

RELATIONSHIP BETWEEN MASS AND LENGTH IN AUSTRALIAN ELAPID SNAKES

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Least squares regression analysis of log mass on both log snout-vent and log total length for individuals of each sex of 14 populations of ten species of Australian elapid snakes indicates that in the 37 most robust data sets isometry occurs in 21 cases, negative allometry in ten cases and positive allometry in six. Isometry seems to be the most common kind of allometry in 'colubroid'-shaped snakes. There are no cases of different kinds of allometry between the sexes in any one species. However, in *Austrelaps ramsayi* both measures of length indicate that mass is relatively greater in males than in females over the middle and large end of the size range. The population of regression lines for log mass on log length for large diurnal, surface-active elapids are bounded by *Austrelaps ramsayi* on the heavy side and by *Pseudonaja textilis* on the light side. These extreme morphological differences may be related to the species' extreme ecological differences. The former species is a frog eating, live-bearing inhabitant of a cool environment with a short growing season, whereas the latter is a lizard, bird and mammal eating, egg-laying inhabitant of a warm environment with a longer growing season. □ *Allometry, elapids, mass, sexual dimorphism.*

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Mass is probably the single most important co-variate of an organism's other biological variables (McMahon & Bonner, 1983; Schmidt-Nielsen, 1984; Calder, 1996). Although there is a vast amount of raw data on mass for Australian vertebrates in the literature, unpublished theses and researchers' notes, little of this information has been collated and summarised. In this paper we analyse published and unpublished data on mass and length in ten species of Australian elapid snakes in order to determine the nature of the allometric relationships and whether sexual dimorphism exists.

MATERIALS AND METHODS

Data on mass (gm) and snout-vent and total length (mm) were gathered from the literature and our own notes (for origin of R. Shine's data and up-dated identifications, see Shine 1977 and 1989, respectively). All data were transformed to base 10 logs prior to analysis.

The relationship between mass and length was analysed initially for each sex using least squares regression. The comparison between mass and each measure of length between the sexes was examined using analysis of covariance with length as the covariant and sex as the factor. Homogeneity of residual mean squares of the regressions was verified prior to the ANCOVA. All analysis was done using SYSTAT 9.0 software. The 0.05, 0.01, and 0.001 levels of

significance are indicated by *, ** and ***, respectively.

Mass data were rejected if the specimen was known to be gravid, and total length data were rejected if the specimen had part of the tail missing.

RESULTS

We found unanalysed data suitable for regression analyses of log mass on log length for 14 populations of ten species of Australian elapid snakes. Data sufficient for a comparison of the regressions between the sexes of the same species were available for nine species (all except *Suta suta* which was only represented sufficiently by males). The results of these analyses are given in Table 1. We also include for the sake of completeness, but do not discuss, some basic regression statistics for *Acanthophis antarcticus* which are the only previously published results with possible relevance for allometry in Australian elapids.

The data are of variable quality for the purposes of our analysis. For example, we discount data for any sex based on fewer than ten specimens. We also discount the data for the female *Notechis ater* as they almost certainly include gravid individuals. The specimens were collected in period of 19 October to 15 February, and although no note was made of whether females

appeared gravid or not (Mirtschin & Bailey, 1990), the collection period coincides with the reproductive season (Shine, 1987b). We also discount the data for *Austrelaps superbus* from King Island due to the apparent rounding off of both lengths and weights, the latter in some cases apparently to the nearest 50g (Fearn, 1994). We also suspect that the relatively low r^2 values for female *Notechis scutatus* from Melbourne may be indicative of an atypical variable (Watharow, 1997, 1999). Finally, we note that the lack of small females in *Hemiaspis signata*, may distort both the allometry and the comparison with males (data R. Shine). In the following discussion we put to one side these qualified data (indicated by italics in Table 1) and focus on the remainder.

DISCUSSION

Methodologically, mass correlates with both snout-vent length and total length about equally well. In those cases where the r^2 values differ, snout-vent length has a higher value in three cases, and total length has a higher value in five cases. However, in no case does the difference exceed 0.01. Furthermore, both length measures gave the same indication of allometry in all cases except for *Pseudechis porphyriacus* from New England. For each sex in this species, the data for the total length indicated a relatively larger increase in mass with length than did snout-vent length. This could be due to a relatively larger increase in mass of the tail with length in this species.

The relationship between mass and length in Australian elapids can be in positive allometry, isometry, or negative allometry, depending on species. However, isometry is the most common form of allometry, occurring in 21 of 37 cases ('total samples' and 'combined' sexes excluded); negative allometry occurs in ten cases, and positive allometry occurs in six cases. In terms of the kind of allometry, there is no difference between the sexes of any species. Therefore we assume that for species represented adequately by only one sex, the allometry of that sex is indicative for the species.

In terms of the kind of allometry shown, the only comparable data set we are aware of is that for 12 species of North American colubrids, a group which is similar in shape and ecology to Australian elapids. The data for these species were based on combined sexes, but they indicated that the mass on length relationship was in isometry in 11 species and in negative allometry in only one, *Heterodon platyrhinos* (Kaufman &

Gibbons, 1975). Hence it may be that isometry is widespread in 'colubroid'-shaped snakes.

Assuming that isometry is the null condition, the cases of negative and positive allometry in Australian snakes are of interest. Negative allometry occurs in *Hemiaspis signata*, *Notechis scutatus* from the New England area, and *Parasuta dwyeri*. Positive allometry occurs in *Notechis scutatus* from Melbourne, *Pseudechis porphyriacus* from Macquarie Marshes and, in terms of total length only, in *P. porphyriacus* from New England. We have no explanation for these differences, but take note of the practical as well as the biological implications of the difference between two populations of the one species, *Notechis scutatus*.

Differences between the sexes in the elevations in the slopes occur in three species: with both measures of length in *Austrelaps ramsayi* and in *Notechis scutatus* from the New England area, and in total length in *Hemiaspis daemeli*. However, in the latter two species, the difference in elevations is so slight that we are reluctant to interpret it. In the case of *Austrelaps ramsayi*, it is clear on both measures of length that mass is relatively greater in males than in females over the middle and large end of the size range (Fig. 1). This may be due to more, or denser, muscle mass as has recently been demonstrated in two colubrids and one viperid in Europe (Bonnet et al., 1998).

The only species in which the residual mean squares of the regressions for each sex were significantly different was *Pseudechis porphyriacus* from the New England area; the unexplained variance in mass was significantly higher in males than in females in both length measures (Table 1). Again we are unable to offer a biological explanation, but we note the statistical implications for other studies of sexual dimorphism in mass on length relationships.

The mass on length regressions examined here form a distribution of roughly similar regression lines. Looking more closely at males only from the largest data sets (basically the Shine data) and restricting the analysis to snout-vent length for simplicity's sake, the boundaries of this distribution of regression lines are set by *Austrelaps ramsayi* on the relatively heavy side and *Pseudonaja textilis* (total sample) on the relatively light side (Fig. 2). The regression lines of the males of *Hemiaspis daemeli*, *H. signata*, *Notechis scutatus*, *Parasuta dwyeri* and *Pseudechis porphyriacus* (not figured to avoid crowding) fall

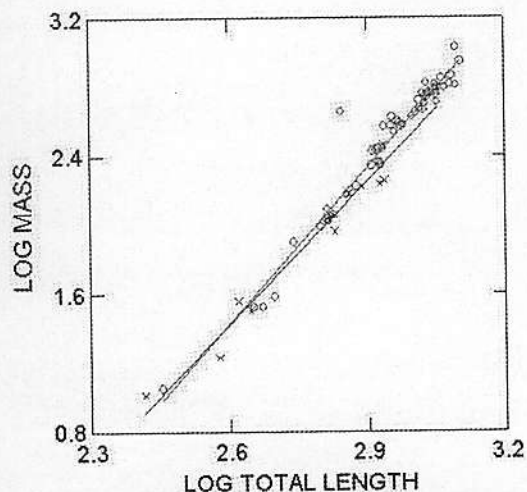


FIG. 1. Plot of log mass on log total length for both sexes of *Austrelaps ramsayi* from the New England area of New South Wales. \circ = males, \times = females.

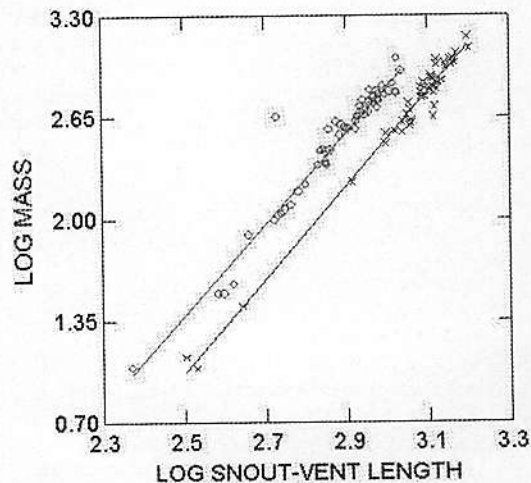


FIG. 2. Plot of log mass on log snout-vent length for males of *Austrelaps ramsayi* (\circ) and *Pseudonaja textilis* (\times).

between the regression lines for *Austrelaps ramsayi* and *Pseudonaja textilis*. In many ways these latter two taxa represent the near extreme ends of the range of diversity of active-searching, surface dwelling Australian elapids. For example, the former occurs at relatively high altitudes with shorter, cooler growing seasons, feeds largely on frogs and is live bearing (Shine, 1987a) whereas the latter occurs at lower altitudes with a longer, warmer growing season, feeds largely on reptiles, birds and mammals and is egg laying (Shine, 1989). We do not know what tissue differences may be contributing to the overall differences in mass in these two species. However, if it is fat, the heavier body in the species occupying the cooler climate with the shorter growing season makes adaptive sense. If it is muscle, the heavier body in the species hunting the generally less active prey and carrying the reproductive load for longer periods is also expected (the mass on length differences in the females of the two species are almost, but not quite, as well separated as in the males). We suspect that *Demansia psammophis* and perhaps *Oxyuranus scutellatus* would be even lighter for their length than is *Pseudonaja textilis*, but we lack the data to test this.

This review of mass and length data for Australian elapids suggests to us several ways to improve the quality of these kinds of data. First, the two measures of length used, snout-vent length and total length, are about equally robust

in their relationship with mass. Hence although both measures are usually taken, either will do by itself. Second, data on mass and length are most useful if specimens with potential confounding features are noted. Specifically, specimens with missing tails, in obvious poor health, recently fed, or gravid should have their condition indicated. Sexes should also be determined. Furthermore, the larger the sample size, the smaller the sampling area, and the more constrained the collecting period, the tighter the mass on length relationship is likely to be. Finally, it would be very useful to have additional data for the smaller species of elapids, as the current data set is primarily for large species.

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TABLE 1. Parameters for least squares regression analysis of log₁₀ weight (g) on log₁₀ length (mm) for ten species of Australian elapid snakes. ci = 95 percent confidence interval of the slope. A slope of 3.00 indicates isometry. All regressions are significant at the 0.001 level.

Species	Regression Parameter					Comparison of Regressions (F values)				
	inter	slope	ci	r ²	n	allometry	homogen	slopes	elevations	Reference
Snout-vent Length										
<i>Austrelaps ramsayi</i> New England										
males	-5.92	2.92	± 0.21	0.93	57	0	1.32 ^{ns}	0.96 ^{ns}	5.01*	R. Shine data
females	-5.48	2.74	± 0.28	0.97	13	0				
<i>A. superbus</i> Melbourne										
males	-3.16	1.94	0.66	0.90	6	-	2.22 ^{ns}	4.95*	-	Watharow, 1997, 1999
females	-5.80	2.86	0.54	0.93	10	0				
<i>A. superbus</i> King Island										
males	-2.98	1.95	0.40	0.85	20	-	2.96 ^{ns}	13.34**	-	Fearn, 1994; Fearn & Munday, 1995
females	-8.60	3.82	1.24	0.84	9	0				
<i>Hemiaspis daemeli</i> Macquarie Marshes										
males	-6.20	2.95	± 0.25	0.96	26	0	2.38 ^{ns}	0.02 ^{ns}	0.81 ^{ns}	R. Shine data
females	-6.10	2.92	± 0.40	0.94	15	0				
combined	-6.15	2.93	± 0.22	0.95	41	0				
<i>H. signata</i> New England area										
males	-4.79	2.39	± 0.26	0.94	24	-	1.08 ^{ns}	0.12 ^{ns}	1.32 ^{ns}	R. Shine data
females	-5.02	2.49	± 0.57	0.85	17	0				
<i>Notechis ater</i> Flinders Ranges										
males	-10.81	2.43	± 0.57	0.94	9	0	1.07 ^{ns}	3.38 ^{ns}	6.89***	Data in Mirtschin & Bailey, 1990
females	-13.89	2.92	± 0.44	0.95	39	0				Data in Mirtschin & Bailey, 1990

TABLE 1. (cont.)

Species	Regression Parameter						Comparison of Regressions (F values)			
	inter	slope	ci	r ²	n	allometry	homogen	slopes	elevations	Reference
<i>Notechis scutatus</i> Melbourne area										
males	-7.39	3.38	± 0.36	0.94	26	+	1.34 ^{ns}	4.52*	-	Data in Watharow, 1997
females	-5.29	2.63	± 0.67	0.79	20	0				
<i>N. scutatus</i> New England area										
males	-5.35	2.66	± 0.15	0.95	73	-	1.13 ^{ns}	1.45 ^{ns}	4.42*	R. Shine data
females	-5.66	2.79	± 0.15	0.97	51	-				
<i>Parasuta dwyeri</i> New England area										
males	-5.31	2.63	± 0.23	0.93	39	-	1.37 ^{ns}	0.057 ^{ns}	1.28 ^{ns}	R. Shine data
females	-5.17	2.58	± 0.31	0.91	31	-				
combined	-5.17	2.58	± 0.18	0.93	70	-				
<i>Pseudechis porphyriacus</i> Macquarie Marshes										
males	-7.04	3.25	0.17	0.98	37	+	1.47 ^{ns}	12.08**	-	R. Shine data
females	-3.35	2.02	0.58	0.91	7	-				
<i>P. porphyriacus</i> New England area										
males	-6.68	3.12	0.20	0.89	128	0	3.37***	-	-	R. Shine data
females	-6.67	3.11	0.19	0.96	49	0				
<i>Pseudonaja textilis</i> Macquarie Marshes										
males	-6.15	2.89	± 0.52	0.83	27	0	1.05 ^{ns}	1.20 ^{ns}	0.004 ^{ns}	R. Shine data
females	-7.78	3.42	± 0.80	0.91	9	0				
combined	-6.17	2.90	± 0.18	0.97	37	0				
<i>P. textilis</i> New England area										
males	-6.54	3.02	± 0.14	0.99	18	0	1.36 ^{ns}	0.05 ^{ns}	0.83 ^{ns}	R. Shine data
females	-6.49	3.00	± 0.18	0.99	11	0				
combined	-6.56	3.03	± 0.10	0.99	29	0				
<i>P. textilis</i> Total Sample										
males	-6.46	2.99	± 0.14	0.98	45	0	1.09 ^{ns}	0.05 ^{ns}	0.32 ^{ns}	R. Shine data
females	-6.54	3.01	± 0.15	0.99	20	0				
combined	-6.52	3.01	± 0.10	0.99	65	0				
<i>Suta suta</i> New South Wales										
males	-5.90	2.83	± 0.24	0.98	14	0	-	-	-	A. Greer data and Shine, 1988
Total Length										
<i>Acanthophis antarcticus</i> Eyre Peninsula										
combined	-6.76	3.09	?	0.97	206	?	?	?	?	Johnston, 1987
<i>Austrelaps ramsayi</i> New England area										
males	-6.42	3.02	± 0.19	0.95	54	0	1.01 ^{ns}	2.23 ^{ns}	5.09*	R. Shine data
females	-5.76	2.76	± 0.29	0.97	13	0				
<i>Austrelaps superbus</i> Melbourne area										
males	-3.24	1.93	0.68	0.89	6	-	1.31 ^{ns}	2.59 ^{ns}	1.00 ^{ns}	Watharow, 1997, 1999
females	-5.80	2.86	0.54	0.93	10	0				
<i>A. superbus</i> King Island										
males	-3.72	2.14	0.44	0.84	20	-	3.08 ^{ns}	11.22**	-	Fearn, 1994; Fearn & Munday, 1995
females	-9.44	3.99	1.34	0.83	9	0				
<i>Hemiaspis daemeli</i> Macquarie Marshes										
males	-6.54	2.99	± 0.25	0.96	26	0	2.00 ^{ns}	0.01 ^{ns}	6.25*	R. Shine data
females	-6.41	2.97	± 0.36	0.95	15	0				

TABLE 1. (cont.)

Species	Regression Parameter						Comparison of Regressions (F values)			
	inter	slope	ci	r ²	n	allometry	homogen	slopes	elevations	Reference
<i>Hemiaspis signata</i> New England area										
males	-5.20	2.46	± 0.25	0.95	23	-	1.12 ^{ns}	0.09 ^{ns}	4.26*	R. Shine data
females	-5.39	2.55	± 0.54	0.86	17	0				
<i>Notechis ater</i> Flinders Ranges										
males	-11.62	2.49	± 0.59	0.93	9	0	1.10 ^{ns}	2.54 ^{ns}	7.26*	Data in Mirtschin & Bailey, 1990
females	-14.49	2.95	± 0.24	0.94	38	0				
<i>Notechis scutatus</i> Melbourne area										
males	-7.80	3.43	± 0.29	0.93	46	+	1.97 ^{ns}	6.47*	-	Data in Watharow, 1997
females	-5.58	2.67	± 0.72	0.76	19	0				
<i>Notechis scutatus</i> New England Area										
males	-5.77	2.74	± 0.14	0.96	70	-	1.25 ^{ns}	0.06 ^{ns}	5.71*	R. Shine data
females	-5.80	2.76	± 0.15	0.97	48	-				
<i>Parasuta dwyeri</i> New England area										
males	-5.51	2.65	± 0.23	0.93	39	-	2.07*			R. Shine data
females	-5.30	2.58	± 0.31	0.91	31	-				
combined	-5.25	2.56	± 0.18	0.93	70	-				
<i>Pseudechis porphyriacus</i> Macquarie Marshes										
males	-7.52	3.33	± 0.17	0.98	36	+	1.33 ^{ns}	11.66**	-	R. Shine data
females	-3.75	2.10	± 0.62	0.92	6	-				
<i>P. porphyriacus</i> New England										
males	-7.20	3.23	± 0.20	0.89	117	+	3.51***	-	-	R. Shine data
females	-7.20	3.22	± 0.20	0.96	44	+				
<i>Pseudonaja textilis</i> Macquarie Marshes										
males	-7.05	3.10	± 0.65	0.80	25	0	1.15 ^{ns}	0.43 ^{ns}	0.06 ^{ns}	R. Shine data
females	-8.21	3.47	± 0.86	0.90	9	0				
combined	-6.49	2.92	± 0.20	0.96	35	0				
<i>P. textilis</i> New England										
males	-6.66	2.98	± 0.10	0.99	16	0	3.11 ^{ns}	0.019 ^{ns}	0.52 ^{ns}	R. Shine data
females	-6.72	3.00	± 0.21	0.99	10	0				
combined	-6.71	3.00	± 0.10	0.99	26	0				
<i>P. textilis</i> Total sample										
males	-6.64	2.97	± 0.13	0.98	41	0	1.37 ^{ns}	0.05 ^{ns}	0.59 ^{ns}	R. Shine data
females	-6.72	2.99	± 0.16	0.99	19	0				
combined	-6.70	2.99	± 0.10	0.98	60	0				
<i>Suta suta</i> New South Wales										
males	-5.98	2.79	± 0.24	0.98	14	0	-	-	-	A. Greer data