

Snake body size frequency distributions are robust to the description of novel species

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Abstract. The accurate interpretation of body size frequency distributions (BSFDs) has important implications for understanding large-scale ecological and evolutionary patterns because they are shaped by ecological and evolutionary processes. However, incomplete species sampling, resulting either from a paucity of reliable body size data or because those species have not yet been detected/described, also has the potential to influence BSFD shape and skew when missing species are disproportionately large or small. Missing species may thus influence the skew of a BSFD, misleading subsequent interpretations. In contrast to many vertebrate taxa, the BSFDs of snakes appears to be log-normal, with no significant skew. However, the influence of imperfect species sampling on these distributions has however not been previously evaluated. We collated body size data and date of description for 300 species of elapid, and 264 species of viperid snakes and assessed the shape and skew of the BSFD of each clade. Next we tested the hypothesis that date of description was related to body size in each clade. We show that the BSFDs of elapid and viperid snakes are both log-normal, with no significant skew. Moreover we demonstrate size-related differences in the probability of detection (as measured by year of description) among elapids and vipers: in both lineages, species with larger body size tend to have been described earlier. However, simulations testing the effect of the addition of novel, small-bodied species revealed that the distributions of elapids and vipers are not highly vulnerable to becoming significantly skewed in the future. Our results support current interpretations of BSFDs in snakes that suggest a lack of size-associated biases in the speciation and extinction rates of this clade.

Key words: bias; body size frequency distribution; date of description; Elapidae; Viperidae.

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INTRODUCTION

The relationships between body size and the ecology, behavior, and physiology of an organism (Peters 1983, Brown et al. 1993) have made body size one of the most widely studied aspects of macroecology (Blackburn and Gaston 1994, Gaston and Blackburn 1999, 2000, Smith and Lyons 2013). Moreover, measures of body size are among the easiest of biological traits to measure,

and are thus known for most taxa. Accordingly, body size, and more specifically, body size frequency distributions (BSFDs), are widely used to inform ecological and evolutionary studies (Holling 1992, Gaston and Blackburn 1999, 2000, Collen et al. 2004, Nash et al. 2013, Smith and Lyons 2013). As such, critical evaluation of the biases that may influence the shape of the BSFDs, and thus their interpretation, is essential (Blackburn and Gaston 1998).

Within a clade of organisms, BSFDs are essentially shaped by differential rates of speciation and extinction with respect to body size (Maurer et al. 1992). Nonbiased speciation and extinction rates produce log-normal BSFDs without significant skew (Maurer et al. 1992) and deviations from this null are interpreted as evidence for size-biased evolution of body size. However, this approach is susceptible to imperfect BSFDs which arise when taxa that are absent from a sample, either because of a lack of reliable body size data or because they have yet to be detected/described, are disproportionately large or small (Blackburn and Gaston 1998). Thus, a distribution for a clade may appear log-normal in shape when in reality it is log-skewed, changing the interpretation of body size evolution within the clade (Blackburn and Gaston 1998).

One manner in which imperfect BSFDs arise is through size-associated differences in the probability of a species being discovered and described, as measured by the relationship between body size and year of description (Blackburn and Gaston 1994). This trend may result from a multiple factors including body size-associated detection probabilities or body size-geographic range size relationships (Gaston and Blackburn 2000). Relationships between body size and date of description have been demonstrated for multiple taxa including: beetles (Gaston 1991, Stork et al. 2015); butterflies (Gaston et al. 1995); birds (Gaston and Blackburn 1994); carnivores (Collen et al. 2004); neo-tropical mammals (Patterson 2001); and some herpetofauna (Reed and Boback 2002). This pattern generally manifests as a significant negative relationship between body size and year of description, suggesting that species missing from the current BSFD sample are on average likely to be smaller bodied. Thus, the addition of missing taxa to the sample could significantly skew a BSFD that is currently perceived as log-normal (Blackburn and Gaston 1994, 1998, Boback and Guyer 2003).

Snakes (Reptilia: Squamata: Serpentes) form a highly successful monophyletic vertebrate radiation (Wiens et al. 2012) of approximately 3500 species with a near-global distribution (Greene 1997, Uetz 2013). Because of their simplified body plan (the lack of large appendages reduces the number of morphological targets available for selection that may confound measures of mass or

length), snakes provide an ideal clade of organisms in which to investigate macroecological and macroevolutionary body size patterns. However, indeterminate growth and large ontogenetic variation in body size pose important challenges to the investigation of variation in body size as a species trait for snakes and other ectothermic vertebrates in general (Nash et al. 2014). Despite of these challenges, several authors have investigated BSFDs for subsets of snakes (Reed and Boback 2002, Boback and Guyer 2003). Importantly, Boback and Guyer (2003) showed that the BSFD for a sample of 618 species of snakes globally (approximately 18% of all species) was log-normal, with no evidence of the significant skew that characterizes the BSFDs of many other clades of organisms (Brown and Maurer 1989, Blackburn and Gaston 1994, Brown 1995). On the basis that the relatively complete North American snake fauna shows a similar log-normal distribution (Reed and Boback 2002), Boback and Guyer (2003) concluded that the “atypical” non-skewed distribution detected for snakes globally was robust. However, the susceptibility of the global snake BSFD, or indeed the BSFD of any major snake clade, to missing species, remains to be assessed.

Here we show that the existing BSFDs of two monophyletic clades of advanced snakes, the elapids and the vipers, are log-normally distributed with limited skew in accordance with the finding of Boback and Guyer (2003). Next, in each clade, we test the hypothesis that body size is negatively correlated with year of description, suggesting that novel species would tend to be smaller on average than the currently described fauna. Finally, we simulate the discovery of novel taxa for each clade based on the relationship between body size and year of description, and test the hypothesis that the addition of novel species will significantly skew the BSFD in each clade, respectively, in the future. In doing so, we demonstrate that the BSFDs for these clades are likely to be robust to the addition of novel small-bodied species, providing confidence in their validity.

MATERIALS AND METHODS

Study species

Vipers (Reptilia: Squamata: Viperidae) and Elapids (Reptilia: Squamata: Elapidae) are both

ecologically and morphologically diverse monophyletic radiations of macrostomatan snakes characterized by the evolution of highly derived venom delivery mechanisms (Greene 1997). Together they comprise approximately 680 species (~350 elapids, ~330 vipers) representing nearly one fifth of all snakes (Uetz 2013), and include species that occupy aquatic (marine and freshwater) and terrestrial (including fossorial, rupicolous and arboreal) habitats (Greene 1997).

Data sources

We used the Reptile Database (Uetz 2013) as a taxonomic guideline and information source to gather date of description for each species. Next, we sought maximum reported total length from the literature for each species, drawing information from a range of sources (see Appendices S1 and S2). We chose maximum total length of the largest sex as the most appropriate measure of size because it was more frequently reported than snout-vent length (Hampton 2011). Moreover maximum total length is less variable than mass, which fluctuates widely depending on nutritional and reproductive states (Boback and Guyer 2003, Terribile et al. 2009, Hampton 2011). We recognize that this situation is not ideal as numerous hypotheses regarding the drivers of body size evolution focus on physiological determinants making mass a more appropriate measure. However, length–mass relationships for snakes scale linearly for all major groups (Feldman and Meiri 2013), suggesting that the distribution of body lengths is likely to approximate the distribution of mass within each clade. Moreover, Nash et al. (2014) demonstrated that for macroecological studies of species with indeterminate growth (such as snakes), maximum reported body size provides a more powerful summary measure of body size than mean body size.

Analyses

We tested for normality of BSFDs using Shapiro–Wilks Test implemented in Statistica (Statsoft 2001). Next we calculated skewness (g_1), the standard error of the skew (SE_{g_1}), and the test statistic (Z) as g_1/SE_{g_1} (Zar 1999) for each clade. To test the significance of the skew we assumed a critical value of two

corresponding to an approximate two-tailed probability of 0.05. To estimate potential changes in the BSFDs for each clade we estimated mean decadal rate of description during the 20th century for elapids and vipers as 9.1 ± 4.9 species-decade⁻¹ and 11.1 ± 3.8 species-decade⁻¹, respectively. Accordingly we assumed an annual rate of description of one species per year for the purposes of our model. We simulated the addition of 150 novel species to each clade, each with a body size drawn randomly from a normal distribution (mean: based on the regression line of year of description on body size; standard deviation [SD]: based on the average SD of the body sizes for species described in each decade). We ran each simulation 1000 times, assessed g_1 and its significance for each simulation, and calculated the likelihood of the clade developing a significant skew after 150 yrs simply as the proportion of the simulations that were significantly skewed.

RESULTS

We gathered body size data for 300 species of elapids (~85% of described species; S1), and 264 species of viperids (~80% of described species; S2). Statistical analyses performed on log-transformed continuous data (and illustrated by log-transformed body size class frequency distribution; Fig. 1) revealed normal distributions (Elapids: $W = 0.996$, $P = 0.67$; Vipers: $W = 0.991$, $P = 0.099$) for both elapids and vipers. Moreover, neither clade showed evidence of significant skew (Elapids: $g_1 = 0.018$, $Z_{g_1} = 0.12$, $P = 0.45$; Vipers: $g_1 = 0.28$, $Z_{g_1} = 1.86$, $P = 0.063$). Both elapids and vipers show a modal log-transformed body size of 2.9–3.1, equating to a modal length of 790–1258 mm.

Elapids ($r = -0.32$, $R^2 = 0.099$, $P < 0.001$, Fig. 2a) and vipers ($r = -0.31$, $R^2 = 0.091$, $P < 0.001$, Fig. 2b) show significant declines in body size in relation to year of description, confirming the possibility that the discovery of smaller bodied species in the future has the potential to skew the BSFD of each clade toward smaller sizes. However, results of our simulations (Table 1) suggest that the BSFD of elapids is highly unlikely (~0.1%) to become significantly skewed in the future. Although more likely (~9%), the BSFD for vipers

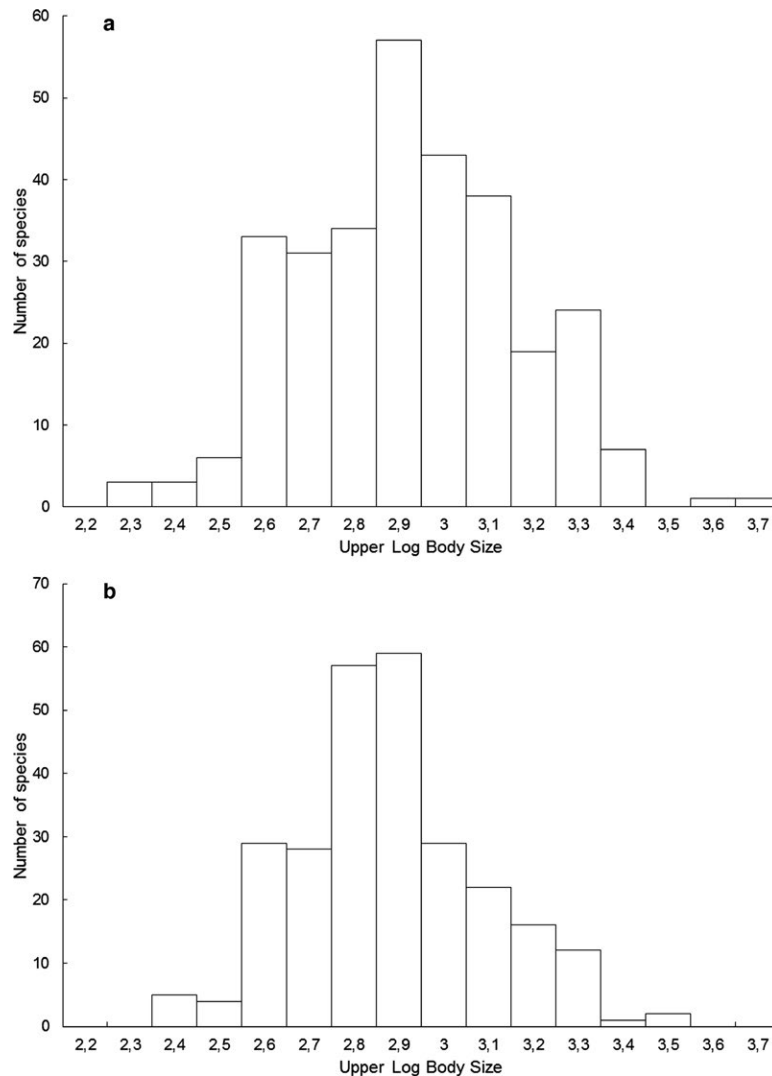


Fig. 1. Frequency distributions of log-transformed maximum total length (mm) for (a) 300 species of elapid snakes and (b) 264 species of viperid snakes. X-axis labels represent the upper value for that class such that taxa that fall between log 3.6 (4000 mm) – log 3.7 (5000 mm) are classed at log 3.7.

does not appear highly susceptible to becoming significantly skewed in the future.

DISCUSSION

Elapids and vipers have approximately log-normal body size frequency distributions. However, both clades show clear trends toward the early description of large-bodied species, and later description of small-bodied species. Accordingly, undescribed species are likely to be smaller bodied, on average, than the modal

size class of each clade. Should these trends hold true into the future, the description of novel small-bodied species have the potential to skew the BSFD toward smaller body sizes. Such a shift would indicate that currently reported BSFDs for these clades (and possibly snakes in general — Reed and Boback 2002, Boback and Guyer 2003), and their interpretation, represent artifacts of imperfect detection probability rather than a lack of size-associated biases in speciation and extinction rates. However, for elapids and vipers, our simulations

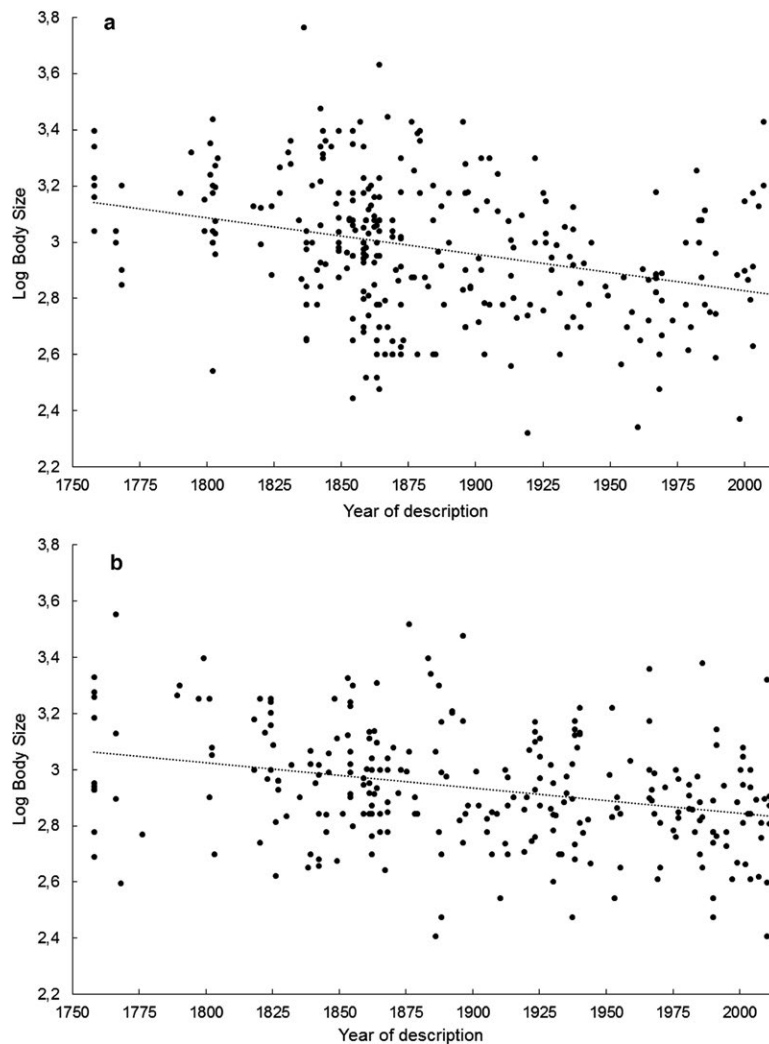


Fig. 2. Relationship between year of description and log-transformed maximum total length (mm) for (a) 300 species of elapid and (b) 264 species of viperid snakes. Dashed lines represent significant linear regression fits.

Table 1. Current and predicted future body size frequency distribution (BSFD) skew for elapids and vipers, as well as the proportion of significantly skewed distributions (Prop. Skewed) given the simulation of 150 novel species.

Clade	Scenario	Skew	Prop. Skewed
Elapids	Current	0.02	
	Future	0.08 ± 0.06	0.001
Viperids	Current	0.28	
	Future	0.14 ± 0.06	0.094

demonstrate that the current nonskewed BSFDs are likely robust to future species descriptions, suggesting that interpretations of the BSFD for

these groups is valid and that body size does not appear to have been significant in determining broad-scale speciation and extinction rates within the clades.

Our analysis shows that two major caenophidian clades produce modal body sizes of approximately 1 m. This finding is in line with Boback and Guyer (2003) who inferred an optimal body length for all snakes of approximately 1.0 m, based on an analysis of 618 species from most major lineages. However, at similar lengths, vipers are significantly heavier than elapids (Feldman and Meiri 2013). Feldman and Meiri's (2013) allometric relationships estimate that within this modal size class, vipers would weigh more than

twice as much as elapids (vipers \approx 520 g; elapids \approx 250 g; based on a total length of 1.0 m). This discrepancy has implications for invoking hypotheses regarding metabolic determinants of optimality (e.g., Brown et al. 1993) based on length as a measure of body size. Comparative data for other lineages of snakes may offer insights regarding how the difference between modal mass and length classes may be influenced by foraging and reproductive modes, both of which are known to influence mass-length relationships in snakes (Feldman and Meiri 2013).

Our data and approach include two inherent constraints. Firstly, while maximum total length is likely to be a useful approximation of body size, the maximum value within any sample is likely to increase as sample size increases. As such, species that have been known for longer periods of time are more likely to have produced larger specimens. However, this bias is unlikely to account completely for the overall trend in the two clades, as the change in absolute maximum length through increased sampling for any one species is likely to be small in relation to the overall range of body sizes within the rest of the clade. Secondly, our model assumes a regular rate of description, from which predicted body size is estimated. Rate of description among both groups is variable and shows influence of significant historical events (e.g., few species described during the period following World War 2; many species described following expansion of European colonies in the new world). These idiosyncrasies make predicting rates of description problematic. However, in the context of attempting to predict body sizes based on imperfect and highly variable data, we think that our assumed rate of one species-year⁻¹ provides a realistic proxy for this parameter in the absence more empirically accurate estimates.

Given the utilization of BSFDs in ecology and evolutionary studies, an understanding of biases associated with such distributions is essential. We identified body size biases in the description of species (and thus detection) as one potential source of bias, but demonstrate that this bias is unlikely to change the shape of the BSFDs for those clades in the future. Our results support the hypothesis that snakes in general (Boback and Guyer 2003) have a log-normal BSFD that is unlikely to be an artifact of missing species.

Moreover, our finding emphasizes that despite exhibiting notable variation in body size, the recent and rapid evolution of elapids and vipers was probably unrelated to body size.

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