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## **Life-history evolution in Australian snakes: a path analysis**

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**Abstract** I recently attempted to investigate interspecific patterns in ecological traits of Australian snakes using univariate statistical techniques (Shine 1994), but high intercorrelations among variables (especially with mean adult body size) made it difficult to interpret the observed patterns. In the present paper, I attempt to tease apart causal factors using multivariate (path) analysis on the same data set (103 species, based on dissection of >22000 museum specimens). Two separate path analyses were conducted: one that treated each species as an independent unit (and thus, ignored phylogeny) and the other based on independent phylogenetic contrasts. Path coefficients from the two types of analyses were similar in magnitude, and highly correlated with each other, suggesting that most interspecific patterns among traits may reflect functional association rather than phylogenetic conservatism. Path analysis showed that indirect effects of one variable upon another (i.e., mediated via other traits) were often stronger than direct effects. Thus, even when two variables appeared to be uncorrelated in the univariate analysis, this apparent lack of relationship sometimes masked strong but conflicting indirect effects. For example, a tradeoff between clutch size and offspring size tends to mask the direct effect of mean adult body size on clutch size. Path analysis may also suggest original causal hypotheses. For example, interspecific allometry of sexual size dimorphism (as seen in Australian snakes, and many other animal groups) may result from a strong effect of another allometrically-tied trait (offspring size) on growth trajectories of females.

**Key words** Allometry · Life history · Reproduction · Sexual dimorphism · Snake

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## Introduction

Despite an increasing scientific interest in the life-history traits of reptiles, available data are still strongly biased towards lizards – especially, phrynosomatid species living in temperate-zone habitats in the New World. For example, our understanding of life-history evolution in snakes lags well behind that for lizards. In order to detect and interpret broad trends in the adaptive radiations of squamates, we will require much broader data sets, from a much wider array of species and places (Seigel 1993). One group of snakes for which we do have extensive data are the Australian species. I have gathered ecological information from dissections of >22000 museum specimens of 103 species (Shine 1994a), the largest compilation for any southern-hemisphere reptile radiation. Even with such a large data set, however, the analysis and interpretation of evolutionary changes in life-history traits is fraught with difficulty. The reliance on correlation to infer causation is a formidable problem when so many life-history traits are highly intercorrelated, and often tied allometrically to body size. Even if we can distinguish trait correlations due to functional relationship from those due to phylogenetic conservatism (Harvey and Pagel 1991), we are still left with a bewildering array of correlations among traits, such that multiple causal hypotheses are consistent with the data. This is exactly the situation with Australian snakes. When I attempted to detect and interpret overall patterns using univariate statistics, I was frustrated by the high intercorrelations among variables and (especially) the high correlation of most variables with absolute body size (Shine 1994a). Multivariate statistics are better suited to disentangling such effects, and in the present paper I report an attempt to identify causal processes using a multivariate approach (path analysis) to the same data set.

Path analysis offers a promising technique for teasing apart correlations that result from indirect pathways (whereby there is no functional relationship between the two variables) from those produced by functional relationships. The procedure works by quantifying relation-

ships among variables based on a *a priori* model (the path diagram) that includes both direct and indirect effects of one variable upon another. Inevitably, the conclusions derived from a path analysis depend on the subjective judgements made by the investigator at the outset of the study: especially, which hypotheses are incorporated in the original path diagram. Thus, my rationale for selecting hypotheses is provided below. I constructed a path diagram to incorporate the following hypotheses and predictions:

1. *Evolutionary changes in dietary composition favor phylogenetic shifts in mean adult body size.* My rationale for this hypothesis was the correlation between body size and diet in Australian snakes, both within and among species: only the largest snakes specialise on mammalian prey (Shine 1994a). I considered the reverse causal connection (larger body size favors a dietary shift towards larger prey) to be less likely in evolutionary terms.
2. *Shifts in dietary habits influence optimal offspring size.* Because snakes are gape-limited predators, offspring may need to be a certain size at birth or hatching if they are to ingest a specific prey type (e.g., Nussbaum 1985). Thus, for example, I expected that the evolution of specialisation on larger prey (e.g., mammals rather than frogs) might favor an evolutionary increase in offspring size. Again, the reverse causal hypothesis (shifts in offspring size favor shifts in dietary habits), although plausible, seems less likely to be valid.
3. *Increases in mean adult body size favor increases in clutch size and offspring size, but there is a tradeoff between these two traits.* I based this hypothesis upon extensive published work showing allometric increases in both traits, and a tradeoff between them (e.g., Seigel and Ford 1987).
4. *Increases in offspring size favor delayed maturation in females.* This hypothesis was based on the notion that selection for increased offspring size should favour increased maternal body size, so that females can more easily accommodate the larger offspring (Andersson 1994; Shine 1994b). Because males do not carry the developing offspring, male body size at maturation should not be affected by offspring size. Similarly, clutch size should not affect female body size at maturation, because smaller female snakes simply produce smaller clutches, whereas offspring size is typically relatively constant over a wide range of female body sizes (Seigel and Ford 1987). Thus, offspring size, but not clutch size, might be expected to influence the evolution of female body size. I also predicted that *changes in growth trajectory* (especially, the proportion of maximum size at which maturation occurs) *are allometrically tied to mean adult body size*, based on consistent interspecific patterns in other taxa (e.g., Andrews 1988; Shine and Charnov 1992).
5. *The direction and degree of sexual size dimorphism is influenced by mean adult size, by the growth trajectories of the two sexes and by dietary composition.* These hypotheses were based on the general allometry of sexual

size dimorphism in snakes and other taxa (e.g., Shine 1993; Andersson 1994), the importance of growth trajectories as proximate determinants of dimorphism in adult size (e.g., Madsen and Shine 1994a), and comparative evidence for sex-specific divergence in dietary habits and trophic morphology in snakes (Shine 1993, 1994b).

6. *The sex ratio of adult specimens collected is affected by adult size, relative sizes at maturation, and sexual size dimorphism.* This hypothesis was based on interspecific allometry in sex ratios and sexual dimorphism (e.g., Shine 1993, 1994b), the notion that relative sizes at maturation should influence the relative numbers of adults of each sex in the population, and the idea that sex differences in activity patterns are tied to mating systems (which in turn influence dimorphism: Shine 1994b).

## Materials and methods

In any path analysis, the first step is to construct the path diagram – a representation of hypothesised causal relationships among variables. If the focus of the study is on the *evolution* of traits, such a path diagram incorporates putative links in terms of selective pressures. Thus, the diagram is based on the hypothesis that a phylogenetic shift in one trait (such as mean adult body size) imposes selection for a shift in another trait (such as offspring size). The nature of these causal relationships is thus fundamentally different from those used in path diagrams that model direct functional links between traits within short time spans (e.g., looking at processes occurring during a single reproductive season – King 1993). The path diagram contains residual variables as well as the independent and dependent variables. Residual variables quantify the proportion of variation in the dependent variable that is not explained by the multiple regression model (Kingsolver and Schemske 1991). Path coefficients are standardised partial-regression coefficients, obtained from a multiple regression on standardised variables for each dependent variable in the path diagram. Because the analysis is based on standardised variables, indirect effects of one variable on another can be calculated by multiplying path coefficients along all the pathways linking the two variables. The effect coefficient is the sum of the effects exerted along all of these pathways. The unit of such coefficients is the standard deviation of the variable; thus, a path coefficient of +0.5 means that an increment of 1 SD in the independent variable causes an increment of 0.5 SD in the dependent variable. Inclusion or exclusion of paths based on statistical significance of individual path coefficients is not recommended (Kingsolver and Schemske 1991), but my overall path diagram is strongly supported statistically. For example, all of the multiple regressions used to generate path coefficients for species mean values explained significant variation in the dependent variable ( $P < 0.0001$ ).

To address the problem of phylogenetic conservatism (i.e., correlation due to common inheritance rather than any functional relationship between the two features), I carried out two separate path analyses using the same path diagram. The first analysis (=“tips”, because it used the tips of the phylogenetic tree) was based on species mean values, and treated each species as an independent unit. Thus, any correlation between two traits might be due to either phylogenetic conservatism or adaptation. The second analysis was based on independent phylogenetic contrasts, whereby I superimposed mean trait values for each species onto a phylogenetic hypothesis (a cladogram), and calculated independent evolutionary contrasts (e.g., Harvey and Pagel 1991). Using this technique, the amount of evolutionary change in one variable can be compared to the amount of change in another variable. Correlat-

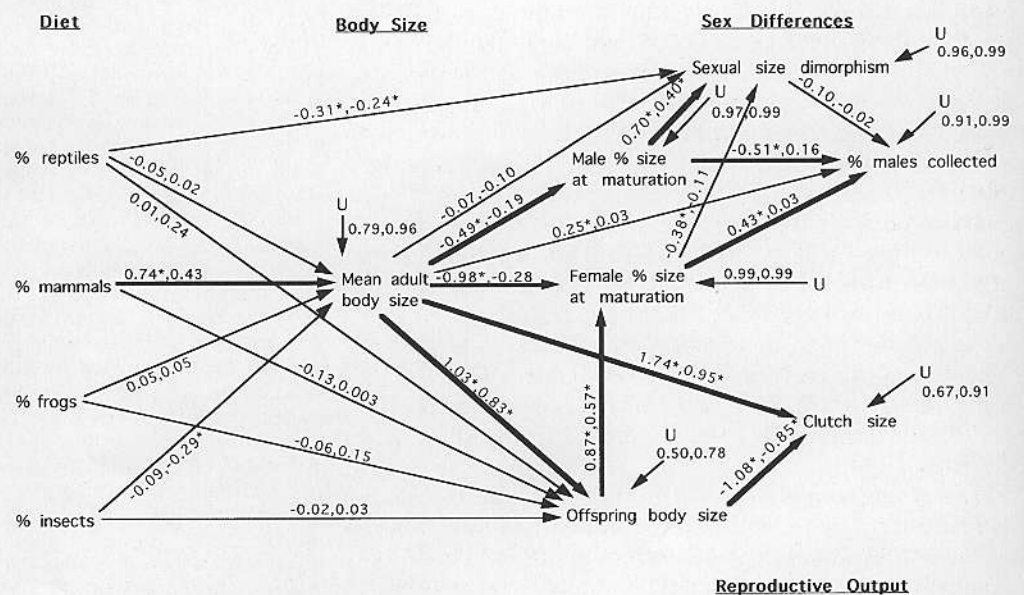
tions due to common inheritance will be deleted from these data, but if two traits are functionally related, phylogenetic shifts in one of them are likely to be accompanied by concurrent shifts in the other.

The data sets and phylogenetic hypotheses used in this paper are taken from my previous summaries (Shine 1994a, Appendix 1; Shine 1994b, Appendix 1). They include mean values for 11 ecological variables for 103 species of Australian snakes of four major Families. The species studied range from small fossorial typhlopids to large arboreal pythons, and include venomous as well as nonvenomous species. I used snout-vent length (SVL) as the measure of body size in all analyses. Sex differences in body size were quantified using the methods of Lovich and Gibbons (1992), whereby the mean adult SVL of the larger sex was divided by that of the smaller sex, and the difference between this value and 1.0 was used as the index of dimorphism (arbitrarily assigned to be positive if females were the larger sex, and negative if males were larger). This index has significant statistical advantages over simple ratio measures of sexual size dimorphism (SSD) (Lovich and Gibbons 1992). I used the proportion of the diet composed of reptilian prey as the diet variable to compare to SSD, because reptiles are the main prey type for most Australian snakes (Shine 1994a), and I have documented intraspecific sex differences in the proportion of reptilian prey (Shine 1991).

## Results and discussion

Figure 1 shows the path diagram incorporating the hypotheses listed above, and also displays path coefficients and residual variables. In general, path coefficients based on raw (tips) data and on phylogenetic contrasts were similar (mean path coefficient=0.09 for tips data, 0.09 for phylogenetic contrast data) and path coefficients calculated from these two data sets were highly correlated with each other ( $r=0.89$ ,  $n=30$ ,  $P<0.0001$ ). This similarity suggests that most of the major patterns of relationship among life-history traits result from functional relationships, rather than being artifacts of phylogenetic conservatism. I now consider each of the dependent variables in turn, in light of the results from the path analyses.

**Fig. 1** Path diagram of evolutionary relationships among ecological variables in Australian snakes. Two path coefficients are shown for each pathway: the first from a "tips" analysis that treats each species as an independent unit, and the second from analysis of independent phylogenetic contrasts. *Thick lines* show path coefficients  $>0.40$  (based on "tips" analysis); *asterisks* show path coefficients for which  $P<0.05$ . *U* shows the proportion of total variation in the dependent variable that is not explained by the combination of independent variables used in the analysis



## Mean adult body size

The primary result (from both the "tips" and phylogenetic analyses) is that only one dietary component (the proportion of the diet composed of mammals) strongly influenced body size (Fig. 1). The likely reason for this pattern is that there are few insectivorous snake species in Australia (only typhlopids), and the body sizes of anurophagous and saurophagous snakes overlap almost completely. Thus, interspecific shifts among these dietary categories have little effect on mean adult body sizes. In contrast, shifts to a mammalian diet involve considerable increases in body size. This result parallels that seen in intraspecific comparisons. I have documented several cases in which the proportion of mammalian prey increases with increasing body size within a species (Shine 1989; Shine and Slip 1990), but no instances of size-related shifts between other prey types.

## Offspring size

The path analysis suggests that mean adult size has a strong direct effect on offspring size, whereas dietary habits do not (Fig. 1). The result is a surprising one, in that many authors have predicted that the optimal size at hatching is affected by the types (and thus, sizes) of prey available (e.g., Nussbaum 1985). My analysis suggests that such effects occur, but are mediated through selection on adult size, rather than adjustment of offspring size *per se*. Because the proportion of mammalian prey in the diet exerts the strongest effect on body size, it also exerts the strongest indirect effect on offspring size (0.76 for tips data, 0.36 for contrasts). In comparison, the corresponding direct pathway is much weaker ( $-0.13$ ,  $0.003$ ; see Fig. 1). I note, however, that my conclusions in this respect depend heavily upon the way in which the path diagram was constructed; alternative path diagrams

**Table 1** Path coefficients linking mean adult body size (snout-vent length, SVL) to other ecological traits in interspecific comparisons among Australian snakes. The Table provides path coefficients from two different analyses: a "tips" analysis that treated each species as an independent unit, and a "phylogenetic contrast" analysis based on evolutionary changes in traits

	"Tips" analysis	Phylogenetic contrasts
Effect of body size on:		
Offspring size		
Direct effect	1.03	0.83
Clutch size		
Direct effect	1.79	0.97
Through offspring size	-1.11	-0.89
Effect coefficient	0.68	0.08
Proportion of mean adult SVL at maturation in females		
Direct effect	-0.98	-0.28
Through offspring size	0.90	0.47
Effect coefficient	-0.08	0.19
Sexual size dimorphism		
Direct effect	-0.07	-0.10
Through male maturation size	-0.34	-0.03
Through female maturation size	0.37	0.08
Through offspring size and female maturation	-0.34	-0.05
Effect coefficient	-0.38	-0.10
% Males in collected adults		
Direct effect	0.25	0.03
Through sex dimorphism	-0.001	0.001
Through male maturation size	0.25	-0.03
Through female maturation size	-0.42	-0.008
Through male maturation and dimorphism	0.03	0.001
Through female maturation and dimorphism	-0.03	-0.0004
Through offspring size, female maturation	0.39	0.01
Through offspring size, female maturation and dimorphism	0.03	0.001
Effect coefficient	0.50	0.005

are possible, and might suggest a greater link between prey types and offspring sizes.

#### Clutch size

Mean adult body size exerts a strong effect on clutch size, but this direct effect is opposed by a large negative indirect effect mediated through offspring size (Table 1). That is, larger species have larger clutches, but they also produce larger offspring – and evolutionary increases in offspring size cause reductions in clutch size. Such tradeoffs between clutch size and offspring size are probably widespread, and reflect the need to partition finite resources into reproduction (e.g., Seigel and Ford 1987). Given a fixed upper limit to some resource (such as energy investment or abdominal space available to hold the clutch), an increase in offspring size must inevitably reduce clutch size. The end result of these two conflicting pressures is that clutch sizes increase with body size, but at a slower rate than would occur in the absence of the tradeoff involving offspring size (Table 1).

#### Growth trajectory

In larger species, both sexes tended to mature at a lower proportion of mean adult size (i.e., they kept growing

more after maturation). The same trend is seen in other reptiles (Andrews 1988; Shine and Charnov 1992). The shift in males may be related to male-male combat, which is more common in larger species (Shine 1994a). The consequent fitness advantages of large body size in males may favor continued growth in this sex (Madsen and Shine 1994). In females, the proportion of mean adult body size at maturation was influenced both by allometry and by offspring size (Fig. 1). These effects tend to cancel each other out. An increase in mean adult size favors maturation at relatively small size, but also favors an increase in offspring size, which militates against early maturation. The net result is that changes in mean adult size had less effect on the proportional size at maturation in females than in males (effect coefficients of -0.08 versus -0.49), because male size at maturation was unaffected by offspring size (see Shine 1994b for further analysis of offspring size versus adult male body size).

#### Sexual size dimorphism

The dietary composition variable employed in the analysis (proportion of the diet composed of reptiles) showed significant relationships with SSD in both "tips" and

phylogenetic analyses (Fig. 1). This result supports previous inferences from ecological data, suggesting that dietary divergence between the sexes may influence the evolution of SSD (Shine 1991, 1993). Why are males larger, relative to conspecific females, in larger species of Australian snakes? The path analysis clarifies possible reasons for this allometry. The direct effect of mean adult size on the direction and degree of sex differences in body size was small, but indirect effects were strong (Table 1). Because body size at maturation was highly correlated with mean adult size (e.g., Shine 1990), the relative sizes at which the two sexes achieved maturity strongly influenced the resultant degree of sexual size dimorphism. However, the effect of larger offspring size on female maturation cancelled out the effect of the size-mediated shift in proportional size at maturation in this sex (see above). Thus, the allometry of sexual size dimorphism among these taxa seems to result from a factor (allometry of mean offspring size) that influences maturation patterns in females but not males (Table 1). The end result is isometry of relative maturation size in females, and allometry in males – so that the degree of SSD shows strong allometry.

These pathways also mean that the degree of SSD is correlated with relative offspring size ("tips" data:  $n=92$ ,  $r=0.22$ ,  $P<0.03$ ), because the latter variable influences female size at maturation, which in turn influences mean adult female size and thus, SSD. Weatherhead and Tøtterød (1994) recently documented a correlation between SSD and relative offspring size in birds, and interpreted it in terms of epistatic genetic effects. The relationships described above suggest an alternative explanation for their pattern.

#### Sex ratio of adults in collections

The proportion of adult males in museum collections tended to increase with mean adult body size. The trend was due primarily to a direct effect of size, combined with a tendency for males to outnumber females in species in which males attain maturity at a small proportion of mean adult size (Fig. 1). As noted above, the latter effect probably reflects an association between growth trajectories and the mating system: males tend to mature at a lower proportion of mean adult size in species that show male-male combat (Shine 1994a). Males engaged in combat bouts are notoriously insensitive to danger and thus, such a mating system may make males more vulnerable to predators (including museum collectors). Also, earlier maturation in males should directly increase the numbers of adult males in the population relative to the number of adult females. However, these trends were opposed by an indirect effect working through size at female maturation (Table 1). The much lower path coefficients for phylogenetic contrast analyses (Table 1) suggest that such effects may largely reflect phylogenetic conservatism (e.g., in the mating system) rather than functional relationships.

The use of path analysis thus helps to clarify relationships among ecological variables in Australian snakes. In particular, this technique was successful in partitioning observed correlations into biologically interpretable direct and indirect effects. Perhaps the strongest result to emerge from these analyses is that overall correlations among traits (as summarised in effect coefficients) are often the result of several significant indirect as well as direct effects. In several cases, the magnitude of the indirect effects is greater than that of the direct effects. The allometry of sexual size dimorphism offers a good example. Males are larger relative to females in species of larger absolute body size. The path analysis suggests that this allometry is due primarily to changes in growth trajectories, and to effects of offspring size on female growth patterns, rather than to a direct effect of body size *per se* (Table 1). In other cases, such as the relationship between mean adult size and clutch size, the overall correlation actually masks a major indirect effect that is very strong, but works in the opposite direction of the direct effect (Table 1).

How do these conclusions differ from those reached by univariate analyses of the same data set (Shine 1994a)? The primary conclusion from univariate analyses was the importance of allometry: most of the traits examined were significantly correlated with mean adult body size. Path analysis of the same data confirmed the existence of strong correlations between body size and other attributes (as is evident from the effect coefficients in Table 1) but suggested that (1) many of these effects are indirect rather than direct; and (2) even where no overall effect of body size on another trait is apparent, a direct effect may be present (and strong) but masked by conflicting strong indirect effects. Indeed, indirect effects were strong enough to obscure the correlation between the magnitude of direct effects and effect coefficients ( $n=9$ ,  $r^2=0.16$ ,  $P=0.15$ ).

Multivariate analyses may also generate new hypotheses about causal processes underlying general patterns. Perhaps the most exciting idea to emerge from the present analysis is a possible explanation for a general pattern: allometry of the degree of sexual size dimorphism in many lineages. In many taxa, males tend to be larger, relative to conspecific females, in species of large absolute body size than in smaller taxa (e.g., Reiss 1989; Andersson 1994). The same trend occurs in the Australian snakes (Table 1; Shine 1994a, b). The path analysis suggests that this allometry results from a strong effect of relative offspring size on the body size at maturation in females. Although the offspring of small species are smaller *in absolute terms* than offspring of larger taxa, they are larger *relative to maternal size*. This is true in many kinds of animals (e.g., Andrews 1982; Reiss 1989; Andersson 1994). The path analysis suggests that this increase in relative offspring size favors later maturation in females (i.e., at a larger body size) whereas sizes at maturation in males are (unsurprisingly) unaffected by offspring size. Because absolute body size at maturation strongly affects mean adult body size (e.g., Shine 1990), the delay in maturation of females, relative to males, re-

sults in a trend to female-biased sexual size dimorphism in smaller species (Table 1). It would be interesting to examine data on other animal taxa, to see whether this process offers a plausible mechanism for the general allometry of sexual size dimorphism.

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