Australian Journal of Ecology (1994) **19**, 395–408

Comparative ecology of *Varanus* in the Great Victoria Desert

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Abstract The ecologies of seven desert species of monitor lizards (*Varanus*), which are very variable in size, are described and compared. Data are reported on abundance, anatomy, behaviour, body temperature relationships, daily activity patterns, diet, growth, habitat and microhabitat, prey size, reproduction, seasonal patterns of activity, sexual dimorphisms, and tracks. As many as six of the seven species occur together in sympatry at one study site. New results reported here are merged with extensive data collected over the past quarter of a century to provide a comprehensive and detailed overview of numerous aspects of the natural history and ecology of the seven species in the Great Victoria Desert. One species of pygmy monitor has evolved large clutch size for unknown reasons. A food web for 40 species of desert lizards is presented. Hutchinsonian ratios of head lengths (larger/smaller) are significantly greater in two observed assemblages of sympatric varanids than in a null model consisting of all possible pairs of species of all Australian varanids. Evolution of body size and the two adaptive radiations of *Varanus* in Australia are discussed.

Key words: comparative ecology, deserts, food webs, Hutchinsonian ratios, monitor lizards, sympatry, *Varanus*.

INTRODUCTION

Currently, 40 species of monitor lizards (genus *Varanus*) are recognized, some 26 of which occur in Australia, where they are known as 'goannas' (a corruption of iguana, a Spanish and English word for a group of large herbivorous New World lizards). All but one (the herbivorous Phillipine *Varanus olivaceus*; Auffenberg 1988) are active predatory species that eat large prey. Monitor lizards live in a wide variety of habitats, ranging from mangrove swamps to dense forests to savannas to arid deserts. Some species are aquatic, some semi-aquatic and others terrestrial, while still others are saxicolous or semi-arboreal or truly arboreal.

Varanus are morphologically conservative but vary widely in size, making this genus a model system for understanding the evolution of body size. Two major lineages have undergone extensive adaptive radiations in Australia: one evolved small body size (subgenus *Odatria*, the pygmy monitors), whereas the other (subgenus *Varanus*) remained large. Australian monitors range from the diminutive pygmy monitor *Varanus brevicauda* (about 20 cm in total length and 8–10 g in mass) to the largest lizard in Australia, the perentie, *Varanus giganteus* (total length may exceed 2.0 m, mass 17 kg). Even larger are the Komodo dragons (*Varanus komodoensis*) of the Lesser Sunda Islands of Indonesia, which attain lengths of 3 m and weights of 150 kg (Auffenberg 1981). Komodos, however, are themselves dwarfed by a closely related, extinct gigantic varanid *Megalania prisca*, originally placed in the genus *Varanus*. This Pleistocene fossil from Australia probably reached 7 m in total length and weighed over 600 kg (Hecht 1975; Auffenberg 1981; Rich 1985). *Megalania* fossils have been dated at 23–25 thousand and 19–26 thousand years before present. *Megalania* teeth were over 2 cm long, curved and, like those of many *Varanus*, with the rear edge serrated for cutting and tearing the skin and flesh of its prey. Several authors have suggested that *V. komodoensis* and *M. prisca* are/were ecological equivalents of large sabre-toothed cats, using a slashing bite to disembowel large mammals (Auffenberg 1981; Akersten 1985; Losos & Greene 1988).

Two distinct adaptive radiations of *Varanus* have taken place in Australia (King *et al.* 1991): the subgenus *Odatria* includes 17 species of pygmy monitors and the subgenus *Varanus* includes 7 larger species of Australian monitors. Two other species, *indicus* and *prasinus*, belong to an Asian clade, and are probably recent migrants to northern Australia.

Australian desert *Varanus* are exceedingly wary, unapproachable and unobservable lizards. One must work very hard for each and every specimen of and each observation on *Varanus*. They do, however, leave conspicuous tracks from which their biology can be deduced. There are seven desert *Varanus* species. Each species leaves its own distinct track. Daily forays of goannas typically cover a distance of 1 km or more. Three species are semi-arboreal: *tristis* and two other little-known small

Accepted for publication February 1994.

species, *caudolineatus* and *gilleni*. These have strongly curved, sharp claws and adpressed limbs. The other four species, *brevicauda, eremius, gouldi* and *giganteus*, are terrestrial (although *gouldi* and *giganteus* will climb when threatened by humans and occasionally for prey).

I have been studying the ecology of Australian desert lizards for 25 years (Pianka 1968, 1969a, 1986). Observations on various aspects of the biology of these seven species of *Varanus* have been reported previously by Pianka (1968, 1969b, 1970a,b, 1971, 1982). During 18 additional months (spring and summer) from October 1989–September 1993, my assistants and I made further observations at three study sites in the western part of the Great Victoria Desert in Western Australia (WA) on five *Varanus* species (numbers of new individuals in parentheses): *brevicauda* (20), *eremius* (33), *tristis* (15 adults and one juvenile), *gouldi flavirufus* (18 adults and 18 juveniles), and *giganteus* (4). Data were collected on anatomy, behaviour, body temperature, diet, habitat and microhabitat, prey size, reproduction, and time of activity. New results are merged with data collected during my previous studies to provide an overview of the natural history and comparative ecology of the seven desert species.

METHODS

At one study site, the L-area, 38–40 km east of Laverton, WA (28°31′S, 122°45.7′E), four species of *Varanus* (*eremius, tristis, gouldi* and *giganteus*) are present. The L-area is a flat desert sandplain with spinifex (*Triodia basedowii*), scattered mallee and *Acacia* bushes, plus marble gum trees (*Eucalyptus gongylocarpa*). About 100 km east is the Red Sands study site, 7 km west of Point Salvation (28°12′S, 123°35′E), where six species of *Varanus* occur (*brevicauda, eremius, gilleni, tristis, gouldi* and *giganteus*). Red Sands is a complex mosaic of sandridges and interdunal flats with a vegetation of spinifex (*Triodia basedowii*), scattered mallee and *Acacia* bushes, plus marble gum trees (*Eucalyptus gongylocarpa*). The third site, the B-area, 4 km south of Red Sands (28°13.5′S, 123°35.5′E), is a homogeneous flat sandplain with large unburned spinifex tussocks (*Triodia basedowii*) plus a few mallees but no marble gum trees. It supports three species of *Varanus*. Two, *brevicauda* and *eremius*, were collected, and numerous diggings indicated the presence of *gouldi*.

Tracks in the sand were a major source of data and aided in locating lizards. Tracks are difficult to see during midday when the sun is high or on overcast days, but are easier to follow when the sun is low in the sky and shadows are long. Tracks are best seen by looking into the light. The track of a running animal is often harder to follow than that of one walking.

Large lizards (some *eremius*, most adult *tristis* and *gouldi* plus all *giganteus*) were captured either by tracking them and then exhuming them from burrows or cutting or chopping them from hollow logs and dead trees. For lizards that were captured when active above ground, body temperature (BT) and air temperature (AT) were taken to the nearest 0.1°C with a thin bulb Schultheis cloacal thermometer. Small lizards, especially *brevicauda, eremius*, plus one juvenile *tristis* and 18 juvenile *gouldi*, were captured in pit traps.

Pit trap lines were established by burying 20 L plastic buckets with their lips flush with the surface. Traps were spaced about 5–10 m apart. Aluminium flyscreen drift fences about 20–25 cm above ground were erected between traps. The total number of traps at each study site was 75 (L-area), 78 (Red Sands) and 75 (B-area). When not being monitored, traps were closed with tight-fitting plastic lids and covered with a 5–10 cm layer of sand. A total of 20 139 trap days were accumulated, with 5731 on the L-area, 9908 at Red Sands, and 4500 on the B-area. Dates spent at each site during 1989–93 are summarized in Table 1. On previous visits during 1966–68 and 1978–79, total numbers of days spent in the field were 207 and 153, respectively.

Captured lizards were weighed to the nearest 0.1 g and measured to the nearest mm, then preserved in 10% formalin for about 1–2 weeks before being transferred to 70% ethanol for permanent storage. All specimens are deposited in the Los Angeles County Museum of Natural History or in the Western Australian Museum.

Later, in the lab, anatomical measurements were taken on the preserved specimens. Head lengths (HL) were measured with vernier calipers to 0.1 mm as the distance from the anterior edge of the ear opening to the tip of the snout. Snout–vent length (SVL) was measured with a metal ruler to 1 mm as the distance from the tip of the snout to the cloacal vent. Hind leg length (HLL) was measured with a metal ruler to 1 mm as the distance from the side of the body to the tip of the longest toe with the hind leg extended as straight as possible perpendicularly to the body. Specimens were dissected and their sex and reproductive condition noted. Testes lengths of males were measured to 1 mm. For gravid females, the size and number of enlarged yolked ovarian and oviducal eggs were recorded, allowing estimation of clutch sizes. Volumes of oviducal eggs were measured by volumetric displacement in narrow-necked graduated cylinders. Relative clutch mass (RCM) was estimated as the ratio of the total volume (= mass) of the preserved oviducal clutch over the fresh body weight of the female, expressed as a percentage. Size of the smallest male with enlarged testes and the smallest female with enlarged yolked eggs allowed estimation of size at maturity for both sexes. Growth rates of juvenile *gouldi* were estimated by plotting size versus date of capture.

Table 1. Dates spent at three study sites in the Great Victoria Desert

Year	L-area	Red Sands	B-area
1989	1–6 October	8–12 October	
	18–21 October	21–27 October	
	28 October–4 November	5–12 November	
	12–20 November	21 November–2 December	
	2–7, 15–17 December	18–26 December	
	29–31 December		
1990	1–2 January	5–14 January	
	14–17 January	20–27 January	
	27 January–8 February	10–23 February	
	24 February–4 March		
	1–6 September	6–13 September	
	18–23 September	24–30 September	
	4–10 October	10–16 October	
	19–26 October	27–31 October	
	2–6 November	8–19 November	
	22–27 November	28 November–3 December	
	8–13 December	14–19 December	
	22–30 December	31 December	
1991	9–15 January	1–6 January	
	24–28 January	16–20 January	
	17–20 February	6–16 February	
		25 February–6 March	
1992	21–29 July	30 July–14 August	12–14 August
	18–22 October	4–17 October	4–17 October
	9–13 November	26 October–8 November	26 October–8 November
	16–22 November	27 November–3 December	23 November–30 November
	16–20 December	7 December–15 December	7 December–15 December
1993		8–21 September	8–21 September

Stomachs were removed from preserved specimens and contents were identified to compile lists of prey species eaten by each species of *Varanus*. Both the number of prey items and the volume were recorded. Volume and mass are assumed to be equivalent (e.g. 1 mL of lizard is assumed to weigh approximately 1 g). Diets are summarized by both total number and total volume of various prey categories, as well as by percentage of total number of prey items and percentage of total volume of prey. Frequency of occurrence of each prey type in the diet, estimated as the percentage of lizard stomachs with food that contained that prey item, was also computed. The stomach of one live medium-sized 1.8 kg *giganteus* was flushed by inserting a plastic tube down the lizard's throat and filling its stomach with water. It was shaken and then held upside down until it regurgitated. Volumes of intact prey items before digestion were estimated by comparison of the sizes of remaining partially digested parts with those of intact whole specimens collected for other purposes.

Losos and Greene (1988) plotted maximum relative mass ratios of the mass of the largest prey item over varanid body mass for 16 species of *Varanus*. Here I report maximal relative prey mass ratios for six desert species of *Varanus* and compare these with those reported by Losos and Greene (1988).

RESULTS

Species accounts

Varanus brevicauda

I have never encountered this diminutive monitor lizard active above ground. Most specimens were collected in pit traps. During August 1967, two were dug from shallow burrows. One must have been active immediately prior to being exhumed as there were fresh tail lash marks at the burrow's entrance and the lizard had a body temperature of 35.4°C, 10°C above ambient air temperature. Four specimens were trapped at Red Sands during 1989–91 and another 16 were trapped during November and December 1992 on the B-area. Sandplain with large, long unburned, clumps of spinifex, is possibly the preferred habitat of *brevicauda*. One female weighing 9.1 g contained an adult 1.5 mL *Ctenotus calurus* skink which constituted 16.5% of the *brevicauda's* body weight. The smallest male with enlarged testes was 82 mm SVL and the smallest gravid female was 94 mm SVL. The typical monitor lizard threat posture and behaviour have been conserved in the evolution of these tiny monitors, which hiss and lunge with throat inflated.

Varanus caudolineatus

This small species is semi-arboreal, preferring habitats with mulga trees, which offer small hollows that provide tight-fitting retreats. However, *caudolineatus* do forage on the ground. Three of 13 active specimens observed were on the ground when first sighted. Moreover, one stomach contained a ground-dwelling *Rhynchoedura ornata* gecko (Pianka 1969b). Others contained tails and intact *Gehyra* (arboreal geckos). One specimen (SVL 111 mm, estimated mass 15 g) contained an intact 3 mL *Gehyra* (20% of its mass). Gut contents of a sample from Atley Station consist largely of scorpions and ground-dwelling spiders (Thompson & King, unpubl. data), and Thompson (1993) suggests that these monitors forage on the ground by searching the burrows of prey species. Movements of *caudolineatus* marked with a radioactive tracer (Thompson 1993) were much more restricted than those of other varanid species, suggesting a sedentary life style. Both sexes mature at about 91 mm SVL.

Varanus eremius

Judging from the frequency of their unique and conspicuous tracks, *Varanus eremius* are common in the Australian sandy deserts (Pianka 1968). They are active all year long, but are wary and seldom seen. Nevertheless, much can be inferred from *eremius* tracks, which I have followed over several hundred kilometres on foot. Individuals usually forage over great distances (up to 1 km). Tracks indicate little tendency to stay within a delimited area; home ranges are large. They are attracted to fresh holes and will often visit human diggings within a few days. In contrast to *gouldi*, *eremius* do not dig for their prey, but rather rely upon catching it above ground. I have noted *eremius* tracks intercept those of a smaller lizard with evidence of an ensuing tussle. One *eremius*, weighing 42.5 g, had eaten a *Ctenophorus inermis* with a body mass of 12.2 mL (28.7% of its body mass).

An *eremius* was observed to attack another lizard (*Ctenotus calurus*) from ambush in a *Triodia* tussock. Over 70% of the *eremius* diet by volume consists of other lizards. Large grasshoppers, cockroaches, centipedes or scorpions constitute most of the remainder (Pianka 1982). Nearly any other lizard species small enough to be subdued is eaten. In a typical foraging run, an individual *eremius* visits, and goes down into, several burrows belonging to other lizard species, especially the complex burrow systems of the nocturnal skink *Egernia striata*. These activities do not include digging, but could be to search for prey, for thermoregulation or for escaping predators. An *eremius* knows the positions of the burrows it has visited, since it usually runs directly to the nearest one when disturbed.

The smallest gravid female *eremius* had a SVL of 110 mm, and the smallest male with enlarged testes had a SVL of 116, suggesting that females may reach sexual maturity earlier than males. Mating activity was suggested by two *eremius* that were trapped in the same pit on the B-area on 23 November 1992. The male was 151 mm SVL with 10 mm long testes and the 113 mm SVL female contained 4 yolked ovarian eggs 10 mm in diameter.

Varanus tristis

Varanus tristis consume other lizards, nestling birds, and probably bird eggs (Pianka 1971, 1982). Lizard prey include agamids, geckos and various species of *Ctenotus*. One specimen had actually eaten a small thorny devil, *Moloch horridus* (estimated intact volume about 5 mL). A *tristis* weighing 220 g had eaten a large adult aganid *Pogona minor* (estimated volume 50 mL), constituting 22.7% of its body mass. Another *tristis* weighing 330 g had eaten a 57 mL *Pogona minor*, which constituted 17.3% of its mass. *Varanus tristis* drag the base of their tails and leave a very distinctive track with a wide tail mark (Pianka 1971). Tracks typically run more or less directly from tree to tree, most of which they climb looking for food. These large, climbing, predatory lizards must threaten hole-nesting parrots. Galahs have been observed to attack and repel them from their nesting trees. Activity is highly seasonal and the animals rely on building up fat reserves during periods of food abundance to get them through lean periods (Pianka 1971). Both sexes achieve sexual maturity at about 200 mm SVL. A large adult male *tristis* and a gravid female were tracked to the same dead marble gum hollow log on 15 November 1978 at Red Sands; the male's testes were 13 and 14 mm long and the female contained 8 large oviducal eggs.

Varanus gouldi

Varanus gouldi has a strongly seasonal period of activity during the six warm months (September to February) in the Great Victoria Desert. It is completely inactive from March to August (Pianka 1970b). Both sexes achieve sexual maturity at SVL of about 250 mm. Courting or copulating pairs of *gouldi* were seen on 17 and 21 November 1978 and 14 December 1989. Males had enlarged testes (20 and 23.5 mm long) and females contained large yolked ovarian eggs (20–25 mm diameter).

Varanus gouldi capture most of their prey (predominantly lizards and reptile eggs) by digging. They appear to have a very keen sense of olfaction, using their long, forked tongues extensively (Pianka 1970b). Geckos are important prey (dug up in their diurnal retreats), but many diurnal species of lizards are also eaten (*Ctenophorus, Ctenotus, Lerista, Lialis, Menetia, Moloch, Pogona,* and other *Varanus*, including *brevicauda, caudolineatus, gilleni* and *gouldi*). They also eat reptile eggs, and juvenile mammals and birds. These lizards very probably will eat any other lizard that they can catch. Among specimens I have examined, the largest relative prey mass was a *Pogona minor* estimated to weigh about 25 g eaten by a *gouldi* that weighed 180 g, about 13.9% of its body mass.

Varanus giganteus

The perentie, *Varanus giganteus*, attains a total length of more than 2 m. They have been hunted by Aborigines and are exceedingly unapproachable. Their food may once have included small hare wallabies and other mid-sized marsupials, many of which have become extinct. Nowadays, perenties feed on other species of lizards and on introduced European rabbits (several scats examined contained large amounts of hair). The flushed stomach contained a half-digested *Varanus gouldi*, estimated probable body mass about 400 g, about 20% of the perentie's overall body mass.

During 207 days in the field in over 16 months in 1966–68, I encountered only two live perenties (one at the edge of sandplain country near a breakaway and the other at a tor area south of Sandstone) and found no evidence of perentie tracks in the sandy desert. In 1979, I found one perentie, far away from rock outcrops at my sandridge desert site, Red Sands. This animal had several deep burrows. A decade later, during 1989–91, perenties were more abundant at Red Sands. I tracked four different individuals, and judged that several others were present by the size of their footprints and lengths of stride. In addition, I saw a dozen other individuals, several in sandy habitats, while driving to and from my study sites. I speculate that perenties have increased in abundance in the Great Victoria Desert over the past 25 years, probably in direct response to the increased abundance of introduced European rabbits (*Oryctolagus cuniculus*). Rabbits were scarce in the Great Victoria Desert during 1966–68, were moderately abundant during 1978–79, and had become quite common by 1988–93 (pers. obs). Perenties could also be expanding their geographic range southwards and eastwards. I have positively identified two very large individuals crossing the road between Menzies and Leonora, one near Lake Goongarrie (30°01′S, 121°10′E), and the other 46 km south of Leonora.

General patterns

Morphology

Varanus are morphologically conservative. Anatomical measures of adult *Varanus* of each of the seven species are given in Table 2. Head lengths and hind leg lengths are strongly correlated with snout–vent lengths, both within and across species. Relative hind leg length (HLL/SVL) is smallest in *brevicauda* (24%) and largest in *gouldi* (43%). In *gouldi* and *tristis*, no sexual dimorphisms in body proportions were apparent in regressions of HL on SVL, or of HLL on SVL. In both species, adult males tend to be larger than adult females, although outlying females occasionally attain the size of males. However, at a given SVL, adult females tend to be slightly heavier than adult males. In *eremius*, males have longer heads than females of the same SVL (Table 3). Analysis of covariance of log-transformed data shows that this difference is statistically significant ($F = 7.608$, $P = 0.007$). Head lengths of adult male *gouldi* are significantly larger (*t*-test, $P < 0.01$) than those of females (Table 3). No sexual size dimorphism in head size was discernible in *tristis*. Although sample sizes are small for *brevicauda* (9 males and 10 females), females average slightly larger (mean SVL = 93.9 mm) than males (mean

Table 2. Anatomical measurements for adult *Varanus* (mm)

Species	Head length			Snout–vent length			Hind leg length		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
brevicauda	14.0	0.8	19	92.3	5.2	19	22.0	1.3	19
caudolineatus	17.0	1.6	13	101.2	12.4	13	34.9	4.2	13
eremius	24.8	2.0	69	144.3	9.5	69	53.7	4.1	69
giganteus	120.9	21.3	8	689.0	127.6	8	250	54.2	4
gilleni	24.5	2.0	3	152.3		4	45.5	1.0	4
gouldi	50.3	5.0	79	310.8	33.5	79	133.1	16.3	79
tristis	38.1	3.3	97	231.4	21.3	97	91.5	7.8	94

Table 3. Head length statistics for adult male and female *Varanus* and significance levels of *t*-tests for comparisons between the sexes (in mm)

Species	Males			Females			Significance level (*P*)
	Mean	SD	*n*	Mean	SD	*n*	
brevicauda	14.5	0.7	9	13.5	0.5	10	<0.05
eremius	25.3	2.0	47	23.7	1.6	22	<0.01
gouldi	52.6	5.0	43	47.6	3.4	36	<0.01
tristis	38.7	3.1	60	37.1	3.3	37	0.05 NS

NS = not significant.

Table 4. Statistics on body temperatures (°C) recorded from active *Varanus*

Species	Body Temperature Mean	SD	*n*	Slope of regression of BT on AT
caudolineatus	37.8	3.45	10	0.71
eremius	37.3	3.24	75	0.22
giganteus	36.7	2.67	3	—
gilleni	37.4	—	2	—
gouldi	37.7	2.86	78	0.38
tristis	34.8	3.84	46	0.60

BT = body temperature; AT = ambient air temperature.

SVL = 90.4 mm). However, as in *eremius*, head lengths of male *brevicauda* are significantly longer than those of females (ANCOVA, $F = 17.471$, $P = 0.0007$).

Body temperature relationships

Body temperature relationships are very similar among the six species of *Varanus* for which data are available (Table 4). *Varanus tristis* has lower and more variable body temperatures than other species. Some active individuals had high body temperatures. For example, six *eremius* had body temperatures of 42.0°C, 42.0°C, 42.2°C, 42.4°C, 42.4°C and 43.2°C. Three *gouldi* had active body temperatures of 42.0°C, 42.0°C, and 44.7°C. Two *tristis* had body temperatures of 44.2°C and 47.3°C, temperatures which would be lethal for most other animal species, suggesting that *Varanus* possess exceedingly high critical thermal maxima.

Diet and trophic relationships

Previous work has established that *eremius* eats 14 other species of lizards (Pianka 1968, 1982). In 32 new stomachs analysed in the present study, *Ctenotus piankai* (2 individuals) was added to the list of prey species (Table 5). No new species of lizard prey were discovered in the 15 new *tristis* stomachs examined. Six new species of lizard prey were found in the stomachs of 36 new *gouldi* (Table 5), bringing the total number of species of its lizard prey to 27 (Pianka 1970b, 1982). *Varanus gouldi* is cannibalistic and also preys upon *brevicauda*, *caudolineatus* and *gilleni*. Among 17 *brevicauda* with food in their stomachs, one specimen had eaten a *Ctenotus calurus*. The food web among these 40 species of lizards (Table 5) is shown in Fig. 1. Note that *gouldi* is a keystone predator.

Updated, revised summaries of stomach contents including new specimens for each of the various species are given in Tables 5, 6, 7, 8, 9 and 10. As indicated in the species accounts, *Varanus* often consume relatively large prey; both average prey size and maximal prey size are correlated with SVL and HL.

From November to February of 1990 and 1991, a series of 18 newly hatched juvenile *gouldi* were collected. Table 8 summarizes the stomach contents of 14 juvenile *gouldi* (preserved SVL vary from 104 to 152 mm) with prey in their stomachs (4 others had empty stomachs). Like adult *gouldi*, juveniles prey heavily on other species of lizards, which constitute 38.8% of their diet by volume. Lizard prey species eaten by juveniles include *Lerista bipes* (2), *Menetia greyi* (1), juvenile *Ctenophorus isolepis* (2), hatchling *Ctenotus quattuordecimlineatus* (1), *Ctenotus colletti* (1) and *Ctenotus dux* (1). One specimen's stomach contained the tail of an unidentified *Ctenotus* skink.

Reproductive biology

Enlarged yolking ovarian eggs and shelled oviducal eggs were found in several females in *brevicauda*, *eremius*, *tristis* and *gouldi*, increasing sample sizes reported previously. Clutch size data are summarized in Table 11. Average clutch sizes for *giganteus* and *gilleni* are 9.3 ($n = 3$) and 4.3 ($n = 4$), respectively (James *et al.* 1992). Two female *brevicauda* each contained two newly ovulated eggs in their oviducts (still unshelled and not yet elongated). One female (28 November 1992) had a fresh body weight of 12.5 g and contained two eggs 12 mm in diameter with a total mass of 2.5 mL (RCM = 20.0%). The other (9 December 1992) weighed 8.9 g and contained two unshelled eggs 10 mm in diameter with a total mass of 1.2 mL (RCM = 13.5%). One female *eremius* weighing 38.3 g (2 December 1989) contained three shelled oviducal eggs with a total mass of 5.2 mL (RCM = 13.6%). Relative clutch masses and sample sizes are given in

Table 5. Lizard species eaten by various species of *Varanus*

Prey species	*brevicauda*	*caudolineatus*	*gilleni*	*eremius*	*tristis*	*gouldi*	*giganteus*
Varanus brevicauda						x	
Varanus caudolineatus					x	x	
Varanus gilleni						x	
Varanus gouldi						x	x
Ctenophorus inermis				x		x	
Ctenophorus isolepis				x		x	
Gemmatophora longirostris				x			
Moloch horridus					x	x	
Pogona minor					x	x	
Ctenotus ariadnae						x	
Ctenotus atlas						x	
Ctenotus brooksi					x		
Ctenotus calurus	x			x			
Ctenotus colletti					x	x	
Ctenotus dux				x		x	
Ctenotus grandis				x	x	x	
Ctenotus helenae					x	x	
Ctenotus leonhardii						x	
Ctenotus leusueri				x			
Ctenotus pantherinus				x	x		
Ctenotus piankai				x			
Ctenotus quattuordecimlineatus				x	x	x	
Ctenotus schomburgkii				x		x	
Lerista bipes				x	x	x	
Lerista muelleri						x	
Menetia greyi				x		x	
Morethia butleri				x			
Delma butleri				x			
Lialis burtonis						x	
Diplodactylus ciliaris						x	
Diplodactylus conspicillatus						x	
Diplodactylus pulcher						x	
Diplodactylus stenodactylus						x	
Gehyra		x	x		x		
Heteronotia binoei			x				
Nephrurus laevissimus						x	
Rhynchoedura ornata		x				x	

Table 11. The average clutch size of *tristis*, 10 eggs (range 5–17), was more than double that of other species.

Growth rate Before preservation, the eight smallest hatchling *gouldi* individuals collected between late December and early January had fresh (live) SVL ranging from 110 to 118 mm. Juvenile *gouldi* grow rapidly, reaching estimated SVL of about 150 mm in February, within about 50 days of hatching (Fig. 2). One recently hatched *tristis* measuring 72 mm SVL was trapped on 3 March 1991 at Red Sands; this individual was not black like adults but was banded boldly with black and beige. No *tristis* specimens between 72 and 190 mm SVL were ever collected, strongly suggesting that 14 subadult *tristis* measuring between 190 and 230 mm captured from October to March represent yearlings. If so, growth in *tristis* is also rapid. I have not yet encountered a hatchling of the pygmy monitors *brevicauda, caudolineatus, eremius* or *gilleni.*

Seasonality of activity Numbers of *Varanus* of each species collected during different months of the year, plus the number of days spent in the field are given in Table 12. Sampling effort during winter (April–August)

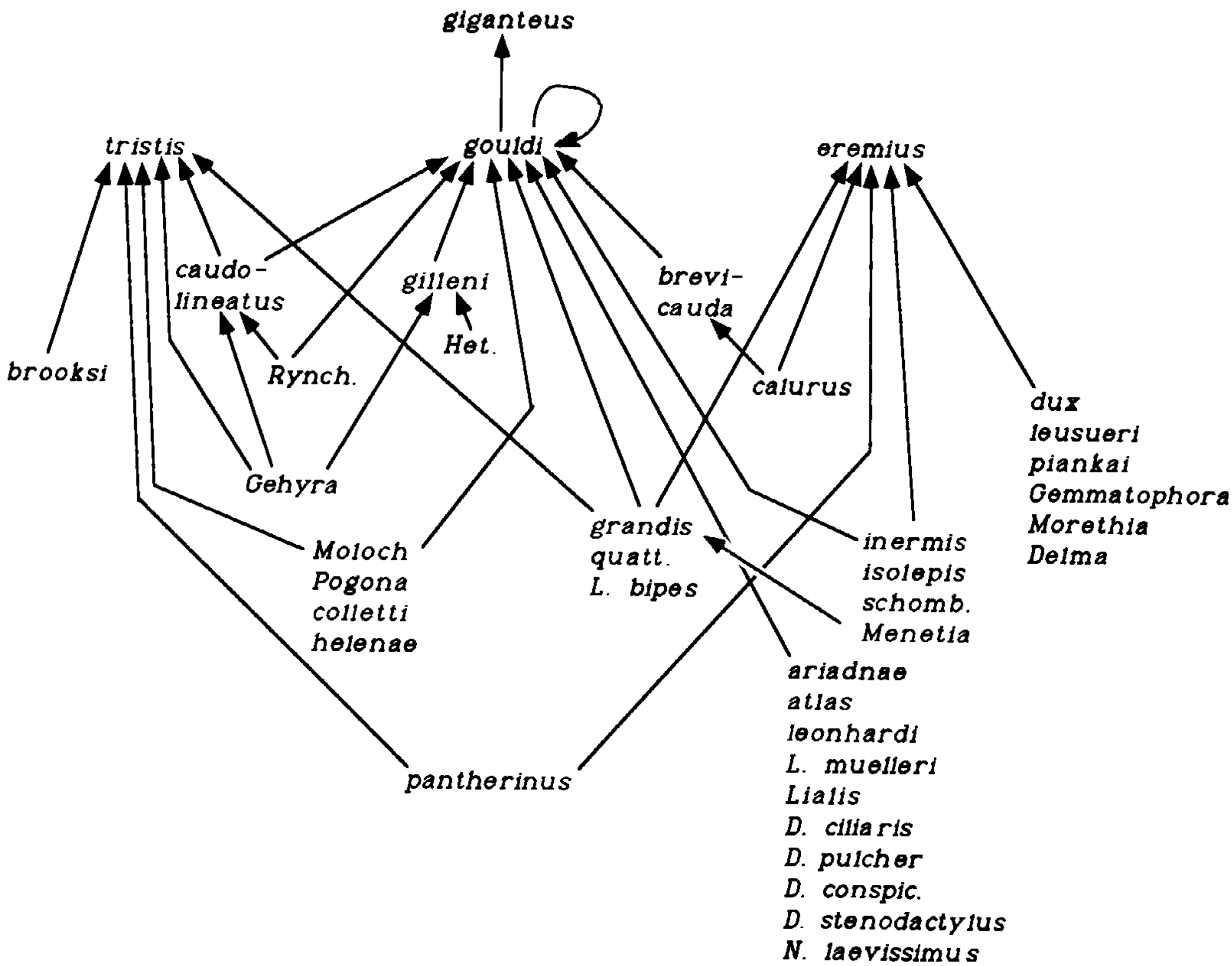

Fig. 1. Food web involving 40 species of lizards in the Great Victoria Desert showing known prey–predator interactions. Other interactions not depicted doubtlessly occur as well. Note that *Varanus gouldi* is a keystone species, which consumes numerous other lizard species as well as three other species of *Varanus* (it is also cannibalistic).

Table 6. Summary of the stomach contents of 26 (17 new) *Varanus brevicauda* with food in their stomachs (9 other stomachs were empty)

Prey species	Number	Volume (mL)	Per cent of total number	Per cent of total volume	Frequency (% stomachs)
Centipedes	3	2.6	8.3	20.3	11.5
Spiders	3	1.0	8.3	7.8	11.5
Grasshoppers	4	2.1	11.1	16.4	15.4
Cockroaches	1	0.1	2.8	0.8	3.9
Beetles	6	0.5	16.7	3.9	23.1
Caterpillars	2	0.8	5.6	6.3	3.9
Other larvae	6	0.4	16.7	3.1	8.3
Unidentified insects	7	1.1	19.4	8.6	26.9
Lizards	1	1.5	2.8	11.7	3.9
Reptile eggs	3	2.7	8.3	21.1	7.7
Totals	36	12.8	100.2	100.0	

Frequencies based on 26 stomachs.

Table 7. Summary of the stomach contents of 82 (22 new) *Varanus eremius* with food in their stomachs (48 other stomachs were empty)

Prey species	Number	Volume (mL)	Per cent of total number	Per cent of total volume	Frequency (% stomachs)
Centipedes	2	1.0	2.04	0.9	2.4
Spiders	1	0.1	1.02	0.1	1.2
Scorpions	3	2.7	3.06	2.5	3.7
Grasshoppers	28	16.6	28.57	15.1	31.7
Cockroaches	3	3.0	3.06	2.7	3.7
Caterpillars	1	0.1	1.02	0.1	1.2
Unidentified insects	7	2.6	7.14	2.4	8.5
Lizards	53	83.6	54.08	76.2	57.3
Totals	98	109.7	100.0	100.0	

Frequencies based on 82 stomachs.

Table 8. Summary of the stomach contents of 79 (16 new) *Varanus gouldi* with food in their stomachs (25 other stomachs were empty)

Prey species	Number	Volume (mL)	Per cent of total number	Per cent of total volume	Frequency (% stomachs)
Centipedes	15	55.1	4.4	8.0	13.9
Spiders	16	26.2	4.7	3.8	12.7
Scorpions	14	52.5	4.1	7.6	17.7
Wasps	1	0.5	0.3	0.1	1.3
Grasshoppers	31	40.5	9.1	5.9	19.0
Cockroaches	11	26.3	3.2	3.8	12.7
Phasmids/mantids	1	0.9	0.3	0.1	1.3
Beetles	52	48.4	15.3	7.0	21.5
Moths	2	3.0	0.6	0.4	2.5
Caterpillars	15	28.4	4.4	4.1	7.6
Pupae	1	1.0	0.3	0.2	1.3
Unidentified insects	16	16.3	4.7	2.4	13.9
Lizards	50	225.4	14.7	32.7	46.8
Birds	2	12.0	0.6	1.7	2.5
Eggs	104	130.6	30.6	19.0	21.5
Mammals	2	9.0	0.6	1.3	2.5
Unidentified vertebrates	2	4.0	0.6	0.6	2.5
Bones	5	8.5	1.5	1.2	6.3
Totals	340	688.6	100.0	100.0	

Frequencies based on 79 stomachs.

Table 9. Summary of the stomach contents of 14 juvenile *Varanus gouldi* with food in their stomachs (4 other stomachs were empty)

Prey species	Number	Volume (mL)	Per cent of total number	Per cent of total volume	Frequency (% stomachs)
Spiders	4	2.2	13.33	12.2	21.4
Hymenoptera	1	0.4	3.33	2.2	7.1
Grasshoppers	2	0.15	6.67	0.8	14.3
Cockroaches	10	4.6	33.33	25.5	21.4
Caterpillars	1	0.3	3.33	1.7	7.1
Unidentified insects	2	2.1	6.67	11.6	14.3
Insect pupae	1	1.3	3.33	7.2	7.1
Lizards	9	7.0	30.0	38.8	50.0
Totals	30	18.05	100.0	100.0	

Frequencies based on 14 stomachs.

Table 10. Summary of the stomach contents of 75 (11 new) *Varanus tristis* with food in their stomachs (25 other stomachs were empty)

Prey species	Number	Volume (mL)	Per cent of total number	Per cent of total volume	Frequency (% stomachs)
Spiders	3	3.5	2.2	0.8	4.0
Ants	5	0.5	3.7	0.1	1.3
Grasshoppers	46	48.4	33.6	11.2	36.0
Cockroaches	9	7.3	6.6	1.7	10.7
Phasmids/mantids	2	2.0	1.5	0.5	2.7
Beetles	1	3.0	0.7	0.7	1.3
Cicada	1	1.0	0.7	0.2	1.3
Caterpillars	3	3.0	2.2	0.7	1.3
Unidentified insects	20	24.1	14.6	5.6	26.7
Lizards	35	301.7	25.6	69.9	44.0
Birds	3	31.7	2.2	7.3	2.7
Reptile eggs	6	4.0	4.4	0.9	2.7
Bones	2	1.1	1.5	0.3	2.7
Leaves	1	0.5	0.7	0.1	1.3
Totals	137	431.8	100.2	100.0	

Frequencies based on 75 stomachs.

Table 11. Frequency of incidence of individuals with varying numbers of enlarged yolked ovarian eggs plus those with shelled eggs in their oviducts among five species of *Varanus* in the Great Victoria Desert

Number of eggs	*brevicauda*	*caudolineatus*	*eremius*	*tristis*	*gouldi*
1					
2	4 (3)		3 (1)		
3		1	4 (2)		
4		3	5 (1)		1
5		1 (1)		1	3
6		1	2		4 (1)
7					2 (1)
8				5 (4)	3
9				2	
10				6 (2)	
11				2 (2)	
12				1	
13					
14				1 (1)	
15				1 (1)	
16					
17				1 (1)	
Mean clutch size (*n*)	2.0 (4)	4.3 (6)	3.6 (14)	10.1 (20)	6.2 (13)
RCM (*n*)	16.7 (2)		15.3 (3)	16.2 (11)	13.9 (2)

Numbers in parentheses are oviducal clutches (body of table) and sample sizes for mean clutch size and relative clutch mass (RCM).

was relatively small, but *eremius* were collected during four of the five colder months. In contrast, no *gouldi* was ever encountered during the six month period March–August. Such size-related seasonal differences in times of activity among these varanids could reduce interspecific competition. All species are most active during spring (October–November), which is probably the mating season.

Fat bodies Stirling (1912) commented on the large size of fat bodies in two emaciated captive perenties. Fat bodies are often quite large in *brevicauda, eremius, tristis* and *gouldi*. Fat bodies allow *Varanus* to take advantage of periods of food abundance, storing up reserves that facilitate survival during food shortages imposed by drought.

Table 12. Numbers of *Varanus* collected during different months of the year, with total number of days spent in the field during each month

Month	*brevicauda*	*caudolineatus*	*gilleni*	*eremius*	*tristis*	*gouldi*	*giganteus**	Days
January	1		1	10	2	27	2	102
February		8		12	13	18	2	90
March		1		9	8		2	40
April							1	3
May				5				17
June				7	1			22
July				8				12
August	2			11	4			32
September				13	13	13	2	54
October	2		1	19	27	24	7	112
November	11	3		21	25	23	1	127
December	6	2		11	10	20	3	115
Totals	22	14	2	126	103	125	20	725

*Includes activity inferred from fresh tracks and road kills, as well as actual sightings.

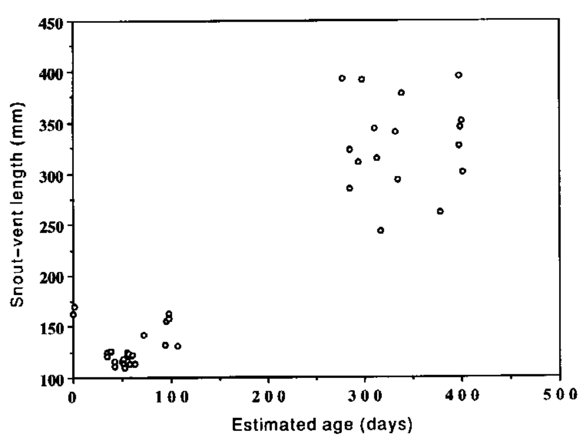

Fig. 2. Snout–vent length of juvenile *Varanus gouldi flavirufus* plotted against estimated age as inferred from date of collection. Except for two aberrant large juveniles at day 0, the smallest hatchlings are clustered about day 50. These lizards appear to grow rapidly, reaching SVL of 150 mm within about 50 days (day 100). Both sexes achieve sexual maturity at 1 year of age at about 250 mm SVL.

DISCUSSION

Male varanids could attain longer SVL than females either because survivorship is higher among males or because sexual selection favours larger size, *per se*. In the absence of data on survivorship, these alternatives cannot be separated. Young adult male *Cnemidophorus tigris* (Teiidae) grow faster than young adult females (Anderson & Vitt 1990). Sexual dimorphisms in head lengths have been noted in other species of scincid and teiid lizards (Fitch 1981; Simbotwe 1985; Vitt & Cooper 1985; Anderson & Vitt 1990). Chasing, clasping, biting fights and ritualized combat displays have now been observed between male monitors of many different species (Murphy & Mitchell 1974; Twigg 1988; Carter 1990; Thompson *et al.* 1992 and references therein). Presumably, sexual selection for fighting ability among males favours larger head lengths because males that win fights with other males gain access to more females and thus have higher reproductive success.

In an analysis of the costs and benefits of lizard thermoregulatory strategies, Huey and Slatkin (1976) identified the slope of the regression of body temperature against ambient environmental temperature as a useful indicator (in this case, an inverse measure) of the degree of passiveness in regulation of body temperature. On such a plot a slope of one indicates true poikilothermy or totally passive thermoconformity (a perfect correlation between air temperature and body temperature), whereas a slope of zero reflects perfect thermoregulation. Lizards span this spectrum. Among active diurnal heliothermic species, regressions of body temperature on air temperature are flat (for several species, including some quite small ones, slopes do not differ significantly from zero); among nocturnal species, slopes of similar plots are typically closer to unity (Pianka 1986). Various other species (nocturnal, diurnal and crepuscular), particularly Australian ones, are intermediate, filling in this continuum of thermoregulatory tactics (Pianka 1986). Slopes of regressions of body temperature on ambient air temperature were calculated for four of the seven species of *Varanus* (Table 4). The data suggest *eremius* and *gouldi* are good thermoregulators, while the arboreal species, *caudolineatus* and *tristis*, do not thermoregulate as well.

Diets of *gouldi* vary greatly in different parts of its wide geographic range. In the tropical part of northern Australia, four sympatric species of *Varanus* use different macrohabitats (Shine 1986), which in turn expose them to different prey species. Data from stomach flushing (Shine 1986) suggest that the diet of *gouldi* in the Northern Territory is dominated, by volume, by mammals and lizards (scorpions, spiders, grasshoppers, beetles and insect larvae are also eaten). The diet of *gouldi* near Perth, Western Australia, is dominated by mole crickets and spiders (Thompson, pers. comm. 1993). In the Great Victoria Desert, the most important foods of adult *gouldi* by both numbers and volume are reptile eggs, lizards and beetles (Table 8). Juvenile *gouldi* consume many cockroaches and lizards (Table 9).

Losos and Greene (1988) plotted maximal prey mass, expressed as a proportion of monitor mass, for 16 species of *Varanus* (their datum point for *komodoensis* is excluded here because the lizards do not actually eat an entire water buffalo). These data, plus six data points from the present paper, are plotted in Fig. 3. About half the species plotted, including all of those from the Great Victoria Desert, consume quite large prey items relative to their own body size.

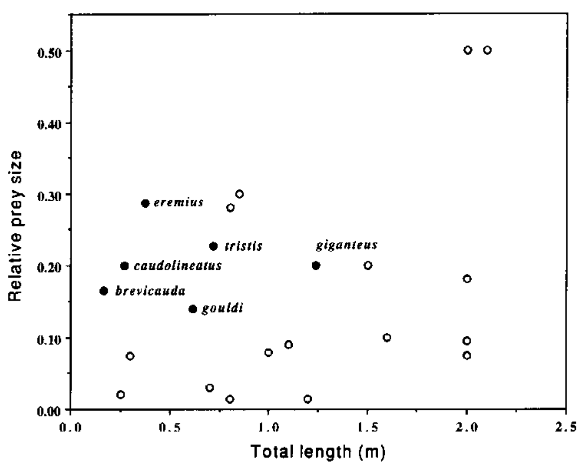

Fig. 3. Relative maximal prey size, expressed as a fraction of lizard mass, plotted against estimated total length among 22 species of *Varanus* (partially based on a figure from Losos and Greene [1988] with new data from the present study [6 solid circles]). Half the species plotted, including all those from the Great Victoria Desert, consume quite large prey items relative to their own body size.

Four species of *Varanus* occur on the L-area: one mid-sized arboreal species (*tristis*) plus small (*eremius*), medium (*gouldi*) and large (*giganteus*) terrestrial species. At Red Sands, six species of *Varanus* occur in sympatry (*brevicauda, eremius, gilleni, tristis, gouldi* and *giganteus*), two of which are arboreal (*gilleni* and *tristis*). Monitors in both these assemblages vary widely in size. Both average prey size and the size of the largest prey items eaten are greater for larger species than they are for smaller species.

Size differences between closely related sympatric species have been implicated as being necessary for coexistence (Hutchinson 1959), and even in the 'assembly' of communities (Case *et al.* 1983), although there has been considerable dispute over the statistical validity of these patterns (Grant 1972; Horn & May 1977; Grant & Abbott 1980). There may be a definite limit on how similar two competitors can be and still avoid competitive exclusion. Character displacement in average mouthpart sizes is often about 1.3, and the length ratio of 1.3 has been suggested as a crude estimate of just how different two species must be to coexist. (For body mass, a ratio of 2 corresponds to the length ratio of 1.3.) Table 13 gives Hutchinsonian ratios (Hutchinson 1959; Schoener 1984) of average head lengths among the seven species. Only two of 21 ratios are below 1.3, *caudolineatus/brevicauda* and *eremius/gilleni*. Both are between pygmy monitors, and both are between an arboreal and a terrestrial species. In addition, *caudolineatus* and *brevicauda* are not sympatric at the study sites and *gilleni* was rare (1 specimen) in sympatry with *eremius* at Red Sands.

Perhaps the most thorough analysis of Hutchinsonian ratios (Schoener 1984) comes from size ratios among all possible pairs and triplets of the 47 species of accipiter hawks. Frequency distributions of expected size ratios were generated for all possible combinations of species, which were then compared with existing accipiter assemblages. Schoener found a significant paucity of low size ratios among real assemblages, strongly suggesting size assortment. Following Schoener (1984), head lengths of 24 species of Australian *Varanus* were estimated from data on maximum SVL (Greer 1989). Among the seven desert species (Table 1), which include size extremes and

Table 13. Hutchinsonian ratios of head lengths (larger/smaller) of various pairs of species of *Varanus*

Species	*caudolineatus*	*gilleni*	*eremius*	*tristis*	*gouldi*	*giganteus*
brevicauda	1.22	1.75	1.78	2.73	3.61	8.67
caudolineatus		1.44	1.46	2.24	2.96	7.11
gilleni			1.01	1.56	2.06	4.94
eremius				1.54	2.03	4.88
tristis					1.32	3.17
gouldi						2.40

both major lineages, average adult head length is strongly correlated with average adult SVL ($r = 0.999, P<0.001$).

The linear regression equation derived from these seven species

$$\text{Head length} = -2.07 + 0.1773 \times \text{SVL}$$

was then used to estimate head lengths for the other 17 species.

Ratios of larger/smaller for all possible pairs of species were computed ($n = 276$) and a cumulative frequency distribution was assembled. This represents a null model of expected size ratios against which distributions of ratios in observed assemblages can be compared. In both real assemblages in the Great Victoria Desert, there are significantly more high Hutchinsonian ratios than expected in random subsamples drawn from the species pool of all Australian varanids (Fig. 4). (Kolmogorov-Smirnov d_{max} statistics: Red Sands 0.175 ($n = 15$), $P<0.05$; L-area 0.167 ($n = 6$), $P \sim 0.08$). Such high Hutchinsonian ratios suggest that either size assortment or character displacement has resulted in extant assemblages that differ in size.

James *et al.* (1992) reported average clutch sizes of 2–5 among seven species of Australian pygmy monitors (subgenus *Odatria*), similar to those of most species examined here (Table 11). However, *tristis* has an average clutch size of 10 eggs and three females with shelled eggs in their oviducts had clutches of 14, 15 and 17. What ecological factors could have favoured the rapid evolution of large clutch size in *tristis*? Relative clutch mass is similar among the four species for which data are available (Table 12), demonstrating that high fecundity in *tristis* is achieved at the expense of egg and neonatal size. Arboreality cannot explain the high fecundity because *caudolineatus* has a lower clutch size. Very little is known about juvenile *tristis* (I have only collected one individual), but if they live at low densities in unusual microhabitats such as mallees and, hence, experience lower levels of competition from adults or less predation than do juveniles of other species, a smaller size could be tolerated. Further research is needed to resolve this intriguing question.

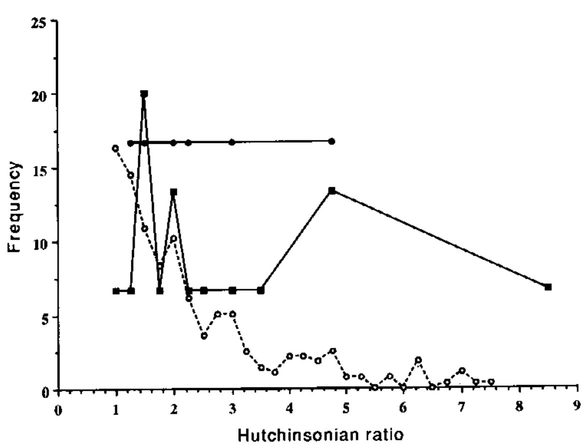

Fig. 4. Frequency distribution of Hutchinsonian ratios of head lengths (larger/smaller). (--O--) 276 interspecific pairs of all possible combinations between all species of Australian *Varanus*; this represents a null model expected from random samples of the available species pool. The solid lines represent two observed assemblages of 4 and 6 species of varanids at the L-area (—●—) and Red Sands (—■—); observed assemblages exhibit large ratios more frequently than expected suggesting either size assortment or character displacement.

Most students of *Varanus* believe that the genus arose in Eurasia (McDowell & Bogart 1954), where the majority of the 10 subgenera still occur today, but others argue for a Gondwanan origin (K. Aplin, pers. comm.). Varanids are considered to be a late Tertiary invader of Australia because the earliest Australian fossils date from the middle Miocene of South Australia. The invasion of Africa produced only four species (all large) of *Varanus* (*albigularis*, *exanthematicus*, *griseus* and *niloticus*), which were recently demonstrated to be a monophyletic lineage (King *et al.* 1991).

In contrast, extensive adaptive radiations have taken place in Australia in two distinct evolutionary lineages: the subgenus *Odatria* includes 17 species of pygmy monitors, while the subgenus *Varanus* includes the 7 larger species of Australian monitors plus *komodoensis*. Small size appears to have evolved only one other time in *Varanus*, in the lineage of the Asian clade that led to *karlschmidti* and *prasinus*. The extensive adaptive radiation of pygmy monitors in Australia suggests a question: Why haven't varanids in other parts of the world evolved small body size? Why haven't more species of *Varanus* evolved in Africa, Asia and southeast Asia? Has the presence of small predatory mammals such as viverids and small foxes precluded African and Asian adaptive radiations of *Varanus*? If so, why have small marsupial predators such as dasyurids been unable to usurp the niche? Large size appears to have evolved several times. What factors allowed the adaptive radiation of the subgenus *Varanus* in Australia? Several workers have suggested that the arrival of varanids on a continent in which other terrestrial vertebrates had not yet completely occupied the carnivore niche provided varanids with an opportunity to diversify to fill many empty niches (Storr 1964; Pianka 1969a; Hecht 1975). Note, however, that some marsupial predators, such as dasyurids, thylacines and *Thylacoleo*, were present in Australia during the adaptive radiations of varanids. As Hecht (1975) notes, 'The real question is what occupied the varanid adaptive zone before the arrival of the lizards and why did the marsupials not fully occupy the zone?'

ACKNOWLEDGEMENTS

This research was financed by grants from the National Geographic Society, the John Simon Guggenheim Memorial Foundation, a senior Fulbright Research Scholarship, the Australian–American Educational Foundation, the University Research Institute of the Graduate School at the University of Texas at Austin, the Denton A. Cooley Centennial Professorship in Zoology at the University of Texas at Austin, the US National Science Foundation, the US National Aeronautics and Space Administration, plus my own pocketbook. For logistic support, I am indebted to the staffs of the Department of Zoology at the University of Western Australia and the Western Australian Museum plus the staffs of Conservation and Land Management, both at Kalgoorlie and at the Western Australian Wildlife Centre at Woodvale. Assistance in the fieldwork was generously given by Helen L. Dunlap, William F. Giles, Daniel Bennett, the late Wayne Saunders, and Magnus Peterson. Gad Perry and the editor Mike Bull carefully read the manuscript and made numerous useful suggestions for improvements.

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