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Ecological and evolutionary implications of diet in monitor lizards

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A survey of 35 species indicates that monitor lizards (*Varanus*) typically hunt over large areas, search in particular microhabitats, and feed frequently on a wide variety of prey, many of which are relatively small. There is ontogenetic, seasonal, and geographic variation in diet. With some exceptions, invertebrates are the predominant prey, but rare predation on vertebrates is often energetically significant. A few monitors specialize on prey types that occur as occasional items in the diet of species with more generalized diets; these include crabs, snails, orthopterans, lizards, and large mammals. For most species, prey specialization occurs via habitat selection and a variety of prey types and sizes are eaten, as expected for widely searching predators. Comparisons with other anguimorphans suggest that derived features of *Varanus* are associated with high body temperature and activity levels; specialized chemoreception; and rapid, skillful capture of hidden and/or potentially hard to catch prey. Occasional ingestion of moderately large prey is primitive for Varanoidea (Helodermatidae + Varanidae), accentuating a trend that is perhaps primitive for anguimorphan lizards. Reduction of very large prey prior to ingestion is a derived attribute within *Varanus*, seen infrequently in several larger species and commonly in *V. komodoensis*. This study illustrates the synthesis of comparative natural history in a phylogenetic context, a method that addresses the history of organismal change.

KEY WORDS:—Feeding – Varanidae – lizard evolution – adaptive radiation.

CONTENTS

INTRODUCTION

Monitor lizards (genus *Varanus*) range from 0.28 m to more than 3.0 m in total length (TL) and occupy deserts, savannas and tropical habitats in the Old World (Mertens, 1942a). Most are terrestrial, but several species are arboreal and a few are semi-aquatic. Approximately two-thirds of the 37 living species

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occur in Australia (Cogger, 1983), where the genus is ecologically most diverse. Fossils demonstrate that varanids were once worldwide in the Northern Hemisphere, and that a Pleistocene species (*V. priscus*) reached a TL $\leqslant 7$ m (Hecht, 1975; Estes, 1983a; Pregill, Gauthier & Greene, 1986).

Monitor lizards have long fascinated lay people and naturalists, and recent research has demonstrated a number of unusual physiological, morphological and behavioural attributes. Discussions of these traits often refer to roles in feeding, and a particularly persistent assertion has been that monitors are specialists on large vertebrate prey. This is correct for one well-studied species (*Varanus komodoensis*; Auffenberg, 1981), but little information is available on the natural diets of most monitors, and several recent studies are inconsistent with previous speculation (e.g. Pianka, 1970a; Auffenberg & Ipe, 1983; Greene, 1986).

Here we report stomach contents of *Varanus* in museums and summarize literature on their feeding biology. Using those data and information on phylogeny, we address five questions: (i) How are diets characterized in terms of prey taxonomy and relative size? (ii) What factors influence dietary variation? (iii) What tactics are used to locate and subdue prey? (iv) How has feeding biology evolved in *Varanus*, and within the larger clade Anguimorpha? (v) Which morphological, physiological and behavioural characteristics of monitors are likely to have arisen as feeding adaptations? Our study illustrates the synthesis of comparative natural history in a phylogenetic context, a method that addresses the history of organismal change (Lauder, 1982; Greene, 1986).

METHODS AND LIMITATIONS

We examined approximately 400 specimens of *Varanus* in the American Museum of Natural History; Bernice P. Bishop Museum; California Academy of Sciences (CAS); Field Museum of Natural History; Museum of Comparative Zoology, Harvard University (MCZ); and Museum of Vertebrate Zoology, University of California, Berkeley. One hundred and eighty-six specimens of 22 species contained identifiable stomach contents. Invertebrates usually were identified to the ordinal, vertebrates to the familial or generic level. Weights were recorded after monitors and intact prey had been briefly drained and blotted of excess fluid. Original weights of some partial items were estimated by comparison with complete specimens of the same species. Prey/predator mass ratios (MR) were calculated from known or estimated weights. Counts of fragmentary body parts were used to estimate the minimum number of individual prey. The "importance index" is the sum of the MRs for that prey type divided by the sum of all prey MRs, and accounts for the size of the prey items and the predator (Greene, 1986). We assigned non-intact prey items the mean MR for that type in that species.

Most literature reports only consider the frequency of prey and their size relative to other prey items (see Hyslop, 1980; Webb, Manolis & Buckworth, 1982). For conclusions on foraging behaviour, we need to know the frequency and size of prey types, the number of predators consuming each prey type, the distribution of number of items taken by individual predators and the relative size of predators and prey. For example, if prey size increased linearly with predator size, larger items would not be more important simply because they constitute a greater proportion of the total prey volume or mass of a sample. Although relative metabolic requirements decrease with increased predator size (but see Dryden, Green, King & Losos, in review) and the energetic value and digestibility of prey types differ, MR serves as a first approximation of the energetic contribution of different items when information on the digestibility, assimilation efficiencies, and caloric content of prey are not available. Failure to report predator-prey sizes might also mask ontogenetic shifts in foraging behavior. The Appendix presents details that can be integrated in future studies of predator-prey interactions (*cf.* Greene, 1988).

Potential biases include the tendency for museums to have few large, intact specimens, and for the stomachs of large individuals of the larger species to be empty more frequently than those of smaller individuals of the same species. Only nine stomach contents in our study exceeded 1.0 m in TL, and only two were longer than 1.5 m. We disregarded very small invertebrates in stomachs with partially digested vertebrates (mainly lizards; most anurans were little digested) and thus perhaps secondarily ingested (*cf.* Jackson, Campbell & Campbell, 1974). Although chitinous parts can persist in the stomachs of reptiles for several months (Garnett, 1985), those remains are fragmentary and would not affect calculations of MR. For species in which there is little evidence of predation on vertebrates, secondary ingestion is not likely. For species which eat vertebrates, particularly anurans, some bias in the observed proportions of prey may result. Monitors that recently ate relatively large prey might be less active and thus less vulnerable to capture than those containing small items, but we have no evidence of such a bias. Moreover, captive *Varanus* typically bask after large meals, rather than seek seclusion (unpublished observation), and non-heliophilic snakes that do seek cover after eating large meals nevertheless are collected (e.g. Greene, 1983, 1984).

Assigning non-intact items mean MR for intact items of that prey type is probably appropriate in most cases. The importance of orthopterans in the diet of *Varanus exanthematicus* is probably exaggerated, however, because the only intact orthopteran probably had a larger MR (0.045) than the other four would have had. Cases where we found no intact prey of a given type were assigned an index value of 0.000 (Table 1). The only significant prey types affected are reptile eggs and lepidopterans in *V. bengalensis* and roaches in *V. gilleni* and *V. glauerti*.

RESULTS

Varanus acanthurus: Australia, arid habitats, TL 0.7 m (Cogger, 1983). Orthopterans, beetles, cockroaches and lizards (Agamidae, Gekkonidae, Scincidae) were the most common items in 127 stomachs. No relationship was found between monitor size and prey size, but larger lizards generally contained more items (King, in press). Orthopterans were the predominant prey, by total number of individuals and frequency of occurrence, in 21 stomachs we examined. Most stomachs contained one or two items, but a 294 g *V. acanthurus* has eight lepidopteran larvae and a 119 g specimen had seven grasshoppers.

Varanus bengalensis: Southern Asia, eurytopic, TL 1.5–2.0 m (Mertens, 1942c). Bengal monitors are generalists, eating many invertebrates, particularly beetles and orthopterans. A variety of vertebrates are eaten, primarily by larger

TABLE 1. Importance indices of various prey types. The importance index is calculated for all monitor species for which weighable prey are available for four or more specimens. Data on *Varanus prasinus* are from Greene (1986). Calculations for *V. giganteus* include data from King *et al.* (unpublished observations) and Horner (personal communication). Calculations on *V. gilleni*, *V. glauerti*, *V. glebopalma*, *V. pilbarensis*, *V. primordius* and *V. storri* include data from Losos, King and James (unpublished observations). An importance index value of a prey type for a species requires at least one intact item. Prey >0.05 and >0.10 is the importance index value of all prey items with relative mass (MR) >0.05 and >0.10. Prey types in a species' diet for which we have no intact prey items are indicated by an asterisk. MR >0.100 incicated by bold type

	Species							
	V. acanthurus	*V. bengalensis*	*V. exanthematicus*	*V. giganteus*	*V. gilleni*	*V. glauerti*	*V. glebopalma*	*V. gouldii*
Prey types								
Lizards	**0.310**	**0.198**	0.000	**0.618**	**0.406**	**0.132**	**0.660**	**0.741**
Reptile eggs	0.000*	0.000*	0.007	0.000*	0.000	0.000*	0.001	0.000*
Frogs	0.000	**0.307**	**0.407**	0.000	0.000	0.000	0.041	0.000
Mammals	0.000	0.000*	0.000	**0.352**	0.000	0.000	0.000	0.000*
Fish	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Orthopterans	**0.430**	**0.100**	**0.345**	0.030	**0.284**	**0.433**	**0.297**	**0.209**
Beetles	0.000	**0.202**	0.050	0.000	0.063	0.000	0.000	0.005
Lepidopterans	**0.252**	0.000*	0.093	0.000	0.000	0.048	0.000	0.023
Phasmids	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Roaches	0.000	0.000	0.000	0.000	0.000*	0.000*	0.000	0.004
Unidentified								
Larvae	0.000	0.019	0.000	0.000	0.000	0.000*	0.000	0.000
Arthropods	0.000*	0.000*	0.000*	0.000	0.000*	0.000*	0.000	0.000*
Spiders	0.008	0.101	0.000	0.000	**0.247**	**0.386**	0.000*	0.000
Scorpions	0.000	0.002	0.000	0.000	0.000*	0.000	0.000	0.000*
Millipedes	0.000	0.000	0.052	0.000	0.000	0.000	0.000	0.000
Centipedes	0.000	0.000	0.000	0.000*	0.000*	0.000	0.001	0.017
Crabs	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Molluscs	0.000	0.071	0.046	0.000	0.000	0.000	0.000	0.001
Isopods	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Vertebrates	**0.310**	**0.505**	**0.407**	**0.970**	**0.406**	**0.132**	**0.660**	**0.741**
Prey >0.05	0.000	0.000	**0.479**	**0.471**	**0.497**	0.000	**0.311**	**0.533**
Prey >0.10	0.000	0.000	**0.339**	0.000	0.000	0.000	0.000	**0.533**

	Species							
	V. griseus	*V. indicus*	*V. niloticus*	*V. prasinus*	*V. rudicollis*	*V. salvadori*	*V. storri*	*V. tristis*
Prey types								
Lizards	**1.000**	**0.261**	0.000	0.000	0.000	**0.443**	0.000*	**0.740**
Reptile eggs	0.000	**0.106**	0.000	0.000	0.000	0.000	0.000	0.000
Frogs	0.000	0.015	0.047	0.000	**0.544**	0.098	0.000	**0.152**
Mammals	0.000	**0.116**	0.000	**0.221**	0.000	0.000	0.000	0.000
Fish	0.000	**0.125**	0.000	0.000	0.000	0.000	0.000	0.000
Orthopterans	0.000*	**0.219**	0.013	**0.689**	**0.272**	**0.425**	**0.971**	0.027
Beetles	0.000	0.000*	0.000	0.000*	0.000*	0.000	0.000*	0.000
Lepidopterans	0.000	0.000*	0.000	0.000*	0.000	0.000	0.015	0.000
Phasmids	0.000	0.000	0.000	0.090	0.000	0.000	0.000	0.000
Roaches	0.000	0.011	0.000	0.000*	0.008	0.000	0.000*	0.029
Unidentified								
Larvae	0.000	0.001	0.000*	0.000	0.000	0.000	0.000*	0.000
Arthropods	0.000	0.000*	0.000*	0.000*	0.052	0.000*	0.000*	0.000*
Spiders	0.000	0.025	0.000*	0.000*	0.068	0.000	0.000*	0.053
Scorpions	0.000	0.000	0.000	0.000	0.010	0.000*	0.000	0.000
Millipedes	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Centipedes	0.000	0.000*	0.000	0.000*	0.010	0.031	0.014	0.000*
Crabs	0.000	**0.110**	0.000*	0.000	0.000*	0.000*	0.000	0.000
Molluscs	0.000	0.012	**0.940**	0.000	0.000	0.003	0.000	0.000*
Isopods	0.000	0.000	0.000	0.000	0.035	0.000*	0.000	0.000
Vertebrates	**1.000**	**0.623**	0.047	**0.221**	**0.544**	**0.541**	0.000	**0.892**
Prey >0.05	**0.633**	**0.369**	**0.449**	**0.754**	0.000	0.000	0.000	**0.855**
Prey >0.10	**0.633**	0.000	0.000	**0.754**	0.000	0.000	0.000	**0.855**

individuals. Prey include orthopterans, beetles, termites, ants, dermapterans, dipteran larvae, caterpillars, centipedes, spiders, snails, crabs, crayfish, fish, lizards, snakes, birds, rats, squirrels, hares, musk shrews, anuran eggs and carrion (Henry, 1912; Deraniyagala, 1931; Brongersma, 1947; Harrison, 1955; Minton, 1966; Sharma & Vazirani, 1977; Sharma, 1980; Auffenberg & Ipe, 1983; Subba Rao & Kameswara Rao, 1984). Several varanids have been found with large numbers of one prey type (Minton, 1966). A 0.41 m snout-vent length (SVL), 1.85 kg gravid female had a toad and seven invertebrates in its stomach (Harrison, 1955). The mean MR of 29 juveniles was 0.0169; the largest was 0.0798 (Auffenberg & Ipe, 1983). Anurans were the most important prey in Andhra Pradesh, India, though seasonal variation was apparent (Subba Rao & Kameswara Rao, 1984); for example during the summer the lizards entered streams to catch fish and aquatic insects. Rodents and hares were often dug out of nests, and carrion was commonly taken. Subba Rao & Kameswara Rao (1984) followed a monitor for 3 km, whereupon it joined five or six others feeding on a dead deer. They also observed a 1 m TL monitor catching an adult Indian bandicoot rat (*Bandicota bengalensis*). Based on Walker *et al.* (1975) and museum specimens of *V. bengalensis*, the MR might have exceeded 0.50. One individual contained 50+ beetles, 40 maggots, 8 caterpillars, 4 orthopterans, a gecko and a scorpion (Sharma, 1980). Beetles were the most common prey by number and frequency in 16 stomachs we examined. Most vertebrates were eaten by larger individuals, although some smaller specimens also took them (contra Auffenberg & Ipe, 1983). Large individuals often took many relatively small arthropods; for example, a 546 g specimen contained five beetles (MRs <0.0006), four insect pupae, one grasshopper and one caterpillar. Three others contained 14, 13 and 13 items, respectively. No other specimen contained more than three items.

Varanus brevicauda: Australia, deserts, TL 0.25 m (Cogger, 1983). Nine specimens contained 13 prey, including reptile eggs, grasshoppers, beetles, roaches, caterpillars and isopods (Pianka, 1970a).

Varanus caudolineatus: Australia, arboreal, TL 0.3 m (Cogger, 1983). The most important prey in 83 stomachs were roaches, grasshoppers and geckos; others were spiders, centipedes, a skink, a cicada, a beetle and a moth (Pianka, 1969a; Losos, King & James unpublished observations). We found a 1.3 g tail-less gecko (*Gehyra fenestra*) in a 16.5 g specimen (MR = 0.0791), and at least one orthopteran in another.

Varanus dumerilii: South-eastern Asia, Borneo, and nearby archipelagos, TL 1.2 m (Mertens, 1942c). One had ants in its stomach (Barbour, 1921). A 784 g specimen that we examined ate at least four crabs, one of which weighed 3.6 g (MR = 0.0046); a 1.1 g spider (MR = 0.0014); and a 0.4 g insect larva (MR = 0.0005). Two others ate at least two and one crabs.

Varanus eremius: Australia, deserts, TL 0.5 m (Cogger, 1983). Lizards (at least 14 species, three families) and grasshoppers were the most frequent prey in 60 stomachs (Pianka, 1968, 1982) and accounted for 72.6% of all prey by volume. Four *V. eremius* we examined ate three skinks (*Ctenotus sp.*, MRs = 0.060, 0.041), an unidentified skink, an orthopteran, and an unidentified insect.

Varanus exanthematicus: Sub-Saharan South Africa, open habitats, TL *c.* 2 m (Mertens, 1942c). Savanna monitors reportedly wait near flowers in trees to eat birds, capturing them with a sweep of the tail (Rose, 1962). One from South

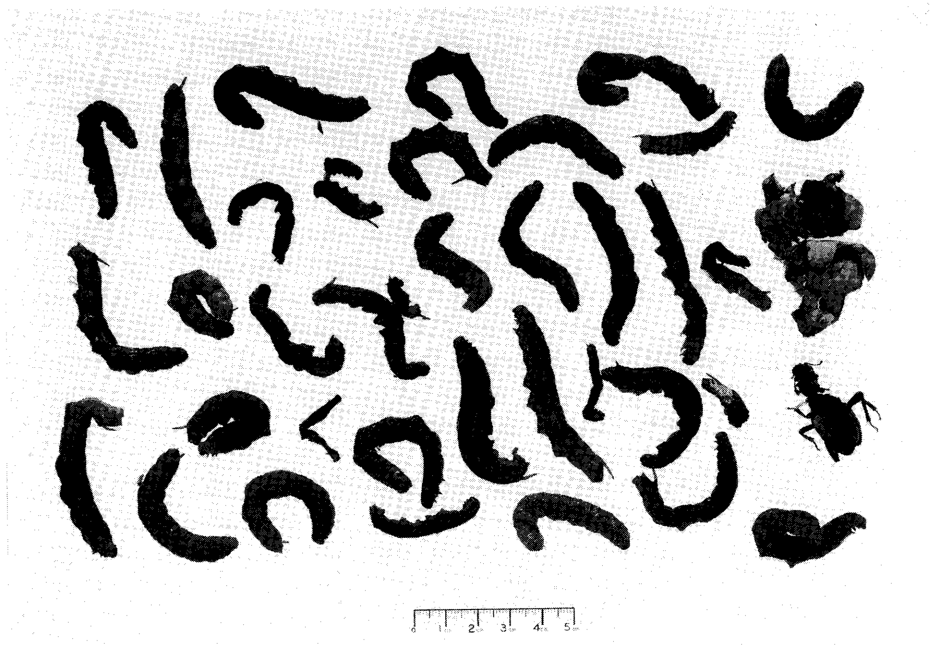

Figure 1. Entire stomach contents of an adult *Varanus exanthematicus* (1.31 kg, MCZ 129896). See text for details.

Africa contained 2 juvenile tortoises and a grasshopper (de Waal, 1978). Beetles, millipedes, caterpillars and orthopterans were the most important items in 24 stomachs from Senegal; three had eaten lizard eggs, including one that contained 11 *V. exanthematicus* eggs. Other prey were snails, centipedes, a hymenopteran and a scorpion. The lizards tended to eat many items (1–105/stomach, $\bar{x} = 35.3$), and many of a particular type. For lizards that had eaten a particular prey, the mean number of millipedes was 29.1, of beetles 10.0, of orthopterans 9.4 and of lizard eggs 10.7 (Cissé, 1972). Insects predominated in ten specimens we examined. More than half had eaten beetles, and they were the only type eaten by more than two individuals. Snails and lepidopteran larvae were also important items by number. The only vertebrates were eaten by small monitors; a 42.4 g *V. exanthematicus* ate a 7.4 g ranid frog (MR = 0.1745) and a 147 g specimen took a 13.4 g *Bufo sp.* (MR = 0.0912). All large specimens contained only relatively small invertebrates. One 1.31 kg specimen contained 35 lepidopteran larvae, ranging from 0.7 to 3.0 g (MR = 0.0005–0.002), a 1.9 g beetle (MR = 0.0015) and a reptile egg (Fig. 1). A 1.47 kg specimen contained four beetles, the largest weighing 2.9 g (MR = 0.0020). The range in items per stomach was great; two individuals had more than 30 items and three other specimens contained four or more items.

Varanus flavescens: Asia, TL *c.* 1 m (Mertens, 1942c). A 656 g specimen that we examined had eaten an earthworm and a winged insect.

Varanus giganteus: Australia, deserts, TL 2 m (Cogger, 1983). Perenties reportedly eat lizards, snakes, birds, eggs and small mammals; one captured an immature kangaroo, "then, placing his forefeet on the body, it tore out pieces of flesh like a dog" (Stirling, 1912). *Varanus giganteus* on Barrow Island off the coast of Western Australia dig up and eat sea turtle eggs (Butler, 1970). A 896 g specimen ran down and ate a 21 g agamid, *Lophognathus longirostris* (MR = 0.0234, Horner, personal communication). A 2.7 kg specimen had eaten a 255 g rodent (MR = 0.094), and four had eaten 1–3 lizards (King, Green & Butler, unpublished observations). Four had eaten orthopterans and one had also eaten a centipede. Twenty-seven scats from Barrow Island consisted primarily of sea turtle eggs and hatchlings and medium-sized mammals (King *et al.*, unpublished observations). At a construction camp on Barrow Island, perenties forage amidst camp for small mammals, patrol beaches for turtle nests, and lie in wait under vehicles for scavenging gulls. The latter are captured in short sprints. A 2 m animal sprinted 30 m to catch and devour a 1.5 m TL perentie stuck in a fence (Butler, personal communication). A 0.72 m SVL, 5 kg *V. giganteus* contained by far the largest prey we found, a 100 g agamid, *Pogona barbatus* (MR = 0.02).

Varanus gilleni: Australia, arboreal, TL 0.3 m (Cogger, 1983). Three geckos, two grasshoppers and a scorpion were found in six stomachs (Pianka, 1969a, 1982). Orthopterans, spiders and beetles were the most important prey by number in 64 stomachs (Losos, King & James, unpublished observations); eight specimens had eaten five lizards and four lizard tails. Other prey included roaches, scorpions, a bird's egg, an ant and a termite. We found a grasshopper in one specimen.

Varanus glauerti: Australia, arid habitats, TL 0.8 m (Cogger, 1983). Orthopterans and spiders were the most important prey by number in 29 *V. glauerti*; roaches, caterpillars, lizards and a reptile egg were also eaten (Losos, King & James, unpublished observations).

Varanus glebopalma: Australia, TL 1 m (Cogger, 1983). Twenty-eight of 30 *V. glebopalma* had eaten vertebrates. Twenty-six had eaten 1–4 lizards (Pygopodidae, Scincidae, Varanidae) and five had eaten anurans. Orthopterans, a spider and a centipede were also eaten (Losos, King & James, unpublished observations). One specimen we examined had eaten a relatively small skink.

Varanus gouldii: Australia and New Guinea, eurytopic, TL 1.6 m (Cogger, 1983). The most important prey in 63 specimens from the Great Victoria Desert were lizards and reptile eggs (Pianka, 1970b). Twenty-one species of lizards (Agamidae, Scincidae, Varanidae, Gekkonidae) were eaten, including several primarily arboreal species. In tropical Northern territory, the most important prey in 40 specimens were orthopterans, caterpillars, reptile eggs and beetles (Pengilley, 1981; Shine, 1986). Other prey were centipedes, spiders, scorpions, crabs, ants, a cicada, a moth, a phasmid, a wasp, roaches, fish, frogs, lizards, a snake, birds and nestlings, a mouse, a marsupial cat and a bandicoot (White, 1952; Pianka, 1970b; Pengilley, 1981; Shine, 1986).

Varanus gouldii eats the eggs of 5% of the *Crocodylus johnstoni* nests laid along a stretch of the McKinlay River (Webb, 1982). Caterpillars, reptile eggs, beetles and orthopterans were the most important prey in 30 lizards; others included arachnids, orthopterans, beetles, centipedes, ants, fish, frogs, lizards (Agamidae, Gekkonidae, Scincidae, and Varanidae), two birds, a caterpillar, a snake, a mouse, a marsupial cat, a bandicoot, a cidada and a crab (Shine, 1986). Lizards and orthopterans were the predominant prey in 20 stomachs we examined; only one had eaten reptile eggs. A 1.04 kg specimen contained four nocturnal terrestrial geckos (*Diplodactylus conspicillatus*, *D. steindachneri*), which presumably were dug out of burrows. Mammal remains perhaps represent scavenging; one lizard contained a chunk of meat, while the other contained a large, essentially intact rib and no other mammalian remains (*cf.* Bustard, 1970; Pianka, 1970b; King & Green, 1979). Most specimens contained three items or less, but a 1.15 kg lizard contained five caterpillars, the largest weighing 1.6 g (MR = 0.001); two orthopterans (MR = 0.002); and a large, well-digested lizard. Two others contained six and five items.

Varanus grayi: Philippine Islands, arboreal, TL 1.8 m. This species regularly feeds on fruits and seeds of several species, including palms and figs, as well as snails, birds, and birds' eggs (Auffenberg, 1979).*

Varanus griseus: Northern Africa to Asia Minor, deserts, TL 1.5 m (Mertens, 1942c). Vertebrates are the most important prey of *V. griseus*, including skinks, lacertids, agamids, turtles, snakes and small mammals (Corkill, 1928; Flower, 1933; Mosauer, 1934; Mertens, 1942a; Anderson, 1963; Gauthier, 1967; Arnold, 1984). Schmidt & Marx (1957) found a lacertid (MR = 0.02; weights determined by examination of the specimens) in a 0.31 m SVL specimen. An 0.85 m TL lizard was found with a 0.64 m TL horned viper (*Cerastes cerastes*) in its stomach (Gauthier, 1967). The major prey in 32 stomachs were lizards (primarily skinks and lacertids, also agamids), gerbils, scorpions and coleopterans; colubrid snakes and a bird were also taken (Vernet & Grenot, 1973). Vertebrates were the most important prey in 410 fecal pellets of *V. griseus* in Israel (Stanner & Mendelssohn, 1986). Only 5 pellets failed to contain vertebrates, and the most important prey were rodents, lizards, snakes, birds and eggs (bird, snake and lizard). Other vertebrates were turtles, hares, shrews and a toad. Six hedgehogs and a cat were probably scavenged. Invertebrates were found in more than 90% of the stomachs, including coleopterans, hemipterans, ants, orthopterans, gastropods, ticks, spiders, scorpions, pseudoscorpions, roaches, wasps, mantids, neuropterans, lepidopteran pupae, flies, siphonapterans and arthropod eggs. Seven of nine prey in seven stomachs we examined were lizards; snake ventral scales were found in one stomach. As a result of the preponderance of vertebrates in their diet, *V. griseus* has the second largest mean MR (Fig. 5).

Varanus indicus: New Guinea, coastal northern Australia and throughout Micronesia, arboreal, TL $\geqslant 1$ m (Cogger, 1983). Snails, arthropods, rats, shrews, crabs and earthworms were the most common prey in 54 lizards from Guam; bird eggs, lizards, a snake and a lizard egg were also eaten. Relatively large prey were taken by small *V. indicus*, whereas large individuals ate many relatively small items. One 2.2 kg individual contained a slug and detritus; a 1.8 kg male had three rail eggs and two earthworms. Some *V. indicus* ate giant toads (*Bufo marinus*) with fatal consequences for both (Dryden, 1965). Six monitors from the Caroline Islands contained crabs, lizards, a *V. indicus* egg and a rat (Uchida, 1966). In New Guinea, *V. indicus* eats the eggs and chicks of *Aplonis metallica* (Silva, 1966) and crocodile eggs (Hall & Johnson, 1987; P. M. Hall, personal communication). We found a variety of prey in 41 specimens, but

*Note added in press: Auffenberg (1988) showed that the correct name for *V. grayi* is *V. olivaceus* and provided extensive information on the diet of this primarily frugivorous lizard. See AUFFENBERG, W., 1988. *Gray's Monitor Lizard*. Gainesville, Florida; University Presses of Florida.

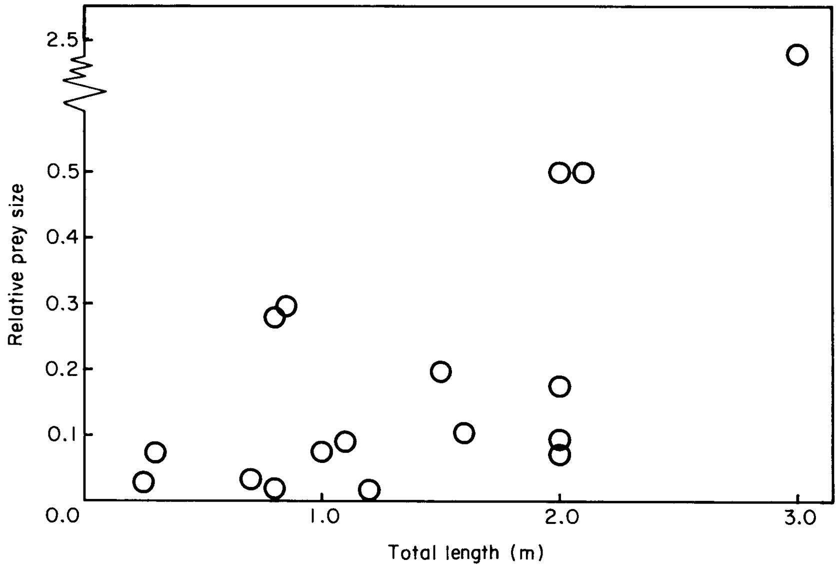

Figure 2. MR *vs.* maximum TL for varanids. Each point represents the maximum MR value for a species.

the most important were lizards, particularly skinks, reptile eggs, orthopterans and crabs. Mammals and snails were of minor importance, and no evidence of earthworm consumption was found. As with *V. exanthematicus*, most relatively large prey were found in the stomachs of small individuals. However, although many large *V. indicus* contained relatively small items, there were exceptions. As *V. indicus* grows, it continues to eat arthropods and small lizards, but adds larger mammals and crabs to its diet. No *V. indicus* contained more than one vertebrate and only three contained more than three items. Most notably, a 0.70 kg lizard contained a 6.5 g frog (MR = 0.009), ten reptile eggs, and an insect wing, and a 268 g specimen had a 6.5 g katydid (MR = 0.024), a 0.1 g hatchling skink (MR = 0.0004), two reptile eggs, and three insect larvae. Our large sample demonstrates significant geographic variation in diet. Four of 16 specimens from New Guinea and its offshore islands contained vertebrates. By contrast, 17 of 25 *V. indicus* from small Pacific Islands (primarily the Caroline and Solomon Islands) preyed upon vertebrates ($\chi^2 = 7.24S$, $P<0.01$). This is partly a result of more young *V. indicus* (which primarily eat skinks) in the non-New Guinea sample and of the tendency for New Guinea specimens to contain fewer prey items ($\bar{x} = 1.44$ *vs.* $\bar{x} = 2.20$ for non-New Guinea specimens). Whether this variation is due to differences in prey availability, shifts in habitat use, or competitive pressures from the other four species of *Varanus* in New Guinea is unknown.

Varanus kingorum: Australia, rocky habitats, TL 0.4 m. (Cogger, 1983). Orthopterans, roaches, a termite and an insect egg were found in three specimens (Losos, King & James, unpublished observations).

Varanus komodoensis: Komodo and nearby islands, terrestrial, TL 3 m (Auffenberg, 1981). Up to approximately eight months of age, *V. komodoensis* is arboreal and primarily takes lizards and insects. After this age, it becomes terrestrial and take rodents and birds. Large individuals prey primarily on deer and boar. Terrestrial individuals also scavenge, though it is unclear to what extent scavenging natural carcasses (as opposed to those left by zoologists and tourists) is important. An examination of 4728 fecal pellets from the islands of Komodo, Padar and Flores indicated that deer, boar and rodents are the most important prey. Others included lizards, snakes, birds and their eggs, goats, civets, water buffalo, beetles, grasshoppers, snails, a clam, crabs, fish, sea turtles and their eggs, a shrew, bats, dogs, crab-eating macaques and porcupines (Auffenberg, 1981; see also Burden, 1928; Darevsky & Kadarson, 1964; Lincoln, 1974). The prey killed and eaten by large *V. komodoensis* can be very large. Auffenberg (1981) estimated the maximum weight of a 3 m Komodo dragon as 250 kg, and observed that one of these lizards can consume as much as 80% of its body weight in one meal. Water buffalo as large as 590 kg have been killed by *V. komodoensis* (the claim by Auffenberg & Ipe (1983) that a *V. komodoensis* killed a water buffalo 608 times heavier than itself is surely a misprint).

Varanus mertensi: Australia, aquatic, TL 1 m (Cogger, 1983). Hermes (1981) observed a *V. mertensi* catching fish trapped in a water hole, and Stewart (1982) saw one eat a crayfish. The most important prey in 31 Northern Territory animals were crabs. Others were beetles, spiders, orthopterans, hemipterans, amphipods, shrimp, fish, frogs, reptile eggs, a dragonfly, an ant, a snake, a bird and a mammal. In 34 Western Australia specimens, the most important prey by number were bugs, beetles, shrimps and amphipods; others were spiders, dragonflies, orthopterans, crabs, fish, frogs, reptile eggs, a bird and a mammal (Shine, 1986). A 448 g individual we examined had a crab (*c.* 10 g, MR = 0.22) and an insect wing; another contained a crab and three grasshoppers.

Varanus mitchelli: Australia, aquatic, TL 0.6 m (Cogger, 1983). Fish, orthopterans and spiders were the most important prey in 43 stomachs; others were crabs, beetles, roaches, caterpillars, ants, frogs, reptile eggs, a centipede, a skink, a hemipteran, a bird and a mouse (Shine, 1986). A 106 g specimen we examined contained a frog and a 0.2 g cicada (MR = 0.002).

Varanus niloticus: Africa, eurytopic, TL 2 m (Mertens, 1942c). Invertebrates and small vertebrates were the most common prey of *V. niloticus*. Snails were a major part of the diet of adults in Cameroon; one contained eight large snails, another two large and several smaller snails, three orthopterans, an insect larvae, and 71 slugs. Most snail shells had been removed prior to ingestion (Lönnberg, 1903). Large *V. niloticus* eat relatively small prey and frogs were the most common prey in 20 stomachs (Cowles, 1930). The most important prey in 32 specimens from Senegal were beetles and orthopterans (Cissé, 1972); others were caterpillars, spiders, "myriapodes", fish, frogs, lizards, *V. exanthematicus* eggs, rodents, a snail, a turtle and a bird. A *V. niloticus* attacked a juvenile duiker (Bourquin & Channing, 1980). *Varanus niloticus* in Uganda primarily scavenged garbage (Edroma & Ssali, 1983); they ate birds, rodents, a snake, a turtle, lizards, *V. exanthematicus* eggs, fish, crabs, orthopterans, hemipterans, caterpillars, termite alates, millipedes, spiders and earthworms (Schmidt, 1919; Cowles, 1930; Cissé, 1972; Edroma & Ssali, 1983; Dial & Vaughan, 1987). Nile monitors are also well known predators on crocodile eggs and young (e.g. Corbet, 1960; Cott, 1961; Mohda, 1967). Orthopterans, snails, and slugs were the major prey in the ten stomachs we examined. Only two items had MRs greater than 0.01, 1.1 g and 0.7 g slugs in the stomach of a 15.4 g *V. niloticus*

(MR = 0.071 and 0.046). The relatively smallest prey were 13 snails, with maximum weights of 5 g each, found in the stomach of a 2.27 kg monitor (MR = 0.002); it also contained an arthropod and was the only individual with more than three prey.

Varanus panoptes: Australia, terrestrial, 1.5 m (Cogger, 1983; Shine, 1986). An individual observed digging at scorpion burrows had four scorpions and beetle parts in its stomach (Koch, 1970, as *V. gouldii*; *cf.* Storr, 1980). The most important prey by number in 77 specimens were orthopterans, ants, lepidopteran larvae and pupae, and frogs; others were spiders, centipedes, roaches, hemipterans, beetles, trichopterans, crabs, fish, lizards (Agamidae, Scincidae, Varanidae), snakes, rodents, a bandicoot, an echidna, reptile eggs and a bird (Shine, 1986).

Varanus pilbarensis: Australia, rocky habitats, TL 0.5 m (Cogger, 1983). Johnstone (1983) observed one catching orthopterans. Three specimens had eaten orthopterans, a spider and a skink (a 12.5 g *Ctenotus fallens* in a 70 g monitor; MR = 0.18; Losos, King & James, unpublished observations).

Varanus prasinus: New Guinea and Australia, arboreal, TL 0.9 m (Greene, 1986). The major prey in 29 specimens were orthopterans, which were found in 22 specimens and constituted 68.1% of all items; others included beetles and their larvae, roaches, a stick insect, a centipede, a spider and a rodent. Most prey were relatively small, but the rodent was 29.6% of the weight of the *V. prasinus* that had eaten it; a 4.6 g katydid taken by a 41 g juvenile was relatively large (MR = 0.112; Greene, 1986). According to Sprackland (1982: 15), "... fecal analyses were used to ... define the natural diet [of *V. prasinus*] ... frogs comprised 55% of the sample by weight. The rest ... consisted of geckos (17%), plant matter (12%), and various soft-bodied insects and vertebrates". However, frogs are typically undetectable in the feces of reptiles (e.g., Fitch, 1965; Jackson *et al.*, 1974); and Greene (1986) failed to find frogs, lizards or plants in the stomachs of emerald monitors. In the absence of further details, we exclude those items from the natural diet of *V. prasinus*.

Varanus primordius: Australia, rocky habitats, TL 0.25 m (Cogger, 1983). Six specimens contains five ants, four orthopterans, a roach, a neuropteran larva, a reptile egg, and two lizards, including a 1.3 g gecko in a 11.5 g lizard (MR = 0.11; Losos, King & James unpublished observations).

Varanus rosenbergi: Australia, eurytopic, TL 1 m (Cogger, 1983). The most frequent prey in 47 *V. rosenbergi* from Kangaroo Island, South Australia, were roaches, orthopterans, spiders, beetles, centipedes, larvae, scorpions, macropods, rodents, birds, lizards and lizard eggs. Others included possums, frogs, gastropods, crabs, isopods, lepidopterans, mantids, ants, isopods and aluminium foil; mammals, particularly rodents, were most important by volume (King & Green, 1979). King & Green reported that *V. rosenbergi* scavenge kangaroos and perhaps other prey from road kills. A 770 g *V. rosenbergi* that we examined contained two orthopterans (maximum weight 5 g, MR = 0.007), a lepidopteran chrysalis and an unidentified vertebrate bone.

Varanus rudicollis: Malay Peninsula, Borneo, and nearby islands, arboreal, TL 1.2 ⩾m (Mertens, 1942a). Only insects were found in specimens from Sumatra (Werner, 1900). Five we examined had eaten a large number of small prey; only a 7.4 g microhylid frog found in a 437 g *V. rudicollis* (MR = 0.017), had MR >0.01. This species had the second greatest mean number of prey items per stomach and the second lowest mean MR (Table 2). No prey type was predominant; for example, the specimen mentioned above also had two other frogs (MR = 0.004, a cluster of frog eggs, a spider (MR = 0.001), a crab, an orthopteran and an insect in its stomach.

Varanus salvadori: New Guinea, forests, TL ⩾3 m. This species eats birds and their eggs (Auffenberg, 1981).

Varanus salvator: Asia, aquatic, TL >2 m (Cogger, 1983). *Varanus salvator* eats primarily vertebrates and crustaceans. Laidlaw (1901) and Gadow (1901) reported that it eats flying squirrels, tortoises, rats and dung beetles. Lönnberg (1903) found an agamid in one lizard. A five foot monitor in Burma had 40 frogs in its stomach and another jumped out of its mouth (Smith, 1930). Deraniyagala (1931) reported that *V. salvator* ate carrion, fish, crocodiles, snakes, mammals, birds, crustaceans, and crocodile and turtle eggs; he found a tortoise, *Melanochelys trijuga*, with a carapace 160 mm long and 105 mm wide in the stomach of a 2.1 m TL *V. salvator*, and observed a 1.2 m TL individual subduing and eating a 1.8 m snake (*Ptyas mucosus*). Two snakes of that size (CAS) weighed *c.* 750 g. The regression of log weight on log SVL for 12 *V. salvator* with stomach contents predicts that a 1.2 m TL lizard would weigh 1.5 kg ($r^2 = 0.99$). Thus, the MR was *c.* 0.50. Smith (1932) stated that coastal *V. salvator* spend much time hunting on the shore for crustaceans and molluscs. Grandison (1972) found a mouse deer in a 1.8 kg, 1.45 m TL *V. salvator*; if the deer had attained maximum size, it might have constituted considerably more than 50% of the lizard's weight (*cf.* Walker *et al.*, 1975). Peltz (1986) observed

TABLE 2. Mean relative mass ratio of prey items. Fragmented items are assigned the mean MR for that prey type. MR-Largest is the mean largest intact prey item for each individual. N is the number of specimens containing intact prey items. See Table 1 for souces of data other than this paper

Species	N	# Items	MR-Mean	MR-Largest	MR-Range
V. acanthurus	7	24	0.011	0.013	0.000004–0.033
V. bengalensis	9	29	0.005	0.019	0.0002–0.039
V. caudolineatus	1	1	0.079	0.079	
V. dumerilii	1	3	0.022	0.005	0.0014–0.0046
V. eremius	2	2	0.051	0.051	0.041–0.060
V. exanthematicus	8	69	0.007	0.047	0.0001–0.18
V. giganteus	5	7	0.020	0.030	0.001–0.094
V. gilleni	10	13	0.024	0.031	0.006–0.073
V. glauerti	13	14	0.008	0.008	0.003–0.019
V. glebopalma	12	18	0.016	0.016	0.003–0.075
V. gouldii	11	24	0.012	0.017	0.0001–0.10
V. griseus	4	6	0.052	0.068	0.019–0.197
V. indicus	18	25	0.018	0.023	0.0004–0.090
V. mertensi	1	1	0.002	0.002	
V. mitchelli	1	1	0.002	0.002	
V. niloticus	4	18	0.008	0.020	0.0005–0.071
V. pilbarensis	2	3	0.039	0.093	0.005–0.18
V. prasinus	7	12	0.031	0.052	0.003–0.30
V. primordius	2	2	0.078	0.061	0.008–0.11
V. rosenbergi	1	1	0.007	0.007	
V. rudicollis	4	15	0.002	0.006	0.0001–0.017
V. salvator	6	11	0.009	0.014	0.001–0.049
V. storri	4	4	0.026	0.019	0.010–0.028
V. timorensis	1	1	0.057	0.057	
V. tristis	10	16	0.054	0.060	0.002–0.28
V. varius	3	18	0.022	0.022	0.0004–0.065

V. salvator foraging in the water along river and estuary edges, in open plains, and on beaches, where they dug up sea turtle nests. Orthopterans, frogs, lizards, and crabs were the major prey in 12 specimens we examined; only two had more than three items. A 375 g monitor had eaten two skinks, six orthopterans and a frog. An 81.4 g individual had 11 orthopterans in its stomach.

Varanus scalaris: Australia and New Guinea, arboreal, TL 0.6 m (Cogger, 1983). A 145 g lizard ate nine orthopterans; three others ate an insect, a scorpion, and a skink.

Varanus semiremex: Australia, semi-aquatic, TL 0.6 m (Cogger, 1983). *V. semiremex* eats geckos, crabs, fish and insects (Bustard, 1970; Cogger, 1983). Crabs were found in three specimens; one lizard had eaten a frog (Losos, King & James, unpublished observations).

Varanus spenceri: Australia, terrestrial, TL 1.2 m (Cogger, 1983). Six contained orthopterans, mammal hair, isopods, an elapid snake and an agamid lizard (Pengilley, 1981).

Varanus storri: Australia, rocky habitats, TL 0.25 m (Cogger, 1983). Peters (1973) stated that grasshoppers, spiders and a gecko, *Heteronotia binoei*, are the main prey of *V. storri*. Orthopterans were the most frequent items in 26 specimens; others were beetles, roaches, ants, myrmeleontid larvae, lizards, a caterpillar, a centipede and a spider (Losos, King & James unpublished observations).

Varanus timorensis. Timor, arboreal, TL 0.6 m (Cogger, 1983). A 21.1 g *V. timorensis* from Timor had eaten a scorpion and a 1.2 g typhlopid snake (*Ramphotyphlops sp.*; MR = 0.057).

Varanus tristis. Australia, arboreal, TL 0.8 m (Cogger, 1983). Nestling birds might be a major prey item based on behavioural observations, although only three were found in 64 stomachs containing food. Lizards were the most important prey by volume (71.4%). Orthopterans were also important. Other items included ants, cockroaches, phasmids, reptile eggs, a beetle and a cicada (Pianka, 1971, 1982). Orthopterans and lizards were important items in 20 stomachs we examined, but roaches and spiders also were major prey by number and frequency. Of the species for which we have an adequate sample, *V. tristis* had the largest average MR (Table 2). The relatively largest prey was a 35 g agamid, *Ctenophorus reticulatus*, in a 126 g *V. tristis* (MR = 0.28). Only three lizards had more than two, and none had more than four items per stomach. Only one of five lizards that had eaten a vertebrate had anything else in its stomach.

Varanus varius: Australia, semi-arboreal, TL >2 m (Cogger, 1983). Bustard (1970) noted that "when searching for food, they examine a fairly small area intensively" and observed an individual apparently searching for eggs and hatchling birds in tree holes. Vestjens (1977) observed predation by *V. varius* on birds' nests; only eggs were taken, with the exception of one cormorant chick. The lace monitor eats nestling and adult birds and rabbits, birds' eggs, lizards, snakes, rodents, turtle eggs, frogs, spiders, grasshoppers, phasmids, hemipterans, bees, beetles, ants and carrion. (Anonymous, 1909; Broadbent, 1910; Grogerley, 1922; Carter, 1924; Hindwood, 1926; Waite, 1929; Hyem, 1936; Kaveney, 1958; Bustard, 1970; Vestjens, 1973, 1977; Kennerson, 1980). A 616 g individual we examined contained 13 orthopterans, 0.5–0.9 g (MR = 0.001); two insect larvae, 1.4 g (MR = 0.002) amd 0.8 g (MR = 0.001); and a 0.3 g snail

(MR = 0.001). A 258 g monitor had eaten a 0.1 g hatchling skink (MR = 0.0004). The smallest *V. varius*, a 12.3 hatchling, had eaten the relatively largest item, an insect >0.8 g (MR >0.065).

DISCUSSION

Dietary characteristics

Most *Varanus* eat a variety of invertebrates and an occasional larger vertebrate. Orthopterans, beetles and/or lizards are often the most important prey by number. Several species (e.g. *V. glebopalma*, *V. griseus*, *V. prasinus*), however, specialize on a few prey types. The important indices for 16 species indicate that lizards and frogs are often the most important prey energetically (Table 1), as are molluscs, orthopterans, and lepidopteran larvae and chrysali in some cases. Even when vertebrates represent only a small fraction of all prey items, the few that are eaten may be of major energetic importance (*cf. V. bengalensis*, *V. prasinus*, and *V. salvator*). Conversely, some items that are eaten in large numbers might not be of great energetic importance (e.g. lepidopterans in *V. exanthematicus*, orthopterans in *V. tristis*, reptile eggs in *V. indicus*).

Our data support Shine's (1986) conclusion that differences in habitat utilization explain interspecific dietary differences among some sympatric *Varanus*. For example, the species for which aquatic organisms are important are often found near water bodies (e.g. *V. dumerilii*, *V. mertensi*, *V. mitchelli*, *V. semiremex*). Four of the five species for which the importance index of lizards is greater than 0.500 are arid zone species (*V. giganteus*, *V. gouldii*, *V. griseus*, and *V. tristis*; *V. gouldii* also gets into the tropics, but mammals are of increased dietary importance there (Shine, 1986)). There are exceptions, however; both *V. indicus* and *V. salvator* are found near water, but lizards and orthopterans are the two most important prey for these species. Geographic differences in habitat use and/or prey availability probably are important sources of intraspecific variation in diet. *Varanus gouldii*, a habitat generalist, relies on different prey in arid and tropical areas (see above). *Varanus giganteus* eats many sea turtle eggs on Barrow Island, a prey type that is unavailable in the Australian outback. Geographic variation in diet is also known for *V. indicus*, *V. mertensi* and *V. mitchelli*.

Varanids also might specialize on seasonally abundant prey, as shown for *V. mitchelli* (Shine, 1986) and *V. bengalensis* (Subba Rao & Kameswara Rao, 1984). Pianka (1982, 1986) and Shine (1986) stressed the intelligence of varanids, and Shine (1986) argued that individuals learn to specialize on particular prey types. Intrapopulational variations might also result from differences in microhabitat utilization (e.g. *V. panoptes*, Shine, 1986).

A number of lizards display ontogenetic dietary shifts (Greene, 1982), including several varanids. *Varanus niloticus* switches to eating snails as it grows (e.g. Lönnberg, 1903). Three of the four largest *Varanus niloticus* (>925 g) had eaten vertebrates, but only one of the six smallest contained vertebrate remains ($P<0.02$, Kolomogorov one-sample test). Two of the three largest *V. bengalensis* had mammal remains in their stomachs; none of the other 13 had eaten mammals ($P \ll 0.01$). Nine of 15 items in the 12 *V. indicus* less than 50 g are lizards; of 68 items in 29 larger *V. indicus*, only three were lizards ($P \ll 0.01$). All six specimens which ate crabs are among the 19 largest specimens (>195 g; $P \ll 0.01$). Young *V. komodoensis* prey upon arboreal lizards and insects, whereas adults capture and feed upon large mammals (Auffenberg, 1981). However, large prey may not be available to smaller *V. komodoensis*, which are probably also forced into arboreality to avoid cannibalism by terrestrial adults (Auffenberg, 1981). Crocodilians exhibit a similar transition; hatchlings and juveniles generally eat invertebrates, while older specimens take larger vertebrates (e.g. Valentine, Walther, McCartney & Ivy, 1972; Taylor, 1979; Webb *et al.*, 1982; Hutton, 1987). Like *Varanus komodoensis*, larger individuals are capable of dismembering large prey (Neill, 1971), whereas smaller specimens eat their prey whole.

An individual becomes able to subdue and devour larger prey items as it grows. But in most species, larger individuals continue to prey on small prey, though it appears that the very smallest sized prey are taken less frequently. However, a positive relationship between body size and size of the *largest* prey is found in seven of the eight species for which we have data for more than three specimens (only the regression for *V. bengalensis* is significant, but the probability that the relationship for 7 or 8 of 8 species would be positive is $P < 0.05$ by the binomial test, one-tailed).

If prey size does not always increase with predator size, then the number of prey eaten by larger individuals should increase to meet increased energetic demands, a trend observed in *Varanus acanthurus* by King (in press). The slope of the regression of number of prey items against predator size is positive for 9 of the 11 species for which we have data for more than three specimens (the exceptions are *V. bengalensis* and *V. salvator*). Although none of the regressions differs significantly from zero, there are a disproportionate number of positive slopes ($P < 0.05$, binomial test, one-tailed), which suggest that larger monitors generally eat more prey items than smaller conspecifics.

Numerous authors have assumed that monitors eat relatively large prey items, and Pough (1973) stated that insectivory is not energetically profitable for a lizard greater than 300 g. From a behavioral viewpoint, these assumptions are not true. *Varanus glebopalma*, *V. griseus*, and adult *V. komodoensis* prey entirely or mostly upon vertebrates. Large specimens of some of the larger species (e.g. *V. giganteus* and *V. salvator*) may also be primarily carnivorous. However, most species of monitors, regardless of size, are primarily insectivorous and mean prey sizes appear small (Table 2). The data for *V. exanthematicus* demonstrate that no absolute constraint on insectivory exists; there were no vertebrates in 28 specimens (size unknown) examined by Cissé (1972) and the two frogs we found were in small specimens. This moderately large species (max. *c.* 2–3 kg) is almost entirely insectivorous (Fig. 1). Other examples of large monitors ($\gtrsim$300 g) eating numerous small items are *V. bengalensis*, *V. gouldii*, *V. niloticus*, *V. prasinus*, *V. rudicollis*, *V. salvator* and *V. varius*.

The importance indices (Table 1), however, indicate that vertebrates are the most energetically important prey for most large varanids. There are three exceptions: adult *Varanus exanthematicus* are primarily insectivorous. Adult *V. niloticus* primarily eat snails (Lönnberg, 1903, but see above), and this is reflected in their high importance index. However, that value is based on only four specimens with weighable stomach contents. *Varanus niloticus* is also known to eat reptile eggs and vertebrates; more extensive data probably will alter these results. *Varanus prasinus* rarely eats vertebrates; by number and importance index, orthopterans are most important for that species. Anecdotal reports suggest that vertebrates may be of even greater energetic importance for the largest varanids (*cf. V. salvator*), which either prey upon or scavenge them. The importance of large prey is variable among smaller varanids; for example, orthopterans are by far the most important prey of *V. storri*, but lizards are most important for *V. gilleni*.

Vezina (1985) has suggested that among terrestrial carnivorous vertebrates, predator-prey mass ratios are an increasing function of predator species size. Varanids appear to follow this trend, though a much larger database is necessary (Fig. 2). We suggest that the ontogenetic change in *Varanus komodoensis* reflects an enhanced ability of larger individuals to capture and tear through the skin of relatively and absolutely larger prey. Consequently, only larger monitors are capable of killing and eating prey that cannot be swallowed whole (Darevsky & Kadarsan, 1964). It would not be surprising to find that larger individuals of the other large species also eat larger prey than would be expected on the basis of extrapolation from the prey size of smaller individuals. (Recall, however, that *V. komodoensis* is not just a scaled up version of smaller species. It is stocky, with a relatively short tail and broad snout, and had vertically inclined quadrates, which perhaps facilitate large gape (Auffenberg, 1981)). Field observations suggest that this may, indeed, be the case for *V. bengalensis* (Subba Rao & Kameswara Rao, 1984), *V. giganteus* (Stirling, 1912) and *V. salvator* (Grandison, 1972).

Hunting tactics

The available data suggest that hunting behaviour of most varanids is as expected for widely searching predators, for which search time is high and handling time low (Schoener, 1971). Such predators should only investigate habitats likely to yield desirable prey, but, when foraging, should pursue any item greater than the minimum size for which the energetic gain at least equals the costs of prey capture and handling (MacArthur & Pianka, 1966). Pianka (1968, 1986) and King (in press) suggested that varanids follow such a strategy, and our data agree for almost all species. Large monitors continue to eat all but the smallest prey items. Behavioural observations indicate that varanids forage over large distances and spend a disproportionate amount of time investigating particular portions of their environment that might prove especially profitable, such as tree trunks, burrows and under piles of elephant dung (Minton, 1966; Subba Rao & Kameswara Rao, 1984; and Auffenberg, 1984 for *Varanus bengalensis*; Pianka, 1968, 1982, 1986 for *V. eremius*; Pianka, 1970b, 1986 for *V. gouldii*; Saint Girons & Saint Girons, 1959; Anderson, 1963; Arnold, 1984; and Stanner, 1985 for *V. griseus*; Auffenberg, 1981 for *V. komodoensis*; Edroma & Ssali, 1983 for *V. niloticus*; Gadow, 1901 for *V. salvator*; Pianka, 1971, 1982, 1986 for *V. tristis*; and Stebbins & Barwick, 1968; Bustard, 1970; and Horn, 1980 for *V. varius*). Among potential lizard prey, *V. giganteus* solely eats agamids, in contrast to other Australian varanids, which eat skinks and geckos but only rarely ingest agamids. Whether this indicates a difference in foraging strategy requires further study (e.g. contrast Horner (above p. 386) with Pianka, 1968, 1970b, 1971; Bustard, 1968, 1970).

More detailed studies are available for two species. Only *Varanus komodoensis* has been extensively studied in the field (Auffenberg, 1981); its behaviour is tailored to capturing very large mammals and thus atypical for the genus. In spacious greenhouses, *V. bengalensis* hunted as widely as possible, preferentially investigating areas that had been successful in the past and intensively searching areas, such as leaf litter and rotting logs, that were likely to prove beneficial (Auffenberg, 1984).

Perhaps some varanids adopt a sit-and-wait hunting mode to capture a particular prey type (*cf.* Huey & Pianka, 1981). Large *Varanus komodoensis* lie in wait near game trails and ambush large mammals (Auffenberg, 1981). *Varanus mertensi* sometimes moves through small pools, using the body and tail to herd fish and invertebrates into a small area (Hermes, 1981; Shine, 1986). A few other varanids have been observed apparently using sit-and-wait tactics to capture active prey (Pianka, 1982; Subba Rao & Kameswara Rao, 1984).

Evolutionary significance

A major impetus for our survey was the recurrent claim that varanids specialize on large vertebrate prey, that they have various morphological and physiological adaptations for that role (e.g. Bennett, 1973; Pough, 1973; Rieppel, 1979), and that as such they are ecological analogues of placental carnivores. Having examined dietary variation in monitor lizards, we now require a phylogenetic perspective to assess patterns of correlated dietary and phenotypic diversification. Ideally, we need to know the relationships among living and fossil *Varanus* and of enough successive outgroups to establish transformation sequences for size, habitat, hunting behaviour and diet (*cf.* Lauder, 1982, Greene, 1986).

The only comprehensive survey of osteology and external morphology among living *Varanus* did not provide explicit analyses of character change and relationships within the genus (Mertens, 1942a, b). Subsequent studies of proteins, chromosomes and hemipenes (Holmes, King & King, 1976; Branch, 1982; King, Mendgen & King, 1982) are partially concordant with Mertens' essentially phenetic subgeneric groupings, but are also contradictory among themselves. Furthermore, there is a moderately rich fossil record for varanines (Estes, 1983a), and no effort has been made to integrate those taxa with living forms in terms of phylogeny. Consequently, we used commonality within the genus and comparisons with successive outgroups (see Maddison, Donoghue & Maddison, 1984) to determine evolutionary polarities for attributes among *Varanus*.

The closest relatives of *Varanus* are lanthanotines, including living *Lanthanotus* and fossil *Cherminotus* (Borsuk-Bianynicka, 1984; Pregill *et al.*, 1986), neither of which exceeds 0.5 m in total length. *Lanthanotus borneensis* is a tropical burrowing animal, and is known to eat earthworms and crustaceans (Pregill *et al.*, 1986; Greene & Schwenk, unpublished observations). The sister taxon of Varanidae is Helodermatidae, including two living species and several fossil taxa, the only known venomous lizards. Helodermatids reach a maximum length of 1 m, inhabit deserts and tropical dry forests, and feed on insect larvae, reptiles, birds, eggs and nestling mammals, some of which are relatively very large (Beck, 1986;

Lowe, Schwalbe & Johnson, 1986, Pregill *et al.*, 1986). Varanines, lanthanotines and helodermatids form a well corroborated group, the Varanoidea.

The relationships of varanoids to other Anguimorpha are uncertain (Gauthier, 1982; Estes, 1983a). Most fossil necrosaurids were less than 1 m TL, but *Eosaniwa* was a much larger animal (Estes, 1983b). Living and fossil xenosaurids are less than 0.5 m TL, and usually inhabit moist, forested regions; *Xenosaurus grandis* eats mainly insects and rarely other lizards (Presch, 1981; McDiarmid & Greene, unpublished observations), whereas *Shinisaurus crocodilurus* eats tadpoles, fish and aquatic invertebrates (Fan, 1931). Living and fossil anguids range from very small to *c.* 1.0 m TL and occupy a variety of habitats. Most species of anguids inhabit non-desert areas and evidently feed mainly on invertebrates, although some occasionally take small vertebrates (e.g *Elgaria multicarinata*, Cunningham, 1956).

Excluding the Australian desert radiation, which is derived within the genus (Mertens, 1942a; Branch, 1982; Estes, 1983a), most monitors live in tropical savannah and/or forest habitats. Living *Varanus* range from *c.* 0.3 to 3.0 m, and most fossil forms span approximately the same total lengths (Estes, 1983a). The Pleistocene *V. priscus* was exceptional, perhaps reaching 7 m in TL. We agree with Mertens (1942a) that *Varanus* was primitively neither exceptionally small nor large, but rather was an animal *c.* 0.5–1–5 m TL, within the size range encompassed by living *V. tristis*, *V. gouldii*, and *V. exanthematicus*, as well as almost all other anguimorphans.

Given phylogenetic relationships among anguimorphans and the above summary of their natural history, a parsimonious conclusion is that the feeding biology of a primitive *Varanus* was approximately like that of living *V. bengalensis* and *V. gouldii*: it hunted over wide areas, occasionally climbing trees and entering water; it used chemoreception to search for hidden prey in particular microhabitats; it fed frequently on large numbers of relatively small prey (MR often less than 0.01); the occasional ingestion of relatively larger vertebrates, perhaps as carrion, was energetically significant; and the latter perhaps involved dismemberment prior to ingestion, using the forefeet and jerking movements of the head. Nothing that we know about living or fossil anguimorphans suggests that monitors originally had one of the specialized diets seen in a few living species.

If our scenario is correct, there is no convincing case for particular characteristics of varanines being adaptively related to the capture or ingestion of 'large' vertebrate prey (see also Smith, 1986). Monitors are undeniably derived and unique in morphology, physiology, and behaviour, but the adaptive significance for those attributes should be sought in aspects of their natural history that are derived at the same level in the phylogeny of Anguimorpha, viz., that are unique to and derived for *Varanus*. Comparisons with other anguimorphans suggest that derived attributes of varanines include unusually high preferred body temperatures and activity levels (e.g. Bennett & Ruben, 1979; King, 1980; Bickler & Anderson, 1986), and the ability to capture and subdue prey types that are capable of rapid and effective escape (e.g. flying and jumping insects, lizards). Intensive hunting over large areas and use of chemoreception to locate hidden prey in particular microhabitats are characteristic of other anguimorphans as well, although these behavioural attributes are probably enhanced and thus further derived in varanids (Pregill *et al.*, 1986).

The ability to capture elusive prey might be of special importance. Anguimorphans generally do not apprehend prey with the tongue—that organ is specialized for chemoreception—and they rely instead on seizing food initially with the jaws (McDowell, 1972; Schwenk, 1984, 1985). Frazzetta (1962, 1983, 1986) argued that cranial kinesis improves the ability of a carnivorous lizard to precisely grasp and retain a mobile prey item. That ability might be enhanced by the long necks and generally long, pointed muzzles of varanines and by their capacity for rapid locomotion. Hidden, highly mobile animals figure prominently in the diets of monitors, and we are impressed by the efficacy with which captive *Varanus bengalensis*, *V. gilleni*, *V. salvator* and *V. tristis* seize prey. In contrast, captive blunt-headed anguimorphans often have difficulty catching fast moving or saltating prey (*Shinisaurus crocodilurus*, two species of *Heloderma*, Greene, unpublished observations).

If our conclusions about the primitive adaptive syndrome of *Varanus* are correct, several derived themes within the genus can be identified. These include predation on hard-shelled molluscs (*V. niloticus*), crustaceans (*V. dumerilii*), orthopterans (*V. acanthurus*, *V. glauerti*, *V. prasinus*), lizards (*V. glebopalma*, *V. griseus*), and large mammals (*V. komodoensis*, perhaps others). Each of these prey types is seen occasionally in the more generalized diets of other species in the genus. In some cases the derived diets are associated with morphological specializations, such as the molariform teeth, heavy skull, and bowed mandibles of *V. niloticus* (Lönnberg, 1903; Rieppel & Labhardt, 1979; Estes & Williams, 1984); the green color, prehensile tail, and grasping feet of *V. prasinus* (Greene, 1986); the broad skull and nasal valves of *V. dumerilii* (Sprackland, 1976; Krebs, 1979); the modified jaw suspension and serrated dentition of *V. komodoensis* (Auffenberg, 1981); and perhaps interspecific differences in gross gut morphology (Sprackland, 1982).

Akersten (1985) discussed *Varanus komodoensis* as a possible behavioural and ecological analogue of saber-toothed cats, in that those lizards use a slashing bite to disembowel large mammals (Auffenberg, 1981). Other authors alluded to *Varanus* as an analogue of placental predators on vertebrates, and speculated that the lack of the latter in Australia facilitated varanid radiation on that continent (e.g. Storr, 1964; Pianka, 1969b; Pough, 1973; Hecht, 1975; Schall & Pianka, 1978; Branch, 1981). Our findings suggest a refinement of those views, in that most monitors are not and probably never have been largely predators on vertebrates, at least in terms of frequency. Many other predators (including various invertebrates, birds, etc., as well as *some* placental carnivores) overlap with *Varanus* in their effects on invertebrate prey populations and are in that sense analogous. If we are looking for creatures with analogous effects on the behavioral ecology of their prey, as a result of diet and hunting techniques, some monitors do closely resemble certain endothermic predators. Giant forms such as *V. komodoensis* and *V. priscus* parallel large felids (e.g. *Panthera leo*, Schaller, 1972). Our proposed archetypal monitor, however, is more reminiscent of a small, insectivorous fox (e.g. *Otocyon megalotis*, Nel, 1978) or some viverrids (e.g., *Viverra tangalunga*, Macdonald & Wise, 1979).

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APPENDIX

Frequency is the number of specimens containing a given prey type. Mean per stomach is the number of prey items divided by the number of individuals eating that prey type.

	n	%Total	Frequency	Mean per stomach ± S.D.
Stomach contents of 21 *Varanus acanthurus*				
Reptilia				
egg	1	2.2	1	1.00
Sauria				
Scincidae				
Lerista sp.	1	2.2	1	1.00
unidentified	1	2.2	1	1.00
unidentified	2	4.3	2	1.00
Arthropoda				
Arachnida	2	4.3	2	1.00
Insecta				
Hemiptera	1	2.2	1	1.00
Lepidoptera				
chrysalis	8	17.4	1	8.00
Orthoptera				
grasshoppers	25	54.3	10	2.50 ± 2.17
unidentified	1	2.2	1	1.00
unidentified	2	4.3	2	1.00
Unidentified	2	4.3	2	1.00
Total	46		21	2.19 ± 2.14
Stomach contents of 16 *Varanus bengalensis*				
Amphibia				
Anura				
Bufonidae				
Bufo melanostictus	2	2.7	1	2.00
Ranidae				
Rana sp.	1	1.4	1	1.00
unidentified	2	2.7	2	1.00

Appendix 1 *Cont.*

	n	%Total	Frequency	Mean per stomach ± S.D.
Reptilia				
eggs	12	16.2	1	12.00
Sauria				
Agamidae				
Calotes versicolor	1	1.4	1	1.00
Scincidae	1	1.4	1	1.00
Mammalia				
Rodentia	3	4.1	1	3.00
Unidentified	1	1.4	1	1.00
Arthropoda				
Arachnida				
Araneae	4	5.4	3	1.33 ± 0.58
Scorpiones	1	1.4	1	1.00
Solifugae	1	1.4	1	1.00
Insecta				
Coleoptera	17	23.0	5	3.40 ± 2.00
Lepidoptera				
larvae	13	17.6	4	3.25 ± 4.50
Orthoptera				
grasshoppers	4	5.4	4	1.00
Tettigoniidae	1	1.4	1	1.00
Unidentified	5	6.8	2	2.50 ± 2.12
Mollusca				
slugs	1	1.4	4	1.00
snails	3	4.1	2	1.50 ± 0.71
Total	74		16	4.63 ± 4.91
Stomach contents of 10 *Varanus exanthematicus*				
Amphibia				
Anura				
Bufonidae	1	1.1	1	1.00
Ranidae				
Tomopterna cryptotis	1	1.1	1	1.00
Reptilia				
egg	1	1.1	1	1.00
Arthropoda				
Diplopoda	3	3.3	2	1.50 ± 0.71
Insecta				
Coleoptera	12	13.0	6	2.00 ± 1.55
Lepidoptera				
larvae	38	41.3	2	19.00 ± 22.63
Orthoptera				
crickets	3	3.3	1	3.00
unidentified	2	2.2	1	2.00
Unidentified	1	1.1	1	1.00
Mollusca	30	32.6	1	30.00
Total	92		10	9.20 ± 14.01
Stomach contents of 21 *Varanus gouldii*				
Reptilia				
eggs	2	3.7	1	2.00
Sauria				
Agamidae	2	3.7	2	1.00
Gekkonidae				
Diplodactylus conspicillatus	2	3.7	1	2.00
D. steindachneri	2	3.7	1	2.00
Scincidae				
Ctenotus sp.	2	3.7	1	2.00
unidentified	3	5.6	3	1.00
Varanidae	1	1.9	1	1.00
unidentified	1	1.9	1	1.00
Mammalia	2	3.7	2	1.00

Appendix 1 *Cont.*

	n	%Total	Frequency	Mean per stomach ± S.D.
Arthropoda				
Arachnida				
Scorpiones	1	1.9	1	1.00
Chilopoda	3	5.6	3	1.00
Insecta				
Blattoidea	3	5.6	1	3.00
Coleoptera	3	5.6	3	1.00
Lepidoptera				
chrysalis	1	1.9	1	1.00
larvae	5	9.3	1	5.00
Orthoptera				
grasshoppers	10	18.5	7	1.43 ± 0.53
unidentified	6	11.1	2	3.00
Unidentified	2	3.7	2	1.00
Mollusca				
slugs	1	1.9	1	1.00
unidentified	2	3.7	2	1.00
Total	54		21	2.62 ± 2.06
Stomach contents of 7 *Varanus griseus*				
Reptilia				
Sauria				
Scincidae				
Chalcides ocellatus	3	33.3	2	1.50 ± 0.71
C. sepsoides	1	11.1	1	1.00
unidentified	1	11.1	1	1.00
unidentified	2	11.1	2	1.00
Serpentes	1	11.1	1	1.00
Arthropoda				
Insecta				
Orthoptera	1	11.1	1	1.00
Total	9		7	1.29 ± 0.76
Stomach contents of 41 *Varanus indicus*				
Pisces				
Periophthalmidae				
Periophthalmus cf. *koelreuteri*	1	1.2	1	1.00
Unidentified	2	2.4	2	1.00
Amphibia				
Anura	2	2.4	2	1.00
Reptilia				
eggs	19	22.9	5	3.80 ± 3.94
Sauria				
Gekkondiae				
Lepidodactylus lugubris	1	1.2	1	1.00
Scincidae				
Sphenomorphus concinnatus	1	1.2	1	1.00
*S.*sp.	1	1.2	1	1.00
unidentified	8	9.6	8	1.00
unidentified	1	1.2	1	1.00
Mammalia				
Rodentia	1	1.2	1	1.00
unidentified	1	1.2	1	1.00
Unidentified vertebrates	2	2.4	2	1.00
Arthropoda				
Arachnida				
Araneae	1	1.2	1	1.00
egg-case	1	1.2	1	1.00
Chilopoda	1	1.2	1	1.00
Crustacea				
Decapoda				
Brachyura	6	7.2	6	1.00

Appendix 1 *Cont.*

	n	%Total	Frequency	Mean per stomach ± S.D.
Insecta				
Blattoidea	1	1.2	1	1.00
Coleoptera	1	1.2	1	1.00
Lepidoptera				
larval skin	1	1.2	1	1.00
Orthoptera				
grasshoppers	1	1.2	1	1.00
Tettigoniidae	4	4.8	3	1.33 ± 0.58
unidentified	9	10.8	8	1.15 ± 0.35
unidentified	8	9.6	4	2.00 ± 2.00
larvae	3	3.6	1	3.00
Mollusca				
snails	1	1.2	1	1.00
unidentified	2	2.4	1	2.00
Unidentified invertebrates	3	3.6	3	1.00
Total	83		41	2.02 ± 2.10
Stomach contents of 10 *Varanus niloticus*				
Amphibia				
Anura				
Bufonidae				
Bufo cf. *regularis*	1	3.1	1	1.00
Reptilia	1	3.1	1	1.00
Aves	1	3.1	1	1.00
Unidentified vertebrate	1	3.1	1	1.00
Arthropoda				
Arachnida	1	3.1	1	1.00
Crustacea				
Decapoda				
Brachyura	1	3.1	1	1.00
Insecta				
Orthoptera				
grasshoppers	4	12.5	3	1.33 ± 0.58
unidentified	1	3.1	1	1.00
unidentified larvae	1	3.1	1	1.00
Mollusca				
slugs	3	9.4	2	1.50 ± 0.71
snails	14	43.8	2	7.00 ± 4.30
Unidentified invertebrates	3	9.4	3	1.00
Total	32		10	3.20 ± 3.85
[Stomach contents of 6 *Varanus rudicollis*]				
Amphibia				
Microhylidae	1	3.6	1	1.00
Rhacophoridae	2	7.1	1	2.00
egg-cluster	1	3.6	1	1.00
Arthropoda				
Arachnida				
Araneae	3	10.7	3	1.00
Scorpiones	4	14.3	1	4.00
Chilopoda	1	3.6	1	1.00
Crustacea				
Decapoda				
Brachyura	3	10.7	2	1.50 ± 0.71
Isopoda	2	7.1	2	1.00
Insecta				
Blattoidea	3	10.7	2	1.50 ± 0.71
Coleoptera	1	3.6	1	1.00
Orthoptera	4	14.3	3	1.33 ± 0.58
Unidentified	1	3.6	1	1.00
Unidentified	1	3.6	1	1.00
Mollusca	1	3.6	1	1.00

Appendix 1 *Cont.*

	n	%Total	Frequency	Mean per stomach ± s.d.
Total	28		6	4.67 ± 2.16
[Stomach contents of 12 *Varanus salvator*]				
Amphibia				
Anura				
Bufonidae				
Ansonia sp.	2	5.6	1	2.00
Rhacophoridae				
Polypedates leucomystax	1	2.8	1	1.00
unidentified	1	2.8	1	1.00
Reptilia				
Sauria				
Scincidae				
Lamprolepis smaragdina	2	5.6	1	2.00
unidentified	1	2.8	1	1.00
Arthropoda				
Arachnida				
Scorpiones	1	2.8	1	1.00
Chilopoda	1	5.6	1	1.00
Crustacea				
Decapoda				
Brachyura	3	8.3	3	1.00
Insecta				
Orthoptera				
crickets	13	36.1	2	6.50 ± 6.36
grasshoppers	1	2.8	1	1.00
unidentified	7	19.4	2	3.50 ± 3.54
Unidentified	2	5.6	1	2.00
Mollusca				
slug	1	2.8	1	1.00
Total	36		12	3.00 ± 3.38
[Stomach contents of 20 *Varanus tristis*]				
Amphibia				
Anura				
Myobatrachidae	1	3.6	1	1.00
Reptilia				
Sauria				
Agamidae	1	3.6	1	1.00
Gekkonidae				
Oedura monilis	1	3.6	1	1.00
Scincidae	2	7.1	2	1.00
Arthropoda				
Arachnida				
Araneae	5	17.9	4	1.25 ± 0.50
Chilopoda	1	3.6	1	1.00
Insecta				
Blattoidea	3	10.7	3	1.00
Cicadidae	1	3.6	1	1.00
Orthoptera				
grasshoppers	5	17.9	4	1.25 ± 0.50
Tettigoniidae	1	3.6	1	1.00
unidentified	1	3.6	1	1.00
Unidentified	1	3.6	1	1.00
Mollusca				
snail	1	3.6	1	1.00
Unidentified invertebrates	4	14.3	3	1.33 ± 0.58
Total	28		20	1.40 ± 0.85