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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 (SVL_{max}). Incubation period of heavier eggs is proportionally less than for smaller eggs at 30 C. SVL_{max} 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 SVL_{max} than for smaller species. Clutch sizes are larger and more variable for larger species; however, clutch sizes for larger species relative to SVL_{max} are smaller than for smaller species. The intraspecific influence of maternal SVL on clutch size is greater than the interspecific influence of SVL_{max} 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.

EVOLUTIONARY 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 body 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-panoptes*), and future taxonomic revisions will probably divide several existing species into more species (e.g., *V. albigularis, 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 [$SVL_{max} = 0.0187$ (SE $\pm$ 0.0198) + 0.328 (SE $\pm$ 0.0173) 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 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 C. To do this, incubation periods for *V. albigularis* are combined for three different water potentials (-150,

−550, −1100 kPa) at each temperature (27, 29, and 31 C) as provided by Phillips and Packard (1994) and the regression equation for the curved line of best fit through these data calculated. Q_{10}-values between 27 and 30 C and 30 and 33 C were calculated (0.48 and 0.77, respectively) and used to adjust all incubation periods to the same standard temperature of 30 C.

Intraspecific relationships between clutch size and maternal SVL were determined from field data for *V. brevicauda, V. caudolineatus, V. eremius, V. gouldii,* and *V. tristis* collected from live Western Australian varanids captured over the last 33 years (Pianka, 1994; supplemented with data collected more recently). Other data were acquired for *V. spenceri* from Pengilley (1981:fig. 2), for *V. olivaceus* from Auffenberg (1988:fig 8.3), for *V. albigularis* from Branch (1991:fig. 11), and for *V. salvator* from Shine et al. (1998). Egg and clutch volumes for wild-caught *V. brevicauda, V. eremius, V. tristis,* and *V. gouldii* were determined by volumetric displacement in graduated cylinders.

Intraspecific analyses of clutch mass, clutch size, and neonate size are undertaken for *V. mertensi.* These data were provided by B. Eidenmüller (pers. comm.) and Eidenmüller and Wicker (1995) from a single pair of *V. mertensi.* This analysis provides an indication of variability among clutch and neonate sizes for captive-bred varanids.

Statistical analyses.—All data were logarithmically transformed to the base 10. Regression analyses are strictly valid only if variance in Y is independent of X and if the independent variable has no measurement error. The X variate is likely to contain errors because SVL_{max} for adult varanids has in a number of circumstances been estimated from an interspecific regression equation of the relationship between SVL and total length and from data accumulated in museums. Measurement of SVL in live and dead specimens is also subject to minor variation depending 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 covariance 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 independent. For data examined here, species means cannot be assumed to be independent because they have evolved as part of a hierarchical phylogeny. Felsenstein's (1985) method of phylogenetically independent contrasts is often used in analysis of such datasets to control for phylogenetic relatedness (Harvey and Pagel, 1991; Christian and Garland, 1996). The *Varanus* phylogeny is not completely resolved and phylogenetic branch lengths are largely unknown even for reported phylogenies (Baverstock 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 additional species from the phylogenetic information reported by Baverstock et al. (1993) and branch lengths for these data reported in Christian 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. flavescens* 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 analysis. Scaling exponents were estimated using phylogenetically independent contrasts calculated by the PDTREE computer program (vers. 5.0) described in Garland et al. (1993).

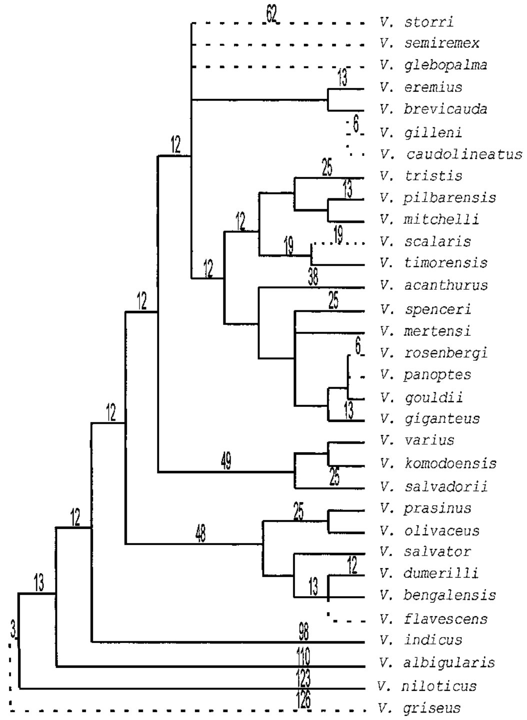

Fig. 1. Phylogeny and branch lengths for *Varanus* used in the phylogenetic analysis. See text for data sources.

RESULTS

Incubation period.—Incubation times (standardized to 30 C) varied widely among species (see Appendix) and are significantly and positively correlated with SVL_{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_{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_{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_{max} (Table 3). The slope of the regression of egg mass on SVL_{max} is 1.51. Mean volume of oviductal eggs for *V. brevicauda, V. eremius, V. tristis,* and *V. gouldii* are 0.92cc ($n = 2$), 1.94cc ($n = 3$), 3.45cc ($n = 11$, SE ± 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_{max} and egg mass is reduced from r^2 of 0.78 to 0.43, and the slope of regressions on SVL_{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

TABLE 1. THE RELATIONSHIP BETWEEN INCUBATION PERIOD AT 30 C AND NEONATE SVL (m), NEONATE TL (m), NEONATE BODY MASS (g), MAXIMUM ADULT SVL (m) AND INDIVIDUAL EGG MASS (g).

Variables	a ± SE	b ± SE	MA	RMA	F_{df}	P	r^2	n
$\log_{10}$ individual egg mass (g)	1.97 (± 0.100)	0.18 (± 0.071)	0.19	0.31	$6.32_{1,13}$	<0.05	0.33	15
$\log_{10}$ neonate body mass (g)	1.89 (± 0.040)	0.25 (± 0.034)	0.25	0.28	$52.50_{1,17}$	<0.01	0.75	19
$\log_{10}$ neonate SVL (m)	0.75 (± 0.293)	0.71 (± 0.150)	0.94	0.96	$22.81_{1,18}$	<0.01	0.56	20
$\log_{10}$ neonate TL (m)	0.61 (± 0.243)	0.67 (± 0.104)	0.78	0.81	$41.02_{1,20}$	<0.01	0.67	22
$\log_{10}$ SVL_{max} (m)	2.31 (± 0.035)	0.37 (± 0.074)	0.42	0.52	$25.75_{1,23}$	<0.01	0.53	25

Values are from the regression equation $\log_{10}$ incubation time at 30 C (days) = $a + b \log_{10}$ X, ± 1 SE, and the slopes of the major axis (MA) and reduced major axis (RMA) regression equations.

TABLE 2. 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) USING PHYLOGENETICALLY INDEPENDENT CONSTRASTS.

Variables	$b \pm$ SE	MA	RMA	F_{df}	P	r^2	n
$\log_{10}$ individual egg mass (g)	0.12 (± 0.085)	0.11	0.31	1.5_{12}	ns	0.11	13
$\log_{10}$ neonate body mass (g)	0.24 (± 0.045)	0.25	0.29	28.8_{13}	<0.01	0.68	14
$\log_{10}$ neonate SVL (m)	0.47 (± 0.251)	1.11	1.05	3.5_{14}	ns	0.20	15
$\log_{10}$ neonate TL (m)	0.57 (± 0.179)	0.85	0.90	10.2_{15}	<0.05	0.41	16
$\log_{10}$ $\mathrm{SVL}_{\max}$ (m)	0.37 (± 0.099)	0.44	0.56	13.7_{18}	<0.01	0.43	19

Values are from the regression equation $\log_{10}$ incubation time at 30 C (days) $= a + b \log_{10}$ X, ± 1 SE, and the slopes of the major axis (MA) 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 $\mathrm{SVL}_{\max}$ 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 $\mathrm{SVL}_{\max}$ 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 $\mathrm{SVL}_{\max}$ 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 $\log_{10}$ clutch size $= -1.58$ (SE ± 0.400) + $\log_{10}$ 1.05 (SE ± 0.164) 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 $\log_{10}$ clutch size = 0 (se ± 0.00) + $\log_{10}$ 1.02 (SE ± 0.384) SVL (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. $\mathrm{SVL}_{\max}$ 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 $\mathrm{SVL}_{\max}$ 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 $\mathrm{SVL}_{\max}$ for intraspecific relationships for $\log_{10}$ clutch size varied significantly among species ($F_{8,156} = 3.5$, $P < 0.05$; 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. albigularis*, 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 $\mathrm{SVL}_{\max}$. 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. albigularis, 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 $\mathrm{SVL}_{\max}$ 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.

Variables	a ± SE	b ± SE	MA	RMA	F_{df}	P	r^2	n
$\log_{10}$ egg mass and $\log_{10}$ maximum SVL of adults	1.83 (± 0.086)	1.51 (± 0.197)	1.81	1.70	$58.4_{1,16}$	<0.01	0.78	18
$\log_{10}$ wild-caught clutch size and $\log_{10}$ maximum SVL of adults	1.16 (± 0.065)	0.65 (± 0.141)	0.88	0.92	$21.1_{1,21}$	<0.01	0.50	23
$\log_{10}$ captive clutch size and $\log_{10}$ maximum SVL of adults	1.22 (± 0.069)	0.81 (± 0.147)	1.10	1.08	$33.6_{1,25}$	<0.01	0.57	27
$\log_{10}$ wild-caught clutch mass and $\log_{10}$ maximum SVL of adults	3.03 (± 0.125)	2.14 (± 0.315)	2.57	2.38	$46.2_{1,12}$	<0.01	0.81	13
$\log_{10}$ captive clutch mass and $\log_{10}$ maximum SVL of adults	3.08 (± 0.100)	2.39 (± 0.224)	2.66	2.54	$113.4_{1,15}$	<0.01	0.88	17
$\log_{10}$ neonate body mass and $\log_{10}$ maximum SVL of adults	1.74 (± 0.077)	1.57 (± 0.148)	1.77	1.70	$112.4_{1,18}$	<0.01	0.85	21
$\log_{10}$ neonate total length and $\log_{10}$ maximum SVL of adults	2.53 (± 0.035)	0.51 (± 0.074)	0.56	0.61	$45.6_{1,21}$	<0.01	0.70	23
$\log_{10}$ neonate SVL and $\log_{10}$ maximum SVL of adults	2.17 (± 0.030)	0.50 (± 0.058)	0.52	0.56	$73.2_{1,18}$	<0.01	0.80	20

Values are from the regression equation $\log_{10} Y = a + b \log_{10} X$, ± 1 SE, and the slopes of the major axis (MA) and reduced major axis (RMA) regression equations.

Slopes of regressions on SVL_{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 113 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 PHYLOGENETICALLY INDEPENDENT CONTRASTS.

Variables	$b \pm$ SE	MA	RMA	F_{df}	P	r^2	n
$\log_{10}$ egg mass and $\log_{10}$ maximum SVL of adults	1.17 (± 0.361)	2.30	1.79	1.05_{14}	ns	0.43	15
$\log_{10}$ wild-caught clutch size and $\log_{10}$ maximum SVL of adults	0.58 (± 0.239)	1.43	1.19	5.88_{19}	ns	0.24	20
$\log_{10}$ captive clutch size and $\log_{10}$ maximum SVL of adults	0.76 (± 0.213)	1.33	1.20	12.53_{19}	<0.01	0.40	20
$\log_{10}$ wild-caught clutch mass and $\log_{10}$ maximum SVL of adults	1.36 (± 0.582)	3.87	2.43	5.49_{12}	ns	0.31	13
$\log_{10}$ captive clutch mass and $\log_{10}$ maximum SVL of adults	1.72 (± 0.458)	2.94	2.34	14.12_{12}	<0.05	0.54	13
$\log_{10}$ neonate body mass and $\log_{10}$ maximum SVL of adults	1.66 (± 0.188)	1.92	1.82	78.38_{16}	<0.01	0.83	17
$\log_{10}$ neonate total length and $\log_{10}$ maximum SVL of adults	0.60 (± 0.080)	0.65	0.69	56.74_{17}	<0.01	0.77	18
$\log_{10}$ neonate SVL and $\log_{10}$ maximum SVL of adults	0.55 (± 0.074)	0.59	0.62	55.64_{15}	<0.01	0.79	16

Values are from the regression equation $\log_{10} Y = a + b \log_{10} X$, ± 1 SE, and the slopes of the major axis (MA) reduced axis (RMA) regression equations.

er latitudes generally oviposit earlier than those from higher latitudes (James et al., 1992) and the onset of reproduction may vary with ambient temperatures (Thompson and Pianka, 1999), our data suggest a difference in incubation period between two Australian subgenera. A number of the smaller Odatrian species [e.g., *V. acanthurus, V. caudolineatus, V. brevicauda, V. eremius, V. tristis* (King and Rhodes, 1982; Pianka, 1994; Thompson and Pianka, 1999)], and perhaps all, from the semiarid and arid regions of Australia, lay their eggs at the beginning of the warmer months (James et al., 1992; Thompson and Pianka, 1999). These eggs incubate over summer and normally hatch toward the end of summer. In contrast, the larger *Varanus* subgenus species [e.g., *V. gouldii, V. rosenbergi, V. varius, V. giganteus* (King and Green, 1979; Pengilley, 1981; Boylan, 1995; pers. obs.)] with longer incubation periods lay their eggs later in summer and eggs incubate over remaining summer months through the much colder winter period before hatching in late spring or summer. This difference in incubation period is evident in Figure 4, where the slope of the regression for odatrians that lay eggs that hatch in the consecutive spring to summer seasons is much flatter than for larger species.

Egg and offspring size.—Phylogenetic and nonphylogenetic 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_{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_{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 *V. 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. storri* 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.

Species	a ± SE	b ± SE	F_{df}	P	r^2	n	SVL, $\bar{x}$ and range (mm)	Clutch $\bar{x}$ and range	CV (%)
Varanus brevicauda	1.73 (± 4.212)	−0.69 (± 2.145)	$0.10_{1,5}$	0.76	0.02	7	92.0, 85–96	2.4, 2–3	22.0
Varanus caudolineatus	−2.64 (± 2.028)	1.64 (± 1.020)	$2.60_{1,4}$	0.18	0.39	6	97.7, 86–109	4.3, 3–6	23.8
Varanus eremius	−2.07 (± 1.693)	1.22 (± 0.790)	$2.37_{1,14}$	0.15	0.14	16	139.6, 110–160	3.6, 2–6	33.2
Varanus tristis	−2.69 (± 1.496)	1.53 (± 0.626)	$5.99_{1,22}$	<0.05	0.21	24	245.2, 199–289	9.8, 5–17	27.4
Varanus gouldii	5.11 (± 5.999)	−1.68 (± 2.407)	$0.49_{1,16}$	0.49	0.03	18	311.2, 280–344	9.4, 4–20	58.7
Varanus spenceri	−6.38 (± 1.306)	2.92 (± 0.499)	$34.3_{1,8}$	<0.01	0.81	10	414.6, 360–500	19.3, 11–31	31.3
Varanus albigularis	−4.70 (± 1.536)	2.26 (± 0.570)	$15.7_{1,28}$	<0.01	0.36	30	501.5, 350–600	27.1, 6–51	43.1
Varanus olivaceus	−15.37 (± 1.001)	6.11 (± 1.284)	$22.6_{1,23}$	<0.01	0.50	25	502.4, 440–590	17.4, 5–50	82.9
Varanus salvator	−6.89 (± 1.001)	2.87 (± 0.361)	$63.2_{1,37}$	<0.01	0.63	39	591.5, 470–770	12.2, 5–22	33.1

Values are from the regression equation $\log_{10} Y = a + b \log_{10} X$, ± 1 SE, range for SVL (mm), clutch $\bar{x}$ 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.

only 13–17% of adult SVL. Why is this so? Optimal offspring size theory (Brockelman, 1975; Pianka, 1976; Charnov and Downhower, 1995) suggests a trade-off of offspring size against clutch size. Most varanid neonates are insectivorous or are general carnivores. A larger body size and gape for smaller species may provide them with a better opportunity to catch and devour prey. For example, a 2-g neonate *V. brevicauda* would have access to a larger range of prey items than would a 1-g neonate because of its body size and gape. This increased size in neonates (and egg size) has possibly been traded-off against clutch size to increase the number of neonates that reach sexual maturity (Madsen and Shine, 1996). For larger species, neonate size is perhaps not as critical a survival factor and species increase their fitness by increasing their clutch sizes. Proportionately larger young for adults of small species is also evident among snakes (Fitch, 1970; Shine, 1978) and other lizards (Andrews and Rand, 1974).

Clutch size and mass.—Clutch size varies within and among *Varanus* species (Fig. 2) although this is not surprising because clutch size can vary in lizards based on the availability of resources during and just before the reproductive period (Pianka, 1970; James and Whitford, 1994; Madsen and Shine, 1996). The low *CV*s for clutch size, egg and neonate mass, and neonate size from 19 clutches from a single pair of mature *V. mertensi* suggest that reproductive output among specific individual varanids remains relatively constant when maintained under similar conditions. The relationship between SVL_{max} and clutch size (log-log) appears to be generally linear for varanids although clutch sizes of larger species are certainly more variable than those of smaller species (Fig. 2). In this regard, *Varanus* are similar to many other lizards—larger reptiles generally have more offspring (Congdon and Gibbons, 1985; Seigel and Ford, 1987; Ford and Seigel, 1989).

Between species, the slope of the regression of clutch size on maternal SVL for the nine wild-caught varanid species is 1.05, and for varanids, using all available data, the allometric relationship between clutch size and SVL_{max} is negative (0.65–0.81). The allometric relationship between SVL_{max} and clutch mass (2.1–2.4) is positive, and for oviductal total egg volume, it is 2.85 using wild-caught data. Volume of the abdominal cavity is intuitively likely to influence clutch mass, a view supported by Qualls and Shine (1995). Therefore, a positive allometric relationship is expected because it is the relationship between the linear measure of SVL and

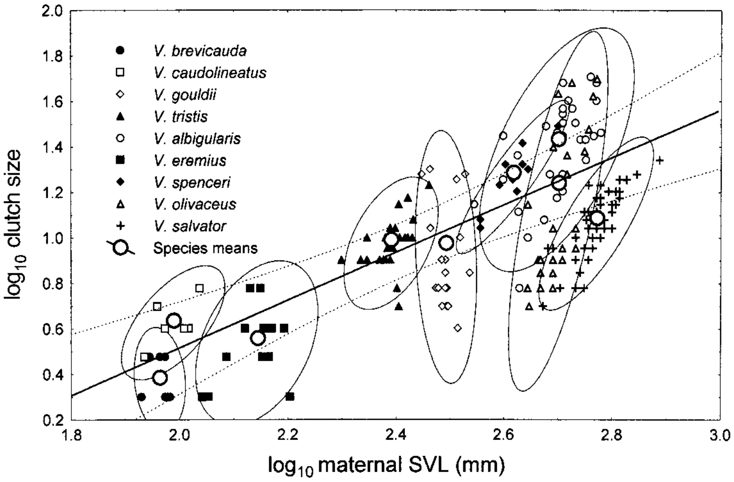

Fig. 2. The relationship between maternal SVL and clutch size for wild-caught varanids. Clutch sizes are for individuals of nine species of varanids, with the regression line and 95% confidence limits drawn from species means (circles), and with ellipses drawn for individual species 95% confidence limits.

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 SVL_{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 would 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. albigularis*, 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* (23%), 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).

	$a \pm$ SE	$b \pm$ SE	F_{df}	P	r^2
$\log_{10}$ individual egg volume (cc) and $\log_{10}$ maternal body mass (g)	−0.56 (± 0.154)	0.51 (± 0.076)	$44.1_{1,2}$	<0.05	0.96
$\log_{10}$ individual egg volume (cc) and $\log_{10}$ maternal SVL (mm)	−3.18 (± 0.511)	1.59 (± 0.226)	$49.6_{1,2}$	<0.05	0.96
$\log_{10}$ total egg volume (cc) and $\log_{10}$ maternal body mass (g)	−0.67 (± 0.110)	0.91 (± 0.055)	$227.4_{1,2}$	<0.05	0.99
$\log_{10}$ total egg volume (cc) and $\log_{10}$ maternal SVL (mm)	−5.36 (± 0.441)	2.85 (± 0.194)	$215.3_{1,2}$	<0.05	0.99

Data come from mean values for wild-caught specimens of *Varanus brevicauda* ($n = 2$), *Varanus eremius* (3), *Varanus tristis* (11), and *Varanus gouldii* (3).

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 exercized 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 SVL_{max} for *Varanus* provide correlation coefficients for the phylogenetically corrected data that are generally lower than for the nonphylogenetically 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 SVL_{max}. 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

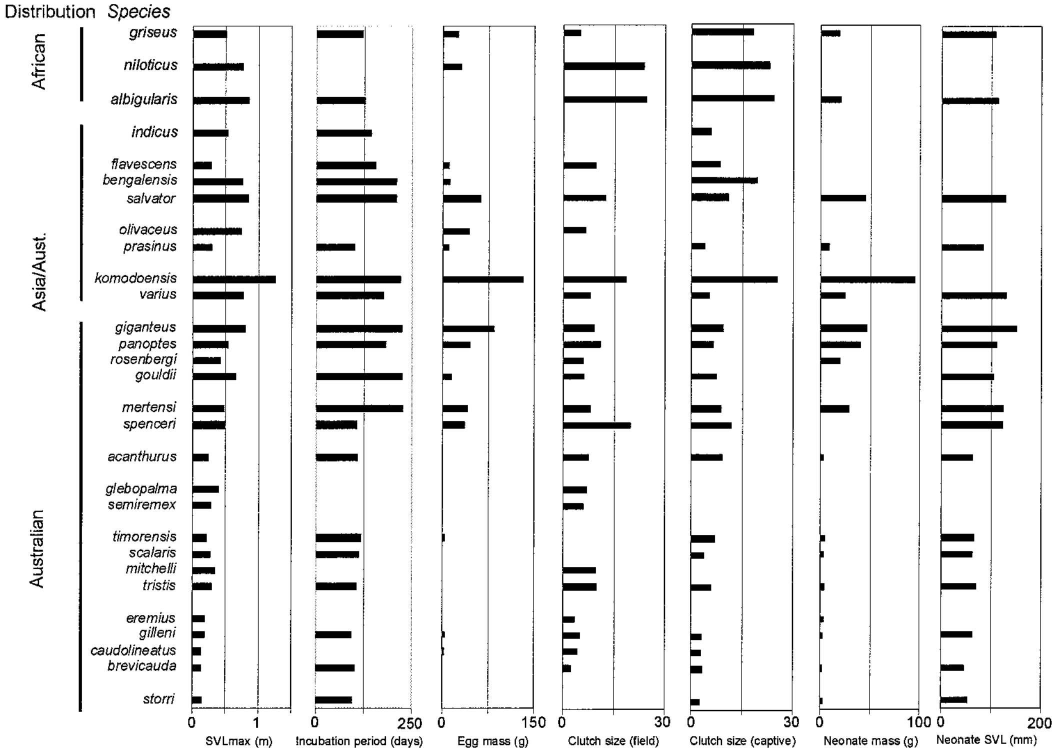

Fig. 3. Relationship between incubation period, egg mass, clutch size, neonate size and mass, and phylogenetic placement and body size for *Varanus* species. Species have been grouped according to they place in the phylogenetic tree (Fig. 1) and their geographic distribution and within this constraint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

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

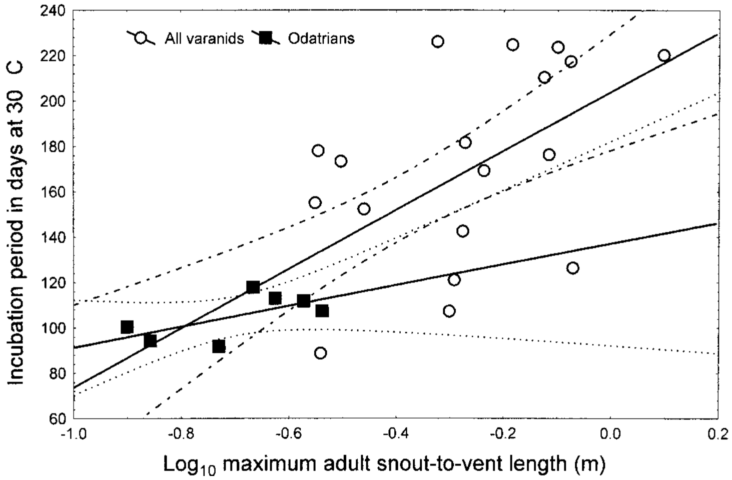

Fig. 4. Relationship between incubation period at 30 C and SVL_{max} for odatrians and all varanids. Regression lines and 95% confidence limits are shown for the odatrians and all the data.

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 tradeoffs between offspring size and increased clutch size to enhance fitness. This appears not to be the case as 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.

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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*.

Varanus species	*Max. SVL (mm)*	*Clutch mass (g)*	*Egg mass (g)*	*Field caught mean clutch size*	*Captive mean clutch size*	*Incubation days at 30 C*	*Neonate mass (g)*	*Neonate SVL (mm)*	*Neonate TL (mm)*	*Source*
acanthurus	237			7.5^{9}	9.2^{28}	108.5^{24}	3.9^{11}	62.9^{11}	151.9^{13}	1
albigularis	850			24.5^{40}	24.3^{3}	126.3^{5}	20.3^{3}	114.4^{2}	272.5^{1}	2
beccarii	(314)				4.0^{2}	178.2^{2}	12.3^{2}	94.3^{2}	238.5^{2}	3
bengalensis	750	230.3^{1}	11.4^{1}		19.3^{4}	210.4^{3}				4
brevicauda	126			2.5^{8}	3.5^{2}	100.4^{2}	1.9^{2}	46.45	95.2^{5}	5
caudolineatus	132		3.1^{1}	4.3^{7}	3.0^{2}					6
eremius	185			3.6^{14}			3.5^{4}			7
exanthematicus	(347)				20.1^{12}	152.2^{1}		89.5^{1}	167.0^{1}	8
flavescens	(281)	254.3^{6}	10.8^{6}	9.6^{5}	8.5^{1}	155.0^{1}				9
giganteus	795	1092.2^{3}	84.1^{3}	9.0^{1}	9.5^{8}	223.7^{4}	46.7^{4}	150.2^{1}	393.0^{4}	10
gilleni	186	15.2^{3}	4.2^{11}	5.25^{4}	3.3^{7}	91.7^{6}	2.9^{3}	63.7^{5}	133.6^{6}	11
glebopalma	397			7.0^{1}						12
gouldii	655	79.7^{6}	15.4^{6}	6.25^{18}	7.3^{14}	224.8^{5}		106.3^{3}	280.5^{5}	13
griseus	(511)	462.6^{1}	25.7^{1}	5.0^{1}	18.0^{1}	121.0^{1}	19.3^{1}	109.1^{1}	132.2^{2}	14
indicus	530				5.7^{3}	142.5^{2}				15
keithhornei	285		7.1^{8}		3.2^{8}	178.0^{1}	10.0^{1}	98.0^{1}	240.7^{1}	16
komodoensis	1250		131.9^{3}	18.7^{17}	25.3^{3}	220.2^{3}	95.2^{1}		357.0^{2}	17
mertensi	475	335.0^{20}	41.0^{19}	8.15^{13}	8.9^{27}	226.0^{5}	29.1^{17}	125.7^{19}	301.9^{12}	18
mitchelli	346			9.8^{5}						19
niloticus	(675)		30.6^{2}	23.8^{1}	23.0^{1}				294.0^{1}	20
olivaceus	730	320.0^{7}	44.2^{7}	6.7^{7}						21
panoptes	535		45.3^{3}	11.0^{3}	6.6^{9}	181.5^{5}	40.1^{9}	111.0^{2}	243.0^{2}	22
prasinus	288		9.9^{1}		4.1^{9}	99.0^{8}	9.2^{3}	84.2^{2}	212.0^{3}	23
rosenbergi	422			6.0^{6}			19.9^{1}			24
rudicollis	580		31.6^{1}		10.4^{5}	169.2^{1}	20.5^{1}		259.0^{1}	25
salvator	(839)	682.0^{12}	62.1^{12}	12.4^{38}	10.9^{23}	209.9^{6}	45.2^{11}	128.9^{5}	354.3^{12}	26
scalaris	268				4.0^{3}	111.7^{1}	3.6^{3}	63.0^{2}	157.0^{1}	27
semiremex	282			5.9^{1}						28
spenceri	500	202.2^{1}	36.7^{1}	19.9^{15}	12.0^{2}	107.2^{1}		124.0^{1}	222.0^{1}	29
storri	139				2.7^{13}	94.2^{9}	2.85^{6}	54.2^{9}	128.6^{8}	30
timorensis	(216)		5.0^{2}		6.9^{12}	117.8^{8}	4.8^{2}	65.8^{2}	129.1^{1}	31
tristis	290			10.0^{21}	6.0^{7}	107.3^{4}	4.4^{5}	70.8^{6}	188.5^{2}	32
varius	765	455.0^{1}		8.0^{27}	5.4^{7}	176.3^{3}	24.9^{29}	130.7^{30}	326.8^{30}	33

The superscripts indicate the number of clutches from which the data were taken. Maximum SVL values in parentheses indicate that they have been estimated from an inter-specific regression equation based on the relationship between SVL and tail length (see text for details). Data sources: [1] Eidenmüller (1994), King and Rhodes (1982), Thissen (1992), Husband (1980), Endfekler (1984, cited in Horn and Visser, 1989), Eidenmüller (cited in Horn and Visser, 1989), Thompson (unpubl.), Krebs (1999); [2] Phillips and Packard (1994), Branch (1991), Haagner (cited in Branch 1991), Staedeli (1962, cited in Horn and Visser (1989), Shaw (1963, cited in Horn and Visser, 1989), Visser (1981, cited in Horn and Visser, 1989); [3] Eidenmüller (1998); [4] Auffenberg (1994), Koop (cited in Horn and Visser, 1989), Klag and Kantz (cited in Horn and Visser, 1989); [5] James (1996), Pianka (1994), Schmida (1974, cited in Horn and Visser, 1989), Thompson (1996, unpubl.); [6] Pianka (1994), Smith (1988), Thompson (unpubl.); [7] Pianka (1994), Thompson (unpubl.); [8] van Duinen (1983), Bayless (1994), Bayless and Reynolds (1992), Bayless and Huffaker (1992), MacInnes (cited in Bayless and Huffaker, 1992); [9] Auffenberg et al. (1989), Visser (1985, cited in Horn and Visser, 1989); [10] King et al. (1989), Irwin (1996b), Irwin (pers. comm.), Bredl and Horn (1987); [11] Gow (1982), Husband (1989), Horn and Visser (1989), Boyle and Lamoreaux (1983), Horn (1978), Broer and Horn (1985, cited in Horn and Visser 1989), Thompson (unpubl.), Eidenmüller (1994); [12] Christian (1977, cited in Greer, 1989); [13] Pianka (1994), Mitchell (1989), Irwin (1986, pers. comm.), Horn and Visser (1989), Doles and Card (1995), Barnett (1979), Thompson (unpubl.), Shine (1986), Brooker and Wombey, (1978, cited in Greer, 1989); [14] Perry et al., (1993), Gupta (1996); [15] Irwin (pers. comm.), Anonymous (1995); [16] Irwin (1996a, pers. comm.); [17] Birchard et al. (1995), Atmosoedirdjo et al. (cited in Horn and Visser, 1989), Auffenberg (1981), Walsh (1993); [18] Eidenmüller (pers. comm.), Irwin (1986, pers. comm.), Horn and Visser (1989), Brotzler (1965 cited in Horn and Visser, 1989), Anonymous (cited in Horn and Visser, 1989), Shine (1986), Bustard (1970, cited in Greer, 1989), Eidenmüller and Wicker (1995), Eidenmüller (pers. comm.); [19] Shine (1986); [20] Cowles (1930), Barbour and Loveridge (1928), Bayless (1992); [21] Auffenberg (1988); [22] Horn and Visser (1989), Shine (1986), Nabors (1997), Eidenmüller (pers. comm.), Dwyer and Bayless (1996), Bayless et al., (1994); [23] Horn and Visser (1989), Carlzen (1982), Barker (1985, cited in Horn and Visser, 1989), Greene (1986), Eidenmüller (1998), Bosch (1999); [24] Ehmann et al. (1991), King and Green (1979), Green et al. (1999); [25] Horn and Visser (1989), Horn and Peters (1982, cited in Horn and Visser 1989), Bayless (1992b); [26] Andrews (1995), Hairston and Burchfield (1990, 1992), Horn and Visser (1989), Andrews and Gaulke (1990), Kratzer (1973, cited in Horn and Visser, 1989), Auffenberg (1985), Shine et al. (1998), Hermann (1999), Wicker et al. (1999), Hoegger (1997, cited in Horn and Visser, 1997) Bowers (1981, cited in Hermann, 1999), Ettling (1992, cited in Hermann 1999), Ott (1997, cited in Hermann 1999), Schmitz (1994, cited in Hermann 1999); [27] Eidenmüller (pers. comm.), Eidenmüller and Wicker (1991); [28] Horn and Visser (1989); [29] Peters (1971), Christian (1979, cited in Greer, 1989), Horn and Visser (1991), Pengilley (1981); [30] Eidenmüller (pers. comm.), Bartlett (1982), Eidenmüller and Horn (1985), Broer and Horn (1985, cited in Horn and Visser, 1989), Eidenmüller (1985, 1994); [31] Horn and Visser (1989), Eidenmüller (pers. comm.), Behrmann (1981, cited in Horn and Visser, 1989), anonymous (1981, cited in Horn and Visser, 1989), Belcher (cited in Horn and Visser, 1989), Eidenmüller (1986), Ruegg (1973, 1974, cited in Horn and Visser, 1989), Broer and Horn (1985, cited in Horn and Visser, 1989), Chippendale (1991); [32] Thompson (unpubl.), Pianka (1994), Broer and Horn (cited in Horn and Visser, 1989), Eidenmüller (1989), Eidenmüller (cited in Horn and Visser, 1989), Christian (1981), Eidenmüller (pers. comm.); [33] Markewell (1983), Horn and Visser (1989), Bredl and Schwaner (1983), Horn and Visser (1989), Boylan (1995), Carter (1999).