-2(\log(L_A) - \log(L_B))$, which is expected to be distributed as a χ^2 with degrees of freedom equal to the difference in the number of parameters in models B and A. Non-nested models can also be compared. In this case, we rely on information-theoretic model selection criteria. For this study, we use the widely applied Akaike Information Criterion, which (in its small sample corrected form) is computed as:

$$\text{AICc} = 2k - 2\log(L) + \frac{2k(k+1)}{n-k-1} \quad (5)$$

(Akaike, 1974; Hurvich and Tsai, 1989). In equation (5), k is the number of estimated parameters, while n and L are as defined above.

In addition to hypothesis testing and model selection, we also tested for absolute model goodness-of-fit by computing the standard χ^2 goodness-of-fit test statistic:

$$\chi^2 = \sum_{i=\min}^{\max} (\text{freq}(i) - p(i) \cdot n)^2 / (p(i) \cdot n). \quad (6)$$

Here, we are just comparing our absolute frequency distribution of caudal vertebrae number to that predicted by each model. In equation (6), ‘min’ and ‘max’ refer to the minimum and maximum observed numbers of caudal vertebrae, respectively, and all other terms have been previously defined. The summation is expected to be distributed as a χ^2 with the number of degrees of freedom (d.f.) determined by $\text{d.f.} = \text{max} - \text{min} - k$. We

assessed model adequacy for each species and model by evaluating its goodness-of-fit given the parameter optimization, where we interpreted a non-significant χ^2 to indicate no significant lack of fit.

Note that we were also able to analytically obtain probability distributions for a given value of m under the simplest model (model 1) presented in this study. Although these results are not shown herein, using maximum likelihood we obtained results that were entirely consistent with those obtained by simulation and given below. This supports the interpretation of our method and results as a ‘simulation-based approximate likelihood method’.

RESULTS

Results from the descriptive analyses

Table 1 shows the results from a descriptive analysis of morphology (SVL and relative tail length), the frequency of tail autotomy, and the number of caudal vertebrae in unbroken tails. Relative tail length, reported here as the mean ratio of tail length over body length from lizards with unbroken tails, was highest in the two grass-bush anoles (*A. krugi* and *A. pulchellus*), and was lower and similar among the remaining three species. Caudal vertebrae number in unbroken tails was similar in all species except for *A. cristatellus*, which had relatively few caudal vertebrae (Table 1). Finally, the frequency of tail autotomy also differed among species. The highest autotomy frequencies were found in *A. cristatellus* and *A. evermanni* (Table 1).

Results from the simulation-based model estimation

We found very good fit between our estimated models and the empirical data. For four of the five species in this study, we found no significant lack of fit in the best fitting model as assessed using a χ^2 test (Table 2). We found significant lack of fit in the best fit model only in the *A. cristatellus* data set (Table 2).

We think it most likely that the lack of fit in this case is due to subtle inadequacies of our models, which only became evident when sample sizes were very large ($n = 924$ for this species). However, lack of fit might also be because *A. cristatellus* was the only species in this study for which our sample contained specimens from several distinct populations, although the majority were from one site (Cayo de Tierra, Vieques), as noted earlier. Populations of *A. cristatellus* included in our study did not differ significantly in relative tail length or tail autotomy frequency, but there were significant differences between populations in snout-to-vent length and in the number of caudal vertebrae in intact tails (although in the latter case this difference was very slight – less than one vertebra).

To test for the possibility that lack of fit in *A. cristatellus* was due to mixing collections from different sites, we separately analysed the specimen series of *A. cristatellus* collected from Vieques, which composed the majority (77%) of the *A. cristatellus* specimens used in this study. In this case, the lack of fit persisted but was marginally non-significant in the best fitting model (χ^2_{34} , $P = 0.09$). We hesitate to over-interpret this finding as it seems consistent with both of our hypotheses for lack of fit in the *A. cristatellus* data set when analysed as a whole. We also note that the simulation-based parameter estimates in the best fitting model for the Vieques *A. cristatellus* data ($\hat{m} = 0.80$, $\hat{a} = 5.40$, $\hat{s} = 0.76$) are quite similar, but not

Table 2. Goodness-of-fit for each model and simulation-based maximum likelihood parameter estimates

Species	Model	d.f.(χ^2)	χ^2	$P(\chi^2)$
<i>A. cristatellus</i> ($n = 924$)	(1)	36	303.77	<0.001
	(2)	35	109.29	<0.001
	(3)	35	105.62	<0.001
	(4)	34	54.486	0.0144
<i>A. evermanni</i> ($n = 94$)	(1)	40	69.079	0.0029
	(2)	39	41.477	0.3632
	(3)	39	43.635	0.2809
	(4)	38	34.590	0.6279
<i>A. gundlachi</i> ($n = 108$)	(1)	41	60.985	0.0230
	(2)	40	43.036	0.3426
	(3)	40	34.356	0.7217
	(4)	39	32.075	0.7761
<i>A. krugi</i> ($n = 115$)	(1)	41	31.614	0.8538
	(2)	40	20.156	0.9962
	(3)	40	23.667	0.9813
	(4)	39	18.574	0.9977
<i>A. pulchellus</i> ($n = 73$)	(1)	41	37.358	0.6333
	(2)	40	26.831	0.9449
	(3)	40	28.273	0.9178
	(4)	39	24.464	0.9666

Note: The best fit model for each species (see Table 3) is indicated in **bold** font. A non-significant χ^2 indicates no significant lack of fit. *Anolis cristatellus* was the only species for which no model showed non-significant lack of fit [although model (4) was close to being non-significant]. Degrees of freedom (d.f.) is the difference between the maximum and minimum number of caudal vertebrae, minus the number of estimated parameters in each model.

identical, to the parameter estimates obtained for all *A. cristatellus* analysed collectively (see Table 3), suggesting at least some effect of mixing samples from different populations.

Table 3 shows the simulation-based maximum likelihood estimated (sMLE) parameter values for all models and all species, together with the approximate log likelihood of each model and the small sample-corrected Akaike Information Criterion (AICc). Since each of models (1) through (3) is a special case of model (4), the likelihood of model (4) is guaranteed to be greater than or equal to the likelihoods of models (1) through (3). [Similarly, models (2) and (3) are guaranteed to have likelihoods greater than or equal to that of model (1).] However, information theory suggests that in picking the best model for inference, we should penalize parameterization (Akaike, 1974). Thus, although model (4) contains the greatest number of parameters, it is not guaranteed to be chosen by model selection unless it adds sufficient information relative to simpler models. Table 3 shows the selected model for each species in **bold** font. The most heavily parameterized model was chosen for *A. cristatellus* and *A. evermanni*, whereas we chose simpler models for tail

Table 3. Parameter estimates, approximate likelihoods, and AICc values for four models of tail autotomy in five species of Puerto Rican anoles

Species	Model	k	\hat{m}	\hat{a}	\hat{s}	$-\log(L)$	AICc
<i>A. cristatellus</i> ($n = 924$)	(1)	1	0.387	0.000	1.000	-3331.4	6664.7
	(2)	2	0.825	5.859	1.000	-3258.9	6521.9
	(3)	2	0.305	0.000	0.632	-3257.1	6518.1
	(4)	3	0.775	4.740	0.754	-3237.0	6480.1
<i>A. evermanni</i> ($n = 94$)	(1)	1	0.391	0.000	1.000	-347.1	696.3
	(2)	2	0.836	5.920	1.000	-339.9	683.9
	(3)	2	0.315	0.000	0.658	-340.2	684.5
	(4)	3	0.807	5.740	0.741	-337.8	681.9
<i>A. gundlachi</i> ($n = 108$)	(1)	1	0.523	0.000	1.000	-367.4	736.9
	(2)	2	0.813	2.988	1.000	-362.5	729.0
	(3)	2	0.436	0.000	0.551	-357.0	718.2
	(4)	3	0.678	1.433	0.647	-357.0	720.3
<i>A. krugi</i> ($n = 115$)	(1)	1	0.491	0.000	1.000	-403.2	808.4
	(2)	2	0.814	3.287	1.000	-399.8	803.8
	(3)	2	0.451	0.000	0.801	-401.1	806.2
	(4)	3	0.794	3.020	0.895	-399.5	805.2
<i>A. pulchellus</i> ($n = 73$)	(1)	1	0.454	0.000	1.000	-254.5	511.1
	(2)	2	0.804	3.518	1.000	-252.4	508.8
	(3)	2	0.413	0.000	0.770	-252.8	509.8
	(4)	3	0.799	3.706	0.893	-252.1	510.5

Note: The best fit model for each species is indicated in **bold** font. Parameters of the models are: m , the probability of mortality in a predator encounter resulting in either mortality or autotomy (thus making $1 - m$ the probability of autotomy); a , the expected number of predation events per individual in the population before they appear in our sample (also age 'cut-off,' see text); and s , a scaling parameter in the β -distribution of the probability of tail breakage over its length ($s < 1.0$ indicates a tail that is stronger towards its base; see Fig. 2).

autotomy in the other species in the study (Table 3). Figure 3 shows the observed and expected frequency distributions for tail length in terms of the number of caudal vertebrae in which the expectation is derived from the best fitting model in Table 3. Note that the observed and expected distributions are for caudal vertebrae number in lizards with both intact and regenerated tails (thus the large peaks at the right side of each distribution contain counts of lizards with original tails; Fig. 3).

Some factors limit the comparability of the parameter estimates across models. In particular, there appear to be strong interactions among the parameters in more complex models. For example, within each species, the models with the lowest estimated mortality rates (i.e. predator efficiencies), m , are those in which a is forced to be 0.0. Thus, comparing the sMLE value of m in model (4) for *A. cristatellus* (the best fitting model for this species) with the sMLE(m) in model (3) for *A. gundlachi* (the best fitting model for *A. gundlachi*; Table 3) would be misleading, because although m for *A. cristatellus* and *A. gundlachi* are fairly similar when both are estimated using the full model ($\hat{m} = 0.775$ and

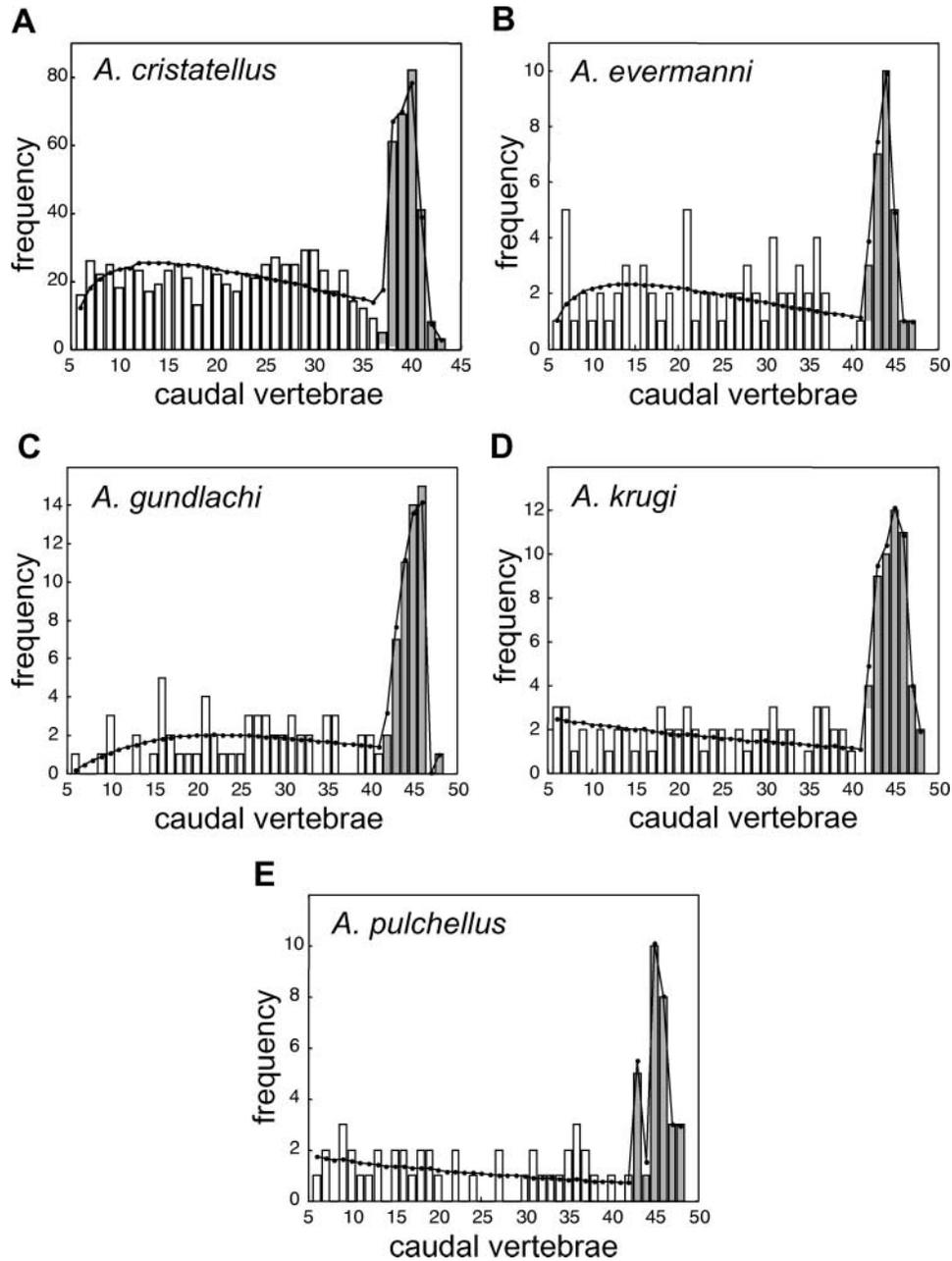


Fig. 3. Frequency histograms of the number of caudal vertebrae in five species of Puerto Rican lizards (bars), together with predicted frequencies under the best fit model of tail autotomy for each species. Note that the distributions contain lizards with both broken/regenerated and intact tails; shaded (and partially shaded) bars indicate intact tails. Species are as follows: (A) *A. cristatellus*; (B) *A. evermanni*; (C) *A. gundlachi*; (D) *A. krugi*; and (E) *A. pulchellus*. Best fit models and parameter estimates are given in Table 3. The only species for which we found significant lack of fit in the best model was *A. cristatellus* (Table 2).

$\hat{m} = 0.678$, respectively), they are quite different when compared across models and species (Table 3).

As such, when comparing each pair of species we fit only the full models. To compare autotomy in different species, we first enumerated all possible pairings. Because order matters (one species in each pair will provide the model for likelihood estimation, whereas the other will provide the data; Table 4), for five taxa there were $5 \times (5 - 1) = 20$ such comparisons in the present study. We compared tail autotomy in each pair of species by fixing the parameters m and s based on their sMLEs in the first species and then evaluating the likelihood of this model in the second species. Since we think that the best fit value for the parameter a is in part due to our sampling strategy, which may have unintentionally differed among species (see Methods), we decided to allow a to be optimized in each analysis. For each pair of species we thus obtained two likelihoods. First, we estimated the maximum likelihood for tail autotomy in species 2 (column species in Table 4), given that all three parameters were optimized, and second, we estimated the likelihood in species 2,

Table 4. A comparison of species under the full model (model 4)

Model	Data	<i>Anolis cristatellus</i>	<i>Anolis evermanni</i>	<i>Anolis gundlachi</i>	<i>Anolis krugi</i>	<i>Anolis pulchellus</i>
<i>A. cristatellus</i>						
	$\log(L(A.c.)) =$	-3237.0	-338.0	-358.0	-400.6	-253.3
	$-2\log(\text{LR}) =$	0.000	0.479	1.937	2.273	2.402
	$P(\text{LR}) =$	1.000	0.787	0.380	0.321	0.301
<i>A. evermanni</i>						
	$\log(L(A.e.)) =$	-3239.0	-337.8	-357.9	-401.0	-253.5
	$-2\log(\text{LR}) =$	3.985	0.000	1.728	2.985	2.935
	$P(\text{LR}) =$	0.136	1.000	0.421	0.225	0.231
<i>A. gundlachi</i>						
	$\log(L(A.g.)) =$	-3250.0	-339.2	-357.0	-403.5	-255.4
	$-2\log(\text{LR}) =$	26.018	2.845	0.000	7.943	6.603
	$P(\text{LR}) =$	<0.001	0.491	1.000	0.019	0.037
<i>A. krugi</i>						
	$\log(L(A.k.)) =$	-3245.8	-338.8	-360.5	-399.5	-252.5
	$-2\log(\text{LR}) =$	17.497	1.947	6.902	0.000	0.859
	$P(\text{LR}) =$	<0.001	0.378	0.032	1.000	0.651
<i>A. pulchellus</i>						
	$\log(L(A.p.)) =$	-3246.7	-338.3	-360.5	-399.6	-252.1
	$-2\log(\text{LR}) =$	19.357	1.071	6.901	0.099	0.000
	$P(\text{LR}) =$	<0.001	0.585	0.032	0.952	1.000

Note: We used the simulation-based maximum likelihood parameter estimates for m and s from the row species to calculate the likelihood for the column species. We optimized a in each case. We computed P -values by comparing two times the likelihood ratio of the compared model and the best fit model to a χ^2 distribution with two degrees of freedom (for the two additional parameters, m and s , estimated in the best fit model). Significant likelihood ratios indicate significantly different models of tail autotomy in the two species.

given that parameters m and s are forced to assume their maximum likelihood values for species 1, and only a was optimized (row species in Table 4). We then compared these two likelihoods using a likelihood ratio test.

Table 4 shows the results from this analysis. In general, we had difficulty rejecting alternative models for all species except *A. cristatellus*. As in our analysis of model goodness-of-fit (see above, Table 2), this finding may be a consequence of very good sampling effort in *A. cristatellus* ($n = 924$) compared with the other species, which may have enabled us to more easily reject the models for tail autotomy derived from most other species.

DISCUSSION

In the following, we first outline biological interpretations of the model parameters in this study. We then discuss possible ecological interpretations for the parameter estimates we obtained in our study of Puerto Rican anoles.

Interpretation of the model parameters

The mortality parameter, m

The mortality parameter is the probability of mortality given a predator encounter (where $1 - m$ is the probability of tail autotomy, and predator encounters not resulting in death or injury are ignored). Since m is the probability of a predation event being successful for the predator (given that it results in either success, i.e. consumption, or tail autotomy), m is also a measure of predatory efficiency (Schoener, 1979). Note that our estimates of m in the best fitting models were quite high; higher than rates of predator success estimated in many other studies (e.g. Vermeij, 1982). It should be kept in mind that predator efficiency in the present study only considers the success rate of predation attempts resulting in either prey mortality or autotomy, ignoring predation attempts resulting in neither, and thus we expect our estimates of m to be higher than estimates of predator success rate calculated when all types of failed predation attempts are included.

Like Schoener (1979), we find that predator efficiency (m in this study) and the frequency of tail autotomy are negatively correlated in the simplest model of tail autotomy, model (1). In fact, in spite of our complex method of model estimation, for model (1) we find that $1 - \hat{m}$ is almost approximately equal to the frequency of autotomy, as predicted by Schoener (1979), with the estimated rate of predator efficiency, m , and the raw frequency of autotomy strongly negatively correlated ($r_{\hat{m}, frequency} = -0.98$; Fig. 4). However, we also find that when additional complexity is added to our model, the sign of the relationship between the absolute frequency of tail autotomy and m actually reverses (Fig. 4). Closer examination of this pattern (not shown) reveals that the correlation between the frequency of injury and the estimated predator efficiency is negative for models in which a is set to 0.0, and positive for models in which a is estimated. We think that this could mean that if our sampling had not been biased with respect to age, we might have found that the frequency of individuals with regenerated tails was indeed higher in species with low predator efficiency (and vice versa) in our best fitting models, consistent with the prediction of Schoener (1979). (Although in this case we would probably have to accommodate heterogeneous predation pressure across age classes; also noted below.)

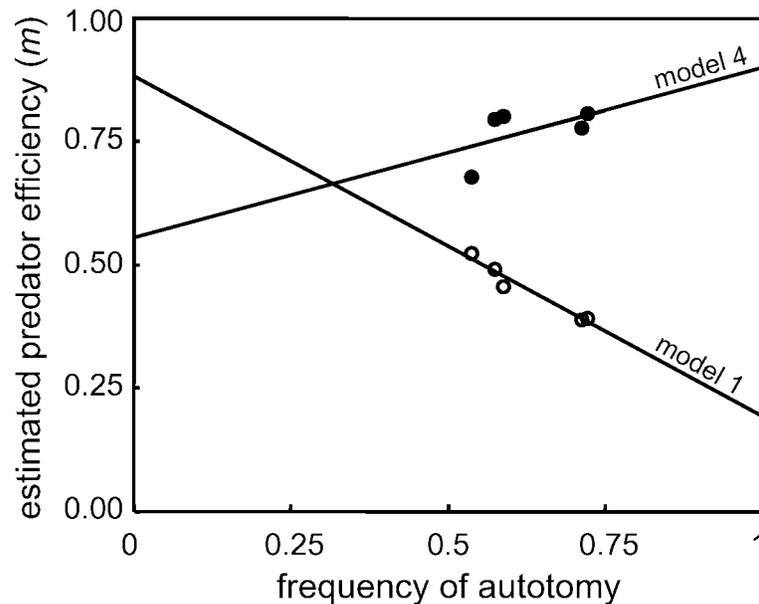


Fig. 4. Estimated predator efficiency (\hat{m}) as a function of the observed frequency of broken and regenerated tails for each of the five species in the study. m was estimated either under the simple mortality model [model (1): open dots] or under the full model [model (4): solid dots], which contains mortality, heterogeneity in the strength of tail over its length, and a parameter to correct for age-biased sampling. Details of each model are in the text.

The sampling threshold (age) parameter, a

The sampling threshold parameter, a , is the age cut-off above which an individual will be included in our sample, and below which it will be excluded (in which age is a relative value, which is in terms of the expected number of predation events from hatching to reaching the sampling threshold for our study). As previously discussed, the possible interpretations of this parameter are varied, depending on our sampling strategy. For example, if our sample included only adults of comparable actual ages from each species (say, only individuals of age t), then a/t would be interpretable as the rate of predation per lizard per unit of time, and $(1 - m)^a$ would be the probability of any lizard surviving from hatching until time t (under the assumption that m is constant over time).

Unfortunately, the sampling strategy in this study was not designed to estimate predation rate, and as such we collected lizards opportunistically. Furthermore, m is unlikely to be consistent across age classes, and among juveniles of different species. Consequently, the age bias in each sample is likely to be just as much a function of the facility of collecting each species as it will be reflective of differences in predation rate among species.

If variation in \hat{a} among species was in fact wholly due to different sampling strategies for different species, then we might expect that the variability in age (substituting size for age in the present study) would negatively covary with \hat{a} . This is because if we only collected terminal size lizards in one species (high a), the coefficient of variation in age and size should be low; whereas if we collected lizards more widely varied in age and thus size (low a), the coefficient of variation should be relatively high. In fact, contrary to this prediction,

we found a slightly positive relationship between \hat{a} and the coefficient of variation for size among the five species in this study ($r = 0.242$). This suggests that our estimates of \hat{a} are not solely a function of the sampling strategy employed for each species, and might indeed reflect differences in predation pressure among species. In spite of this suggestive result, as we did not control for age or size in our sampling effort, we hesitate to over-interpret \hat{a} and consider it to be primarily a ‘nuisance’ parameter in our models.

In an idealized data set, we would like to have had extensive and unbiased sampling from not only adult males, but also juveniles and females. However, these data would introduce additional complexity to the problem because the pressures and consequences of predation are unlikely to be identical across these different groups. We plan to investigate these possibilities in future studies.

Tail strength, s

We found that incorporating heterogeneity in the strength of the lizard’s tail across its length improved the model fit to the data in three of five species. In these species, predictably, the model parameter estimates suggested that the probability of autotomy increases towards the tip of the tail. Since anole tails are thickest at the base, this seems sensible.

The two species in which the best fitting model did not include the parameter s , *A. krugi* and *A. pulchellus*, are both grass-bush specialists (Table 1). Grass-bush anoles tend to have very long, slender tails. Our model provides the testable prediction that the tail in these species is more or less uniformly breakable across its length. Whether uniform tail strength means that the tail is uniformly fragile or uniformly strong cannot be determined from our data. Prior studies have used weights attached to the lizard’s tail to test the force required to produce autotomy (e.g. Quattrini, 1952; Brattstrom, 1965; reviewed in Bellairs and Bryant, 1985), and this type of experiment could easily be adapted to test the breaking force of the tail across its length for the species in our study. In the absence of such an experimental analysis, direct experience with these species (by L.J.R.) suggests that it is more plausible that *A. krugi* and *A. pulchellus* have uniformly strong (rather than uniformly fragile) tails.

The ecology of autotomy in Puerto Rican anoles

In this section, we interpret our tail measurements and model parameter estimates in the specific context of the ecology of Puerto Rican anole species. As we have stressed above, we offer these perspectives with caution; nonetheless, our results invite interesting interpretation that we hope will stimulate further research.

Although the classic ecomorph categories were not the primary focus of this study, a cursory comparison of Tables 1 and 3 shows some suggestive patterns. In particular, there is no notable tendency towards resemblance between the trunk-ground species, *A. cristatellus* and *A. gundlachi*. In fact, in the best fit model parameter estimates, *A. cristatellus* is much more numerically similar to *A. evermanni*, a trunk-crown anole, than it is to the more ecologically and morphologically similar *A. gundlachi* (Table 3). It is possible that predation intensity and predator efficiency do not vary considerably among trunk-ground and trunk-crown ecomorphs, or equally plausibly, that the ecology of predation is largely determined by species-specific or population-specific factors. Field study has shown that predation intensity might be similar between *A. evermanni* and *A. gundlachi* (Lister, 1981); however, an empirical measure of predator efficiency would be required to predict whether similar levels

of predation should lead to similar frequencies of autotomized and regenerated tails in these species. Comparison of autotomy frequency across populations and for more species may shed light on these possibilities.

However, the parameter estimates of the model, particularly the estimates for m and s , are virtually identical between the two grass-bush anoles, *A. krugi* and *A. pulchellus*. We expect this may result from similar morphologies and ecologies shared by these grass specialists; however, we cannot rule out an effect of shared history, as *A. krugi* and *A. pulchellus* are sisters in the context of the species sampled in this study (Fig. 1), although they are not especially closely related (Brandley and de Quieroz, 2004; Nicholson *et al.*, 2005). Both *A. pulchellus* and *A. krugi* are found almost exclusively in dense, grassy cover and previous research has shown that these species are highly similar in morphology as well as in sprinting and jumping performance (Losos, 1990). In these species, the tail probably serves a different functional role relative to the other species examined – the centre of mass of *A. pulchellus* and *A. krugi*, as well as other grass-bush anoles, is displaced towards the hindlimbs (Losos, 1990). Given a different functional role for the tail, it is plausible that these species also differ substantially from the other species in this study in their tendency to autotomize the tail. The estimates of predator efficiency (m) in the grass-bush anoles are high in the favoured models, although this does not distinguish them absolutely from other species. This may seem counterintuitive, as one might expect the greater relative tail length in these species to lead to better chances of escape through autotomy. This is because if predators strike lizards indiscriminately along their total length, and tail strikes are non-lethal with some probability, then longer relative tails should confer higher survival. However, if these species are less likely to autotomize their tails in a predatory encounter (because, for instance, the tail is critical for locomotion in these species), greater overall tail length may lead to greater expected predator efficiency. As discussed above, studies are needed to establish whether these species drop their tails more or less readily compared with other anoles.

Future studies and conclusions

Although we treat these patterns as tentative, we hope that future studies will test their generality. We recommend further investigation into autotomy parameters in *Anolis* ecomorphs of other Greater Antillean islands, as well as study of additional ecological specialists. In particular, it would be interesting to compare patterns observed in the Puerto Rican grass-bush anoles to similar long-tailed anoles elsewhere in the Caribbean, and it would likewise be interesting to assess the pattern and rate of autotomy in anoles with remarkably short tails, such as members of the twig ecomorph category.

Other factors in addition to those modelled in the present study might also influence the frequency and pattern of tail autotomy. For example, our models do not incorporate any cost to autotomy, even though various studies have demonstrated such a cost (e.g. Ballinger and Tinkle, 1979; Dial and Fitzpatrick, 1981; Fox and Rostker, 1982; Salvador *et al.*, 1995; Gillis *et al.*, 2009). This cost can come in the form of decreased locomotor performance (Ballinger, 1973; Gillis *et al.*, 2009) or decreased growth (Ballinger and Tinkle, 1979; but see Fox and McCoy, 2000), but be manifest as an increased susceptibility to subsequent predation attempts (Congdon *et al.*, 1974; Downes and Shine, 2001). There is also some evidence that environmental factors can affect the probability that a lizard will autotomize its tail in response to a predator strike. In particular, Brattstrom (1965) showed that temperature can influence the force required to autotomize the tails of the side-blotched lizard, *Uta stansburiana*, with autotomy taking place more easily at lower

temperatures. In the present study, we obtained very good fit of our models in spite of ignoring these nuances. Incorporating the several additional parameters that would have been required to fit more complicated models (e.g. a parameter for increased susceptibility; a parameter describing the gradual abatement of heightened susceptibility over time) would have been computationally prohibitive in a comparative study of several species, although we would encourage future authors to incorporate additional complexity into similar studies.

Our model makes some unrealistic assumptions. For example, regeneration is assumed to be instantaneous. In natural populations, regeneration may be rapid, but not instantaneous. We also assume that the system is at equilibrium. If the predation regime is constant over time, this may be a safe assumption. However, if a new predator has been recently introduced into the system (e.g. Losos *et al.*, 2004), then it may not yet have reached equilibrium. The rate at which equilibrium is approached will be directly proportional to the rate of predation.

In the present study, we examined the frequency and pattern of tail autotomy in five species of Puerto Rican anoles. We found that the frequency of autotomy differed significantly among species. We used the novel approach of Monte Carlo simulation-based likelihood optimization to identify the best fitting of four ecological models for tail loss in each species. We found that in two of the five species the most complex model was the best fitting model, whereas in the other three species we selected simpler models. In particular, for *A. gundlachi* the best fit model did not include age bias in the sample, while in *A. krugi* and *A. pulchellus* the best fit model did not include heterogeneity in the tail tensile strength. Finally, we note a strong ecomorph effect of the grass-bush ecology on the parameter estimates of the best fit models; however, this ecomorph effect does not appear to extend to the other classes included in the study.

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