

ENCYCLOPEDIA OF AUSTRALIAN REPTILES

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Introduction

The **Encyclopedia of Australian Reptiles** is an attempt to summarise all the biological information on the reptiles of Australia that may be of interest to a general reader as of August 2006. It is intended for herpetologists and naturalists; students at a secondary, tertiary and post-graduate level; researchers, and bureaucrats involved with Australian reptiles.

The Encyclopedia does not aid in the identification of Australian reptiles. For this, one of the many good Australia-wide or regional guides should be consulted.

The Encyclopedia offers special assistance to New South Wales users (its ultimate supporters) in listing species that occur in this state in blue, whereas all other species are listed in red. Also, the only maps available to date are those for species that occur in New South Wales.

Using the Encyclopedia

The easiest way to use the Encyclopedia is to ‘word search’ it for the name of any taxonomic group, say a particular species, or any concept, say, ‘sexual dimorphism’.

How to Cite the Encyclopedia

The Encyclopedia should be cited as follows.

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Encyclopedia of Australian Reptiles - Varanidae

Varanids are powerful lizards with somewhat elongate bodies and short limbs, giving them a slightly slinky look. They range in size from *Varanus brevicaudis* with a maximum snout-vent length of about 120 mm and a maximum weight of about 18 g up to the *Varanus komodoensis* with a maximum snout-vent length of about 1 340 mm and a maximum weight of about 54 000 g (Auffenberg, 1981). Despite this large size range, varanids are rather similar in shape, primarily in the length of the tail relative to the body. Only one genus, *Varanus*, is recognised, but this genus is subdivided into several subgenera.

About 58 living species of varanids currently recognised (Böhme, 2003). Today, varanids occur in Africa, southern Asia and in the southwest Pacific region. However, they are most numerous, by far, in Australia.

Varanids are widespread on mainland Australia and occur in almost all terrestrial habitats. However, they are absent from Tasmania.

The closest living relative of the varanids is a somewhat elongate, secretive lizard, *Lanthanotus*, from Borneo. And the closest relatives of these two groups are the two beaded lizards in the genus *Heloderma* from the warm arid and semi-arid regions of western North America (Estes *et al.*, 1988).

In Australia, goannas are primarily ground dwelling, semi-arboreal or semi-aquatic, depending on the species. In the first case they may occur primarily either in flat or rolling countryside or in rocky areas; in the second case, they usually forage on the ground and shelter in vegetation, and in the third case they occur along creeks and billabongs.

As far as is known, goannas have a home range within which most of their activities occur.

Many, but not all, goannas have a high aerobic scope; that is, compared to other lizards, they can achieve and maintain higher levels of oxygen-based metabolism compared to their resting rates than can other lizards. This means they can achieve and maintain higher levels of activity than can other lizards over prolonged periods. These high levels of activity may be most useful in foraging and in escape. Australian goannas with a relatively high aerobic scope are *V. gouldii*, *V. panoptes* and *V. rosenbergi*; in contrast, *V. mertensi* has an aerobic scope not appreciably different from other lizards (Christian and Conley, 1994).

All Australian goannas eat a wide variety of animal food, including in many, if not all, species a variety of invertebrates. Many species also eat carrion.

All Australian goannas range widely in foraging for food. Some of the larger species may cover more than a kilometre in a day's activity.

All goannas lay eggs and clutch sizes are variable within species.

The common Australian name for the lizards in this family is "goanna". This is probably a corruption of the word "iguana", the name for a number of large lizards in the New World (e.g., Galapagos Iguana and Green Iguana) to which, perhaps, the early European settlers thought the Australian species might be related (Cogger, 1959). A common name elsewhere

for the lizards is "monitors", a name probably arising from the habit of many of the larger species of standing up on their back legs to survey the surrounds or in defence. In Australia, the common names for individual species may include either the name "goanna" or "monitor".

Several books have been written on the natural history of varanids both worldwide (King and Green, 1993b; Bennett, 1995, 1998; De Lisle, 1996; Steel, 1996; Pianka and King, 2004) and in Australia (Vincent and Wilson, 1999), and these provide overviews of the family as a whole. There are also two books dedicated to the husbandry of varanids (Kirschner, Müller and Seuffer, 1996; Eidenmüller, 1997; see also Bennett, 1998).

Varanus acanthurus

Distribution. The species is widespread in the north central and western parts of Australia.

It also occurs on a number of islands. In Western Australia, these include: Augustus I. (Storr, 1980a), Barrow I. (Case and Schwaner, 1993), Hermite I. (Storr, 1980a), Legendre I. (Storr, 1980a), Lowendall I. (Storr, 1980a), Montebello I. (Storr, 1980a), South Muiroon I. (Storr, 1980a) and West Lewis I. (Storr, 1980a).

Habitats. The species has been recorded from the following habitats: sparse, short grasses and forbs under *Acacia* (Dryden *et al.*, 1990).

Activity. During the active season, the species shelters in rock crevices and under boulders (Dryden *et al.*, 1990).

Shelter sites. In captivity, the young are said to dig extensive burrows (Kuhn and Julander, 1999). This suggests that wild individuals may also dig their own burrows.

In the wild, the species has been found in burrows about 300 mm (one foot) deep and 915 (three feet) long (W. Scheville, in Loveridge, 1934).

Thermal biology. In captivity, the animals bask (Kuhn and Julander, 1999).

Water relations. The mean water content of this species has been measured at 70.3 percent (n =19) (Dryden *et al.*, 1990).

In an experimental situation, the rate of evaporative water loss at 35° C (in terms of the log-log relationship) had a slope of 2.13 which was extremely high compared to other goannas tested at the same time (Thompson and Withers, 1997). This means that the rate of water loss increases much faster with increasing size than in other species. Why this species should have such a high slope is not clear. And the mystery is compounded by another study at 30° C in which the slope was only 0.42 (Green, 1969, as reported in Thompson and Withers, 1997).

The equation for the study with the high rate of change in the rate of water loss with size is: log rate of evaporative water loss (mg/h) = 2.13 log body mass (g) -2.45 (Thompson and Withers, 1997).

Diet. In the wild, the species eats arthropods such as beetles (D. King, in Jones, 1983; Losos and Green, 1988), cockroaches (D. King, in Jones, 1983; Losos and Green, 1988) and orthopterans (D. King, in Jones, 1983; Losos and Green, 1988) and vertebrates such as lizards (Losos and Green, 1988). In one study, of the total food items, grasshoppers made up 44 percent, beetles 17 percent and cockroaches six percent (D. King, in Jones, 1983).

In captivity, the young goannas eat arthropods such as cockroaches (Husband, 1979b; Thiessen, 1993; Krebs, 1999), crickets (Husband, 1979b; Thiessen, 1992, 1993; Kuhn and Julander, 1999), grasshoppers (Husband, 1979b; Thiessen, 1993), locusts (Krebs, 1999) and mealworms (Husband, 1979b); lizards such as geckos and skinks (Husband, 1979b) and small mammals (Husband, 1979b; Thiessen, 1993) or small mammal parts (Kuhn and

Julander, 1999). They also eat egg yolk (Krebs, 1999), beef heart (Krebs, 1999) and mince (Kuhn and Julander, 1999). Young individuals do not eat waxworms (Thissen, 1992).

As they grow, the young goannas begin eating pink mice (Thissen, 1992).

Fat storage. In captivity, the tails of post-laying females are said to sometimes be "shrunk" (Kuhn and Julander, 1999). This suggests that fat may be stored in the tail and used by gravid females.

Male combat. Behaviour interpreted as male combat has been observed in captivity (Thissen, 1992, 1993), but no details were published other than the combat was bloodless.

Courtship and mating. In captivity, when a male is newly introduced into a female's cage, he often presses on the substrate a part of his tail several centimetres posterior to the cloaca while walking and waves the tail. This is speculated to be marking behaviour (Krebs, 1999), although what is deposited and where it comes from is unclear.

Pictures of mating pairs show the male's body extending diagonally over the female's body (Thissen, 1992; fig. on p. 33, 1993: fig. 1; Krebs, 1999: fig. 1).

In captivity, copulation is said to last "for hours or even all day" (Kuhn and Julander, 1999). And egg laying is said to occur as early as two weeks after copulation (Kuhn and Julander, 1999).

Seasonality of reproduction. In the wild, females carry oviducal eggs between late winter and mid-spring (15 August - 21 November) (King and Rhodes, 1982).

Clutch size. Clutch size ranges 2-11 (Husband, 1979b; King and Rhodes, 1982; Erdfelder, 1984; Thissen, 1992, 1993; Eidenmüller, 1994).

There is a significant positive correlation between female snout-vent length and clutch size ($r^2 = 0.65$, $P < 0.05$, $n = 8$) (King and Rhodes, 1982). However, there is no significant correlation between female post-laying weight and clutch size ($r^2 = 0.25$, $P = 0.25$, $n = 7$) (data in Krebs, 1999: table 3).

Frequency of reproduction. In captivity, one female produced two clutches in each of two successive seasons and both clutches in each season were separated by 42 days (Thissen, 1993).

Eggs. Measurements and weights of freshly laid eggs are tabulated below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	28	18	-	18	18	-	-	-	Krebs, 1999
30-32	-	-	14-15	-	-	-	-	-	Krebs, 1999
-	-	-	-	-	-	-	4.3	9	Krebs, 1999
-	-	-	-	-	-	-	4.4	15	Krebs, 1999
-	-	-	-	-	-	-	4.5	6	Krebs, 1999
-	-	-	-	-	-	3.3-5.2	4.5	31	Krebs, 1999

-	-	-	-	-	-	-	4.7	13	Krebs, 1999
-	-	-	-	-	-	-	4.5	18	Krebs, 1999
-	-	-	-	-	-	-	5.5	11	Krebs, 1999
-	-	-	-	-	-	-	5.5	15	Krebs, 1999
32-33	-	8	18-19	-	8	-	6.0	8	Erdfelder, 1984
-	-	-	-	-	-	-	6.6	11	Krebs, 1999

There is no significant relationship between female post-laying weight and mean egg mass ($r^2 = 0.17$, $P = 0.36$, $n = 7$)(data in Krebs, 1999: table 3). In other words, heavier females lay clutches in which the mean egg weight does not differ significantly from that of smaller females.

The eggs gain weight throughout development, presumably through the uptake of water. One egg increased 140 percent in weight during development (Krebs, 1999).

Nesting. In captivity, females are said to begin digging burrows a week prior to laying. The eggs are laid usually at night. The female is said to take care in arranging the eggs once laid. She also backfills the nest (Kuhn and Julander, 1999).

In captivity, females are said to defend their laying sites from other cagemates, including stronger males (Krebs, 1999).

Nests. A nest in nature was dug into soil graded up along the side of a road. The nest burrow was S-shaped, about 25 mm in diameter and about 400 mm below the surface of the ground. It appeared as if the nest had been filled in with soil (Husband, 1979b).

Relative clutch mass. Relative clutch mass in seven captive breedings ranged 0.24-0.57 (mean = 0.41)(data in Krebs, 1999).

Incubation. The incubation times under various incubation temperatures are given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
26-28	-	144-172	-	7	Krebs, 1999
27-28.5	-	111	111	1	Thissen, 1992,1993
27-28.5	-	117-133	-	5	Thissen, 1993
27-28.5	-	113-139	-	8	Thissen, 1993
27-28.5	-	120-122	121.3	3	Thissen, 1993
26-30	-	101-121	-	7	Eidenmüller, 1994
26-30	-	131-147	-	6	Eidenmüller, 1994
28-30	-	123	-	1	Krebs, 1999
28-30	-	120-141	-	5	Krebs, 1999
28-30	-	125-154	-	12	Krebs, 1999
29	29	140-169	-	7	Erdfelder, 1984
29-30	-	118-140	-	14	Krebs, 1999
29-31	-	94-100	-	14	Krebs, 1999

30-31	-	84-98	-	-	Kuhn and Julander, 1999
31-32	-	79-82	-	8	Krebs, 1999
-	-	138	138	3	Erdfelder, 1984

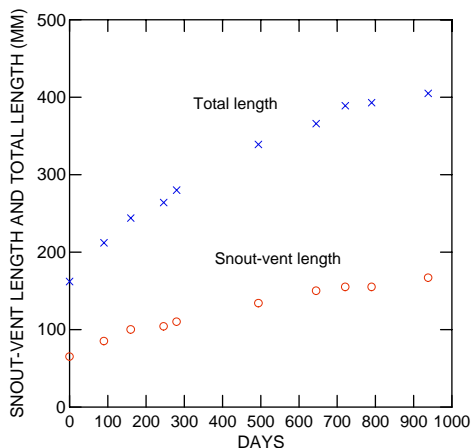
Hatching. In the wild, hatching occurs in early summer (4 January)(Husband, 1979b).

Hatchlings. Measurements and weights of hatchlings are tabulated below.

Snout-vent Length (mm)			Total Length (mm)			Weight (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
63-69	65.7	8	153-167	160.9	8	-	-	-	Husband, 1979b
60	60	1	135	135	1	-	-	-	Thissen, 1992, 1993
-	51	-	-	-	-	-	-	-	Kuhn and Julander, 1999
-	-	-	135	135	1	3.5	3.5	1	Thissen, 1993
-	-	-	130-145	137.5	2	3.5-3.9	3.7	2	Thissen, 1992
-	-	-	137-164	151	21	2.9-4.5	4.0	21	Krebs, 1999
-	62	7	-	-	-	-	4.0	7	Eidenmüller, 1994
-	63	6	-	-	-	-	4.4	6	Eidenmüller, 1994
-	-	-	145-172	-	7	7.0-9.5	-	7	Erdfelder, 1984

Hatchlings can start feeding within the first two days of life (Thissen, 1993).

Growth. The growth in snout-vent length and in total length is available for one specimen raised in captivity since hatching (see accompanying figure based on data in Husband, 1979b).



One captive hatchling grew in total length at a rate of 0.91 mm/day over the first 40 days of life (data in Thissen, 1992).

Among wild-caught specimens, the smallest male with active sperm measured only 89 mm in snout-vent length, but all males above 120 mm in the presumed mating season had active sperm. The smallest female with oviducal eggs measured 140 mm in snout-vent length (King and Rhodes, 1982).

In captivity, males can engage in combat at an age of 19 months and mate at 20 months, and females have mated at 15 (Erdfelder, 1984) and 18 months (Thissen, 1993). Some keepers even claim that individuals can breed when less than one year old (Kuhn and Julander, 1999).

Allometry. The growth rate of one specimen in captivity (see Growth) shows that, at least in the young, the growth rate in total length is faster than the growth rate in snout-vent length, which means that with growth, the tail is becoming ever increasingly longer relative to snout-vent length. This is a common pattern in lizards.

Sex ratio. Among museum specimens that could be confidently sexed, the number of males (98) did not differ significantly from the number of females (107)(King and Rhodes, 1982).

Maximum size. The species reaches a snout-vent length of 237 mm and a total length of 630 mm (Storr, 1980a).

Karyotype. The species has a diploid chromosome number of 40 (King *et al.*, 1982). Females have a sex chromosome: one member of pair nine being nearly twice as long as its opposite number (King *et al.*, 1982).

The species is unusual in showing a chromosome polymorphism in both sexes in the central and western part of the range. Pair six can consist of two metacentric chromosomes, one metacentric and one acrocentric or two acrocentric chromosomes. To judge from the condition in closely related species, the primitive condition is probably two metacentric chromosomes, the acrocentric chromosome being the evolutionary novelty (King *et al.*, 1982). Why this polymorphism evolved is unknown.

Predators. The species' only recorded predators are pythons (Browne-Cooper, 1998).

Parasites. The species' only known endoparasites are nematodes (round worms) (Jones, 1983, 1991).

Literature. Boulenger, 1885; Sternfeld, 1919; Loveridge, 1934; Thomson and Hosmer, 1963; Greer, 1969; Husband, 1979b; Brunn, 1982; King, Mengden and King, 1982; King and Rhodes, 1982; Jones, 1983; Erdfelder, 1984; Losos and Green, 1988 (possibly a composite of *V. acanthurus* and *V. baritji*); Horn and Visser, 1989; Dryden, Green, King and Losos, 1990; Jones, 1991; Thissen, 1992; Case and Schwaner, 1993; Thissen, 1993; Wicker, 1993; Eidenmüller, 1994; Thompson and Withers, 1994; Wick, 1996; Horn and Visser, 1997; Thompson and Withers, 1997; Browne-Cooper, 1998; Jones, 1998; Kuhn and Julander, 1999; Krebs, 1999; Michelsen, 2000; in den Bosch, 2001.

Varanus baritji

Lemon-throated Monitor

Distribution. The species occurs only in the Top End of the Northern Territory north of the Katherine River (King and Horner, 1987; fig. 3; Bedford and Husband, 2003).

Habitats. The species occurs in woodlands (Sweet, 1999).

Daily activity. The goannas forage under conditions of low light intensity (Sweet, 1999).

Shelter sites. The species shelters in burrows under large rocks (Sweet, 1999; Bedford and Husband, 2003).

Agonistic behaviour. Observations on two mature males in an enclosure with four females gave no indication of any agonistic interaction between the two males, despite their both having mated with the same female (Bedford and Husband, 2003). In other words, no male combat was observed.

Diet. In the wild, the animals eat arthropods such as beetles (Losos and Green, 1988), caterpillars (Losos and Green, 1988), grasshoppers (Losos and Green, 1988), isopods (Losos and Green, 1988), roaches (Losos and Green, 1988) and spiders (Sweet, 1999). It also eats vertebrates in the form of squamate eggs (Losos and Green, 1988).

In captivity, juveniles eat cockroaches, crickets, gecko tails and kangaroo mince (Bedford and Husband, 2003).

Foraging behaviour and prey handling. Field observations indicate that the species forages under conditions of low light intensity (Sweet, 1999).

One of its main prey types is large spiders. The goannas extract the spiders from their burrows, beat them on the ground to the extent that they lose their appendages and many of their setae and then swallowed (Sweet, 1999).

Courtship and mating. A courting male bobbed his head, followed the female and bit her neck (Bedford and Husband, 2003).

Seasonality of reproduction. In individuals kept in captivity near the natural range of the species, courtship occurred in the early winter dry season (late June-early July) and females laid their eggs in mid to late winter (19 August-September) (Bedford and Husband, 2003).

Frequency of reproduction. In captivity, one female laid two successive clutches in one season, one in August and another in September (Bedford and Husband, 2003).

Clutch size. Clutch size ranges 5-9 with a mean of 7.3 (Bedford and Husband, 2003).

Nests. In captivity, females bury their eggs in sand and then lie across the closed nest (Bedford and Husband, 2003).

Eggs. Measurements and weights of freshly laid eggs are tabulated below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	35.2	5	-	16.6	5	-	5.6	5	Bedford and Husband, 2003
-	30.0	9	-	16.5	9	-	4.6	9	Bedford and Husband, 2003
-	31.2	8	-	15.8	8	-	4.4	8	Bedford and Husband, 2003

Incubation. The incubation times under various incubation temperatures are given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
32	32	103	103	1	Bedford and Husband, 2003
c. 32	c. 32	110	110	8	Bedford and Husband, 2003
c. 32	c. 32	104	104	6	Bedford and Husband, 2003

Hatchlings. Measurements and weights of hatchlings are summarised in the following table.

Snout-vent Length (mm)	Total Length (mm)	Weight (g)	

Range	Mean	N	Range	Mean	N	Range	Mean	N	Reference
-	57.7	8	-	-	-	-	3.7	8	Bedford and Husband, 2003
-	59.5	6	-	-	-	-	3.6	6	Bedford and Husband, 2003

Growth. It has been asserted that captive-bred young can double their mass in two months (Bedford and Husband, 2003).

Maximum size. The largest measured specimen had a snout-vent length of 200 mm (Bedford and Husband, 2003).

Predators.

Parasites.

Literature. King and Horner, 1987; Losos and Green, 1988; Sweet, 1999; Bedford and Husband, 2003.

Varanus brevicauda

Short-tailed Goanna

Distribution. The species is widespread throughout the arid regions of the central western two-thirds of the continent. It only occurs near the coast at the western limit of its range.

Habitats. The species occurs in sand dunes (Gillam *et al.*, 1978) and sand dunes/sand plains with a tussock grass understorey and a scattered shrub overstorey (Fyfe *et al.*, 1999: fig.3; see also Pianka, 1970).

A detailed study of the distribution of the species across the entire topography of a dune, found the species occurred about equally frequently on crest, slope and interdune (Downey and Dickman, 1993).

Activity. The fact that the species is usually caught in pit traps (Pianka, 1994) suggests that it is primarily, if not exclusively, ground dwelling.

There is an interesting observation of how this species deals with sheet flooding that can follow prolonged heavy rain in the arid regions where this species lives. At the edge of a flood water, an individual was seen under the water stretching itself out of a burrow and just managing to get its nose above the surface. Its tail and rear legs were in the burrow and its front legs were tucked alongside its body. Upon approach, it tried to withdraw backwards into the burrow (Jackson, 2001). This observation raises the possibility that many burrow-inhabiting species may stay in their burrows during flood, especially if the floods are of short duration. It also implies that they are able to withstand short periods without oxygen.

Shelter sites. The species has occasionally been found in holes (Slater, 1964) and burrows (Pianka, 1970, 1994)

Thermoregulation. In captivity, the species basks under a heat lamp (Fyfe *et al.*, 1999).

Agonistic behaviour. In captivity, mature males will fight (Fyfe *et al.*, 1999).

Water relations. The rate of evaporative water loss relative to body mass has been measured for a variety of different sized individuals of this species at 35° C. Although an equation was produced, the relationship was not significant and hence is not reported here (Thompson and Withers, 1997).

Diet. In the wild, the goannas eat arthropods, squamate eggs and lizards (Pianka, 1970, 1994). In one study, each of these prey types comprised 88.9, 2.8 and 8.3 percent of the total number of prey items eaten (n = 36)(Pianka, 1994).

In captivity, the young eat crickets and mealworms (Thompson, 1996c) and adults eat cockroaches, mealworms and mealworm pupae (Fyfe *et al.*, 1999).

Fat is stored in abdominal fat bodies, which can be quite large (Pianka, 1994).

Seasonality of reproduction. Shortly after being captured in the wild, a female mated in early spring (16-17 October). This female laid eggs 17 days after her last mating (Thompson, 1996c).

Clutch size. Clutch size ranges 2-4 (Pianka, 1970a, 1994; Schmida, 1974; Thompson, 1996c; Fyfe *et al.*, 1999), with a recorded mean of 2.4 (n = 7, Thompson and Pianka, 2001).

There is no significant association between female snout-vent length and clutch size ($r^2 = 0.02$, $P = 0.76$, $n = 7$; Thompson and Pianka, 2001).

Eggs. Measurements and weights for freshly laid fertile eggs are summarised below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	-	-	-	-	-	1.66-1.80	1.73	2	Fyfe <i>et al.</i> , 1999
23-25	24.0	3	12	12.0	3	2.07-2.19	2.13	3	Fyfe <i>et al.</i> , 1999

Incubation. Incubation periods are given in the following table.

Incubation Temp. (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
29	29	107	107	2	Thompson, 1996c
29	29	108-109	108.5	2	Thompson, 1996c
30	30	80	80.0	1	Fyfe <i>et al.</i> , 1999
31	31	71-73	-	3	Fyfe <i>et al.</i> , 1999

Hatchlings. Hatchling measurements and weights are summarised below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	-	-	80	80	3	-	-	-	Schmida, 1974
43	43	1	82	82.0	1	1.12	1.12	1	Fyfe <i>et al.</i> , 1999
55	55.0	3	104	104.0	3	1.71-1.83	1.78	3	Fyfe <i>et al.</i> , 1999

40-48	46.4	5	88-100	95.2	5	1.3-2.3	1.9	5	Thompson, 1996c
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Growth. In captivity, growth of a single individual from hatching to seven months of age (taken here as 214 d) was nearly linear and averaged 0.17 mm/day in snout-vent length and 0.03 g/day in mass (data in Fyfe *et al.*, 1999).

In another case, one hatchling grew over the first 30 days of life at an average rate of 0.05 g/day (data in Thompson, 1996).

Sexual maturity can be achieved in males (large testes) at a snout-vent length as small as 82 mm and females (gravid) at a snout-vent length as small as 94 mm (Pianka, 1994).

Maximum size. The species attains a snout-vent length of 118 mm and a total length of 230 mm (Storr, 1980a).

Predators. The species' only recorded predator is another goanna, *Varanus gouldii* (Pianka, 1970a, 1994).

Defence. In captivity, two day old young arch their neck and extend their gular pouch in response to a human hand (Thompson, 1996). Adults will hiss and lunge with the throat extended (Pianka, 1994).

Parasites.

Literature. Boulenger, 1898; Slater, 1964; Pianka, 1970a; Schmida, 1974; Gillam, Cawood and Honner, 1978; Mebs, 1979; Downey and Dickman, 1993; James, 1994; Pianka, 1994; James, 1996; Thompson, 1996c; Thompson and Withers, 1997; Fyfe, Munday and Comber, 1999; Jackson, 2001.

Varanus caudolineatus

Distribution. The species occurs in the more arid parts of western Western Australia.

Habitats. The species inhabits open shrubland and woodland (Pianka, 1969c; Thompson, 1993; Thompson and King, 1995), often with a hummock grass understorey (Thompson, 1993; Thompson and King, 1995). The substrates are usually loamy (Thompson, 1993; Thompson and King, 1995) or sandy (Thompson *et al.*, 1992).

Activity. The species is both ground dwelling and arboreal (Pianka, 1969c, 1994). It may occur as high as two metres above the ground (Pianka, 1969c).

The species is mostly, if not exclusively, active during the warmer months, e.g., November-March (Pianka, 1969). It is also diurnal in its surface activity, with most active animals being seen between 1000 and 1620 h (mean = 1300 h) (Pianka, 1969c).

Shelter sites. The species shelters under exfoliating bark (Pianka, 1969c) and in the hollow stems and trunks of dead shrubs and trees (Pianka, 1969, 1994; Thompson *et al.*, 1992; Thompson, 1993; Thompson and King, 1995; pers. obs.). It often wedges itself snugly into

the hollows of dead branches (Thompson, 1993; Pianka, 1994). It also shelters occasionally in rock crevices (Pianka, 1969c).

Thermal relations. The body temperatures of ten active individuals ranged 34.0-40.8° C with a mean of 37.8° C (Pianka, 1969c, 1982, 1994).

The slope of the regression of body temperature on ambient air temperature was 0.71 (n = 10) (Pianka, 1994). Theoretically a slope of 1.0 would indicate no thermoregulation and a slope of 0 would indicate perfect thermoregulation (Huey and Slatkin, 1976). Hence, it appears as if this species is not a particularly good thermoregulator.

Water relations. The rate of evaporative water loss relative to body mass has been measured for a variety of different sized individuals of this species at 35° C. An equation was produced, but the relationship was not significant and is not reported here (Thompson and Withers, 1997).

Diet. In the wild, the species feeds on a variety of arthropods, including centipedes, cicadas, grasshoppers, moths, roaches, spiders (Pianka, 1969c; Losos and Green, 1988; Thompson and King, 1995). It also takes small vertebrates such as geckos (Pianka, 1969c, 1994; Losos and Green, 1988; Thompson and King, 1995) and skinks (Thompson and King, 1995).

In captivity, hatchlings feed on cockroaches and crickets (Thompson and Thompson, 2002).

Foraging behaviour. Although the goannas are often sheltering off the ground in vegetation, their diets indicate that they probably forage on the ground (Thompson and King, 1995).

Male combat. Male combat has been observed in late spring (18 December). It consisted of two males embracing each other head to head with their front and rear legs while intermittently rolling horizontally along the ground and arching their body from snout to tail. The purpose of the combat appeared to be to throw the opponent on its back. The animals also bit each other, but without breaking the skin (Thompson *et al.*, 1992).

Seasonality of reproduction. Wild-caught males had maximum testis size in winter (July-August) (Pianka, 1969).

Wild-caught females have laid eggs in late spring (16 December) (Thompson and Thompson, 2002).

Clutch size. Clutch size ranges 3-6 (Pianka, 1969c; Smith, 1988; Retes and Bennett, 2001; Thompson and Pianka, 2001; Thompson and Thompson, 2002), with a reported mode of four (Pianka, 1969) and a reported mean of 4.3 (n = 6; Thompson and Pianka, 2001).

There is no significant association between female snout-vent length and clutch size ($r^2 = 0.39$, $P = 0.18$, $n = 6$; Thompson and Pianka, 2001).

Frequency of reproduction. In captivity, females are said to be able to produce 5-6 clutches within the period of four months, followed by a quiescent period of eight months (Retes and Bennett, 2001).

Relative clutch mass. Relative clutch mass ranges 24-47.5 percent (Smith, 1988; Thompson and Thompson, 2002).

Incubation. Incubation periods are given in the following table.

Incubation Temp. (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
-	-	65-80	-	-	Retes and Bennett, 2001
29-31	-	77	77	4	Thompson and Thompson, 2002

Hatchlings. Hatchling measurements and weights are summarised below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
54-57	54.7	4	105-120	108.7	4	1.8-2.1	19.5	4	Thompson and Thompson, 2002

Hatchlings begin feeding after five days (Thompson and Thompson, 2002).

Growth. In the wild, both males and females are said to reach sexual maturity at a snout-vent length of about 91 mm (Pianka, 1994).

In captivity, the young are said to be able to reach sexual maturity at an age of five months (Retes and Bennett, 2001).

Maximum size. The species attains a snout-vent length of 132 mm and a total length of 320 mm (Storr, 1980a).

Predators. The species' recorded predators include other goannas (Pianka, 1969, 1994).

Defence. When approached by a human predator, a goanna may move around to the other side of a tree or branch, or enter a hollow (Thompson *et al.*, 1992).

Parasites. The species' only recorded endoparasites are nematodes (round worms) (Jones, 1991, 1992a, 1995c).

Literature. Pianka, 1969c; Schmida, 1975; Pianka, 1986; Storr and Harold, 1980; Bush, 1987; Losos and Green, 1988; Smith, 1988; Jones, 1991; Jones, 1992a; Thompson, Withers and Thompson, 1992; Thompson, 1993; Thompson and Withers, 1994; Jones, 1995c; Thompson and King, 1995; Thompson, Bradshaw and Withers, 1997; Thompson and Withers, 1997; Retes and Bennett, 2001; Thompson and Pianka, 2001; Thompson and Thompson, 2002.

Varanus eremius

Distribution. The species occurs in the arid central and western parts of Australia (Pianka, 1968: fig. 2).

Habitats. The species occurs primarily in habitats with hummock grass (Pianka, 1968), and it occurs primarily on sandy substrates (Pianka, 1968; Downey and Dickman, 1993).

A detailed study of the distribution of the species across the entire topography of a dune, found the species occurred about equally frequently on crest, slope and interdune areas (Downey and Dickman, 1993).

Seasonal activity. In contrast to some larger sympatric species such as *Varanus gouldii*, this species can be active during the winter as well as during the warmer parts of the year, e.g., in the Great Victoria Desert (Pianka, 1968).

Daily activity. During the warmer time of year, the species is most active in the morning and shelters during the hottest part of the day, but during the winter, it is active primarily at mid-day (Pianka, 1968).

To judge from its tracks, a single individual can move as much as a kilometre in a day (Pianka, 1968, 1982, 1994). This suggests that the species has a very large home area or that it is nomadic.

Shelter sites. The species may occasionally shelter in *Egernia* burrows (Pianka and Giles, 1982).

One specimen was found in a burrow on the top of a sand dune (Thomson and Hosmer, 1963), but whether it sheltering or foraging was not clear.

In the presence of a human predator, the goanna will flee to a burrow. And its direct flight to a burrow suggests that it knows where the burrows in its vicinity are located (Pianka, 1968, 1994).

Thermal biology. The body temperatures of 75 active individuals had a mean of 37.3° C (Pianka, 1994, see also Pianka, 1982). And six individuals had body temperatures in the range 42-43.2° C (Pianka, 1994).

The slope of the regression of body temperature on ambient air temperature was 0.22 (n = 75) (Pianka, 1994). Theoretically a slope of 1.0 would indicate no thermoregulation and a slope of 0 would indicate perfect thermoregulation (Huey and Slatkin, 1976). Hence, it appears as if this species is pretty good thermoregulator.

Water relations. The rate of evaporative water loss relative to body mass has been measured for a variety of different sized individuals of this species at 35° C. The equation describing the relationship is: $\log \text{rate of evaporative water loss (mg/h)} = 0.87 \log \text{body mass (g)} - 0.135$ (Thompson and Withers, 1997).

Diet. In the wild, the goanna eats mainly large insects and lizards, including dragons, geckos, pygopodids and skinks (Pianka, 1968, 1982, 1994; Losos and Green, 1988; Jones, 1995b). In one study, over 70 percent of the diet was lizards (Pianka, 1994). However, it also occasionally eats mice (W. Schevill, in Loveridge, 1934).

Fat is stored in abdominal fat bodies, which can be quite large (Pianka, 1994).

Foraging behaviour. On individual was observed to attack a skink from an ambush in a grass hummock (Pianka, 1994). But whether this was a purposeful or serendipitous ambush is unknown.

Seasonality of reproduction. In males, testes volumes are largest in spring (September-November) (Pianka, 1968). In females, large ovarian follicles can occur between spring and early summer (October-January) (Pianka, 1968, 1982, 1994), and oviducal eggs can occur in early summer (January) (Pianka, 1968).

Clutch size. Clutch size ranges 2-6 (Pianka, 1968, 1982; Thompson and Pianka, 2001), with recorded means of 3.6 (n = 16, Thompson and Pianka, 2001) and 4.1 (n = 8, Pianka, 1982).

There is no significant association between female snout-vent length and clutch size ($r^2 = 0.14$, $P = 0.15$, $n = 16$; Thompson and Pianka, 2001).

Growth.

Size at sexual maturity. Sexual maturity is attained at a snout-vent length of at least 116 mm in males (large testes) and at 110 mm in females (gravid) (Pianka, 1994).

Maximum size. The species reaches a snout-vent length of 164 mm and a total length of 460 mm (Storr, 1980a).

Sexual dimorphism. Head length relative to snout-vent length is significantly greater in males than in females (Pianka, 1994).

Predators.

Defence.

Parasites. The species' only recorded parasites are nematodes (round worms) (Jones, 1995b-c).

Literature. Lucas and Frost, 1895; Loveridge, 1934; Thomson and Hosmer, 1963; Pianka, 1968; Storr, 1980a; Pianka, 1982; Pianka and Giles, 1982; Downey and Dickman, 1993; Jones, 1995b-c; Thompson and Withers, 1997.

Varanus giganteus

Perentie

Distribution. The species is widespread throughout the arid interior of Australia from the coast of western Western Australia to eastern Queensland. It also occurs on Barrow Island, off the coast of Western Australia.

Habitats. The species occurs on open sand plains (Pianka, 1994; pers. obs.) and on sand ridges (Pianka, 1994). It is often associated with rock outcrops and breakaways (Irwin, 1997).

Seasonal activity. On Barrow Island, the species is active year around (King *et al.*, 1989).

Daily activity. The species is diurnal in its activity on the surface (King *et al.*, 1989) and retreats to shelters during the night (King *et al.*, 1989).

Although the species is usually seen only on the ground, the fact that they are attracted to and will attack bait hung in trees (Irwin, 1997), suggests that they can also climb.

Shelter sites. The species shelters in burrows (Pianka, 1982; King *et al.*, 1989) and in rock crevices and caves (Irwin, 1997).

Thermal biology. The body temperature of active animals rises during the morning, peaks at midday and declines in the late afternoon (King *et al.*, 1989).

In one study, the body temperatures of active individuals ranged 37.6- 38.8° C (n = 2 in Pianka, 1982a) and had a mean of 36.7° C (n = 3 in Pianka, 1994). In the former two cases, the body temperatures were 10.5-12.8° C higher than the ambient air temperatures (Pianka, 1982a). In another study, the body temperatures of four animals ranged 31.0-40.9° C with a mean of 36.1° C (109/4, King *et al.*, 1989).

The maximum recorded body temperature, which indicates the maximum temperature tolerated by the animals, was 40.9° C (King *et al.*, 1989).

Diet. In the wild, perenties feed on both invertebrates and vertebrates. Invertebrate prey includes arthropods such as grasshoppers and spiders, and vertebrate prey includes lizards (Pianka, 1994), snakes (King *et al.*, 1989), birds (King *et al.*, 1989) and small mammals (Finlayson, 1958; King *et al.*, 1989; Robinson, 1992; Pianka, 1994).

On Barrow Island, which is a sea turtle nesting locality, Perenties eat turtle eggs and hatchlings (King *et al.*, 1989).

The species is cannibalistic (King *et al.*, 1989).

Perenties also eat carrion; that is, they are scavengers (King *et al.*, 1989).

In captivity, juveniles eat week-old mice and adults eat rabbits (Bredl and Horn, 1987).

Fat is stored in abdominal fat bodies, which can be quite large (Stirling, 1912).

Male combat. In captivity, two males were said to combat by assuming a bipedal stance (Card, 1994).

Seasonality of reproduction. Among mature specimens in museum collections, males had large testes in spring (October-November) (King *et al.*, 1989).

One female contained oviducal eggs in spring (November) (King *et al.*, 1989).

Clutch size. Clutch size ranges 8-13 (Bredl and Horn, 1987; Irwin, 1997).

Nesting and nests. In captivity, a female may dig several “test” nest burrows before digging the one she will use. The burrow is dug with the front feet (Irwin, 1997). Completed nest burrows range in length from 0.5 to 1.5 m in length (Bredl and Horn, 1987; Irwin, 1997).

After laying her eggs, the female back-fills the burrow using both her head and her front legs (Bredl and Horn, 1987; Irwin, 1997). She uses the head to cave in the substrate over the eggs and then taps it down with her snout. This activity can be so vigorous that all four legs come off the ground. The female also uses the head to push the loose substrate at the entrance of the burrow down into the burrow (Irwin, 1997). After filling the hole, the female rubs her belly over the site, thereby destroying the signs of her digging activity (Bredl and Horn, 1987).

Should an egg be found outside the unfilled burrow, the female may roll the egg toward the burrow, pick it up in her mouth and place it into the burrow and then continue filling the burrow (Irwin, 1997).

In captivity, one female laid her eggs at intervals of 5-10 minutes (Irwin, 1997).

In captivity, a female’s behaviour may become more aggressive to conspecific enclosure mates, even the male that fathered her clutch (Irwin, 1997). Other males, not fathers to the clutch, may also become aggressive to a male father after the female has nested. The aggressor may chase and bite the other male, inflicting deep lacerations on the base of the latter’s tail (Irwin, 1997).

Eggs. Measurements and weights of freshly laid eggs are tabulated below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	78.0	10	-	50.0	10	-	82.0	10	Bredl and Horn, 1987
-	85.0	8	-	42	8	-	90.0	8	Bredl and Horn, 1987
83.0-91.0	87.3	13	43.5-46.0	44.5	13	92-101	95.6	13	Irwin, 1997

For one clutch of eggs, much more of the variability in egg mass was accounted for by egg length ($r^2 = 0.073$, $P < 0.001$) than egg width ($r^2 = 0.03$, $P = 0.54$)($n = 13$) and the coefficient of variation for egg length (0.03) was nearly twice that for egg width (0.0165) (data in Irwin, 1997). Why goanna eggs should vary more in length than in width is not clear, unless it indicates that the width of the female's reproductive tubes and passageways is a limiting factor.

Incubation. Incubation periods are given in the following table.

Incubation Temp. (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
-	-	-	200	-	Irwin, 1997
-	-	228-233	-	-	Irwin, 1997
-	-	-	234	-	Irwin, 1997
-	-	-	249	-	Irwin, 1997

30-32	-	228	228.0	1	Bredl and Horn, 1987
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Hatching. Published pictures of hatchlings emerging from the eggs suggest that the hatchlings cut a hole only large enough for them to escape, instead of making extensive slashings in the egg shell. The pictures also show that the hatchlings usually cut the exit hole in the middle fourth-fifths of the egg and not at an end (Bredl and Horn, 1987: fig. 2; Irwin, 1997: fig. p. 28).

Hatchlings. Hatchling measurements and weights are summarised below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
144-155	150.2	6	368-381	375.3	6	30-50	40.0	6	Bredl and Horn, 1987 ¹

1. Five of these six individuals were assisted in hatching.

Growth. Six captive hatchlings (five of which were assisted in their hatching) grew in the first month of life an average of 0.88 mm/d in snout-vent length, 2.47 mm/d in total length and 0.88 g/d in weight (data in Bredl and Horn, 1987).

Allometry. The mean ratio tail length/snout-vent length of six captive hatchlings (see above) was not markedly different between the time of hatching (1.50) and a month later (1.54) suggesting that tail length may have been growing in isometry with snout-vent length in this time (data in Bredl and Horn, 1987).

Size. This is the largest lizard in Australia in terms of both length and weight. The maximum accurately recorded snout-vent length measurement is 880 mm (King *et al.*, 1989; King and Green, 1993), the maximum total length is 1960 mm (King and Green, 1993) and the maximum weight is 17 kg (Butler, 1970).

The relationship between mass and both snout-vent length and total length is strongly exponential, with mass increasing markedly in relation to length beyond a snout-vent length of about 500 mm (King and Green, 1993: fig. 1). In other words, beyond a snout-vent length of about 500 mm, the animals start bulking up.

Predators. Large Perenties often allow close approach by humans (White, 1979; Horn and Visser, 1988; pers. obs.), and they can be very docile when captured (Pianka, 1982). Why they are so passive is unclear, especially when it seems likely that up until recently Aboriginal people would have hunted them for food and Europeans would have molested them or even tried to kill them.

Defence. The species' full defensive display consists of a raised stance on stiff legs, an arched back and tail, and an extended throat pouch (Horn and Visser, 1988: fig. 2; Fyfe, 1995). A threatened animal may also open its mouth (Horn and Visser, 1988: fig. 10).

Some individuals may flee into trees when confronted by people (Horn and Visser, 1988: fig. 11)

Parasites. The species' only recorded ectoparasite is the tick *Amblyomma calabyi* (Sharrad and King, 1981), and its only recorded endoparasites are nematodes (round worms) (Jones, 1985, 1991).

Human uses. Aboriginal people are said to hunt Perenties for food, but Aboriginals in some area think they are poisonous (Robinson, 1992).

Conservation.

Literature. Stirling, 1912; Zietz, 1914; Finlayson, 1958; Cogger, 1965; Butler, 1970; White, 1979; Brunn, 1980; Storr, 1980a; Horn, 1981; Saint-Girons, Rice and Bradshaw, 1981; Sharrad and King, 1981; Pianka, 1982; Jones, 1985; Green, King and Butler, 1986; Bredl and Horn, 1987; Horn and Visser, 1988; Losos and Green, 1988; King, Green and Butler, 1989; Visser and Horn, 1989; Jones, 1991; James, Losos and King, 1992; Robinson, 1992; King and Green, 1993; Card, 1994; Pianka, 1994; Fyfe, 1995; Thompson, Heger, Heger and Withers, 1995; Irwin, Engle and Mackness, 1996; Lee, 1996; Irwin, 1997.

Varanus gilleni

Distribution.

Habitat. The species occurs in woodland/shrubland (Delean, 1980), often with a hummock grass understorey (Pianka, 1969c) and growing on sand plains (Pianka, 1969c) or sandridges (Pianka, 1982; pers obs.).

Activity.

Shelter sites. The species often shelters under loose bark (Pianka, 1969c; Gow, 1982a) and in the hollows of dead trees and shrubs (Delean, 1980; Pianka, 1982; pers. obs.).

Diet. In the wild, the species eats arthropods such beetles (Losos and Green, 1988; James *et al.*, 1992), chilopods (James *et al.*, 1992), orthopterans (Pianka, 1969c; Losos and Green, 1988; James *et al.*, 1992), roaches (Losos and Green, 1988; James *et al.*, 1992), scorpions (James *et al.*, 1992) and spiders (Pianka, 1969c; Losos and Green, 1988; James *et al.*, 1992) and vertebrates such as bird eggs (Losos and Green, 1988; James *et al.*, 1992) and lizards (Pianka, 1969c; Losos and Green, 1988; James *et al.*, 1992). In one study, orthopterans, spiders and beetles made up 30.2, 17.4 and 15.1 percent, respectively, of all items (n = 86) eaten (James *et al.*, 1992). [See also Pianka, 1982]

In captivity, hatchlings eat crickets (Horn, 1978), wax moths (both adults and larvae) (Horn, 1978), small grasshoppers (Gow, 1982a) and skinks (Gow, 1982a). Larger individuals eat cockroaches (Eidenmüller and Wicker, 1997), crickets (Polleck, 1980a; Eidenmüller and Wicker, 1997), grasshoppers (Polleck, 1980a; Eidenmüller and Wicker, 1997), mealworms (Eidenmüller and Wicker, 1997), geckos (Bustard, 1979; Gow, 1982a) and small mice (Polleck, 1980a).

Foraging behaviour. The species' gecko prey may be grasped anywhere on the body, but they are always swallowed head-first (Bustard, 1979). A goanna can subdue and swallow a gecko up to 40 percent of its own body mass (Bustard, 1979).

Courtship and mating. In captivity, courting males wave their heads and tongue flick the females (Eidenmüller and Wicker, 1997).

In mating, the male lies diagonally across the back of the female and often bites the skin of her neck. Copulation can last up to half an hour (Polleck, 1980a: fig. p. 20).

Seasonality of reproduction. In males, testes are largest in late winter and early spring (September-October)(Pianka, 1969c).

Wild-caught females have given birth in captivity in late winter (18-19 September)(Gow, 1982a).

Clutch size. Clutch size ranges 1-7 (Horn, 1978; Gow, 1982a; James *et al.*, 1992; Eidenmüller and Wicker, 1997) with recorded means of 4.0 (n = 19)(James *et al.*, 1992).

There is a significant positive association between female snout-vent length and clutch size ($r^2 = 0.30$, $P = 0.015$; James *et al.*, 1992).

The size of females and their clutch sizes are in the following table.

Female Snout-vent Length (mm)	Clutch Size	Reference
131	4 (only 3 laid)	Horn, 1978
150	4	Gow, 1982a
160	7	Gow, 1982a

Nesting. One captive female buried her eggs in sand under a water container during the night or early morning (Gow, 1982a).

Eggs. Measurements and weights of freshly laid eggs are tabulated below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
28-30	28.3	3	18	18.0	3	-	-	-	Gow, 1982a

Incubation. Incubation periods are given in the following table.

Incubation Temp. (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
26-29	-	106-112	-	3	Eidenmüller and Wicker, 1997
26-29	-	124-131	-	2	Eidenmüller and Wicker, 1997
26-29	-	101-111	-	2	Eidenmüller and Wicker, 1997
28	28	95-101	-	-	Card, 1994
29	29	95-96	-	-	Broer and Horn, 1985
29-30	-	c. 91 ± 3	-	1	Horn, 1978
30	30	87-89	-	-	Broer and Horn, 1985
-	-	103-104	-	3	Gow, 1982a

Hatchlings. Hatchlings have an egg tooth (Horn, 1978) with which they slit the eggshell. They remain in the egg for up to 10 hours, withdrawing the head back into the shell if disturbed (Horn, 1978).

Hatchlings may take up to 24 hours to emerge completely from the eggs after first slitting the shell (Gow, 1982a). With the egg shell slit, the goannas stick their heads out, turn from side to side and tongue flick, and pull back into the eggs if disturbed (Gow, 1982a).

Measurements and weights for hatchlings are summarised in the following table.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	65	2	-	-	-	-	3.4	2	Eidenmüller and Wicker, 1997
-	65	2	-	-	-	-	3.1	2	Eidenmüller and Wicker, 1997
-	63	3	-	-	-	-	3.4	3	Eidenmüller and Wicker, 1997
c. 53	c. 53	1	110	110	1	2.2	2.2	1	Horn, 1978
61-65	63.5	3	134-138	135.7	3	-	-	-	Gow, 1982a

Hatchlings may start feeding within 18 hours of completely leaving the egg (Gow, 1982a).

Growth. In the first 30 days of life, one captive hatchling grew in snout-vent length and weight at rates of 0.17 mm/d and 0.057 g/day (data in Horn, 1978).

Maximum size. The species reaches a snout-vent length of 186 mm (Pianka, 1982a)

Sexual dimorphism. Based on adult specimens in museum collections, the mean snout-vent length of males (122.8 mm, sd = 15.2, n = 67) and females (126.9 mm, sd = 18.6, n = 74) is not significantly different ($t = 1.42$, $P = 0.15$)(data in James *et al.*, 1992).

Predators. The species' only recorded predator is the goanna, *Varanus gouldii* (Pianka, 1969c, 1994).

Defence.

Parasites.

Literature. Lucas and Frost, 1895; Zietz, 1914; Thomson and Hosmer, 1963; Pianka, 1969c; Murphy and Mitchell, 1974; Martin, 1975; Carpenter, Gillingham, Murphy and Mitchell, 1976; Horn, 1978; Bustard, 1979; Delean, 1980; Polleck, 1980a; Storr, 1980a; Barnett, 1981; Gow, 1982a; Pianka, 1982; Polleck, 1982; Boyer and Lamoreaux, 1983; Broer and Horn, 1985; Bickler and Anderson, 1986; Pianka, 1986; Losos and Greene, 1988; James, Losos and King, 1992; Card, 1994; Eidenmüller, 1994; Eidenmüller and Wicker, 1997; Thompson and Withers, 1997; Polleck, 2001.

Varanus glauerti

Distribution. The species occurs disjunctly in two areas of northern Australia: the Kimberley in Western Australia and the Top End of the Northern Territory (Rankin *et al.*, 1987).

Habitats. The species occurs only in areas of extensive sandstone outcrops (Rankin *et al.*, 1987; Sweet, 1999) with a woodland or forest vegetative cover (Sweet, 1999).

Daily activity. The species is active during the day (Shea *et al.*, 1988; Sweet, 1999). There are also serendipitous observations of nocturnal activity during mid-summer (Shea *et al.*, 1988). However, a much longer and more intense field study found no indication of nocturnal activity (Sweet, 1999).

In the Kimberley, the goanna is partially aquatic (Shea *et al.*, 1988).

The species forages both on the ground (Shea *et al.*, 1988) and in trees (Rokylle, 1989; Sweet, 1999).

Home range. Radio-tracking individual animals has shown that the goannas occupy distinct home ranges. Home ranges vary in size from 1.25 to 7.36 ha, and there is a strong positive correlation between the goanna's snout-vent length and the size of the home range. Within its home range, an animal may move from one side to another in the course of a day. To a human observer, at least, the boundaries of the home range correspond with no obvious features in the landscape (Sweet, 1999).

Agonistic behaviour. In an intensive field study in the Northern Territory, only one agonistic interaction was observed. During the probable breeding season, a larger male chased a smaller male along the branch and trunk of a partially hollow tree (Sweet, 1999). However, on other occasions, several males were seen in proximity to each other in association with a female and no agonistic behaviour occurred.

Diet. In the wild, the lizards eat arthropods such as lepidoptera larvae, orthopterans, roaches spiders and vertebrates such as squamate eggs, lizards (James *et al.*, 1992). The majority of the items eaten are orthopterans and spiders, which make up 38.3 and 29.8 percent, respectively, of all the items (n = 47) eaten (James *et al.*, 1992).

Foraging behaviour. The species appears to be an active forager. It spends much time in the hollow parts of trees and scratching sounds and debris falling through hollows suggest the goanna searches the rotting interiors of trees for prey (Sweet, 1999).

Fat storage. In the Northern Territory, mature males lack fat bodies and appear dehydrated during the mid-dry season (last week of July)(Sweet, 1999).

Courtship and mating. In the Northern Territory, mating has been observed during the early to mid-dry season (mid-May - mid-July) (Sweet, 1999).

Seasonality of reproduction. In the Northern Territory, females are gravid in the mid-dry season (20 June - early July) and lay their eggs in the mid-dry (mid-July)(Sweet, 1999).

Clutch size. Clutch size ranges 3-12 (James *et al.*, 1992; Retes and Bennett, 2001), with a recorded mean of nine (Retes and Bennett, 2001).

Frequency of reproduction. In captivity, individual females have produced as many as eight clutches in eight months (Retes and Bennett, 2001).

Incubation. Incubation is said to take about 90-110 days (Retes and Bennett, 2001).

Hatchlings. Hatchlings are said to have a total length of approximately 180 mm (Retes and Bennett, 2001).

Growth. In captivity, the lizards are said to reach sexual maturity (criterion not stated) at an age of about seven months (Retes and Bennett, 2001).

Maximum size. The species reaches a snout-vent length of 246 mm (sex male; Sweet, 1999), a total length of 790 mm (Storr, 1980a) and a weight of 141 g (sex male; Sweet, 1999).

Predators.

Defence. The species flees to rock crevices (Shea *et al.*, 1988).

In areas where humans leave it alone, some individuals become tame enough to climb on quiescent humans (Rokylle, 1989).

Parasites. The species' only known endoparasites are nematodes (round worms) (Jones, 1988, 1991).

Literature. Mertens, 1957; Storr, 1980a; Rankin, Horner and King, 1987; Shea, Weigel, Harwood, Floriani and Hemsley, 1988; Jones, 1988; Rokylle, 1989; Jones, 1991; Sweet, 1991; James, Losos and King, 1992; Keirans, King, Sharrad, 1994; Pianka, 1995; Retes and Bennett, 2001; Izaber, 2003.

Varanus glebopalma

Distribution. The species occurs disjunctly in the Kimberley region of Western Australia and the far northern part of the Northern Territory (Storr, 1980a).

It occurs on a number of islands. In Western Australia it occurs on Boongaree I., Byam Martin I., Katers I., Koolan I., Osborne I. and Uwins I. (Storr, 1980a).

Habitats. The species occurs in rocky habitats (R. Miller, in Mitchell, 1955; Rokylle, 1989; Valentic, 1994; Sweet, 1999) supporting woodland and forest (Sweet, 1999).

Activity. The species is active primarily during the day (Shea *et al.*, 1988; Sweet, 1999). There are also occasional observations of activity at twilight (Valentic, 1994) and at night (Shea *et al.*, 1988), but a much longer and more intense field study revealed no indications of nocturnal activity (Sweet, 1999).

The species is largely ground dwelling and can climb rock walls (Rokylle, 1989).

The goannas occupy distinct home ranges, which can be revealed by monitoring radio-tracked animals. Measured home ranges vary in size from 3.50 to 7.76 ha, and there is a

strong positive correlation between the goanna's snout-vent length and the size of the home range. Within its home range, an animal may move from one side to another in the course of a day (Sweet, 1999).

Diet. In the wild, this goanna eats arthropods such as centipedes (Losos and Green, 1988), chilopods (James *et al.*, 1992), orthopterans (James *et al.*, 1992; Sweet, 1999) and spiders (Losos and Green, 1988; James *et al.*, 1992) and vertebrates such as frogs (Losos and Green, 1988; James *et al.*, 1992; Sweet, 1999), squamate eggs (James *et al.*, 1992) and lizards (Valentic, 1994; Sweet, 1999). Lizards eaten include agamids (Valentic, 1994), pygopodids (Losos and Green, 1988), scincids (Losos and Green, 1988) and varanids (Losos and Green, 1988). In one study, lizards and orthopterans made up the 54.9 and 27.7 percent of all items (n = 65) eaten (James *et al.*, 1992).

In the Top End of the Northern Territory, there is a seasonal shift in diet, driven largely by prey availability and accessibility. As the wet season progresses, ground cover becomes thicker, making it more difficult for the goannas to find lizards, but also as the wet season progresses, grasshoppers become more common. The prey prevalence of the goannas shifts accordingly (Sweet, 1999).

Foraging behaviour. The species is at least partially a sit and wait predator. Individuals have been seen sitting at the edge of a rock and then rapidly descending to the ground to catch prey (Sweet, 1999).

The observation of a goanna running down a medium-size dragon lizard over a distance of 30 m (Valentic, 1994), suggests that it can capture prey by pursuit.

Fat bodies. Individuals contain large fat bodies during the dry season (June-August)(Sweet, 1999).

Seasonality of reproduction.

Clutch size. The only recorded clutch size is five (James *et al.*, 1992).

Eggs.

Incubation.

Hatchlings.

Maximum size. The species attains a snout-vent length of 355 mm and a total length of 1020 mm (Storr, 1980a).

Sexual dimorphism. Based on adult specimens in museum collections, the mean snout-vent length of males (274.3 mm, sd = 42.2, n = 43) is significantly greater than the snout-vent length in females (247.2 mm, sd = 40.7, n = 17) ($t = 2.26$, $P < 0.03$)(data in James *et al.*, 1992).

Predators.

Defence. The species flees to deep rock crevices (Shea *et al.*, 1988).

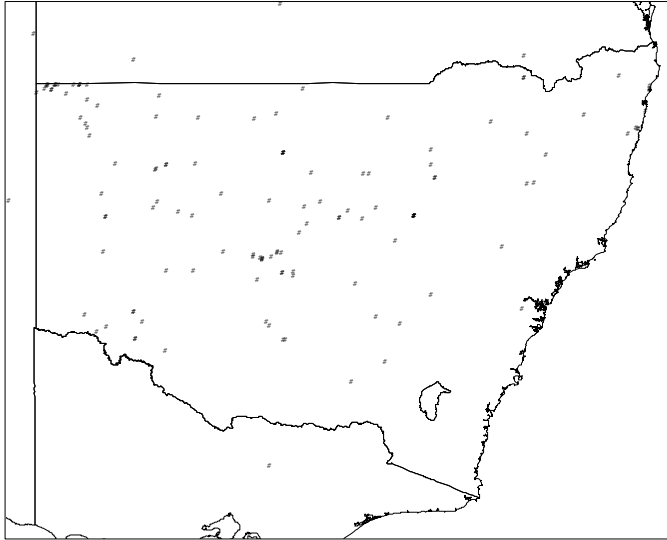
Parasites. The species' only recorded endoparasites are nematodes (Jones, 1988, 1991).

Literature. Mitchell, 1955; Christian, 1977c; Horn and Schürer, 1978; Swanson, 1979; Storr, 1980a; Shea, Weigel, Harwood, Floriani and Hemsley, 1988; Jones, 1988; Rokylle, 1989; Jones, 1991; James, Losos and King, 1992; Keirans, King and Sharrad, 1994; Valentic, 1994; Christian, 1997; Sweet, 1999.

Varanus gouldii

Sand Goanna

Distribution. The species is widespread throughout Australia, being absent only from the cool mesic southwestern and southeastern corners of the continent.



The distribution in New South Wales as based on voucher specimens in the collections of the Australian Museum is shown in the accompanying map.

Habitats. The species occurs in herblands (Shea *et al.*, 1988), shrublands (Shea *et al.*, 1988), tall open heath (Maryan, 1996) and woodlands (Shine, 1986; Shea *et al.*, 1988; Blamires, 2000) with sandy or loosely consolidated soils.

A detailed study of the distribution of the species across the entire topography of a dune, found the species occurred about equally frequently on crest, slope and interdune (Downey and Dickman, 1993).

Seasonal activity. In some areas, such as the Great Victoria Desert, the species is active between late winter and mid-summer (September-March) and is inactive between late summer to late winter (March-August) (Pianka, 1968, 1970b, 1982). When the lizards emerge from their winter quiescence, they are often thin and their fat bodies tiny (Pianka, 1982).

Daily activity. The species is primarily active during the day (Shine, 1986: fig. 1; Shea *et al.*, 1988; Couper *et al.*, 2002). However, it has also occasionally been seen hunting in the early hours of darkness (Trembath, 2000).

It is almost exclusively terrestrial (Pianka, 1982), only occasionally fleeing to a tree (Pianka, 1970b).

Tracks indicated that one individual moved a distance of more than 1.5 km during the course of its daily activity (Pianka, 1970b).

Shelter sites. The species shelters in burrows (W. Schevill, in Loveridge, 1934), either of its own or another species' making. At least one individual has been observed plugging its burrow from the inside with its snout (Couper *et al.*, 2002).

When confronted by a human predator, some individuals will flee to trees (W. Schevill, in Loveridge, 1934; Pianka, 1970b). However, this seems to be the extent of the species' arboreality.

Thermal biology. Sixty-eight active individuals had an overall mean body temperature of 37.7° C (Pianka, 1994, see also Pianka, 1970, 1982). And three individuals had body temperatures in the range 42.0-44.7° C (Pianka, 1994).

The slope of the regression of body temperature on ambient air temperature was 0.38 (n = 78) (Pianka, 1994). Theoretically a slope of 1.0 would indicate no thermoregulation and a slope of 0 would indicate perfect thermoregulation (Huey and Slatkin, 1976). Hence, it appears as if this species is a moderately good thermoregulator.

Water relations. The rate of evaporative water loss relative to body mass has been measured for a variety of different sized individuals of this species at 35° C. The equation describing the relationship is: log rate of evaporative water loss (mg/h) = 0.82 log body mass (g) - 0.012 (Thompson and Withers, 1997).

The significance of an individual soaking in the mouth of its burrowing which it prevented from flooding by inflating itself is unclear (Wild, 2005).

Diet. In the wild, these goannas eat a very large range of prey including invertebrates (Pianka, 1970b, 1982; Shine, 1986; Henle, 1989a; Jones, 1995b), fish (Shine, 1986), frogs (Shine, 1986), squamate eggs (Pianka, 1970b, 1982), lizards (Pianka, 1970b, 1982; Shine, 1986; Jones, 1995b), snakes (Shine, 1986), birds (Pianka, 1970b, 1982; Shine, 1986) and mammals (Pianka, 1970b, 1982; Shine, 1986).

In one study, lizard prey occurred in 46.8 percent of goanna stomachs (n = 79) and eggs comprised 30.6 percent of prey items (n = 340) (Pianka, 1994, see also Pianka, 1982).

The species is cannibalistic (Pianka, 1994).

The goanna eats carrion, including poisoned baits (Pianka, 1970b).

In captivity, hatchlings refuse crickets but eat skinks; however, hatchlings can be enticed to feed on crickets but getting them to start feeding on wriggling skink tails and then introducing the crickets (Barnett, 1979). Adults can be maintained on a diet of commercial kangaroo meat (Christian and Conley, 1994).

Fat is stored in abdominal fat bodies, which can be quite large (Pianka, 1994).

Foraging behaviour. The species' tracks and diggings suggest that it hunts for much of its food by digging, probably after picking up the scent of buried prey with its tongue (Pianka, 1970b, 1982).

Seasonality of reproduction. In central and western Western Australia, females carry yolking follicles in mid- to late spring (22 October - 7 December) (Pianka, 1970, 1994). They can also carry oviducal eggs in late spring (22 November - 11 December) (Pianka, 1970).

In the northern part of the Northern Territory, females carry oviducal eggs in mid-summer (January-February) (Shine, 1986).

Clutch size. Clutch size ranges 3-20 (Pianka, 1970b, 1982; Barnett, 1979; Mitchell, 1990; Thompson and Pianka, 2001), with recorded means of 6.0 (n = 3; Shine, 1986) and 9.4 (n = 18; Thompson and Pianka, 2001).

There is no significant association between female snout-vent length and clutch size ($r^2 = 0.03$, $P = 0.49$, $n = 18$; Thompson and Pianka, 2001).

Eggs. Measurements and weights of freshly laid eggs are tabulated below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
42.8-44.3	43.5	2	24.2-27.2	25.7	2	14.9-18.0	16.5	2	Mitchell, 1990

Nesting habits.

Incubation. The incubation times under various incubation temperatures are given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
28	28	228-237	232.5	2	Mitchell, 1990
28	28	229-235	-	-	Card, 1994
30-32	-	169-172	171	3	Barnett, 1979
-	-	208	208	1	Barnett, 1979

Hatchlings. Measurements and lengths of hatchlings are tabulated below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	110	-	-	260	-	-	-	-	Barnett, 1979
94-96	95	2	-	-	-	-	-	-	Shine, 1986

Growth. Maturity is reached at a snout-vent of approximately 320 mm in males and 270 mm in females (Shine, 1986: table 1).

Size at sexual maturity. In Western Australia, both sexes are said to attain sexual maturity at a snout-vent length of about 250 mm (Pianka, 1994), although the evidence for this was not provided.

Size. The largest measured individual was a male with a snout-vent length of 425 mm (Shine, 1986).

Predators. Recorded predators include the varanid *Varanus giganteus* (Pianka, 1994), the elapid snake *Pseudechis australis* (Kirkpatrick and Hancock, 1981) and birds of prey (Fyfe, 1981a). It is also eaten by its own species (Pianka, 1994).

Defence. When confronted by a predator or a member of its own species, the species often stands high on its digits, arches it back, inflates its neck and hisses. This behaviour may be followed by a tail lash and a lunge (Pianka, 1970: fig. 1; Delean, 1981).

Parasites. The species is infected by a number of endoparasites including: nematodes (round worms) (Jones, 1983; 1986a, 1988, 1991, 1995b-c) and pentastomes (tongue worms) (Bosch, 1991 and references therein).

Conservation.

Literature. Zietz, 1914; Loveridge, 1934; Longley, 1947; Mertens, 1958; Thomson and Hosmer, 1963; Bartholomew and Tucker, 1964; Warburg, 1965b; Pianka, 1968; Bustard, 1970; Pianka, 1970a-b; Green, 1972; Johnson, 1972; Floyd, 1973; Johnson, 1976; Barnett, 1979; Green and King, 1978; King, 1980; Storr, 1980a; Delena, 1981; Fyfe, 1981b; Kirkpatrick and Hancock, 1981; Pengilley, 1981; Pianka, 1982; Jones, 1983; Morley and Morley, 1984; Mansergh and Huxley, 1985; Polis and Myers, 1985; Green, Kind and Butler, 1986; Irwin, 1986; Jones, 1986a; Shine, 1986; Jones, 1988; Shea, Weigel, Harwood, Floriani and Hemsley, 1988; Green, King and Butler, 1989; Henle, 1989a; Sadlier and Shea, 1989; Mitchell, 1990; Jones, 1991; Goonan and Mann, 1992; Thompson and Withers, 1992; Case and Schwaner, 1993; Downey and Dickman, 1993; Garrett and Card, 1993; Card, 1994; Christian and Conley, 1994; Pianka, 1994; Annable, 1995a; Card, 1995; Christian, Corbett, Green and Weavers, 1995; Jones, 1995b-c; Maryan, 1996; Thompson and Withers, 1997; Blamires, 2000; Trembath, 2000; Couper, Covacevich and Amey, 2002; Wild, 2005.

Varanus indicus

Mangrove Monitor

Distribution. In Australia, the species occurs in near coastal areas in the Top End of the Northern Territory and in the northern part of Cape York Peninsula (Covacevich and Couper, 1991a: fig. 387) and on several islands in the Torres Strait, e.g., Boigu (Clarke, 2004) and Campbell (Limpus *et al.*, 1983).

Habitats.

Seasonal activity.

Daily activity.

Diet. In the wild, Mangrove Monitors eat invertebrates, such as crabs (Webb *et al.*, 1977; Jones, 2004), snails (Jones, 2004) and insects (Jones, 2004), and vertebrates such as frogs (Jones, 2004), lizards (Jones, 2004), snakes (Jones, 2004), reptile eggs (Jones, 2004) and birds (Jones, 2004).

The lizards also eat carrion, such as rotting crocodile eggs (Webb *et al.*, 1977).

Seasonality of reproduction.

Clutch size.

Nesting. The species has been reported as nesting nocturnally in captivity (Irwin *et al.*, 1996), but the significance of this behaviour in the wild remains to be seen.

Eggs.

Incubation.

Hatchlings.

Predators.

Parasites. The species recorded endoparasites are nematodes (round worms) (Schad, 1962; Jones, 2004).

Literature. Schad, 1962; Webb, Messel and Magnusson, 1977; Limpus, Miller, Baker and McLachlan, 1983; Irwin, Engle and Mackness, 1996; Phillip, Böhme and Ziegler, 1999; Jones, 2004; Smith, 2004

Varanus keithornei

Distribution. The species occurs only in the Iron and McIlwraith Ranges of Cape York Peninsula (Czechura, 1980; Irwin, 1994).

Habitats. The species has been found in open forest (Eucalyptus dominant) (Czechura, 1980) and semi-deciduous mesophyll vine forest (Czechura, 1980).

Seasonal activity. The species is active in the open during the winter dry season (August) (Czechura, 1980) and well as in the end of the dry season in spring (November)(Irwin, 1994). If the species is active in the mid-dry season, it is probably active year- around.

Daily activity. The species is active in the open during the day (Irwin, 1994).

It is both ground dwelling (J. Winter, in Czechura, 1980; Irwin, 1994) and arboreal (Czechura, 1980; Irwin, 1994). It may climb as high as 15 m (J. Winter, in Czechura, 1980).

The tail is prehensile (Czechura, 1980), which is probably an adaptation to its arboreal habits.

Shelter sites. The goannas shelter in rotting logs and hollow tree limbs (Irwin, 1994).

Diet. Wild-caught individuals passed faeces containing the remains of beetles, cockroaches, tree crickets (Irwin, 1994).

Foraging behaviour. The prey taken by the species (above) suggests that it forages, at least partly, for litter-dwelling prey (Irwin, 1994).

Seasonality of reproduction.

Clutch size.

Eggs.

Nesting. In captivity, nesting is said to occur at night (Irwin et al., 1996) but no further details are available.

Incubation.

Hatchlings.

Predators.

Parasites.

Literature. Czechura, 1980 (as *V. prasinus*); Wells and Wellington, 1985; Sprackland, 1991b (as *V. teriae*); Irwin, 1994 (as *V. teriae*); Irwin, Engle and Mackness, 1996; Holthuis, 1997; Sprackland, Smith and Strimple, 1997a-b; Covacevich and Couper, 1998; Hoser, 1998e; Shea, 1998; Ziegler and Böhme, 1998; Cogger, 1999; International Commission on Zoological Nomenclature, 2001

Varanus kingorum

Distribution.

Habitats. The species occurs in rocky habitats (Weigel, 1985).

Seasonal activity.

Daily activity.

Shelter sites. The species shelters in horizontal rock crevices (Weigel, 1985).

Agonistic behaviour. In captivity, males begin chasing and biting one another at an age of about three months (Eidenmüller, 1999, 2001).

Diet. In the wild, the species eats orthopterans, roaches, termites and insect eggs (Losos and Green, 1988).

In captivity, hatchlings have been maintained on a diet of crickets and grasshoppers, and adults have been maintained on cockroaches, crickets, grasshoppers and large mealworms (Eidenmüller, 1999, 2001).

Seasonality of reproduction.

Clutch size. Clutch size ranges 2-6 (James *et al.*, 1992; Eidenmüller, 1999, 2001) with a mean of 4.6 (n = 5) (Eidenmüller, 1999, 2001).

Frequency of reproduction. In captivity, where they are subsidised, one female laid two successive clutches separated by 94 days in one year and two further clutches separated by 64

days in the following year (Eidenmüller, 1999, 2001). And another female laid 14 clutches in as many months (Retes and Bennett, 2001).

Eggs. Measurements of eggs are given in the accompanying table.

Length (mm)			Width (mm)			Weight (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	15	6	-	7	6	-	-	-	Eidenmüller, 1999, 2001

Incubation. Incubation at different temperatures is given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
27-29	-	108-126	121.5	6	Eidenmüller, 1999, 2001
27-29	-	107-115	110.7	6	Eidenmüller, 1999, 2001
27-29	-	102-112	107.3	4	Eidenmüller, 1999, 2001
27-29	-	103-105	104.0	2	Eidenmüller, 1999, 2001
27-29	-	104-110	106.3	3	Eidenmüller, 1999, 2001
?	?	65-80	-	-	Retes and Bennett, 2001

Hatchlings. Measurements and weights for hatchlings are summarised below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	-	-	-	c. 150	-	-	-	-	Retes and Bennett, 2001
48-53	50	6	136-145	140.3	6	1.8-2.1	1.9	6	Eidenmüller, 1999, 2001
47-55	51.3	6	131-136	133.0	6	1.6-2.0	1.7	6	Eidenmüller, 1999, 2001
51-52	51.5	4	131-136	133.7	4	2.0-2.2	2.1	4	Eidenmüller, 1999, 2001
44-46	45.0	2	131-136	133.5	2	1.5-1.6	1.55	2	Eidenmüller, 1999, 2001
48-50	49.3	3	131-136	133.0	3	1.6-1.7	1.7	3	Eidenmüller, 1999, 2001

Growth. In captivity, females can lay their first clutches, albeit infertile, at an age of about six months (Eidenmüller, 2001).

Size at sexual maturity. In captivity, successful mating occurred between two individuals measuring about 70 mm in snout-vent length (Eidenmüller, 1999, 2001).

Maximum size. The species attains a snout-vent length of 114 mm (Storr, 1980a).

Predators.

Parasites.

Literature. Storr, 1980a; Weigel, 1985 (as *V. minor*); Losos and Green, 1988; James, Losos and King, 1992; Eidenmüller, 1999; Eidenmüller, 2001; Retes and Bennett, 2001; Eidenmüller, 2003

Varanus mertensi

Mertens' Water Monitor

Distribution. The species occurs across the northern part of Australia from the Kimberley to northcentral Queensland.

Habitats. The species is usually found around water bodies, either still or flowing (Cogger and Lindner, 1974; Schürer and Horn, 1976; Shine, 1986; Shea *et al.*, 1988; Blamires, 2000).

Seasonal activity. The species is seen more frequently during the warm wet season than during the cool dry season (Shine, 1986). However, the species is active on the surface during the latter period (Schürer and Horn, 1976).

Daily activity. The species is diurnal (Shine, 1986: fig. 1) and semiaquatic (Schürer and Horn, 1976; Shea *et al.*, 1988; Blamires, 1999). It is primarily ground dwelling but is also occasionally found off the ground in vegetation (Shine, 1986).

The capacity to increase the aerobic metabolism is significantly less in this species than in other species of goannas. In fact, the capacity of this species is no greater than in species from some other lizard families (Christian and Conley, 1994). Why this species should lack the apparent increased capacity for high levels of oxygen based metabolism seen in other goannas is unknown.

Thermal relations. During late autumn (last week of May), the species can be seen in sunny patches (Schürer and Horn, 1976), suggesting that it is basking. One individual caught in water in late autumn has a body temperature of 18° C (Schürer and Horn, 1976).

Water relations. The field water turnover, that is, the rate at which water passes through the body of the animal, is relatively high in this species (Christian *et al.*, 1996). This is perhaps not too surprising as water is unlikely to be a limiting resource in the species' habitat, which always includes water.

Part of the reason for the species' high rate of water turnover is that it has a high rate of overall evaporative water loss; that is, it loses water through the skin, lungs, eyes and mouth membranes at a relatively high rate. In young goannas, the mean rates at 20° and 35° C are 0.52 mg/g/h and 1.95 mg/g/h (Thompson and Withers, 1998). At the latter temperature, at least, this rate is much higher than for comparable sized (by weight) goannas, none of which are as closely associated with water as this species (Thompson and Withers, 1998). Again, in a habitat in which water is not a scarce resource, there is no need for special water conservation measures.

Locomotion. The lizards swim with lateral undulations of their body and tail with their front and rear limbs tucked back along the side of their body and tail, respectively (Schürer and Horn, 1976).

Diet. In the wild, the species eats a wide variety of prey including invertebrates and vertebrates. Invertebrate prey includes include arthropods such as beetles, dragonflies, hemipterans, orthopterans, spiders and crustaceans such as amphipods, crabs and shrimps (Losos and Green, 1988). And vertebrate prey includes fish (Shine, 1986; Losos and Green, 1988), frogs (Shine, 1986; Losos and Green, 1988), reptile eggs (Shine, 1986; Losos and Green, 1988), snakes (Shine, 1986; Losos and Green, 1988), birds (Losos and Green, 1988) and mammals (Shine, 1986; Losos and Green, 1988).

In captivity, hatchlings and juveniles eat crickets, small fish, pink mice (Brotzler, 1965) and raw meat (Thompson and Withers, 1998). Adults eat cockroaches (Eidenmüller, 1995; Eidenmüller and Wicker, 1995), crabs (Eidenmüller, 1995; Eidenmüller and Wicker, 1995), crickets (Eidenmüller, 1995; Eidenmüller and Wicker, 1995), small fishes (Eidenmüller, 1995; Eidenmüller and Wicker, 1995), adult mice (Murphy, 1972; Eidenmüller, 1995; Eidenmüller and Wicker, 1995) and commercial kangaroo meat (Christian and Conley, 1994).

Foraging behaviour. The species herds and corrals small fish with its body in shallow, drying pools. It moves sideways in the pool, and when it is close to the bank, it draws its head and tail into a C-shaped trap. It then probes the trap for fish with its head if the water is cloudy or stabs at the fish from above, if the water is clear (Hermes, 1981; I. Morris, in Shine, 1986).

In captivity, juveniles tongue flick underwater and occasionally chase large fish (Eidenmüller, 1995).

Courtship and mating. In captivity, males head-bob during courtship. Copulation can start in the water and then continue on land (Eidenmüller, 1995) or occur entirely in water (Polleck, 1999). Copulation lasts about 10 - 20 minutes (Eidenmüller, 1995; Polleck, 1999), and only one copulation occurs per season (Eidenmüller and Wicker, 1995).

In captivity, the interval between copulation and egg laying ranges 21-25 days (Eidenmüller and Wicker, 1995; Polleck, 1999; see also Eidenmüller, 1995). This is a very narrow range and suggests either that copulation occurs at a very precise time in the female's ovulation cycle or, more likely, that copulation stimulates ovulation (pers. obs.).

Reproduction. The smallest mature male measured had a snout-vent length of 330 mm and the smallest mature female had a snout-vent of 310 mm (Shine, 1986: table 1).

Females with large yolking follicles have been recorded throughout the wet season (December-March) and gravid females have been recorded in the first half of the dry season (April, June)(Shine, 1986). These data suggest that the eggs may be laid during the dry season (Shine, 1986).

Clutch size. Clutch size ranges 3-14 (Brotzler, 1965; J. Bredl, in Bustard, 1970; Shine, 1986; Eidenmüller, 1991; Eidenmüller, 1995; Eidenmüller and Wicker, 1995; Polleck, 1999), with recorded means of 6.9 (n = 10, Shine, 1986) and 7.0 (n = 19, Thompson and Pianka, 2001).

There was no correlation between clutch size and snout-vent length in the one instance in which the relationship was examined ($r = 0.54$, $P > 0.05$, $n = 10$, Shine, 1986).

Occasionally, one egg may contain two (Eidenmüller and Stein, 1991; Eidenmüller, 1995) or even three (Krauss and Horn, 2004a-b) young.

Frequency of reproduction. In captivity, one female laid three clutches separated by periods of 58 and 86 days (data in Polleck, 1999).

Eggs. Measurements and weights for freshly laid eggs are summarised below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	65	5	-	28	5	-	-	-	Polleck, 1999
60-65	-	6	30	30	6	-	-	-	Eidenmüller, 1995
							41.3	15	Thompson and Pianka, 2001

Incubation. Incubation at different temperatures is given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
-	-	285-317	-	2	Eidenmüller, 1991
27-28	-	265-316	-	6	Eidenmüller, 1995; Eidenmüller and Wicker, 1995
27-28	-	285-317	-	6	Eidenmüller and Wicker, 1995
27-28	-	286-304	-	6	Eidenmüller and Wicker, 1995
27-28	-	293-327	-	7	Eidenmüller and Wicker, 1995
27-28	-	258-308	-	6	Eidenmüller and Wicker, 1995
27-28	-	229-277		8	Eidenmüller and Wicker, 1995
27-28	-	193-305		6	Eidenmüller and Wicker, 1995
27-28	-	239-306		8	Eidenmüller and Wicker, 1995
27-28	-	204-294	-	7	Eidenmüller and Wicker, 1995
28	28	191-235	218	5	Polleck, 1999
28	28	220-305	257	6	Polleck, 1999
29	29	182-202	192	3	Brotzler, 1965
30	30	193-217	205	2	Brotzler, 1965

As can be seen from the table, even at the same incubation temperature, there is a broad range of hatching times within single clutches. Indeed, one clutch of six eggs took 220-305 days to hatch (Polleck, 1999), a span of 85 days. For eggs of one clutch incubated under similar conditions, these broad ranges for single clutches seem very large and raise the question of what other factors may have influenced the incubation time. It would be especially interesting to examine the stage of embryonic development of the eggs of a single clutch at laying for possible differences in the degree of development of the eggs at deposition.

Hatchlings. Measurements and lengths of hatchlings are tabulated below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
#	#	#	252-270	264.3	4	23.6-27.9	25.7	4	#
-	122	8	-	-	-	-	26.7	8	Eidenmüller and Wicker, 1995
-	119	4	-	-	-	-	27.1	4	Eidenmüller and Wicker, 1995
-	124	8	-	-	-	-	27.5	8	Eidenmüller and Wicker, 1995
-	121	6	-	-	-	-	28.0	6	Eidenmüller and Wicker, 1995
-	122	6	-	-	-	-	28.0	6	Eidenmüller, 1995
-	125.2	15	-	180.2	9	-	29.6	14	Thompson and Pianka, 2001
-	131	6	-	-	-	-	33.0	6	Eidenmüller and Wicker, 1995
-	132	7	-	-	-	-	32.4	7	Eidenmüller and Wicker, 1995
-	125	6	-	-	-	-	30.8	6	Eidenmüller and Wicker, 1995
-	131	7	-	-	-	-	32.7	7	Eidenmüller and Wicker, 1995
-	127	6	-	-	-	-	33.6	6	Eidenmüller and Wicker, 1995
110	110	1	260	260	1	-	-	-	Polleck, 1999
100-110	104	5	240-260	248	5	-	-	-	Polleck, 1999
100-120	107	6	230-250	242	6	-	-	-	Polleck, 1999

The single surviving hatchling from an egg with two yolks measured 100 mm in snout-vent length (Eidenmüller, 1991, 1995) and 235 mm in total length (Eidenmüller, 1991). This is at the small end of the overall size range for hatchlings and suggests, not illogically, that the amount of yolk determines the size of the hatchling.

Size. An equation predicting mass (g) from snout-vent length (cm) is: $\ln \text{ mass} = 2.64 + 0.11 \ln \text{ snout-vent length}$ ($n = 14$, Shine, 1986).

The species reaches a snout-vent length of 475 mm (Storr, 1980a) and a total length of 1130 mm (Storr, 1980a).

Predators. In fleeing potential predators in captivity, the species can run bipedally, that is, on its rear legs. The trunk is held at an angle of about 45° and the front legs are held against the body (Murphy and Lamoreaux, 1978a).

When cornered, the lizard may rise up in a bipedal stance, arch the neck and extend the throat (Murphy and Lamoreaux, 1978a)>

Defence. The species usually flees to water (Shea *et al.*, 1988; Blamires, 2000) but sometimes it will flee to other forms of cover, such as rock piles (Shea *et al.*, 1988).

Parasites. The species' only known endoparasites are nematodes (round worms) (Jones, 1988).

Literature. Glauert, 1951; Mitchell, 1955 (as *V. varius* - USNM 128386); Worrell, 1956 (as *V. bulliwallah*); Mertens, 1958; Mertens, 1963; Anonymous, 1965; Brotzler, 1965; Bustard, 1970; Murphy, 1972; Cogger and Lindner, 1974; Schürer and Horn, 1976; Swanson, 1976; Murphy and Lamoreaux, 1978a; Storr, 1980a; Hermes, 1981; Shine, 1986; Jones, 1988; Losos and Green, 1988; Eidenmüller, 1990; Eidenmüller and Stein, 1991; Christian and Conley, 1994; Philippen, 1994; Eidenmüller, 1995; Eidenmüller and Wicker, 1995; Christian, Weavers, Green and Bedford, 1996; Wesiak and Irwin, 1996; Eidenmüller and Wicker, 1998; Thompson and Withers, 1998; Blamires, 1999a; Polleck, 1999; Blabbers, 2000; Frappell, Schultz and Christian, 2002.

Varanus mitchelli

Distribution.

Seasonal activity. The species is seen more frequently during the wet season than during the dry season (Shine, 1986).

Daily activity. The species is primarily diurnal (Shine, 1986: fig. 1). It occurs both on the ground and in trees (Shine, 1986).

Habitat. The species is almost always found close to water (Shine, 1986).

Diet. In the wild, the goanna eats a wide variety of both invertebrate and vertebrate prey. Invertebrate prey includes arthropods such as ants (Losos and Green, 1988), beetles (Losos and Green, 1988), caterpillars (Losos and Green, 1988), centipedes (Losos and Green, 1988), hemipterans (Losos and Green, 1988), orthopterans (Losos and Green, 1988), spiders (Losos and Green, 1988) and crustaceans such as crabs (Losos and Green, 1988). Vertebrate prey includes fish (Shine, 1986; Losos and Green, 1988), frogs (Shine, 1986; Losos and Green, 1988), reptile eggs (Shine, 1986; Losos and Green, 1988), lizards (Shine, 1986; Losos and Green, 1988), birds (Losos and Green, 1988) and mammals (Shine, 1986; Losos and Green, 1988). The diversity of the diet probably reflects the opportunistic nature of feeding in the species, and the aquatic prey such as crabs and fish reflect its semi-aquatic behaviour.

In captivity, adults eat small fish (whole or strips) and mice (Peters, 1968, 1971d).

Seasonality of reproduction. Gravid females can be found at the beginning of the dry season (April-June)(Shine, 1986), and they presumably lay their eggs during this season (Shine, 1986).

Clutch size. Clutch size ranges 7-12, with a mean of 9.8 (n = 5, Shine, 1986).

Eggs.

Incubation.

Hatchlings.

Growth.

Size at sexual maturity. The smallest mature male measured had a snout-vent length of 230 mm and the smallest mature female had a snout-vent length of 210 mm (Shine, 1986: table 1).

Size. An equation predicting mass (g) from snout-vent length (cm) is: $\ln \text{ mass} = 1.18 + 0.16 \ln \text{ snout-vent length}$ (n = 22, Shine, 1986).

The species reaches a snout-vent length of 346 mm (Peters, 1971d) and a total length of about 680 mm (Peters, 1971d).

Predators.

Defence. When fleeing a human predator, the species flees to water or to trees, or runs away (Shine, 1986).

Parasites. The species' only known endoparasites are nematodes (round worms) (Jones, 1988).

Literature. Mertens, 1958; Peters, 1968; Peters, 1969b; Peters, 1971d; Shine, 1986 a-b; Jones, 1988; Losos and Green, 1988.

Varanus panoptes

Distribution. The species occurs in two disjunct areas. The subspecies *V. p. panoptes* occurs across the northern parts of the continent from the Kimberley to northern Queensland and *V. p. rubidus* occurs in central western Western Australia. The dorsal ground colour is brownish in the former and reddish in the latter, reflecting perhaps the general substrate colours of the two areas.

The species occurs on a number of islands. In Western Australia it occurs on Dolphin Island (Storr, 1980a). In Queensland it occurs on Lizard Island; indeed, it is the "lizard" of Lizard Island.

Habitat. The species occurs in a variety of habitats including beaches (Cameron and Cogger, 1992; Blamires, 2000, 2004), beach dune grasslands (Blamires, 2004), grasslands (Shine, 1986), mangroves (Blamires, 2000), woodland (Shine, 1986; Blamires, 2000), mangroves (Blamires and Nobbs, 2000), monsoon forest (Blamires, 2000), open forest (Cameron and Cogger, 1992), riparian forest (Blamires, 2000) and vine forest (Cameron and Cogger, 1992).

In one long-term study of the goannas on and around a sea turtle nesting beach in the Northern Territory, the lizards were often found on the beach and the dunes behind the beach. However, they or their spoor were only occasionally found in nearby mangroves and salt flats and they were never found in monsoon forest (Blamires, 2004).

The species also occurs in settled areas (Cameron and Cogger, 1992).

Seasonal activity. In the Top End of the Northern Territory, the species is active year around (Blamires, 2001, 2004).

Daily activity. The species is primarily diurnal (Shine, 1986: fig. 1; Blamires and Nobbs, 2000). However, it has also been seen occasionally active in the early evening (Lyons and Frisby, 1996). Interestingly, these nocturnally active individuals sometimes seem warmer to the touch than the air temperature, perhaps demonstrating the thermal inertia of large reptiles.

Shelter sites. The goannas shelter in burrows that are presumably dug by themselves (Blamires, 2001). On one stretch of beach dune habitat in the Top End of the Northern Territory, the number of shelter burrows and the depth of the shelter burrows are positively correlated (Blamires, 2001). In other words, whatever prompts the goannas to dig shelter burrows, also seems to prompt them to dig them deeper. And what that something may be is perhaps indicated by the negative correlation between both the number and depth of the shelter burrows with both the minimum sand-surface temperature and the maximum sand temperature at 50 cm, the number of burrows peaking in mid-winter (July) (Blamires, 2001; fig. 3). In other words, it looks as if falling sand temperatures cause the goannas to dig shelter burrows more often and to dig them deeper. This may be a thermoregulatory device. During cooler weather, the goannas are digging in more often and digging in deeper, perhaps in an effort to access the higher soil temperatures at depth.

Water relations. The rate of evaporative water loss relative to body mass has been measured for a variety of different sized individuals of this species at 35° C. The equation describing the relationship is: $\log \text{ rate of evaporative water loss (mg/h)} = 0.89 \log \text{ body mass (g)} - 0.27$ (Thompson and Withers, 1997).

Diet. In the wild, the species eats a wide variety of prey including both invertebrates and vertebrates. The invertebrate prey includes arthropods such as ants (Losos and Green, 1988), beetles (Losos and Green, 1988; Blamires, 2004), centipedes (Losos and Green, 1988), hemipterans (Losos and Green, 1988), lepidopteran larvae and pupae (Losos and Green, 1988), orthopterans (Losos and Green, 1988; Blamires, 2004), roaches (Losos and Green, 1988; Blamires and Nobbs, 2000; Blamires, 2004), scorpions (Koch, 197) and trichopterans (Losos and Green, 1988) and crustaceans such as crabs (Blamires, 2004). Vertebrate prey includes fish (Shine, 1986), frogs (Losos and Green, 1988; Valentic, 1994c), sea turtle eggs and hatchlings (Blamires and Guinea, 2003; Blamires, 2004); lizards (Shine, 1986; Blamires, 2004), snakes (Shine, 1986; Blamires, 2004), reptile eggs (Shine, 1986; Blamires, 2004) and mammals (Shine, 1986; Blamires, 2004).

The species also eats carrion, e.g., dead fish (Shine, 1986; Blamires, 2004).

In captivity, the young eat small insects such as cockroaches, dead baby mice and beef heart dipped in egg yolk. The adults eat cockroaches, day old chicks, young mice and rats (Schardt, 2001a) and commercial kangaroo meat (Christian and Conley, 1994).

Foraging strategy. The goannas often dig for buried prey (Blamires, 2001).

One goanna, observed at very close range, found and ate in succession 18 buried frogs (probably *Limnodynastes ornatus*) in the mid-morning. The earth where each frog was found was indistinguishable from the surrounding earth to a human observer. This observation shows the power of a monitor's ability to find buried prey items, probably by vomerolfaction, that is, picking up scent with its tongue (Valentic, 1994c).

Male combat. The males engage in combat. This takes the form of a standing embrace (Cogger, 2000: p. 367 where the two combatants have presumably just toppled over). This form of combat is typical of the larger species of goannas.

Courtship and mating. In captivity, copulation may last 10-30 minutes (Schardt, 2001a), and females can deposit eggs within four weeks of the first copulation of the season (Schardt, 2001a).

Seasonality of reproduction. In northern Australia, females have large ovarian follicles at the end of the wet season (February) and are gravid in the early dry season (April) (Blamires and Nobbs, 2000; Shine and Sadlier, 2000). These data suggest that the eggs may be laid in the dry season.

In captivity, one female laid a single clutch each year for three successive years (Schardt, 2001a).

Clutch size. Clutch size ranges 7-13 (Shine, 1986; Blamires and Nobbs, 2000; Schardt, 2001a; Shea and Sadlier, 2001), with means of 11.0 (n = 4, data in Shine, 1986 and Shea and Sadlier, 2001).

Eggs. Measurements and weights for freshly laid eggs are summarised below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
64-72	68.4	12	37-40	38.5	12	52-60	58.2	12	Schardt, 2001a

Incubation. Incubation at different temperatures is given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
27, 29	-	197	197.0	1	Schardt, 2001a
27, 29	-	185-214	-	7	Schardt, 2001a
27, 29	-	177-202	193	10	Schardt, 2001a

Hatching. The time between the first slitting of the egg and the complete emergence of the hatchling from the egg can take up to 36 h (Schardt, 2001a).

Hatchlings. Measurements and lengths of hatchlings are tabulated below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
125-133	129	10	300-325	311	10	31-46	41.4	10	Schardt, 2001a
130	130.0	1	305	305.0	1	45	45.0	1	Schardt, 2001a
115-142	-	7	290-342	-	7	32-52	-	7	Schardt, 2001a
105-106	105.5	1	-	-	-	-	-	-	Shine, 1986

Growth.

Size at sexual maturity. In the Top End of the Northern Territory, sexual maturity is attained by a snout-vent length of 380 mm in males and 310 mm in females (Shine, 1986: table 1).

Size. The largest specimen measured is a male with a snout-vent length of 670 mm (Shine, 1986).

An equation predicting weight (g) from snout-vent length (cm) is $\ln \text{ mass} = 4.32 + 0.06 \ln \text{ snout-vent length}$ ($n = 29$; Shine, 1986).

Sex ratio. In the wild in the Top End of the Northern Territory, adult males ($n = 43$) are much more commonly encountered than adult females ($n = 10$) ($X^2 = 20.5$, $P < 0.05$) (Shine, 1986).

Predators. Juveniles are known to be preyed upon by cats (Cameron and Cogger, 1992).

Defence. When confronted by a large predator (a human), the species often stands on its rear legs and tail and looks at the predator and then usually flees by running on all four legs and sometimes accelerating to run on just the two rear legs (Blamires, 2000). It may also flee to water and swim with its legs tucked back alongside its body and tail (Blamires and Nobbs, 2000).

Parasites. The species' only known endoparasites are nematodes (round worms) (Jones, 1983, 1988, 1991).

Literature. Koch, 1970 (as *V. gouldii*); Storr, 1980a; Jones, 1983; Shine, 1986a-b; Böhme, 1988; Jones, 1988; Bedford, 1991; Böhme, 1991; Jones, 1991; Bennett, 1992; Cameron and Cogger, 1992; James, Losos and King, 1992; Thompson and Withers, 1992; Schildger, Frammer, Sporle, Gerwig and Wicker, 1993; Christian and Conley, 1994; Christian, 1995; Christian, Corbet, Green and Weavers, 1995; Christian and Weavers, 1996; Irwin, 1996; Irwin, Lyons and Frisby, 1996; Lyons and Frisby, 1996; King, 1997; Thompson and Withers, 1997; Sprackland, Smith and Strimple, 1997; Thompson and Withers, 1997; Böhme and Ziegler, 1998; Shea and Cogger, 1998; Sprackland, Smith and Strimple, 1998; Blamires, 1999; Blamires and Nobbs, 1999; Gentry, 1999; Hoser, 1999; Schardt, 1999, as *V. g. gouldii*; Schultz, Christian and Frappell, 1999; Blamires, 2000; International Commission on Zoological Nomenclature, 2000; Blamires and Nobbs, 1999; Blamires, 2001; Schardt, 2001a; Shea and Sadlier, 2001; Blamires and Guinea, 2003; Blamires, Guinea and Prince, 2003; Blamires, 2004.

Varanus pilbarensis

Distribution. The species occurs in the Pilbara area of western Western Australia.

Habitats.

Activity.

Diet. In the wild, the goannas eat arthropods such as orthopterans (Johnstone, 1983) and spiders (Losos and Greene, 1988) and vertebrates such as skinks (Losos and Greene, 1988).

In captivity, young individuals eat crickets (Eidenmüller and Langner, 1998), and adults eat cockroaches, crickets, grasshopper and beetle larvae (Eidenmüller and Langner, 1998).

Courtship and mating. A courting male may scratch the base of the female's tail with the claws of his rear foot. During mating he lies diagonally across her back (Eidenmüller and Langner, 1998: fig. 4). Copulation may last several hours (Eidenmüller and Langner, 1998).

Seasonality of reproduction.

Clutch size. Clutch size ranges 3-6 (James *et al.*, 1992; Eidenmüller and Langner, 1998; see also Retes and Bennett, 2001), with means of 2.5 (n = 2)(James *et al.*, 1992) and 4.0 (n = 6) (data in Eidenmüller and Langner, 1998).

Frequency of reproduction. In captivity, females are said to be able to produce up to six clutches in a period of 2-3 months followed by a quiescent period of 8-9 months (Retes and Bennett, 2001). Within the laying period, successive clutches are said to be separated by usually two weeks (Retes and Bennett, 2001).

The only actual data on the frequency of reproduction in captivity is from one female which for six successive clutches had inter-clutch intervals ranging 56-83 days (mean = 63.6 days, n = 5) (Eidenmüller and Langner, 1998).

Eggs. Measurements and weights for freshly laid eggs are summarised below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	20	5	-	10	5	-	-	-	Eidenmüller and Langner, 1998

Incubation. Incubation at different temperatures is given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
27	27	112-116	114.3	3	Eidenmüller and Wicker, 1997
27	27	99	99.0	1	Eidenmüller and Langner, 1998
27	27	136	136.0	1	Eidenmüller and Langner, 1998
27	27	120	120.0	1	Eidenmüller and Langner, 1998
27	27	99	99.0	1	Eidenmüller and Langner, 1998
27	27	106	106.0	1	Eidenmüller and Langner, 1998

Incubation is also said to take between 65-80 days (Retes and Bennett, 2001).

Hatchlings. Measurements and weights for hatchlings are summarised in the following table.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
47-52	50.0	3	125-127	126.0	3	1.8-2.3	2.1	3	Eidenmüller and Langner, 1998

52	52.0	1	136	136.0	1	2.3	2.3	1	Eidenmüller and Langner, 1998
55	55.0	1	141	141.0	1	2.9	2.9	1	Eidenmüller and Langner, 1998
57	57.0	1	151	151.0	1	2.9	2.9	1	Eidenmüller and Langner, 1998
59	59.0	1	151	151.0	1	2.9	2.9	1	Eidenmüller and Langner, 1998
59	59.0	1	151	151.0	1	3.1	3.1	1	Eidenmüller and Langner, 1998
-	-	-	-	c. 130	-	-	-	-	Retes and Bennett, 2001

Growth. In captivity, young lizards are said to be able to reach sexual maturity at an age as early as eight months (Retes and Bennett, 2001).

Maximum size. The species reaches a snout-vent length of 169 mm and a total length of about 470 mm (Storr, 1980a).

Predators.

Parasites.

Literature. Storr, 1980a; Johnstone, 1983; Losos and Green, 1988; James, Losos and King, 1992; Pianka, 1995; Eidenmüller and Langner, 1998; Retes and Bennett, 2001.

Varanus prasinus

Distribution. In Australia, the species is known from only a few islands in the Torres Strait, i.e., Boigu (Clarke, 2004), Duan, Mer (Günther, 1877, 1879; Boulenger, 1885) and Moa (Whittier and Moeller, 1993; Wilson, 1996; Wilson and Swan, 2003).

Habitats. The species occurs in mangrove forest (Clarke, 2004).

Seasonal activity.

Daily activity. The species is active in the open during the day (Clarke, 2004) and is arboreal (Clarke, 2004).

Thermal relations. The species has been described as basking (Clarke, 2004).

Shelter sites.

Diet.

Seasonality of reproduction.

Predators.

Parasites.

Literature. Günther, 1877; Günther, 1879; Boulenger, 1885; Whittier and Moeller, 1993; Wilson, 1996; Clarke, 2004.

Varanus primordius

Distribution. The species occurs in the interior regions of the Top End of the Northern Territory.

Habitats.

Daily activity. To the extent that the species is observed on the surface, it seems to be diurnal (Husband, 2001a-b).

Shelter sites. The species sometimes shelters under building debris that are usually well embedded in the substrate (Husband, 2001a-b).

Thermoregulation. The species basks (Husband, 2001a-b). Gravid females especially seem to increase their basking time (Husband, 2001a-b).

Agonistic behaviour. In captivity, males will fight severely (Husband, 2001a-b).

Diet. In the wild, the goannas eat a variety of invertebrates including ants (Losos and Green, 1988), centipedes (Husband, 2001a-b), cockroaches (Husband, 2001a-b; Losos and Green, 1988), crickets (Husband, 2001a-b), neuropteran larvae and orthopterans (Losos and Green, 1988). They also eat vertebrates such as squamate eggs (Losos and Greene, 1988) and lizards (Losos and Green, 1988; Husband, 2001a-b).

In captivity, both juveniles and adults eat invertebrates such as crickets and cockroaches (Husband, 2001a-b).

Courtship and mating. In captivity, courting males display “fast jerky head movements and vigorous tongue flicking” while pursuing females (Husband, 2001a-b).

In captivity, the time between mating and egg-laying ranges 14-21 days (Husband, 2001a-b).

Seasonality of reproduction.

Nesting. Prior to egg-laying, the female may dig several “test” holes (Husband, 2001a-b). Females usually lay their eggs in the “late evening” (Husband, 2001a-b).

Clutch size. In captivity, clutch size ranges 2-5 (mean = 3.4) (n = 8) (Husband, 2001a-b).

Eggs. Measurements and weights for freshly laid eggs are summarised below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
18.0-19.0	18.6	4	10.5-11.0	10.8	4	1.3	1.3	4	Husband, 2001a-b
19.5-20.5	19.9	5	11.0-13.0	12.2	5	1.6-1.8	1.7	5	Husband, 2001a-b
20.0-20.5	20.3		10.5-11.0	10.9	4	1.4-1.5	1.7	4	Husband, 2001a-b
21.0	21.0	2	12.0-12.5	12.3	2	1.7	1.7	2	Husband, 2001a-b
20.0	20.0	3	10.0	10.0	3	1.8-1.9	1.9	3	Husband, 2001a-b
25.0	25.0	2	12.5	12.5	2	2.2	2.2	2	Husband, 2001a-b

24.0-25.0	24.5	2	12.5-13.0	12.7	2	2.2-2.4	2.3	2	Husband, 2001a-b
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Incubation. Incubation at different temperatures is given in the following table.

Incubation Temperature (°C)			Incubation Period (Days)			Reference		
Range	Mean		Range	Mean	N			
28.5-30	-		121	121.0	2	Husband, 2001a-b		
28.5-30	-		95-103	99.0	2	Husband, 2001a-b		
28.5-30	-		86-88	-	4	Husband, 2001a-b		
28.5-30	-		132-133	-	4	Husband, 2001a-b		

Hatchlings. Measurements and weights for hatchlings are summarised below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
41	41.0	2	95-98	96.5	2	1.0-1.5	1.3	2	Husband, 2001a-b
41-44	42.3	4	93-99	96.0	4	1.2-1.5	1.3	4	Husband, 2001a-b
41-45	42.7	4	90-100	96.5	4	1.2-1.4	1.3	4	Husband, 2001a-b
47-48	47.5	2	106.6-112	109.3	2	2.0-2.1	2.0	2	Husband, 2001a-b
49-50	49.5	2	108.5-116	112.3	2	2.0-2.3	2.1	2	Husband, 2001a-b

Maximum size. The largest measured male and specimen had a snout-vent length of 119 mm. The largest measured female had a snout-vent length of 111 mm. The male weighed 32.8 g and the female weighed 24.8 g; however, both specimens were captive, so it is not clear how their weight might compare to individuals in the wild (Husband, 2001a-b).

Predators.

Parasites.

Literature. Mertens, 1942a-b, d; Mertens, 1958b; Mertens, 1963; Storr, 1966b; Losos and Green, 1988; James, Losos and King, 1992; Bedford and Christian, 1996; Husband, 2001a-b.

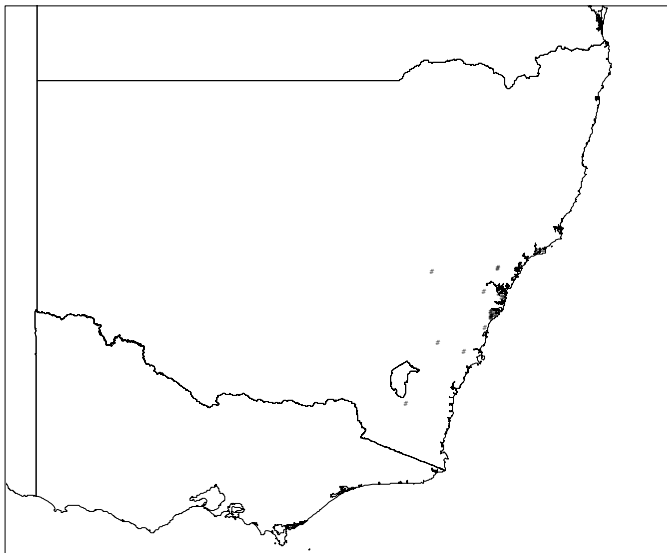
Varanus rosenbergi

Rosenberg's Goanna

Distribution. The species is disjunctly across southern Australia.

It occurs on a number of different islands throughout its range. In South Australia it occurs on Boston I., Finders I., Kangaroo I. (Storr, 1980a), Louth I., Reevesby I. (Tubb, 1938), Spilsby I., St Peter I., Taylor I. and Thistle I. (Mirtschin and Jenkins, 1985; Robinson *et al.*, 1985; Schwaner, 1985). However, the goannas indigenous versus introduced status is in dispute for all except Kangaroo I. and Thistle I., where the populations are agreed to be natural. The goannas may have been introduced on the other islands in the belief that they would eat the island's snakes.

The distribution in New South Wales, based on voucher specimens in the collections of the Australian Museum, is shown in the accompanying map.



Habitats. The species occurs in open grassy areas with light vegetative cover (Green and King, 1978), sand ridges with light vegetative cover (Green and King, 1978), heath (Maryan and Robinson, 1987b) and open woodland with a heath understorey (Watharow, 1998b).

Seasonal activity. On Kangaroo Island, one of the southernmost localities for the species, the animals are active all year around; that is, they are active not only in spring, summer and autumn but also in winter on suitable days (Green and

King, 1978; King, 1980). However, the animals may move away from open areas during winter (Green and King, 1978; King, 1980).

The metabolic rate in animals from Kangaroo Island varies with the season. The standard metabolic rate under standard conditions (35° C) is significantly higher in summer than in autumn and significantly higher in autumn than in winter (Christian and Conley, 1994). In general, the baseline metabolic rate appears to be tracking the actual activity levels of the animals.

Daily activity. The species is primarily diurnal (king, 1980). However, some activities such as digging nesting holes may extend into the early night (Ehmann *et al.*, 1991).

It is semi-arboreal (Watharow, 1998b).

Home ranges overlap considerably, suggesting that the animals are not territorial (Green and King, 1978).

Shelter sites. On Kangaroo Island, the species shelters in burrows (Green, 1972b; King, 1977; Green and King, 1978) that they dig themselves (King, 1980). And as might be expected, the temperature in the burrows is less variable than the ambient air temperature (Greer, 1972b: fig. 1).

The mean depths of the burrows inhabited are significantly shallower in summer (137.1 m, n = 15) than in winter (180.0, n = 22)(King, 1980).

Different animals may use the same burrow on different nights, and sometimes two animals may occur in the same burrow (Green and King, 1978).

Thermal relations. On Kangaroo Island, the body temperatures of goannas active between mid-spring and early autumn (November-April) ranged 32.4-37.6° C with a mean of 35.1° C (n = 14)(King, 1980). And at Dunsborough, southwestern Western Australia, the body temperatures of goannas active in late spring (November-December) ranged 35.2-37.4° C with a mean of 36.4° C (King, 1980). In general, body temperatures of active goannas are higher in summer than in winter (King, 1980).

The species basks (Maryan and Robinson, 1987b).

Water relations. The mean water content by mass of this species has been measured as 73.0 percent (n = 44/?, sd = 4.1); Green *et al.*, 1991).

In the wild, the rate of water loss in the four seasons is in the order summer > spring > autumn > winter (Green, 1972b). This is order is to be expected given that water loss is a function of the lizards body temperature and activity as well as the seasonal temperature and humidity.

The rate of evaporative water loss relative to body mass has been measured for a variety of different sized individuals of this species at 30° C (Green, 1969) and 35° C Thompson and Withers, 1997). The equation describing the relationship at 35° C is: log rate of evaporative water loss (mg/h) = 1.32 log body mass (g) – 1.37 (Thompson and Withers, 1997).

Within any lizard species, the eye is relatively smaller in small individuals than it is in large individuals. As a consequence, the moist cornea of the eye loses proportionally more water in smaller individual than in larger individuals. This difference has been measured in this goanna. Water loss from the eye represents 64.9 percent of total evaporative water loss in an immature individual (15 g) but only 16.7 percent a mature individual (Green, 1969, as cited in Thompson and Withers, 1997).

Diet. The species eats a variety of both invertebrate and vertebrate prey. Invertebrate prey include arthropods such as beetles (King and Green, 1979; Losos and Green, 1988), centipedes (Losos and Green, 1988), chilopods (King and Green, 1979); cockroaches (King and Green, 1979; Watharow, 1998b; Watharow, 1998b), lepidopterans (Losos and Green, 1988), mantids (Losos and Green, 1988), orthopterans (Losos and Green, 1988), scorpions (King and Green, 1979; Losos and Green, 1988) and spiders (King and Green, 1979; Watharow, 1998b) and crustaceans such as crabs (Losos and Green, 1988) and isopods (Losos and Green, 1988). Vertebrate prey includes frogs (King and Green, 1979; Losos and Green, 1988), squamate eggs (King and Green, 1979; Losos and Green, 1988), lizards (Rose,

1974; King and Green, 1979; Watharow, 1998b), birds (King and Green, 1979; Losos and Green, 1988) and small mammals (King and Green, 1979; Overton, 1987; Losos and Green, 1988).

The species also eats carrion (Losos and Green, 1988; Watharow, 1998b).

In captivity, the goannas can be maintained on a diet of commercial kangaroo meat (Christian and Conley, 1994).

Courtship and mating. On Kangaroo Island, mating has been observed in early summer (4-5 January) (King and Green, 1979).

Seasonality of reproduction. On Kangaroo Islands, females have only small follicles in late autumn and early spring (May-October) but one female had oviducal eggs in mid-summer (February) (King and Green, 1979).

On Kangaroo Island, a female was seen digging a nest in mid-summer (21 February) (King and Green, 1979). In the Sydney area, females digging into termite mounds, presumably to lay their eggs, have been observed twice, both times in late summer (mid-February and early March).

Clutch size. The clutch size ranges 3-19 (King and Green, 1979; Ehmann *et al.*, 1991), with recorded mean of 15.3 (n = 4; King and Green, 1979).

Nesting. Females often lay their eggs in active termite mounds situated on the ground (King and Green, 1979; Ehmann *et al.*, 1991; King and Green, 1999; Vincent and Wilson, 1999; Gaikhorst, 2002; fig. 1). The termites seal off the breached mound and hence enclose the eggs for the duration of their incubation. The termite mound presumably provides physical protection for the eggs (the termites seem to ignore the eggs) as well as a constant warm temperature and high humidity that would seem to be the ideal environment for the incubation of eggs.

In the Sydney area, females digging into termite mounds, presumably to lay their eggs, have been observed twice. The digging took two to three days and continued into the night until at least 2200 h. On both occasions, the female doing the digging was accompanied in the vicinity by a slightly larger and more wary individual of undetermined sex. In both instances, the two goannas stayed around the termite mound for two to five weeks (Ehmann *et al.*, 1991).

The goannas dig through the hard outer layer of the termite mound and into the soft, flaky inner core where the termites live (Ehmann *et al.*, 1991). Probes placed into a mound near the freshly laid eggs showed that the temperature varied from 33.3° to 38.6° C (mean = 36.2° C) and the relative humidity was never lower than 92 percent (Ehmann *et al.*, 1991).

The observation of old dead eggs in different stages of decomposition in termite mounds suggests that the same mound may be used on more than one occasion (Ehmann *et al.*, 1991).

The only termite mounds the goanna has been observed using are those of *Nasutitermes*, specifically *N. exitiosus* on the east coast, the same genus as used by the sympatric *Varanus varius*.

Eggs. Dimensions of fertile eggs are shown in the table below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	-	-	-	-	-	-	25.6	3	Green <i>et al.</i> , 1991

The egg shell comprises 2.64-2.88 percent (mean = 2.80, n = 3) of the egg's total mass (Green *et al.*, 1991), and 66.7-71.1 percent (mean = 68.6, n = 3) of the egg's content consists of water (Green *et al.*, 1991).

The eggs expand after being laid, presumably through the uptake of water from the substrate (Ehmann *et al.*, 1991).

Hatchlings.

Growth. The smallest gravid female specimen recorded had a snout-vent length of 255 mm (Case and Schwaner, 1993); hence this can be taken as the best estimate of the minimum size at maturity.

Size. The snout-vent length of the largest measured specimen was about 489 mm (Case and Schwaner, 1993: table 3).

Sex ratio. On Kangaroo Island, out of a total of 45 specimens collected initially without regard to their sex but subsequently sexed on the basis of the gonad, 37 proved to be males and 8 females (King and Green, 1979). This is a significant bias in favour of males ($X^2 = 18.7$, $P < 0.0001$)(see also Case and Schwaner, 1993).

On the mainland, the difference between the number of males (26) and females (10) was just on statistical significance ($P = 0.05$)(Case and Schwaner, 1993).

Predators.

Parasites. The species' recorded endoparasites are nematodes (round worms)(Johnson and Mawson, 1941; Jones, 1983).

Conservation status.

Literature. Tubb, 1938; Johnston and Mawson, 1941 (as *V. varius* from Kangaroo Island); Mertens, 1958; Green, 1969; Green, 1972b (Flinders Chase, Kangaroo Island study site; Calperum mainland study site = *V. gouldii*; King, 1977; Green and King, 1978; King and Green, 1979; King, 1980; Storr, 1980a; Saint-Girons, Rice and Bradshaw, 1981; Jones, 1983; Mirtschin and Jenkins, 1985; Robinson, Mirtschin, Copley, Canty and Jenkins, 1985; Schwaner, 1985; Maryan and Robinson, 1987b; Overton, 1987; Losos and Green, 1988; Dryden, Green, King and Losos, 1990; Ehmann, Swan, Swan and Smith, 1991; Green, Dryden and Dryden, 1991; Case and Schwaner, 1993; Christian and Conley, 1994; Christian

and Weavers, 1994; Shea, 1994; Belan and Bull, 1995; Christian and Weavers, 1996; Thompson and Withers, 1997; Watharow, 1998; Green, McKelvey and Rismiller, 1999; Rismiller and McKelvey, 2000; Twigg, Kok, Kirkpatrick, Winifred and Burrow, 2001; Gaikhorst, 2002.

Varanus scalaris

Distribution. The species is widely distributed across the northern part of Australia from the vicinity of Broome, Western Australia to Mackay, Queensland. It also occurs on islands in the Torres Strait and in southern New Guinea opposite Cape York.

Habitat. The species occurs in woodland (Sweet, 1999; Blamires, 2000), savanna woodland (Christian and Bedford, 1996), savanna woodland with an acacia shrub understorey (Christian *et al.*, 1996), melaleuca woodland with dense speargrass understorey (Valentic, 1996a) and monsoon forest (Blamires, 2000).

Seasonal activity. Although the species is seen more frequently during the wet season than during the dry season (Shine, 1986), it is active year around (Christian and Bedford, 1996; Christian *et al.*, 1996).

Most measures of the species' metabolic rate, that is, standard, resting and field metabolic rates, are significantly lower during the dry season than during the wet season (Christian *et al.*, 1996). The mean differences for the standard and the field rates were 47.5 and 47 percent, respectively. However, maximum metabolic rates, as determined from lizards running on a treadmill, were not significantly different between the dry and wet season (Christian *et al.*, 1996).

The lizards' aerobic scope, that is, the difference between maximum and standard metabolic rates was 20 (Christian *et al.*, 1996). Varanids as a group have high metabolic scopes, which mean they can maintain much higher levels of constant activity, as opposed to bursts of activity, than can other lizards.

Daily activity. The species is primarily diurnal (Shine, 1986; Christian *et al.*, 1996) and is active on both on the ground (Christian *et al.*, 1996) and off the ground in woody vegetation (Shine, 1986; Christian *et al.*, 1996) or derivatives of such vegetation, such as fence posts (Christian *et al.*, 1996).

In captivity, the species is said to remain "very shy" even after being in confinement for a long time (Peters, 1969d).

Thermal biology. The body temperature of the species differs between the dry (cool) and wet (warm) seasons. The mean body temperatures in the field at pre-dawn, morning, midday and late afternoon were 18.5, 24.7, 35.6 and 34.1° C, respectively, in the dry season and 21.7, 33.7, 38.9 and 33.7° C, respectively, in the wet season. For each time period, the differences were significantly lower in the dry season than in the wet season except for the late afternoon period (Christian and Bedford, 1996). Other data also indicate that during the warmest part of the day, that is, between about 12 noon and 1700 h, the mean body temperature of active animals is lower in dry season (35.6° C) than in the wet season (37.7° C) (Christian *et al.*, 1996). The lower morning and midday temperatures, especially, the latter, during the dry season may be due to a behavioural change in the lizards, as the environmental temperatures available to them do not seem to be limiting (Christian and Bedford, 1996).

Shelter sites. The species shelters in holes and hollows in wood, such as trees and fence posts (Christian and Bedford, 1996; Valentic, 1996a).

Agonistic behaviour. Agonistic interaction between two captive males is said to have been similar to another species but not actually described (Horn, 1985). The interaction in the other species involved two animals lining up sideways head to tail and displaying with neck bent, gular area extended, back arched and legs extended stilt like.

In captivity, one male drove away two other males and a female at feeding time (Chippendale, 1991).

Diet. In the wild, the species eats arthropods such as orthopterans and scorpions and vertebrates such as skinks (Losos and Green, 1988; see also Christian *et al.*, 1996).

In captivity, the goannas eat insects (Peters, 1969d) such as crickets (Chippendale, 1991; Eidenmüller and Wicker, 1991) and earthworms (Chippendale, 1991). They also eat vertebrates such as fish (Peters, 1969d), frogs (Peters, 1969d; Chippendale, 1991), lizards (Peters, 1969d), raw egg (Peters, 1969d), young mice (Peters, 1969d; Chippendale, 1991), meat (Peters, 1969d) and canned dog food (Chippendale, 1991).

Foraging behaviour. The goannas move around in a manner that suggests they forage actively (Christian *et al.*, 1996) instead of relying on ambush.

In captivity, gravid females may continue feeding normally up until the day of egg laying (Chippendale, 1991).

Courtship and mating. In captivity, mating occurs only during a six week period, and in this period, mating between the same two animals may occur several times a day (Chippendale, 1991).

Seasonality of reproduction.

Frequency of reproduction. In captivity, one female laid two clutches of eggs separated by an interval of 85 days. However, the second clutch consisted of only one egg (Eidenmüller and Wicker, 1991).

Clutch size. Clutch size ranges 1-6 (Chippendale, 1991; Eidenmüller and Wicker, 1991).

Nests. In captivity, the eggs are laid in dry soil and loosely covered (Chippendale, 1991).

Eggs.

Incubation. Incubation periods at different temperatures are given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
#	#	139-140	#	#	Rüegg, 1974
27-28	27.5	134	134	1	Eidenmüller and Wicker, 1991
27-28	27.5	132-136	134.0	2	Eidenmüller and Wicker, 1991
28-30	-	121-122	121.5	2	Chippendale, 1991
28-30	-	136-140	138.0	2	Chippendale, 1991

29	29.0	114-116	-	-	Broer and Horn, 1985
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Hatchlings. Measurements and weights for the hatchlings are summarised below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
57-62	59.5	2	148	148.0	2	3.1-3.2	3.15	2	Eidenmüller and Wicker, 1991
57-63	60.0	2	144-159	151.5	2	4.1-4.2	4.15	2	Chippendale, 1991 ¹
65	65.0	1	175	175.0	1	5.0	5.0	1	Eidenmüller and Wicker, 1991
63-70	66.5	2	153-162	157.5	2	5.3	5.3	1	Chippendale, 1991 ¹

1. Total length data based on the assumption that the total length data in original paper was in fact tail length data.

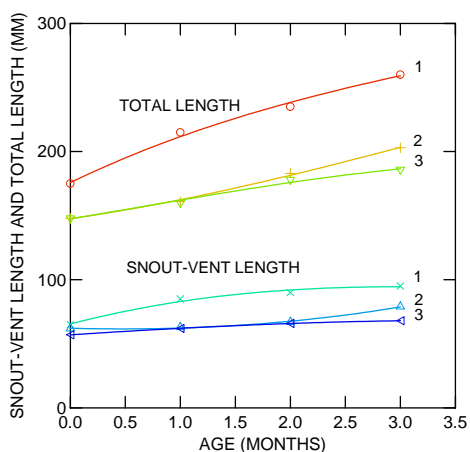
In captivity, hatchlings may begin feeding within 3-6 days (Chippendale, 1991; Eidenmüller and Wicker, 1991).

Growth. In captivity under uniform conditions throughout the observation period, the fastest growth rates over three months (calculated here as 91.5 d) for three hatchlings were: 0.33 mm/d for snout-vent length, 0.93 mm/d for total length and 0.10 g/d for weight (data in Eidenmüller and Wicker, 1991: table 1).

Similar data for four hatchlings also kept under uniform conditions were: 0.10 mm/d in snout-vent length (over 790 days), 0.27 mm/d in total length and 0.037 g/d (over 1189 days) (data in Chippendale, 1991, based on the most conservative estimate of the time period over which the data were gathered and on the assumption that the data for total length was really for tail length). The two sets of data together demonstrate the well-known result of fastest growth rates at younger ages.

Maximum size. The species reaches a snout-vent length of 253 mm and a total length of about 590 mm (Storr, 198-0a).

Allometry. A plot of growth in total length and snout-vent length for three hatchlings during the first three months of life (see graph) suggests that the tail grows at a faster rate than the snout-vent length; that is, it is in positive allometry to the snout-vent length (data in Eidenmüller and Wicker, 1991).



Predators.

Parasites. The only endoparasites recorded for the species are nematodes (round worms)(Jones, 1988).

Literature. Mertens, 1941; Mertens, 1950; Mertens, 1958 (as *V. (Odatia) timorensis similis*); Peters, 1969d (as *V. timorensis similis*); Schmida, 1971(*V. timorensis similis*); Rüeegg, 1973; Rüeegg, 1974 (as

V. timorensis similis); Broer and Horn, 1985 (as *V. timorensis similis*); Horn, 1985 (as *V. timorensis similis*); Jones, 1988; Losos and Green, 1988; Eidenmüller and Wicker, 1991; Cameron and Cogger, 1992 (as *V. timorensis*); Tidemann, Palmer, Boyden and Hunt, 1992; Bedford and Griffiths, 1995; Pianka, 1995; Christian and Bedford, 1996; Christian, Green, Bedford and Newgrain, 1996; Valentic, 1996a (as *V. timorensis similis*); Sweet, 1999; Blamires, 2000.

Varanus semiremex

Distribution.

Habitats. The species occurs in mangrove forests (Peters, 1969d) and melaleuca swamps (P. Reeders, in Cameron and Cogger, 1992).

Activity. In captivity, the species may soak for several hours in its water dish, especially before shedding (Peters, 1969d). But how this may relate to the species' habits in the wild is unclear.

Shelter sites. In the wild during the day, the species has been seen in cavities in dead branches of mangroves (Peters, 1969d).

Thermoregulation. The species has been reported to bask, both in the wild (P. Reeders, in Cameron and Cogger, 1992) and in captivity (Peters, 1969d).

Diet. Food items found in the stomachs of museum specimens, and hence presumably taken by the animals in the wild, include only crabs (Losos and Green, 1988) and frogs (Losos and Greene, 1988).

In captivity, the species eats insects, geckos (Polleck, 1982), eggs (presumably of birds) (Peters, 1969d), young birds (Peters, 1969d), mice (Peters, 1969d; Polleck, 1982) and pieces of meat (Polleck, 1982).

Male combat. In captivity, males engage in combat (Horn, 1985). In the initial phase, the two individuals face off head to tail with heads bent down, throats extended, backs raised, sides flattened and legs held stilt-like. They move slowly closer to each other such that one individual occasionally touches the flank of the other, but without biting. If one individual breaks from this encounter and "flees", it is followed by the other individual much as a female is followed by a courting male. The dominant, pursuing male overtakes the subservient male and grasps him around the pelvis with the rear leg. The two individuals then turn belly to belly with the subservient male grasping the dominant male around the body with both front and rear legs. The dominant individual may bite the subordinate individual. Sometimes the two individuals separate anteriorly, but maintain the grip at the pelvis. The bout ends with the two animals suddenly separating.

Seasonality of reproduction. A female measuring 230 mm in snout-vent length was carrying two eggs, presumably oviducal eggs and not ovarian "eggs", in mid spring (November) (James *et al.*, 1992).

Clutch size. The only recorded clutch size is two (James *et al.*, 1992).

Eggs.

Incubation.

Hatchlings.

Growth.

Maximum size. The snout-vent length of the largest measured male (and specimen) was 272 mm and the largest measured female 255 mm (James *et al.*, 1992).

Predators.

Parasites.

Literature. Peters, 1869; Kinghorn, 1923; Mertens, 1961; Stettler, 1966; U. Peters, 1969d; Dunson, 1974; Friend and Russell, 1979; Polleck, 1980b; Polleck, 1982; Horn, 1985; Losos and Greene, 1988; Cameron and Cogger, 1992; James, Losos and King, 1992.

Varanus spenceri
Spencer's Monitor

Distribution.

Habitat. The species is found primarily on tussock grasslands growing on blacksoil plains (Pengilley, 1981; Valentic, 1995).

Daily activity. The species is primarily diurnal, but a record of one specimen out on a warmish (23° C) night in heavy rain showers suggests that it may be also occasionally be active after dark (Valentic, 1995).

Shelter sites. The species may shelter in burrows. One female was seen entering a burrow about 30 minutes before sunset (Pengilley, 1981). It is not clear if the goannas dig their own shelter burrows or use burrows made by other animals.

Diet. In the wild, the goanna eats a variety of both invertebrate and vertebrate prey. Invertebrates include arthropods such as cockroaches (Valentic and Turner, 1997), isopods (Pengilley, 1981), grasshoppers (Pengilley, 1981) and orthopterans in general (Losos and Green, 1988) and crustaceans such as crabs (Losos and Green, 1988). Vertebrates include dragons (Pengilley, 1981; Valentic and Turner, 1997), skinks (Valentic and Turner, 1997), snakes (Pengilley, 1981) and mammals (Pengilley, 1981).

In captivity, hatchlings eat meal worms and baby mice (Peters, 1969c); juveniles eat insects (Peters, 1970), raw eggs (Peters, 1969c; Peters, 1970) and heart (Peters, 1969c; Peters, 1970), and adults eat mice and rats (Peters, 1968; Peters, 1970).

Reproduction. Females are gravid in early spring (late September to early October) (n = 15) (Pengilley, 1981; Valentic and Turner, 1997).

Clutch size. Clutch size ranges 11-31 (Peters, 1969c; Pengilley, 1981; Valentic and Turner, 1997; Thompson and Pianka, 2001), with recorded means of 18.7 (n = 13, Pengilley, 1981) and 19.3 (n = 10, Thompson and Pianka, 2001).

Data on female snout-vent length and clutch size are given in the following table.

Female Snout-vent Length (mm)	Clutch Size	Reference
435	13	Valentic and Turner, 1997

There is a significant positive relationship between female snout-vent length and clutch size ($r^2 = 0.79$, n = 13, $P < 0.01$; Pengilley, 1981 and $r^2 = 0.81$, n = 10, $P < 0.01$; Thompson and Pianka, 2001).

Eggs. Dimensions of fertile eggs are shown in the table below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
47.3-49.6	47.8	5	30.0-31.0	30.6	5	-	-	-	Pengilley, 1981
-	52	18	-	36	18	-	-	-	Peters, 1969c

Incubation. Incubation at different temperatures is given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
29.5	29.5	123-130	-	11	Peters, 1969c

Hatchlings. Measurements and weights for the hatchlings are summarised below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
124	124	1	222	222	1	-	-	-	Peters, 1969c

Growth. Growth rates in captivity can be remarkably variable. For example, at two years of age, total length among four individuals from the same clutch ranged 350-501 mm (Peters, 1970). Presumably, all four individuals would have been raised under the same, good conditions.

Predators.

Parasites. The species' only recorded ectoparasites are ticks (Valentic and Turner, 1997). Its recorded endoparasites include nematodes in the digestive track (Valentic and Turner, 1997).

Literature. Lucas and Frost, 1903; Peters, 1968; Peters 1969c; Peters, 1970; Peters, 1971; Christian, 1979; Horn, 1981; Pengilley, 1981; Peters, 1986; Losos and Green, 1988; Green and King, 1993; Valentic, 1995; Valentic and Turner, 1997; Schultz, Christian and Frappell, 1999.

Varanus storri

Distribution.

Habitats. The species has been found in grasslands (Peters, 1973a) and open mixed eucalypt woodland with open grassland patches on clay soil (McAlpin, 2000).

Seasonal activity.

Daily activity. The goannas are active on the surface during the day; at night, they shelter in burrows (Peters, 1973a).

In captivity, individuals changed colour in response to temperature change and in interactions with individuals of their own or other species. In terms of temperature, the goannas were greyish under cool conditions but turned a vivid, rusty-orange dorsally under warm conditions (35° C) (Sprackland, 1980).

Shelter sites. The species digs its own shelter burrows in captivity (Bartlett, 1982). Hence it seems likely that the burrows the animals use in the wild (Peters, 1973a; McAlpin, 2000) are also dug by them and not another animal.

The burrows are often, if not always, under rocks (Peters, 1969d, 1973a; McAlpin, 2000) and are said to be U-shaped (Peters, 1973a).

Agonistic behaviour. In captivity, both males (M. Vincent, in Husband, 2001) and females (Eidenmüller and Horn, 1985) will fight severely. Females may also attack males, but then subsequently mate with them (Flugi, 1990).

In a "small piece of grassland in the wild, 22 individuals consisting of 13 males, seven females and two juveniles were found in their "respective" burrows (Peters, 1973a). This separation in a small area suggests that the animals may not tolerate each other's immediate presence.

However, at the same time, the presence of a large number of individuals in a small area suggests that the animals may live in loose social groups (Peters, 1973a).

Diet. The stomach contents of museum specimens included arthropods such as ants (Losos and Green, 1988; James *et al.*, 1992), beetles (Losos and Green, 1988; James *et al.*, 1992), centipedes (Losos and Green, 1988), chilopods (James *et al.*, 1992), lepidopteran larvae (Losos and Green, 1988; James *et al.*, 1992), neuropteran larvae (James *et al.*, 1992), orthopterans (Losos and Green, 1988; James *et al.*, 1992), roaches (James *et al.*, 1992), spiders (Losos and Green, 1988; James *et al.*, 1992) and termites (James *et al.*, 1992) and vertebrates such as lizards (James *et al.*, 1992). In one study, orthopterans accounted for 47.2 percent of all the items (n = 53) eaten (James *et al.*, 1992).

In captivity, adults eat crickets (Sprackland, 1980; Flugi, 1990), mealworms (Peters, 1969d), egg yolk (Flugi, 1990), fish strips (Peters, 1969d), lizards (Peters, 1969d; Sprackland, 1980), baby mice (Flugi, 1990), red meat strips (Peters, 1969d) and dog food (Flugi, 1990).

Courtship and mating. Mating as observed in captivity involves the male biting and holding the female on the neck and scratching her inguinal region (Peters, 1969d). In some cases at least, the male also lies diagonally across the back of the female (Eidenmüller and Horn, 1985). Copulations can last 30-50 minutes (Peters, 1969d).

Seasonality of reproduction. In northern Queensland, females are gravid in early spring (late September)(Peters, 1973a).

Clutch size. Clutch size ranges 1-6 eggs (James *et al.*, 1992; Eidenmüller and Horn, 1985), with recorded means of 3.9 (n = 7)(James *et al.*, 1992).

There is a significant positive association between female snout-vent length and clutch size ($r^2 = 0.58$, $P = 0.05$; James *et al.*, 1992).

Frequency of reproduction. In captivity, one female produced two clutches in a period of 111 days (Eidenmüller and Horn, 1985).

Eggs. Dimensions of fertile eggs are shown in the table below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
29-32	30.5	2	19	19.0	2	-	-	-	Eidenmüller and Horn, 1985

The mean dimensions of 8 x 6 mm given in one report (Flugi, 1990) are clearly too small and represent more than a simple order of magnitude type error.

Incubation. Incubation at different temperatures is given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
22-28	-	117	117.0	2	Flugi, 1990
24-31	-	105	105.0	2	Flugi, 1990
22-29	28.0	105-107	106.0	2	Eidenmüller and Horn, 1985
22-29	28.0	109-112	111.0	3	Eidenmüller and Horn, 1985
28.5-29.5	29.0	103	103.0	2	Eidenmüller and Horn, 1985
29	29.0	102-103	-	-	Broer and Horn, 1985
#	#	102-103	102.5	2	Eidenmüller and Horn, 1985
#	#	#	72	#	Rese, 1984

Hatchlings. Measurements and weights for hatchlings are summarised below.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	-	-	133-137	135.0	2	2.0-2.3	2.1	2	Eidenmüller and Horn, 1985

-	-	-	110	110.0	1	3.5	3.5	1	Flugi, 1990
-	-	-	125-133	129.0	2	4	4.0	2	Flugi, 1990
-	-	-	117-125	121.0	3	4.8-5.3	5.1	3	Eidenmüller and Horn, 1985
-	-	-	126-130	128.0	2	7.1-7.4	7.3	2	Eidenmüller and Horn, 1985
57	57.0	1	133	133.0	1	-	-	-	Bartlett, 1982

Note the more than threefold difference in weight of the largest (7.4 g) and smallest (2.0 g) hatchling, especially given the greater total length of the smaller hatchling.

Maximum size. The largest total length measured for the species is 440 mm for a male from Queensland (Peters, 1969d).

Sexual dimorphism. Based on adult specimens in museum collections, the mean snout-vent length of males (110.4 mm, sd = 14.1, n = 27) and females (110.5 mm, sd = 11.3, n = 11) is not significantly different ($t = 0.02$, $P = 0.98$)(data in James *et al.*, 1992).

Predators.

Defence. In captivity, an individual vibrated the tip of the tail when confronted by a human hand, another lizard or large prey item. On substrates, this resulted in an audible “buzz”. And when grasped on the body, the tail was brought forward and the spiny tail raked across the hand (Sprackland, 1980).

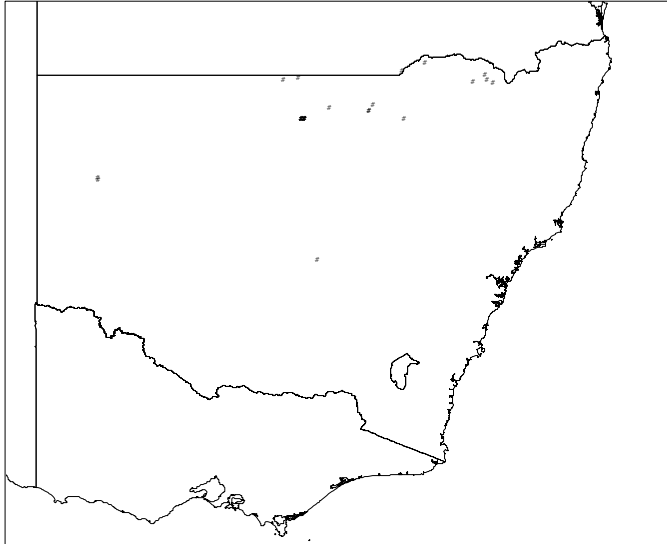
Parasites. The species' only known endoparasites are nematodes (round worms) (Jones, 1988, 1991).

Literature. Zietz, 1914; Mertens, 1942, 1963, 1966; Mudrack, 1969; Peters, 1969d; Peters, 1973a-b; Sprackland, 1980; Storr, 1980a; Stirnberg and Horn, 1981; Bartlett, 1981c; Bartlett, 1982; Broer and Horn, 1985; Eidenmüller and Horn, 1985; Rese, 1986; Jones, 1988; Losos and Green, 1988; Flugi, 1990; Jones, 1991; James, Losos and King, 1992; Eidenmüller, 1994; McAlpin, 2000.

Varanus tristis

Distribution. The species is widespread through northern and central Australia.

The distribution in New South Wales based on voucher specimens in the collections of the Australian Museum is shown in the accompanying map.



Geographic variation. Adults in populations in western Australia have dark heads and necks, with the dark colour becoming less intense posteriorly (subspecies *tristis*), while adults from northern and eastern Australia are paler and more uniformly patterned (subspecies *orientalis*). The function of the dark pigment in western populations is unknown.

Habitat. In the Top End of the Northern Territory, the species occurs in woodland (Sweet, 1999).

In central Western Australia, the species occurs primarily where there are large eucalypts (Pianka, 1971), often with hummock grass understorey on a sand substrate (Bennett, 1993).

Seasonal activity. In western Australia, the species appears to be active only between late winter and early summer (August-January) (Pianka, 1971).

Daily activity. The species is primarily diurnal (Christian, 1981; Thompson *et al.*, 1998). It inhabits both rock outcrops (S. White, in Zietz, 1914; Christian, 1981; Fitzgerald, 1983) and trees (S. White, in Zietz, 1914; Christian, 1981; Fitzgerald, 1983; Shine, 1986).

During the course of a day, a single animal may move more “hundreds” of metres and return to the nocturnal shelter that it occupied on the previous night (Thompson *et al.*, 1999).

Corrected for differences in body size, mean distances moved in one day are significantly greater in males than in females (Thompson *et al.*, 1999). The longest recorded movement for a male was 890 m and for a female 345 m (Thompson *et al.*, 1999).

Shelter sites. The species shelters in hollow logs and in the hollows of tree branches (Thompson *et al.*, 1999).

When chased on the ground by humans, it will flee to the tops of trees (S. White, in Zietz, 1914).

Thermal biology. In the wild, 48 active individuals had a mean body temperature of 34.8° C (Pianka, 1994, see also Pianka, 1982). Two individuals had body temperatures of 44.2 and 47.3° C (Pianka, 1994). However, these temperatures seem exceptionally high, and the

highest body temperature shown by six telemetered individuals was 42.5 C, which may be closer to the true voluntary upper thermal limit (Thompson *et al.*, 1998).

In one study of the body temperatures of active lizards, the slope of the regression of body temperature on ambient air temperature was 0.60 (n = 46) (Pianka, 1994). Theoretically a slope of 1.0 would indicate no thermoregulation and a slope of 0 would indicate perfect thermoregulation (Huey and Slatkin, 1976). Hence, it appears as if this species is only moderately good thermoregulator.

In a more indicative study of the body temperatures in the species, six telemetered individuals were followed between early morning and early evening in a period between late winter and early spring (11 September – 8 November). In the aggregate, body temperature rose throughout the morning to a broad peak about 33° C in the early afternoon and then declined steadily in the late afternoon and early evening (Thompson *et al.*, 1998). However, it was impossible to determine how if at all the lizards actually thermoregulated as the temperature trace is one that would be expected from a passive body placed on the surface.

The species has a very distinctive basking posture: the tail is curled in a large arc forward over its body (Christian, 1981: diag. 9; see also McDonald, 1999).

In captivity, the animals seem to seek out warm spots, either a heat lamp or a heat pad (McDonald, 1999), suggesting that they are actively regulating their body temperature.

Water relations. The rate of evaporative water loss relative to body mass has been measured for a variety of different sized individuals of this species at 35° C. The equation describing the relationship is: $\log \text{rate of evaporative water loss (mg/h)} = 0.92 \log \text{body mass (g)} - 0.56$ (Thompson and Withers, 1997).

The rate of water loss in this species appears to be low compared to other all other Australian species tested (Thompson and Withers, 1997: fig. 2, but no statistical comparison is available). This result is particularly surprising considering that the species is rather thin and lanky for its snout-vent length, suggesting a relative high surface volume to mass, and hence might have been expected to lose water at least at a similar rate if not faster than in other more robust species. As the species spends much of its time foraging off the ground in trees where it would be subject to increased risk of dehydration due to increased wind flow, its overall low rate of water loss may reflect some adaptive mechanism to reduce water loss.

Diet. In the wild, the goannas eat a variety of invertebrates and vertebrates. Invertebrate prey includes arthropods such as beetles (Pianka, 1971, 1982), orthopterans (Pianka, 1971, 1982; Losos and Green, 1988), phasmids (Pianka, 1971, 1982) and spiders (Losos and Green, 1988). Vertebrate prey includes squamate eggs (Pianka, 1971, 1982), lizards (Pianka, 1971, 1982; Losos and Green, 1988) and birds (Pianka, 1971, 1982).

In one study, lizards occurred in 46.9 percent of stomachs (n = 64) and grasshoppers occurred in 35.9 percent. Grasshoppers also constituted 34.7 percent of all prey items (n = 121) and lizards constituted 26.5 percent (Pianka, 1982).

In captivity, the adults eat arthropods such as cockroaches (McDonald, 1999; Schardt, 2001b), crickets (McDonald, 1999; Schardt, 2001b), and grasshoppers (Schardt, 2001b) and vertebrates such as young mice (McDonald, 1999; Schardt, 2001b).

Fat is stored in abdominal fat bodies, which can be quite large (Pianka, 1994).

Foraging behaviour. The species' tracks suggest that it moves fairly directly from one tree to another, presumably ascending each tree and then descending and moving on (Pianka, 1971, 1982). There is a single observation of an individual chasing a *Lophognathus longirostris* up the trunk and into the crown of a c. 8 m palm tree, showing that the goanna will actually engage in active pursuit of prey (Peterson and Metcalfe, 2004).

Courtship and mating. In captivity, courtship, such as it is, appears to involve the male tongue flicking and nudging the neck and back of the female, scratching her cloacal region with his rear claws, and then pushing his tail beneath hers to apply his cloaca to hers. Copulations can last from a few seconds to many minutes (McDonald, 1999).

Gravid females may stop feeding a few days prior to laying their eggs (Schardt, 2001b).

Seasonality of reproduction. In western Western Australia, females can carry yolking follicles between early and mid-spring (29 September – early November) (Pianka, 1971, 1982, 1994), and they can carry oviducal eggs in mid-spring (21 October – 19 November) (Pianka, 1982; Thompson *et al.*, 1999).

In the Northern Territory, the species lays its eggs in late winter (mid-September) (Christian, 1981).

Clutch size. Clutch size ranges 5-17 (Mitchell, 1955; Pianka, 1971, 1982, 1994; Husband, 1981; McDonald, 1999; Schardt, 2001b; Thompson and Pianka, 2001), with recorded means of 9.8 (n = 24, Thompson and Pianka, 2001) and 10.2 (n = 19, Pianka, 1982).

There is a significant positive association between female snout-vent length and clutch size ($r^2 = 0.21$, $P < 0.05$, n = 24; Thompson and Pianka, 2001).

Frequency of reproduction. In captivity, one female produced four clutches of eggs in one "season". The interval between clutches varied from 31 to 36 days. The female had not mated between her second and third clutches, suggesting that sperm can be stored for at least the length of the interval between the two clutches, 35 days (McDonald, 1999; see also Schardt, 2001b).

Nests. One female dug her nest about 200 mm below the surface in the roots of a dead tree (Thompson *et al.*, 1999). This observation indicates that females will lay their eggs in the ground, but whether they also lay them in the tree hollows where they shelter remains to be seen.

Eggs. Dimensions of freshly laid eggs are shown in the table below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
30-35	33.1	7	16-18	17	7	4.2-4.4	4.3	7	Schardt, 2001b

The eggs take up water from the substrate during development. For example, seven eggs gained an average of 11.8 percent in weight during the first 100 days of incubation (Schardt, 2001b).

Hatching. Hatchlings may not leave the egg completely for up to 26 hours after first slitting the shell (Schardt, 2001b).

Incubation. Incubation at different temperatures is given in the following table.

Incubation Temperature (°C)		Incubation Period (Days)			Reference
Range	Mean	Range	Mean	N	
27.5-29	-	108-111	-	7	Schardt, 2001b
28	-	105	105	1	McDonald, 1999
29	-	96-105	-	11	McDonald, 1999
29	29.0	117-122	-	-	Broer and Horn, 1985

Hatchlings. Measurements and weights for hatchlings are given in the following table.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	57	7	-	161	7	-	4.1	7	Schardt, 2001b
62-67	63.9	11	168-216	186	11	3.4-4.9	4.4	11	McDonald, 1999

Growth. A very young individual (snout-vent length 72 mm) found in an area of western Australia where adults are very dark on the head, neck and anterior body, was itself paler and more uniformly patterned (Bennett, 1993: fig. p. 37). This suggests that the dark pigmentation of the western population is acquired with growth.

Size at sexual maturity. The size at sexual maturity is asserted to be at a snout-vent length of about 200 mm (Pianka, 1994), although the evidence for this was not given.

Maximum size. The species attains a snout-vent length of 280 mm and a total length of 750 mm (Storr, 1980a).

Sexual dimorphism. Based on data in the literature from throughout the range (Mitchell, 1955), there is no significant difference in the snout-vent length in males (130-288 mm, mean = 216 mm, n = 10) and females (160-288 mm, mean = 213 mm, n = 7)(Mann-Whitney U = 38, P = 0.77), although admittedly the sample sizes are small.

Predators.

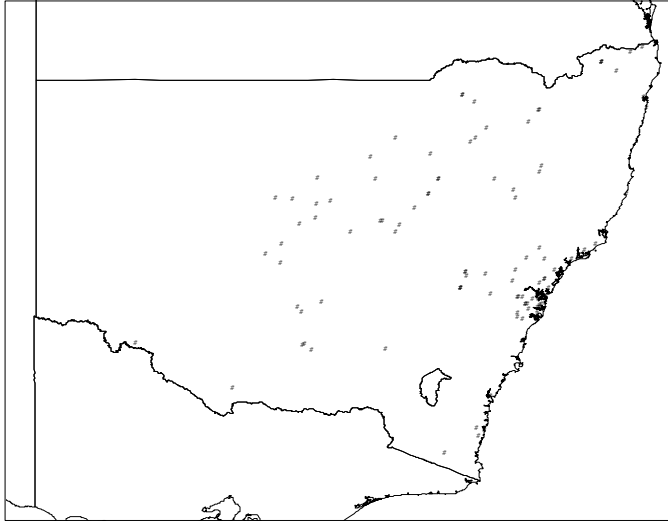
Parasites. The species' only recorded endoparasites are nematodes (Jones, 1986a, 1988, 1991, 1995b).

Literature. Gray, 1832 (as *Odatria punctata*); Schlegel, 1839 (as *Monitor tristis*); Stirling and Zietz, 1893; Fry, 1913; Zietz, 1914; Mitchell, 1955; Mertens, 1957; Mertens, 1958; Pianka, 1971; Fyfe, 1979; Fyfe, 1980; Christian, 1981; Brunn, 1982; Pianka, 1982; Fitzgerald, 1983; Stammer, 1983; Schmida, 1985; Jones, 1986a; Jones, 1988; Eidenmüller, 1989; Maryan, 1989; Jones, 1991; Bennett, 1993; Pianka, 1994; Jones, 1995b; Hollamby and Creeper, 1997; Thompson and Withers, 1997; McDonald, 1999; Thompson, DeBoer and Pianka, 1999; Thompson and Pianka, 1999; Thompson, Pianka and DeBoer, 1999; O'Dell, 2001; Schardt, 2001b; Peterson and Metcalfe, 2004.

Varanus varius

Lace Monitor

Distribution. The species occurs widely along the coast and hinterland of eastern Australia between central Queensland and southeastern South Australia.



The distribution in New South Wales as based on voucher specimens in the collections of the Australian Museum is shown in the accompanying map.

Habitats. The species occurs in woodland (Henle, 1989a) and closed forest. In drier country, it usually occurs only in woodland along rivers (Henle, 1989a).

Activity. The species is entirely diurnal in its activity and indeed usually only on sunny days

(Seebacher and Grigg, 2001). The species is both terrestrial and arboreal (Kingston, 1980; Henle, 1989a). It will climb as high as 20 m (Kingston, 1980).

At night, Lace Monitors shelter in hollow logs (Carter, 1990, 1992), hollow trees (Carter, 1992; Seebacher and Grigg, 2001), burrows in the ground or rocks (Carter, 1992; Seebacher and Grigg, 2001) and burrows in termite mounds (Carter, 1990, 1992). The goannas also occasionally use human-built nest boxes made of timber (Menkhorst, 1984). Over winter, they shelter in burrows of another animal's making (Annable, 1995a) or in hollows in standing trees (Carter, 1992). Goannas over-wintering in tree hollows usually stay in the same hollow all winter long, but occasionally they may move to a near-by tree (Carter, 1992).

Lace Monitors tend to occupy a local area or home range within which they carry out most of their activities. However, within these home areas most of the time is actually spent in a smaller core area (Carter, 1992). Home areas can range in size from approximately 13.9 to 127.5 ha. The home areas of different goannas can overlap broadly which suggests that the home areas are not defended from other goannas, that is, their home areas are not defended territories (Carter, 1992).

There is no relationship between the size of the home areas and the size of the goanna (Weavers, 1983; Carter, 1992). This is probably because habitats are not uniform, and factors such as the distribution of food and shelter sites may be more critical than sheer area in determining the size of a goanna's home area.

There is also no significant difference in the size of the home areas of males and females (Carter, 1992).

Thermoregulation. On warm and sunny days, Lace Monitors emerge from their shelters in the morning and bask. When basking initially, they often turn their body toward the sun and flatten the back in order to have as much exposure to the sun as possible (Stebbins and

Barwick, 1968; Weavers, 1983; Carter, 1992). They then begin their daily activities and during this time maintain a mean body temperature in the range 34 to 36° C (Bartholomew and Tucker, 1964; Stebbins and Barwick, 1968; Seebacher and Grigg, 2001). In the evening, they retreat to their shelters (Stebbins and Barwick, 1968; Carter, 1992; Seebacher and Grigg, 2001).

When heating in the morning, the heart rate rises and along with it the circulation which hastens the warm up time. Conversely, when cooling with falling temperatures in the evening, the heart rate slows which slows the cool down time (Bartholomew and Tucker, 1964; Stebbins and Barwick, 1968; Seebacher and Grigg, 2001). Interestingly, at the same temperature, the difference between the warming heart rate and the cooling heart rate is greater, the lower the temperature. In other words this difference, or "hysteresis", increases with lower temperature (Seebacher and Grigg, 2001). This effect, which is likely to be widespread in lizards (see *Pogona barbata*), is expected if heart rate really is used to achieve and maintain an optimal body temperature.

Lace Monitors rarely let their body temperature rise above 38.1 C (Weavers, 1983; #) and temperatures of 43.0 to 44.5° C are lethal if not lowered immediately (Spellerberg, 1972). Conversely, a low body temperature of about 5.0° C renders the animal so immobile that it can not right itself if turned on its back (Spellerberg, 1972).

In the southern part of their range, where winter is most severe, Lace Monitors curtail their activities during winter but may emerge to bask on warm days and occasionally to move short distances, such as to change shelter sites (Weavers, 1983). In southeastern New South Wales, activity usually begins in the last part of August or the first part of September and ceases in April (Carter, 1992; Guarino, 2001).

Parentetically, the heart rate in this species varies from about 9° C in a cool, inactive individual to about 65° C in a warm, mildly active one (Seebacher and Grigg, 2001).

Diet. Lace Monitors look for food by actively searching instead of waiting in ambush for prey to come their way. When hunting, they move slowly through the habitat in their home area searching in crevices and holes and occasionally pausing to scratch out some prospective shelter with one of the front feet. The tongue is flicked in and out and the head moved from side to side, as if sensing the environment both with their eyes and tongue. When harassed by birds, they flatten themselves on the ground for a short period and then resume foraging (Carter, 1992).

In the wild, the species eats a variety of invertebrates (Rose, 1974; Vestjens, 1977; Weavers, 1989; Carter, 1992; Tasoulis, 1992; Guarino, 2001) and vertebrates. The vertebrate prey include fish (Weavers, 1989; Webber, 1993), frogs (Towerton and Lemckert, 2001), reptile eggs (Vestjens, 1977; Carter, 1992; Guarino, 2001) – including some identified as the species' own eggs (Weavers, 1989), lizards and snakes (Fleay, 1950; Rose, 1974; Losos and Green, 1988; Weavers, 1989; Carter, 1992; Guarino, 2001), bird eggs (Vestjens, 1977), birds (Vestjens, 1977; Kingston, 1980; Weavers, 1989; Carter, 1992; Guarino, 2001; Kingston, 1980) and mammals (Fleay, 1950; Irvine, 1957; Vestjens, 1977; Weavers, 1989; Carter, 1992; Guarino, 2001) including possibly bats (Mansergh and Huxley, 1985). Fish can be caught by diving ("T." Simmons, in Webber, 1993).

In captivity, the species eats egg yolk (Longley, 1945), insects such as locusts (Horn and Visser, 1989), pieces of raw and cooked meat (Longley, 1945), lizards such as *Physignathus lesueurii* (water dragons), *Tiliqua scincoides* (eastern blue-tongue lizards) and *Varanus gouldii* (sand goannas) (Hoser, 1993) and small mammals (Horn and Visser, 1989).

The species also eats carrion (Horn, 1980; Kennerson, 1980; Ward and Carter, 1988; Carter, 1992) and human garbage (Weavers, 1989; Hoser, 1998d; Carter, 1992). Carrion can be at almost any stage of decomposition, varying from freshly killed through maggot infested to dry skin and bones (Ward and Carter, 1988).

There is apparently no relationship between a Lace Monitor's size and the size of its prey (Weavers, 1989). In other words, large monitors eat small prey and small monitors eat large prey.

Goannas can swallow prey that is large relative to their size. For Lace Monitors, the largest recorded meal relative to the goanna's size is a 500 g rabbit eaten by a 1200 g goanna. The rabbit was 42 percent of the goanna's own weight (Weavers, 1989).

Lace Monitors can exhibit a surprisingly "light" touch when eating certain food. For example, in captivity, they can pick up chicken eggs in the mouth and swallow them intact (Fleay, 1950; Horn, 1980:fig. 11). This "light touch" is probably the most efficient way to eat a liquid food wrapped in a delicate package by a predator whose long thin tongue may not be too efficient at lapping.

The fact that Lace Monitors feed on non-moving prey, especially buried prey such as invertebrate larvae, suggests that they are finding the prey by vomerolfaction and not sight.

The fact that Lace Monitors eat carrion and can also eat a huge amount of food in proportion to their body weight raises the issue of how sensitive they may be to 1080 baits laid to poison feral mammals such as foxes and pigs. Unfortunately, the experimental work that has been done to test the species' sensitivity was inconclusive. The poison will kill these goannas, but whether their likely normal intake would kill them or not could not be determined (McIlroy *et al.*, 1984). But it might be noted that the goannas would almost certainly find and eat the poison and that it is hardly likely to be good for them.

The species propensity for carrion also leads to it being caught in baited traps set for other species (Newsome *et al.*, 1983).

Lace Monitors are the second largest native terrestrial carnivore in the current Australian fauna (Weavers, 1989). At a maximum weight of 14.0 kg, it is second only to the Perentie, another species of goanna, at 17.0 kg.

Drinking. Lace Monitors drink by submerging the tip of the snout (to just short of the nostrils) in water and lapping with the tongue through a slightly opened mouth for about half a minute. Then the head is raised and tilted back to assist in swallowing (Horn, 1980).

Male combat. Males engage in one-on-one combat. These struggles look like something between ballroom dancing (Breedon and Breedon, 1972: fig. #) and a wrestling match (Worrell, 1963: plate 30), the two combatants embracing each other tightly and trying to

overpower the other. The "fights" often involve biting and scratching (Twigg, 1988; Phillips, in Carter, 1992) but mainly appear to be primarily a test of strength or stamina.

There are relatively few dates recorded for combats, but those available suggest the combats occur in late November (Twigg, 1988). The purpose of the matches is unclear, but may determine which males hold sway in a particular area, and this in turn may help determine a male's chances of mating.

Mating. In southeastern New South Wales, mating occurs between mid-November and early January in animals in the wild (Carter, 1990, 1992) and in the end of October and the beginning of November in animals in "natural" enclosures (Bredl and Schwaner, 1983). During the mating season, males can be extremely aggressive to one another. However, females are rarely if ever aggressive to other individuals, males or females, except perhaps at a nest (Carter, 1990).

The behaviour of males at least suggests that they can track other individuals, both male and female, using vomerolfaction (Carter, 1990), that is, the scent picked up by the tongue and tested in Jacobsen's organ in the roof of the mouth.

Females may mate with more than one male over a period of a few days. They may also mate with one male as many as 16 times in a few hours. Each copulation lasts only a few minutes (Carter, 1990).

When a courting male approaches a female, he carries his head raised and often jerks his head from side to side in a "spasmodic, shuddering fashion" (Carter, 1990; Horn, 1991). In contrast, females tend to keep their head and body low to the ground. The scent that the goannas give off probably comes primarily from the cloaca, which from its position is often in contact with the ground (Carter, 1990).

When mating, the male lies across the top of the female's body, raises the female's tail by reaching over her tail with the leg on the same side as his head and uses the hemipenis of that same side. In subsequent matings between the pair over the next few hours, the male often alternates the way he lies across the female and hence which hemipenis is used (Carter, 1990).

A few days or weeks before laying, the females reduces her feeding, but resumes shortly after laying (Horn, 1991).

The period between the last observed mating and egg laying ranges from 31 to 35 days in captive animals (Bredl and Schwaner, 1983; Horn and Visser, 1989).

In captivity, a female that had just laid eggs defended her nest box from a cagemate female but not her cagemate male, the father of her fertilised eggs (Horn, 1991).

Seasonality of reproduction. In the southern half of their range, females carry yolking follicles between late October and early December and oviducal eggs from mid-November to mid-January (Carter, 1992). They lay their eggs in mid-summer (13 January) (Boylan, 1995).

Frequency of reproduction.

Clutch size. Clutch size varies from 4 to 15 (Irvine, 1957; Bredl and Schwaner, 1983; Horn and Visser, 1989; Horn, 1991; Carter, 1992; Annable, 1995a; Horn *et al.*, 1997; Krauss and Horn, 2004a-b).

Females reproduce every year.

Eggs. Dimensions of fertile eggs are shown in the table below.

Length (mm)			Width (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
67	67	5	40	40	5	-	-	-	Anonymous in Hoser, 2003
64.6-72.4	68.3	7	34.2-36.5	35.2	7	45.0-50.5	48.4	7	Horn, 1991
73.5-74.8	74.1	5	33.0-35.7	34.1	5	45.1-50.8	49.1	5	Horn <i>et al.</i> , 1997
69.0-70.0	69.5	2	39.5-41.0	40.3	2	-	-	-	Markwell, 1983
70	70	5	40	40	5	c 65	c 65	5	Bredl and Schwaner, 1983
65-78	74.3	5	34.5-37.5	35.8	5	48.0-60.2	55.0	5	Horn, 1991

Curiously, freshly laid eggs apparently show no sign of embryonic development (Carter, 1992). This may be one reason that goanna eggs in general take longer to develop than similar sized eggs of other lizards and snakes.

Nesting habits. In the wild, Lace Monitors lay their eggs in active termite mounds (Cogger, 1959; Worrell, 1963), which can be either in trees (Longley, 1945; Fleay, 1953, 1960; Tasoulis, 1992; Annable, 1995a; Boylan, 1995) or on the ground (Boylan, 1995). There is no reliable record of a wild Lace Monitor nesting anywhere other than termite mounds (Carter, 1992). This makes the species continued existence dependent on the termite species whose mounds they use.

In southeastern Australia, two species of termites build mounds above the ground: *Coptotermes lacteus* and *Nasutitermes exitiosus*. However, the goannas only use the mounds of *Nasutitermes* whose softer outer layer makes them easier to dig into (Weavers, 1983; Carter, 1992). The mounds of *Nasutitermes* consist of three layers: outer, inner and central nursery. The goannas lay their eggs in the nursery.

The only recorded laying times are from captivity, and those from within the natural range of the species are from mid-December, both in central New South Wales (Markwell, 1983) and in South Australia (Bredl and Schwaner, 1983).

The young goannas are apparently released from their termite mounds by an adult, most likely the female (Cogger, 1967). The basis for this conclusion is circumstantial but convincing. First, hatchlings can almost certainly not dig through the hard inner layer of mound material but adults can. Second, it is females that do the majority of burrowing in termite mounds (Carter, 1992). Third, the tunnels dug by adults clearly lead to the nursery chamber. And fourth, a female has been observed digging into termite mound that contained hatchlings (Mertens, 1987). However, the critical missing piece of information in this set of observations is the demonstration that it is the female that laid the eggs that actually digs the hatchlings out. This observation will require marking a nesting females and monitoring the

release of the young or comparing the genetics of any young in a mound being excavated by a female (Carter, 1992).

In captivity, a female dug into a termite mound in which her presumed young were hatching. She was also aggressive at the time to handlers (Boylan, 1995).

How females know when to dig out their young is unclear. The young make no sound audible to humans and their movements and scratchings make only a faint sound. But perhaps this faint noise is enough to a well-tuned maternal ear or perhaps the young release an odour recognised by the female (Carter, 1992).

The benefits of nesting in a termite mound are many. During incubation, the eggs experience a fairly narrow range of temperatures and humidities that are conducive to the development of reptile eggs. And they are protected from predators, floods and inclement weather.

Eggs only do well in healthy, active termite mounds. Moribund mounds or mounds that die during the course of egg development, usually lead to the death of the eggs (Carter, 1992). Strangely, the termites appear to not attack the eggs. This may be due some substance adhering to or emanating from the eggs that inhibits the attacks (Carter, 1992). Such a substance, if it does exist, might be of importance in protecting human structures from termites (Carter, 1992).

In captivity, some females have been observed to nest at night (H.-G. Horn, in Irwin *et al.*, 1996), but it is not clear whether this is normal behaviour.

Incubation. The recorded incubation periods for Lace Monitor eggs, all based on observations in captivity, range from 153 to 317 days based on observations in captivity (Bredl and Schwaner, 1983; Markwell, 1983; Horn, 1991; see Table below) and 288 to 294 days based on nests in the wild (Carter, 1992).

Incubation Temperature (°C)		Incubation Period Days			Reference
Range	Mean	Range	Mean	N	
-	-	317	317	2	Markwell, 1983
28	28	225-237	231	2	Horn <i>et al.</i> , 1997
28.8	28.8	226-235	-	5	Horn and Visser, 1989
28.8 -29.0	-	226-235	231	5	Horn, 1991
28.8 -29.0	-	232-243	235.9	7	Horn, 1991
29.4	29.4	274	274	1	Anonymous in Hoser, 2003
30	30	191-193	192	3	Horn <i>et al.</i> , 1997
30	30	< 275	-	3	Anonymous in Hoser, 2003
30.5	30.5	280-294	287	2	Anonymous in Hoser, 2003
30-31	-	222	222	3/1	Krauss and Horn, 2004a ¹
30-32	-	153-154	153.7	4	Bredl and Schwaner, 1983

1. Three hatchlings from one egg.

There is one recorded incubation period of only "six weeks" (Fleay, 1950), but compared to all the other records for the species, it seems very likely to be based on an error.

The normal incubation period means that, in the wild, development continues throughout the winter.

In the eggs of one female (but consisting of two clutches) incubated at the same temperature, there was no significant difference between egg size and incubation period ($r^2 = 0.02$, $n = 11$, data from Horn, 1991). In other words, bigger eggs do not take longer to “cook”.

Hatchlings. In captivity, hatchlings make several slits in their egg shells as they are hatching and take from 3 to 30 hours to leave their eggs (Horn, 1991). In the wild, the hatchlings may stay in and around the termite mound in which they hatched for at least 14 days before dispersing (Carter, 1992; Tasoulis, 1992).

Measurements and weights of hatchlings are given in the following table.

Snout-vent Length (mm)			Total Length (mm)			Mass (g)			Reference
Range	Mean	N	Range	Mean	N	Range	Mean	N	
-	-	-	220-225	223.3	3/1	12.0-13.0	12.3	3/1	Krauss and Horn, 2004a ¹
103-210	156.5	2	260-280	270	2	-	-	-	Markwell, 1983
120	120	1	297	297	1	-	-	-	Boylan, 1995
117-120	118.7	4	302-310	305.3	4	32-36	34.0	4	Bredl and Schwaner, 1983
-	-	-	290-360	336	5	33.1-38.2	35.0	5	Horn <i>et al.</i> , 1997
126-139	134	7	327-363	345	7	28.4-35.5	33.2	7	Horn, 1991
133-143	138	4	338-352	354	3	33.0-40.8	36.1	4	Horn, 1991
-	-	-	338-372	354	4	33-40.8	36.1	4	Horn and Visser, 1989
130-150	140	2	340-370	355	2	-	-	-	Anonymous, in Hoser, 2003
-	-	-	-	-	-	-	35.0	-	P. Krauss unpublished, in Krauss and Horn, 2004a

1. Three hatchlings from one egg.

Hatchlings from clutches taken from the wild range 20-31 g in mass (Weavers, 1988; Carter, 1992; Boylan, 1995). In contrast, hatchlings from captive breeding range 28-41 g in mass (Bredl and Schwaner, 1983; Horn, 1991; Horn and Visser, 1991). The reason for the heavier weights of captive-bred animals is not clear. It could be due to natural geographic variation of the stocks represented by the animals in the two groups, or perhaps more likely, to the better nutritional conditions of the captive animals (Horn and Visser, 1991).

The mean mass of the three hatchlings from one egg (12.3 g) was about one-third of the mean mass of hatchlings from normal clutches (c. 33.2-36.1 g) (see table). This suggests that the mass of the hatchling is determined by the mass of the yolk (Krauss and Horn, 2004a), a logical relationship.

In hatchlings from the same female (but two different clutches), there was a significant positive relationship between the original egg mass and the mass of the hatchlings ($r^2 = 0.37$, $n = 11$, data from Horn, 1991). In other words, bigger eggs mean bigger hatchlings.

In their nests, hatchlings appear to sleep for the first three or four days of life and then become more active. Once freed from the mounds, they may stay around the mound for up to 15 days (Carter, 1992). They do not eat the termites that surround them, although they eat

voraciously on grasshoppers once freed from their nest mounds. In captivity, hatchlings generally only start to feed about 7 to 10 days after hatching (Bredl and Schwaner, 1983; Horn, 1991; Horn and Visser, 1991).

Once hatchlings disperse from their nest, they are rarely seen in the wild. All observers attribute this to their great wariness due to their susceptibility to predation at their relatively small size. Observations that adults apparently show no interest in hatchlings still hanging around their termite mound suggests that adults may not regard hatchlings as food (Carter, 1992).

Hatchlings lose the egg tooth within two days of hatching (Carter, 1992).

Like most lizards, the colour pattern of juveniles is brighter and more contrasting than that of adults (pers. obs.).

Growth. In 28 days, three captive hatchlings grew at an average rate of 2.93 mm per day in total length and 1.75 g per day in weight (data in Horn and Visser, 1989)

In 450 days, a zoo-raised hatchling grew at an average rate of 0.47 mm per day in snout-vent length, 1.36 mm per day in total length and 1.06 g per day in weight (data in Boylan, 1995).

In 12 months, the average snout-vent length and weight of seven zoo-raised one month old young increased by 0.31 mm per day and 0.56 g per day, respectively (data in Boylan, 1995).

In southeastern New South Wales, males may become mature at a snout-vent length of about 415 mm and females at about 385 mm (Carter, 1992).

Longevity. Individual Lace Monitors have been kept in captivity for as long as 15 years and seven months. However, as the individual was captured as an adult, it was older than this upon its death (Kennerson, 1979).

Allometry. Mass is in positive allometry with snout-vent length. The relevant regression equation is $\log \text{mass (g)} = 3.33 \log \text{snout-vent length (mm)} - 5.34$ ($r^2 = 0.99$, $P < 0.001$, $n = 43$) with a 95 percent confidence interval for the slope of ± 0.12 (AG, pers obs based on data in the literature). In other words, larger Lace Monitors are heavier relative to their snout-vent length than are smaller individuals.

Sex ratio. In both the wild (Horn, 1980; Hoser, 1998d; Guarino, 2001) and collections (Carter, 1992), males outnumber females by a large margin. The reason for this is unknown, but it may be due to the greater secretiveness of females.

Colour pattern. Throughout the range of Lace Monitors, the colour pattern usually consists of several relatively pale and dark crossbands, which tend to become less distinct with age. However, there is a second colour pattern, which consists of only a few relatively wide, and highly contrasting pale and dark crossbands. This is the so-called "Bell's" pattern (Worrell, 1963; plate 26), and the goannas with it are called "Bell's" goannas. The pattern occurs most commonly on the western slopes of the Dividing Range in the southern part of the range between southeastern Queensland and northeastern Victoria (Horn, 1980), but it can also occur along the east coast, e.g., Kuringai National Park, north of Sydney (Eipper, 2001: fig.

p. 27). It used to be thought that this distinctive pattern occurred only in males (Horn, 1980), but this was probably due to a coincidence arising from the fact that in collections, males generally outnumber females by a large margin, and all the Bells goannas examined just happened to be males. It is now clear that the colour pattern can occur in females as well as males. Hatchlings with the Bell's pattern can be produced by parents with the more common colour pattern (Anonymous in Hoser, 2003)

Predators. Lace Monitors, at least while they are relatively small, are probably eaten by a variety of predators, but the only recorded predators on Lace Monitors of any size are: snakes (Hamon, 2000) and dogs (Webb, 1996, as dingoes).

Lace Monitors are able to learn whether humans are friendly or hostile. For example, around picnic and camping areas, they can become quite tame, even bold, if people leave them alone or even encourage them with handouts of food (Carter, 1992; Mantell, 2001).

Defence. When on the ground and approached by an intruder such as a person, Lace Monitors usually flee to a tree (Fleay, 1950; Irvine, 1957; Carter, 1990, 1992). And once in a tree, the lizards tend to spiral upward, keeping the tree between themselves and the intruder. If the lizards are already in a tree when approached, their first reaction is likely to be just to press themselves closer to the trunk or branch (Horn, 1980). The goannas will climb quite high in trees, up to 20 m (Carter, 1992).

Goannas seem to recognise the human form as something dangerous, because they can be approached quite closely if the human observer wears a "hide" such as an inverted sac, which conceals the human form (Carter, 1988, 1990, 1992). Some modern fashions may be equally effective.

Sometimes Lace Monitors hold their ground when startled. In this case, they may suddenly rise up on their rear legs, arch the neck, inflate the throat and hiss (Irvine, 1957; Bustard, 1970).

When grasped by a human, Lace Monitors often regurgitate their stomach contents and defecate (Guarino, 2001). Whether this is meant to put off the predator or merely lightens the load for flight is difficult to tell. Curiously, as in other large monitors, male Lace Monitors often evert the hemipenes when restrained (#). The function of this behaviour is also unclear.

Parasites. Lace Monitors often carry ticks (Ward, 1989), and sometimes, these ectoparasites actually find their way beneath the level of the skin (Ward, 1989).

The known endoparasites of the species include pentastomids (Heymons, 1939; Riley *et al.*, 1985).

Size. Males are much larger than females (Carter, 1990, 1992). For example, in one study of juvenile and adult goannas, snout-vent length, total length and weight for 46 males and 40 females were: 370 to 765 mm, 1000 to 1935 mm and 510 to 8800 g versus 315 to 525 mm, 920 to 1435 mm and 400 to 2470 g, respectively (Carter, 1992).

The maximum recorded mass is 14.0 kg for a specimen with a snout-vent length of 750 mm and a total length of 1920 mm (Weavers, 1988).

Size affects many physiological functions. One such function that has been measured in Lace Monitors is heart rate, which slows with increasing size (Seebacher, 2000: fig. 4). This is a widespread phenomenon both within and among terrestrial vertebrates.

Conservation. Lace Monitors have several features that suggest they will be able to cope with the increasingly degraded environment of the future. As adults, at least, they are beyond the reach of most exotic predators, such as cats, dogs, foxes, and unarmed humans. Furthermore, they eat dead animals (carrion), exotic species that are especially abundant such as rabbits and foxes, and garbage. They may also be intelligent enough to learn from "bad" experiences involving humans and thus avoid them in the future.

Literature. Waite, 1929 (this account may be largely based on *V. rosenbergi* on Kangaroo Island); Longley, 1945; Fleay, 1950; Fleay, 1953; Irvine, 1957; Cogger, 1959; Fleay, 1960; Worrell, 1963; Bartholomew and Tucker, 1964; Frauca, 1966; Cogger, 1967; Stebbins and Barwick, 1968; Bustard, 1970; Peters, 1970; Spellerberg, 1972; Dale, 1973; Frauca, 1973; Kennerson, 1979, 1980; Horn, 1980; Markwell, 1983; Newsome *et al.*, 1983; Tasoulis, 1983; Weavers, 1983; Bredl and Schwaner, 1983; Menkhorst, 1984; Bredl and Schwaner, 1985; Mansergh and Huxley, 1985; Shea, 1985; Brooker and Wombey, 1986; Goldingay, Daly and Lemckert, 1996; Lunney and Barker, 1986; Shea and Reddacliff, 1986; Mertens, 1987; Wilson, 1987; Twigg, 1988; Ward and Carter, 1988; Weavers, 1988; Henle, 1989a; Horn and Visser, 1989; Ward, 1989; Carter, 1990; Horn, 1991; Horn and Visser, 1991; Carter, 1992; Tasoulis, 1992; Hoser, 1993; Weavers, 1993; Webber, 1993; Murphy, 1994; Annable, 1995a; Boylan, 1995; Webb, 1996; Horn, Visser and Stirnberg, 1997; Stirnberg, 1997; Hoser, 1998d; Jones, 1998; Carter, 1999a-b; Hamon, 2000; Seebacher, 2000; Seebacher and Grigg, 2001; Guarino, 2001; Standen, 2001; Guarino, 2002; Guarino, Georges and Green, 2002; Towerton and Lemckert, 2001; Hoser, 2003; Midtgaard, 2003; Krauss and Horn, 2004a-b.