Allometry of Clutch and Neonate Sizes in Monitor Lizards (Varanidae: Varanus)

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This paper analyzes data from the published literature with the addition of some new information to explore the relationship between varanid body size and reproductive biology. Incubation time for varanid eggs is positively correlated with egg mass, neonate snout–vent length (SVL), and maximum adult snout–vent length (SVLmax). Incubation period of heavier eggs is proportionally less than for smaller eggs at 30 C: SVLmax is positively correlated with egg mass, clutch size, clutch mass, neonate body mass, and neonate SVL. Neonates of larger species have longer SVL but are smaller as a proportion of SVLmax than for smaller species. Clutch sizes are larger and more variable for larger species; however, clutch sizes for larger species relative to SVLmax are smaller than for smaller species. The intraspecific influence of maternal SVL on clutch size is greater than the interspecific influence of SVLmax on clutch size. These results suggest there are greater fitness advantages for smaller species having relatively larger offspring than for larger species, which concurs with results for snakes and other genera of lizards, as well as optimal offspring size theory. Reproductive output also appears to be influenced by maternal abdominal volume. Analysis of phylogenetically corrected data generally concurs with patterns evident in the nonphylogenetically corrected data. Body size has a much greater influence on reproductive output of Varanus than phylogeny.

EvolVutionary influences on reproductive biology in squamate reptiles have been the focus of scientific research for some time (Vitt and Congdon, 1978; Seigal and Fitch, 1984; Shine and Schwarzkopf, 1992). Several broad patterns have been identified in clutch sizes and relative clutch mass (RCM) for lizards. For example, clutch sizes and RCMs are generally lower among lizards than in snakes (Fitch, 1970; Seigel and Fitch, 1984), and widely foraging lizards have lower RCMs than do sit-and-wait predators (Vitt and Congdon, 1978). For many species, clutch or litter size increases with maternal body size (Fitch, 1985; Seigel and Ford, 1987; Shine and Greer, 1991). Clutch size is fixed among geckos and anoline lizards, although some species have multiple clutches in a year (Smith et al., 1973; Kluge, 1987; Werner, 1989). Life-history theory suggests that an animal’s reproductive output is influenced by trade-offs between current and future reproduction, as well as by phylogenetic, anatomical, and resource constraints (Stearns, 1992; Shine, 1992; Qualls and Shine, 1995). For example, Shine (1992) analyzed clutch mass and body shape in a range of snakes and lizards, suggesting that abdominal volume and shape offered plausible explanations for much variation in RCM.

Body size has enormous implications for an animal’s biology, being correlated with numerous life-history traits (Calder, 1984; Charnov, 1993; Harvey and Pagel, 1991). In addition to the above-mentioned variables, reproductive output is also significantly influenced by body size, with clutch or total litter mass generally increasing with maternal body mass. Among reptiles, the range of body sizes within a single taxon is often too small to provide sufficient variability for useful quantitative analyses of intraspecific allometric variability in reproductive output. Interspecific analyses are more common (Shine and Greer, 1991; James et al., 1992; Shine, 1992), although little is still known of the allometric influence on reproductive biology for squamate lizards.

Our objective was to quantify and to attempt to explain both intra- and interspecific allometric relationships between adult size and clutch size and mass, incubation time and neonate size, both within and among species of squamate reptiles. Such a study is best achieved in taxa that display considerable variation on size both within and among species but that also have similar body shape, foraging mode, and minimal phylogenetic differences to minimize the potential impact of these variables on analyses. Extant varanids are useful animals to explore such relationships because they are morphologically conservative (Thompson and Withers, 1997; Pianka, 1995) but vary greatly in size, both within and between species. Clutch sizes also vary intra- and interspecifically (James et al., 1992; Pianka, 1994; Horn and Visser, 1997). Data on clutch and neonate size, incubation
time, and temperature have accumulated over the last 20 years, with much information coming from captive-bred animals. Useful interspecific summaries of available field data are provided by James et al. (1992) and Pianka (1994). Horn and Visser (1989, 1997) summarize data on Varanus reproduction in captivity.

MATERIALS AND METHODS

Considerable confusion exists over nomenclature for some species (e.g., gouldii-pancoptes), and future taxonomic revisions will probably divide several existing species into more species (e.g., V. albogularis, V. exanthematicus, V. gouldii, V. panoptes, V. scalaris, V. tristis, and V. varius; King and Green, 1999). We use Storr's (1980) nomenclature for gouldii and panoptes. Although it might be desirable to analyze reproductive data at the subspecies level to minimize potential errors, subspecies have been grouped and dealt with at species level because most literature data do not indicate subspecies or specific capture location of specimens, precluding any subspecific assignment.

Adult size.—Based on an examination of viviparous and oviparous Lerista bougainvillii, Qualls and Shine (1995) report reproductive output in lizards is influenced by maternal body volume. Data on maternal body volume for Varanus are not available. Abdomen length would be next most useful measure because it is likely to be directly proportional to body volume. However, these data are also unavailable for most species. Presuming abdominal length is strongly positively correlated with SVL, SVL is the next best measure. For this analysis, we presume that Varanus abdomens (and thus body volumes) are similar in shape (Thompson and Withers, 1997), making body volume proportional to body length. Maternal SVL measurements are not available for most literature data on egg mass, clutch size and neonate size. Total length (TL) is not a good measure of body size because it includes tail length, and ends of tails are often missing (Thompson and Withers, 1997). An alternative measure of size is body mass. Body mass is excluded as a suitable measure of size because it depends on an animal's condition and reproductive status at the time of measurement and, again, is not available for most data on Varanus reproductive output. Therefore, we selected maximum reported SVL for each species as the measure of "size" for each species in our allometric analyses. Varanids are generally sexually dimorphic, with males growing larger than females (unpubl. reanalyses of data reported in Thompson and Withers, 1997), but, in the absence of maternal body volumes, body length, and maternal SVL data for most species for which we have accumulated reproductive output data, maximum SVL for the species is the best alternative. Greer (1989) lists SVL_{max} for 24 species of Australian varanids and Thompson and Withers (1997) provide SVL_{max} for 18 species of Western Australian varanids. Data from these two lists form the basis for the SVL_{max} of Varanus species studied here. Data from Auffenberg (1981, 1988, 1994), Branch (1991), Horn and Visser (1991), and personal records were used to supplement these records. Where SVL_{max} for a species was not available, it is estimated from the interspecific regression equation of total length (TL) with SVL \[ SVL_{max} = 0.0187 \times SVL + 0.328 \times TL \] (m \( r^2 = 0.94, P < 0.001 \)) based on the maximum TL reported for the species by De Lisle (1996) and the longest SVL from either Greer (1989) or Thompson and Withers (1997; Appendix).

Data sources.—Data come from two primary sources; captive bred varanids and field observations (wild-caught specimens). These data are not always comparable, but data from field observations remain scarce or nonexistent for many species. Where possible, data from wild-caught and captive-bred records are analyzed separately to enable comparisons. Because few data are available for neonate mass, SVL, and TL for wild-caught specimens, the mean of the combined wild-caught and captive-bred data are presented and used in subsequent analyses. Literature data are often presented in summarized form so that individual egg or clutch mass, clutch size, or neonate size for specific maternal specimens could not be determined. Grand means for species are reported and used in all regression equations for individual egg mass, clutch size and mass, neonate mass, SVL, and TL. Clutch mass was estimated by multiplying mean egg mass by mean clutch size for each species.

Temperature is a major determinant of incubation period (Van Damme et al., 1992; Phillips and Packard, 1994). Incubation temperature among species bred in captivity ranged from 26–33 \( ^\circ \)C, except for a single record for V. brevicauda (Schmida, 1974) deleted from our analyses. When a range of temperatures is reported for incubation, we used the midpoint. To facilitate comparisons, all incubation temperatures were adjusted to 30 \( ^\circ \)C. To do this, incubation periods for V. albogularis are combined for three different water potentials (−150,
data for and maternal SVL were determined from field periods to the same standard temperature of 30 C. and 33 C were calculated (0.48 and 0.77, re- and calculated. Q10-values between 27 and 30 C and 30 and 31 C) as provided by Phillips and Packard (1994) and the regression equation for the curved line of best fit through these data cal- (1991) and the regression equation for the and 33 C indicate that reduced major axis than 0.9 (Harvey and Pagel, 1991). Harvey and differ-ences between the three models are small ing measurement. Length and mass of neonates have also been used as independent variables to following preservation or was “stretched” dur-ing on the extent to which the specimen shrunk mens is also subject to minor variation depend- ing on the bases of SVL and total length and from data accumulated in museums. Measurement of SVL in live and dead speci-mens is also subject to minor variation depend-ing on the extent to which the specimen shrunk following preservation or was “stretched” during measurement. Length and mass of neonates have also been used as independent variables to predict incubation period and these variables may also contain measurement error for the same reasons. Zar (1984) suggests that errors in X variates are often impossible to eliminate in biology. Major axis and reduced major axis analyses can reduce error in both variates, although differences between the three models are small when the coefficient of determination is greater than 0.9 (Harvey and Pagel, 1991). Harvey and Pagel (1991) indicate that reduced major axis technique can yield nonsensical results, because it does not use any information about the co-variance between the Y and X variates, and as a consequence recommend against its use, although Christian and Garland (1996) report major axis exponents in conjunction with linear regression size exponents. All other studies cited for comparative purposes (Blueweiss et al., 1978; Ford and Seigel 1989; James et al., 1992) used least-squares regression. Therefore, we use least-squares regression in all data analyses and comparisons. However, slopes for major axis and reduced major axis analyses are included in tables should readers wish to access these data. Statistical confidence limits of P < 0.05 are used in all analyses.

Linear regression to determine allometric relationships assumes that data points are indepen-dent. For data examined here, species means cannot be assumed to be independent because they have evolved as part of a hierar-chical phylogeny, Felsenstein’s (1985) method of phylogenetically independent contrasts is of-ten used in analysis of such datasets to control for phylogenetic relatedness (Harvey and Pagel, 1991; Christian and Garland, 1996). The Var-anus phylogeny is not completely resolved and phylogenetic branch lengths are largely un-known even for reported phylogenies (Baver-stock et al., 1993; Fuller et al., 1998). We use the phylogeny for Varanidae reported by Fuller et al. (1998), with branch lengths taken from measurements from their figure 4 (D. King, pers. comm., indicated branch lengths shown are indicative of those calculated from the analysis). This phylogeny is supplemented with ad-ditional species from the phylogenetic inform-ation reported by Baverstock et al. (1993) and branch lengths for these data reported in Chris-tian and Garland (1996). Specifically, we have placed into the proposed phylogeny of Fuller et al. (1998) and estimated relative branch lengths for V. storri, V. semiremex, V. glebopalma, V. gilleni, V. spenceri, V. rosenbergi, V. panoptes, and V. indicus from Christian and Garland (1996) and V. fla-vescens and V. griseus from Baverstock et al. (1993). We added V. caudolineatus on the bases of its morphological similarity with V. gilleni and its distribution. The phylogeny used is shown in Figure 1. Where a datum for a variable was unavailable for a particular species that branch was deleted from the phylogeny and from the analy-sis. Scaling exponents were estimated using phylogenetically independent contrasts calculat-ed by the PDTREE computer program (vers. 5.0) described in Garland et al. (1993).
Fig. 1. Phylogeny and branch lengths for *Varanus* used in the phylogenetic analysis. See text for data sources.

**RESULTS**

**Incubation period.**—Incubation times (standardized to 30 C) varied widely among species (see Appendix) and are significantly and positively correlated with SVL$_{\text{max}}$ ($r^2 = 0.53$), individual egg mass ($r^2 = 0.33$), neonate SVL ($r^2 = 0.56$), and neonate body mass ($r^2 = 0.75$); with regression equations shown in Table 1. Slopes of regressions to predict incubation time from the equation $\log_{10}$ incubation time at 30 C (days) = $a + b \log_{10} X$ are as follows: egg mass 0.18, neonate body mass 0.25, neonate SVL 0.71, neonate TL 0.67, and SVL$_{\text{max}}$ 0.37 (Table 1). With phylogenetic effects removed, slopes of regressions on SVL are as follows: egg mass 0.13, neonate body mass 0.24, neonate SVL 0.47, neonate TL 0.57, and SVL$_{\text{max}}$ 0.37 (Table 2). Slopes of phylogenetically corrected and noncorrected regression equations cannot be evaluated for statistical differences because the PDTREE program forces the regression line through the origin. Inspection of slopes and standard errors for phylogenetically corrected and noncorrected exponents suggests that removal of phylogenetic effects has little impact on log$_{10}$-transformed predictors of incubation time. Correlation coefficients are, however, lower for phylogenetically corrected data, implying that there is some phylogenetic effect.

**Egg mass.**—Individual egg mass is positively correlated ($r^2 = 0.78$, $P < 0.05$) with SVL$_{\text{max}}$ (Table 3). The slope of the regression of egg mass on SVL$_{\text{max}}$ is 1.51. Mean volume of oviductal eggs for *V. breviceps*, *V. eremius*, *V. tristis*, and *V. gouldii* are 0.92cc ($n = 2$), 1.94cc ($n = 3$), 3.45cc ($n = 11$, SE $\pm 0.176$), and 7.21cc ($n = 3$), respectively. The slope of the regression of individual oviductal egg volume on maternal body mass (based on species means) is 0.51, and the slope of the regression of individual oviductal egg volume on maternal SVL is 1.56, indicating that oviductal egg volumes decrease proportionally as species maternal mass increases (but the proportional individual oviductal egg volume increases with increases in species maternal SVL). When phylogenetic effects are removed, the correlation between SVL$_{\text{max}}$ and egg mass is reduced from $r^2$ of 0.78 to 0.43, and the slope of regressions on SVL$_{\text{max}}$ is reduced from 1.51 to 1.17 (Table 4), suggesting that phylogeny is correlated with either the dependent or independent variable or both.

**Neonate size.**—Mean neonate mass and SVL as well as individual egg mass for each species are strongly and significantly positively correlated (neonate body mass with neonate SVL, $r^2 = 0.90$, $P < 0.01$; neonate body mass with egg mass

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**Table 1.** The relationship between incubation period at 30 C and neonate SVL (m), neonate body mass (g), maximum adult SVL (m) and individual egg mass (g).

<table>
<thead>
<tr>
<th>Variables</th>
<th>$a \pm \text{SE}$</th>
<th>$b \pm \text{SE}$</th>
<th>MA</th>
<th>RMA</th>
<th>$F_b$</th>
<th>$P$</th>
<th>$r^2$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>log$_{10}$ egg mass (g)</td>
<td>1.97 ($\pm 0.100$)</td>
<td>0.18 ($\pm 0.071$)</td>
<td>0.19</td>
<td>0.31</td>
<td>6.32,13</td>
<td>&lt;0.05</td>
<td>0.33</td>
<td>15</td>
</tr>
<tr>
<td>log$_{10}$ body mass (g)</td>
<td>1.89 ($\pm 0.040$)</td>
<td>0.25 ($\pm 0.034$)</td>
<td>0.25</td>
<td>0.28</td>
<td>52.50,17</td>
<td>&lt;0.01</td>
<td>0.75</td>
<td>19</td>
</tr>
<tr>
<td>log$_{10}$ SVL (m)</td>
<td>0.75 ($\pm 0.293$)</td>
<td>0.71 ($\pm 0.150$)</td>
<td>0.94</td>
<td>0.96</td>
<td>22.81,18</td>
<td>&lt;0.01</td>
<td>0.56</td>
<td>20</td>
</tr>
<tr>
<td>log$_{10}$ TL (m)</td>
<td>0.61 ($\pm 0.243$)</td>
<td>0.67 ($\pm 0.104$)</td>
<td>0.78</td>
<td>0.81</td>
<td>41.02,20</td>
<td>&lt;0.01</td>
<td>0.67</td>
<td>22</td>
</tr>
<tr>
<td>log$<em>{10}$ SVL$</em>{\text{max}}$ (m)</td>
<td>2.31 ($\pm 0.035$)</td>
<td>0.37 ($\pm 0.074$)</td>
<td>0.42</td>
<td>0.52</td>
<td>25.75,23</td>
<td>&lt;0.01</td>
<td>0.53</td>
<td>25</td>
</tr>
</tbody>
</table>

*Values are from the regression equation log$_{10}$ incubation time at 30 C (days) = $a + b \log_{10} X$, $\pm 1$ SE, and the slopes of the major axis (MA) and reduced major axis (RMA) regression equations.
\( r^2 = 0.98, P < 0.01; \) neonate SVL with egg mass
\( r^2 = 0.89, P < 0.01. \) Mean SVL\(_{\text{max}}\) for each species is significantly positively correlated with species means for neonate mass \( (r^2 = 0.85, P < 0.01) \) and neonate SVL \( (r^2 = 0.80, P < 0.01; \) Table 3). Without removal of phylogenetic effects, slopes of regressions on SVL\(_{\text{max}}\) for neonate body mass, SVL and TL are 1.57, 0.50 and 0.51, respectively. Neonates of larger species are longer in absolute size (SVL), however, as a proportion of maximum adult size, neonates of smaller species are proportionately larger than those of larger species. Neonates of larger species are proportionately heavier than those of smaller species. With phylogenetic effects removed, slopes of regressions on SVL\(_{\text{max}}\) of neonate body mass, SVL and TL are 1.66, 0.55, and 0.60, respectively. These values as well as correlation coefficients are similar to those when effects of phylogenetic relatedness are not removed (Tables 3–4).

**Clutch size**—Clutch size varies widely among species (Appendix 1). Interspecific relationships between means of clutch size and means for maternal SVL for nine wild-caught species (\( V. \) albigularis, \( V. \) brevicauda, \( V. \) caudolineatus, \( V. \) eremius, \( V. \) gouldii, \( V. \) olivaceus, \( V. \) salvator, \( V. \) spenceri, \( V. \) tristis) is best expressed by the significant log-log regression equation \( \log_{10} \text{clutch size} = -1.58 (SE \pm 0.400) + \log_{10} \text{SVL} (mm) (F_{1,8} = 40.66, P < 0.001, r^2 = 0.85). \) When phylogenetically corrected, the regression equation for the same data is \( \log_{10} \text{clutch size} = 0 (se \pm 0.00) + \log_{10} 1.02 (SE \pm 0.584) \) SVL\(_{\text{max}}\) (mm) \( (F_{1,7} = 7.01, ns, r^2 = 0.50). \) Although slopes are similar, the noncorrected regression equation is a better predictor of clutch size than the phylogenetically corrected equation which forces a zero intercept. SVL\(_{\text{max}}\) for all species is significantly positively correlated with species means for both field and captive bred clutch sizes \( (r^2 = 0.50; r^2 = 0.57, \) respectively). Slopes of regressions on SVL\(_{\text{max}}\) for clutch size for wild-caught and captive bred specimens are 0.65 and 0.81, respectively. When phylogenetically corrected, slopes are slightly lower at 0.58 and 0.76, and correlation coefficients are also lower (Tables 3–4).

Slopes of regressions on SVL\(_{\text{max}}\) for intraspecific relationships for \( \log_{10} \) clutch size varied significantly among species \( (F_{156} = 3.5, P < 0.05; \) Table 5). Shine and Greer (1991) argue that variance in clutch size should be measured using the coefficient of variation \( (CV) \) instead of the standard deviation. We calculated CV from field data for nine species. The positive correlation \( (r^2 = 0.51, P = 0.16) \) between mean SVL for each species and CV for each species is not statistically significant (Table 5).

The common slope of intraspecific regressions of clutch size on maternal SVL is 2.53. The only significant differences among the nine species are between \( V. \) olivaceus and \( V. \) tristis, \( V. \) olivaceus, and \( V. \) albignarius, and \( V. \) olivaceus and \( V. \) eremius. The steep slope (6.11) for \( V. \) olivaceus undoubtedly is responsible for these differences (Table 5).

Slopes of regressions on SVL are generally higher within species than between species, indicating that maternal SVL influences clutch size more than SVL\(_{\text{max}}\). Comparison of slopes of ellipses estimated to enclose 95\% of the distribution of clutch sizes based on maternal SVL with the interspecific regression line based on all nine species highlights these differences (Fig. 2). Slopes of regressions of clutch size on maternal SVL are significant for five of the six larger species: \( V. \) tristis, \( V. \) spenceri, \( V. \) albignarius, \( V. \) olivaceus, and \( V. \) salvator. It is more difficult to determine the relationship between clutch size and maternal size for smaller species because of limited variation in both clutch size and maternal SVL (see Table 5).

**Clutch mass**—Clutch mass is significantly correlated with SVL\(_{\text{max}}\) for both wild-caught \( (r^2 = 0.81) \) and captive bred \( (r^2 = 0.88) \) varanids.
Table 3. Allometric relationships for egg mass, clutch size, clutch mass, and neonate size with the maximum SVL for adults.

<table>
<thead>
<tr>
<th>Variables</th>
<th>$a$ (SE)</th>
<th>$b$ (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>log$<em>{10}$ egg mass and log$</em>{10}$ maximum SVL of adults</td>
<td>1.83 (0.086)</td>
<td>1.16 (0.065)</td>
</tr>
<tr>
<td>log$<em>{10}$ wild-caught clutch size and log$</em>{10}$ maximum SVL of adults</td>
<td>1.22 (0.069)</td>
<td>0.65 (0.141)</td>
</tr>
<tr>
<td>log$<em>{10}$ captive clutch size and log$</em>{10}$ maximum SVL of adults</td>
<td>3.03 (0.125)</td>
<td>0.50 (0.058)</td>
</tr>
<tr>
<td>log$<em>{10}$ wild-caught clutch mass and log$</em>{10}$ maximum SVL of adults</td>
<td>3.08 (0.100)</td>
<td>0.52 (0.068)</td>
</tr>
<tr>
<td>log$<em>{10}$ captive clutch mass and log$</em>{10}$ maximum SVL of adults</td>
<td>2.17 (0.080)</td>
<td>0.50 (0.068)</td>
</tr>
</tbody>
</table>

Values are from the regression equation $\log_{10} Y = a + b \log_{10} X$, and the slopes of the major axis (MA) and reduced major axis (RMA) regression equations.

Slopes of regressions on $\text{SVL}_{\text{max}}$ for clutch mass are 2.1 and 2.4 for wild-caught and captive specimens, respectively (Table 3). However, removal of phylogenetic effects reduces these slopes to 1.4 and 1.7; correlation coefficients for the phylogenetically corrected data are also lower (Table 4). The slope of the regression of total oviductal clutch volume on maternal body size is 0.91, and the slope for total oviductal clutch volume on maternal SVL is 2.85, indicating that total clutch volume decreases proportionately with maternal mass, but total clutch volume increases with increasing species SVL (Table 6).

Varanus mertensi.—Data from a single pair of captive $V. mertensi$ provide an indication of variability in clutch, and neonate size and mass. Standard error of the mean and CV are indications of variation in reproductive attributes. Mean size for 19 clutches of $V. mertensi$ is 7.0 (SE = 0.23, CV = 14.2%), mean individual egg mass is 41.3 g (SE = 1.61, $n = 15$, CV = 15.1%), mean neonate body mass is 29.6 g (SE = 0.81, $n = 14$, CV = 10.2%), mean neonate SVL is 125.2 mm (SE = 1.15, $n = 15$, CV = 3.6%), and mean TL is 180.2 mm (SE = 2.03, $n = 9$, CV = 3.4%).

Figure 3 summarizes all the data that are arranged by probable geographically distinct clades. This figure illustrates phylogenetic inertia: close relatives tend to be more similar than more distantly related pairs of species, as expected. Moreover, larger species have higher values for all variates and smaller species tend to have lower values.

**Discussion**

**Incubation period.**—Phylogenetic and nonphylogenetic analyses indicate similar trends for the relationship between incubation period with egg and neonate mass and neonate size (Phillips and Millar, 1998). Because individual egg mass, neonate body mass, and neonate SVL are significantly correlated, all three are positively correlated with incubation period. Larger eggs take longer to hatch than smaller eggs, but the allometric relationship is negative. For example, the 3.1 g egg of $V. caudolineatus$ (max. body mass 24 g, max. SVL = 0.132 m) is predicted to take 115 days to hatch at 30 C, whereas the much larger 132 g egg of $V. komodoensis$ (max. body mass 250 kg, max. SVL = 1.25 m) takes slightly less than double the incubation period (220 days). This increase in incubation time for larger species that produce larger eggs is also evident in Horn and Visser (1989, 1997).

Taking into account that specimens from low-
TABLE 4. ALLOMETRIC RELATIONSHIPS FOR EGG MASS, CLUTCH SIZE, CLUTCH MASS, AND NEONATE SIZE WITH THE MAXIMUM SVL FOR ADULTS USING PHYLOGENICALLY INDEPENDENT CONTRASTS.

<table>
<thead>
<tr>
<th>Variables</th>
<th>b</th>
<th>SE</th>
<th>RMA</th>
</tr>
</thead>
<tbody>
<tr>
<td>log10 egg mass and log10 maximum SVL of adults</td>
<td>1.17</td>
<td>0.36</td>
<td>0.58</td>
</tr>
<tr>
<td>log10 wild-caught clutch size and log10 maximum SVL of adults</td>
<td>0.58</td>
<td>0.29</td>
<td>0.59</td>
</tr>
<tr>
<td>log10 captive clutch size and log10 maximum SVL of adults</td>
<td>0.76</td>
<td>0.28</td>
<td>0.76</td>
</tr>
<tr>
<td>log10 wild-caught clutch mass and log10 maximum SVL of adults</td>
<td>1.36</td>
<td>0.58</td>
<td>1.36</td>
</tr>
<tr>
<td>log10 captive clutch mass and log10 maximum SVL of adults</td>
<td>1.88</td>
<td>0.54</td>
<td>1.88</td>
</tr>
<tr>
<td>log10 neonate body mass and log10 maximum SVL of adults</td>
<td>1.82</td>
<td>0.58</td>
<td>1.82</td>
</tr>
<tr>
<td>log10 neonate total length and log10 maximum SVL of adults</td>
<td>1.92</td>
<td>1.92</td>
<td>1.92</td>
</tr>
</tbody>
</table>

Values are from the regression equation \( Y = a + b \times X \), where the slope of the major axis (MA) reduced axis (RMA) regression equations.

Egg and offspring size.—Phylogenetic and non-phylogenetic analyses indicate similar trends for the relationship between egg mass, clutch size and mass, and neonate size and mass with maximum adult SVL (Tables 3–4). For egg (and oviductal eggs) and neonate body mass, the regression slope on SVL\(_{\text{max}}\) is approximately 1.5–1.6, whereas for neonate SVL and TL, slopes are approximately 0.50. Regression slopes for neonate SVL and neonate mass on SVL\(_{\text{max}}\) differ appreciably, as might be expected because the first is a linear-linear relationship and the second is a linear-volume relationship. Larger varanids have proportionately heavier eggs, and their neonates weigh more than for smaller species. For example, the egg mass of Varanus giganteus (87.7 g) is approximately 28 times that of V. caudolineatus (3.1 g), yet the maximum SVL of adult V. giganteus (0.795 m) is only six times larger than that of V. caudolineatus (0.132 m). Larger species obviously can accommodate larger eggs and more of them in their larger abdominal volumes than can smaller species.

SVLs for neonates are considerably longer in smaller species than for larger species. For example, in neonate V. brevicauda and V. storti SVLs are between 36% and 39% of adult SVLs, whereas neonates of larger species, for example, V. albigularis and V. varius, are approximately...
Table 5. Intraspecific Regression Equations for the Relationship between Clutch Size and SVL for Eight Species of Varanids.

<table>
<thead>
<tr>
<th>Species</th>
<th>$a \pm SE$</th>
<th>$b \pm SE$</th>
<th>$F_a$</th>
<th>$P$</th>
<th>$\hat{r}$</th>
<th>$n$</th>
<th>SVL min and range (mm)</th>
<th>Chock $x$ and range (mm)</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Varanus brevicauda</td>
<td>1.73 ($\pm$ 4.212)</td>
<td>-0.69 ($\pm$ 2.415)</td>
<td>0.10,5</td>
<td>0.76</td>
<td>0.02</td>
<td>7</td>
<td>92.0, 85–96</td>
<td>2.4, 2–5</td>
<td>22.0</td>
</tr>
<tr>
<td>Varanus caudolineatus</td>
<td>-2.64 ($\pm$ 2.028)</td>
<td>1.64 ($\pm$ 1.020)</td>
<td>2.06,4</td>
<td>0.18</td>
<td>0.39</td>
<td>6</td>
<td>97.7, 86–109</td>
<td>4.3, 3–6</td>
<td>23.8</td>
</tr>
<tr>
<td>Varanus eremius</td>
<td>-2.07 ($\pm$ 1.693)</td>
<td>1.22 ($\pm$ 0.790)</td>
<td>2.37,14</td>
<td>0.15</td>
<td>0.14</td>
<td>16</td>
<td>139.6, 110–160</td>
<td>3.6, 2–6</td>
<td>33.2</td>
</tr>
<tr>
<td>Varanus tristis</td>
<td>-2.69 ($\pm$ 1.496)</td>
<td>1.53 ($\pm$ 0.626)</td>
<td>5.99,22</td>
<td>&lt;0.05</td>
<td>0.21</td>
<td>24</td>
<td>245.2, 199–289</td>
<td>9.8, 5–17</td>
<td>27.4</td>
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<tr>
<td>Varanus gouldii</td>
<td>5.11 ($\pm$ 5.999)</td>
<td>-1.68 ($\pm$ 2.407)</td>
<td>0.49,16</td>
<td>0.49</td>
<td>0.03</td>
<td>18</td>
<td>311.2, 280–344</td>
<td>9.4, 4–20</td>
<td>58.7</td>
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<tr>
<td>Varanus spenceri</td>
<td>-6.38 ($\pm$ 1.306)</td>
<td>2.92 ($\pm$ 0.499)</td>
<td>34.3,14</td>
<td>&lt;0.01</td>
<td>0.81</td>
<td>30</td>
<td>414.6, 360–500</td>
<td>19.5, 11–31</td>
<td>31.3</td>
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<tr>
<td>Varanus olivaceus</td>
<td>-4.70 ($\pm$ 1.536)</td>
<td>2.26 ($\pm$ 0.570)</td>
<td>15.7,24</td>
<td>&lt;0.01</td>
<td>0.36</td>
<td>30</td>
<td>501.5, 350–600</td>
<td>27.1, 6–51</td>
<td>43.1</td>
</tr>
<tr>
<td>Varanus salvator</td>
<td>-15.37 ($\pm$ 1.001)</td>
<td>6.11 ($\pm$ 1.284)</td>
<td>22.6,21</td>
<td>&lt;0.01</td>
<td>0.50</td>
<td>25</td>
<td>502.4, 440–500</td>
<td>17.4, 5–50</td>
<td>82.9</td>
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</tbody>
</table>

Values are from the regression equation $\log_{10} Y = a + b \log_{10} X$, $X \pm 1$ SE, range for SVL (mm), clutch $x$ and range, and the coefficient of variation for species clutch size. Data for Varanus brevicauda, Varanus caudolineatus, Varanus gouldii, Varanus tristis, and Varanus eremius for wild-caught varanids in central Western Australia, data for Varanus olivaceus taken from figure 8.3 Auffenberg (1988), Varanus spenceri from figure 2, Pengilley (1981), Varanus albigularis from figure 11 Branch (1991), Varanus salvator from figure 3 Shine et al., 1998.

Clutch size and mass—Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data. Clutch size varies with respect to SVLmax and clutch mass. A negative relationship between clutch size and SVLmax is positive for the wild-caught data.
Fig. 2. The relationship between maternal SVL and clutch size for wild-caught varanids. Clutch sizes are for individuals of nine species of varanids, with the regression line and 95% confidence limits drawn from species means (circles), and with ellipses drawn for individual species 95% confidence limits.

a volume determined measure of the combined egg mass. A varanid’s abdomen presumably approximates a cylinder, $V = \pi r^2 \cdot h$, where $V$ is a measure of abdominal body volume and $h$ is a measure of abdominal length. For all varanid data, the slope of the regression of clutch mass on $\text{SVL}_{\text{max}}$ is 2.1 (wild-caught) or 2.4 (captive-bred), suggesting that reproductive output is determined by body volume, as suggested by Qualls and Shine (1995).

Clutch size for $V. gouldii$ does not appear to conform to the pattern of increasing clutch size corresponding with increases in maternal SVL (Fig. 2, Table 5). Perhaps clutch size for $V. gouldii$ is labile and determined more by fat supplies than by female size, but why this be the situation for $V. gouldii$ but not for other species of Varanus? If fat supplies or availability of resources and body volume were two important factors determining clutch size in varanids, this might explain why the intraspecific slopes differ from the interspecific slope of clutch size on maternal SVL (Fig. 2). Another possibility is that data for $V. gouldii$ include several different taxa (this “species” has a very extensive geographic range and may well be a composite of several species).

Clutch sizes of smaller varanids are less variable than those of larger species (Fig. 2, Table 1). For example, wild-caught $V. brevicauda$ and $V. caudolineatus$ lay clutches of only 2–3 and 3–6 eggs (respectively) compared with clutches of 11–31 for $V. spenceri$, 6–51 for $V. albogularis$, and 5–50 for $V. olivaceus$. This pattern is similar to Australian scincids described by Shine and Greer (1991). Shine and Greer (1991) suggested low variance in clutch size for small species could be a result of (1) substantial variation around the optimum integer of clutch size is often too small in absolute terms to increase clutch size, (2) low variance in maternal body size, and (3) small adult body size. Smaller species produce relatively larger eggs and neonates, and, relative to neonate size, adult body size is less variable among small species as compared to larger species. Hence, all three factors suggested by Shine and Greer (1991) probably influence low variability in clutch size for smaller varanids.

Small clutches and low variability in maternal body mass contribute to nonsignificant intraspecific relationships between maternal SVL and clutch size for smaller species. Slopes of regressions of clutch size on SVL within species and between the nine species (1.05) for which field data are presented (Fig. 2, Table 5) are not related in any obvious way. Slopes of intraspecific plots are variable and generally considerably steeper than in the interspecific plot. Therefore, body size influences clutch size within species more than it does between species.

Pianka (1994) reported relative clutch masses for $V. brevicauda$ (16.7%), $V. eremius$ (15.3%), $V. tristis$ (16.2%), and $V. gouldii$ (13.9%) to be smaller than those reported by Auffenberg (1994) for the generally larger $V. bengalensis$ (21%), $V. olivaceus$ (19%), $V. komodoensis$ (19%), and $V. salvator$ (25%), which would indicate that not only do larger varanids have proportionally larger eggs they also invest proportionally more in their clutches.
TABLE 6. THE RELATIONSHIP BETWEEN OVIDUCTAL INDIVIDUAL EGG VOLUME AND TOTAL EGG VOLUME WITH MATERNAL SVL (mm) AND BODY MASS (g).

<table>
<thead>
<tr>
<th>Log 10 Individual Egg Volume (cc) and Log 10 Maternal Body Mass (g)</th>
<th>P</th>
<th>Log 10 Individual Egg Volume (cc) and Log 10 Maternal SVL (mm)</th>
<th>P</th>
<th>Log 10 Total Egg Volume (cc) and Log 10 Maternal Body Mass (g)</th>
<th>P</th>
<th>Log 10 Total Egg Volume (cc) and Log 10 Maternal SVL (mm)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.56 (± 0.154)</td>
<td>0.96</td>
<td>2.18 (± 0.511)</td>
<td>0.06</td>
<td>0.67 (± 0.411)</td>
<td>0.99</td>
<td>5.36 (± 0.441)</td>
<td>0.05</td>
</tr>
<tr>
<td>44.11, 2</td>
<td></td>
<td>49.61, 2</td>
<td></td>
<td>227.41, 2</td>
<td></td>
<td>215.31, 2</td>
<td></td>
</tr>
</tbody>
</table>
| Phylogenetic effects.—The varanid phylogeny used here remains incomplete. Some species are missing and branch lengths are dubious. Moreover, recent authors disagree on phylogenetic affinities of some species (Fuller et al. 1998; Baverstock et al. 1993). In addition, future systematic revision of this genus will doubtlessly subdivide some currently recognized species [e.g., *V. albigularis*, *V. exanthematicus*, *V. gouldii*, *V. panoptes*, *V. scalaris*, *V. tristis*, and *V. varius* (King and Green, 1999)]. Under such circumstances, where substantial change is likely in the primary data used for phylogenetic reconstruction, considerable caution must be exercised in interpreting results from any phylogenetic analyses. In addition, slopes from phylogenetically corrected regression equations where the intercept is forced through the origin cannot be statistically evaluated against slopes of least squares linear regression equations. In the context of these caveats, analyses of egg mass, neonate size, and clutch mass and size with both incubation period and SVLmax for *Varanus* provide correlation coefficients for the phylogenetically corrected data that are generally lower than for the non-phylogenetically corrected data. These data suggest that phylogeny is correlated with either the dependent or independent variable or both. The slopes of the regression lines for phylogenetically corrected and noncorrected data are generally similar indicating that the influence of phylogeny on the general patterns is small. This is confirmed by an inspection of Figure 3. In Figure 3, species have been grouped according to their place in the phylogenetic tree and their geographic distribution and, within this constraint, according to SVLmax. There is no obvious pattern for any of the reproductive variables that reflects phylogeny, but it is apparent that body size is one of the primary determinants of egg mass, incubation period, and neonate size. However, we strongly suggest an entire reanalysis of these data when the systematics of *Varanus* is revised and a better phylogeny is in place.

In summary, body size is a major correlate with reproductive data for *Varanus*, whereas phylogenetic effects are weak. Higher environmental temperatures hasten incubation period of varanid eggs laid in the substrate or termite mounds (Cowles, 1930; Riley et al., 1985; Ehmann et al., 1991). Although incubation period is generally longer for larger species, the relationship is not unitary, with smaller species having proportionally longer incubation periods. The timing of oviposition is also linked with incubation period. Egg incubation periods appear less variable for varanids from habitats that have...
considerable seasonal oscillation in ambient temperature (e.g., central Australia) and lay their eggs in late spring or early in summer and hatch before the colder winter period, as compared with species that lay their eggs later in the warmer months and whose eggs incubate over a longer period including the colder winter months. Neonates of smaller species are proportionally longer than those of larger species. This relative increase in size for neonates of

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**Fig. 3.** Relationship between incubation period, egg mass, clutch size, neonate size and mass, and phylogenetic placement and body size for *Varanus* species. Species have been grouped according to their place in the phylogenetic tree (Fig. 1) and their geographic distribution and within this constraint according to SVLmax.

**Fig. 4.** Relationship between incubation period at 30 °C and SVLmax for odatrians and all varanids. Regression lines and 95% confidence limits are shown for the odatrians and all the data.
smaller species probably provides an important fitness advantage in their capacity of catch and devours prey. The relatively smaller size of neonates of larger species could result from trade-offs between offspring size and increased clutch size to enhance fitness. This appears not to be the case for the slopes for clutch size, and neonate SVL with SVL_{max} are similar. However, as the SVL of neonates increases, the rate of increase in neonate body mass is cubed (presuming the shape remains unchanged). This proportionally more rapid increase in egg/neonate mass with increasing SVL probably prevents a proportional increase in clutch size for larger species. The generally larger intraspecific clutch size slopes with maternal SVL compared with the interspecific slopes for SVL_{max} suggests that abdominal volume changes are greater within Varanus species than among species across a size range. Data from other taxa are necessary to determine whether such patterns are evident in other squamate lizards.

**ACKNOWLEDGMENTS**

We thank B. Eidenmüller, S. Irwin, and H. V. Andrews for providing unpublished data. The assistance of P. C. Withers with the phylogenetic analysis is most appreciated.

**LITERATURE CITED**


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APPENDIX.  Maximum Snout–Vent Length for Species, Mean Clutch Mass, Mean Egg Mass, Mean Clutch Size, Incubation Time Corrected to 30 C, Mean Neonate Body Mass, and Mean Neonate Size for 33 Species of Varanus.

<table>
<thead>
<tr>
<th>Verrucus species</th>
<th>Max SVL (mm)</th>
<th>Clutch mass (g)</th>
<th>Egg mass (g)</th>
<th>Field caught</th>
<th>Captive mean clutch size</th>
<th>Incubation days at 30 C</th>
<th>Neonate mass (g)</th>
<th>Neonate SVL (mm)</th>
<th>Neonate TL (mm)</th>
<th>Source</th>
</tr>
</thead>
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<td>acanthurus</td>
<td>237</td>
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