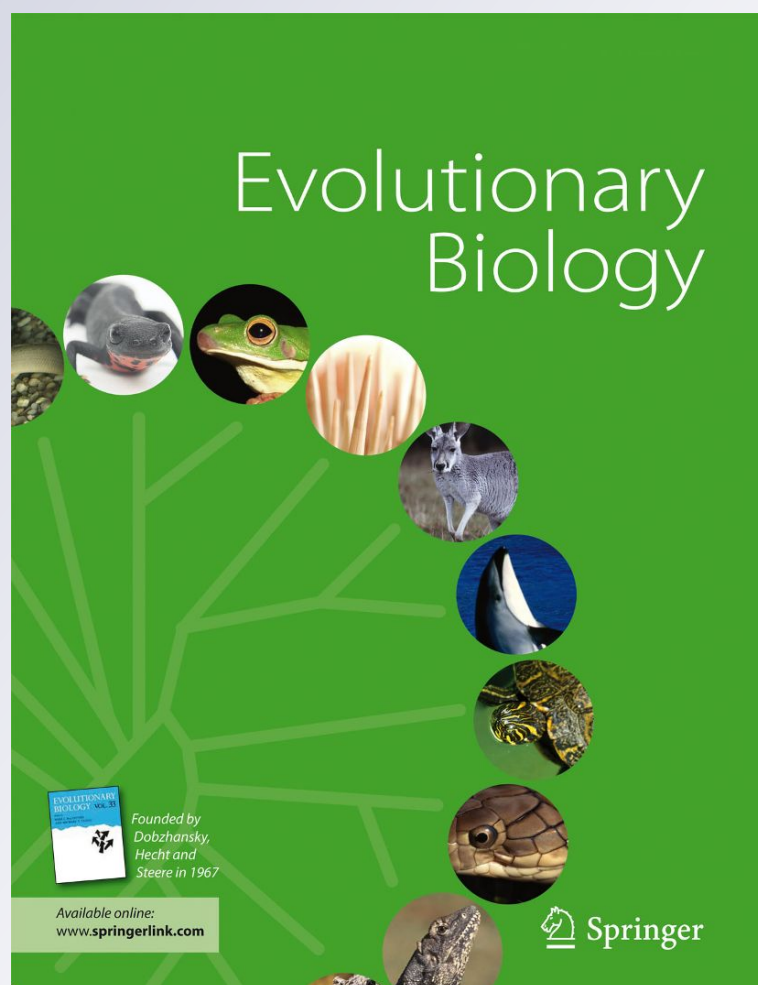# Spatial Dynamics of Body Size Frequency Distributions for North American Squamates

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Spatial Dynamics of Body Size Frequency Distributions for North American Squamates

Christian L. Cox · Scott M. Boback · Craig Guyer

Abstract Scale dependent patterns of body size frequency distributions (BSFDs) have been explained by competition and an evolutionarily optimal body size in mammals. We test these ideas in a vertebrate group that is a model for competition and evolutionary studies by assessing the scale-dependence of BSFDs. BSFDs (body size defined as maximum total length) of North American squamates were assembled for the entire continent, biomes within the continent and local habitat patches within biomes. We described these distributions using skewness, kurtosis, interquartile range (IQR), and an index of evenness. We compared these parameters among spatial scales using Kolmogorov–Smirnov tests and bootstrap simulations. We assessed the relationship between body size and species richness using correlations (Pearsons and Spearmans R). The North American BSFD is bimodal, with a primary mode (240 mm) corresponding to lizards and small snakes and a secondary mode (912 mm) to snakes. Squamate BSFDs varied in a scale dependent fashion for some biomes and local habitat patches for kurtosis (12% of local patches and 10% of biomes more platykurtic), skewness (30% of biomes skewed to the right) and IQR (12% of patches increased). The index of evenness of BSFDs did not vary with spatial scale. Body size of biomes and local habitat patches closely resembles the North American BSFD as species richness increases. We found limited statistical support for the scale-dependency of North American squamate BSFDs (only 12–30% of patches or biomes conformed to the predicted pattern). These results suggest that the mechanisms implicated in scale-dependent patterns of BSFDs for mammals, geographic turnover of modal-sized species and competition within local assemblages may be of diminished importance in squamates. As geographic turnover of modal-sized species is theoretically linked to an evolutionarily optimal body size, this may suggest that optimal size theory is not adequate to predict spatial scaling of BSFDs in squamates.

Keywords Body size · Body size frequency distribution · Squamate · Macroecology · Spatial scaling

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Introduction

Squamate reptiles (a monophyletic group including snakes and lizards) are important models for the study of competition (Pianka and Huey 1978; Roughgarden 1995; Losos 2000; Himes 2003; Luiselli 2006). Research in this area has focused on the role of competition in structuring squamate communities through character displacement, niche segregation, and the evolution of ecomorphs (Pianka and Huey 1978; Williams 1983; Losos 1990, 1995; Roughgarden 1995). Competition often structures communities with respect to body size, resulting in local assemblages that show strong segregation of body sizes (Ricklefs et al. 1981; Losos 1995). However, whether competition is pervasive enough in squamates to be manifested in large-scale macroecological patterns of squamate body size is not well known.

Competition has been used to explain scale-dependent patterns of body size frequency distributions (BSFDs) for mammals of Africa and both North and South America (Brown and Nicoletto 1991; Bakker and Kelt 2000; Kelt and Meyer 2009). As spatial scale decreases, BSFDs flatten as the result of loss of species in the modal size class. Statistically, BSFDs change from highly modal and right skewed for continents to platykurtic with decreased skewness and increased mode for local habitat patches (Brown and Maurer 1989; Brown and Nicoletto 1991). There are two proposed mechanisms that have been implicated in producing this pattern. First, at the local level, competition prevents species from occupying similar body sizes within local assemblages (Brown and Maurer 1989; Brown and Nicoletto 1991). Second, at the regional level a positive relationship between body size and geographic range size leads to geographic turnover of modal-sized species at the local level. Undergirding this pattern is the concept that modal-sized species represent an energetically optimal body size [e. g. mammals (Brown and Maurer 1989; Brown et al. 1993; Marquet and Taper 1998), birds (Maurer 1998), and snakes (Boback and Guyer 2003), but see (Meiri et al. 2005; Raia et al. 2010 and citations within)], and hence attain smaller geographic ranges than species with body sizes above and below the mode (Brown and Maurer 1989; Brown and Nicoletto 1991). Thus as spatial scale decreases, BSFDs become platykurtic due to modal-sized species turnover among local communities (Brown and Maurer 1989; Brown and Nicoletto 1991). While at a local scale assembly of BSFDs may be dominated by recent ecological processes (e.g. competition), historical evolutionary processes are important in structuring BSFDs at large spatial scales.

Body size is governed by physiological and evolutionary processes as well as ecological processes such as competition (Peters 1983; Schmidt-Nielsen 1984; Brown 1995). Physiological constraint has been implicated in limiting minimum body size in endotherms (Brown and Maurer 1989), whereas large body size is associated with low population density, high extinction risk and increased dispersal ability for some taxa (Peters 1983; Brown 1995). Because of the influence of these physiological and evolutionary processes, BSFDs can possess characteristics that are either taxon- or region-specific (Marquet and Cofre 1999; Bakker and Kelt 2000). In fact, recent work has found more evidence of regional, phylogenetic or ecological influences on body size compared to a metabolically optimal body size for large taxonomic clades (Meiri et al. 2005; Meiri 2007; Raia et al. 2010). Examining BSFDs in a clade other than mammals that also experiences strong competition (e.g. squamates), allows us to evaluate the generality of scale-dependency and potentially the proposed evolutionary mechanisms (e.g. optimal size theory) driving this pattern.

Large-scale BSFDs have been characterized for lizards and snakes, which comprise the monophyletic clade of Squamata (Reed and Boback 2002; Boback and Guyer 2003; Olalla-Tarraga et al. 2006; Meiri 2008). While the global BSFD of lizards is unimodal and right skewed (Meiri 2008), the global BSFD of snakes is unimodal but not skewed (Boback and Guyer 2003). The importance of ecological (diet and reproductive mode) and evolutionary (insularity, latitude, and continent of origin) factors in determining large-scale patterns of body size for squamates have been demonstrated (Boback 2003; Olalla-Tarraga et al. 2006; Meiri 2007, 2008). However, the scale-dependency of these BSFDs for squamates is not well known.

We test the role of both competition within local communities and geographic turnover among modal-sized species among squamates in the scaling of North American BSFDs. Studies seeking to discover universal factors shaping body size distributions should focus on monophyletic groups of organisms, because they are likely to experience similar evolutionary constraints (Brown and Maurer 1989). We chose to analyze all squamates because snakes are deeply nested within lizards and thus lizards alone do not comprise a monophyletic group (Vidal and Hedges 2009).

If competition combined with geographic turnover of modal-sized species is the main force driving BSFD patterns in mammals (Brown and Maurer 1989; Brown and Nicoletto 1991), and both competition and geographic turnover of modal species are important in structuring squamate assemblages (Williams 1983; Boback and Guyer 2003), then we expect to see scale-dependent patterns in the BSFDs for North American squamates. To test this, we evaluated North American squamate BSFDs at three different spatial scales (continent, biome, and local habitat patches). We tested the role of competition in structuring body sizes of local assemblages by testing (1) whether body size categories are more evenly filled than a normal distribution and (2) whether they become more evenly occupied as spatial scale decreases. We tested for geographic turnover of modal-sized species by observing whether BSFDs of squamates become less modal, less skewed, and increasingly platykurtic with decreasing spatial scale.

Materials and Methods

Study System

Squamata is the order that includes the suborders of Serpentes (snakes), Lacertilia (lizards) and Amphisbaenia (worm lizards) (Pough et al. 2003). The historically defined group of Lacertilia is paraphyletic when excluding the monophyletic groups of Serpentes and Amphisbaenia,

which are both deeply nested within Lacertilia (Vidal and Hedges 2009). The discussion of any macroecological patterns within a group of organisms only makes sense in the context of a group that has a shared evolutionary history. We thus chose to analyze squamates and snakes, both of which are monophyletic.

Data Collection

We define body size as maximum total length, which is tightly correlated with body mass and is a common measure of body size for squamates (Reed and Boback 2002; Boback and Guyer 2003; Meiri 2007, 2008). Although mass is often considered a better measure of body size, it is not widely available for all squamates (Boback and Guyer 2003; Meiri 2010). Length may be transformed to mass using allometric equations, but this approach requires clade-specific equations (Meiri 2010). Unfortunately, clade-specific allometric equations have been developed for many clades of squamates (Meiri 2010), but these are not available for snakes. Additionally, length as a measure of body size is routinely used in macroecological analyses (Boback and Guyer 2003; Meiri 2008; Blanchet et al. 2010). We obtained body size data (maximum total length) for North American squamates (see Supplementary Table 1) from multiple sources (Conant and Collins 1998; Behler and King 2002; Ernst and Ernst 2003; Stebbins 2003). All body size data were $\log_{10}$ transformed prior to analysis.

We chose to include all squamate species from the United States and Canada in our study (see Supplementary Table 1). We included Mexican species that have geographic ranges that include the United States, but due to the paucity of body size information we did not include all Mexican species. We were conservative taxonomically, only including species that are described in field guides or well supported in the literature (e.g., Conant and Collins 1998; Behler and King 2002; Ernst and Ernst 2003; Stebbins 2003). Most recently described taxa in our study area are the result of dividing geographically widespread taxa into multiple species which lack maximum body size data and may not be thoroughly scientifically reviewed.

North American biomes (regions of climatically and ecologically similar habitat) were defined as in Udvardy (1975), and biome occupancy of each species was determined by published range maps (Stebbins 1997; Conant and Collins 1998; Dixon 2000; Behler and King 2002; Ernst and Ernst 2003; Campbell and Lamar 2004). Local habitat patches were considered small geographic locations of relatively homogeneous habitat (Brown and Nicoletto 1991). Generally, these patches were state or national parks, recreation areas, or biological field stations (see Supplementary Table 2), and ranged in size from 0.6 to 3,300.0 km^2, approximating the range of patches analyzed

in previous studies (Bakker and Kelt 2000; Kelt and Meyer 2009). Species lists for patches were determined from published sources, unpublished reports and personal communications from biologists at field stations (see supplementary Table 2). We restricted our analyses to patches with species richness greater than 15, because some of our analyses are sensitive to low sample size (Sokal and Rohlf 1995). Accordingly, local habitat patches are not evenly distributed within biomes because biomes are not equal in area, species richness varies across biomes, and well-documented squamate assemblages are not evenly distributed across biomes. This should not impact the results of our study, because the pattern and processes of spatial scaling or scale-dependency of BSFDs is not tied to any particular habitat or geographic area (Brown and Maurer 1989; Brown and Nicoletto 1991; Brown 1995).

Statistical Methods

We analyzed North American BSFDs of all squamates in North America (excluding exclusively Mexican species), biomes within North America, and local habitat patches within biomes. For each BSFD, we determined mode, mean, median, interquartile range, skewness and kurtosis. Additionally, BSFDs were tested for unimodality using the Hartigan dip test (Hartigan and Hartigan 1985). To ensure that variation in patch area was not influencing our results, we conducted Pearson's correlation and Spearman's Rank correlation with all patches to determine if patch area is significantly associated with patch assemblage parameters (species richness, median, minimum and maximum total length, kurtosis and skewness) on untransformed, log-transformed (patch size, body size parameters) and square root-transformed (patch size) parameters. We used a square-root transformation to meet the distributional assumptions of parametric statistics (Sokal and Rohlf 1995).

We examined the role of competition in structuring local body size assemblages by examining the extent to which body size categories are filled (evenness) by using EcoSim software (Gotelli and Entsminger 2004). We used an index of evenness which is computed as the variance of the log ratio of all possible ith body sizes to ith $+1$ body size pairs in a distribution (Gotelli and Entsminger 2004). The log ratio body size is equivalent to the difference in values between the log body sizes. Thus, a low index of evenness indicates that the differences between body sizes are evenly spaced, whereas a high index of evenness indicates that the differences between body sizes are variable (Gotelli and Entsminger 2004). We tested whether local habitat patches were more even than a log-normal distribution, and whether evenness increases with decreasing spatial scale using bootstrapping to estimate significance. For each habitat patch, a bootstrap procedure created 1,000 pseudo-assemblages

Table 1 Basic parameters of North American, biome and local habitat patch BSFDs ($\log_{10}$ transformed total length in mm) of squamates

Region	N	Minimum	Maximum	Mean	SD	Median	IQR	Skewness	Kurtosis
North American	232	1.756	3.439	2.703	0.384	2.628	0.665	0.043	−1.110
Biome 2	24	2.182	3.439	2.833	0.377	2.937	0.673	−0.339	−1.079
Biome 4*	16	2.332	3.405	2.941	0.309	3.035	0.444	−0.823*	−0.004
Biome 5*	57	2.114	3.408	2.887	0.354	3.004	0.575	−0.504*	−0.869
Biome 6*	64	1.756	3.420	2.863	0.405	2.966	0.678	−0.615*	−0.523*
Biome 7*[E]	24	2.079	3.439	2.340	0.163	2.368	0.301	0.130	−1.119
Biome 8	88	2.079	3.439	2.655	0.371	2.593	0.636	0.306	−0.997
Biome 11	55	2.146	3.407	2.715	0.376	2.622	0.684	0.193	−1.212
Biome 18	105	1.778	3.420	2.764	0.409	2.706	0.684	−0.106	−1.139
Biome 19	50	2.021	3.407	2.735	0.411	2.652	0.730	0.032	−1.350
Biome 20	23	2.182	3.439	2.805	0.396	2.875	0.669	−0.139	−1.321
Patch 1	23	2.114	3.407	2.841	0.384	2.875	0.658	−0.214	−1.011
Patch 2	29	2.176	3.439	2.807	0.405	2.875	0.793	−0.079	−1.437
Patch 3	16	2.332	3.408	2.971	0.353	3.089	0.626	−0.575	−1.013
Patch 4	33	2.114	3.408	2.880	0.405	3.028	0.720*	−0.411	−1.316
Patch 5*	24	2.114	3.420	3.010	0.359	3.098	0.445	−1.140	0.716
Patch 6*	19	2.114	3.318	2.923	0.352	3.009	0.388	−1.038*	0.370
Patch 7*	23	2.114	3.439	2.892	0.386	3.028	0.594	−0.357	−1.103
Patch 8	21	2.114	3.407	2.880	0.401	2.919	0.733	−0.391	−1.240
Patch 9*	35	2.114	3.420	2.956	0.378	3.035	0.489	−0.728	−0.471
Patch 10	16	2.114	3.420	2.838	0.430	2.897	0.867	−0.226	−1.351
Patch 11	34	2.114	3.420	2.862	0.396	2.897	0.658	−0.333	−1.008
Patch 12	30	2.176	3.439	2.797	0.384	2.755	0.586	0.001	−1.077
Patch 13	28	2.114	3.420	2.892	0.394	3.018	0.712	−0.378	−1.101
Patch 14*	23	2.114	3.408	2.946	0.392	3.064	0.570	−0.817	−0.701
Patch 15	17	2.114	3.408	2.881	0.392	3.035	0.674	−0.675	−0.814
Patch 16	30	2.114	3.408	2.840	0.365	2.986	0.614	−0.423	−1.142
Patch 17*	24	2.114	3.408	2.942	0.402	3.089	0.721	−0.712	−0.910
Patch 18*	30	2.114	3.408	2.906	0.421	3.050	0.787	−0.514	−1.207
Patch 19	24	2.114	3.408	2.824	0.434	2.919	0.882*	−0.182	−1.581*
Patch 20	17	2.114	3.408	2.854	0.418	3.064	0.754	−0.462	−1.288
Patch 21	19	2.114	3.408	2.825	0.456	3.064	0.821	−0.175	−1.878*
Patch 22	23	2.114	3.408	2.847	0.419	3.009	0.737	−0.308	−1.537*
Patch 23	39	2.021	3.439	2.695	0.405	2.568	0.606*	0.259	−1.124
Patch 24	35	2.134	3.439	2.755	0.384	2.681	0.629	0.048	−0.979
Patch 25	16	2.021	3.439	2.586	0.442	2.488	0.700	0.904*	−0.38*

An asterisk next to biome and patch names indicates a significant difference from the North American BSFD (Kolmogorov–Smirnov test). A superscript E next to biome and patch names indicates a significant difference from the biome or North American BSFDs index of evennesss based on bootstrap procedures. A asterisk next to IQR, skewness, or kurtosis values for each habitat patch indicates significantly different values relative to their biome based on bootstrap procedures

identical in the number of species to the actual habitat patch. These pseudo-assemblages were created by randomly drawing from a log-normal distribution with the same mean and standard deviation as the local habitat BSFD, and by randomly drawing from the pool of actual body sizes observed within the local habitat patches' respective biomes. We then compared the actual and random pseudo-assemblages for skewness, kurtosis and IQR. We repeated this procedure comparing biomes to the North

American BSFD. In both cases we used a two-tailed alpha level of 0.05 and inferred that the BSFD differed significantly from a random sample of the more inclusive BSFD when the observed values resided in the extreme 2.5% of the simulated values.

To test for spatial scaling of BSFDs, we used two different statistical approaches. First, we tested whether BSFDs differed statistically among spatial scales. Biome BSFDs were compared to the North American BSFD, and local habitat

patch BSFDs were compared to both biome and North American BSFDs using the Kolmogorov–Smirnov (K–S) two-sample test. Second, we tested how BSFDs differed among spatial scales by comparing kurtosis, skewness and IQR statistics, which measure the degree to which observations cluster around a common mode. Following our predictions, we expected that as spatial scale decreased, skewness and kurtosis would decrease and IQR would increase. We compared these values between spatial scales using the same bootstrapping procedure described above.

If modal-sized species have small geographic ranges, as spatial scale decreases BSFDs should contain fewer and fewer modal-sized species and thus decrease in modality. Therefore, we predicted that as spatial scale decreased, the BSFDs would become increasingly different in central tendency (mean or median) from the largest spatial scale (continent). This should occur because means and medians for a non-modal or uniform distribution are more reflective of bin occupancy and the extreme values in a distribution rather than central tendency. However, as spatial scale (and species richness) increases and distributions become leptokurtic, the mean or median become more reflective of central tendency and should be similar to the continental mean or median, given the predictions of Brown and Nicoletto (1991). We examined the correlation between the magnitude of the difference between biomes or local habitat patches and the North American continent in central tendency and species richness. We used Pearsons correlation to evaluate the relationship between the absolute difference between the mean or median of the North American BSFD and the local (region or patch) BSFD with the species richness of each biome or local habitat patch (square-root transformed). We also plotted the difference between the local habitat patch or biome median and the North American median against species richness of the local region. We predicted that distributions with greater species richness (which are more modal) will have means and medians closer to the North American value, which will result in a significant negative relationship.

All summary statistics and statistical tests were calculated in the statistical program Systat (Systat Software Inc., v. 11.0). Additionally, body size distributions were tested for unimodality using the Hartigan dip test (Hartigan and Hartigan 1985; Hartigan 1985), implemented in the statistical program R (R Development Core Team 2011).

Results

Squamate Distributional Summary

We recorded body size for 232 species of North American squamates (see supplementary Table 1). This BSFD was significantly bimodal (Fig. 1), with a primary mode of 2.60 (240 mm) and a secondary mode of 2.96 (912 mm). The mean and median of this BSFD were 2.50 and 2.57, respectively (Fig. 1; Table 1). We analyzed body size for 10 biomes (with species richness of greater than 15) in North America (Udvardy 1975). None of the biome BSFDs were bimodal, and they possessed a mean and median of 2.75 (range = 2.34–2.94) and 2.78 (range = 2.37–3.04), respectively (Fig. 2; Table 1). We recorded body size for squamates in 25 local habitat patches (see Supplementary Table 2). Only one local habitat patch BSFD was bimodal (Fig. 3; Table 1) and BSFDs for patches possessed a mean and median of 2.86 (range = 2.59–3.01) and 2.94 (range = 2.57–3.10), respectively (Table 1). Local habitat patch area was not significantly correlated with species richness, kurtosis, skewness, median body size, minimum body size, or maximum body size (Ps from 0.09 to 0.81).
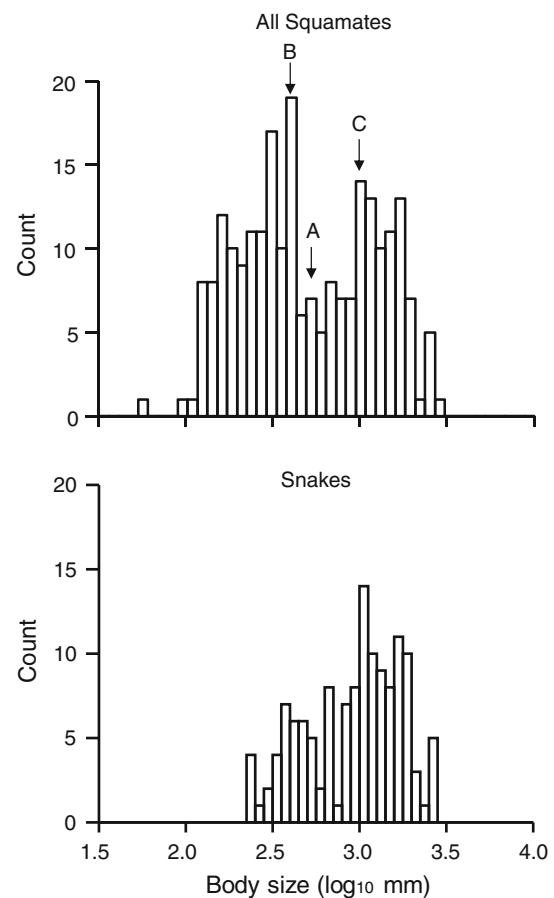

Fig. 1 Body size frequency distribution of North American squamates, with modes approximately corresponding to squamates (**a**), lizards (**b**) and snakes (**c**). Note the bimodality of the North American squamate body size distribution

Evenness of Squamate BSFDs

None of the biomes or local habitat patches differed significantly in the index of evenness from a log-normal distribution. Only one biome, and no local habitat patches possessed a significantly ($Ps > 0.05$) greater index of evenness than the North American or their respective biome BSFDs (Table 1).

Spatial Scaling of Squamate BSFDs

As spatial scale decreases, BSFDs for squamates become flatter in shape (Figs. 1, 2, 3). There were significant differences (K–S two sample test, $Ps < 0.05$) between the North American BSFD and some of the regional (4 of 10 biomes) and local (7 of 25 habitat patches) BSFDs (Table 1). However, no local habitat patch BSFDs were significantly different from their biome BSFDs. Kurtosis was similar among North American (-1.10), biome (mean = -0.943, range = -1.350–0.004) and patch (mean = -0.891, range = -1.878–0.716) BSFDs (Table 1). Only

one biome was significantly more platykurtic compared to the North American BSFD, whereas three patches were significantly more platykurtic compared to their respective biome BSFDs (Table 1). Skewness was similar among North American (0.043), biome (mean = -0.339, range = -0.823–0.306) and patch (mean = -0.348, range = -1.140–0.904) BSFDs (Table 1). Three biomes were significantly more left skewed compared to the North American BSFD, whereas two patches were significantly more skewed (1 to the right, 1 to the left) compared to their respective biomes (Table 1). IQR was quite similar among North American (0.665), biome (mean = 0.607, range = 0.301–0.730) and patch (mean = 0.662, range = 0.388–0.867) BSFDs. Although biome IQR did not differ significantly from the North American BSFD, three patches possessed IQR significantly greater than their respective biomes (Table 1).

As species richness increases, median body size of local regions becomes more similar to the North American median body size (Fig. 4). We found a significant negative relationship ($r^2 = 0.201$, $P < 0.005$) between species
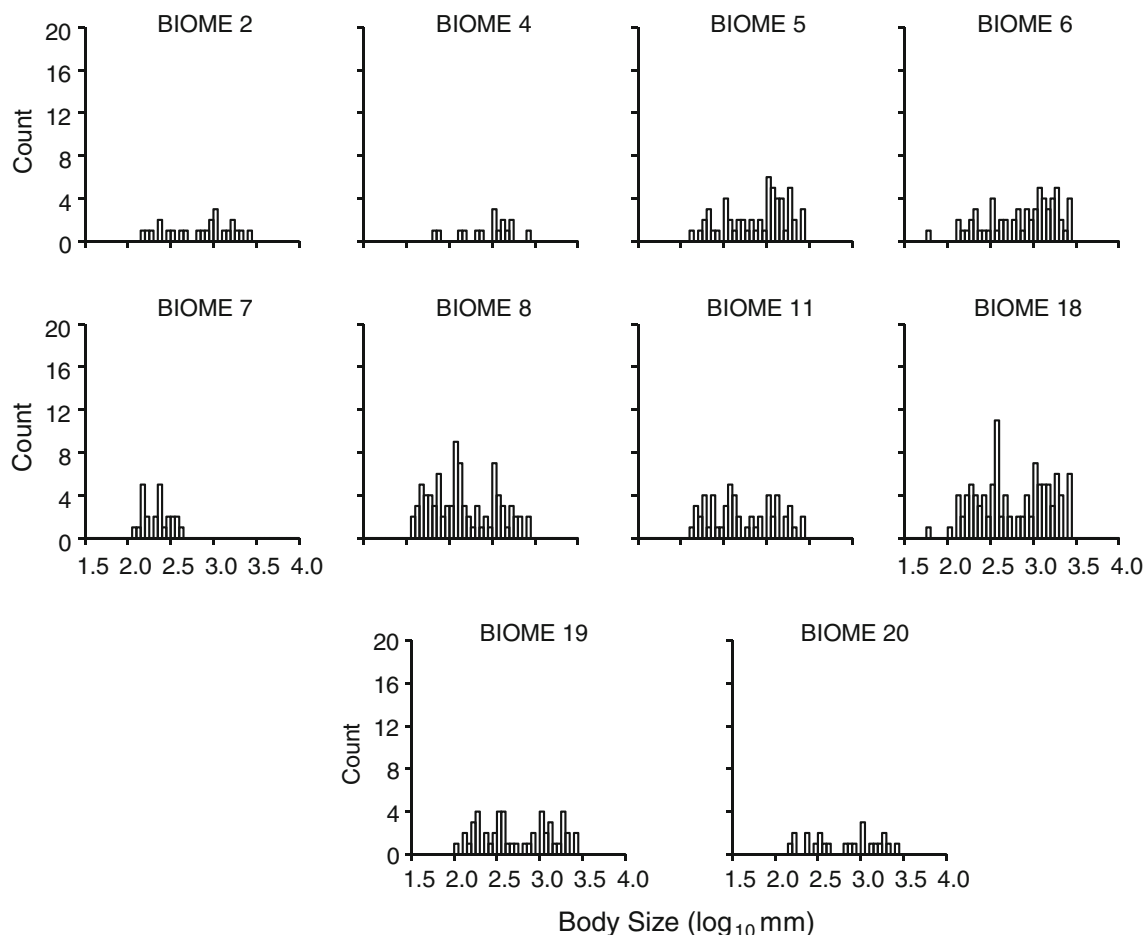

Fig. 2 Biome body size frequency distributions for North American squamates. *X*-axis labels are provided on the *bottom* pane of the figure. *Y*-axis labels are provided on the *left* pane of the figure
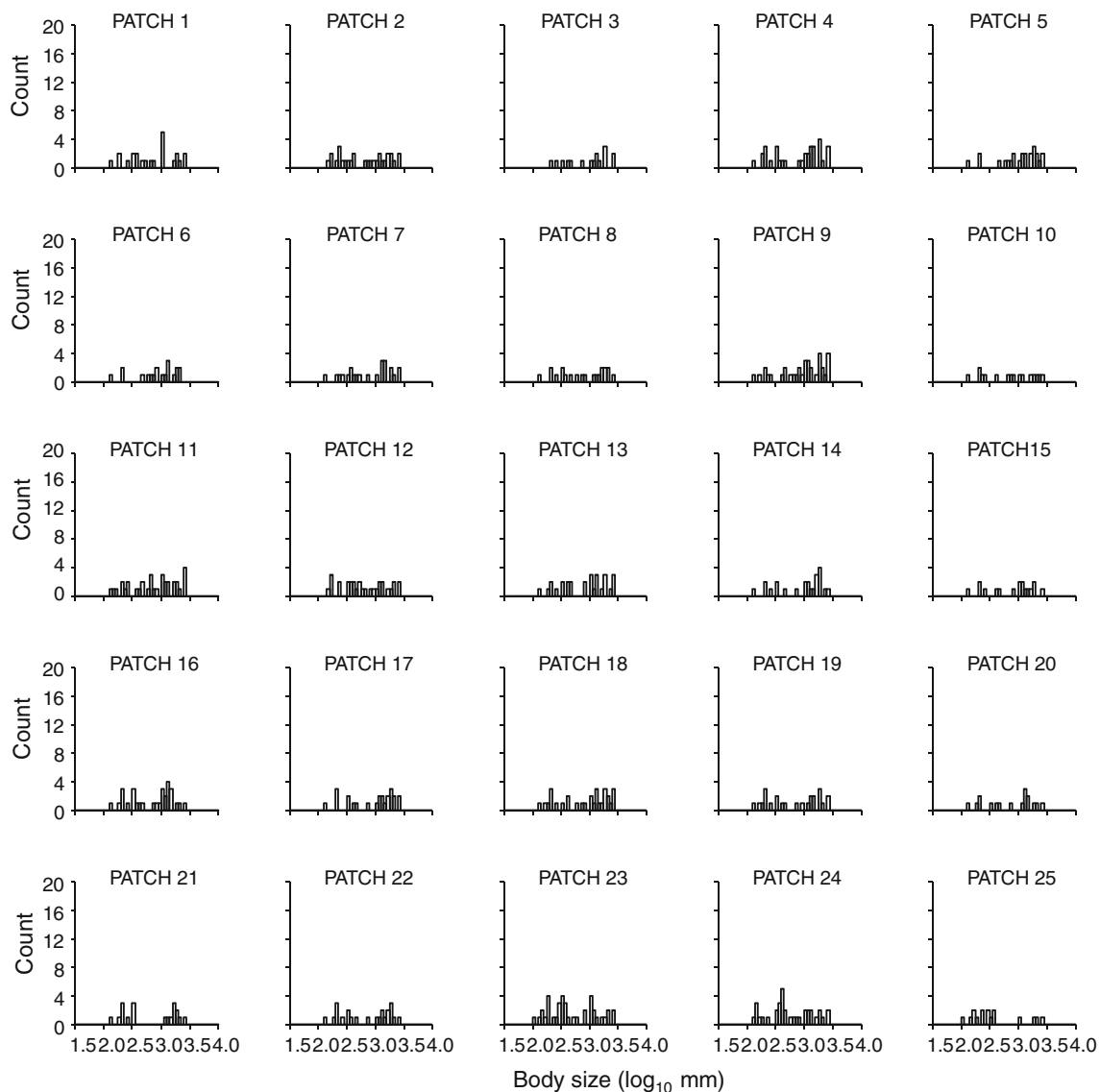
Fig. 3 Local habitat patch body size frequency distributions for North American squamates. *X*-axis labels are provided on the *bottom* pane of the figure. *Y*-axis labels are provided on the *left* pane of the figure

richness of patches and biomes (square root transformed) and the absolute difference between the median of North American and biome or patch BSFDs (Fig. 4). We found a similar negative relationship ($r^2 = 0.298$, $P < 0.005$) between species richness of patches and biomes and the absolute difference between the median of North American and biome or patch BSFDs (data not shown).

Spatial Scaling of Snake BSFDs

Recognizing the divergent ecology and high species richness of the snake radiation, we examined whether snakes differed from all squamates in the scaling of their BSFDs. We recorded and analyzed body size for 132 species of North American snakes. This BSFD was unimodal at all

scales (Fig. 1; Table 2), with a mode of 3.0 (1,000 mm). The mean and median of this BSFD were 2.96 and 3.01, respectively (Table 2). We analyzed body size for 8 biomes and 19 local habitat patches (Table 2). We found similar results to the analysis including all squamates, with no evidence for increasing platykurtosis, increased IQR, or increased evenness with decreasing spatial scale (Table 2).

Discussion

The frequency distribution of body sizes for North American squamates bears several similarities to those of mammals from North America, the Neotropics and Africa. The North American squamate BSFD is bimodal with a primary mode
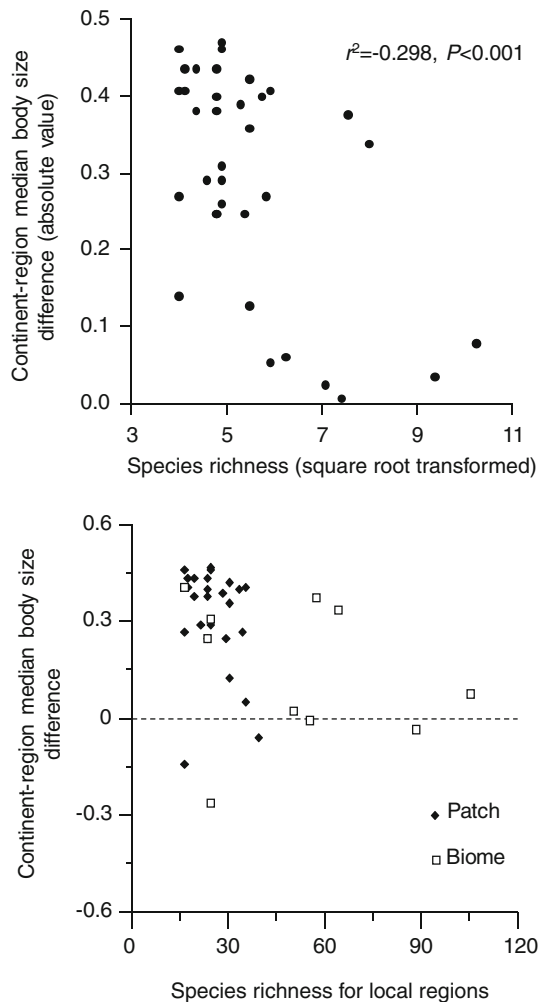
Fig. 4 Difference between median body size of North American squamates and the median body size of smaller regions (patch or biome) plotted against species richness of smaller regions for local habitat patches and biomes, with the continental median indicated by the *dashed line* at zero on the *Y*-axis (*top panel*). Absolute value of the difference between median body size of North American squamates and the median body size of smaller regions (patch or biome) plotted against square root transformed species richness of smaller regions for local habitat patches and biomes (*bottom panel*). As species richness increases, mean and median body size of patches and biomes approach the continental mean and median

that is less than the mean, indicating that the preponderance of species possess small body size. Interestingly, North American BSFDs for lizards and snakes considered separately are unimodal, with modes (2.4 and 3.0) that correspond approximately to the primary and secondary modes (2.6 and 3.0) in the North American squamate BSFD (Reed and Boback 2002). Bimodality has also been reported for eutherian mammals (Caughley 1987) and freshwater fish (Blanchet et al. 2010; but linked to invasive species). BSFDs of mammals at the continental scale for the North American and Neotropics (Brown and Nicoletto 1991; Bakker and Kelt 2000) are also bimodal (Kelt and Meyer 2009), and the mammalian BSFD from Africa is bimodal at all spatial scales (Kelt and Meyer 2009). Despite the bimodality, mammalian BSFDs still appear to scale spatially, demonstrating that unimodality is not necessary to detect a pattern of spatial scaling (Kelt and Meyer 2009). The secondary mode in the BSFD of African mammals has been explained by the species richness of large ungulates (Kelt and Meyer 2009). It appears that the morphological and ecological divergence of snakes from other squamates have led to the evolution of larger body size, which results in a prominent secondary mode in the BSFD of North American squamates (Bakker and Kelt 2000). This increase in size cannot be explained as coordinated evolution of size and limbless locomotion, because the snakelike body form has independently evolved many times within squamates (at least 25 times, Wiens et al. 2006) and none approach the maximum size achieved by snakes. Rather, because snakes represent a deeply nested monophyletic clade within Squamata (Vidal and Hedges 2009), the bimodality of the squamate BSFD is consistent with the idea that morphological diversity evolved early in the squamate tree and subsequent diversification proceeded within the major morphotypes (e.g., Meloro and Raia 2010).

There are two proposed explanations that might explain the bimodality of the North American squamate BSFD. First, the two modes may result from the evolution of fixed differences in body plan and body size between snakes and other clades of squamates early in the evolutionary history of snakes (e.g., Meloro and Raia 2010). Another explanation (similar to that invoked for ungulate mammals) is that the evolutionary, morphological and ecological divergence of snakes from other squamates have led to the evolution of larger body size, which results in a prominent secondary mode in the body size distribution of North American squamates (e.g., Bakker and Kelt 2000). Conversely, unimodal continental BSFDs for groups such as Australian turtles, snakes, and frogs and North American turtles, salamanders, snakes, and frogs are probably driven by the phylogenetically conserved morphology and ecology within each group (Reed and Boback 2002).

For at least three different continents, mammalian BSFDs are scale-dependent, with kurtosis and modality decreasing with spatial scale (Brown and Maurer 1989; Brown and Nicoletto 1991; Marquet and Cofre 1999; Bakker and Kelt 2000; Kelt and Meyer 2009). Surprisingly, we found no evidence that competition lead to increased evenness or uniform distribution of BSFDs of squamates or snakes within local habitat patches (Tables 1, 2). Similarly, we found that while North American squamate BSFDs may appear to be scale-dependent (Figs. 1, 2, 3), this pattern has only weak statistical support for squamates (Table 1), and none for snakes (Table 2). In contrast, the association

Table 2 Basic parameters of North American, biome and local habitat patch BSFDs ($\log_{10}$ transformed total length in mm) of snakes

Region	N	Minimum	Maximum	Mean	S.D.	Median	IQR	Skewness	Kurtosis
North American	132	2.362	3.439	2.958	0.272	3.009	0.451	−0.398	−0.806
Biome 2	16	2.653	3.439	3.060	0.203	3.019	0.380	−0.056	−0.12
Biome 5	45	2.398	3.408	3.003	0.268	3.064	0.435	−0.528	−0.602
Biome 6	48	2.362	3.420	3.016	0.291	3.086	0.197	−0.594	−0.69
Biome 7	23	2.613	3.439	3.097	0.19	3.111	0.405	−0.468	0.745
Biome 8	44	2.398	3.439	2.940	0.276	3.002	0.345	−0.238	−0.864
Biome 11	28	2.568	3.407	3.019	0.239	3.049	0.501	−0.338	−0.723
Biome 18	68	2.362	3.420	2.988	0.295	3.053	0.241	−0.461	−0.868
Biome 19[E]	25	2.681	3.407	3.097	0.198	3.100	0.380	−0.402	−0.385
Patch 1	16	2.431	3.407	3.031	0.276	2.875	0.363	−0.516	−0.135
Patch 2	18	2.591	3.439	3.073	0.244	2.875	0.312	−0.553	−0.254
Patch 4	24	2.505	3.408	3.061	0.283	3.028	0.313	−0.825	−0.406
Patch 5	20	2.69	3.42	3.135	0.211	3.098	0.290	−0.518	−0.667
Patch 6	16	2.307	3.318	3.019	0.267	3.009	0.252	−1.271	2.103
Patch 7	18	2.398	3.439	3.005	0.323	3.028	0.540	−0.479	−1.157
Patch 8	16	2.531	3.407	3.049	0.282	2.919	0.412	−0.661	−0.944
Patch 9*	27	2.362	3.42	3.082	0.281	3.035	0.384	−0.801	0.104
Patch 11	24	2.362	3.42	3.019	0.302	2.897	0.448	−0.393	−0.77
Patch 12	18	2.398	3.439	3.03	0.284	2.755	0.407	−0.51	−0.216
Patch 13	20	2.505	3.42	3.047	0.298	3.018	0.411	−0.474	−1.038
Patch 14*	17	2.505	3.408	3.12	0.24	3.064	0.196	−1.369	1.691
Patch 16	21	2.519	3.408	2.992	0.263	2.986	0.280	−0.603	−0.658
Patch 17	19	2.531	3.408	3.105	0.259	3.089	0.240	−1.079	0.305
Patch 18*	20	2.602	3.408	3.142	0.241	3.050	0.266	−1.051	0.584
Patch 19	16	2.531	3.408	3.079	0.274	2.919	0.335	−0.837	−0.308
Patch 22	16	2.531	3.408	3.074	0.267	3.009	0.289	−1.007	−0.078
Patch 23	20	2.431	3.439	3.004	0.293	2.568	0.352	−0.447	−0.627
Patch 24	20	2.568	3.439	3.005	0.272	2.681	0.435	−0.152	−1.097

An asterisk next to biome and patch names indicates a significant difference from the North American BSFD (Kolmogorov–Smirnov test). A superscript E next to biome and patch names indicates a significant difference from the biome or North American BSFDs index of evennesss based on bootstrap procedures. A asterisk next to IQR, skewness, or kurtosis values for each habitat patch indicates significantly different values relative to their biome based on bootstrap procedures

between species richness and median body size (Fig. 4) is statistically consistent with scale dependency of squamate BSFDs (Fig. 4), indicating that that BSFDs at different spatial scales possess different underlying distributions. In concert, these results may suggest a decreased role for both geographic turnover of modal-sized species and competition in structuring BSFDs at all spatial scales for North American squamates.

Scale-dependency of BSFDs is suggested to be linked to the concept of an optimal body size (Brown et al. 1993), because species within the modal or "optimal" body size range are able to satisfy their energy requirements with smaller home ranges, which leads to smaller geographic range sizes (Brown and Maurer 1989; Brown and Nicoletto 1991). Compared to modal-sized species, body sizes above and below the mode represent species that have larger

geographic ranges, and hence are less likely to experience turnover between local habitat patches (Brown and Maurer 1989; Brown and Nicoletto 1991). Evidence supporting this mechanism include a suggested optimal body size for mammals (Marquet and Taper 1998), and a positive relationship between geographic range and body size for endotherms (Brown and Maurer 1989; Brown 1995; Diniz-Filho and Torres 2002). An optimal body size has been proposed for snakes (Boback and Guyer 2003) and within at least some squamates (venomous snakes of the western hemisphere), geographic range size is positively correlated with body size (Reed 2003).

In the context of optimal size theory, geographic turnover of modal-sized species (and thus scale-dependency of BSFDs) may be more obvious in mammals than squamates or snakes because of the strong constraint on minimum

body size and greater mass-specific metabolic rate of endotherms (Pough 1980). Because ectotherms, such as squamates, have lower energy requirements than endotherms, such as mammals (Pough 1980), an optimal body size for squamates may be impacted more by factors such as resource availability and locomotion constraints (Boback and Guyer 2003). However, while many macroecological patterns such as spatial scaling are based upon the concept of a metabolically optimal size in the absence of competition (Brown et al. 1993), this concept is not without major criticism. After phylogenetic autocorrelation and other factors are taken into account, some authors have failed to find evidence of optimal body size in mammals (Meiri et al. 2004; Raia et al. 2010). Additionally, key predictions of optimal body size are not satisfied in some taxonomic groups (e.g. Roy et al. 2000; Meiri 2007). Our results are also consistent with these ideas and suggest that optimal size theory may not be adequate to predict spatial scaling in temperate squamate assemblages.

One potential mechanism that is independent of optimal size theory that has been implicated in the scale-dependency of mammalian BSFDs is interspecific competition (Brown and Maurer 1989; Brown and Nicoletto 1991). The absence of scale-dependency (especially in the index of evenness) in North American squamates implies that competition is reduced relative to mammals. We suggest two lines of evidence in support of this notion. First, squamate species richness (at least in this study) is lower than mammalian species richness at all spatial scales (Pough 1980; Brown and Nicoletto 1991; Marquet and Cofre 1999; Bakker and Kelt 2000; Kelt and Meyer 2009). Fewer squamate species in local communities can lead to less interspecific competition for resources, and thus less segregation of body sizes among species within those local communities. Second, squamates are ectothermic and have metabolic rates and energy flux that is 5–10% that of endotherms such as mammals (Pough 1980; Nagy et al. 1999). These low energy requirements can result in decreased competition for energy resources relative to endotherms (Pough 1980; Nagy et al. 1999). This diminished competition can result in weaker segregation of body sizes within local communities and thus weaker scale-dependency of squamate BSFDs.

How can we have diminished scale-dependency of BSFDs in a taxonomic group that has been used as a model for interspecific competition? Our results suggest that the importance of competition in certain local communities may not translate into the structure of large spatial scale BSFDs. Additionally, competition research in squamates has been especially prevalent in tropical systems, especially on islands. Tropical systems are vegetationally complex, species rich, and possess high rates of energy flux, all of which can lead to increased competition and specialization

(Currie et al. 1999; Gaston and Williams 2000). Relative to mainland systems, islands contain simplified communities, with reduced species richness, reduced predation pressure (Carlquist 1972; Williamson 1981; Boback 2003; Losos and Ricklefs 2009) and increased interspecific competition (Calsbeek and Cox 2010). In this paper, we focused on temperate fauna because of well described local communities and readily available maximum body size data. However, with increasingly detailed community and body size information from the tropics, research exploring the scale-dependency of squamate BSFDs in continental tropical regions would be a notable advance towards understanding whether species richness is an important factor underlying scale-dependency of BSFDs.

Our study is the first to test for scale-dependency of BSFDs in a vertebrate group other than mammals. We observed that there were differences between squamate BSFDs at different spatial scales. However, we found only limited support for spatial scaling of North American squamate BSFDs, compared to mammals of the North American, Neotropics, and Africa. This research highlights the importance of broad taxonomic and geographic coverage when determining the generality of macroecological patterns and mechanisms. Future research should focus on other taxonomic groups that can offer further insight into the evolutionary mechanisms underlying scale-dependency of BSFDs.

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