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RESEARCH PAPER

Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards

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ABSTRACT

Aim To explore and identify probable mechanisms contributing to the relationships among body size, dietary niche breadth and mean, minimum, maximum and range of prey size in predaceous lizards.

Location Our data set includes species from tropical rainforests, semi-arid regions of Brazil, and from deserts of the south-western United States, Australia and the Kalahari of Africa.

Methods We calculated phylogenetic and non-phylogenetic regressions among predator body size, dietary breath and various prey size measures.

Results We found a negative association between body size and dietary niche breadth in 159 lizard species sampled across most evolutionary lineages of squamate reptiles and across major continents and habitats. We also show that mean, minimum, maximum and range of prey size were positively associated with body size.

Main conclusions Our results suggest not only that larger lizards tend to eat larger prey, but in doing so offset their use of smaller prey. Reduction of dietary niche breadth with increased body size in these lizards suggests that large predators target large and more profitable prey. Consequently, the negative association between body size and niche breadth in predators most likely results from optimal foraging. Though this result may appear paradoxical and runs counter to previous studies, resources for predators may be predictably more limited than resources for herbivores, thus driving selection for more profitable prey.

Keywords

Body size, diet, herbivore, lizard, macroecology, niche breadth, optimal foraging, phylogenetic contrast, predator, prey size.

INTRODUCTION

Evolutionary responses of animals to variation in food availability form the basis for much current theory in community ecology. Optimal foraging theory, for example, posits that, other things being equal (e.g. risk, energetic cost of pursuit), individuals should select food items on the basis of net profitability (MacArthur & Pianka, 1966; Charnov, 1976). Acquiring food items with higher net profitability allows the greatest amount of energy to be allocated to growth, maintenance, reproduction and storage, which affect important organismal characteristics such as body size. Body size is a fundamental trait that varies over several orders of magnitude among organisms within biological communities and has major implications for life history, metabolism, physiology and many other aspects of an organism's ecology (Peters, 1983; Calder, 1996; Brown *et al*., 2004). For example, a tendency exists for larger species to have larger geographical range sizes, whereas the geographical ranges of smaller species are more variable (Brown, 1995; Gaston & Blackburn, 1996). In addition, the positive relationship between body size and home range or territory size is a general and widespread pattern in population biology (Peters, 1983; Calder, 1996).

A key hypothesis invoked to explain the variation in geographical range size is the 'niche breadth hypothesis', which posits that the extent of a species' niche (e.g. diversity of microhabitats occupied, variety of foods eaten, range of physiological conditions tolerated) determines geographical range size (Brown, 1984, 1995). If the niche breadth hypothesis holds, then a positive correlation should exist between body size and niche

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breadth. Support for the niche breadth hypothesis (i.e. positive correlation between geographical range size and habitat niche breadth) exists across many different taxonomic groups (Pyron, 1999; Brändle *et al.*, 2002a; Krasnov *et al.*, 2005). Some of these studies and others have also found a positive correlation between body size and dietary niche breadth (Novotny & Basset, 1999; Brändle & Brandl, 2001; Brändle *et al.*, 2002b).

A possible mechanism to explain the relationship between body size and dietary niche breadth is that because individuals of larger species have larger home ranges (Biedermann, 2003; Ottaviani *et al.*, 2006) and geographical ranges (Brown, 1995; Gaston & Blackburn, 2000), they encounter a wider variety of prey items compared with smaller species, which have smaller geographical and home ranges. In addition to the effect of body size on geographical range size, other mechanisms could explain a positive relationship between body size and niche breadths, particularly with respect to diets. For instance, it has been shown that large predators can detect, capture and consume both small and large prey items, whereas small predators are usually restricted to small prey, partially because they are often gape limited when compared with larger animals (Peters, 1983; Vézina, 1985; Díaz, 1994).

Theoretical and empirical evidence suggests that a positive correlation between dietary niche breadth and body size should be a general and widespread phenomenon. Alternatively, despite the fact that large predators may have access to a wider range of prey items, they might be restricted to use larger prey for at least two non-exclusive reasons. First, large predators might be less efficient in capturing and manipulating very small prey (handling hypothesis). Second, large predators might maximize their energy intake by targeting large prey (optimal foraging hypothesis). Some studies explicitly suggest that an increase in foraging distance leads to an increase in prey size, which links prey size, body size and home range size (Schoener, 1971). Although the first hypothesis is difficult to test across taxa with existing comparative data, the optimal foraging hypothesis makes testable predictions. Minimum and maximum prey size should be positively correlated with predator body size (Brandl *et al.*, 1994). Consequently, no relationship between predator body size and dietary niche breadth would emerge. Alternatively, if maximum prey size increases with predator body size but minimum prey size remains constant, then a positive relationship between body size and dietary niche breadth should exist (see Fig. 1 for details).

Here, we explore the relationship between body size, dietary niche breadth, mean, minimum, maximum and range of prey size for a large data set on predatory lizards. Lizards have proven to be ideal models for ecological studies because they are taxonomically diverse, exhibit a wide range of body sizes, are easily sampled and their diets can be quantitatively summarized and compared (Pianka & Vitt, 2003). We first describe the nature of the relationship between body size and dietary niche breadth and then identify the probable mechanism contributing to this relationship. Lastly, we review the available evidence for a general rule concerning body size and dietary niche breadth.

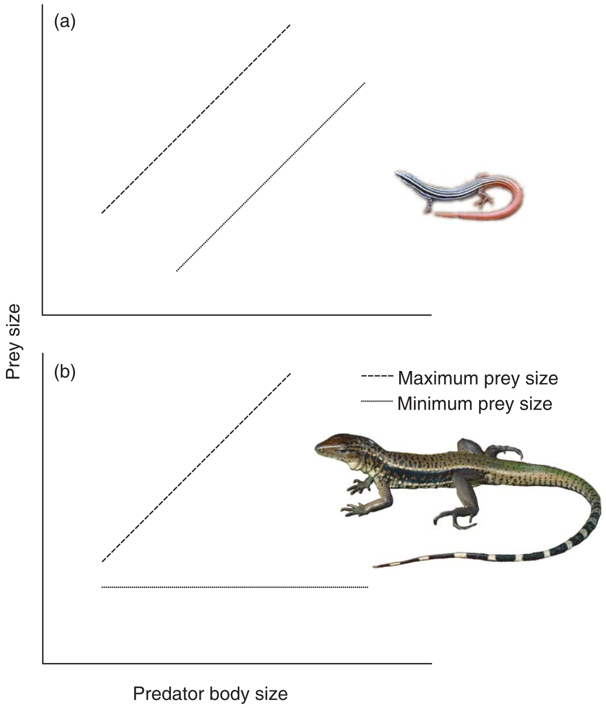

Figure 1 Two different possible scenarios for the relationship between predator and prey size. (a) Both maximum and minimum prey size increases with predator body size. While adding larger items to the diet predators avoid smaller items. Therefore, there is no increase in overall prey diversity in the diet of larger predators. In this case no relationship between body size and niche breadth is expected. (b) Maximum prey size increases with predator body size while minimum prey size remains constant. In this scenario predators add larger items to their diet and still prey on smaller items. Therefore, the overall prey diversity of larger predators is increased. In this case a positive relationship between niche breadth and body size is expected. Upper picture: *Vanzosaura rubricauda* a small-bodied lizard. Lower picture: *Tupinambis longilineus* a large-bodied lizard species. Photos by Laurie Vitt.

MATERIALS AND METHODS

Diets

Initially, we examined diet data collected for 184 lizard species from several localities around the globe, including 91 species from tropical rain forests of Nicaragua, Ecuador and Brazil, and semi-arid regions of north-eastern Brazil (Caatinga) and 93 species from deserts of the south-western United States, Australia and the Kalahari of Africa. The data set is the same as was used in a previous study, which examined how phylogenetic history affects lizard diets (Vitt & Pianka, 2005). We excluded 25 dietary specialists, because dietary specialization has arisen independently in several clades and does not appear to be associated with body size. We considered specialists to be species in which a single prey category represents 80% or more of its diet volumetrically. Dietary specialists have unusually narrow dietary niche breadths and most specialize on ants, termites or plants in the case of herbivores. After excluding these species, we calculated dietary niche breadth (B) for the remaining 159 species using the inverse of Simpson's diversity index (Simpson, 1949):

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where p is the volumetric proportion of prey category i and n is the number of prey categories. Prey categories were based on the identification of each prey item to the level of the order.

Values of niche breadth can vary from 1 (exclusive use of a single prey category) to n (equal use of all prey categories). Simpson's index is an algebraic transformation of Hurlbert's probability of an interspecific encounter (PIE), a diversity index that has good statistical properties and is not dependent on sample size (Gotelli & Graves, 1996). For different analyses (described below), we used the measurements of individual prey items to calculate the mean, minimum, maximum and range of prey item volume for each species. We used mean body mass for all individuals within each species as an estimate of the species' body size because energy use scales with mass. The data used in the analysis, and detailed methods for collection of diet data, prey categories and identification and measurements of prey are available in Appendix S1 in the Supplementary Material.

In addition to the analysis using all species, we conducted a similar analysis of diets of individuals of three well-sampled taxa (species and genera) to determine whether niche breadth and prey size vary with body size (snout–vent length in this case) within taxa. The taxa included were: *Ameiva ameiva* (Teiidae) and species of similar size in the genera *Cnemidophorus* (Teiidae) and *Tropidurus* (Tropiduridae).

Statistical analyses

Because species differ in their evolutionary relatedness, they do not represent independent data points in statistical analyses. Not to account for such evolutionary relationships could result in a reduction in the degrees of freedom and lower statistical power, and may affect parameter estimation (Grafen, 1989; Harvey & Pagel, 1991). To control for phylogenetic relationships, we employed phylogenetic independent contrasts (PIC) (Harvey & Pagel, 1991) using the software CAIC version 2.6.9 (Purvis & Rambaut, 1995). We constructed a composite phylogenetic hypothesis for the 159 lizard species based on several different published phylogenies (see Vitt & Pianka, 2005; Appendix S2). Because we did not have branch length data for the tree topology, we considered all branch lengths to be equal to 1. In the absence of information on branch lengths, this method produces the lowest type I error rates (Purvis *et al.*, 1994). Furthermore, previous studies using different methods to estimate branch lengths reported no difference among methods when performing regressions between two traits (Brandl *et al.*, 1994; Blackburn *et al.*, 1996).

The PIC method assumes a model of character evolution (Brownian motion), and thus if the model is incorrect the analysis may produce results that may be inaccurate (Price, 1997; Losos, 1999). Indeed, some studies have shown that, under extreme deviations from Brownian motion, PIC can be too conservative (i.e. Diniz-Filho & Tôrres, 2002), although the method seems to perform quite well when violations in this assumption are moderate (Martins *et al.*, 2002). Therefore, it may be useful to check assumptions of PIC by verifying whether contrasts are reasonably standardized, and here we did this by exploring the relationship of standardized contrasts and their standard deviation. A significant relationship would imply that contrasts were not adequately standardized and transformations on branch lengths would be necessary to match the assumption of character evolution under Brownian motion (Garland *et al.*, 1992). Some authors, on the other hand, suggest that the results of both phylogenetic and non-phylogenetic analysis should always be presented (Price, 1997; Blackburn & Gaston, 1998). For this reason, in addition to the results of the PIC we also present results of regressions using species as independent data points. However, we acknowledge that this analysis may suffer from the opposite effect and be too liberal.

Next, we performed a linear regression using contrasts of body mass and contrasts of dietary niche breadth, mean, minimum and maximum prey volumes. PIC has an expectation of zero and regressions must pass through the origin. Thus the degrees of freedom remain equal to the number of contrasts (number of nodes minus 1); for details see Garland *et al.* (1992) and Eisenhauer (2003).

In addition to the analysis using all species together, we performed linear regressions of body size against dietary niche breadth and mean prey volume for individuals of *Ameiva ameiva*, *Cnemidophorus* spp. and *Tropidurus* spp. To explore whether lizard head morphology can explain variation in dietary niche breadth, we performed a principal components analysis using the size-corrected head variables: length, width and height. We then computed contrasts of the first principal component and performed a linear regression through the origin of these contrasts against the contrasts of dietary niche breadth. Also, to access whether a larger body is simply a passive outcome of the need for a larger head for feeding or vice versa, we performed a multiple regression with both body size and head size in the model against mean prey size. All variables were log-transformed prior to calculating regressions. All regressions were performed using the software SPSS, version 11.0.

RESULTS

We found no relationship between the standardized contrasts and their standard deviations (very low r-values and all $P > 0.05$), indicating that contrasts are adequately standardized. Body size and dietary niche breadth are negatively related (Fig. 2a, Table 1); as lizard body size increases, the diversity of prey used decreases. Mean, minimum, maximum and ranges of prey sizes were all positively associated with body size (Fig. 2b–e). This result indicates that in addition to shifting diets to include larger prey, larger lizards exclude small prey resulting in the upward shift of minimum prey size with increasing lizard body size (scenario described in Fig. 1a). However, the increase in prey size range with body size suggests that larger lizards can still

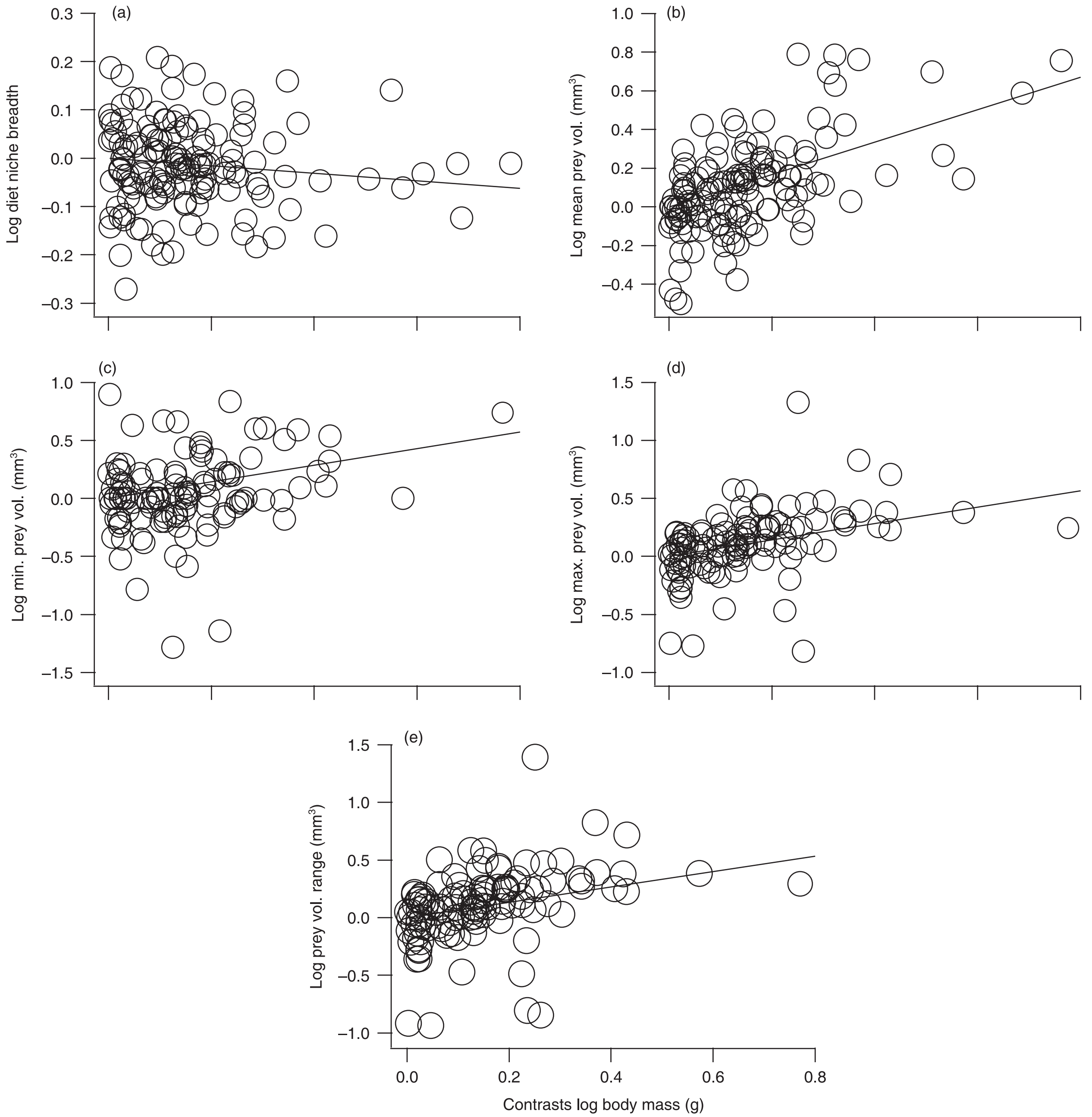

Figure 2 Phylogenetically independent contrasts of body weight vs. (a) contrasts of dietary niche breadth ($r^2 = 0.04$, slope = −0.1, $P < 0.01$); (b) contrasts of mean prey volume ($r^2 = 0.42$, slope = 0.93, $P < 0.01$); (c) contrasts of minimum prey volume ($r^2 = 0.16$, slope = 0.64, $P < 0.01$); (d) contrasts of maximum prey volume ($r^2 = 0.20$, slope = 1.08, $P < 0.01$); and (e) contrasts of prey volume range ($r^2 = 0.17$, slope = 1.03, $P < 0.01$). Note: regressions are calculated with intercepts of zero.

occasionally prey on small items. The analysis using species as independent data points achieved similar results with minor differences in correlation coefficients and slope values (Table 1).

When examining the same relationships within species, we found no correlation between body size and dietary niche breadth, but we still found a positive relationship between body size and mean prey volume (Fig. 3a–f). These results indicate that although larger individuals tend to prey on larger prey, there is no increase in the overall diversity of prey taken by larger individuals.

Even though considerable variation exists in head morphology and much of that is associated with lizard size, our analysis demonstrates that head morphology does not contribute to size-based variation in dietary niche breadth (first principal component of head size vs. Simpson's index of niche breadth, $r^2 = 0.02$, slope = 0.05, $P = 0.84$). Also, our multiple regression using lizard body mass and head size (first principal component) showed that while body mass is related to mean prey size ($P < 0.01$), head size was not ($P = 0.09$).

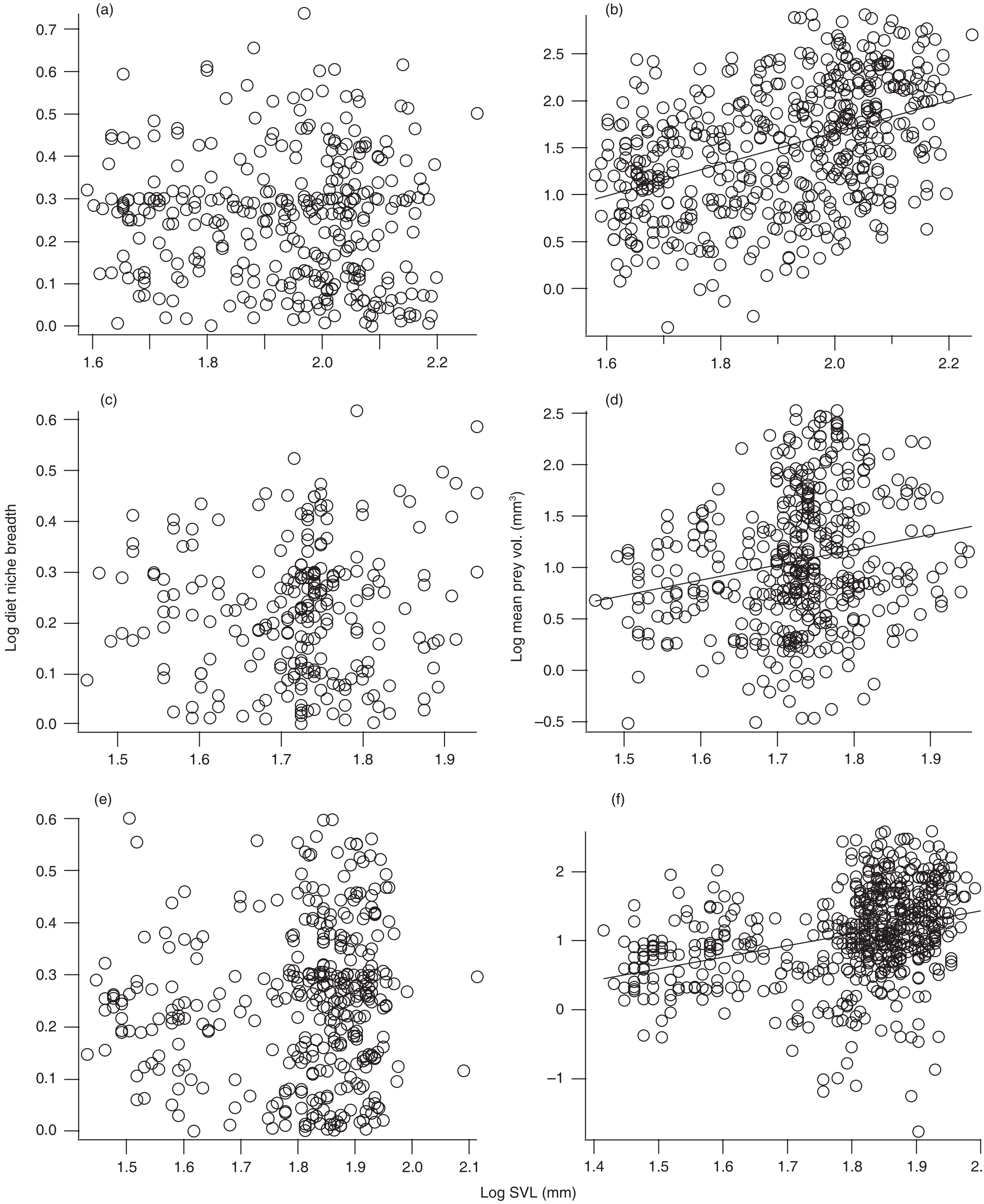

Figure 3 Relationship between snout–vent length (SVL), dietary niche breadth and mean prey volume for individuals within taxa. (a) SVL against dietary niche breadth for *Ameiva ameiva* ($r^2 = 0.06, P = 0.29$); (b) SVL against mean prey volume for *Ameiva ameiva* ($r^2 = 0.42, P < 0.001, y = 1.68x - 1.7$); (c) SVL against dietary niche breadth for *Cnemidophorus* spp. ($r^2 = 0.07, P = 0.34$); (d) SVL against mean prey volume for *Cnemidophorus* spp. ($r^2 = 0.2, P < 0.001, y = 1.5x - 1.5$); (e) SVL against dietary niche breadth for *Tropidurus* spp. ($r^2 = 0.1, P = 0.14$); (f) SVL against mean prey volume for *Tropidurus* spp. ($r^2 = 0.34, P < 0.001, y = 1.68x - 1.9$).

Table 1 Correlation coefficients (r), slopes and degrees of freedom (d.f.) of comparison between body mass and dietary niche breadth, mean, minimum, maximum and prey range volumes using species as independent data points. P-values are omitted because significance levels are biased in non-phylogenetic analysis.

Variable	r	Slope	d.f.
Dietary niche breadth	–0.19	–0.06	157
Mean prey volume	0.73	0.77	142
Minimum prey volume	0.59	0.90	122
Maximum prey volume	0.65	0.71	122
Prey volume range	0.59	0.71	122

DISCUSSION

Our results differ from those reported in other studies using birds (Brändle *et al*., 2002b), butterflies and moths (Wasserman & Mitter, 1978; Brändle *et al*., 2002a) and herbivorous insects (Novotny & Basset, 1999), all of which exhibit positive body size–niche breadth relationships. Nevertheless, some studies have reported a lack of association between dietary niche breadth and body size (Brandl *et al*., 1994). We are not aware of any study that has previously reported a negative relationship between body size and dietary niche breadth. Although our result appears intuitively paradoxical, the frequency distribution of body sizes in general may account for it. The frequency distribution of organisms is heavily skewed toward small body sizes (Gaston & Blackburn, 2000), therefore most prey items available to predators are small-bodied. Exclusion of small prey from the diets of larger lizards, even with the addition of some larger prey in different taxa, may reduce the overall diversity of prey eaten by larger lizards.

We found a positive relationship between prey size range and lizard body size. Therefore, large lizards ingest prey with a larger variability in size. This result has been previously reported for a large spectrum of predators (Vézina, 1985). This probably occurs because of the occasional ingestion of small prey items. This ingestion is not consistent enough to have an impact on dietary niche breadth or affect the relationship between body size and minimum prey size. If large lizards where consistently preying on small items we would not see a positive relationship between body size and minimum prey volume and we would see a positive relationship (or lack of a relationship) between body size and dietary niche breadth. The best explanation for our results is that larger lizards tend to avoid smaller prey either because they are difficult to handle and/or the energetic cost of including them exceeds the energetic gain. For predators with a wide size range of available prey, the optimal strategy should be to selectively target prey offering the maximum net energy gain and selectively exclude those that offer no net gain or actually accrue a net cost to capture. Our results build on other recent evidence for the importance of optimal foraging in ecosystems and large-scale ecological patterns such as the structure of food webs (Beckerman *et al*., 2006).

Even though previously unreported, the relationship we found should be widespread among predators. One possible reason why previous studies have failed to capture this relationship might be that they covered too narrow a range of predator body sizes. In our analysis we used 159 species of lizards from around the globe including some of the smallest and largest species. Our results for individuals within lower taxonomic groups (species and genera) support this argument. Body size variation within *Ameiva ameiva*, species of *Cnemidophorus* and species of *Tropidurus* is low relative to the variation that exists across all lizard species, and we found no relationship between body size and dietary niche breadth within these genera.

A general pattern of increased niche breadth with increasing body size does appear to be the case with respect to habitat/microhabitat and physiological niche axes (Wasserman & Mitter, 1978; Novotny & Basset, 1999; Pyron, 1999). Likewise, in herbivorous insects in which microhabitat niche breadth is a good proxy for dietary niche breadth (e.g. number of host plants), a positive association between body size and niche breadth is consistently reported (Wasserman & Mitter, 1978; Novotny & Basset, 1999). It is not surprising that our results for predators are different from those for herbivores. Small and large herbivores have potential access to the same set of plants, whereas small predators cannot prey on very large prey (gape limitation) and large predators may choose not to prey on very small prey (optimal foraging).

In summary, theory and most empirical data suggest that a positive relationship between body size and niche breadth is a widespread general pattern in macroecology. Nevertheless, the dietary niche breadth of predatory lizards decreased with body size, suggesting that consuming small prey when larger and probably more profitable prey are available is not an optimal foraging strategy; larger predators should target larger prey while avoiding smaller prey. The decrease in dietary niche breadth that we found with increasing predator size appears to result from the general decrease in diversity with body size (prey in this case) that exists in organisms (e.g. many more taxa are small-bodied). We caution ecologists and evolutionary biologists that although some patterns in macroecology appear well-supported (e.g. the right-skewed distribution of organism size), others, such as putative increases in niche breadth with body size, are much more complex and often constrained by patterns at a more basic level.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Species used in the analysis and their measurements.

Appendix S2 Phylogenetic relationships of the 159 lizard species used in the analysis.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2008.00405.x
(This link will take you to the article abstract).

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