Global Ecology & Biogeography (2002) **11**, 41–47

RESEARCH LETTER

Does body size predict dates of species description among North American and Australian reptiles and amphibians?

ROBERT N. REED* and SCOTT M. BOBACK

Department of Biological Sciences, Auburn University, Auburn AL 36849–5414 U.S.A.

ABSTRACT

Which factors determine whether a species is obvious to collectors? For some taxa, species of small body size tend to be described later than large-bodied species, perhaps because large animals are more obvious or easily captured. Thus it has been proposed that current estimates of species numbers within taxa may be biased, as they may not include small species. However, the trend for recently described species to be small-bodied has only been observed in a few higher taxa, and may not be general. Herein, we examine the relationships between body size and date of description for the entire herpetofaunas of North America and Australia (snakes, lizards, turtles, frogs and salamanders). We found that body size is generally a poor predictor of description date in herpetofaunal taxa. Even for most taxa that did exhibit a negative relationship between these variables, recently described species could not be distinguished from a random draw from overall species pools. We interpret our results in the light of the history of exploration of these continents and the biology of reptiles and amphibians.

Key words Amphibians, Australia, body size, date of description, macroecology, North America, randomization, reptiles, species richness estimates.

INTRODUCTION

Within a variety of higher taxa, the probability of describing a species tends to be related to body size (Diamond, 1985; Gaston, 1991; Gaston & Blackburn, 1994; Gaston *et al.*, 1995). In other words, large fierce animals may be rare (Colinvaux, 1980) but large animals do tend to be collected and described earlier than small animals. Our knowledge of faunal diversity both within and among taxa may thus be biased in favour of large species, especially in incompletely surveyed areas such as the tropics. If this bias exists, estimates of species numbers and concomitant conservation planning should be adjusted to account for small and as yet undescribed species within each taxon.

The explanatory power of body size in predicting description dates varies widely among taxa, and has only been examined in some insects, birds and mammals (Gaston, 1991; Gaston & Blackburn, 1994; Patterson, 1994; Blackburn & Gaston, 1995; Gaston *et al.*, 1995). The best evidence for a strong relationship comes from insects, but even among insect taxa this evidence is far from uniform (Gaston, 1991; Gaston *et al.*, 1995). Among South American birds, geographical range size and relative abundance are the best predictors of description date, while body mass is a very poor predictor of description date (Blackburn & Gaston, 1995). Clearly, the assumption that recently described species are small is debatable and further data are needed to assess the generality of this hypothesis.

In this paper we examine relationships between body size and description date for the reptiles and amphibians of North America and Australia. We first use Spearman correlations to test for negative relationships between these variables. Secondly, we examine possible confounding effects of the shape of body size distributions on regression results via randomization tests. Finally, we test the generality of the body size/description date thesis by examination of patterns across higher taxa and between the two continents.

MATERIALS AND METHODS

Our dataset included 1433 species from five higher taxa: lizards, snakes, turtles, frogs, and salamanders, encompassing the entire non-marine herpetofaunas of Australia and North America (exclusive of Mexico). Dates of description were taken from Cogger (2000) for Australian species and Collins (1997) for North American species. Some taxonomic decisions in the latter publication are under debate (Frost *et al.*,

* Corresponding author and current address: Robert N. Reed, Drawer E, Savannah River Ecology Laboratory, Aiken, SC 29802, USA. E-mail: reed@srel.edu

1992; Van Devender *et al.*, 1992); we therefore used Behler (1992) and Conant & Collins (1998) as arbiters of North American species status. Species are often described as unique, then later synonymized with sister taxa, only to be resurrected as full species at a later date. Our methods do not take into account this type of taxonomic shuffling. However, dates of description document when a taxon was first recognized as unique, and are thus appropriate for analysis of description date–body size relationships (Patterson, 1994).

Body size data were compiled from various sources (Stebbins, 1985; Behler, 1992; Conant & Collins, 1998; Cogger, 2000). When sources conflicted for body size of a species, we used the value given in the most recent publication. We used either snout–vent length (SVL) or total length (TL) as indicators of body size, depending on availability. However, use of SVL or TL was uniform within each taxon from a given continent. We used logarithmically transformed ($\log_{10}$) body size data in all analyses. Relationships between body length and date of description were examined separately for each taxon using Spearman correlation analysis.

Within most higher animal taxa examined thus far, the distribution of body sizes is highly right-skewed, even after logarithmic transformation (Brown & Maurer, 1989; Blackburn & Gaston, 1994a; Blackburn & Gaston, 1998). Thus the tendency for recently described species to be small-bodied may be because they are a random sample of the overall size distribution, rather than because they are more difficult to collect and/or describe (Gaston & Blackburn, 1994). It is important to reject this hypothesis before accepting mechanistic explanations for the negative relationship between body size and description date. We thus calculated the skewness of the log-transformed body size distribution of each taxon from each continent to determine if reptiles or amphibians are disproportionately represented by small species, as predicted by previous studies (skewness coefficients were considered significant if the absolute value of skewness divided by the standard error of skewness was greater than 2.0: systat v.9, 1998). We then compared the size distribution of recently described species in a higher taxon (defined here as the most recently described 20% of species) with the overall size distribution of that taxon using simulation tests (following Gaston & Blackburn, 1994), which have higher power than conventional statistics when dealing with non-normal distributions (Crowley, 1992). Within each taxon from each continent, a sample of body lengths equal to 20% of the total number of species in the taxon was drawn randomly and without replacement from the overall distribution. The mean, standard deviation and skewness of the sample were calculated, and the algorithm was repeated 10 000 times. Results from the simulation tests were compared with mean, standard deviation and skewness of the actual log-transformed distribution of the recently described species, under the null hypothesis that the ‘real’ values represent a random draw from the pool of all described species.

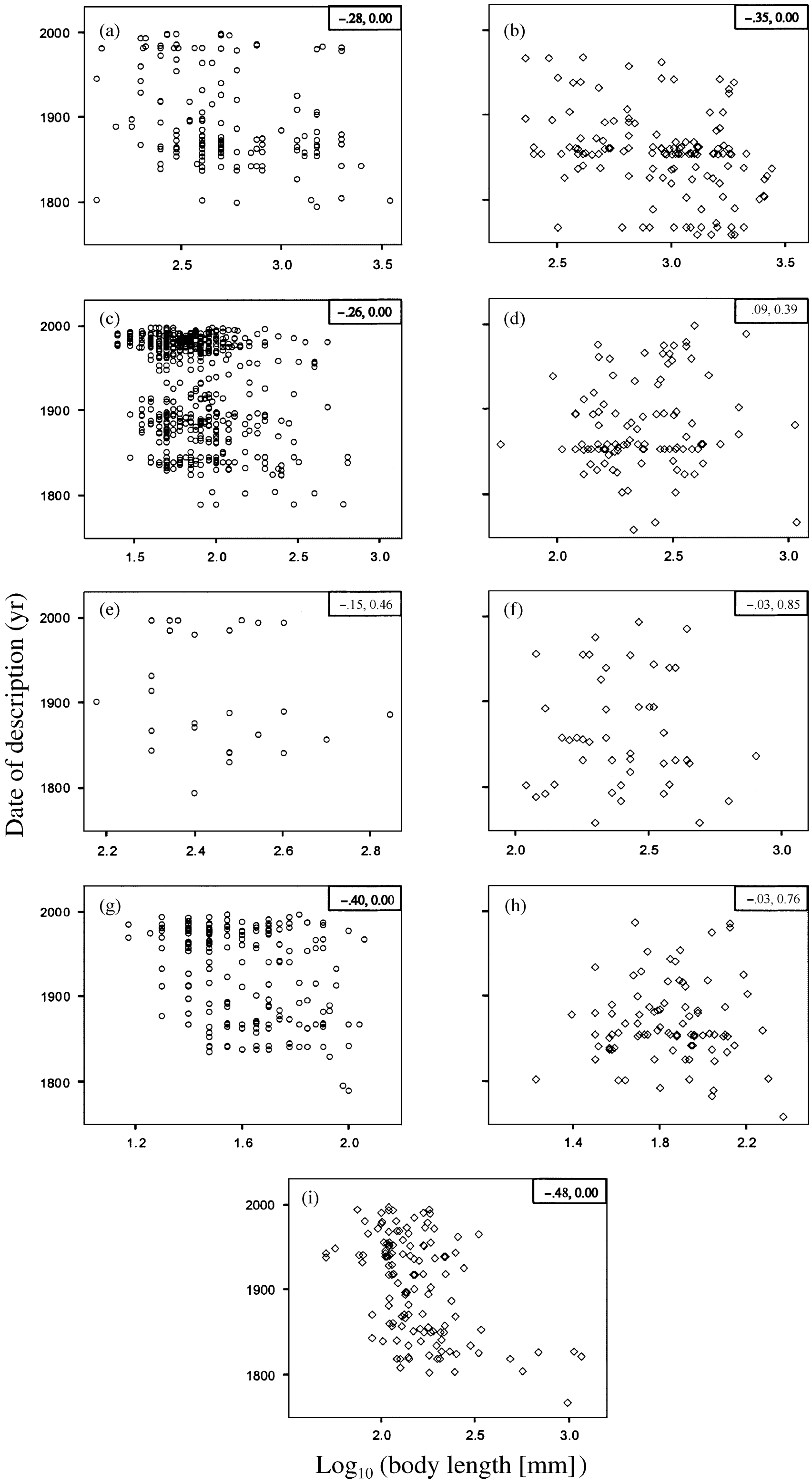
RESULTS

Of nine Australian and North American higher taxa, five exhibited significantly negative correlations between body size and date of description (Fig. 1). This relationship was most pronounced for North American salamanders, North American snakes and Australian frogs, all of which had correlation coefficients < -0.35. Australian lizards and snakes also exhibited significant correlations, but these were not as strongly negative. Examination of correlation coefficients and *P*-values between North American and Australian assemblages revealed that correlations between body size and description date were similar in direction and magnitude for snakes and turtles, but different for frogs and lizards.

All taxa except North American snakes and frogs exhibited right-skewed body size distributions after log-transformation. However, skewness was statistically significant only for North American salamanders, Australian lizards and Australian snakes (Fig. 2).

Simulation tests on mean body size (log-transformed) generally agreed with results from correlations: the same five taxa had recently described species of smaller body size than expected (Table 1, Fig. 1). Among recently described species, however, only Australian lizards displayed less variance in body size ($P = 0.030$) than expected (Table 1), and only North American snakes were more right-skewed than expected ($P = 0.011$), although Australian snakes approached statistical significance ($P = 0.065$). Thus we cannot reject the hypothesis that negative relationships between body size and description date (from correlation results) for many of these taxa are simply due to recently described species comprising a random draw from continental species distributions.

Fig. 1 (opposite) Description dates of North American and Australian reptiles and amphibians, plotted by higher taxon as a function of body size ($\log_{10}$-transformed). *X*-axis for Australian lizards = Log_{10} (snout–vent length [mm]), for all others *x*-axis = Log_{10} (total length [mm]). Boxes in upper right of each panel contain r^2 values followed by *P*-values. Values in bold indicate statistically significant ($P < 0.05$) Spearman correlations. (a) Australian snakes ($n = 150$, mean = 2.71); (b) North American snakes ($n = 132$, mean = 2.96); (c) Australian lizards ($n = 605$, mean = 1.86); (d) North American lizards ($n = 99$, mean = 2.38); (e) Australian turtles ($n = 26$, mean = 2.45); (f) North American turtles ($n = 49$, mean = 2.40); (g) Australian frogs ($n = 210$, mean = 1.60); (h) North American frogs ($n = 89$, mean = 1.84); (i) North American salamanders ($n = 128$, mean = 2.19).



(a)
−.28, 0.00
(b)
−.35, 0.00
(c)
−.26, 0.00
(d)
.09, 0.39
(e)
−.15, 0.46
(f)
−.03, 0.85
(g)
−.40, 0.00
(h)
−.03, 0.76
(i)
−.48, 0.00
Date of description (yr)
Log_{10} (body length [mm])

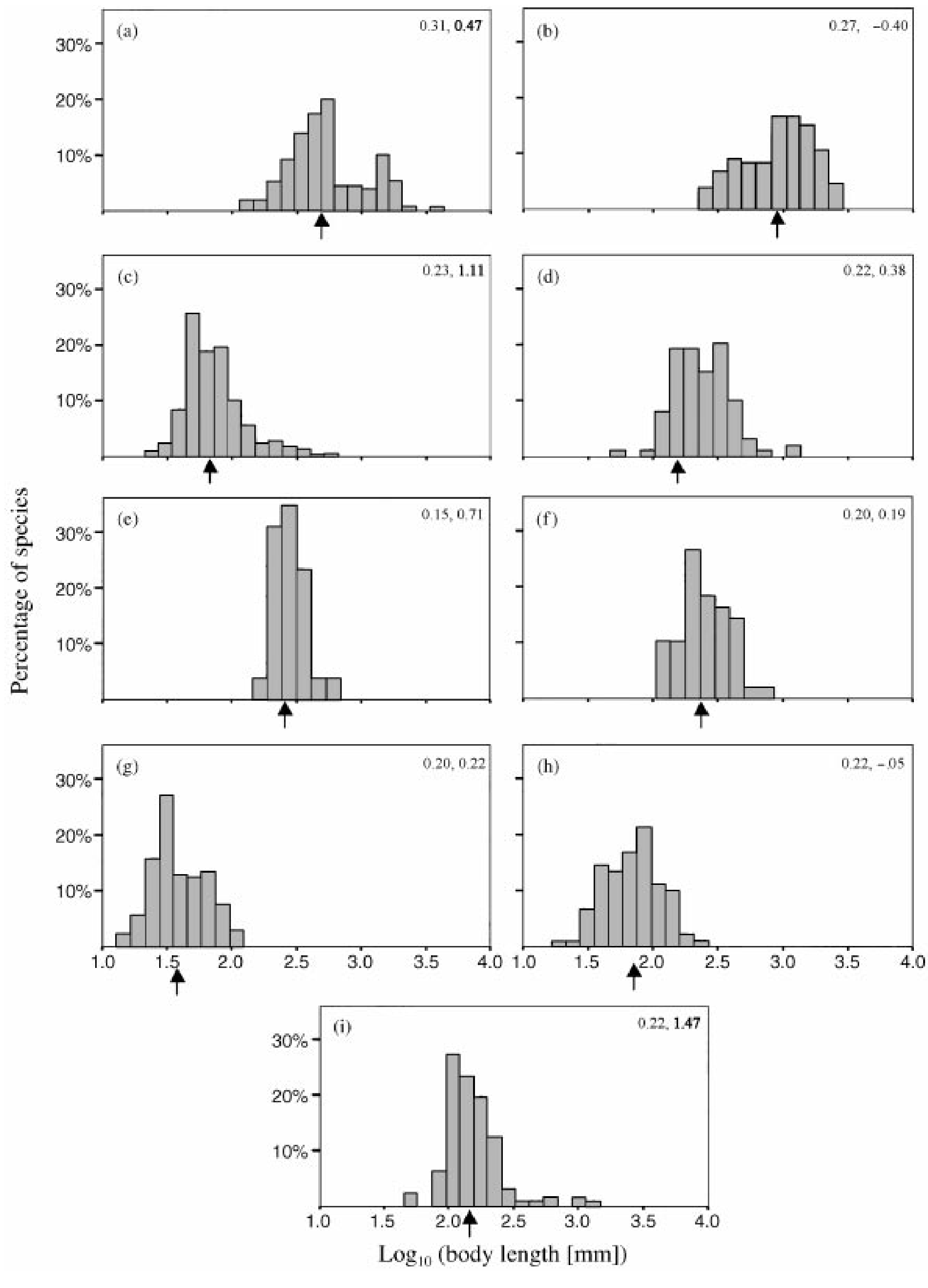


Fig. 2 Frequency distributions of North American and Australian reptiles and amphibians with respect to $\log_{10}$-transformed body size. *X*-axis for Australian lizards (c) = $\log_{10}$ (snout–vent length [mm]), for all others *x*-axis = Log_{10} (total length [mm]). Standard deviation is indicated in upper right of each panel followed by skewness. Values in bold indicate significantly skewed distributions (skewness coefficients were considered significant if absolute value of skewness divided by the SE of skewness was greater than 2, see text). Arrows along the *x*-axes indicate mean values. Panel key as in Fig. 1.

DISCUSSION

The most obvious feature of our results was a marked lack of consistency: relationships between body size and date of description varied widely between continental herpetofaunal taxa. While the relationship was significantly negative for five of nine correlation analyses, these results were tempered by high dispersion of data points and relatively low correlation

Table 1 Results of simulation tests of body size distributions (log_{10}-transformed [mm]) of the most recently described 20% of each higher taxon, sampled from the size distribution of all species in that taxon (by continent; thus each of the nine simulation tests is independent of all others). 'Real distribution' refers to the parameter calculated for recently described species. 'Proportion of simulations' indicates the proportion of 10 000 simulated distributions which was less than or greater than the parameter immediately preceding. Results significant at the 0.05 level are in bold type; none of these retained significance after sequential Bonferroni correction ($N = 53$ possible comparisons across all three test families)

Taxon	Mean (real distribution)	Proportion of simulations		SD (real distribution)	Proportion of simulations		Skew (real distribution)	Proportion of simulations	
		Less	Greater		Less	Greater		Less	Greater
N. American turtles	2.377	0.323	0.677	0.159	0.186	0.814	−0.234	0.293	0.707
Australian turtles	2.422	0.342	0.658	0.126	0.464	0.536	0.789	0.686	0.314
N. American lizards	2.441	0.938	0.062	0.194	0.327	0.673	−0.612	0.083	0.917
Australian lizards	1.815	**0.007**	0.993	0.196	**0.030**	0.97	0.521	**0.012**	0.988
N. American snakes	2.808	**0.002**	0.998	0.290	0.756	0.244	0.243	0.989	**0.011**
Australian snakes	2.618	**0.028**	0.972	0.307	0.504	0.496	0.957	0.935	0.065
N. American frogs	1.903	0.916	0.084	0.193	0.201	0.799	−0.123	0.401	0.599
Australian frogs	1.515	**0.002**	0.998	0.198	0.449	0.551	0.227	0.507	0.493
N. American salamanders	2.103	**0.015**	0.985	0.142	0.064	0.936	0.927	0.374	0.626

coefficients. Only within some higher taxa were recently described species of small body size, and thus the prediction that recent descriptions are biased towards small species lacks generality. North American and Australian snakes displayed roughly equivalent relationships between body size and description date, as did turtles from the two continents, but this equivalence was not observed for other higher taxa. Thus, although these two continents are of similar land surface area, and the earliest species descriptions are from the same period (*c.* the 1750s), the broad patterns of species description rates appear to be generally different. Australia has a much smaller population than the United States and Canada (< 20 000 000, as opposed to > 250 000 000 in the United States alone), and historically there may have been fewer taxonomists and fewer opportunities to encounter new species. Also, extended travel in the arid (and reptile rich) interior of Australia is logistically difficult, and large areas are not serviced by roads.

It is somewhat surprising that only three of nine body size distributions were significantly log-skewed to the right, and that two taxa were actually log-skewed to the left. Log-transformed reptilian and amphibian body size distributions thus may not be generally characterized by either modes at a very small body size or disproportionately low numbers of large-bodied taxa, as predicted in the majority of macroecological literature (e.g. Brown & Maurer, 1989; Blackburn & Gaston, 1994a,b; Blackburn & Gaston, 1998). Taxa that fail to exhibit a log-transformed size distribution that is skewed to the right may be incompletely known, and the distribution may assume the predicted shape as more small species are discovered and described (Blackburn & Gaston, 1994a). While this bias could pertain to some taxa addressed in this paper, it is unlikely to be a strong explanation overall. It is extremely unlikely, for example, that enough North American snakes or frogs (taxa that have been fairly well surveyed) of the appropriate size classes will be discovered to shift overall log-transformed size distributions from a left skew to a strong right skew. Collins (1997) has proposed that a number of allopatric populations of North American reptiles and amphibians should be elevated to full species status. If adopted, this approach could conceivably add a number of species and change the size distributions of higher taxa. His 'new' species are scattered among a wide variety of size classes, however, and so would be unlikely to alter the size distributions appreciably.

What of the five higher taxa in which recently described species *were* of smaller body size? It is tempting to divine ecological or historical mechanisms for these results. However, our simulation tests show that such an attempt would be misguided. For most taxa, skewness and standard deviation parameters derived from size distributions of recently described species did not differ from simulated distributions drawn from their respective overall species pools. These results contrast with findings for the recently described birds of the world (Gaston & Blackburn, 1994); using similar simulation methods, the authors found that these birds are smaller-bodied, have lower variance in body weight and have a size distribution that is more right-skewed than expected.

Why is body size a poor predictor of description date for the majority of reptiles and amphibians? For many species, body size may not be an important factor in whether or not they are apparent to collectors. Male frogs of most species advertise to females via calls during the breeding season, making them obvious to humans regardless of body size. Many snakes of various size classes are nocturnal and/or fossorial and thus rarely encountered, while some large snakes are sedentary and extremely cryptic (e.g. many vipers and pythons: Reinert & Zappalorti, 1988; Shine, 1996). Sophisticated statistical or molecular techniques are increasingly used both to re-define 'established' herpetofaunal groups, and to identify heretofore 'cryptic' species (e.g. Shea, 1998; Highton, 1999); results from these types of recent studies have resulted in major increases in the numbers of described species (especially in Australia). Thus the relative conspicuousness of species of reptiles and amphibians may often be due to factors other than simply body size.

Given that species within a taxon are unlikely to be described at random, which ecological variables may be of greater importance than body size in predicting description date? Among recently described birds, disproportionately many belong to groups that tend to be cryptic, geographically localized, or small (Diamond, 1985). Both geographical range and relative abundance are better predictors of description dates of South American oscine birds than is body size (Blackburn & Gaston, 1995), with geographical range by far explaining the most variance. Unfortunately, an analysis of this sort is not yet possible for all the reptiles and amphibians of these two continents, but we predict that geographical range will greatly affect description date. We also predict that, given historical patterns of European colonization and the logistical difficulties of travel to some areas, species with distributions in central or far northern Australia should have been described at a later date.

In conclusion, it is far too early to generalize about the effects of body size on description dates in animal taxa. We particularly caution researchers against the temptation to estimate the number of species remaining undescribed by using body size/description date relationships. While the enumeration of the species on Earth holds enduring fascination for scientists and lay-people alike, estimating species numbers of incompletely known taxa must be based on hypotheses that are valid for most organisms. Our results indicate that even for the herpetofaunas of two continents that have been intensively studied, general relationships between body size and description date are nebulous at best; estimating species numbers in poorly known regions via extrapolation of these relationships would be fanciful.

ACKNOWLEDGMENTS

We thank T'ai Honda Roulston for writing the computer program used in randomization tests. This paper was improved by the comments of C. Guyer, R. Shine, M. Lomolino, B. Patterson and one anonymous reviewer. RNR and SMB thank the Auburn University Graduate School for support, SMB thanks C.J. and S. Boback for inspiration, and RNR thanks the Fulbright Foundation and the Australian-American Educational Foundation for support.

REFERENCES

Behler, J.L. (1992) *The Audubon Society field guide to North American reptiles and amphibians*. Alfred A. Knopf, New York.

Blackburn, T.M. & Gaston, K.J. (1994a) Animal body size distributions: patterns, mechanisms, and implications. *Trends in Ecology and Evolution*, **9**, 471–474.

Blackburn, T.M. & Gaston, K.J. (1994b) The distribution of body sizes of the world's bird species. *Oikos*, **70**, 127–130.

Blackburn, T.M. & Gaston, K.J. (1995) What determines the probability of discovering a species? A study of South American oscine passerine birds. *Journal of Biogeography*, **22**, 7–14.

Blackburn, T.M. & Gaston, K.J. (1998) The distribution of mammal body masses. *Diversity and Distributions*, **4**, 121–133.

Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243**, 1145–1150.

Cogger, H.G. (2000) *Reptiles and amphibians of Australia*, 6th edn. Reed New Holland, Sydney.

Colinvaux, P. (1980) *Why big fierce animals are rare. An ecologist's perspective*. Penguin Books, Harmondsworth, UK.

Collins, J.T. (1997) *Standard common and current scientific names for North American amphibians and reptiles*, 4th edn updated. Online at http://eagle.cc.ukans.edu/~cnaar/CNAAR/CNAARNA-Checklist.html. Center for North American Amphibians and Reptiles.

Conant, R. & Collins, J.T. (1998) *A field guide to reptiles and amphibians of eastern and central North America*. Houghton Mifflin Company, Boston.

Crowley, P.H. (1992) Resampling methods for computation intensive data analysis in ecology and evolution. *Annual Review of Ecology and Systematics*, **23**, 405–447.

Diamond, J.M. (1985) How many unknown species are yet to be discovered? *Nature*, **315**, 538–539.

Frost, D.R., Kluge, A.G. & Hillis, D.M. (1992) Species in contemporary herpetology: comments on phylogenetic inference and taxonomy. *Herpetological Review*, **23**, 46–54.

Gaston, K.J. (1991) Body size and probability of description: the beetle fauna of Britain. *Ecological Entomology*, **16**, 505–508.

Gaston, K.J. & Blackburn, T.M. (1994) Are newly described bird species small-bodied? *Biodiversity Letters*, **2**, 16–20.

Gaston, K.J., Blackburn, T.M. & Loder, N. (1995) Which species are described first? The case of North American butterflies. *Biodiversity and Conservation*, **4**, 119–127.

Highton, R. (1999) Geographic protein variation and speciation in the salamanders of the *Plethodon cinereus* group with the description of two new species. *Herpetologica*, **55**, 43–90.

Patterson, B.D. (1994) Accumulating knowledge on the dimensions of biodiversity: systematic perspectives on Neotropical mammals. *Biodiversity Letters*, **2**, 79–86.
Reinert, H.K. & Zappaloorti, R.T. (1988) Timber rattlesnakes (*Crotalus horridus*) of the Pine Barrens: their movement patterns and habitat preference. *Copeia*, **1988**, 964–978.
Shea, G.M. (1998) Geographic variation in scalation and size of the black whip snakes (Squamata: Elapidae: *Demansia vestigiata* complex): evidence for two broadly sympatric species. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory*, **14**, 41–61.
Shine, R. (1996) Life history evolution in Australian snakes: a path analysis. *Oecologia*, **107**, 484–489.
Stebbins, R.C. (1985) *A field guide to western reptiles and amphibians*. Houghton Mifflin, Boston.
SYSTAT, Version, 9 Standard Edition (1998) SPSS Science Inc, Chicago.
Van Devender, T.R., Lowe, C.H., McCrystal, H.K. & Lawler, H. (1992) Viewpoint: reconsider suggested systematic arrangements for some North American amphibians and reptiles. *Herpetological Review*, **23**, 10–14.

BIOSKETCHES

Robert N. Reed has broad interests in the ecology and evolution of reptiles and amphibians. Bob's recent projects include evaluation of the efficacy of life history variables in predicting conservation status of elapid snakes, ecology and species isolating mechanisms among sea kraits in Vanuatu, and biology of mangrove monitor lizards on Pacific islands.

Scott M. Boback has interests in tropical and temperate herpetology. Currently, Scott is a PhD student in the Department of Biological Sciences at Auburn University. His recent projects include an investigation of evolutionary patterns of body size variation among insular snakes, the macroecology of snake body size, and foraging ecology of sympatric Neotropical salamanders.