

Feeding ecology of a selective folivore, the thin-spined porcupine (*Chaetomys subspinosus*) in the Atlantic forest

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We studied the feeding ecology of the thin-spined porcupine (*Chaetomys subspinosus*), a small arboreal rodent endemic to the Atlantic rain forest of Brazil and threatened with extinction. We captured and radiotracked 4 free-ranging individuals and collected 1,177 feeding records in 944 h of observation between April 2005 and September 2006. We found that the animal feeds exclusively on the leaves of woody trees, preferring young leaves. Diet composition and foraging pattern did not vary seasonally, although we observed a seasonal variation in the availability of young leaves. Annual diet comprised primarily (90%) 4 plant species, *Albizia pedicellaris*, *Inga thibaudiana*, *Pera glabrata*, and *Tapirira guianensis*. This small subset of plant species contains high levels of both leaf protein and fiber, and most preferred species have the capacity to establish symbiotic associations with nitrogen-fixing bacteria. A diet concentrated in a few taxonomically related, nitrogen-fixing species suggests that in addition to high protein levels other features linked to chemical tolerance and local abundance of food items also influence the use and selection of food by this small browser. We conclude that *C. subspinosus* is more folivorous than previously thought and that it is highly selective in food choice, as expected for a small arboreal mammalian folivore. Because the animals selected pioneers species that are locally abundant, widespread, and typical of early secondary forests, we suggest that food supply is not a limiting factor for the presence of thin-spined porcupines in small disturbed forest patches in the Atlantic forest. DOI: 10.1644/09-MAMM-A-185.1.

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Theory predicts that small herbivorous mammals need to be more selective in their food choice compared to larger species (Milton 1979; Moir 1965; Parra 1978) because the increasing demand for energy per unit of mass in smaller bodies does not correspond to a proportional increase in the relative capacity of the intestinal tract. Therefore, a link between body size and energy budget represents an important ecological constraint for the smaller folivores (Parra 1978).

The thin-spined porcupine (*Chaetomys subspinosus* Olfers, 1818) is a small hystricomorph rodent (1.25–1.75 kg—Oliver and Santos 1991) and one of the smallest arboreal folivores (Eisenberg 1978). It is an elusive, endemic species occurring within a narrow section of the Atlantic rain-forest region that spans from the northern part of the state of Rio de Janeiro to the southern part of Sergipe, Brazil (Oliver and Santos 1991). Because of its endemism and the massive habitat loss within

its range, this species is considered vulnerable to extinction (Catzefflis et al. 2008). Nevertheless, even the basic aspects of its ecology are poorly understood, particularly regarding its feeding ecology. Data about the feeding habits of *C. subspinosus* are limited to anecdotal reports collected from local inhabitants of northeastern Brazil, suggesting that thin-spined porcupines consume a variety of exotic and abundant fruits and seeds, such as jackfruits (*Artocarpus heterophyllus*) and seeds of cacao (*Theobroma cacao*) and the oil palm (*Elaeis guianensis*—Carvalho 1987; Kuniy et al. 2005; Moojen 1952; Nowak and Paradiso 1983). However, studies using recent quantitative and qualitative data from free-



ranging animals concluded that their diet is comprised almost entirely of leaves, with sporadic consumption of flowers and fruits (de Souto Lima et al. in press; Kuniy et al. 2005). Considering that the Atlantic forest harbors one of the highest diversities of plant species in the world (Martini et al. 2007), with a concomitant variety of primary and secondary metabolites, this small arboreal folivore provides valuable insights into the characteristics that lead to dietary selectivity.

We examined the feeding ecology of the thin-spined porcupine in forest remnants located in the core region of the cacao-producing zone in Brazil, as it harbors the largest continuous population of this species (Oliver and Santos 1991). Our aim was to examine the degree of folivory and dietary selectivity of this mammal to identify features that drive its food choices. More specifically, we aimed to assess and quantify the dietary composition of the species and evaluate differences among individuals; analyze the annual patterns of food intake and availability; assess plant species selectivity; and investigate ecological and nutritional features of food resources that could influence the preference of porcupines. Based on assumptions about constraints imposed by body size, we hypothesized that if this small rodent is primarily a folivore, the species must be highly selective regarding its food choice. Because the protein: fiber ratio of food items is a good predictor of food preference in mammalian folivores (Milton 1998), we expected that leaf choice would be driven by these nutritional factors. Moreover, because availability of leaves in the study region varies throughout the year (Mori et al. 1982), we expected seasonal changes in the dietary and foraging patterns of the focal mammal species.

MATERIALS AND METHODS

Study area.—The study was conducted in 3 forest remnants of 0.7, 2.1, and 18 ha (Fig. 1) located in the municipality of Ilhéus, southern Bahia ($14^{\circ}25'–15^{\circ}07'S$, $39^{\circ}32'–38^{\circ}59'W$), Brazil. The mean annual temperature is $24^{\circ}C$, and the average rainfall is 2,000 mm/year. There is not a typical dry season. However, a short dry season can occur in August and September and secondarily in December (Milde and Nitzsche 1985; Mori et al. 1983). The forest remnants studied harbor tree species typical of an arboreal late secondary community (Mori et al. 1983). The most common families are Euphorbiaceae, Araliaceae, Fabaceae, Anacardiaceae, and Moraceae (Fernandez-Giné 2009). The canopy averages 16 m tall with some emergent trees reaching 30 m, and lianas are abundant (Fernandez-Giné 2009). The matrix comprised a mosaic of shade cacao plantations, rubber plantations, early secondary forest, and open areas (Fig. 1).

Radiotracking and feeding observations.—During surveys we located a total of 4 free-ranging, adult thin-spined porcupines within the forest canopy. Once an animal was located, trained personnel climbed the tree and captured the animal by the tail. We immobilized the animal with an intramuscular injection of ketamine (5 mg/kg) and xylazine

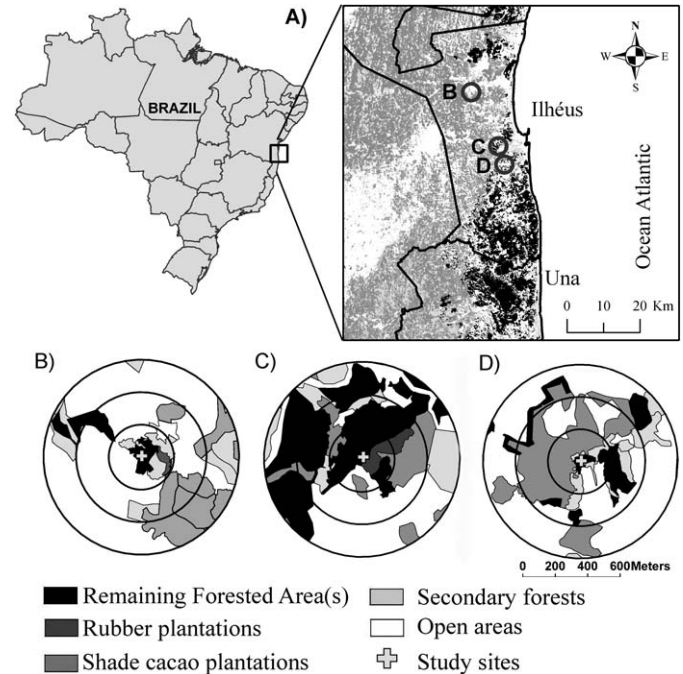


FIG. 1.—Map of the southern part of the state of Bahia showing A) the location of 3 studied remaining forest areas and B–D) their surrounding landscape.

hydrochloride (2 mg/kg). We weighed the animal while sedated and fitted on its neck a ball-chain collar with an attached radiotransmitter weighing 50 g (model 080; Telonics Inc., Mesa, Arizona), which represents $<3\%$ of the body mass. We attached a reflective tape to each transmitter to improve the visual detection of each animal during the observation sessions. Once tagged, the animal was released and assisted until it was able to climb properly. We considered only observations taken after a minimum of 15 days postrelease. All procedures regarding capture, handling, and tagging of animals were conducted under the legal approval and consent of the Brazilian Federal Authority and followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007). We recovered radiocollars after the sampling period.

We followed each tagged porcupine for 2–4 nights each month, alternately for the 1st or 2nd half of the night (1800–0000 h or 0000–0600 h), for a total of 146 observation sessions (Table 1). We observed animals using halogen flashlights and binoculars (8×40). We recorded animal activity by an instantaneous scan-sampling method (Altmann 1974), which recorded the 1st behavior visible in the 1st 2 min of each 10-min interval. We considered a feeding record when an animal was observed eating, handling, or searching for food. During feeding records we recorded the form of the food item (tree, shrub, liana, or epiphyte), the type of item consumed (leaves, fruits, flowers, or other), and the maturity of consumed leaves (young or mature). Because leaves appear monochromatic at night, we considered young leaves (including buds) those that were located up to the 3rd node from the outer part of the tree branch. All feeding trees were tagged and identified to species.

TABLE 1.—Monitoring period and sampling effort of 4 radiocollared *Chaetomys subspinosus* studied in Atlantic forest, Brazil. F = female; M = male.

Individual	Sex	Body mass (g)	Forest fragment size (ha)	Monitoring			
				Period	No. months	No. sessions (nights)	No. hours
CS01	F	1,650	2.1	8 April 2005–17 March 2006	11	35	223
CS02	F	1,650	0.7	13 June 2005–2 July 2006	13	42	271
CS03	M	1,500	18	9 October 2005–27 September 2006	12	35	229
CS04	F	2,000	18	29 October 2005–28 September 2006	11	34	220
Total					17	146	944

Vegetation sampling: species survey and phenology.—We estimated the availability of plant species in the study area by overlaying a grid of 30 × 30-m plots within the limits of the home range of each monitored individual. Home range was determined using the 100% minimum convex polygon method (Mohr 1947) and 5,202 animal localizations obtained simultaneous to activity records (Fernandez-Giné 2009). We used each intersection within the grid as the center for a 10 × 10-m plot. Considering the home range of the 4 porcupines, we established a total of 129 plots (1.29 ha). In each plot we measured and identified all trees with a diameter at breast height ≥ 10 cm. We adopted this lower limit for diameter at breast height inclusion because all species consumed by the porcupines were trees, and only 2% of them showed lower values of diameter at breast height. Using the Mata Nativa version 2.09 program (Cientec 2006), we assessed the local availability of each tree species by calculating the importance value (IV), which is the average of the sum of the relative values of frequency (RF), density (RDe), and dominance (RDo) of each species ($IV = (RF + RDe + RDo)/3$)—Mueller-Dombois and Ellenberg 1974). Frequency was calculated by dividing the number of plots in which a given species is found by the total number of plots sampled. The relative frequency (RF) was the frequency of each individual species divided by the sum of the frequencies of all species multiplied by 100. Density was calculated by dividing the total number of individuals tallied for a given species by the total area of the measured plots in ha. Relative density (RDe) was obtained by dividing the density of each individual species by the sum of the densities of all of the species multiplied by 100. We divided the sum of the basal area of each tree of a species (from all plots) by the total area of all of the measured plots (in m²/ha) to calculate dominance. Relative dominance (RDo) was obtained by dividing the total basal area of each individual species by the sum of the basal areas of all of the species multiplied by 100 (Curtis and McIntosh 1951; Mueller-Dombois and Ellenberg 1974). Therefore, the IV measures the availability of each plant species, taking into account their density, cover, and frequency of occurrence in the area. Values of IV ranged from 0% to 100% (Mueller-Dombois and Ellenberg 1974).

Based on data collected in early samples, we selected 10 individuals (diameter at breast height ≥ 10 cm) of each of the 4 plant species most consumed by the porcupine (40 trees in

total). We then monitored leaf availability each month for 11 months of 2006 excluding October. By visual inspection we used a score of 0–4 to estimate the availability of young and mature leaves of each tree (Fournier 1974). A score of 0 indicated trees with no leaves, whereas 1–4 estimated 4 regular intervals of 25%, from 1–25% (1) to 76–100% (4) of leaf coverage. We measured the monthly availability of young leaves by multiplying the average availability index of each plant species by 25 to transform the index to a percentage of the crown coverage (Bencke and Morellato 2002). A meteorological station located between 3 and 20 km from the forest remnants studied provided the daily rainfall and temperature measurements for 2006. We thus calculated monthly rainfall and monthly average temperature. We calculated daily photoperiod for the study area using Online-Photoperiod Calculator version 1.95 software (Lammi 2001).

Ecological and nutritional features of plant species.—Based on previous studies (Gandolfi et al. 1995; Lorenzi 1992, 1998; Mariano-Neto 2004) and expert opinion (S. Gandolfi, Universidade de São Paulo, pers. comm.; E. Mariano-Neto, Universidade Federal da Bahia, pers. comm.; R. R. Rodrigues, Universidade de São Paulo, pers. comm.), we classified the consumed and available plant species into 2 distinct ecological groups, the pioneer species (early secondary and pioneer tree species) and the nonpioneer species (later secondary and climax species). When information for the plant species was not available, we classified the species as an unidentified ecological group, with exotic species treated separately. We calculated the relative availability of each ecological group of plants as the sum of IVs of each species belonging to this group (Gandolfi et al. 1995).

We also established a binary classification of plant species—fixing and nonfixing species—from Fabaceae using their ability to form symbiotic associations with nitrogen-fixing bacteria (Faria and Lima 2002; Gehring 2003; Roggy and Prévost 1999). For the 7 most commonly eaten plant species (representing 94.7% of the annual diet), we undertook an analysis of the plant's nutritional content by selecting 4 samples of young leaves from each species. We used Weende's method (Hart and Fisher 1971) to assess the levels of dry matter (DM) and mineral matter (MM), total protein content (crude protein levels [CP]), and crude fat levels (ether extract [EE]). The levels of fiber content (acid detergent fiber [ADF]) were assessed using the method of Van Soest (1967).

Porcupine digestive anatomy.—We obtained an illegally hunted specimen. From this we recorded the mass and dimensions of stomach, duodenum, jejunum, ileum, cecum, colon, and rectum.

Data analysis.—We calculated the importance of food items and plant species in the annual diet (dietary composition) by dividing the number of feeding records for that species by the total number of feeding records and transforming the fraction into a percentage. In the same way we calculated the importance of the 4 most-consumed species in the monthly diet of the subject, and we used it to evaluate differences in the frequency of consumption of these species between individuals. We applied 1-way analysis of variance and Tukey post hoc tests to this analysis.

We used the Morisita–Horn index (C_{mH} —Magurran 1988) to calculate the similarity of the annual diet of an individual and the joint diet of the 4 animals in consecutive months. We compared dietary diversity between animals and consecutive months by using the Shannon–Weaver index (H' —Magurran 1988; Pielou 1969) and the method of Hutcheson (1970) based on the t -test (Magurran 1988). For these analyses we used the BIO-DAP program (Thomas and Clay 2000).

We assessed the preference for tree species and ecological groups by applying Ivlev's preference index (E_i —Ivlev 1961), which ranges from -1 (total avoidance) to $+1$ (total preference—Krebs 1989). We applied a detrended component analysis to characterize the nutritional features of each assessed plant species and examined the relationship between nutritional content and Ivlev's preference index (E_i) using the Pearson correlation (r).

We evaluated differences in the frequency of consumption of the 4 most-consumed species between months by linear mixed-modeling procedures using SAS version 8.2 software and a compound symmetry covariance structure (SAS Institute Inc. 2002). We assigned individual animals as a random factor because measurements were repeated using the same animals throughout the year. We used the same procedure to identify variations in foraging patterns throughout the year (monthly differences) using 2 variables, visiting rate (mean number of feeding trees visited per observation session, balanced for 6 h of observation) and exploitation rate (average number of feeding records per feeding tree visited per observation session). Similarly, we used the mixed-modeling procedure, considering autoregressive covariance structure and individual trees as random factors, to identify differences in the availability of young leaves of the 4 most-consumed species among months. Differences were considered statistically significant at $P < 0.05$. In addition, we used general linear models and applied multiple regressions to evaluate the relationship between the climatic factors and the monthly availability of young leaves.

RESULTS

Diet composition.—For the 4 porcupines observed we reported a total of 1,177 feeding records, with positive

identification of the plant parts and plant species consumed in 892 records (75.8%) and 1,136 records (96.5%), respectively. The thin-spined porcupine relied exclusively on leaves, with young leaves representing 87.6% of the total items consumed and only a minor portion of the registers unidentified regarding the state of maturation.

The 4 study animals consumed leaves from 113 individual trees belonging to 17 species and 11 families (Table 2). The family Fabaceae comprised most of the tree species (7), and the majority of the annual diet (80.9%). Among these species, 6 are of the subfamily Mimosoideae and 1 (*Andira fraxinifolia*) of the subfamily Papilionoideae. Two Fabaceae species, *Albizia pedicellaris* and *Inga thibaudiana*, comprised 77.8% of the joint diet of the individuals, representing the bulk of the diet for all individuals. Species such as *Pera glabrata* (Euphorbiaceae) also had a relative importance ($\geq 5\%$) in annual diet of 3 animals (CS01, CS02, and CS03), whereas *Tapirira guianensis* (Anacardiaceae) and *Simarouba amara* (Picramniaceae) were important components in the annual diet of 1 animal (CS01). In addition, 2 thin-spined porcupines consumed leaves from the exotic jackfruit tree (*A. heterophyllus*), which comprised a minor part of their diet (0.83% and 4.74%).

Similarity among diets of individuals.—The dietary similarity among individuals (C_{mH}) varied between 54% and 92% (CS03 versus CS04 = 92%; CS01 versus CS04 = 81%; CS01 versus CS02 = 68%; CS02 versus CS04 = 64%; CS01 versus CS03 = 62%; CS02 versus CS03 = 54%). The 3 plant species dominant in their diets were consumed in different proportions by animals (*A. pedicellaris*: $F_{3,42} = 4.912$, $P < 0.001$; *I. thibaudiana*: $F_{3,42} = 10.649$, $P < 0.001$; *Pera glabrata*: $F_{2,32} = 4.273$, $P = 0.023$). We found a difference in the number of species (5–7 species) and trees (15–40 trees) used by each studied animal (Table 2). Particularly, the composition of the annual diet of porcupine CS02, which lived in the smallest forest fragment, was poorer and less diverse, comprising nearly half the number of trees used by the other porcupines (Table 2).

Diet selection.—We sampled a total of 832 trees from 118 species and 41 families in all sampling plots. Porcupines used $< 15\%$ of the total available tree species in the area. The values of the preference index (E_i) reveal that of the 17 species of trees used for food by the porcupines, 7 were consumed in higher proportion than their local availability ($E_i > 0$), indicating preference (Table 3). Among these, 5 are Fabaceae species potentially or confirmed capable of forming symbiotic associations with nitrogen-fixing bacteria, with 4 species belonging to the tribe Ingea (genera *Albizia* and *Inga*). The remaining plant species were consumed in proportions lower than or approximately equal to their availability, indicating avoidance ($E_i \leq 0$). The majority of these species were consumed only occasionally ($< 1\%$ of feeding records).

Thin-spined porcupines based their diet on protein-rich species, because 6 of the 7 most-consumed species had protein (CP) levels $\geq 16\%$, with the 2 most-consumed species having values $> 19\%$ (Table 3). Most of these species (5 of 7) also

TABLE 2.—Plant species composition, richness, and diversity of the diet of the 4 free-ranging thin-spined porcupines monitored in 3 fragments of the Atlantic forest, Brazil.

Plant species ^a	% feeding records/porcupine ^b				Total
	CS01	CS02	CS03	CS04	
1. <i>Albizia pedicellaris</i> (Fabaceae)	38.0a	76.3b	14.2a	26.1a	42.3
2. <i>Inga thibaudiana</i> (Fabaceae)	22.1a	16.2a	63.3b	50.6b	35.5
3. <i>Pera glabrata</i> (Euphorbiaceae)	16.3a		5.0b	14.6ab	8.4
4. <i>Tapirira guianensis</i> (Anacardiaceae)	10.9a	2.5a			3.4
5. <i>Simarouba amara</i> (Picramniaceae)	9.1				2.2
6. <i>Artocarpus heterophyllus</i> (Moraceae)		4.7	0.8		1.7
7. <i>Schefflera morototoni</i> (Araliaceae)	0.4		0.8	4.2	1.2
8. <i>Inga capitata</i> (Fabaceae)			5.8		1.2
9. <i>Protium warmingianum</i> (Burseraceae)			5.0		1.1
10. <i>Inga affinis</i> (Fabaceae)	1.8			1.9	0.9
11. <i>Parkia pendula</i> (Fabaceae)				2.7	0.6
12. <i>Ecclinusa ramiflora</i> (Sapotaceae)			2.5		0.5
13. <i>Vismia latifolia</i> (Clusiaceae)			1.7		0.4
14. <i>Andira fraxinifolia</i> (Fabaceae)			0.8		0.2
15. <i>Cryptocarya mandiocana</i> (Lauraceae)	0.7				0.2
16. <i>Inga nuda</i> (Fabaceae)	0.7				0.2
17. <i>Myrcia acuminatissima</i> (Myrtaceae)		0.3			0.1
Total feeding records	276	359	240	261	1,136
No. used trees	30	15	40	28	113
No. consumed species	9	5	10	6	17
Shannon's index (H') ^c	1.8a	1.0b	1.6ac	1.4c	1.5

^a Plant species ranked in order of total consumption frequency.

^b Different lowercase letters in the same line indicate statistically significant ($P < 0.05$) differences based on the Tukey post hoc test.

^c Different lowercase letters in the same line indicate statistically significant ($P < 0.05$) differences according to Hutcheson's test (Hutcheson 1970).

were rich in fiber, with ADF values $> 50\%$. In general, the 4 most-consumed species (*A. pedicellaris*, *I. thibaudiana*, *P. glabrata*, and *T. guianensis*) are clearly characterized by a higher DM and ADF values (Fig. 2). However, only the foliar MM was negatively correlated with the E_i values ($r = -0.86$, $n = 7$, $P = 0.012$), and other nutritional features were not significantly correlated (DM: $r = 0.65$, $n = 7$, $P = 0.116$; CP: $r = -0.20$, $n = 7$, $P = 0.657$; ADF: $r = 0.70$, $n = 7$, $P = 0.074$; EE: $r = -0.49$, $n = 7$, $P = 0.253$).

Among the 7 most-consumed species, 5 are among the 10 species that have the highest IVs in the study area (Table 3). Pioneer species were preferred in relation to nonpioneer and exotic species, according to the Ivlev's preference index [(E_i (pioneers) = 0.24; E_i (nonpioneers) = -0.84 ; E_i (exotic) = -0.56). Pioneer species were consumed more frequently (95.7%) than their availability (IV = 58.9%), whereas nonpioneer and exotic groups were consumed less frequently (2.7% and 1.7%, respectively) than their availability (IV (nonpioneers) = 31.9%; IV (exotic) = 3.2%). Species not classified comprised the remaining trees in the study area (IV = 3.2%).

Seasonal variation.—The availability of young leaves was significantly less ($< 50\%$ of prior availability) from June to September (Fig. 3), which was triggered by the lower temperatures and shorter photoperiod in July, only to recover by the end of the period of low rainfall (September–October). Nevertheless, the availability of young leaves was not dependent on the photoperiod ($F_{1,7} = 0.039$, $P = 0.441$), rainfall ($F_{1,7} = 0.668$, $P = 0.440$), or temperature ($F_{1,7} = 2.607$, $P = 0.150$). In addition, the consumption of young

leaves did not follow their availability, because during the period from March to May and July to September of both years the animals consumed young leaves almost exclusively ($> 98\%$; Fig. 3). In contrast, during the period from October 2005 to February 2006, and during June of both years, animals often did not feed at the end of the branches, making the identification of the state of maturity of the consumed leaves difficult.

The composition of the joint diet of the 4 thin-spined porcupines, relative to plant species, was similar during consecutive months, with a C_{mH} index ranging from 72.4% to 96.5% (Table 4). Dietary diversity (H') was similar across the months ($P > 0.05$), with the exception of May and September showing lower diversity values than previous months ($t_{28} = 3.615$, $P < 0.01$; and $t_{36} = 2.051$, $P < 0.05$, respectively) and following months ($t_{44} = 2.427$, $P < 0.05$; and $t_{37} = 2.308$, $P < 0.05$, respectively). We found differences among months in the availability of young leaves of 3 of the 4 most frequently consumed plant species of the diet, *A. pedicellaris* ($F_{10,360} = 6.10$, $P < 0.001$), *P. glabrata* ($F_{10,360} = 3.19$, $P = 0.001$), and *T. guianensis* ($F_{10,360} = 7.02$, $P < 0.001$), but not for *I. thibaudiana* ($F_{10,360} = 1.68$, $P = 0.082$). In general, these woody tree species showed a reduction in young leaf availability in the same period of the year, between June and September (Fig. 3). Nevertheless, significant variation in consumption rates between months was reported only for *A. pedicellaris* ($F_{11,124} = 2.85$, $P = 0.002$), but not for the remaining species (*I. thibaudiana*: $F_{11,124} = 1.85$, $P = 0.052$; *P. glabrata*: $F_{11,124} = 0.71$, $P = 0.730$; and *T. guianensis*: $F_{11,124} = 0.17$, $P = 0.998$).

TABLE 3.—Consumption frequency (%), availability (IV %), selectivity (E_j), and ecological and nutritional characteristics of plant species consumed by radiocollared thin-spined porcupines monitored in fragments of secondary forest in the municipality of Ilheus, southern Bahia.

Plant species (family) ^a	Consumption (% feeding records)		Availability		Selectivity (E_j) ^d	Ecological characteristics ^e	Nutritional characteristics (%) ^f			
			IV % ^b	Rank ^c			DM	CP	ADF	EE
<i>Inga capitata</i> (Fabaceae)	1.23	<0.1	<0.1	>118th	>0.85	p; f	—	—	—	—
<i>Albizia pedicellaris</i> (Fabaceae)	42.34	3.34	3.34	5th	0.85	p; f	33.0	19.5	63.6	1.1
<i>Inga thibaudiana</i> (Fabaceae)	35.48	2.79	2.79	8th	0.85	p; f	31.0	21.4	75.8	0.4
<i>Pera glabrata</i> (Euphorbiaceae)	8.36	1.13	1.13	22nd	0.76	p	33.7	12.7	82.8	0.6
<i>Inga affinis</i> (Fabaceae)	0.88	0.31	0.31	71st	0.48	p; f	—	—	—	—
<i>Andira fraxinifolia</i> (Fabaceae)	0.18	0.1	0.1	112nd	0.28	np; f	—	—	—	—
<i>Protium warmingianum</i> (Bursaceae)	1.06	0.69	0.69	33rd	0.21	np	—	—	—	—
<i>Sinarouba amara</i> (Pteramiaceae)	2.20	2.11	2.11	13rd	0.02	p	35.3	16.6	26.7	2.7
<i>Vismia latifolia</i> (Clusiaceae)	0.35	0.42	0.42	54th	-0.09	p	—	—	—	—
<i>Ecclinusa ramiflora</i> (Sapotaceae)	0.53	0.64	0.64	35th	-0.10	np	—	—	—	—
<i>Parkia pendula</i> (Fabaceae)	0.62	0.92	0.92	27th	-0.20	np; nf	—	—	—	—
<i>Artocarpus heterophyllus</i> (Moraceae)	1.67	2.55	2.55	9th	-0.21	e	16.7	19.9	53.3	2.0
<i>Tapirira gutanensis</i> (Anacardiaceae)	3.43	7.75	7.75	2nd	-0.39	p	30.5	16.0	55.2	1.4
<i>Inga nuda</i> (Fabaceae)	0.18	0.59	0.59	39th	-0.54	p; f	—	—	—	—
<i>Myrcia acuminatissima</i> (Myrtaceae)	0.09	0.64	0.64	36th	-0.76	np	—	—	—	—
<i>Schefflera morototoni</i> (Araliaceae)	1.23	10.58	10.58	1st	-0.79	p	18.9	21.7	40.5	1.2
<i>Cryptocarya mandiocana</i> (Lauraceae)	0.18	2.14	2.14	12nd	-0.85	np	—	—	—	—

^a Plant species ranked in order of preference by Ivlev's (1961) preference index (E_j).

^b Importance values of plant species in the habitat of the animals.

^c Position of the species in terms of importance value among all sampled species.

^d Ivlev's (1961) preference index.

^e p = pioneer species; np = nonpioneer species; e = exotic species; f = non-nitrogen-fixing Fabaceae species; nf = non-nitrogen-fixing Fabaceae species.

^f DM = dry matter; CP = crude protein; ADF = acid detergent fiber; EE = ether extract; MM = mineral matter.

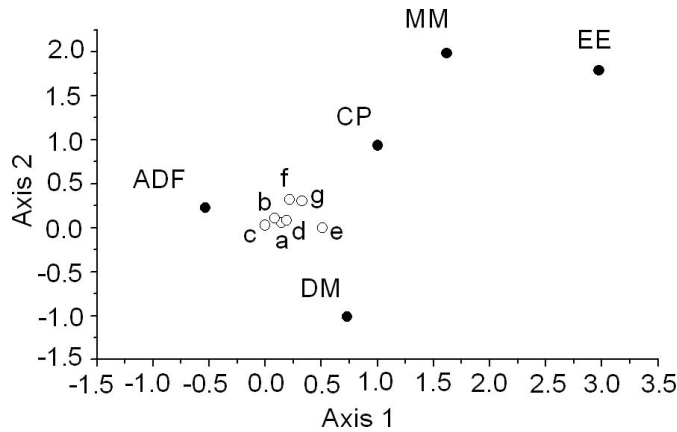


FIG. 2.—Ordination scores for plant species on the 1st and 2nd axis of a detrended component analysis biplot using nutritional features of dry matter (DM) and mineral matter (MM), total protein content (crude protein levels [CP]), crude fat levels (ether extract [EE]), and fiber content (acid detergent fiber [ADF]). Plant species are a) *Albizia pedicellaris*, b) *Inga thibaudiana*, c) *Pera glabrata*, d) *Tapirira guianensis*, e) *Simarouba amara*, f) *Artocarpus heterophyllus*, and g) *Shefflera morototoni*.

Considering the monthly foraging pattern, the mean number of feeding trees visited per observation session (visitation rate) ranged from 1.3 ± 0.5 to 2.3 ± 1.1 (mean \pm SD; $n = 4$) throughout the year, and the exploration rate (mean number of feeding records per tree visited in each observation session) ranged from 3.4 ± 1.6 to 5.4 ± 1.6 (mean \pm SD; $n = 4$). We

observed no variation in the foraging pattern of the thin-spined porcupine throughout the year, because rates of visitation and exploration were statistically similar between months ($F_{11,31} = 0.78$, $P = 0.659$; and $F_{11,31} = 0.63$, $P = 0.790$, respectively).

Digestive anatomy.—The single individual thin-spined porcupine examined showed a simple and small stomach, a large intestine longer than the small intestine, and an enlarged and sacculated cecum. In relation to porcupine length (head + body length = 440 mm), the relative lengths were 26% for stomach, 280% for small intestine, 384% for large intestine, and 94% for cecum. The porcupine weighed 1.1 kg, and percentages of total body mass were 2% for the stomach, 2.3% for small intestine, 16.4% for large intestine, and 13% for cecum.

DISCUSSION

Thin-spined porcupines showed a strictly folivorous diet consisting exclusively of leaves of woody trees without any observation of fruit, flower, seed, or animal intake. This folivorous diet is consistent with previous observations of fecal content, lethargic movements, and feeding activity of the thin-spined porcupines reported from another Atlantic forest location (Chiarello et al. 1997; de Oliveira 2006; de Souto Lima et al., in press). However, de Souto Lima et al. (in press) observed an opportunistic use of flowers, fruits, and shoots when those items were available among the leaves of plant

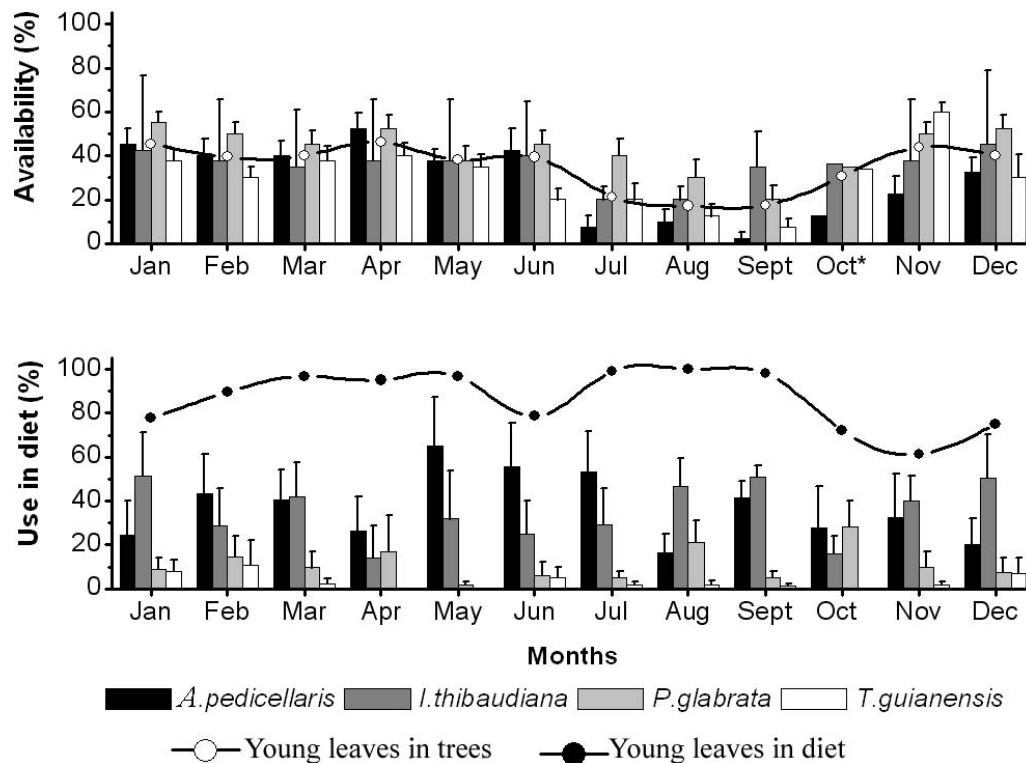


FIG. 3.—Seasonal variation in the availability and consumption of young leaves of plant species by thin-spined porcupines in forest fragments in the southern part of Bahia, Brazil. The values of young leaf availability are from January to December 2006, except for young leaf availability in October (*), which represents the average between values obtained in September and November. The values of young leaves in the diet are from March 2005 to September 2006, and the values shown between March and September represent the average of values obtained in both years.

TABLE 4.—Characteristics of the monthly sampling effort throughout the year, species richness (S) and Shannon–Weaver diversity (H') of the monthly diet of radiocollared thin-spined porcupines, and similarity (Morisita–Horn index [C_{mH}]) of the diet in consecutive months. Different lowercase letters in the same column indicate statistically significant ($P < 0.05$) differences according to Hutcheson's test (Hutcheson 1970).

Month	No. sessions	No. porcupines	Richness (S)	Diversity (H')	Similarity (C_{mH})
Jan.	12	4	6	1.50a	—
Feb.	14	4	6	1.53a	0.965
Mar.	13	4	7	1.61a	0.961
Apr.	7	3	6	1.68a	0.879
May	14	4	4	1.02b	0.856
Jun.	16	4	8	1.58a	0.957
Jul.	17	4	7	1.57a	0.934
Aug.	8	3	7	1.69a	0.724
Sep.	17	4	5	1.24c	0.868
Oct.	10	4	7	1.72a	0.753
Nov.	8	4	6	1.55a	0.826
Dec.	10	4	6	1.66a	0.844
Total	146	4	17	—	—

species highly consumed. This opportunistic use might also have occurred during our study but went undetected due to the greater height of the forest canopy in southern Bahia. Nevertheless, the degree of folivory reported in both studies is greater than that observed for other tropical erethizontids (Charles-Dominique et al. 1981; Emmons and Feer 1997; Santos-Junior 1998), and *C. subspinosus* probably is one of the most-folivorous species within its family. We did not observe the animals drinking water, an adaptation commonly associated with strictly arboreal folivores such as koalas (*Phascolarctos cinereus*) and greater gliders (*Petauroides volans*—DeG Gabriele et al. 1978). The anatomy of the digestive tract, described here for the 1st time, might suggest that the thin-spined porcupine is a cecal fermenter, similar to other porcupine species, with typical adaptations for high-fiber diets and conservation of water (Felicetti et al. 2000; Johnson and McBee 1967; Parra 1978).

Our results do not support previous anecdotal observations of the consumption of fruits or nuts from exotic species, such as cacao, jackfruit, or oil palm (Kuniy et al. 2005; Moojen 1952; Nowak and Paradiso 1983). The thin-spined porcupine concentrated its feeding on a few plant species that represented a small subset of the total species available within its home range. Two of the 4 most-consumed plant species in our study area also were consumed frequently (>75% of the dietary composition) by individuals observed in a forest area located 750 km south of our study region (de Souto Lima et al. 2009), showing a consistent pattern of dietary composition spanning a larger geographical area.

Nutritional features alone were insufficient to explain why some of the most-consumed species were preferred more than others by the thin-spined porcupines. This is evidenced by the absence of correlation between the index of preference and the main nutritional characteristics. We expected that leaf choice would be driven by the protein: fiber ratio of food items,

following the hypothesis of Milton (1998). However, this ratio was not a good predictor of food preference in this case. Six of 7 most-consumed species have crude protein values above 16%, which is high in comparison to values observed for neotropical tree species (Barreto 2007; Sambuichi 2002), even among nitrogen-fixing species within Fabaceae (Roggy et al. 1999). Thus, leaf protein might be a critical variable for these herbivores. By contrast, the fiber levels (ADF) were higher in the 4 most-consumed and preferred plant species than in other species evaluated, with values comparable to leaves eaten by large-bodied primates such as the colobines and indriids (Powzyk and Mowry 2003; Waterman and Kool 1994). Thus, low fiber levels apparently were not an important factor in the selection of plant species by thin-spined porcupines.

In addition to protein content, some features associated with tree species capable of symbiosis with nitrogen-fixing bacteria apparently play an important role in food choice by the thin-spined porcupine. Species of Fabaceae were preferred among plant species available within the home range of an animal, even among those plant species with high-protein content. The preference for these plant species relative to other high-protein species could be due to foliar production and secondary metabolites. The association with nitrogen-fixing bacteria supplies more nitrogen for plants, which in turn can increase their growth rates (foliar expansion and substitution) and leaf biomasses (Kursar and Coley 2003; Roggy et al. 1999). By relying on food resources that are more abundant and predictable in space and time, the animal can maximize the rate of food intake while minimizing the energy expenditure and risks in searching for food (Emlen 1966; Schoener 1971). Thus, the selection for these plant species can be an important behavioral strategy for a primarily arboreal folivore whose dietary nature and small body size impose restrictions on its energy budget (Eisenberg 1978; McNab 1978). Species from the monophyletic clade of Fabaceae tend to share chemical defense strategies (Wink and Mohamed 2003). Thus, it is possible that thin-spined porcupines are selecting related species due to the presence of specific types or levels, or both, of secondary metabolites of which they might be more tolerant.

Young leaves in general, and from the 4 most-consumed species, were available in Ilheus throughout 2006. However a significant decline in leaf production occurs in the dry season (July–September), similar to the seasonal pattern in foliar production observed in this region by Mori et al. (1982). The assessment of leaf availability was not carried out during 2005 when some of the behavioral data were collected. However, apart from availability and consumption of young leaves, we noticed no significant alteration in the composition of the diet throughout the sampling period, either in terms of plant species or the foraging pattern of the animals. The variation in diet diversity between consecutive months was influenced only by the less-consumed species because the frequency of consumption of the 4 most-consumed species, in general, was continuous throughout the year. In addition, thin-spined porcupines maintained a consistent pattern of consumption

of young leaves throughout the year, similar to that observed for maned sloths in the Atlantic rain forest (Chiarello 1998). In both cases it is likely that young leaves are always available in sufficient levels to allow continuous consumption, although a noticeable seasonal variation in availability may occur.

Our study shows that these small rodents appear to be strict folivores and highly selective in food choice, in agreement with assumptions associated with constraints imposed by body size. However, the selection of plant species is not explained entirely by primary nutritional content, and the extent to which features such as the presence, composition, and levels of feeding deterrents drive food selection by thin-spined porcupine is yet to be determined. Although thin-spined porcupines showed a diet based on a few plant species, these are pioneer species characteristic of early secondary forests (Gandolfi et al. 1995; Lorenzi 1992, 1998; Mariano-Neto 2004). A core diet relying heavily on pioneer, abundant, and widespread species allows thin-spined porcupines to thrive even in small, disturbed forest patches highly impacted by edge effect, such as the forest remnants assessed in the present study. In the current state of fragmentation and disturbance of the remaining Atlantic forest, populations of thin-spined porcupines are vulnerable to habitat loss and a myriad of anthropogenic pressures, although food supply may not be the most limiting.

RESUMO

Nós estudamos a ecologia alimentar do ouriço-preto (*Chaetomys subspinosus*), um pequeno roedor arborícola endêmico da Mata Atlântica do Brasil e ameaçado de extinção. Nós capturamos e radiomonitoramos 4 indivíduos em vida-livre e coletamos 1.117 registros de alimentação em 944 horas de observação entre abril de 2005 e setembro de 2006. Nós encontramos que os animais se alimentaram exclusivamente de folhas de árvores, preferindo folhas jovens. A composição da dieta e o padrão de forrageio dos animais não variou sazonalmente, embora nós observamos que houve variação sazonal na disponibilidade de folhas jovens. A dieta anual deles foi constituída primariamente (90%) de 4 espécies de plantas, *Albizia pedicellaris*, *Inga thibaudiana*, *Pera glabrata* e *Tapirira guianensis*. Este pequeno grupo de espécies de planta contem altos níveis de proteína e fibra, e as espécies mais preferidas tem capacidade de estabelecer associação simbiótica com bactérias fixadoras de nitrogênio. A dieta concentrada em poucas espécies taxonomicamente aparentadas e fixadoras de nitrogênio sugere que em adição aos altos níveis de proteína, outros fatores ligados à tolerância química e abundância local de alimento podem influenciar o uso e seleção de alimento por estes pequenos podadores. Nós concluímos que *C. subspinosus* é mais folívoro do que se pensava e que é altamente seletivo na escolha do alimento, como esperado para um pequeno mamífero folívoro arborícola. Uma vez que os animais selecionam espécies pioneiras, localmente abundantes, amplamente distribuídas e típicas de florestas secundárias iniciais, nós sugerimos que a oferta de

alimento não é um fator limitante à presença do ouriço-preto em fragmentos de florestas pequenos e perturbados ao longo da Mata Atlântica.

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