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Feeding ecology of the pygmy gecko *Coleodactylus natalensis* (Squamata: Sphaerodactylidae) in the Brazilian Atlantic Forest

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ABSTRACT. We studied the feeding ecology of a population of *Coleodactylus natalensis* Freire, 1999, an endemic gecko of Atlantic Forest fragments in the state of Rio Grande do Norte, northeastern Brazil. Lizards (N = 49) were collected manually through active search in the four habitats of Parque Estadual Dunas de Natal, type locality of the species. In the laboratory, we measured the lizards and registered the number of consumed prey items identified to Order, its dimensions and frequencies. We also collected samples of leaf litter in each habitat to determine prey availability. Females were significantly larger than males, but head size did not differ between the sexes. The most important prey categories in the diet of *C. natalensis* based on number, volume and frequency were Isopoda and Araneae. Prey categories with highest importance indices in the diet were Isopoda, Araneae, Homoptera and Gryllidae. The diets of adult males and females were similar with respect to prey size, but differed qualitatively, mainly due to the larger trophic spectrum of females. We found some variations on trophic niche breadths and food preferences of lizards between habitats, but in general niche breadths were intermediate, and the most elected prey categories were Isopoda, Araneae, Homoptera and Thysanoptera. High electivities for Isoptera and Gryllidae occurred only in the open habitats (restinga and dunes), and for Mantodea in the forested habitats (high and low forest). Collembola was consumed in the same proportion of the environment, and Acarina and Formicidae had negative values of electivity, indicating rejection. We conclude that the population studied seems to have a selective diet, preferring relatively large prey items that are less abundant in the leaf litter, and possibly avoiding potentially toxic prey.

KEY WORDS. Arthropods; diet; electivity; leaf litter; lizards.

Lizards of the genus *Coleodactylus* Parker, 1926 (Sphaerodactylidae) inhabit the leaf litter of South American tropical forests, and are the smallest species in their respective lizard assemblages (e.g., Freire 1996, Vitt & Zani 1998, Vitt *et al.* 2005). The ecological consequences of the extremely reduced size of sphaerodactyl lizards have been documented and discussed by some authors (e.g., MacLean 1985, Vitt 2000, Steinberg *et al.* 2007). The small body allows these lizards to explore a singular dietary niche among vertebrates, and to take advantage of tiny prey items, which are apparently abundant in leaf litter but are not eaten by most larger lizards (Vitt *et al.* 2005). Ecological studies performed on *Coleodactylus* species were mostly carried out on Amazonian populations, primarily *Coleodactylus amazonicus* (Andersson, 1918) (Ramos 1981, Vitt & Caldwell 1994, Vitt *et al.* 2005, Carvalho Jr *et al.* 2008) and *C. septentrionalis* (Vanzolini, 1980) (Vitt & Zani 1998, Vitt *et al.* 2005). In recent years, some studies on *C. meridionalis* (Boulenger, 1888) have been conducted in the Brazilian Atlantic Forest and Cerrado (Dias *et al.* 2003, Werneck *et al.* 2009), and on *C. brachystoma* (Amaral, 1935) in Cerrado (Brandão & Motta 2005).

The Natal pygmy gecko, *C. natalensis* Freire, 1999, is an endemic species of Atlantic Forest remnants of the state of Rio Grande do Norte, northeastern Brazil (Freire 1999, Sales *et al.* 2009, Freire *et al.* 2010). It is the smallest species in the genus (males and females reach a maximum snout-vent length of 22 and 24 mm, respectively – Freire 1999), and one of the smallest lizard species of South America. The few ecological data available for *C. natalensis* include the spatial distribution of lizards by habitats in the Parque Estadual Dunas de Natal – PEDN (Freire 1996, Capistrano & Freire 2009), the thermal ecology of a population from another Atlantic Forest remnant, the Parque Estadual Mata da Pipa – PEMP (Sousa & Freire 2011), and short notes about reproduction, diet and natural predators (Lisboa *et al.* 2008, Sousa & Freire 2010, Sousa *et al.* 2010). These studies have shown that this lizard is a passive termoregulator that lives in the leaf litter deposited on the soil and displays a preference for shaded forest habitats (high and low forest in PEDN), but also occurs in the leaf litter of less shaded habitats (restinga and beach dunes in PEDN), although in lower abundance.

The fact that *C. natalensis* is a species with restricted geographic distribution, currently limited to a few fragmented forest areas, underscores the importance for ecological data capable of subsidizing conservation strategies and management of populations in different areas. In this sense, we describe here aspects of the feeding ecology of *C. natalensis* in the Atlantic Forest of northeastern Brazil. The study had three main objectives: (1) to determine diet composition; (2) to identify possible sexual differences in diet; and (3) to examine food preferences.

MATERIAL AND METHODS

This study was conducted at the PEDN, the type locality of *C. natalensis*. The PEDN is the second largest urban park in Brazil, with 9 km long covering 1172.8 ha, and encompasses an area of coastal dunes colonized by plants and animals of different Morphoclimatic Domains (*sensu* AB'SABER 1977), such as Atlantic Forest and Caatinga (FREIRE 1996). Bordered by an urban area, it shows indications of human disturbance, and is situated at the northern border of the Atlantic Forest, along the coastline of the city of Natal, state of Rio Grande do Norte (05°48'-05°53'S and 35°09'-35°12'W). The string of dunes in Natal extends in a SE-NW direction, due to the predominantly southeasterly trade winds. The fine-grain sandy-quartzitic soil is non-consolidated and has low fertility. Mean temperatures are constant throughout the year, averaging 26.2 ± 5.0°C, and relative humidity remains 79.4 ± 3.1% year-round. Based on years 1990-2006 annual rainfall averaged 1554.3 mm (Source: Empresa de Pesquisas Agropecuárias do Rio Grande do Norte – EMPARN).

The PEDN has four habitats, defined according to the physiognomy of the vegetation (FREIRE 1990, 1996): (I) interdune high forest, situated in valleys at least 30 m deep and interspersed with series of dunes fixed by tall vegetation reaching up to 20 m high (*Caesalpinia echinata* Lam. and *Ficus* spp., for example); (II) low forest on fixed dunes, covered predominately by 3 to 7 m high shrub vegetation such as *Eugenia* spp.; (III) restinga vegetation, present on the top of dunes (therefore subjected to more sunlight) and characterized by the marked presence of *Anacardium occidentale* L., *Myrcia* sp. and large clumps of bromeliads like *Aechmea lingulata* (L.) Baker and *Hohenbergia* sp.; and (IV) mobile beach dunes, generally without vegetation or with a sand-fixing herbaceous cover, sometimes with sparse brushlands, home to species such as *A. occidentale* L., *Chrysobalanus* sp. and *Pilosocereus* sp.

The field work consisted of monthly trips to the study area from December 2006 to November 2007. Searches were conducted on four 1,370 to 2,427 m pre-existing trails that run through the four habitats of PEDN. Lizards were collected manually in all four habitats through active search from 08:00 to 12:00 h and from 14:00 to 18:00 h. In the laboratory, they were measured (see below) and dissected to remove stomach contents, then fixed in 10% formalin, preserved in 70% alcohol, and deposited at the Coleção Herpetógica do Departamento de Botânica, Ecologia e Zoologia (CHBEZ) of the Universidade Federal do Rio Grande do Norte (UFRN). We identified the sex of individuals based on sexual dichromatism of the species (FREIRE 1999) and the bulge at the base of the tail, typical in Sphaerodactylidae males. Using a caliper with an accuracy of 0.05 mm and a stereomicroscope, we took the following measures from each lizard collected: snout-vent length (SVL) from the tip of the snout to the anterior end of cloaca, head length (HL) from the posterior edge of the tympanum to the tip of the snout, and head width (HW) at the widest point on the skull. Analysis of variance (ANOVA) was used to test for sexual differences in body size (SVL). Sexual differences in head size (HL, HW) were tested using the analysis of covariance (ANCOVA) with SVL as covariate.

Stomach contents were placed on petri dishes and analyzed under a stereomicroscope. Individual prey items were identified taxonomically to Order (Family in some cases) and measured (length and width) to the nearest 0.01 mm using precision calipers. Prey volume (V) was estimated with the formula for a prolate spheroid (DUNHAM 1983): $V = 4/3\pi(\text{length}/2)(\text{width}/2)^2$. The frequency of occurrence (number of stomachs containing the prey category *i*, divided by the total number of stomachs) and the numerical and volumetric percentages of each prey category were determined for pooled stomachs. The importance index (I) was calculated for each prey category as the sum of the occurrence, numerical and volumetric percentages divided by three. The G-test was used to test for sexual differences in diet composition (based on numeric proportions of prey categories in the pooled stomachs), and the Mann-Whitney U test was used to test for sexual differences in the number of prey items ingested and prey size measurements (mean and maximum prey length and width). We excluded lizards with only unidentified items or empty stomachs for these analyses. The dietary niche breadth from numeric percentages of prey was calculated for pooled stomachs in each habitat using the Levins' standardized niche breadth (B_A), a standardized measure of Simpson's diversity index (KREBS 1999), which varies from 0 (exclusive use of a single prey category) to 1 (equal use of all prey categories).

To assess the supply of food available for *C. natalensis*, 16 samples of 30 L of leaf litter were collected, four per habitat. These samples were placed in a Berlese-Tullgren funnel and the sampled invertebrate material was identified to Order and deposited at the CHBEZ. Invertebrate diversity in the leaf litter sample was calculated for each habitat using the Shannon-Wiener diversity index (MAGURRAN 1988): $H' = -\Sigma pi \log_n pi$, where *pi* is the proportion of individuals in the taxonomic category *i*. The electivity of prey was calculated using the Ivlev's electivity index (KREBS 1999): $IEI = (ri - ni)/(ri + ni)$, where *ri* is the percentage of prey category *i* in diet, and *ni* is the percentage of prey category *i* in environment. The values of this index range from -1 to +1, with values near +1 indicating preference, values near -1 indicating rejection, and values near 0 indicating consumption in the same proportion of the environment. We registered some individuals of the taxa Neuroptera, Lepidoptera (larvae), Chilopoda, Dermaptera and Scorpiones in the leaf litter samples, but they were not included in the analyses of electivity because they were not potential prey for *C. natalensis* (i.e., they were too large to be eaten by lizards). Spearman's correlation was used to verify the relationship between availability and consumption of prey items in each habitat.

Statistical tests were performed using SPSS 16.0 software for Windows (except for G-test, which was performed in BioEstat 5.0 software). Before performing parametric tests, all variables were tested for normality and homoscedasticity of variances. Significance was assessed based on $\alpha = 0.05$.

RESULTS

We collected a total of 49 specimens of *C. natalensis* for dietary analysis (26 adult females, 22 adult males and one juvenile). Females (20.3 ± 1.9 mm, range: 17.0-23.8 mm, N = 26) were significantly larger in SVL than adult males (19.1 ± 1.3 mm, range: 16.4-22.0 mm, N = 22; $F_{1,46} = 5.149$, p = 0.02). We found no sexual differences in head size (ANCOVA, HL – $F_{2,45}$ = 2.242, p = 0.14; HW – $F_{2,45}$ = 0.050, p = 0.82).

Of the 49 stomachs examined, only three (6.1%) were empty. We recognized 18 prey categories in the diet of *C. natalensis*, in which the most important in terms of number, frequency and volume were Isopoda and Araneae (Tab. I); Collembola, Isoptera, Homoptera, Pseudoscorpiones, Orthoptera (Gryllidae) and Thysanoptera were also well represented. The prey categories with highest importance indices were Isopoda, Araneae, Homoptera and Gryllidae (Tab. I). The 107 identifiable prey items removed from the stomachs averaged 1.6 ± 1.1 mm in length (range: 0.1-6.3 mm), 0.8 ± 0.6 mm in width (range: 0.1-3.0 mm) and 1.4 ± 3.7 mm^3 in volume (range: 0.001-28.2 mm^3). The mean number of prey categories per stomach was 1.4 ± 1.1 (range: 1–5) and mean number of prey items per stomach was 2.1 ± 1.9 (range: 1-8).

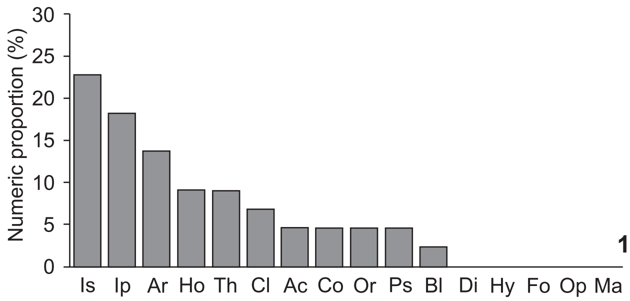
Based on numeric proportions, the diets of males and females differed significantly (G = 30.640, p = 0.009), mainly due to the larger spectrum of prey categories used by females and the absence of termites in the diet of females (Figs. 1 and 2). Despite the qualitative differences in diet, males and females did not differ significantly in the number of food items ingested and prey size measurements (Tab. II).

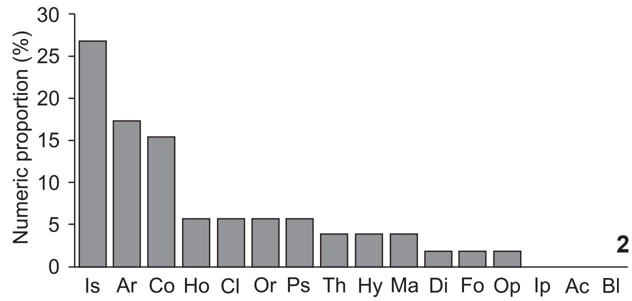
The dietary niche breadth of the lizards collected in the high forest habitat (N = 20) was 0.542; in low forest (N = 14), 0.685; in restinga (N = 9), 0.574; and in dunes (N = 6), 0.541. The invertebrate taxa most frequently found in the leaf litter of all four habitats were Acarina, Collembola, Formicidae, Pseudoscorpiones and Isoptera (Tab. III). Invertebrate diversity in leaf litter was higher in low forest (H' = 1.958), followed by high forest (H' = 1.370), dunes (H' = 1.318) and restinga (H' = 0.891).

Table I. Diet composition of *Coleodactylus natalensis* (N = 49) in Parque Estadual Dunas de Natal, state of Rio Grande do Norte, Brazil. (F) Frequency of occurrence; (N) number of prey items, (V) volume (mm^3), (I) importance index, (U.A.R.) unidentified arthropod remains.

Taxon	F (%)	N (%)	V (%)	I
Arachnida				
Acarina	1 (2.1)	2 (1.8)	<0.1 (<0.1)	1.3
Araneae	13 (28.2)	16 (14.9)	43.8 (12.0)	18.4
Opiliones	1 (2.1)	1 (0.9)	1.6 (0.4)	1.1
Pseudoscorpiones	6 (13.0)	6 (5.6)	1.3 (0.3)	6.3
Crustacea				
Isopoda	13 (28.2)	24 (22.4)	81.2 (22.3)	24.3
Diplopoda	1 (2.1)	1 (0.9)	<0.1 (<0.1)	1.0
Hexapoda				
Blattodea	1 (2.1)	1 (0.9)	0.7 (0.1)	1.0
Coleoptera	6 (13.0)	6 (5.6)	1.0 (0.2)	6.3
Collembola	5 (10.8)	10 (9.3)	2.6 (0.7)	6.9
Homoptera	7 (15.2)	7 (6.5)	31.7 (8.7)	10.1
Hymenoptera				
Formicidae	1 (2.1)	1 (0.9)	1.9 (0.5)	1.2
Others	1 (2.1)	2 (1.8)	<0.1 (<0.1)	1.3
Isoptera	3 (6.5)	8 (7.4)	14.4 (3.9)	5.9
Mantodea	2 (4.3)	2 (1.8)	1.1 (0.3)	2.1
Orthoptera (Gryllidae)	5 (10.8)	5 (4.6)	34.8 (9.5)	8.3
Thysanoptera	3 (6.5)	6 (5.6)	0.8 (0.2)	4.1
Insect eggs	1 (2.1)	4 (3.7)	0.2 (<0.1)	1.9
Shed skin	5 (10.8)	5 (4.6)	45.2 (12.4)	9.3
U.A.R.	–	–	100.1 (27.5)	–

We found some variations on food preferences between habitats, but in general the most elected prey categories among the lizards were Isopoda, Araneae, Homoptera and Thysanoptera (Tab. III). High electivities for Isoptera and Gryllidae occurred only in the open habitats (restinga and dunes), and for Mantodea in the forested habitats (high and low forest). Collembola was consumed in the same proportion of the environment in all habitats, and some prey categories such as Acarina and Formicidae had negative values of electivity, indicating rejection (Tab. III). Correlations between diet composition and prey availability in each habitat were all non-significant (high forest – $r_s = 0.00$, p = 0.99; low forest – $r_s = 0.01$, p = 0.94; restinga – $r_s = 0.02$, p = 0.94; dunes – $r_s = 0.04$, p = 0.86). Acarina was massively the most abundant taxon in the leaf litter, but had minimal importance in the diet of *C. natalensis* (Tab. III). For this reason, we repeated the correlation analyses without Acarina; the same results were observed, with absence of relationship between diet composition and prey availability (high forest – $r_s = -0.12$, p = 0.60; low forest – $r_s = 0.11$, p = 064; restinga – $r_s = 0.19$, p = 0.48; dunes – $r_s = 0.13$, p = 0.61).





Figures 1-2. Numeric proportions of prey categories ingested by (1) adult males (N = 22) and (2) adult females (N = 26) of *Coleodactylus natalensis* in Parque Estadual Dunas de Natal, state of Rio Grande do Norte, Brazil. Prey categories are as follows: (Ac) Acarina, (Ar) Araneae, (Bl) Blattodea, (Cl) Coleoptera, (Co) Collembola, (Di) Diplopoda, (Fo) Formicidae, (Ho) Homoptera, Hy = Hymenoptera (except Formicidae), (Is) Isopoda, (Ip) Isoptera, (Ma) Mantodea, (Op) Opiliones, (Or) Orthoptera (Gryllidae), (Ps) Pseudoscorpiones, (Th) Thysanopera.

Table II. Average values of quantitative variables analyzed for the diet of adult males and females of *Coleodactylus natalensis* at the Parque Estadual Dunas de Natal, state of Rio Grande do Norte, Brazil. Z values refer to the Mann– Whitney U test.

Variables	Males (N = 19)	Females (N = 21)	Z	P
Number of prey items	2.16 ± 1.70 (1-6)	2.43 ± 1.56 (1-8)	-1.09	0.27
Maximum prey length	2.13 ± 1.23 (0.5-4.5)	2.81 ± 1.65 (0.4-6.3)	-1.43	0.15
Mean prey length	1.30 ± 0.63 (0.5-3.0)	1.55 ± 0.87 (0.3-4.0)	-0.89	0.37
Maximum prey width	1.37 ± 0.67 (0.5-3.0)	1.65 ± 0.90 (0.2-3.0)	-0.97	0.33
Mean prey width	0.79 ± 0.40 (0.3-2.0)	0.83 ± 0.41 (0.1-1.7)	-0.51	0.61

DISCUSSION

The diet of *C. natalensis* was composed mainly of arthropods, most categorically represented by Isopoda and Araneae. Other prey categories like Homoptera and Gryllidae were also well represented. All these categories are comprised of relatively large prey compared to *C. natalensis*, with just few individuals filling the entire space inside the stomach of the lizards. Tiny prey with high abundance in the leaf litter such as Acarina and Collembola had little importance in the diet of *C. natalensis*. Most prey items consumed by the lizards are readily mobile and thus typical for sit-and-wait foragers (Huey & Pianka 1981). The low frequency of individuals with empty stomachs suggests that this population is in a positive energetic balance (sensu Huey *et al.* 2001).

When the diet composition of *C. natalensis* is compared with that of *C. meridionalis*, a congeneric, close species, some differences are evident. In a population of *C. meridionalis* from Cerrado (N = 11) studied by Werneck *et al.* (2009), the diet was dominated by termites (Isoptera), and the most important prey in the diet of *C. natalensis* (Isopoda, Araneae and Homoptera) were absent or had little importance for *C. meridionalis*. Termites were also the predominant prey for a population of *C. meridionalis* from the Atlantic Forest in the state of Alagoas, northeastern Brazil (E.M.X. Freire, unpublished data). With respect to *C. amazonicus* in the Amazon region, Vitt *et al.* (2005) found that the diets of six populations (N = 220) were composed predominantly of Collembola, Isoptera, Homoptera and insect larvae. Although *C. amazonicus* is a sphaerodactyl gecko with similar body size to *C. natalensis*, their diet includes a higher frequency of tiny prey items that are probably more abundant in the environment, especially Collembola and Isoptera. However, *C. amazonicus* also consumes larger prey such as insect larvae, Orthoptera and Araneae. The composition of the diets of these populations of *C. amazonicus* are quite similar to one another. They differ from the diets of *C. natalensis* populations in that the former contains more prey items of relatively smaller size in higher frequencies. Prey size measures (mean prey length, width and volume) from the populations of *C. amazonicus* studied by Vitt *et al.* (2005) were smaller than the values obtained for *C. natalensis* in this study.

Some studies on lizards have shown that morphological differences between males and females might result in differences in diet composition (Fitch 1978, Schoener *et al.* 1982, Preest 1994). However, sexual dimorphism in size does not necessarily imply feeding differences between the sexes. Some studies on sexually dimorphic lizards have not found sexual differences in types and sizes of the prey ingested (e.g., Kolodiuk *et al.* 2010, Menezes *et al.* 2011, Sales *et al.* 2011). For *C. natalensis*, despite the sexual dimorphism in body size, the diets of males and females were very similar in terms of number of prey items ingested, and prey size. Females had, however, a trophic spec-

Table III. Number of prey items ingested by *Coleodactylus natalensis* and abundance in the leaf litter of potential prey to the lizards in the four habitats of Parque Estadual Dunas de Natal, state of Rio Grande do Norte, Brazil. Values of Ivlev's Electivity Index (IEI) with an asterisk (*) indicate preference. Lizard samples: high forest = 20, low forest = 14, restinga = 9, dunes = 6.

Taxon	High Forest			Low Forest			Restinga			Dunes		
	Diet	LL	IEI	Diet	LL	IEI	Diet	LL	IEI	Diet	LL	IEI
Arachnida												
Acarina	2	3763	-0.80	–	884	-1	–	3241	-1	–	1441	-1
Araneae	5	15	0.97*	3	35	0.52*	1	20	0.84*	7	14	0.95*
Opiliones	–	9	-1	–	2	-1	1	2	0.98*	–	1	-1
Pseudoscorpiones	–	50	-1	3	72	0.22	1	47	0.66*	2	45	0.57*
Crustacea												
Isopoda	10	17	0.98*	9	1	0.99*	5	2	0.99*	–	8	-1
Diplopoda	–	18	-1	1	23	0.24	–	20	-1	–	6	-1
Gastropoda	–	1	-1	–	–	–	–	–	–	–	–	–
Hexapoda												
Blattodea	–	10	-1	–	17	-1	1	5	0.95*	–	2	-1
Coleoptera	–	10	-1	5	12	0.88*	1	14	0.88*	–	28	-1
Collembola	3	597	0	4	132	0.06	2	321	0.19	1	85	0
Embioptera	–	3	-1	–	3	-1	–	2	-1	–	10	-1
Heteroptera	–	42	-1	–	1	-1	–	–	–	–	–	–
Homoptera	2	1	0.99*	4	5	0.93*	–	–	–	1	–	1*
Hymenoptera												
Formicidae	–	334	-1	–	46	-1	1	93	0.43	–	187	-1
Others	2	1	0.99*	–	–	–	–	–	–	–	–	–
Isoptera	–	59	-1	–	50	-1	1	9	0.92*	7	10	0.96*
Mantodea	1	–	1*	1	–	1*	–	–	–	–	1	-1
Orthoptera (Gryllidae)	–	35	-1	3	31	0.57*	1	3	0.97*	1	7	0.84*
Psocoptera	–	1	-1	–	9	-1	–	5	-1	–	5	-1
Thysanoptera	–	–	–	2	–	1*	1	–	1*	3	–	1*
Thysanura	–	–	–	–	–	–	–	–	–	–	1	-1
Symphyla	–	17	-1	–	4	-1	–	2	-1	–	–	–
Nematoda	–	3	-1	–	–	–	–	–	–	–	–	–

trum slightly larger than males (females: 13 prey categories, males: 11 prey categories; Figs 1 and 2), and this fact, combined with the absence of termites in the diet of females, resulted in a significant difference between the sexes.

The absence of a relationship between the diet composition of *C. natalensis* and prey availability in the leaf litter indicates that individuals are selective about what they eat, rather than preying on all small invertebrates available in the environment. This trend was confirmed by the values of the Ivlev's Electivity Index, which indicated preferences for some prey categories, such as Isopoda and Araneae, and rejection of others like Acarina and Formicidae. Lizards of the genus *Coleodactylus* have a developed nasal chemosensory (Cooper 1995), and are possibly able to detect and discriminate prey by chemical cues. Therefore, rejection of Acarina and Formicidae may be associated with chemosensory avoidance, since many ants and mites produce chemical defenses that may be noxious for predators (Vitt & Pianka 2005, Saporito *et al.* 2007). Chemical discrimination of prey, allowing identification of highly profitable items and avoidance of potentially toxic prey, is widespread among scleroglossans (Vitt & Pianka 2005).

We conclude that *C. natalensis* is a carnivorous lizard with a diet composed mainly of Isopoda and Araneae, which are relatively large prey items with low relative abundance in the leaf litter. Tiny prey items with high abundance in the environment such as Collembola and Isoptera are not predominant in the diet of *C. natalensis*, contrasting with the diets of other sphaerodactyl geckos of similar body size, such as *C. meridionalis* and *C. amazonicus*. Data indicates that *C. natalensis* is selective in food use and avoids some potentially toxic prey.

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