ARTICLES

Introductory note. – The following article is a previously unpublished manuscript by Dennis King (1942-2002). It was slated to appear together with King and Rhodes (1982, Sex ratio and breeding season of *Varanus acanthurus*, Copeia 1982:784-787), but for some reason did not. Ruth Allen King has kindly consented to publication in *Biawak*, and provided a copy of Dennis's manuscript and data sheets. I have reconstructed the lost Fig. 1 from the original data and corrected a few typographical errors, but the manuscript is otherwise unchanged.

This is the most detailed dietary analysis available for *V. acanthurus*. The specimens examined here overlap partially with those analyzed by Losos and Greene (1988, Biol. J. Linn. Soc. 35:379-407) and James, Losos and King (1992, J. Herp. 26:128-136), and are included in a summary by Dryden (2005, Varanoid Lizards of the World, pp. 298-307); thus, the data in these four contributions should be viewed as complementary, but not strictly additive.

Samuel S. Sweet

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The Diet and Foraging Strategy of *Varanus acanthurus*

DENNIS KING
[*deceased*]

Agriculture Protection Board of Western Australia,
Bougainvillea Avenue, Forrestfield,
Western Australia, 6058

Abstract - The diet of 127 *Varanus acanthurus*, as revealed by stomach contents, consisted mainly of invertebrates (principally Orthoptera, Coleoptera and Dictyoptera) and lizards. There was no apparent relationship between predator and prey size within the sample but larger individuals tended to eat more food items than did smaller ones. These findings are consistent with predictions on the diet of intensive foragers. No seasonality in feeding activity of *V. acanthurus* could be demonstrated.

Although there are numerous references to the diet and foraging strategy of varanid lizards (Pianka 1973, Pough 1973, Regal 1978) there have been few studies of their diet based on the examination of the contents of substantial numbers of stomachs (King and Green 1979). Varanids are active carnivores and intensive foragers (Pianka 1973, Regal 1978, King and Green 1979, Auffenberg 1981) which have been reported as feeding "primarily upon the eggs and young of vertebrates and the adults of smaller species" (Pianka 1973), although a number of species are known to eat large numbers of invertebrates (Pianka 1969a, 1970b, 1971, 1982, Cisse 1972, King and Green 1979, Greene 1980).

The relationship between predator and prey size in lizards has been discussed by Pianka (1969b and 1982) who stated as a generalization that small lizards or species tend to take smaller prey than larger individuals or species. Pough (1973) suggested that insect-sized prey would not be an energetically efficient diet for large carnivorous lizards; Pianka (1968a) pointed out, however, that *V. eremeus*, which forages widely, could not afford to pass by large insects because of the uncertainty of finding and capturing larger prey. Griffiths (1980) predicted that predators which use a strategy of foraging widely would feed mainly on small prey.

The stomach contents of a large sample of preserved specimens of the medium-sized Ridge-tailed Monitor (*Varanus acanthurus*) in several Australian museums were examined to establish what they eat and to determine whether or not their diet was consistent with the predator-prey size relationship discussed above.

Materials and Methods

Specimens examined are held in the reptile collections of the Northern Territory Museum, Western Australian Museum and Queensland Museum. The stomachs (n = 201) were removed and individual prey items in those containing food (n = 127) were identified to species, where possible, for vertebrates and to the level of order for invertebrates. The longest dimension of each relatively intact prey item was measured with vernier calipers and the item was ascribed to a category of "target-size" using templates based on the area it would present to a predator (Webb et al 1982). The templates used differed in shape, but each had the same surface area as others of that category. The linear dimensions of each category are double those of the previous one, and thus each target size area increases by a factor of 4 over the previous one. The surface area of Target Size 4 is 4.0 sq cm (Webb et al 1982). Snout vent length and head length of each monitor were measured with calipers, and a regression of snout-vent length on head length was calculated from specimens which were not twisted or contorted ($r^2 = 0.95$) so that head length could be used as the standard measure of lizard size (HL = 0.12241 SV + 8.20134 for males and 0.11154 SV + 8.45319 for females).

Results

The majority of the items found in the stomach contents were invertebrates (Table 1), with grasshoppers, beetles and cockroaches comprising almost 2/3 of the total number of food items (Table 1). Grasshoppers occurred in 50% of stomachs and made up 17% of food items. The largest items in the diet were lizards (agamids, gekkonids and scincids) but these occurred in only 14.5% of stomachs containing food and constituted only 7% of all food items (Table 1). All lizards eaten fell into target-sizes of TS 5 to TS 7. Other prey items were found infrequently and then only in small numbers (Table 1). Plant material occurred in 15% of the stomachs, but as it all consisted of mature leaves, it did not appear to have been selected as food, and was presumably accidentally ingested when capturing or eating prey.

Table 1. Food items in stomachs of 127 *Varanus acanthurus*.

Item	No. of stomachs	% Occurrence	Total minimum # of items	% of total items
Grasshoppers (Orthoptera)	63	50	134	44
Beetles (Coleoptera)	29	24	53	17
Unidentified Insects	25	20	27	9
Lizards (Agamidae, Scincidae,Gekkonidae)	18	14.5	23	7
Cockroaches (Dictyoptera-Blattaria)	16	13	17	6
Egg cases (Orthoptera)	8	6.5	10	3
Spiders (Arachnida)	8	6.5	9	3
Slaters (Isopoda)	4	3.2	9	3
Caterpillars (Lepidoptera)	5	4	6	2
Cicadas (Hemiptera)	3	2.4	5	2
Snails (Mollusca)	3	2.4	3	1
Stick Insects (Dictyoptera-Mantodea)	2	1.6	2	trace
Centipedes	2	1.6	2	trace
Ant lion (Myrmeleonydiae)	1	0.8	1	trace
Robber fly (Diptera)	1	0.8	1	trace
Cricket (Orthoptera)	1	0.8	1	trace
Mantispid (Neuroptera)	1	0.8	1	trace
Tick (Acarina)	1	0.8	1	trace
Bone fragment	1	0.8	1	trace
Unidentified carrion	1	0.8	1	trace
Plant material	19	15+	?	?

Table 2. Target sizes of prey eaten by different size classes of *V. acanthurus*.

	Head length (mm) 15.0-19.9		Head length (mm) 20.0-24.9		Head length (mm) 25.0-29.9		Head length (mm) 30.0 +	
Target Size	No. of Items	% of Items	No. of Items	% of Items	No. of Items	% of Items	No. of Items	% of Items
2	0	0	3	6	0	0	0	0
3	0	0	6	12	8	13	3	4
4	5	50	19	38	22	33	37	45
5	4	40	26	32	29	45	41	49
6	1	10	4	8	6	9	0	2
7	0	0	2	4	0	0	0	0
Total	10		50		65		83	

There was no significant relationship between size of *V. acanthurus* and the size of food items eaten. In lizards with HLs from 15.0 - 19.9 mm, the mean greatest dimension of prey items was 2.39 mm ± 0.49 (range 1.0 - 5.9, n = 10) and the values for other size classes were:
20.0 - 24.9 mm, X = 2.52 ± 0.36 (0.4 - 14.0, n = 50),
25.0 - 29.9 mm, X = 2.25 ± 0.19 (0.5 - 9.7, n = 65),
and >30.0 mm, X = 2.05 ± 0.12 (0.6 - 7.5, n = 83).
There was also no relationship between size class of the lizards and target-size of their prey (Table 2). The majority of items (70 - 94%) eaten by all classes were in TS 4 and TS 5 and lizards in the largest size class had eaten the fewest items in TS 6 and TS 7 (Table 2).

The relationship between lizard size and the number of reasonably intact prey items found in them is shown in Figure 1. The slope of the regression line (0.12) is significant ($p = 0.028$) despite the low regression coefficient ($r^2 = 0.062$). All lizards which contained five or more prey items had head lengths >25.0 mm.

A high percentage of stomachs collected in each month contained food items (Table 3), an indication that in most areas *V. acanthurus* probably feeds during all months of the year.

Table 3. Percentage of stomachs of *V. acanthurus* which contained food, by month of collection.

Month	No. of stomachs examined	Stomachs containing food	% stomachs containing food
JAN	10	4	40
FEB	14	9	64
MAR	9	5	55
APR	22	18	82
MAY	25	13	52
JUN	18	7	39
JUL	16	10	63
AUG	24	10	42
SEPT	17	11	65
OCT	20	16	80
NOV	3	3	100
DEC	23	17	74
Total	201*	123*	

* Contents of 4 additional stomachs, for which no month of collection was recorded, were also examined

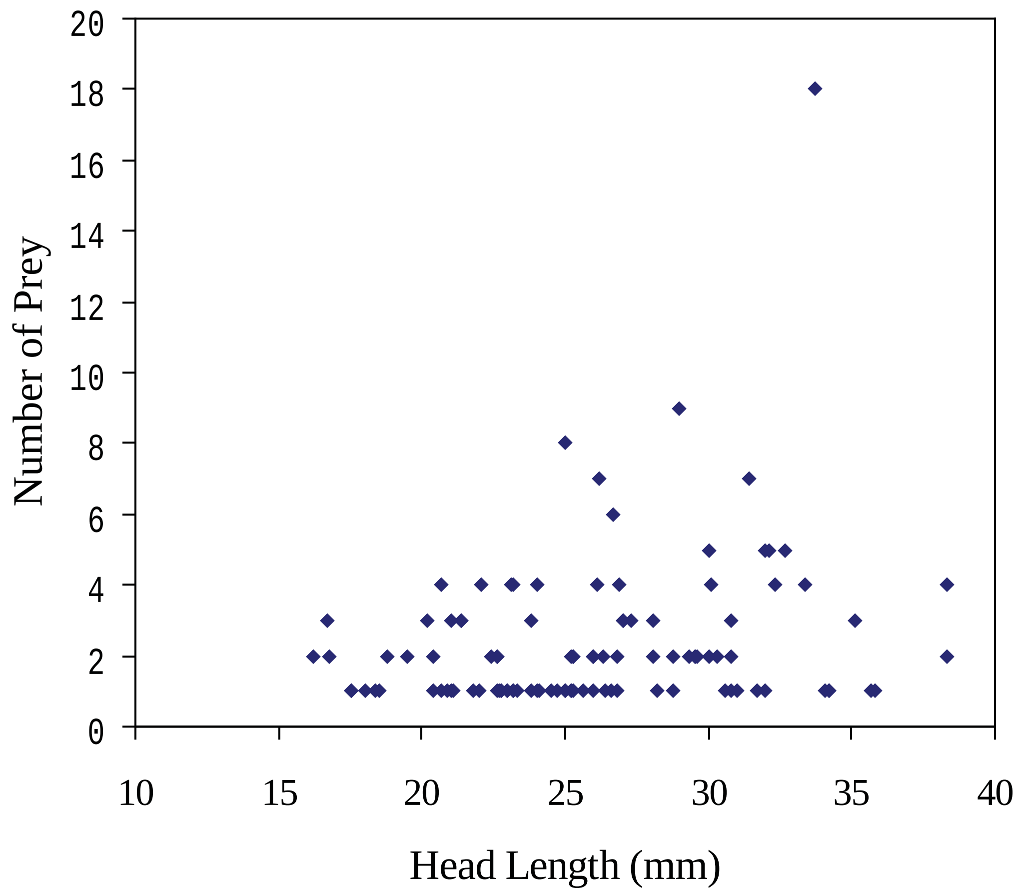

Figure 1. Relationship of head-length to number of prey items found in *V. acanthurus* [the 18 items record includes 17 beetles plus grasshopper fragments].

Discussion

The diet of *V. acanthurus* consists mainly of insects and lizards, as stated by Bustard (1970) and Cogger (1975), and is similar to that of other small and medium-sized species of Australian varanids (Pianka 1968, 1969a, 1970a, b, 1971, King and Green 1979). Varanids have morphological (Rieppel and Labhardt, 1979) and behavioural (Loop 1974) adaptations which enable them to feed on large prey, and large species such as *V. komodoensis* (Auffenberg 1981) and *V. giganteus* (King et al., unpubl. data) appear to feed mainly on large vertebrates. Nevertheless, the majority of food items eaten by *V. acanthurus* were invertebrates (Table 1) as has been reported for other small and medium-sized varanids (Pianka 1968, 1970b, 1971, Cisse 1972, Greene 1980). Despite having a low frequency of occurrence in the diet of *V. acanthurus*, lizards represented a large percentage of the total volume of food consumed.

Although a relationship between size of a predator and of its prey has been shown in other species of lizards (Pianka 1969b, Auffenberg 1978, 1981) no such relationship was apparent in *V. acanthurus* (Table 2). However, as stated by Pianka (1968), it may well be energetically inefficient for a lizard which forages widely to ignore large insects when they are encountered, given the uncertainty of finding larger vertebrate prey. Most *V. acanthurus* are smaller than the 300 g Pough (1973) gives as the upper limit at which eating insects would be efficient; however, medium-sized species of varanids which are above that upper limit do eat considerable amounts of invertebrates (Cisse 1972, King and Green 1979, Greene 1980).

Perhaps the diet of varanid lizards should be viewed in the same way as that recently suggested for crocodiles, in that while the maximum size of prey eaten increases with size of the predator, the ability to eat small prey is maintained, and the size of prey most commonly eaten may change only marginally with increased body size (Webb et al. 1982).

Varanid lizards generally forage over considerable distances (Pianka 1968, 1970a, 1971, 1982, Green and King 1978, Auffenberg 1978, 1981, Regal 1978) and aspects of their anatomy and physiology are well suited to a wide-foraging strategy. They have well-developed olfactory and visual systems (Auffenberg 1978, 1981), a high aerobic scope and capacity for rapidly repaying oxygen debt (Bennett 1972), and show evidence of remembering potential food sources (Auffenberg 1978, 1981). The major energetic cost for intensive foragers is in searching, and the consequent low handling cost predicts that they should, to a large extent, feed upon small prey (Griffiths 1980), retaining flexibility and a relative generality of diet (Pianka 1978, Regal 1978). The optimal strategy for such predators is that they should eat essentially all the palatable food they encounter (Pianka 1978). Pianka (1982, Table 6), in a comparison of 6 species of Australian varanid lizards in the arid zone, has recently shown that although prey size tends to increase with the size of the species of predators, even the largest species examined still ate substantial numbers of small prey items. In addition over half of the prey items eaten by *V. gouldii*, which was the largest species for which he provided dietary data, were less than 1.1 cc. It appears that while varanid lizards may seek large prey items, they also take small prey when they are encountered. The irregular seasonal conditions and unreliability of the availability of large prey in the arid and semi-arid regions of Australia may frequently result in several species of varanid lizards relying heavily on invertebrates as their main prey. Large invertebrates may thus form the major portion of the diet of many varanid lizards in these regions for prolonged periods.

Stomach contents of larger lizards tended to contain more food items than did those of smaller individuals (Fig. 1).

The high percentages of *V. acanthurus* stomachs containing food during each month (Table 3) indicate that there is no annual period of inactivity characterising the species throughout its range, despite the pronounced seasonality in reproductive condition (King and Rhodes, 1982).

Varanus acanthurus seems to be a species which is an opportunist feeder, which forages widely, and is active throughout the year. Its diet contains a wide range of food items and the majority of these are invertebrates.

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