Reproductive Biology and Diets of Goannas (Reptilia: Varanidae) from Australia

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ABSTRACT. — Aspects of the reproductive biology and diets of nine species of Varanus from the seasonal tropics and temperate zones of Australia were examined by dissection of 386 preserved museum specimens. We investigated whether morphological and habitat diversity in the varanids was expressed in reproductive and dietary diversity. Most species from seasonal tropical areas had enlarged testes in the dry season (June-October) and females with oviductal eggs were collected at the end of the dry season and the beginning of the wet season (September-January). However, three species seemed to be exceptions to this trend, with an extended reproductive season (V. storri), or reproductive activity in the late wet season (V. semiremex and V. kingorum). A diversity of reproductive seasons for varanids from seasonal tropical regions in Australia was also found in a review of the literature. Temperate zone species had enlarged testes in spring (September-November) and laid eggs in spring or late summer. Clutch sizes ranged from 1-7 eggs. Regression slopes of maternal SVL and clutch size seemed to be higher for the smaller-bodied species compared to the larger-bodied species, but sample sizes were too low to compare them statistically. A review of reproductive data on Australian varanids suggested that some large-bodied species (e.g., V. varius) had relatively small clutch sizes. Most species had generalized diets with lizards and orthopterans being the most important prey. Large-bodied species such as V. giganteus and V. glebopalma tended to eat larger prey items, and specialized on vertebrate prey. Varanus semiremex ate mostly aquatic prey. Diets were relatively similar for most species but appear to be influenced by body size and habitat.

The family Varanidae consists of one extant genus (Varanus) with about 35 species distributed throughout tropical Africa, southern Asia, and Australia (Greer, 1989). Varanids are most diverse in Australia, where 25 species range in body size from the smallest living species of Varanus (V. brevicauda) at 8 g, to Australia's largest lizard, the perentie (V. giganteus), at 17 kg (Butler, 1970; Cogger, 1986; Weavers, 1988). Despite this large range of body sizes, varanids are relatively conservative in body plan (Shine, 1986; Greer, 1989), and appear also to be relatively similar in their ecologies: most varanids have generalized diets, dominated by small invertebrates, with a few large vertebrate prey (Losos and Greene, 1988); reproductive cycles appear to be similar in their timing (Bustard, 1970; King and Green, 1979; King and Rhodes, 1982; Pianka, 1986; Horn and Visser, 1989).

Although the varanids appear to be superficially similar in their ecologies, this generalization seems to be based on meager data. Varanids can be found in most major climatic regions in Australia (seasonal tropics, arid, semiarid, and mesic-temperate) occupying a range of habitats (semi-aquatic, terrestrial and arboreal). After assessing the ecological literature on varanids, Shine (1986) asked, "Is this ecological homogeneity a real phenomenon, or simply an artifact of insufficient data?" In this study we examine nine species of Australian varanids in an attempt to evaluate some of the ecological diversity of the group. We chose species covering a 1000-fold range in body mass, and species from many different habitats and climatic regimes, for an examination of reproductive biologies and diets.

Only two species of Varanus, V. komodoensis and V. olivaceus, have been studied in detail (Auffenberg, 1981, 1988). Captive husbandry has provided data on the reproductive biology (e.g., behavior, incubation periods, clutch sizes) of a number of Australian species (Horn, 1978; Horn and Visser, 1989), but the reproductive biologies of only six species of Australian varanids have been examined in the field (King and Green, 1979; King and Rhodes, 1982; Shine, 1986). Similarly, the feeding biology of most of the Australian species in the field is poorly known. Of the species examined in this study,

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TABLE 1. Numbers of reproductive male and female *Varanus* examined for each month, with total sample size shown in parentheses. The periods when most adults seem to be reproductive are underlined. See Methods for the definition of "reproductive" males and females. Species from temperate zone climates are asterisked; the remainder are from seasonal tropical climates.

	Sex	J	F	M	A	M	J	J	A	S	O	N	D
V. glauerti	♂	—	0 (3)	—	0 (1)	0 (5)	4 (5)	2 (3)	7 (13)	—	1 (2)	—	—
	♀	—	0 (1)	—	—	—	—	—	1 (1)	—	—	1 (1)	—
V. glebopalma	♂	—	1 (2)	—	0 (2)	0 (6)	1 (8)	2 (4)	10 (10)	2 (2)	1 (1)	3 (4)	—
	♀	1 (1)	0 (3)	—	—	0 (1)	0 (3)	0 (1)	0 (2)	0 (3)	0 (1)	—	2 (2)
V. kingorum	♂	—	1 (1)	—	—	0 (1)	—	—	—	—	—	—	—
	♀	—	1 (1)	—	—	—	—	—	—	—	—	—	—
V. primordius	♂	—	0 (2)	—	—	—	—	—	—	3 (3)	1 (1)	—	1 (1)
	♀	—	0 (1)	—	—	—	—	—	—	—	—	—	0 (1)
V. semiremex	♂	—	1 (1)	2 (2)	1 (1)	0 (1)	—	—	—	—	0 (1)	0 (1)	0 (2)
	♀	0 (1)	—	0 (2)	—	0 (2)	—	—	—	—	0 (2)	1 (1)	0 (2)
V. storri	♂	1 (5)	0 (5)	0 (2)	0 (1)	1 (4)	0 (4)	1 (1)	—	1 (1)	1 (1)	3 (3)	—
	♀	0 (2)	1 (1)	1 (2)	0 (1)	—	1 (1)	1 (1)	—	2 (2)	1 (1)	—	—
V. gilleni*	♂	0 (8)	2 (7)	1 (4)	1 (5)	0 (5)	3 (6)	1 (2)	3 (5)	1 (2)	15 (20)	1 (8)	—
	♀	1 (8)	3 (5)	1 (5)	0 (4)	1 (4)	0 (3)	—	0 (1)	2 (3)	9 (26)	3 (6)	—
V. pilbarensis*	♂	—	0 (1)	—	0 (1)	—	—	1 (1)	1 (1)	—	2 (2)	—	—
	♀	—	—	—	—	—	—	—	—	1 (1)	—	—	1 (1)

season). Sample sizes were low for adult *V. kingorum* but reproductive males and females were collected toward the end of the wet season. Temperate zone species had enlarged testes in early to mid spring (August to October).

Adult female varanids with yolking follicles usually appeared in the populations during the period when the testes of males were enlarged. Species from seasonal-tropical climates had vitellogenic follicles or oviductal eggs during the latter stages of the dry season and during the wet season (October to February; Table 1). Temperate zone species had oviductal eggs in spring (October and November) and summer (February). Long periods over which females with oviductal eggs could be found (e.g., *V. gilleni*) suggest that some females may produce more than one clutch of eggs per season. However, this suggestion was not confirmed by the presence of concurrent vitellogenic follicles and oviductal eggs or corpora lutea in the preserved specimens.

TABLE 2. Reproductive variables for *Varanus* species examined in this study. SVL in mm; N_1 is the number of adult males and females examined; N_2 is the number of reproductive females in the collections. Uncertainty around the estimate for SVL at maturity was due to a lack of specimens in the critical size range. *Varanus giganteus* and *V. primordius* are omitted due to a lack of specimens in museum collections.

Species of Varanus	Estimated SVL at maturity		x̄ adult SVL ± SD [N₁] Upper extreme of SVL		x̄ clutch size ± SD Extremes [N₂]
	♂	♀	♂	♀	
V. gilleni	100	95	122.8 ± 15.2 [67] 161	126.9 ± 18.6 [74] 170	4.0 ± 1.2 2-7 [19]
V. glauerti		≈150	198.3 ± 19.3 [31] 228	178.3 ± 7.8 [3] 185	3.0 — [2]
V. glebopalma		≈170	274.3 ± 42.2 [43] 343	247.2 ± 40.7 [17] 369	5.0 — [1]
V. kingorum		—	103.5 ± 9.2 [2] 110	92.0 [1] 92	2.0 — [1]
V. pilbarensis		—	144.7 ± 19.9 [6] 172	120.5 ± 10.6 [2] 128	2.5 ± 1.0 — [2]
V. semiremex		≈150	214.4 ± 33.3 [10] 272	228.0 ± 14.6 [7] 255	2.0 — [1]
V. storri	89	93	110.4 ± 14.1 [27] 139	110.5 ± 11.3 [11] 126	3.9 ± 1.6 1-6 [7]

Reproductive Variables.—Mean SVLs of adult males and females were similar for the smaller species (*V. gilleni* and *V. storri*), but in the larger species males were on average larger than females (Table 2). Snout-vent length at maturity was larger for male *V. gilleni* than for females, but the reverse was true for *V. storri*. Sample sizes in the critical size range were low for the remainder of the species and size at sexual maturity could only be estimated.

Clutch sizes ranged from 1–7 eggs (Table 2). There were only two species in which sufficient reproductive females were available to compute a regression of clutch size with maternal SVL: in both *V. gilleni* and *V. storri*, the linear regressions were significant (*V. gilleni*, clutch size = 0.035SVL − 0.487, $r^2 = 0.3$, $P = 0.015$; *V. storri*, clutch size = 0.108SVL − 8.46, $r^2 = 0.58$, $P = 0.05$), and significantly different from each other in slope (ANCOVA, slopes $F_{1,22} = 4.4$, $P = 0.05$). Fig. 1 shows a plot of clutch size against maternal body size for all individuals of all species examined. Clutch sizes of large-bodied species (*V. glauerti*, *V. semiremex*, and *V. glebopalma*) were smaller than expected based on the relationship between maternal SVL and clutch size in the small-bodied species. The only reproductive female *V. semiremex* examined had two eggs and a *V. glebopalma* had a clutch size of five eggs. The regression of clutch size with maternal SVL with all species included (regression 1 in Fig. 1), accounted for only 8% of the variance in clutch size among species. Even with the larger species omitted from the analysis, only 28% of the variance in clutch size was explained by the regression with maternal body size (regression 2 in Fig. 1).

Diets.—Prey items found in the stomachs of four common species in museum collections are summarized in Table 3. The stomach contents of the other five species investigated are summarized as follows: six *V. giganteus* with stomach contents contained 14 prey items. Lizards comprised 50% by number of the prey, with orthopterans (31.1%), chilopods (7.1%), and mammals (7.1%) making up the remainder. Three *V. kingorum* contained eight prey items, of which orthopterans made up 50% of the total number. Blattids (25%), isopterans (12.5%), and insect eggs (12.5%) made up the remainder of the prey items. Three *V. pilbarensis* contained five prey items, of which orthopterans were the most common prey items (60%), followed by lizards (20%) and spiders (20%). Six *V. primordius* contained 15 prey items which constituted formicids (ants, 33%), orthopterans (27%), lizards (13%), squamate eggs (7%), blattids (7%), neuropteran larvae (6%), and unidentified insects (6%). Four *V. semiremex* contained four prey items of two taxa, crustaceans (Brachyura, 75%) and frogs (25%).
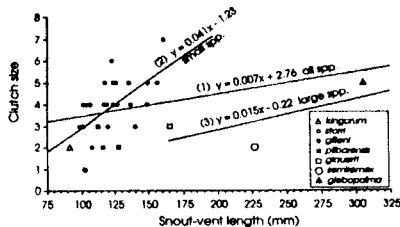

FIG. 1. Scatter plot of clutch size against maternal SVL for seven species of *Varanus* examined in this study. Regression 1 uses the data for all species (n = 32; $r^2 = 0.084$; $P > 0.5$); regression 2 uses only the data for small-bodied species with *V. glebopalma* and *V. semiremex* omitted (n = 30; $r^2 = 0.281$; $P = 0.0016$); and regression 3 uses the data for the three largest species only.

Orthopterans and lizards dominated the diet of every species except *V. semiremex*, which relied on aquatic prey. Two species, *V. giganteus* and *V. glebopalma*, appear to be lizard specialists, whereas four others prey primarily on orthopterans (*V. kingorum*, *V. pilbarensis*, *V. primordius*, and *V. storri*). *Varanus gilleni* had the most diverse diet, with five prey types (lizards, spiders, blattids, coleopterans, and orthopterans) that were eaten by more than 10% of the individuals.

Importance index values indicate that several prey types that were relatively insignificant numerically may be energetically important (Table 3). For example, mammals accounted for only 7% of the total number of prey eaten by *V. giganteus*, but had relatively high II (Table 4). Similarly, lizard prey constituted 10.5% of the total number of items eaten by *V. gilleni* and had an II of 0.406. Conversely, some prey taxa that were common in the diet may be unimportant energetically (e.g., coleopterans in *V. gilleni* and frogs in *V. glebopalma*). Lizard prey had high IIs in the diets of all species except *V. storri*.

DISCUSSION

Reproductive Biology.—There appear to be only slight differences among temperate zone species in the timing of oviposition and testis enlargement: all species laid eggs in the late spring and summer (October–January). A review of the reproductive data available on Australian varanids supports this general result (Table 5). Many authors have noted the relatively invariant timing of reproduction in temperate zone squamates (e.g., Fitch, 1970) where temperature seems to be the controlling factor. In the tropics, however, temperatures are high year-round and do not limit the activity of reptiles. In these environments, rainfall may be more important than temperature in determining when reproduction occurs. In this study we found diversity

no dietary data are available on four species (*V. glauerti, V. kingorum, V. primordius* and *V. semiremex*), and the diets of two other species are known from only single observations (*V. glebopalma* and *V. pilbarensis*).

THE SPECIES

We examined nine species covering almost the maximum range in body sizes of Australian varanids, and species from many different habitats and climatic regions. A brief outline of the comparative sizes and climatic zones occupied by the species examined is presented below.

Maximum recorded snout-vent lengths (SVL) for the species from largest to smallest (Greer, 1989) are *V. giganteus* (800 mm), *V. glebopalma* (350 mm), *V. semiremex* (260 mm), *V. glauerti* (230 mm), *V. gilleni* (190 mm), *V. pilbarensis* (170 mm), *V. storri* (130 mm), *V. kingorum* (120 mm), and *V. primordius* (110 mm).

The species studied are found in two major climatic regions: arid and semi-arid zones (*V. giganteus, V. gilleni, V. pilbarensis*), and seasonal tropical zones (*V. glauerti, V. glebopalma, V. kingorum, V. primordius, V. semiremex* and *V. storri*). The seasonal tropics in northern Australia (north of 20°S latitude) have high year-round diurnal temperatures (>30 C) with strongly seasonal rainfall (wet-dry topics). Monsoonal rainfall begins in December and lasts until April. From May until November little or no rainfall is received and the region becomes increasingly dry (see James and Shine, 1985, for more details of the climate). In the arid and semi-arid regions of central Australia, rainfall is low (around 250 mm annual average) and unpredictable, and there is a marked difference between daily summer and winter temperatures.

Most of the species from the seasonal tropics occur in rocky habitats (*V. glauerti, V. glebopalma, V. kingorum, V. primordius*, and *V. storri*), although *V. semiremex* is an inhabitant of coastal mangrove forests. Of the species occurring in arid and semi-arid zones, one is arboreal (*V. gilleni*), and two are found in rocky habitats.

METHODS

We examined 386 preserved specimens in collections of the Australian Museum, the Northern Territory Museum, the Queensland Museum, the South Australian Museum, and the Western Australian Museum. Sample sizes for each species are: *V. giganteus*, n = 19; *V. gilleni*, n = 149; *V. glauerti*, n = 47; *V. glebopalma*, n = 70; *V. kingorum*, n = 7; *V. pilbarensis*, n = 10; *V. primordius*, n = 12; *V. semiremex*, n = 24; and *V. storri*, n = 48. Dietary data were collected for all nine species examined, but reproductive data were available for only eight species due to a lack of reproductive adult *V. giganteus*.

Each specimen was measured for SVL (mm), blot-dried, weighed, and dissected with a mid-ventral incision. The reproductive data recorded were: sex; state of maturity (immature or mature); stage of reproductive cycle (reproductive or non-reproductive); level of development of gonads in reproductive females (yolking ovarian follicles or oviductal eggs); and clutch sizes from females with enlarged vitellogenic follicles (>3 mm diameter), oviductal eggs or macroscopically visible corpora lutea. Stage of maturity for males was judged by the appearance of the testes and epididymides, which were small and without obvious convolutions in immature specimens. Immature females had only small follicles in the ovary (<1.0 mm diameter) and had thin, strap-like oviducts. Males were judged to be reproductive if their testes and epididymides were turgid and white, whereas reproductive females were those with either yolking ovarian follicles or oviductal eggs. Approximate size at sexual maturity was determined from the overlap in the SVL of the largest specimen that was judged to be immature and the smallest reproductive specimen.

Stomach contents were removed and invertebrate prey items were identified to order, whereas vertebrate prey items were identified to species if possible. Substantially intact prey items were blot-dried and weighed. The mass ratio (MR = prey mass/predator mass) was calculated for each intact prey item (Greene, 1986; Losos and Greene, 1988). Counts of fragmentary body parts were used to estimate the minimum number of individual prey. Fragmented prey items were assigned the mean MR for that prey taxon in that species of *Varanus*. The Importance Index (II, hereafter) for each prey taxa for a species is the sum of MRs for that prey taxa divided by all MRs for that species (Greene, 1986; Losos and Greene, 1988). The advantages and limitations of the II are discussed in Losos and Greene (1988). Prey that may have been secondarily ingested (e.g., small insects from a stomach that also contained a well-digested insectivorous lizard [see Jackson et al., 1974]) were not included in the analysis.

RESULTS

Male and Female Reproductive Seasons. —The species from seasonal-tropical climates were reproductive at a range of different times of the year (Table 1). *Varanus glauerti* and *V. glebopalma* had enlarged testes and epididymides from June to October (mid-dry season). *Varanus storri* with enlarged testes could be found at most times of the year, but were primarily collected in the late dry or early wet season (November), and male *V. semiremex* had enlarged testes when collected in February, March, and April (late wet

TABLE 3. Percentages of the total number of prey (%no.) and frequency of each prey taxon (F[x]) in the stomachs of four common species of *Varanus* examined in this study. Sample sizes given in parentheses are: (1) the total number of prey items found; and (2) the number of individuals with prey in their stomachs. Total numbers of individuals examined are given in the text.

Prey taxon	V. gilleni %no. (86)	V. gilleni F[x] (64)	V. glauerti %no. (47)	V. glauerti F[x] (29)	V. glebopalma %no. (65)	V. glebopalma F[x] (30)	V. storri %no. (53)	V. storri F[x] (26)
Vertebrata								
Amphibia								
Anura[1]	—	—	—	—	12.3	16.7	—	—
Reptilia								
Egg	—	—	2.1	3.4	2.0	3.3	—	—
Sauria[2]	10.5	12.5	8.5	13.8	54.9	87.7	9.4	19.2
Aves								
Egg	1.2	1.6	—	—	—	—	—	—
Unidentified	1.2	1.6	—	—	—	—	—	—
Arthropoda								
Arachnida								
Araneae	17.4	23.4	29.8	34.5	1.5	3.3	1.9	3.8
Scorpiones	2.3	3.1	—	—	—	—	—	—
Chilopoda	2.3	3.1	—	—	1.5	3.3	1.9	3.8
Insecta								
Blattodea	9.3	12.5	12.8	20.7	—	—	3.8	7.7
Coleoptera	15.1	17.2	—	—	—	—	7.5	15.4
Hymenoptera								
Formicidae	1.2	1.6	—	—	—	—	11.3	3.8
Isoptera	1.2	1.6	—	—	—	—	1.9	3.8
Lepidoptera larvae	—	—	4.2	6.9	—	—	1.9	3.8
Neuroptera larvae	—	—	—	—	—	—	3.8	3.8
Orthoptera	30.2	31.3	38.3	51.7	27.7	40.0	47.2	65.4
Unidentified insect	4.7	6.3	—	—	—	—	3.8	7.7
Unidentified larvae	—	—	2.1	3.4	—	—	1.9	3.8
Unidentified item	3.5	4.7	2.1	3.4	—	—	3.8	7.7

[1] Three frogs eaten by *V. glebopalma* were *Litoria* sp.
[2] Identifiable lizard prey items were (1 per species unless otherwise indicated): (a) *Varanus gilleni*: *Diplodactylus taeniatus*, *Gehyra* sp., *Ctenotus leonhardii*; (b) *Varanus glauerti*: *Heteronotia binoei*, *Cryptoblepharus* cf. *plagiocephalus*; (c) *Varanus glebopalma*: *Delma borea*, *Carlia triacantha* (2), *Carlia* sp. (3), *Ctenotus* sp. (6), *Cryptoblepharus littoralis*, *Lerista walkeri*, *Morethia ruficauda*, *Morethia* sp., *Notoscincus ornatus*, *Sphenomorphus isolepis*, *Sphenomorphus* sp., *Varanus glauerti*, *Varanus* sp.; (d) *Varanus storri*: *Ctenotus* sp.

in the timing of reproduction of varanids from the seasonal tropics. Male *V. glauerti*, *V. glebopalma*, and *V. primordius* had enlarged testes in the dry season (June–September) and females laid their eggs at the end of the dry season, or in the wet season (November–January). In *V. storri*, reproductive males and females were found over many months of the year (this result may be in part due to variation in timing at different localities throughout the broad geographic range of *V. storri*). In contrast to other species from the seasonal tropics, both *V. kingorum* and *V. semiremex* appear to be reproductive during the wet season. A review of the timing of reproduction in other varanids from the seasonal tropics also indicates a diversity of reproductive seasons for species in the seasonal tropics compared with species from the temperate zone (Table 5). This result is consistent with an inter-familial diversity of reproductive seasons for sympatric scincid, agamid and varanid lizards in the Alligator Rivers Region of

northern Australia (James and Shine, 1985; Shine, 1986), and for sympatric iguanid (Vitt and Lacher, 1981; Vitt and Goldberg, 1983) and gekkonid lizards (Vitt, 1986) in seasonal tropical regions in Brazil.

The diversity of reproductive seasons for lizards in the wet-dry tropics suggests that rainfall is not an overriding cue for reproduction in seasonal tropical climates, as seems to be the case for temperature in the temperate zone. Some of the hypotheses proposed to account for the timing of copulation and oviposition in varanids from the seasonal tropics include avoidance of nest-flooding in semi-aquatic species (Shine, 1986), softer substrate for digging nests during the wet season (Auffenberg, 1981), and timing egg-hatching to coincide with a period of high prey abundance (Wikramanayake and Dryden, 1988). Based on an estimated incubation period of 3 to 4 months for most of the species from tropical areas examined in this study (Horn and Visser, 1989), it is likely that

TABLE 4. Importance index values of prey in the diets of seven species of *Varanus*. Importance index value for a prey type is the sum of the MRs (mass ratios, see text) for the prey divided by the sum of all MRs. *Varanus semiremex* and *V. kingorum* are omitted because there were no intact prey items of the taxa shown in the small number of stomachs examined. Zero values with an asterisk indicate that the prey taxon was found in the diet of the *Varanus* species but none was intact and no estimate of the MR could be made.

Prey taxon	V. giganteus	V. gilleni	V. glauerti	V. glebopalma	V. pilbarensis	V. primordius	V. storri
Anura	0.0	0.0	0.0	0.041	0.0	0.0	0.0
Sauria	0.618	0.406	0.132	0.660	0.882	0.965	0.0*
Squamate eggs	0.0*	0.0	0.0*	0.001	0.0	0.0	0.0
Mammalia	0.352	0.0	0.0	0.0	0.0	0.0	0.0
Araneida	0.0	0.247	0.386	0.0*	0.039	0.0	0.0*
Chilopoda	0.0*	0.0	0.0	0.001	0.0	0.0	0.014
Coleoptera	0.0	0.063	0.0	0.0	0.0	0.0	0.0*
Lepidoptera	0.0	0.0	0.048	0.0	0.0	0.0	0.015
Neuroptera	0.0	0.0	0.0	0.0	0.0	0.035	0.0
Orthoptera	0.030	0.284	0.433	0.297	0.079	0.0	0.971

eggs laid in the second half of the dry season would hatch during the wet season when invertebrate abundance is high. Although there is superficial support for the hypothesis that eggs are laid to coincide hatching with periods of high invertebrate abundance for some of the species, it is impossible to assess alternative hypotheses without detailed autecological studies.

Analyses of clutch-size relationships among the species were hampered by the low sample sizes of reproductive females for some species. Two small-bodied species, *V. gilleni* and *V. storri*, had similar clutch sizes after adjustment for maternal body size, with an extra egg added for every 25 mm increase in maternal SVL. Clutch sizes for the larger-bodied species (*V. semiremex* and *V. glebopalma*) were below the regression for the smaller-bodied species, and smaller than the clutch sizes of previously studied *Varanus* of similar body size (Table 5). For example, *V. gouldii* (SVL 300 mm) and *V. mitchelli* (SVL 240 mm) have clutch sizes of up to 12 eggs (Shine, 1986) compared with only five eggs for *V. glebopalma* (SVL 250 mm), or two eggs for *V. semiremex* (SVL 230 mm).

A plot of log mean clutch size against log mean maternal SVL for many of the Australian species of *Varanus* (Fig. 2; data summarized in Table 5) indicates that clutch sizes generally follow a linear allometric relationship, as has been found for lineages of Australian scincid and agamid lizards from different climatic zones (James and Shine, 1988). However, clutch sizes for three species (*V. giganteus*, *V. semiremex*, and *V. varius*) seem to be lower than expected from their relative body sizes, though the clutch size reported here for *V. semiremex* may be erroneously low since larger clutch sizes have been reported for captive specimens (clutches of 6 and 14 eggs, H-G. Horn, pers. comm.). Rela-

tively low clutch sizes in *V. giganteus* and *V. varius* may be the result of a trade-off between clutch size and egg size in these large species (Vitt and Price, 1982), but we have too few data on egg size to test this prediction. The major departures from a linear allometric relationship between maternal size and clutch size in varanids are unusual compared with relatively strong trends in scincid and agamid lizards (James and Shine, 1988).

Despite the superficial similarity of varanids, the diversity of body sizes, climatic regions and habitats occupied by Australian varanids is reflected in a diversity of reproductive characteristics of the species, even at the simple level of investigation attempted in this study. Recent studies have identified phylogenetic relatedness as a major source of variation in the life histories of squamates (Dunham and Miles, 1985). Accordingly, attempts to refine theories of life-history evolution should concentrate on closely-related species. Varanids represent a taxon of lizards which are apparently closely related, and at the same time offer a diversity of species occurring in many different habitats. We suggest that varanids may be a good taxon for testing models of life-history evolution among closely-related species over a range of environmental situations.

Diets.—Substantial dietary information previously existed for only two of the species examined in this study: *V. giganteus* and *V. gilleni*. As with previous studies, we found that vertebrates predominate in the diet of *V. giganteus* (King et al., 1989), and lizards (tails) and orthopterans are major prey of *V. gilleni* (Pianka, 1969). We also confirmed previous statements that *V. storri* eats mainly orthopterans, and *V. semiremex* utilizes aquatic prey. The diet of most of the species examined is composed of a wide

TABLE 5. Review of reproductive information on Australian *Varanus*. Only field records or captive breeding records within the natural geographic range of a species were accepted for the timing of reproduction. Captive breeding records were used to complement field data for clutch sizes.

Species of *Varanus*	Body size[1] (mm)	Climatic zone of distribution[2]	Months of year when reproductive ♀♀ collected	Mean clutch size ± SD [extremes, n]		Authority
V. acanthurus	160	seasonal tropics/arid	Aug–Nov	7.5 ± 2.7	[3–11, 8]	King and Rhodes (1982)
				7.9 ± 3.4	[4–17, 14]	Horn and Visser (1989)
V. brevicauda	90	arid zone	Oct–Dec	2.3 ± 0.5	[2–3, 4]	Pianka (1970a); Schmida (1974); James (unpubl. data)
V. caudolineatus	100	arid zone	Nov–Dec	4.1 ± 1.1	[3–6, 7]	Pianka (1969); Smith (1988)
V. eremius	120	arid zone	Oct–Feb	4.1 ± 1.0	[3–6, 8]	Pianka (1968, 1982)
V. giganteus	600	arid zone	Nov	9.3 ± 1.5	[8–11, 3]	Bredl and Horn (1987); Horn and Visser (1988); King et al. (1989)
V. gilleni	130	arid zone	Sept	4.3 ± 0.9	[3–5, 4]	Pianka (1969); Horn (1978); Gow (1982); Broer and Horn (1985); H-G. Horn, pers. comm.
V. gouldii flavirufus	280	arid zone	Oct–Dec	6.4 ± 1.4	[4–8, 11]	Pianka (1970b, 1982)
V. gouldii gouldii	300	seasonal tropics	Dec–Feb	5.8 ± 3.6	[3–11, 4]	Pengilley (1981); Shine (1986)
V. mertensi	360	seasonal tropics	Mar–Jun	12.6 ± ?	[10–14, 5]	Brotzler (1965); Bustard (1970)
				6.9 ± 2.6	[3–11, 10]	Shine (1986)
V. mitchelli	240	seasonal tropics	Apr–Jun	9.8 ± 1.9	[7–12, 5]	Shine (1986)
V. panoptes	390	seasonal tropics	Feb–Mar	11.0 ± 2.0	[9–13, 3]	Shine (1986)
V. rosenbergi	360	cool temperate	Nov–Feb	13.3 ± 3.0	[10–19, 8]	King and Green (1979)
V. scalaris[3]	170	seasonal tropics	—	5.0 ± 2.0	[3–7, 3]	Rüegg (1974); Broer and Horn (1985)
V. spenceri	380	seasonal tropics/arid	Sept–Oct	19.3 ± 5.1	[11–31, 14]	Peters (1969, 1971); Pengilley (1981)
V. storri	110	seasonal tropics	Sept	2.5 ± 0.6	[2–3, 4]	Bustard (1970); Bartlett (1982); Eidenmüller and Horn (1985)
V. tristis	220	seasonal tropics/arid	Oct–Nov	10.2 ± 2.8	[5–17, 19]	Pianka (1971, 1982); Broer and Horn (1985)
V. varius	550	temperate zone	Dec–Jan	5.6 ± 1.3	[4–7, 5]	Bredl and Schwaner (1983); Weavers (1988); Horn and Visser (in press)

[1] Estimated average SVL of reproductive adult females from references cited above, Cogger (1986), Storr et al. (1983) and the present study.

[2] Geographic distribution from Cogger (1986) and Storr et al. (1983).

[3] Reported as *V. timorensis similis* (Horn and Visser, 1989).

variety of invertebrates, with the occasional vertebrate, usually a lizard. A few species, however, do seem to specialize on particular prey types. The apparent specialization of *V. glebopalma* on lizard prey is matched only by the specialization of Old World *V. griseus* (Stanner and Mendelssohn, 1986).

Varanids are generally widely-foraging predators, searching over large areas and eating any prey they encounter (Losos and Greene, 1988; Greer, 1989). Most differences in diet, however, seem to be the result of differences in habitat and geographic distribution (Shine, 1986; Losos and Greene, 1988). Many species of varanids in the Australian deserts (e.g., *V. eremius* and *V. gouldii*) prey heavily on vertebrates, primarily lizards (Pianka, 1982), which reflects both the diversity and abundance of lizards in arid Australia (Morton and James, 1988). *Varanus semiremex*, like other semi-aquatic species (e.g., *V. mertensi* and *V. mitchelli*, Shine, 1986), feeds on aquatic prey, and dietary differences between sympatric species such as *V. glauerti* and *V. glebopalma* are possibly related to habitat differences. However, the relative body size of a species also plays a role in shaping diet. Large-bodied varanids tend to specialize on vertebrate prey (Auffenberg, 1981; Weavers, 1989), which is both absolutely and proportionately larger (Losos and Greene, 1988).

Despite the large range in body sizes of the species examined (1000-fold range in body mass between *V. giganteus* and *V. gilleni*), and the range of climatic zones and habitats occupied, the diets of varanids are relatively conservative, with lizards and orthopterans being the main prey. Possibly the most important factor determining the composition of the diet of varanids is the habitat in which a species lives. Reproductive characteristics were more variable, with a diversity of seasons of reproduction in the tropics, and relatively low clutch sizes in some of the larger-bodied species. The results from this preliminary study, using material available in museum collections, indicate worthwhile areas for future research in the reproductive biology of varanids. But low sample sizes in museum collections highlight the need for autecological research on Australian varanids.

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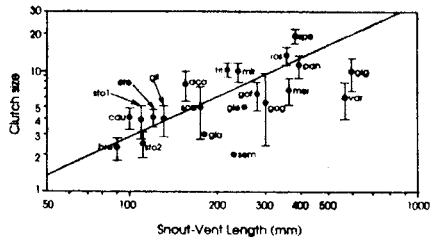

Fig. 2. Mean SVL of adult females versus mean clutch size (log scale) for 18 species of Australian *Varanus* examined in this study and from literature (Table 5). Vertical bars show ±2 SE of the mean (see Tables 2 and 5 for sample sizes). The fitted regression (using mean SVLs and mean clutch sizes) has the equation clutch size $= 0.033 \text{SVL} - 0.527$ ($r^2 = 0.661$) and was calculated for the data from 18 species, omitting *V. semiremex*, *V. giganteus* and *V. varius* (see text). Note that although there is a general increase in clutch size with the body size of the species, the larger-bodied species have relatively small clutch sizes. Abbreviations for species names are: aca = *V. acanthurus*; bre = *V. brevicauda*; cau = *V. caudolineatus*; ere = *V. eremius*; gig = *V. giganteus*; gil = *V. gilleni*; gla = *V. glauerti*; gle = *V. glebopalma*; gog = *V. gouldii gouldii*; gof = *V. gouldii flavirufus*; mer = *V. mertensi*; mit = *V. mitchelli*; pan = *V. panoptes*; ros = *V. rosenbergi*; sca = *V. scalaris*; sem = *V. semiremex*; spe = *V. spenceri*; sto = *V. storri*; tri = *V. tristis*; var = *V. varius*. *Varanus storri* is plotted twice because of the difference in mean clutch size reported in this study ("sto1") compared to that reported in the literature ("sto2"; see Table 5).

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