

Ecological observations on the Gargoyle Gecko, *Rhacodactylus auriculatus* (BAVAY, 1869), in southern New Caledonia

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Abstract. Ecological niches of squamate reptiles are delineated by diet, microhabitat use, and activity period. In the current study field data were gathered to characterize the ecology of *Rhacodactylus auriculatus* with regard to these three axes. *Rhacodactylus auriculatus* regularly consume a wide taxonomic and ecological variety of arthropods, lizard prey including geckos and skinks, and various plant materials including floral parts and sap. Based upon the variety of dietary constituents and the regularity with which they are utilized, *R. auriculatus* may have the most atypical of all gekkonid diets. *Rhacodactylus auriculatus* partition their microhabitat with conspecifics based on perch height, presumably to avoid aggressive interactions. During winter in southern New Caledonia, *R. auriculatus* were most active from one to four hours after sunset.

Key words. Diplodactylidae, *Rhacodactylus auriculatus*, New Caledonia, ecology, diet, activity, microhabitat.

Introduction

The gargoyle gecko, *Rhacodactylus auriculatus*, is a commonly kept and bred diplodactylid gecko. It is the smallest of six recognized species in the genus, reaching only about 125 mm SVL (SAMEIT 1986, BAUER & SADLER 2000). *Rhacodactylus auriculatus* occurs in both humid forest and maquis (a shrub-dominated habitat underlain by ultramafic substrates) across the southern third of the New Caledonian mainland (Grande Terre) from sea level to nearly 1000 m, but appears to be absent from the Isle of Pines and its satellite islets (BAUER & SADLER 1994a, 2000). It has recently been recorded from numerous isolated areas in the north of the island (WHITAKER et al. 2004), and the taxonomic status of these populations is under investigation (BAUER et al., unpublished).

Although there is a large body of captive data about the species (e.g., MERTENS 1964, RÖSLER 1988, HENKEL 1991, PETHER 1999, TYTLE 2000, DE VOSJOLI et al. 2003, BACH 2004, HENKEL & SCHMIDT 2007), field-based observations are more limited, and have chiefly been based on opportunistic data gathering (e.g., ROUX 1913, MEIER 1979, BAUER & VINDUM 1990, BAUER & SADLER 1994b, 2001, DE VOSJOLI & FAST 1995, SEIPP & HENKEL 2000). The information available, however, suggests that *R. auriculatus* has a particularly diverse diet that is highly atypical for geckos, incorporating vertebrate prey, mollusks, and plant material, as well as a broad range of arthropods (BAUER & RUSSELL 1990, BAUER & SADLER 1994b, SNYDER et al. 2008). The preferred habitats of this species are shrubby maquis vegetation, primary and secondary forest edges, and the ecotonal region between forest and maquis, although it

is also known to utilize mangroves and strand vegetation (BAUER & VINDUM 1990, BAUER & SADLER 2000). Within these areas, *R. auriculatus* is most frequently encountered on shrubs, saplings, and trees of small diameter. It is often found within a few meters of these and is regularly active on the ground, at least seasonally, in association with foraging and mating (BAUER & SADLER 2000).

In order to establish a more complete picture of the autecology of *Rhacodactylus auriculatus*, a field study was undertaken to quantify aspects of microhabitat use and activity and to assess diet during the cool period of the austral winter.

Materials and methods

Study site and specimen documentation

Rhacodactylus auriculatus were studied in Le Parc Provincial de la Rivière Bleue (22°06'S, 166°39'E) in the southern part of the Province Sud on the Grande Terre of New Caledonia (Figures 1–2). The park is a protected area with limited access. It was selected because of its location in the center of the known contiguous distribution of *R. auriculatus* (BAUER & SADLER 2000). The site contained both humid forest and maquis habitats (Figure 2). Other geckos in the study area included *Bavayia septuiclavus*, chiefly in maquis and *R. ciliatus*, *R. sarasinorum*, *Eurydactylodes symmetricus*, and *Bavayia geitaina* in forest. The study took place from 22 June 2004 to 4 August 2004 during the cool New Caledonian winter season. Data were recorded on a total of 30 nights within this interval as heavy rains occasionally precluded locating geckos by eye-shining. Transects

were followed along unpaved roads within the Parc Rivière Bleu, typically from 18:00 to 22:30 h (although on warmer nights, when activity remained high, searching continued until 01:00 h). Searches were not randomized but were concentrated in areas found to be most productive.

Geckos were located primarily by eye-shining and captured by hand. For each specimen SVL (mm), total body mass (g), tail condition (original versus regenerated), sex, and age class (juvenile [< 88 mm SVL] versus adult) were recorded. A permanent black marker was used to write a unique number on the ventral surface of the body so that individuals could be recognized when recaptured. Such markings are lost at ecdysis, but this occurs less frequently at cooler temperatures and lower metabolic rates (ALEXANDER & BROOKS 1999) and none of the recaptured geckos shed during the period of the study. Nonetheless, to ensure unambiguous identification of individuals digital photographs were taken to record color pattern, which is highly variable in this species (MEIER 1979, HENKEL 1986, BAUER 1990, WIRTH & PEUKERT 2009; Figures 3A–B) and can be used to identify individuals.

Habitat and activity

For each specimen captured the following data were recorded: time of collection, latitude and longitude, elevation, weather condition, phase of moon, vegetation type (maquis or forest), perch height (m), and perch diameter (mm). Geographic coordinates were recorded with a Magellan GPS, elevations were determined using a barometric

altimeter, and measurements of vegetation were made with a tape measure (perch height) and digital caliper (perch diameter). Temperature was recorded each night at the beginning of each search period. Ambient light was calculated using data from the U.S. Naval Observatory site (http://aa.usno.navy.mil/data/docs/RS_OneDay.html), which provides information about percent reflected visible moonlight and moonrise/set time.

Single factor ANOVAs and regression analyses were performed in order to investigate the relationship between perch height and diameter and gecko mass, SVL, and sex, and between temperature, ambient light, and precipitation and average hourly capture rate.

Diet

Diet was determined through stomach flushing. Although this method does not retrieve items that have passed below the pyloric sphincter, it has been found to be highly reliable at recovering stomach contents and is non-destructive (LEGLER 1977, LEGLER & SULLIVAN 1979). The mouth was held open by a plastic cuff and a human infant feeding tube with sub-terminal holes to decrease pressure placed on the pyloric sphincter was connected to a 10 cc syringe and passed down the throat to the center of the stomach (JAMES 1990). Approximately 10 cc of water (adjusted for body size) was injected into the stomach. This was repeated 3–5 times unless stomach contents were regurgitated sooner, in which case one additional flushing took place to ensure the removal of all stomach contents. Stomach contents

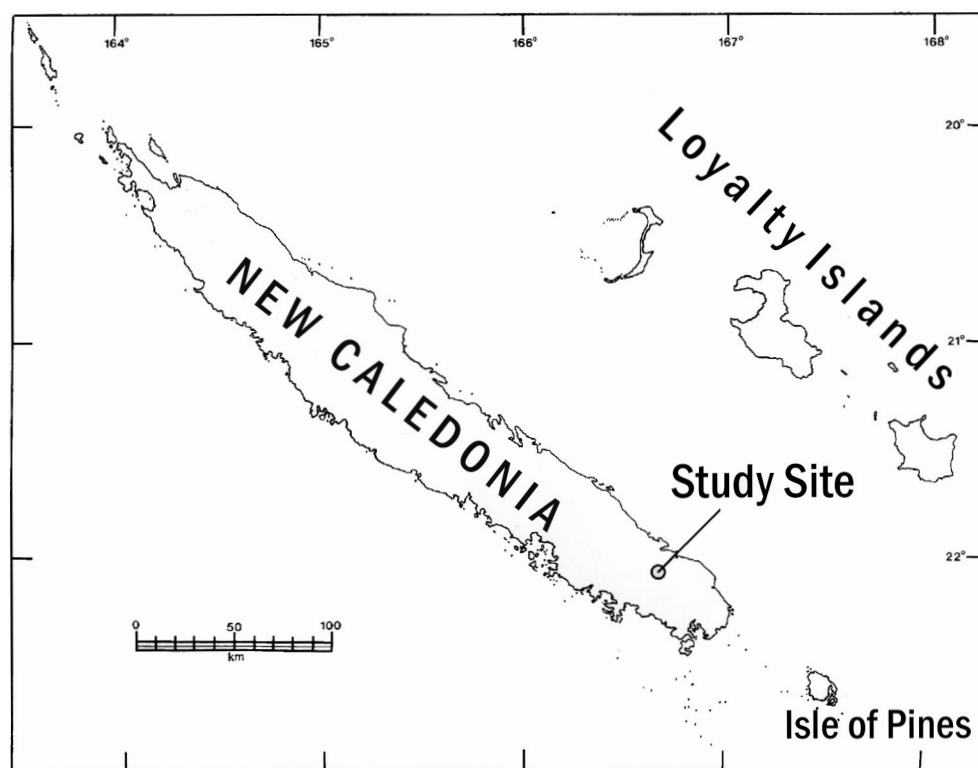


Figure 1. Map of New Caledonia showing the position of the study site (Parc Rivière Bleue).

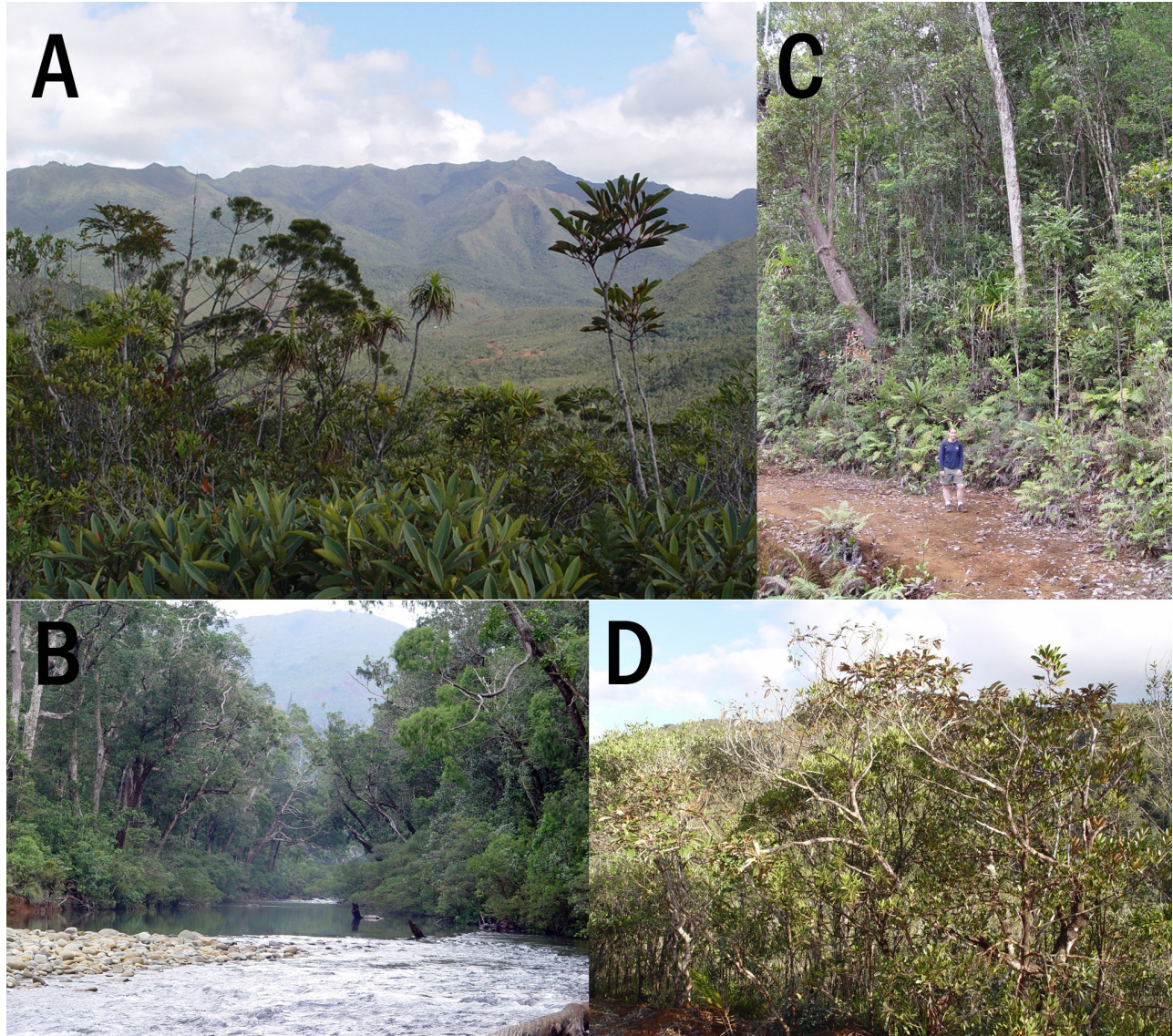


Figure 2. Habitat of *Rhacodactylus auriculatus*. (A) View of the Rivière Bleue valley from an adjacent hilltop. (B) View of the Rivière Bleue from the Pont Germain showing humid forest trees flanking the banks. (C) Humid forest vegetation near a roadside in the Parc Rivière Bleue. Such roads served as transects for locating *Rhacodactylus auriculatus*. (D) Maquis vegetation, characterized by low canopy and generally small-diameter trees and shrubs along a roadside transect in Parc Rivière Bleue.

were stored in 70% alcohol for subsequent identification. Specimens were released at the site of capture. Stomach flushing resulted in no fatalities or obvious damage to the geckos. Specimens weighing less than 12 g and those that had been stomach-flushed within the previous seven days were not examined for dietary items.

Dietary niche breadth for *Rhacodactylus auriculatus* was calculated by number and volume of items in each food category using the Shannon index of diversity (PIANKA 1966, PEET 1974, PIELOU 1977, CASTANZO & BAUER 1993, 1997, VITT 1995). Prey items were identified to the lowest taxonomic possible and larval coleopterans and lepidopterans were treated as prey categories separate from adults. Calculations were based on the combination of results of the present study and previously published quantitative dietary data (BAUER & DEVANEY 1987; BAUER & SADLER 1994b).

Results

Microhabitat

One hundred and two captures, representing 88 unique specimens, were made (Figure 4). Six specimens were recaptured once and four were recaptured twice. Thirteen *Rhacodactylus auriculatus* were found in humid forest and 89 were found in maquis. All individuals found in the humid forest were located along the roadside or at the ecotone with maquis, where *Bavayia septuiclavus* was also common. The mean (\pm S.D.) perch diameter for *R. auriculatus* recorded in humid forest was 40.0 ± 46.9 mm and the mean perch height was 1.6 ± 0.8 m. The mean perch diameter and height for specimens recorded in the maquis was 21.0 ± 23.2 mm and 1.8 ± 1.1 m, respectively.

Differences between mean perch height usage for males, females, and juveniles were statistically significant ($P =$

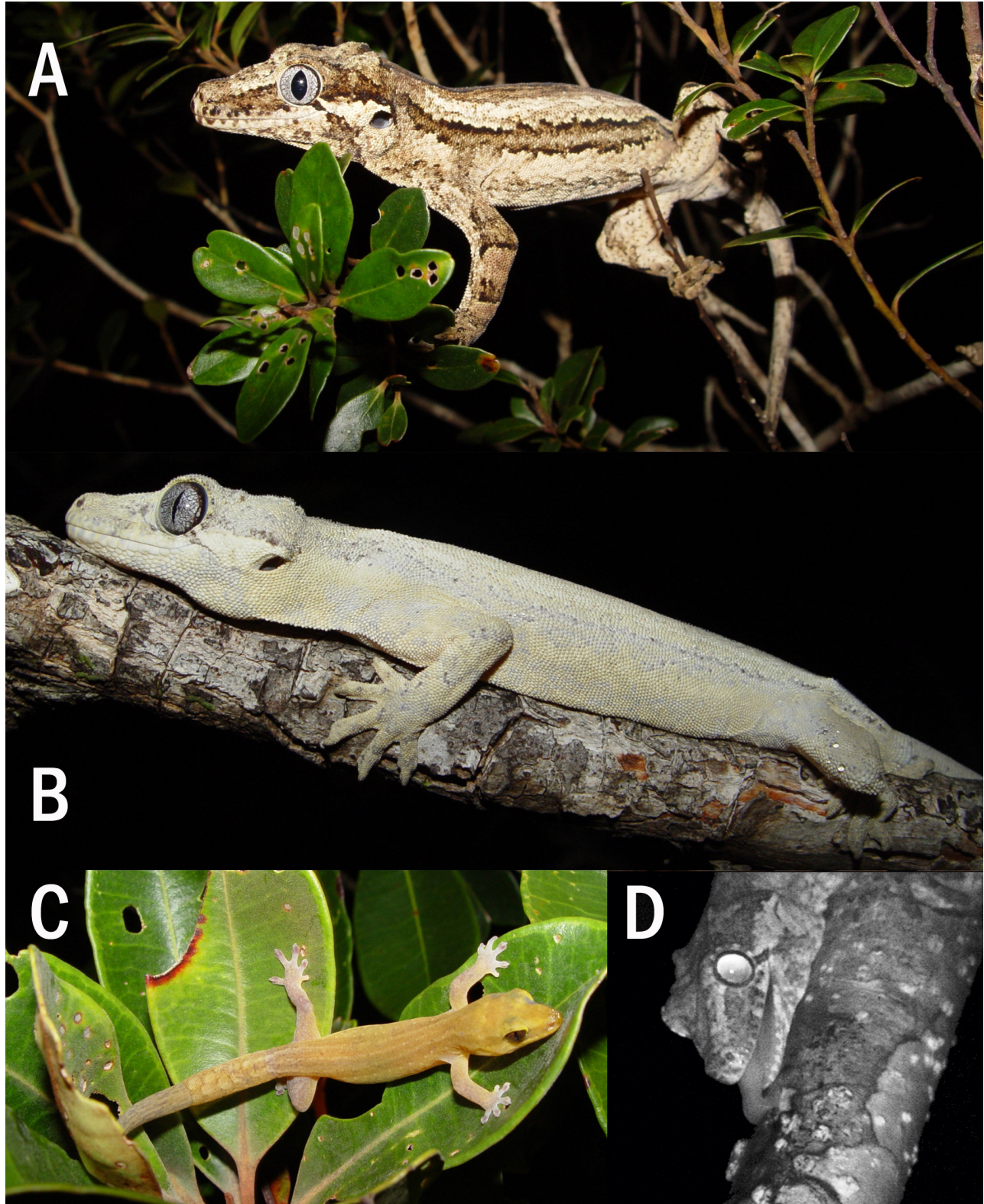


Figure 3. (A, B) Two representative *Rhacodactylus auriculatus* showing diversity in color and pattern at Rivière Bleue. (C) *Bavayia septuiclavis*, the most common small gecko occurring at Parc Rivière Bleue and a confirmed dietary item for *Rhacodactylus auriculatus*. (D) Infrared video still of an adult female *Rhacodactylus auriculatus* licking sap from a *Cunonia macrophylla* (Cunoniaceae).

0.049; Tab. 1). Female *R. auriculatus* occupied the highest perches on average (2.0 ± 1.2 m), whereas males and juveniles occupied average perch heights of 1.9 ± 0.9 m and

1.4 ± 0.7 m, respectively. Heavier animals were more likely to be found on higher perches ($r^2 = 0.065$, f ratio = 6.71, degrees of freedom = 1, 97; P value = 0.011). The relation-

ship between perch height and SVL was non-significant ($P = 0.077$). Likewise, ontogenetic stage, body mass or SVL were not related to perch diameter (Tab. 1).

Activity

Specimens were captured from 43 minutes after sunset until six hours and 38 minutes after sunset (local times between 18:05 and 00:10 hrs). The highest capture rates occurred between one and four hours after sunset, although this is not necessarily indicative of peak activity as search effort was not random. Nighttime temperatures during the study period ranged from 14.3 to 21.9°C at the beginning of field work each night. There were no significant relationships between hourly capture rate and temperature ($r^2 = 0.292$, $P = 0.394$) or ambient light ($r^2 = 0.896$, $P = 0.108$), although the highest average hourly capture rate (2.29 specimens/hr) occurred at 90% ambient light. Field observations suggested that light precipitation was also related to increased activity in *R. auriculatus*, but this was not found to be statistically significant ($P = 0.313$).

Diet

Sixty-six stomach flushings were performed, three on recaptured specimens. Food items were found in 14 of the 66 (21.2%) stomachs flushed, yielding a total of 18 prey items (Tab. 2). Fifteen of the 18 items were animal prey, 13 of which were arthropods, comprising 86.7% by number and 93.9% by volume of the total animal prey items recovered. The majority of arthropods recovered showed little sign of digestion. Two vertebrate prey items, constituting 13.3% by number and 6.1% by volume of the total animal prey, were recovered. One was the forelimb of *Caledoniscincus atropunctatus* and the other the thoracic region and humerus of a small gecko (probably *Bavayia septuiclavis*; Figure 3C). These were recovered from different adult male *R. auriculatus* captured in open maquis. Remaining items included shed gecko skin, found in two stomachs, and an unidentifiable gelatinous mass recovered from one stomach. Outside of the context of the main study an adult female (36 g, 122.8 mm SVL) was observed and filmed drinking sap from a *Cunonia macrophylla* (Figure 3D) over a period of three nights (SNYDER et al. 2008).

Dietary niche breadth for *Rhacodactylus auriculatus*, derived from cumulative data (multiple studies), based on the number of prey items consumed per prey category was 2.43, and by volume 1.94 (Tab. 3).

Discussion

Spatial Use

Rhacodactylus auriculatus has been recorded from open and closed maquis as well as humid forest (BAUER & SADLER 2000), usually on trees and shrubs at heights of 3–5 m, although specimens have also been found on fence posts, on the ground, under rocks, and under the loose bark of trees (BAUER & VINDUM 1990, SEIPP & HENKEL 2000). In the present study all specimens were found perched on trees

Table 1. Relationships between attributes of *Rhacodactylus auriculatus* (sex/age class [male, female, or juvenile], mass, SVL) and microhabitat parameters (perch height and perch diameter). Statistically significant P values are indicated in bold.

ANOVAs		r^2	f	d.f.	P
Perch Height	Class	–	3.11	2,91	0.049
Perch Diameter	Class	–	1.66	2,84	0.196
Regression Analyses					
Perch Height	Mass	0.065	6.71	1,97	0.011
Perch Height	SVL	0.032	3.19	1,97	0.077
Perch Diameter	Mass	0.008	0.369	1,97	0.814
Perch Diameter	SVL	0.002	0.639	1,97	0.221

and shrubs, the majority (87.3%) in maquis vegetation. The primary use of maquis and humid forest edge habitats by *R. auriculatus* appears to separate them spatially from their similarly sized congeners *R. ciliatus* and *R. sarasinorum*, both of which also occur at Rivière Bleue, perhaps reducing interspecific competition.

Microhabitat may be utilized differentially based on a variety of habitat features including substrate type, plant species, perch height and/or diameter, and retreat sites (JAMES & M'CLOSKEY 2002). In our study the difference in perch diameters used between habitats was not statistically significant due to small sample size in forest, but it is of interest that humid forest specimens were found on much larger-diameter perches but at the same height as in the maquis. This suggests that *R. auriculatus* may select perches primarily based upon height rather than perch diameter and is consistent with our findings that perch height, but not diameter, is significantly related to size and sex in this species. Our results that heavier individuals were more likely to be found on higher perches than lighter individuals parallels SEIPP & HENKEL's (2000) observations that young *R. leachianus* occupied much lower perches than did adults and is consistent with the hypothesis that perch segregation serves to reduce aggressive interactions among conspecifics (POUNDS 1988, IRSCHICK et al. 2005). There is little comparative information available for perch use by gekkotan lizards. PIANKA & PIANKA (1976) reported height above ground for three species they considered to be arboreal, but made no distinction between size, age, or sex. For the sphaerodactylid gecko *Gonatodes humeralis*, MIRANDA & ANDRADE (2003) reported statistically significant differences in perch height for males and females, but only during the rainy season. It is likely that perch use in *Rhacodactylus auriculatus* is also temporally labile and that seasonal variations in intraspecific segregation related to reproductive activity, prey availability, or environmental conditions occur.

Activity

In the present study, the highest capture rates occurred from one to four hours after sunset (1900–2200 h). This is consistent with qualitative statements by BAUER & SADLER (2000) that *R. auriculatus* are most active from sunset

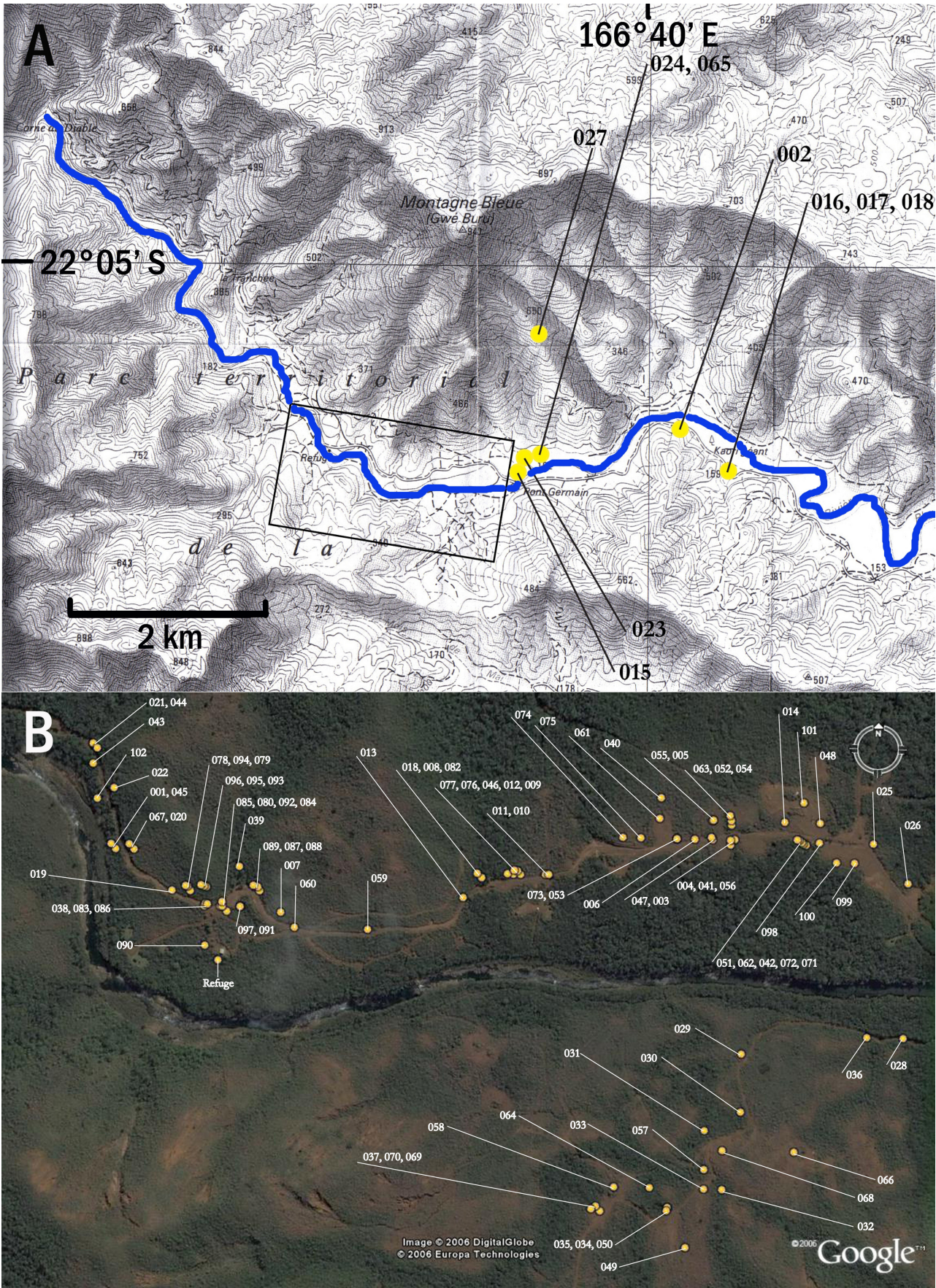


Table 2. Stomach contents from the 14 specimens of *Rhacodactylus auriculatus* from Parc Rivière Bleue that contained food items during the austral winter of 2004. Prey, by category, are listed by absolute number and percent of: total items consumed, stomachs containing prey type, volume of all items consumed, and mass (blotted dry) of all items consumed. Shed skins and amorphous plant material consumed are not included in the percentages calculated but are indicated below the main table. Note that the values under “stomach” exceed the total animal prey values because a single specimen may contain more than one prey type.

Prey Taxon	Items		Stomachs		Volume		Mass	
	number	% total	number	% total	cm ³	% total	g	% total
Araneae	1	6.7	1	7.1	0.15	12.6	0.09	17.6
Diptera								
Tupulidae	2	13.3	2	14.3	0.03	2.5	0.04	7.8
Coleoptera								
adult	3	20.0	3	21.4	0.05	4.2	0.05	9.8
larvae	3	20.0	3	21.4	0.23	19.3	0.17	33.3
Lepidoptera								
adult	2	13.3	2	14.3	0.22	18.4	0.06	11.8
larvae	1	6.7	1	7.1	0.05	4.2		
Phasmodidae	1	6.7	1	7.1	0.39	32.7	0.07	13.7
Scincidae								
<i>Caledoniscincus atropunctatus</i>	1	6.7	1	7.1	0.01	0.8	0.02	3.9
Diplodactylidae								
<i>Bavayia</i> spp.	1	6.7	1	7.1	0.06	5.3	0.01	2.0
Total Animal Prey	15	100	14	100	1.19	100	0.51	100
Other								
Shed gecko skin	2		2	14.3	2.26		0.79	
Gelatinous mass	1		1	7.1	0.30			

to 21:00–22:00 h. Although diurnal activity was not monitored in this study, a radiotelemetered female *R. auriculatus* studied opportunistically at the same time (SNYDER et al. 2008) was found to rotate around its perch, following the sun. Such limited diurnal activity, presumably related to basking, has also previously been noted in gargoyle geckos (MEIER 1979, BAUER 1990, BAUER & VINDUM 1990).

We did not find a relationship between capture rate and either precipitation or ambient light. Higher ambient light could facilitate prey location by nocturnal reptiles, but may also subject them to higher risk of predation themselves (PERRY & FISHER 2005). Native nocturnal predators of *R. auriculatus* are few, but barn owls (*Tyto alba*) are a potential threat and do occur in the study area. The few studies that have been done on nocturnal geckos suggest that most are more active under higher light conditions. BOUSKILA et al. (1992) and REICHMANN (1998) found that *Stenodactylus doriae* (a terrestrial, nocturnal, desert-dwelling gecko) is most active during moonlit nights, although they

change their behavior under such conditions, presumably to avoid predators. However, at least some species, such as *Crossobamon e. evermanni*, serve as counter examples and are inactive during bright nights (SZCZERBAK & GOLUBEV 1996).

Diet

In the present study, conducted during the austral winter, 21.2% of stomachs flushed contained food items, which is comparable to BAUER & DEVANEY's (1987) results for samples collected in May–June 1985, in which two of nine (22%) *R. auriculatus* contained prey. In contrast, 19 of 21 (90.5%) specimens contained food items in BAUER & SADLER's (1994b) dietary examination of *R. auriculatus* specimens collected in the austral spring–summer (although some prey items were retrieved from the hindgut, which was not accessed in the present study). Such a seasonal difference is expected as cooler temperatures reduce the activity levels of both ectothermic predators and their prey, reducing both the likelihood of obtaining prey and the need to do so (HUEY et al. 2001). The generally high proportion of empty stomachs in *R. auriculatus*, regardless of season, is not unexpected as HUEY et al. (2001) found that gekkonids had the highest percent of empty stomachs of all lizards they reviewed. In addition, they found that regardless of phylogeny, a high proportion of empty stomachs was associated with species occupying higher trophic levels and with nocturnality, both traits characterizing *R. auriculatus*.

Left page: Figure 4. Capture sites of *Rhacodactylus auriculatus* within the Parc Rivière Bleue. Each numbered locality represents a capture site. (A) Topographic map (Serie Orange 1:50000 4834 St. Louis, Institut Géographique National, Paris) of the north-western portion of the Parc Rivière Bleue. Course of the Rivière Bleue indicated in blue. Outlined rectangle indicates the main area of capture sites and corresponds to the area shown in greater detail in B. (B) Satellite image (Google Earth) of the main study area, showing the course of the Rivière Bleue and park roads and trails used for sampling transects.

Table 3. Diet of *Rhacodactylus auriculatus*. Data derived from multiple sources; superscripts denote data sources: (1) BAUER & DEVANEY (1987), (2) BAUER & SADLER (1994), (3) this study. Data presented by percent by number and percent by volume of total prey items recorded. Total number and total volume are listed parenthetically. Previous studies did not provide prey volumes, thus all data in the volume column are derived from the present study. Unlike Tab. 2, shed skins and unidentified material are included in the totals calculated. *Note that BAUER & SADLER (1994) reported 14 anthers, 20 stamens, and one leaf from their sample of *R. auriculatus* gut contents, but we have treated these plant parts as three items for the purposes of our calculations. See text for details of calculation of niche breadth.

Prey Taxon	Number	Volume
Chilopoda	0.92 (1) ²	–
Araneae	11.01 (12) ^{2,3}	4.00 (0.15)
Hemiptera: Cicadidae	0.92 (1) ²	–
Coleoptera (adult)	13.76 (15) ²³	1.33 (0.05)
Coleoptera (larvae)	2.75 (3) ³	6.13 (0.23)
Diptera: Tephritidae	2.75 (3) ^{2,3}	0.80 (0.03)
Lepidoptera (adult)	2.75 (3) ^{2,3}	5.87 (0.22)
Lepidoptera (larvae)	29.36 (32) ^{2,3}	1.33 (0.05)
Hymenoptera undetermined	1.83 (2) ²	–
Hymenoptera: Formicidae	0.92 (1) ²	–
Phasmatodea	1.83 (2) ^{2,3}	10.40 (0.39)
Orthoptera: Gryllidae	1.83 (2) ²	–
Orthoptera: Gryllacridoidea	3.67 (4) ²	–
Orthoptera: Ensifera	1.83 (2) ²	–
Blattidae	3.67 (4) ²	–
Unidentified Insecta	2.75 (3) ^{1,2}	–
Total Arthropoda	82.57 (90)	29.87 (1.12)
Mollusca: Pulmonata	0.92 (1) ²	–
Plant Material*	2.75 (3) ²	–
Vertebrata: <i>Bavayia</i>	1.83 (2) ^{1,3}	1.60 (0.06)
Vertebrata: <i>Caledoniscincus</i>	5.50 (6) ^{2,3}	0.27 (0.01)
Total Vertebrata	7.34 (8)	1.87 (0.07)
Shed skin	5.50 (6) ^{2,3}	60.27 (2.26)
Unidentified	0.92 (1) ³	8.00 (0.30)
Total Ingested Material	100.00 (109)	100.00 (3.75)
Niche breadth	2.43	1.94

Arthropods were the most numerous dietary constituent recovered, as is typical for virtually all geckos (PIANKA & PIANKA 1976, PIANKA & HUEY 1978, SNYDER 2007). However, the large size of some prey items, particularly the single phasmid consumed (32.7% by volume of the total animal prey), is noteworthy and corroborates the tendency of this species to take large prey noted by BAUER & SADLER (1994b).

As expected based on earlier studies (BAUER & DEVANEY 1987, BAUER & SADLER 1994b), vertebrate prey items were also recovered from *R. auriculatus*, although they constituted only 6.1% by volume and 13.3% by number of the total prey items. The low volume of the vertebrate prey is a reflection of their fragmented condition and the conservative means by which the volume of vertebrate prey was calculated. The volume of the single skink prey was based only on the arm recovered, as the skink itself may

have either escaped or been consumed. Based on comparisons with museum specimens, an entire *Caledoniscincus atropunctatus* of comparable forearm length would be approximately 97 mm in total length and have a volume of 1.8 cm³. This value would represent 62.4% by volume of the total animal prey consumed. Likewise, the gecko consumed would have also accounted for a much higher percentage by volume of the total animal prey had its whole body been recovered.

Lizard prey in the diet of *R. auriculatus* have previously been reported by BAUER & DEVANEY (1987), BAUER & SADLER (1994b), and SEIPP & HENKEL (2000), who observed a *R. auriculatus* stalk and consume a *Bavayia septuiclavis* in the wild. SEIPP & HENKEL (2000) also claimed that “wild *R. auriculatus* have proved to be partly cannibalistic.” Our results document that both geckos and skinks are consumed by *R. auriculatus* in winter, although only 3.0% (present study) of gargoyle geckos examined during the cool season contained lizard prey compared to 23.8% of specimens collected in warmer months (BAUER & SADLER 1994b). The regular consumption of vertebrates by geckos is rare (BAUER 1990). Notable exceptions include *Cyrtodactylus cavernicolus* (HARRISON 1961), and *Gekko gekko* (BOULENGER 1912, SMITH 1935), and especially pygopodids of the genus *Lialis* (PATCHELL & SHINE 1986). Whether all *R. auriculatus* include lizards in their diets is unknown, but BAUER & RUSSELL (1990) argued that the dentition of this species was unique among gekkotans and consistent with a diet of soft-bodied prey items, such as vertebrates.

The ingestion of flower parts by *R. auriculatus* has long been known (BAVAY 1869) and has been confirmed by the recovery of anthers, stamens, and possibly pollen from the stomach of preserved specimens (BAUER & SADLER 1994b), and by recent observations (BAUER & SADLER 2001) of feeding on *Geissois* sp. (Cunoniaceae) in the field. Feeding on the sap of *Cunonia macrophylla* was also documented during the period of this study and previously (SNYDER et al. 2008). Although the regular use of plant material of any kind is rare in lizards (KING 1996), and geckos in particular (COOPER & VITT 2002), it is most often associated with insularity (BAUER 1990, PEREZ & CORTI 1993, VAN DAMME 1999). Other geckos known to regularly to opportunistically ingest nectar, sap, and other plant parts include *Hoplodactylus* spp. and *Naultinus* spp. from New Zealand (EIFLER 1995, WHITAKER 1987a, 1987b), *Phelsuma* spp. from the Mascarenes and Seychelles (VINSON & VINSON 1969, GARDNER 1984, McKEOWN 1993), and *Lepidodactylus* (PERRY & RITTER 1999) and *Gehyra* (GIBBONS & CLUNIE 1984, DELL 1985, COUPER et al. 1995, LETNIC & MADDEN 1998) in Australia and the tropical Pacific.

The majority of gecko species are small nocturnal insectivores (LOVERIDGE 1947, KLUGE 1967, BUSTARD 1968, PIANKA & PIANKA 1976, PIANKA & HUEY 1978, VITT & ZANI 1997, MIRANDA & ANDRADE 2003), but geckos have been reported to consume diverse prey items such as tadpoles, birds, mice, bats, snakes and other lizards, often conspecifics (ROUX 1913, POLIS & MYERS 1985, MITCHELL 1986, BAUER 1990). However, many of these observations are based on animals in captive conditions or are anecdotal records of anomalous single events rather than evidence of regular patterns of consumption. The regular acquisition of both lizard prey and plant materials, along with arthropods,

suggests that *Rhacodactylus auriculatus* may have one of the most diverse of all gekkotan diets. Compared with 19 other gekkotans for which data were available (SNYDER 2007), *R. auriculatus* had the highest dietary niche breadth by prey category. Mean dietary niche breadth for the other taxa was 1.59 ± 0.81 (range 0.00–2.40), whereas in *R. auriculatus* it was 2.43 (Tab. 3). By volume *R. auriculatus* had a dietary niche breadth of 1.94 compared to a mean dietary niche breadth of 1.74 ± 0.78 (range of 0.06–2.62) in other gekkotans. The comparatively lower dietary niche breadth by volume as compared to number may, in part, be due to the propensity of *R. auriculatus* to take large soft-bodied prey items, but is also partly an artifact of the lower number of prey categories (10 versus 21) for which volumetric data were available (these were not reported in earlier studies). Dietary niche breadth comparisons are useful in comparing diets (PIANKA 1966, CASTANZO & BAUER 1993, 1997, VITT 1995), but account only for the number of categories utilized and not for the taxonomic or ecological diversity of the categories. However, in the case of *R. auriculatus*, the prey categories certainly are reflective of a wide taxonomic and ecological range of dietary constituents.

Resource Partitioning

Diet, microhabitat use and activity period (PIANKA 1973, SCHOENER 1977, HOWARD & HAILEY 1999) are the three main resource-partitioning axes along which lizards segregate. In the relatively simple lizard communities of New Caledonia, the arboreal *Rhacodactylus auriculatus* is clearly ecologically segregated from most skinks, which are chiefly terrestrial or subfossorial, diurnal, and strictly insectivorous (BAUER & DEVANEY 1987). Although it is probable that gargoyle geckos share the same basic activity period with most other New Caledonian geckos, significant size differences from the endemic species of *Bavayia* and *Eurydactylodes*, as well as all gekkonine geckos, almost certainly force differences in both microhabitat use (particularly oviposition sites and retreats) and, concomitantly, in diet. Among its congeners on Grande Terre, *R. auriculatus* is certainly separated from *R. chahoua*, *R. leachianus*, and *R. trachyrhynchus* by microhabitat. These species are typically exclusively arboreal, and tend to occupy perches relatively high in the canopy (BAUER & SADLIER 2000), descending only for specialized activities, such as oviposition (HENKEL 1991). For *R. sarasinorum* and *R. ciliatus*, similarly-sized congeners that occur in sympatry with *R. auriculatus* and are also often active at lower levels within the vegetation, diet may serve as the primary resource partition.

Relatively little is known about the ecology of arboreal night-active geckos (VITT & PIANKA 1994, PIANKA & VITT 2003). The information gathered in this study helps elucidate the natural history of *R. auriculatus* and provides the context within which further studies may be conducted. Given the many threats to these geckos, including habitat destruction through mining and deforestation, predation by introduced animals including rats, dogs, and cats, and exploitation by the illegal pet trade, such studies, which may provide invaluable data for use in the management of these magnificent geckos and their habitats, should be a priority.

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References

- ALEXANDER, G. J. & R. BROOKS (1999): Circannual rhythms of appetite and ecdysis in the elapid snake, *Hemachatus haemachatus*, appear to be endogenous. – *Copeia*, **1999**: 146–152.
- BACH, S. (2004): Haltung und Nachzucht des Höckerkopfgeckos, *Rhacodactylus auriculatus* Bavay, 1869. – *DRACO*, **5**(18): 82–87.
- BAUER, A. M. (1990): Gekkonid lizards as prey of invertebrates and predators of vertebrates. – *Herpetological Review*, **21**: 83–87.
- BAUER, A. M. & K. D. DEVANEY (1987): Comparative aspects of diet and habitat in some New Caledonian lizards. – *Amphibia-Reptilia*, **8**: 349–364.
- BAUER, A. M. & A. P. RUSSELL (1990): Dentitional diversity in *Rhacodactylus* (Reptilia: Gekkonidae). – *Memoirs of the Queensland Museum*, **29**: 311–321.
- BAUER, A. M. & R. A. SADLIER (1994a): The terrestrial herpetofauna of the Ile des Pins, New Caledonia. – *Pacific Science*, **48**: 353–366.
- BAUER, A. M. & R. A. SADLIER (1994b): Diet of the New Caledonian gecko *Rhacodactylus auriculatus* (Squamata, Gekkonidae). – *Russian Journal of Herpetology*, **1**: 108–113.
- BAUER, A. M. & R. A. SADLIER (2000): The Herpetofauna of New Caledonia. – *Society for the Study of Reptiles and Amphibians*, Ithaca.
- BAUER, A. M. & R. A. SADLIER (2001): New data on the distribution, status, and biology of the giant New Caledonian geckos (Squamata: Diplodactylidae: *Rhacodactylus* spp.). – *Amphibian and Reptile Conservation*, **2**: 24–29.
- BAUER, A. M. & J. V. VINDUM (1990): A checklist and key to the herpetofauna of New Caledonia, with remarks on biogeography. – *Proceedings of the California Academy of Sciences*, **47**: 17–45.
- BAVAY, A. (1869): Catalogue des reptiles de la Nouvelle-Calédonie et description d'espèces nouvelles. – *Mémoires de la Société Linnéenne de Normandie*, **15**: 1–37.
- BOULENGER, G. A. (1912): A Vertebrate Fauna of the Malay Peninsula: Reptilia and Batrachia. – Taylor and Francis, London.
- BOUSKILA, A., D. EHRLICH, Y. GERSHMAN, I. LAMPL, U. MOTRO, E. SHANI, U. WERNER & Y. L. WERNER (1992): Activity of a nocturnal lizard (*Stenodactylus doriae*) during a lunar eclipse at Hazeva (Israel). – *Acta Zoologica Lilloana*, **41**: 271–275.
- BUSTARD, H. R. (1968): The ecology of the Australian gecko, *Gehyra variegata*, in northern New South Wales. – *Journal of Zoology*, London, **154**: 113–138.
- CASTANZO, R. A. & A. M. BAUER (1993): Diet and activity of *Mabuya acutilabris* (Reptilia: Scincidae) in Namibia. – *Herpetological Journal*, **3**: 130–135.

- CASTANZO, R. A. & A. M. BAUER (1997): Comparative aspects of the ecology of *Mabuya acutilabris* (Squamata: Scincidae), a lacertid-like skink from arid south western Africa. – *Journal of African Zoology*, **112**: 109–122.
- COOPER, W. E. & L. J. VITT (2002): Distribution, extent, and evolution of plant consumption by lizards. – *Journal of Zoology*, London, **257**: 487–517.
- COUPER, P. J., J. A. COVACEVICH & S. K. WILSON (1995): Sap feeding by the Australian gecko *Gehyra dubia*. – *Memoirs of the Queensland Museum*, **38**: 396.
- DELL, J. (1985): Arboreal geckos feeding on plant sap. – *Western Australian Naturalist*, **16**: 69–70.
- DE VOSJOLI, P. & F. FAST (1995): Notes from a herpetological field trip to New Caledonia, part two. Notes on three species of New Caledonian geckos of the genus *Rhacodactylus*. – *The Vivarium*, **6**(6): 26–29, 53–54.
- DE VOSJOLI, P., F. FAST & A. REPASHY (2003): *Rhacodactylus*, The Complete Guide to their Selection and Care. – Advanced Visions Inc., Vista, California.
- EIFLER, D. A. (1995): Patterns of plant visitation by nectar-feeding lizards. – *Oecologia*, **101**: 228–233.
- GARDNER, A. S. (1984): The evolutionary ecology and population systematics of day geckos (*Phelsuma*) in the Seychelles. – Unpublished PhD. dissertation, University of Aberdeen.
- GIBBONS, J. R. H. & F. CLUNIE (1984): Brief notes on the voracious gecko *Gehyra vorax*. – *Domodomo*, **2**: 34–36.
- HARRISON, T. (1961): Niah's new cave-dwelling gecko: habits. – *Journal of the Sarawak Museum*, **10**: 277–282.
- HENKEL, F. W. (1986): Bemerkungen über einige *Rhacodactylus*-Arten. – *herpetofauna*, **8**(42): 6–8.
- HENKEL, F. W. (1991): Zur Kenntnis der diplodactylinen Gecko-Gattung *Rhacodactylus* FITZINGER, 1843. Aspekte von Freileben, Haltung und Nachzucht. – *Salamandra*, **27**: 58–69.
- HENKEL, F. W. & W. SCHMIDT (2007): *Rhacodactylus ciliatus* und *Rhacodactylus auriculatus*. – *Herpeton*, Offenbach.
- HOWARD, K. E. & A. HAILEY (1999): Microhabitat separation among diurnal saxicolous lizards in Zimbabwe. – *Journal of Tropical Ecology*, **15**: 367–378.
- HUEY, R. B., E. R. PIANKA & L. J. VITT (2001): How often do lizards “run on empty”? – *Ecology*, **82**: 1–7.
- IRSCHICK, D. J., B. VANHOYDONCK, A. HERREL & J. J. MEYERS (2005): Intraspecific correlations among morphology, performance, and habitat use within a green anole lizard (*Anolis carolinensis*) population. – *Biological Journal of the Linnean Society*, **85**: 211–221.
- JAMES, C. D. (1990) A refinement of the stomach flushing technique for small scincid lizards. – *Herpetological Review*, **21**: 87–88.
- JAMES, S. E. & R. T. M'CLOSKEY (2002): Patterns of microhabitat use in a sympatric lizard assemblage. – *Canadian Journal of Zoology*, **80**: 2226–2224.
- KING, G. (1996): *Reptiles and Herbivory*. – Chapman and Hall, London.
- KLUGE, A. G. (1967): Higher taxonomic categories of gekkonid lizards and their evolution. – *Bulletin of the American Museum of Natural History*, **135**: 1–59.
- LEGLER, J. M. (1977): Stomach flushing: a technique for chelonian dietary studies. – *Herpetologica*, **33**: 281–284.
- LEGLER, J. M. & L. J. SULLIVAN (1979): The application of stomach-flushing to lizards and anurans. – *Herpetologica*, **35**: 107–110.
- LETNIC, M. & K. MADDEN (1998): The gecko *Gehyra australis* feeding on the sap of *Acacia holosericea*. – *Western Australian Naturalist*, **21**: 207–208.
- LOVERIDGE, A. (1947): Revision of the African lizards of the family Gekkonidae. – *Bulletin of the Museum of Comparative Zoology*, **98**: 1–469.
- McKEOWN, S. (1993): *The General Care and Maintenance of Day Geckos*. – Advanced Vivarium Systems, Lakeside.
- MEIER, H. (1979): Herpetologische Beobachtungen auf Neukaledonien. – *Salamandra*, **15**: 113–139.
- MERTENS, R. (1964): Neukaledonische Riesengeckos (*Rhacodactylus*). – *Der Zoologische Garten (N.F.)*, Leipzig, **29**: 49–57.
- MITCHELL, J. C. (1986): Cannibalism in reptiles: a worldwide review. – *SSAR Herpetological Circulars*, **15**: i–iii, 1–37.
- MIRANDA, J. P. & G. V. ANDRADE (2003): Seasonality in diet, perch use, and reproduction of the gecko *Gonatodes humeralis* from eastern Brazilian Amazon. – *Journal of Herpetology*, **37**: 433–438.
- PATCHELL, F. C. & R. SHINE (1986): Food habits and reproductive biology of the Australian legless lizards (Pygopodidae). – *Copeia*, **1986**: 30–39.
- PEET, R. K. (1974): The measurement of species diversity. – *Annual Review of Ecology and Systematics*, **5**: 285–307.
- PEREZ, M. V. & C. CORTI (1993): Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). – *Bonner zoologische Beiträge*, **44**: 63–83.
- PERRY, G. & R. N. FISHER (2005): Night lights and reptiles: observed and potential effects. – pp. 169–191 in RICH, C. & T. LONGCORE (eds.): *Ecological Consequences of Artificial Night Lighting*. – Island Press, Washington DC.
- PERRY, G. & M. RITTER (1999): *Lepidodactylus lugubris* (mourning gecko). Nectivory and daytime activity. – *Herpetological Review*, **30**: 166–167.
- PETHER, J. (1999): In search of a giant. Part 2: The care and breeding of three species of *Rhacodactylus* in captivity. – *International Reptilian*, **5**(10): 11–17.
- PIELOU, E. C. (1975): *Ecological Diversity*. – John Wiley & Sons, New York.
- PIANKA, E. R. (1966): Convexity, desert lizards, and spatial heterogeneity. – *Ecology*, **47**: 1055–1059.
- PIANKA, E. R. (1973): The structure of lizard communities. – *Annual Review of Ecology and Systematics*, **4**: 53–74.
- PIANKA, E. R. & R. B. HUEY (1978): Comparative ecology, niche segregation, and resource utilization among gekkonid lizards in the southern Kalahari. – *Copeia*, **1978**: 691–701.
- PIANKA, E. R. & H. D. PIANKA (1976): Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. – *Copeia*, **1976**: 125–142.
- PIANKA, E. R. & L. J. VITT (2003): *Lizards: windows to the Evolution of Diversity*. – The University of California Press, Berkeley.
- POLIS, G. A. & C. A. MYERS (1985): A survey of intraspecific predation among reptiles and amphibians. – *Journal of Herpetology*, **19**: 99–107.
- POUNDS, A. J. (1988): Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. – *Ecological Monographs*, **58**: 299–320.
- REICHMANN, A. (1998): The effect of predation and moonlight on the behavior and foraging mode of *Stenodactylus doriae*. – Unpublished M.S. thesis, Ben Gurion University, Israel.
- RÖSLER, H. (1988): Nachzucht von *Rhacodactylus auriculatus*. – *Die Aquarien- und Terrarienzeitschrift*, **41**: 282–283.
- ROUX, J. (1913): Les reptiles de la Nouvelle-Calédonie et des Îles Loyalty. – pp. 79–160 in SARASIN, F. & J. ROUX (Eds.): *Nova*

- Caledonia, Zoologie I, Lieferung II. – C. W. Kreidel's Verlag, Wiesbaden.
- SAMEIT, J. (1986): *Rhacodactylus auriculatus* (Bavay) (Reptilia: Sauria: Gekkonidae). – Amphibien/Reptilien Kartei, Beilage in Sauria, **8**: 43–44.
- SCHOENER, T. W. (1977): Competition and the niche. – pp 35–136 in GANS, C. & D.W. TINKLE (eds.): *Biology of the Reptilia*, Volume 7. Ecology and Behavior. – Academic Press, London.
- SEIPP, R. & F. W. HENKEL (2000): *Rhacodactylus* – Biology, Natural History & Husbandry. – Edition Chimaira, Frankfurt.
- SMITH, M. A. (1935): The Fauna of British India including Ceylon and Burma. Reptilia and Amphibia, Vol. II. Sauria. – Taylor & Francis, London.
- SNYDER, J. P. (2007): The autecology of *Rhacodactylus auriculatus*: a natural history study of gargoyle geckos. – Unpublished M.S. thesis, Villanova University.
- SNYDER, J. P., L. A. SNYDER & A. M. BAUER (2008): *Rhacodactylus auriculatus* (Gargoyle Gecko). Sap feeding. – *Herpetological Review*, **39**: 93.
- SZCZERBAK, N. N. & M. L. GOLUBEV. (1996): Gecko Fauna of the USSR and Contiguous Regions. – Society for the Study of Amphibians and Reptiles, Ithaca.
- TYTLE, T. (2000): Natural history, captive maintenance and reproduction of the gargoyle gecko (*Rhacodactylus auriculatus*). – *Reptiles*, **8**(2): 10–12, 14, 16, 18–19.
- VAN DAMME, R. (1999): Evolution of herbivory in lacertid lizards: effects of insularity and body size. – *Journal of Herpetology*, **33**: 663–674.
- VINSON, J. & J. M. VINSON (1969): The saurian fauna of the Mascarene Islands. – *Mauritius Institute Bulletin*, **6**: 203–320.
- VITT, L. J. & E. R. PIANKA (1994): *Lizard Ecology*. – Princeton University Press, Princeton.
- VITT, L. J. (1995): The ecology of tropical lizards in the caatinga of northeast Brazil. – *Occasional Papers of the Oklahoma Museum of Natural History*, **1**: 1–29.
- Vitt, L. J. & P. A. Zani (1997): Ecology of the nocturnal lizard *Thecadactylus rapicauda* (Sauria: Gekkonidae) in the Amazon Region. – *Herpetologica*, **53**: 165–179.
- WHITAKER, A. H. (1987a): Of herbs and herps – the possible roles of lizards in plant reproduction. – *Forest and Bird*, **Aug. 1987**: 20–22.
- WHITAKER, A. H. (1987b): The roles of lizards in New Zealand plant reproductive strategies. – *New Zealand Journal of Botany*, **25**: 315–328.
- WHITAKER, A. H., R. A. SADLER, A. M. BAUER & V. A. WHITAKER (2004): Biodiversity and Conservation Status of Lizards in Threatened and Restricted Habitats of North-Western New Caledonia. – Report by Whitaker Consultants Limited to Direction du Développement Économique et de l'Environnement, Province Nord, Koné, New Caledonia.
- WIRTH, M. & D. PEUKERT (2009): Zur Haltung und Nachzucht des Höckerkopfgeckos, *Rhacodactylus auriculatus*. – *DRACO*, **9**(36): 55–63.