Russian Journal of Herpetology Vol. 1, No. 2, 1994, pp. 108 – 113

DIET OF THE NEW CALEDONIAN GECKO *Rhacodactylus auriculatus* (SQUAMATA, GEKKONIDAE)

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Submitted March 1, 1994.

The diet of the large New Caledonian gekkonid lizard, *Rhacodactylus auriculatus* is highly varied and most prey items taken are relatively large. In addition to many types of arthropods, this lizard also includes geckos and especially skinks in its diet. It also appears to feed on pollen. Saurophagy in this species was previously predicted on the basis of dental morphology, whereas the inclusion of flower parts in the diet was signaled by observations reported in the 19th Century.

Key words: Gekkonidae, *Rhacodactylus auriculatus*, diet, saurophagy, pollen.

Rhacodactylus auriculatus is one of the smaller members of the giant carphodactyline forest geckos and is endemic to the forests and maquis vegetation of the southern ultramafic region of New Caledonia. Its diet in captivity has been reported to include crickets, waxworms, bananas and mango (Rösler, 1988, 1989) and it has been suggested (Mertens, 1964; Bauer, 1985; Bauer and Vindum 1990) that insects and fruit were probably also part of the natural diet of this species. The wild diet of this species also includes snails (Bauer and Russell, 1990), flowers (Bavay, 1869), and most surprisingly, other lizards. In an analysis of the diets of New Caledonian forest lizards, Bauer and DeVaney (1987) reported the presence of a single adult specimen of the small endemic New Caledonian gecko *Bavayia sauvagii* in the stomach of *R. auriculatus*.

Bauer (1990a; Bauer and Russell, 1990) proposed that the enlarged, caniniform teeth unique to *R. auriculatus* might reflect a specialization for feeding on vertebrates, or other large, soft-bodied prey. This hypothesis, based on inference from the morphology of other saurophagous lizards and supported by the identification of one lizard prey item from a single stomach, has remained untested by more representative dietary data. Dietary records for all species of *Rhacodactylus* are difficult to obtain, chiefly because these large, attractive geckos are often kept alive in captivity before being prepared as museum specimens. The availability of gut contents from a series of specimens sacrificed shortly after capture provides an opportunity to obtain a more representative picture of the wild diet of *R. auriculatus* and offers the possibility of evaluating the hypothesis that the dentition of this species is functionally adapted to the diet.

MATERIAL AND METHODS

Stomach and intestinal contents were obtained from a series of 21 specimens of *Rhacodactylus auriculatus* collected in southern New Caledonia (Mt. Gouemba, Pic du Pin, and Mt. Dore) in December 1978 by Ross Sadlier and Peter Rankin and housed in the herpetological collection of the Australian Museum, Sydney (AMS). Lizard snout-vent lengths were recorded with vernier calipers to the nearest 0.1 mm. Both stomach and intestine were examined for prey items. Pooled gut contents were stored in 70% ethanol. Although the inclusion of hindgut contents in dietary analyses may have small (Schoener, 1989) or large (Floyd and Jenssen, 1984) effects on interspecific prey diversity comparisons, they can only be beneficial in the context of determining dietary scope in single taxon studies. Prey items were identified at least to order or family (to genus or species for vertebrate prey). For fragmented prey, head capsules, elytra or other body parts were used to estimate the minimum number of individuals represented. Because most of the prey items recov-

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ered were fragmentary, consistent estimates of prey volume or mass could not be calculated.

RESULTS

The geckos examined ranged from 76.2 to 119.6 mm SVL (x = 102.2 mm), encompassing the size range from juveniles to large adults. Nineteen of the 21 geckos examined contained food items in the stomach, hindgut, or both. Nine specimens, all of which also contained food, had pinworms (*Oxyurus* sp.) in their hindguts. Levels of infestation ranged from two to 20 parasites per lizard (x = 6.33). A single nematode resembling *Trichuris* spp. was located in the stomach of one specimen only (AMS 78337). This is noteworthy as members of this parasite have previously been reported only from mammals and irds. A similar, although morphologically distinct genus, *Capillaria*, however is known from a variety of amphibian and reptile hosts. Both types of worms represent new parasite records as the only nematode parasite previously reported from an element of the New Caledonian herpetofauna is *Angiostrongylus cantonensis*, a metastrongylid recorded in the introduced frog, *Litoria aurea* (Ash, 1968).

A total of 82 animal prey items were found in the 19 guts containing prey and animal prey items per stomach ranged from 1 to 26 (x = 4.32) (Table 1). Arthropods comprised the majority of the prey (76 items; 92.7%), with insects constituting the majority (84.2%) of these. Lepidopteran larvae (mean length 14.4 mm for intact individuals, n = 12) accounted for 31 items, but these were concentrated in the stomachs of only three lizards, and 26 of these were taken from a single specimen. Beetles were also significant in the diet, with 12 items being found in eight guts. Orthopterans, while not as common, were among the largest prey items, with adult gryllacridoids measuring up to 30 mm (excluding ovipositor). The single largest insectan prey item was a phasmid (minimum length 50 mm). Other insect groups were not well represented in the guts examined (see Table 1). In addition to insects, spiders were an important food source, with a minimum of 11 individuals found in nine *Rhacodactylus* stomachs. Most spiders were represented by isolated chelicerae or leg segments, so identification to lower taxonomic level was not possible. A centipede was represented by a single body segment in AMS 78118, the same individual that had eaten the phasmid.

In addition to arthropods, prey items also included part of the operculum of a pulmonate gastropod and parts of five skinks assignable to the genus

TABLE 1. Gut Contents of 19 Specimens of *Rhacodactylus auriculatus*

Prey taxon	Items		Guts	
	number	% total	number	% total
Araneomorphae	11	13.4	9	47.4
Chilopoda	1	1.2	1	5.3
Insecta				
Blattodea	4	4.9	4	21.1
Coleoptera				
Curculionidae	3	3.7	2	10.5
Elateridae	1	1.2	1	5.3
unidentified	8	9.8	7	36.8
Diptera				
Tipulidae	1	1.2	1	5.3
Hemiptera				
Cicadidae	1	1.2	1	5.3
Hymenoptera				
Formicidae	1	1.2	1	5.3
unidentified	2	2.4	2	10.5
Lepidoptera				
adult	1	1.2	1	5.3
larvae	31	37.8	3	15.8
Orthoptera				
Ensifera	2	2.4	1	5.3
Gryllacridoidea	4	4.9	3	15.8
Gryllidae	2	2.4	1	5.3
Phasmatodea	1	1.2	1	5.3
Unidentified	2	2.4	2	10.5
Mollusca				
Pulmonata	1	1.2	1	5.3
Vertebrata				
Caledoniscincus	5	6.1	5	26.3
Total Animal Prey	86	100	19	100
Other gut contents				
Shed gecko skin	4		4	21.1
Plantae				
Anthers	14		1	5.3
Stamens	20		1	5.3
Leaf	1		1	5.3

Note: The number of items of each prey type and the number of lizard guts containing at least one item of each prey type are presented, along with the percentage representation of each prey type by item in the diet and the percentage of all lizard guts containing each prey type.

Caledoniscincus. The remains identified included: one left innominate bone and femur (AMS 78336), one pes (AMS 78337), one partial frontal bone, one otic capsule, one humerus, one pelvis and two partial femora (AMS 78334), one frontal bone, left and right mandibles, one maxilla, one prefrontal and one postfrontal (AMS 78119), and and entire lizard (preserved wet weight 0.58 g, SVL = 24 mm) (AMS 78338). Although no specific assignment could be made in the case of the skeletal remains, the entire lizard was a *C. austrocaledonicus.* Only this species and the very similarly sized and proportioned *C. atropunctatus* occur within the range of *Rhacodactylus auriculatus*. The whole lizard was the largest single item retrieved from the stomach of any gecko, although the size of fragments suggests that some spiders, the phasmid and some gryllacridoids were probably comparable to the skink prey in volume. The only other vertebrate material recovered from the guts of *Rhacodactylus auriculatus* was shed gecko skin, found in four of the specimens examined.

Plant material was found in three stomachs. One lizard contained a large leafy plant part that would appear to have been ingested accidentally, the other two lizards, however, contained anthers and stamens, respectively.

DISCUSSION

Although there are extensive anecdotal references to gekkonid diet (e.g., Loveridge, 1947), detailed analyses of gut contents have been limited. For virtually all taxa studied, arthropods have been the dominant prey type. Termite specialists are common, especially in arid regions (Pianka and Pianka, 1976; Pianka and Huey, 1978; Simbotwe, 1983; Pianka, 1986), but most species appear to be arthropod generalists (see Perry and Brandeis, 1992). Beetles, spiders and orthopterans are commonly the most important components of such generalized gecko diets, in both arboreal (Bustard, 1968a; Henle, 1990; Bobrov, 1992) and terrestrial species (Bustard, 1968b; Pianka and Pianka, 1976; Pianka and Huey, 1978; Pianka, 1986; Semenov and Borkin, 1990). This is true whether prey categories are ranked by number of prey items ingested or by prey volume (or mass).

With regard to its arthropod constituents, the diet of *Rhacodactylus auriculatus* is rather typical of most geckos, although there is a tendency for relatively large prey items to be taken. A similar pattern is also seen in the carphodactyline gecko *Phyllurus platurus*, the only other large non-terrestrial gecko to be investigated (Doughty and Shine, in press), although centipedes and cockroaches were more important in the diet of this species than that of *R. auriculatus*. Perhaps significantly, *P. platurus* has also been reported to eat small geckos (Ehmann, 1992). Predation on vertebrates is, predictably, more often a feature of geckos of larger size. Bauer (1990b) reviewed gecko predation on other vertebrates. Although he listed a minimum of 37 species that preyed on vertebrates (mostly other lizards), the significance of vertebrate prey as dietary items has not been fully established in the majority of taxa. Data from those few saurophagous geckos for which large samples are available, *Nephrurus* spp. (Pianka and Pianka, 1986), *Chondrodactylus angulifer* (Pianka and Huey, 1978), and *Teratoscincus* spp. (summarized in Szczerbak and Golubev, 1986; Semenov and Borkin, 1990), confirm that vertebrate prey are rarely taken (although they may make up a large part of the volume of prey consumed). The presence of lizard remains in six of 22 guts containing food in *R. auriculatus* (including data from Bauer and DeVaney, 1987; Bauer and Russell, 1990) would appear, therefore, to indicate that this species is more of a "specialist" on lizard prey than most other geckos.

Bauer and Russell (1990) regarded the caniniform dentition of *R. auriculatus* to be an adaptation of such specialization, although their conclusions were based only on the presence of one gekkonid stomach content and inference from tooth form in other squamates, such as those teiids (Presch, 1974) and crotaphytids (Hotton, 1955) that feed on vertebrate prey. Such caniniform teeth are certainly atypical of most gekkonids (Sumida and Murphy, 1987) and the occurrence of lizard remains in more than one fourth of dietary samples corroborates the hypothesis of dentitional adaptation. If dentition is a limiting factor in the successful utilization of lizard prey by geckos, the relative rarity of such prey in the diets of such large geckos as *Nephrurus* spp. and *Phyllurus* spp. is not surprising, as these taxa possess numerous, very small, blunt teeth (Bauer, 1990a), typical of generalized arthropod-feeders.

The lizards most often reported in the diet of geckos are other geckos, often congeners or even conspecifics (Bauer, 1990b). Skinks have only been reported from the diet of *Nephrurus milii* (McPhee, 1979) and *N. asper* (Gow 1979). The rarity of these items in the diet of geckos probably reflects differ-

ences in both typical activity period and substrate preference of representatives of these two families. The prey items taken by *Rhacodactylus auriculatus* may reflect this species' peculiar activity pattern. Although it is chiefly arboreal, it may be found on the ground quite frequently, although exclusively at night (Bauer and Vindum, 1990). The bulk of the prey items could have been taken either on the ground or in the vegetation. The skinks, however, are thought to be exclusively terrestrial. It is probable that sleeping skinks were taken by the geckos from their terrestrial retreats, but it is also possible that *R. auriculatus* forages by day on the ground or that *Caledoniscincus* may climb to low perches in vegetation at night (although neither of these interpretations is supported by our extensive field observations of these lizards).

Caledoniscincus austrocaledonicus is the commonest vertebrate in virtually all habitat types in New Caledonia except closed forest. This, combined with its surface-active habits and small size account for its frequent occurrence in the diet of a variety of predatory vertebrates. It has previously been shown to make up part of the diet of the introduced frog *Litoria aurea* (Bauer and Vindum, 1990) and of its own congener *Caledoniscincus festivus* (Bauer and DeVaney, 1987; Bauer and Vindum, 1990), and is probably at least occasionally taken by other, larger lizards. Predation by birds has not been well documented, but photographs of the kingfisher *Halcyon sanctus canacorum* and island thrush, *Turdus poliocephalus xanthopus* carrying lizards (Hannecart and Letocart, 1980, 1983) appear to represent this species, and other saurophagous birds in New Caledonia probably also take this skink. Feral cats and house cats also frequently take small skinks (Bauer and Sadlier, 1993), and *C. austrocaledonicus*, owing to its abundance and preference for open habitats, including those disturbed by human activity, are probably often eaten.

The only other animal remains identified from the stomach contents examined were shed skins of the *Rhacodactylus auriculatus* themselves, and a single snail. The ingestion of sloughed skins is a common phenomenon among geckos (Bustard, 1968a; Perry and Brandeis, 1992) and molluscs may be a minor, but typical, component of the diet in a variety of geckos. Snails have previously been reported from the diet of *R. auriculatus* (Bauer and Russell, 1990), as well as a number of gekkonine geckos (e.g., *Gehyra variegata* [Bustard, 1968a]; *Ebenavia inunguis* [personal observation]).

Finally, the plant material found in the stomachs of three of the specimens examined deserves some comment. Most authors have tended to dismiss occasional plant parts in gekkonid diets as accidentally ingested (Perry and Brandeis, 1992). This may be so in many cases, especially when the plant material is found in conjunction with herbivorous arthropods or with prey, such as gastropods, that may be adherent to leaves or other plant parts. The occurrence of fruit, nectar, or pollen in the guts of lizards, however, is generally indicative of the use of plant products as a regular dietary component (Whitaker, 1987).

It has been recognized for some time that lizards may be significant as pollinators in a number of widely scattered island ecosystems (Vinson and Vinson, 1969; Elvers, 1977; Whitaker, 1987). New Zealand geckos of the genera *Hoplodactylus* and *Naultinus*, both closely related to the New Caledonian carphodactyline geckos, are known to feed on nectar from a variety of plants, most notably pohutukawa (*Metrosideros excelsa*), and other myrtaceous plants (Whitaker, 1987). Whitaker (1987) observed large numbers of *Hoplodactylus pacificus* feeding on inflorescences. He reported pollen smears from the throat of geckos, but did not mention the ingestion of stamens or anthers in association with nectivory. The reward for New Zealand lizards appears to be nectar alone (Whitaker, 1987), although gekkonine geckos of the genus *Phelsuma* have been known to eat pollen (Evans and Evans, 1980; Cheke, 1984), which may be a significant source of nutrition for at least some species (Gardner, 1984). Whitaker (1987) suggested that a reassessment of the pollination biology of other brush-structured flowers, to determine if geckos might be significant pollinators.

It was not possible to determine if pollen grains were absent, had been digested or had been overlooked in the guts of the *Rhacodactylus auriculatus* we examined. Nonetheless, the original notes taken at the time of gut emptying indicate that some stomachs contained a "gelatinous mass" that might represent an aggregate of partially digested pollen. Gardner (1984) reported the presence of pollen grains in all regions of the gut, but did not report the presence of stamens or anthers in any of the specimens he examined. Bavay's (1869) observations of *R. auriculatus* feeding on *Geissois* flowers can be confirmed by our results. The stomachs of two lizards contained stamens or anthers of flowers that appear to represent some plant of the same family (Cunoniaceae). This group includes numerous species endemic to the lateritic

southern third of New Caledonia. Alternatively, these may represent material from the superficially similar inflorescences of certain myrtaceous plants, which are also well-represented in this area of New Caledonia.

Significant differences in diet with age, sex, season and locality are known to exist in at least some geckos (Bustard, 1968a; Henle, 1990; Perry and Brandeis, 1992). We cannot address seasonal variability in our sample and our sample size is too small to effectively address sexual and geographic variation in diet. The latter, would be expected to be minimal, however, as the habitat of *Rhacodactylus auriculatus* is relatively homogeneous (Bauer and Vindum, 1990) and occupies a small area (maximum of 5000 km^2) in the southern third of New Caledonia. No pronounced sexual dimorphism exists in this species, and maximum sizes of males and females are comparable. Age (or size) relationships might be thought to be important in determining the maximum size of prey taken, however. Specimens in our sample ranged from juveniles of less than 80 mm SVL or less to large adults of approximately 120 mm SVL. However, the largest prey classes, skinks and gryllacridids, were distributed across all lizards sizes. The large size of these geckos relative to all prey classes probably places little restriction on the possible prey of all except the very young *R. auriculatus*, for which no dietary information is available.

Samples remain inadequate for a quantitative analysis of diet in *Rhacodactylus auriculatus*, comparable to those available for desert geckos (e.g., Pianka, 1986). Nonetheless, it is apparent that this species, although catholic with respect to the range of dietary items consumed, utilizes a combination of resources that is rare or perhaps unique among geckos. It is likely that vertebrates form a regular and significant portion of the diet in this species, perhaps to a greater extent than in any gecko studied to date. The utilization of pollen is also relatively rare among geckos, although it may be more frequent among island species than had been realized. The latter dietary specialization does not seem to be accompanied by any peculiar morphological correlates and may be an option available to many or most geckos under appropriate ecological circumstances. The association of lizard-feeding habits with a highly modified dentition, however, is unique among geckos and may reflect both the significance of such prey in the diet and the special requirements for subjugation and handling of prey of this type.

Acknowledgements. We thank the authorities of the Service du Patrimoine Naturel for permission to collect in New Caledonia, and Eric Larsen for assistance with the identification of insect fragments.

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