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Diet and Arboreality in the Emerald Monitor, *Varanus prasinus*, with Comments on the Study of Adaptation

Harry W. Greene

A Contribution in Celebration of the Distinguished Scholarship of Robert F. Inger on the Occasion of His Sixty-Fifth Birthday

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MURRA, J. 1946. The historic tribes of Ecuador, pp. 785–821. *In* Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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Diet and Arboreality in the Emerald Monitor, *Varanus prasinus*, with Comments on the Study of Adaptation

Abstract

Forty-seven prey items from 29 museum specimens demonstrate that *Varanus prasinus* eats mainly katydids and other small arthropods. An "importance index," used to consider prey frequency and relative prey mass simultaneously, demonstrates that infrequent predation on large walkingsticks and small rodents also might make significant energetic contributions to the diet. Prey typically were swallowed headfirst, and a large, spinose walkingstick evidently was dismembered prior to ingestion. Hatchlings emerged from termite nests and fed there.

Varanus prasinus is unique among living varanids in having bright green coloration, a prehensile tail, and feet apparently specialized for grasping. It thereby resembles other arboreal, tropical forest lizards of the family Chamaeleontidae and of the iguanid genus *Polychrus,* probably as a result of adaptive convergence. Number of species per lineage is correlated positively with degree of morphological specialization among these taxa.

Varanus prasinus, chamaeleontids, and *Polychrus* are used to illustrate a modification of Gould and Vrba's conceptual treatment of adaptation. If natural selection and adaptation are separated conceptually, the latter can be identified by the coincidence of features and performance advantages as derived attributes within a clade. As such, the study of adaptation is independent of and complementary to investigations of optimal design and convergence.

Introduction

Lizards of the family Varanidae vary in adult total length from ca. 0.3 to 3 m, occur in habitats as different as tropical wet forests and temperate deserts, and exhibit substantial diversity in diet. Several species are known to eat vertebrates (e.g., Cowles, 1930; King & Green, 1979; Auffenberg, 1981; Pianka, 1982); others eat insects (e.g., Pianka, 1970); and one might be largely a frugivore (Auffenberg, 1979). Popular literature and morphological studies abound with statements that particular features of varanids are adaptations for feeding on large prey, despite the fact that very little evidence supports this point and some contradicts it (Greene, 1982; Auffenberg & Ipe, 1983). A thorough consideration of the role of feeding in varanid evolution is currently hampered by the lack of detailed natural history information on many species in this interesting family.

The present paper describes aspects of the feeding biology of *Varanus prasinus,* one of the most distinctive and poorly known living varanids. Information is provided on diet, prey-predator size relationships, and feeding behavior in adults and hatchlings. Comparisons with other monitors and with ecologically similar lizards in two other families are then used to support a hypothesis of adaptive convergence for certain morphological attributes of these species.

The concept of adaptation has come under heavy criticism in recent years, so I first present a modification of Gould and Vrba's (1982) approach to

the topic. Because this method requires phylogenetic information, I also discuss the relationships of *Varanus prasinus* with certain other taxa. My findings suggest that the exquisite green coloration, unusual foot structure, and long, prehensile tail of *V. prasinus* are adaptations for arboreal hunting.

Conceptual and Systematic Perspectives

Adaptation and Phylogeny

Gould and Vrba (1982) proposed that a feature be regarded as an adaptation only if its origin was associated with a specified task and an increase in fitness. Operationally, this is tantamount to saying that a feature and a performance advantage are derived simultaneously within a population or a clade, except that Gould and Vrba also specified the action of natural selection in their concept of adaptation. In their terminology, an exaptation is a feature that promotes increased performance of a task that was not associated with the origin of that feature. Gould and Vrba suggested that adaptations often would be difficult to identify, implied that exaptations might be widespread, and coined the term aptation to encompass the two.

Reactions to the approach taken by Gould and Vrba (1982) have been mixed, perhaps in part because they emphasized the potential role of exaptations in evolution and only implicitly identified a method for distinguishing them from adaptations. Kiltie (1985) found their conceptual distinction useful, but used the default term aptation in discussing his data. Brown (1982) and Reif (1984) criticized them for confusing preadaptation and exaptation (but see Gould & Vrba, 1982, p. 11), and Brown asserted that most evolutionary biologists are interested in ". . . natural populations instead of fossils, and variation among individuals rather than among species and higher taxa . . . ." Dobson (1985) did not cite Gould and Vrba, but pitted "historical origin" (as indicated by the presence of an attribute throughout all or most of a monophyletic group) against "superior adaptiveness in recent environments" (as indicated by convergent features among species).

If the goal of evolutionary biology is to understand the history of life, the views expressed by Brown (1982) and Dobson (1985) are unnecessarily narrow. After all, cetaceans are characterized by finlike limbs, but the fact that this diverse monophyletic group originated millions of years ago (Gingerich et al., 1983) does not make an aquatic lifestyle in extant whales irrelevant to understanding the evolution of their appendages. Surely most evolutionary biologists *are* interested in diversification, adaptive or otherwise, beyond the level of populations in the present! Even if the distinction between preadaptation and exaptation does not prove useful, Gould and Vrba's (1982) paper is important because it emphasized the historical context for adaptation and the need to separate factors involved in the origin of a feature from its current utility.

Adaptation and natural selection should be separated conceptually (cf. Burian, 1983; Fisher, 1985) so that it is not necessary to confirm or assume the past action of the latter in order to study the former. Adaptation and exaptation then can be distinguished by accepting a particular phylogeny; examining the distribution of morphological, functional, and ecological character states among related taxa; and determining if features and performance advantages are coincident as shared, derived traits (fig. 1a; see also Wanntorp, 1983; Coddington, 1985; Gauthier & Padian, 1985; Luke, 1986). Enhanced performance should be measured in the living members of a monophyletic group and compared to that exhibited by organisms possessing the antecedent condition, as seen in sister taxa or experimentally altered individuals. In this framework, an adaptive hypothesis can be rejected if a performance advantage is shown to be derived at a level either more restricted or more inclusive than that of the feature with which the advantage is associated. If the performance advantage is more restricted within a group, the feature is an exaptation for that task (fig. 1b). If it is more widely distributed (fig. 1c), the feature is irrelevant to the task (i.e., neither an adaptation nor an exaptation for that task).

The approach taken here entails a common problem in phylogenetic analysis, namely parallelism. As with any other characteristic of organisms, we only can assume parsimoniously that a derived attribute common to all or most members of a higher taxon is homologous (e.g., the four-chambered heart in mammals, flapping flight in birds, etc.), and abandon this conclusion if there is evidence to the contrary. For example, an adaptive hypothesis can be rejected if it is shown that the performance advantage was irrelevant when the feature originated, as with paleontological evidence that a habitat or prey type relevant to the advantage was not present (fig. 1d).

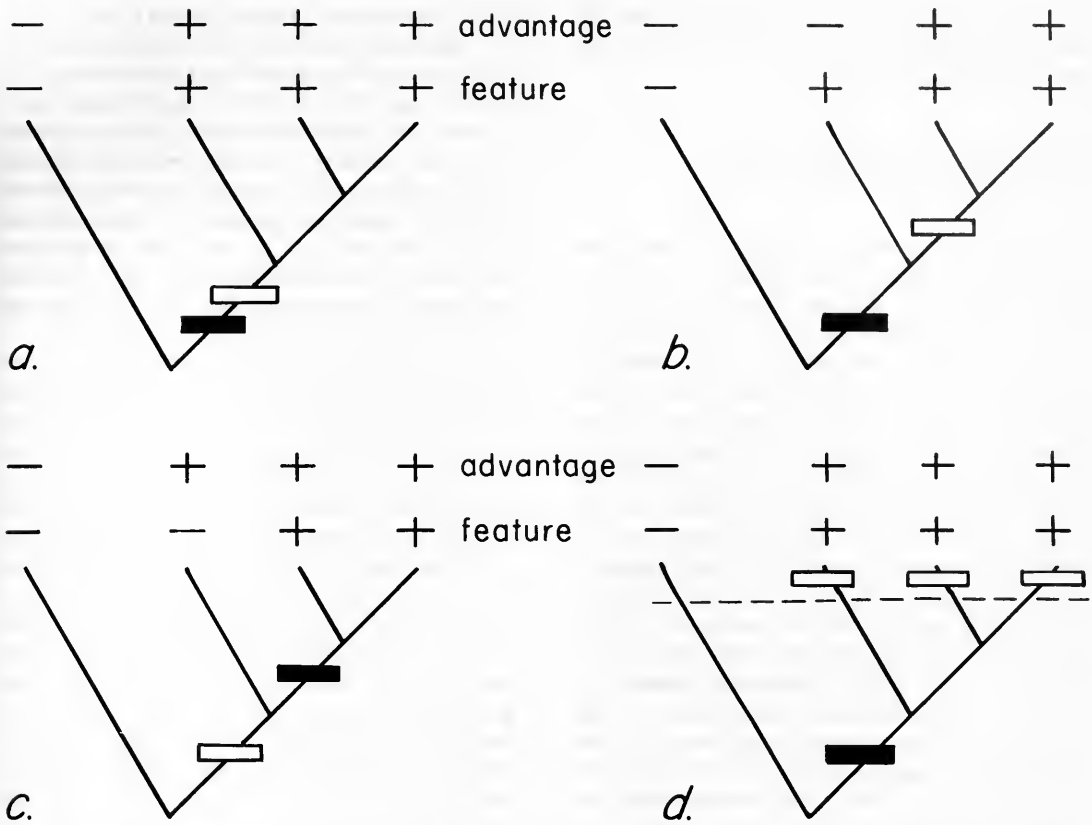

FIG. 1. (**a-c**), Origins of features (solid bars) and performance advantages (open bars), as inferred from the distribution of derived (+) and primitive (−) attributes among four taxa. Same symbols in (**d**), except that the dotted line indicates independent evidence of the earliest time at which a performance advantage could possibly have originated, regardless of its distribution among taxa. See Adaptation and Phylogeny for additional details.

There are at least two advantages to this modification of Gould and Vrba's (1982) formulation. First, by decoupling patterns and processes, the concepts of adaptation and exaptation become empirically tractable for historical analyses in evolutionary biology (Lauder, 1982). Evolutionary processes and adaptive patterns merge at the level of differences among individuals in a population (Fisher, 1985), but there remain real difficulties in studying past selection. Given a phylogeny for the organisms in question, however, this problem need not preclude the study of adaptive patterns among taxa. The possible roles of natural selection, heterochronic processes, chance, and other phenomena in producing and sorting variation—in creating adaptive patterns—should be relegated to other analytic approaches (e.g., Arnold, 1986) and to inference.

A second advantage of a phylogenetic approach to studying adaptations is that it removes the necessity for using optimality as a criterion in identifying adaptations (cf. Levins & Lewontin, 1985). This does not negate the value of optimality approaches in evolutionary biology (e.g., Oster & Wilson, 1978; Kingsolver & Koehl, 1985). For example, with independent criteria for perfection (in the sense of engineering design) and adaptation, it might be possible to determine under what conditions the former is most closely approached (cf. Gans, 1983). In the same vein, it is traditional to view convergence as evidence for adaptation, because independently derived similarity is presumed to indicate parallel selection for a particular solution to a problem (Mayr, 1983; Dobson, 1985). That assumes the burdens of an optimality approach and can be circular (Levins & Lewontin, 1985), and convergence also might implicate factors other than adaptation (e.g., constraint). Those problems are removed if convergence is viewed only as independently derived similarity (Wake,

1982), selection is not associated necessarily with adaptation, and the latter is identified separately in each taxon (Fisher, 1985).

Evolutionary Relationships in the Anguimorpha

Although intrageneric groupings have been proposed (Holmes et al., 1976; Branch, 1982), a detailed, rigorously supported phylogeny is not available for varanids. I therefore cannot exclude on the basis of intrafamilial comparisons alone the possibility that any particular feature of *Varanus prasinus* is primitive for a higher taxon (either Varanidae or more inclusive), the rest of whose members lack ecological traits unique to the emerald monitor. The closest living relative of varanids is the monotypic Lanthanotidae, and the sister taxon of these two families is the Helodermatidae; together, the three constitute the Varanoidea. The relationship of varanoids to other families in the Anguimorpha is uncertain (Gauthier, 1982; Estes, 1983). Accordingly, I noted coloration, use of the tail, and foot structure for representatives of the families Anguidae (*Abronia, Diploglossus, Elgaria, Gerrhonotus*), Helodermatidae (*Heloderma*), and Xenosauridae (*Xenosaurus*) on the basis of specimens in the Museum of Vertebrate Zoology, University of California, Berkeley, literature accounts, and personal observations. For the Lanthanotidae, I based my notations on the literature and examination of a live *Lanthanotus borneensis* in the Senckenberg Museum, Frankfurt am Main, West Germany. I consider an attribute to be derived in *Varanus prasinus* if it is absent in other varanoids and rare or absent in other anguimorphs.

Methods

The stomach contents of all *Varanus prasinus* in the American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); California Academy of Sciences, San Francisco (CAS); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); National Museum of Natural History, Washington, D.C.; and Bernice P. Bishop Museum, Honolulu, were examined. To the extent possible, I recorded collecting data, snout–vent length (SV), total length (TL), and head width (HW, across the retroarticular processes of the mandibles) for the lizards; and orientation in the gut, identity, minimum number of items, and linear dimensions (LD, maximum length and diameter) for each prey (exclusive of legs, antennae, and ovipositor). If not otherwise stated, orientation in the gut and prey dimensions could not be determined. The mass (M) of items that were at least approximately intact and the lizards that had contained them were weighed after each was blotted briefly on a paper towel.

I used a Wild dissecting microscope to study the feet of *Varanus* in the MVZ, including *V. acanthurus, V. bengalensis, V. exanthematicus, V. gouldii, V. griseus, V. indicus, V. komodoensis, V. niloticus, V. prasinus, V. rudicollis, V. salvator, V. tristis,* and *V. varius* (the *V. komodoensis* is a tanned skin; all others are intact specimens stored in alcohol). The sample thus included more than one-third of the extant species and most of the ecological, morphological, and size diversity within the family. Specimens of *Polychrus* in the MVZ were also examined because it appeared that this iguanid genus might resemble *V. prasinus* in certain features. Finally, I handled two living adult emerald monitors at the Dallas Zoo and obtained observations on their behavior from J. B. Murphy (pers. comm.).

Results

Diet of Adults

Twenty-nine *Varanus prasinus* contained 47 prey items. The monitors were apparently subadults or adults (SV = 150–335 mm, TL = 520–830 mm; Loveridge [1948] recorded maximum TL = 845 mm for a specimen with SV = 295 mm). Four specimens came from three islands in the D'Entrecasteaux Group, off the southeastern tip of New Guinea; one from Aru Island; and 24 from Irian Jaya and Papua New Guinea. The localities thus spanned ca. 141°–151°E longitude and ca. 3°–10°S latitude, much of the range of this lizard in New Guinea. They included the subspecies *V. p. prasinus, V. p. beccari,* and *V. p. bogerti* (Mertens, 1950), and were collected between 1928 and 1967 from sea level to at least 830 m elevation.

Thirty-two prey items were katydids (Orthoptera, Tettigoniidae), 14 of which had been swal-

lowed headfirst (LD = 8 × 28 mm to 11 × 63 mm, N = 9; M = 1.0–4.6 g, N = 7). Thirteen other invertebrate prey included two grasshoppers (Orthoptera, Acrididae); one iridescent green beetle (Coleoptera, ca. 24 mm in diameter, M = 1.9 g); three coleopteran larvae, one of which was swallowed headfirst (LD = 6.3 × 37.9 mm, M = 0.5 g); two roaches (Blattodea), both swallowed headfirst (LD = 10 × 29 mm, 19 × 20 mm, M = 0.6 g); three unidentified insects; one centipede (Chilopoda, ca. 8 mm wide) swallowed doubled up; and one spider (Arachnida).

The relatively largest invertebrate prey was a katydid (LD = 11 × 63 mm, M = 4.6 g) in a subadult *Varanus prasinus* (MCZ 101298; SV = 150 mm, HW = 14.2 mm, M = 41 g), swallowed headfirst. The largest invertebrate prey in an adult *V. prasinus* was a spectacular walkingstick (Phasmatodea), probably *Eurycantha* sp., in the stomach of a large male from Marienberg, Papua New Guinea (FMNH 14103; SV = 280 mm, HW = 27.5 mm, M = 313 g). The stick insect (LD = 19 × 124 mm, M = 12.2 g) had been swallowed headfirst. Specimens of *Eurycantha* that I examined (at CAS) have the body and legs armed grotesquely with sharp spines, and it is noteworthy that some legs of the prey were not in the stomach of the monitor.

The only vertebrate prey was a murid rodent of the genus *Melomys,* probably *M. moncktoni,* in a monitor from Kubuna, southeastern Papua New Guinea (AMNH 59051; SV = 255 mm, M = 135 g). The prey was largely digested, but based on comparisons of the teeth with intact *Melomys,* it weighed ca. 40 g. Rodents of this genus are terrestrial and/or semiarboreal, and *M. moncktoni* is widespread in the lowlands of Papua New Guinea (W. Z. Lidicker, Jr., pers. comm.).

Each monitor's stomach contained one to six items (mode = 1, mean = 1.62, N = 29). Stomachs with multiple prey items contained, respectively: four katydids; two katydids; five katydids and one rodent; one katydid and one centipede; three katydids and one coleopteran larva; one spider and one coleopteran larva; and one katydid and one roach (N = 2). Prey/predator mass ratios (MR) were 0.0032–0.296 ($\bar{x}$ = 0.045, N = 12); excluding the large walkingstick and rodent, mean MR for 10 arthropods was 0.021. None of the unweighable orthopterans appeared to have been larger than 4 g, so modal MR for all 47 prey was probably ca. 0.01. The relatively largest items were the walkingstick (MR = 0.04), the katydid in the subadult (MR = 0.11), and the rodent (MR = 0.296).

Nest and Hatchlings

Two specimens (MVZ 74904 and 74905) have obvious umbilical scars, SVs of 83 and 84 mm, and TLs of 218 and 224 mm, respectively. They were collected 23 October 1962, on the upper Baiune River, Papua New Guinea. R. G. Allen saw the lizards "hatch in termite nests and feed there later to emerge as one of the large long-tailed species" (sic, field notes of A. H. Miller, 24 October 1962, on file in MVZ). Their stomachs were empty, but the colons contained unidentifiable debris and several insect eggs, perhaps those of termites. Two *Varanus prasinus* hatched at the Dallas Zoo on 4 October 1978; they had TLs of 205 and 210 mm and weighed 10.0 and 8.4 g. One died the day after hatching, and the other fed readily on crickets.

Feeding Behavior

J. B. Murphy observed at least 100 feeding events by *Varanus prasinus* in the Dallas Zoo. Two-week-old mice were seized by the nape of the neck, slammed against the substrate, raked and eviscerated with the claws, and swallowed headfirst. Mice were raked with the claws as swallowing commenced, which appeared to align the prey with the long axis of the monitor's head. Approximately five minutes were required to subdue mice and five minutes to swallow them. Crickets were simply seized and swallowed headfirst. Other captive varanids (*V. acanthurus, V. gilleni, V. gouldii, V. indicus, V. mitchelli, V. tristis*) of similar or smaller size did not eviscerate mice prior to ingestion. Once, an emerald monitor descended from tree limbs to a bowl of young mice, and briefly suspended itself from a branch using only its tail.

Habitat and External Morphology

The emerald monitor is found in extreme northern Australia and throughout much of New Guinea, in rain forests, palms, mangroves, and cocoa plantations (Schlegel, 1839; Room, 1974; Czechura, 1980; Cogger et al., 1983). On mainland New Guinea, *Varanus prasinus* is a brilliant green lizard, often with a dorsal pattern of irregular black crossbands (for color illustrations see Müller & Schlegel, 1845; Kundert, 1974; Grzimek, 1984), while on certain offshore islands and in northern Australia, populations are uniformly black (Mer-

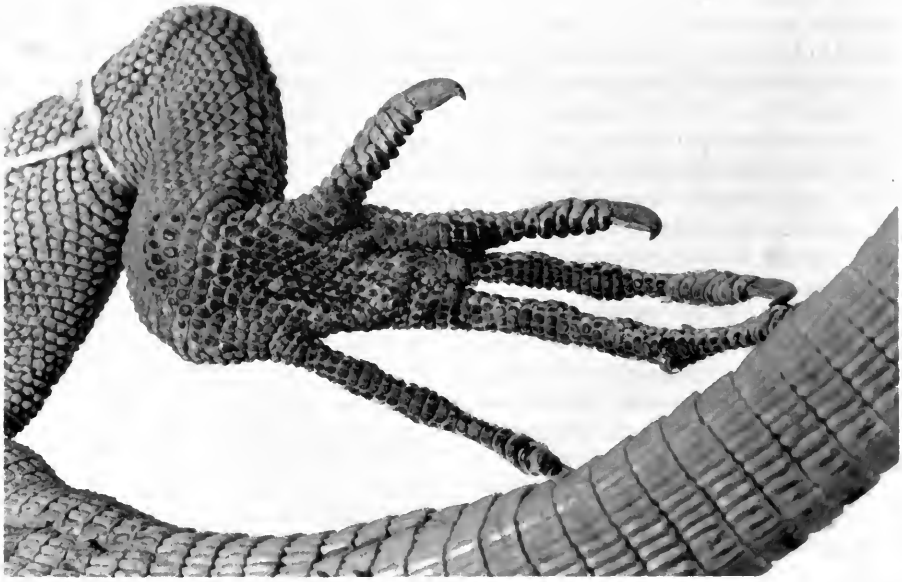

FIG. 2. Ventral view of left hind foot of *Varanus prasinus* (MVZ 74906), from 8 mi N Bulolo, Papua New Guinea. Snout–vent length of the lizard is 275 mm.

tens, 1950; Czechura, 1980). Although several varanids are known to climb frequently (e.g., Smith, 1930; Pianka, 1982), no other living monitor is bright green (Mertens, 1942a). *Lanthanotus borneensis* is dark reddish brown in life. Among other anguimorphs, only a few species of anguids are green (e.g., *Abronia taeniata,* males of *Barisia monticola*; pers. obs.). I regard green color as derived in *V. prasinus.*

The tail of *Varanus prasinus* is prehensile (i.e., able to support the animal's weight, terminology of Emmons & Gentry, 1983), unusually long compared to those of most other varanids, and has a blunt tip (Mertens 1942b, 1950; Czechura, 1980). Live animals, while struggling to escape, readily coiled the distal part of their tails around my fingers. Prehensile tails are unknown in other varanids, helodermatids, and xenosaurids, and only sporadically present in anguids (e.g., *Abronia deppii, Gerrhonotus liocephalus*; pers. obs.). Semiprehensile tails are known for some anguids (e.g., Blair, 1950), helodermatids (Alvarez del Toro, 1982), and *Lanthanotus* (Proud, 1978). I interpret a fully prehensile tail as derived in *V. prasinus.*

Czechura (1980, p. 105) noted that climbing in *Varanus prasinus* is also aided by ". . . the structure of the surface tissue on the soles of fore and hind feet. These surfaces are covered by soft black tissue, which feels sticky on contact and appears to give additional support to the climbing animal." The MVZ specimens of *V. prasinus* possess black subdigital scales, juxtaposed in transverse rows of three to four scales each, such that their distal edges are elevated from the surfaces of the fingers and toes (fig. 2). Subdigital scales on the distal phalanges have dark pigment reduced to the centers, as do all scales on the hands and feet. The digits, palms, and soles on the live animals I examined were not soft or sticky to the touch.

There are enlarged subdigital, palmar, and plantar scales on *Varanus acanthurus* and *V. tristis,* but in those species only the centers of some scales are darkly pigmented (fig. 3). The feet were not sticky to the touch on a live *V. tristis* I examined. The hands and feet of *V. indicus* resemble those of *V. prasinus,* but the former species has an irregular light and dark color pattern and its dark subdigital scales are not arranged in transverse rows. The anguids, helodermatids, xenosaurids, *Lanthanotus,* and nine other varanids I examined

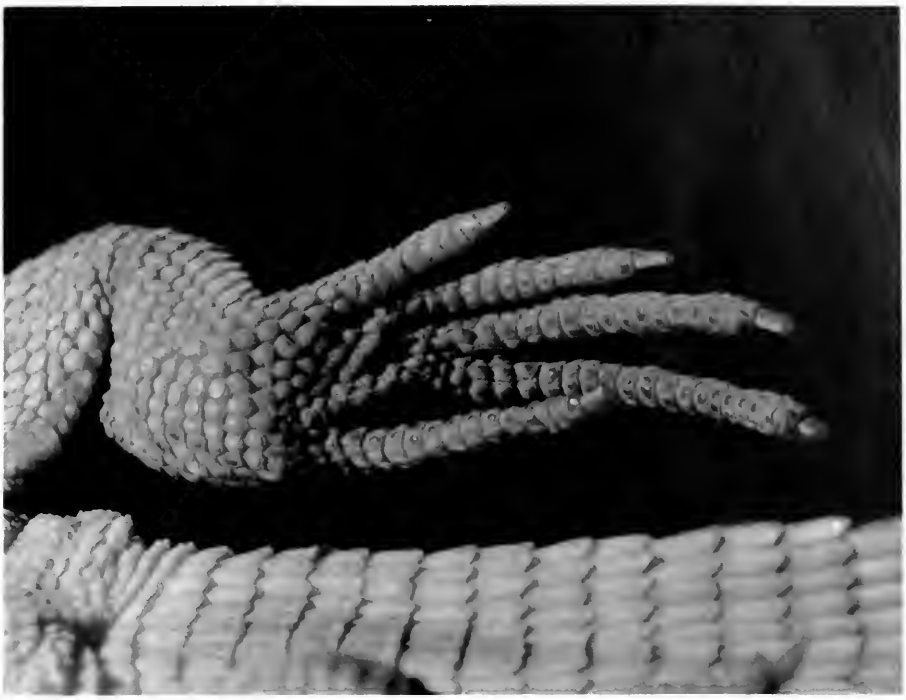

FIG. 3. Ventral view of left hind foot of *Varanus acanthurus* (MVZ 81648), from Charter's Towers, Queensland, Australia. Snout–vent length of the lizard is 123 mm.

exhibit several foot morphologies, but none of them has rows of darkly pigmented, juxtaposed scales as in *V. prasinus.*

Background Observations on Other Taxa

Neotropical iguanids of the genus *Polychrus* are green and have long, semiprehensile tails (Gorman et al., 1969; Hoogmoed, 1973; Vanzolini, 1983). Hoogmoed (1973) noted keels on the free margins of subdigital scales of *P. marmoratus* and suggested that they aid in climbing. Peterson (1983) illustrated these structures for *P. marmoratus* and confirmed their presence in *P. acutirostris, P. gutturosus,* and *P. peruvianus.* I observed similar subdigital keels in *P. femoralis* and *P. liogaster,* the remaining species in the genus.

Vitt and Lacher (1981) found that stomachs of 105 *Polychrus acutirostris* from Brazil contained a variety of arthropods and fruit, but orthopterans predominated. Stomach contents of 16 *P. marmoratus* from northern and western South America indicate a similar diet for that species (Beebe, 1944; Hoogmoed, 1973; Duellman, 1978). One *P. liogaster* (MVZ 36455, Bolivia, 49.3 g) contained a cicada (Homoptera, Cicadidae, MR = 0.028), a grasshopper (Orthoptera, Acrididae, MR = 0.01), a beetle (Coleoptera, Cerambycidae, MR = 0.006), and seven fruits with hard seeds (5 × 10 mm).

Old World chamaeleontids (especially species of *Chamaeleo*) are often green and are characterized as a family by strongly prehensile tails, highly projectile tongues, zygodactylous feet, and several visual specializations (Bellairs, 1969; Harkness, 1977). There is surprisingly little information available on the natural diets of chameleons, but a few species are known to feed frequently on orthopterans (Burrage, 1973; Schifter, 1984).

Discussion

General Remarks

Varanus prasinus feeds mainly on arthropods, usually relatively small katydids, but large walkingsticks and rodents are also taken occasionally. These data probably reliably represent the diet,

despite the modest sample size, because a single prey type predominates in specimens that were collected from diverse localities over a period of four decades. Consideration of stomachs with multiple items further suggests that the sample primarily mirrors variation within, rather than among, individuals (cf. Arnold, 1977). Although a captive *V. prasinus* ate bananas (Mertens, 1971), there is no evidence of plants in the natural diet of this species.

With the exceptions of *Varanus bengalensis* (Loop, 1974; Auffenberg, 1984) and *V. komodoensis* (Auffenberg, 1981), the role of prey characteristics in the feeding behavior of monitors remains largely unknown. Stomach contents indicate that *V. prasinus* typically swallows prey headfirst (of 19 items, this orientation in the gut could be determined for 18; one was swallowed doubled up). A large, spinose walkingstick evidently was partially dismembered before ingestion, perhaps with the raking movements observed in captive monitors. These findings suggest an array of prey handling behavior that merits further study.

Some larger monitors in more terrestrial habitats also lay eggs in termite mounds, nest in burrows, or exhibit intraspecific variation in this regard (Auffenberg, 1981, 1983; review of Riley et al. [1985] omitted Longley [1945], who reported the eggs of *Varanus varius* in a termite nest, high up in a tree). Cowles (1930) pointed out that termitaria provide a favorable microclimate for incubation of the eggs of *V. niloticus* in Africa, and subsequent authors have emphasized that effect and protection from predators (Magnusson et al., 1985; Riley et al., 1985). The observations of *V. prasinus* suggest that immediate accessibility of a rich food source for the young might be another advantage to reptiles nesting in termitaria. Moreover, if the use of termite nests proves typical for several species, it might represent a behavioral homology with potentially interesting implications for the early evolution of varanids (cf. Greene & Burghardt, 1978).

Relative Prey Size

Varanus prasinus is comparatively large among extant lizards (cf. Pough, 1980) and, because approximately 98% of its diet by frequency consists of arthropods, this species might seem to contradict Pough's (1973) suggestion that a large lizard could not catch enough insects to make a living. Large prey, however, might be rare in the diet and yet significant. If average MRs of 0.021, 0.122, and 0.296 are multiplied by 44 small arthropods, one walkingstick, and one rodent (frequencies of those items in adult *V. prasinus*), respectively, the resulting "importance indices" (each of these products divided by the sum of the products) are 0.69, 0.09, and 0.22. This simulation is at best a crude approximation of the overall diet of an individual (e.g., it ignores differences in digestibility among prey), but it demonstrates that even the occasional ingestion of relatively large walkingsticks and rodents might be energetically significant (in this case, roughly 31% by relative prey mass).

Conversely, it is clear that fairly small arthropods are an important part of the diet of this moderately large lizard (at least 69% by relative prey mass). If the frequency of large items is exaggerated by small sample size, arthropods might be the *only* significant prey type for *Varanus prasinus*. These comments emphasize the need for additional data to address conclusively the problem of functionally important variables in lizard feeding biology (Greene, 1982; Estes & Williams, 1984).

Hunting Adaptations

I propose that the green coloration, prehensile tail, and unusual feet of *Varanus prasinus* facilitate carefully controlled, unobtrusive movements on small limbs, vines, or leafy vegetation and thereby enable the lizards to capture katydids and other arboreal creatures. Prey that can propel themselves from a perch probably present special capture problems for a predator, and such escape tactics are widespread among animals in tropical forests (e.g., Robinson, 1969; Emmons & Gentry, 1983; pers. obs.). Furthermore, tropical katydids and walkingsticks often are colored cryptically and active nocturnally (Robinson, 1973; pers. obs.), and monitors are known to search methodically in particular microhabitats for hidden prey (e.g., *V. bengalensis,* Auffenberg, 1984; *V. tristis,* Pianka, 1982). Ridges on the feet of some birds are thought to enhance maneuverability on perches (Bock & Miller, 1959), and perhaps the raised subdigital scales of *V. prasinus* also do that. A plausible mechanism is that they increase the number of frictional edges in contact with the substrate (Hecht, 1952; Peterson & Williams, 1981; Cartmill, 1985). The function of dark pigment in this case is unknown, but melanin reduces wear on bird feathers (Burtt, 1979) and might do so for lizard

skin. Prehensile tails also provide additional frictional support for a climbing lizard (Tornier, 1899; Cartmill, 1985).

The situation for *Varanus prasinus* is equivalent to Figure 1a, except that here the derived features and performance advantage characterize a single taxon. Green coloration, a prehensile tail, a regular arrangement of black foot scales, and a diet of katydids are unique to this species among varanids, and these attributes are lacking even in other members of the subgenus *Odatria* (Mertens, 1942b) that climb regularly and occasionally eat arthropods (e.g., *V. tristis,* Pianka, 1982). For this reason, alternatives such as constraint and exaptation (Gould & Vrba, 1982) seem less likely than adaptive divergence to explain their concordant presence in *V. prasinus.* It is important to note, however, that if *V. acanthurus, V. prasinus,* and *V. tristis* are related such that the dark aspects of their subdigital scales are homologous, then only the extreme development of that character can be interpreted as an adaptation for hunting in tropical forest foliage by *V. prasinus.*

A brief comparison of *Varanus prasinus* with certain other arboreal tropical lizards is instructive. The closest living relatives of chamaeleontids and *Polychrus* are agamids and other iguanids, respectively, which lack primitively green coloration, prehensile tails, and specialized grasping feet (Etheridge, *in* Paull et al., 1976; Estes, 1983; Peterson, 1983). The independently derived morphological similarities among chamaeleontids, *Polychrus*, and *V. prasinus* are concordant with dietary similarities. As such they present a good *prima facie* case for adaptive convergence, and I propose that the relevant task for all three is to stalk stealthily and seize wary, arboreal, saltatory, and flying prey. It is interesting to note that species richness among these lineages parallels the extent of morphological specialization exhibited by each of them. *Varanus prasinus* is modified in minor ways relative to other varanids; the approximately 90 species of chamaeleontids share a number of features that are associated with arboreal hunting, and are highly derived relative to agamids; and, lastly, the six species of *Polychrus* are intermediate in their deviation from ancestral iguanid characteristics.

My findings emphasize the likelihood that adaptive convergence in external morphology is a widespread phenomenon in lizards (e.g., Williams & Peterson, 1982; Luke, 1986). Conclusive treatment of this generalization will require comprehensive information on the functional morphology, natural history, and systematic relationships of these animals.

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Addendum

I learned of Mitchell's (1964) illustration of the foot scalation of *Varanus glebopalma* after this manuscript was accepted for publication. That species is approximately the same size as *V. prasinus,* has a black and gray dorsal pattern, inhabits sandstone outcrops in xeric parts of northwestern Australia, and feeds primarily on scincid lizards (J. B. Losos, pers. comm.). The soles of its feet are characterized by polished dark areas in the center of each scale, and thus closely resemble the condition in *V. prasinus.*

An evolutionary assessment of the similarities

between *Varanus glebopalma* and *V. prasinus* will require more information on varanid relationships than is available currently. As noted above, the darkened soles of *V. prasinus* cannot be adaptations for predation on orthopterans that live on tropical foliage if those features are retained from a non-rain forest ancestor (as might be the case if *V. glebopalma* and *V. prasinus* are sister taxa). On the other hand, my adaptive interpretation of the darkened foot scales of *V. prasinus* is not affected by their presence in *V. glebopalma* if the similarity is not homologous, although the possibility of functional convergence would still merit study.

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