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Consumption of arbuscular mycorrhizal fungi by spiny rats (*Proechimys semispinosus*) in eight isolated populations

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ABSTRACT. The consumption of arbuscular mycorrhizal fungi (AMF) by *Proechimys semispinosus* (Central American spiny rat) was assessed via microscopic examination of faecal material for the presence of AMF spores. Mycophagy (indicated by the presence of spores) was compared among individual spiny rats residing on eight isolated islands in Gatun Lake, Panama during January and July 1996. Spores and sporocarps of *Sclerocystis coremioides* and spores from at least four species of *Glomus* were present in 77% of the 231 faecal samples examined. The proportion of faecal samples that contained AMF spores did not differ between spiny rat sex, age classes or months of sampling or with island area. However, there was a positive relationship between the proportion of samples containing spores and rodent density in January, and a marginally significant positive trend in July. Increased consumption of AMF on islands that supported high densities of spiny rats may have resulted from increased competition for primary food resources (fruits and seeds).

KEY WORDS: glomalean fungi, mycophagy, Panama, spore dispersal, tropical rodent

INTRODUCTION

Most trees in tropical regions rely on arbuscular mycorrhizal fungi (AMF) for seedling establishment and improved growth (Alexander *et al*. 1992, Janos 1980a). Field studies have shown that plants that host AMF commonly have improved uptake of phosphorus (Merryweather & Fitter 1996, Sanders & Koide 1994), which is frequently the limiting nutrient in the tropics (Janos 1987). Following the disturbance of tropical soils, AMF inoculum is often severely reduced or eliminated (Alexander *et al*. 1992, Cuenca & Lovera 1992, Fischer *et al.* 1994). These soils may thus require the re-introduction of AMF from an outside source to facilitate forest regeneration (Janos 1980b). Other studies

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have found reduced root densities (root gaps) associated with tree falls (Ostertag 1998, Sanford 1989, Wilcynski & Pickett 1993). Such small-scale disturbances may contribute to the heterogeneity of AMF inoculum available to seedlings within intact forests (see Janos 1992). Therefore, the movement of AMF within forests and the dispersal of AMF inoculum to adjacent disturbed soils may be critical for the re-establishment of tropical forests.

Although the extension of mycelia and roots from infected plants may serve as a mechanism for the slow dispersal of AMF (Powell 1979), dispersal may be hastened through the movement of spores (MacMahon & Warner 1984). However, such movement of AMF spores is limited by their largely hypogeous (underground) formation (Gerdemann & Trappe 1974). There is some evidence that spores may be dispersed via wind erosion of soil in arid regions of North America (Allen *et al*. 1989), but this mechanism probably is not common in humid locations. Numerous studies have shown that small mammals in temperate regions of North America and Australia consume AMF species that produce sporocarps (Claridge & May 1994, Fogel & Trappe 1978, Maser *et al*. 1978, McGee & Baczocha 1994) and defecate the spores in a viable condition (Allen & MacMahon 1988, Reddel *et al*. 1997, Rothwell & Holt 1978, Trappe & Maser 1976). Therefore, small-mammal mycophagy (fungus consumption) may serve as an important spore-dispersal mechanism.

Despite the dependence of most tropical trees on AMF and accelerating levels of forest disturbance in tropical regions, only two studies have addressed AMF mycophagy by tropical small mammals (Janos *et al*. 1995, Reddel *et al*. 1997). Furthermore, the majority of studies (both temperate and tropical) that have examined the consumption of mycorrhizal fungi are restricted to single populations of mammals. By comparing several populations of a single species, the effects of population-level characteristics (e.g. rodent densities) on mycophagy can be addressed. Accordingly, faecal pellets from individuals in eight isolated populations of a neotropical forest rodent, *Proechimys semispinosus* (Central American spiny rat), were examined for the presence of AMF spores. Spiny rats are one of the most ubiquitous and abundant rodents throughout lowland forests of Central America (Eisenberg 1989). Although this echimyid is thought to be primarily frugivorous and granivorous (Adler 1995), other species of *Proechimys* have been reported to include AMF in their diets (Emmons 1982, Janos *et al*. 1995). This study was conducted to determine whether (1) *P. semispinosus* consumes AMF, (2) AMF consumption among populations of *P. semispinosus* differs between seasons (rainy and dry), and (3) forest patch size and spiny rat age, sex and density influence the consumption of AMF.

METHODS

Study sites

This study was conducted on eight small islands in Gatun Lake, central Panama. The lake was created when the Chagres River was dammed during

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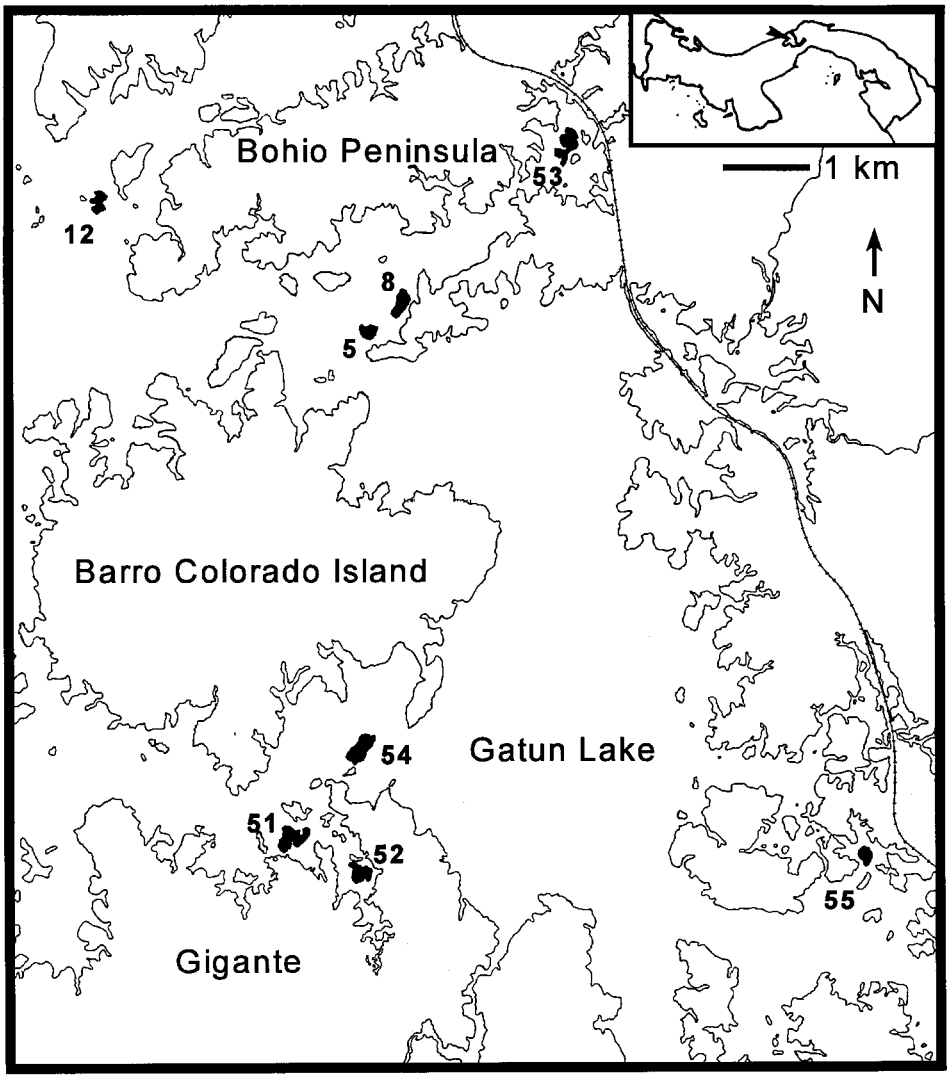

Figure 1. Locations of the eight study islands in Gatun Lake; the inset shows the location of Gatun Lake in Panama.

construction of the Panama Canal. As a result, over 200 hilltops were isolated as islands and are covered now with tropical moist forest. Eight islands ranging in size from 1.7 to 3.7 ha were selected for this study (Figure 1). *Proechimys semispinosus* is apparently the only rodent that maintains persistent populations on islands of less than 17 ha (Adler & Seamon 1991). Therefore, selecting islands that only support spiny rats allows for population-level comparisons without having to untangle confounding interactions with other small-mammal species within complex communities.

The study area has highly seasonal rainfall, which averages *c*. 2600 mm per

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year on Barro Colorado Island (Windsor 1990). Over 90% of total annual precipitation falls during an 8-mo rainy season, which is followed by a severe dry season lasting from mid-December to the end of April (Windsor 1990). The islands were sampled during January and July 1996 to include both seasons.

Sampling procedures

On each island, a permanent sampling grid consisting of sampling stations placed 20 m apart and covering the entire island was established. A single wire mesh live-trap (26.5-cm × 17-cm × 13-cm, manufactured in Taichung, Taiwan) baited with ripe banana was placed on the ground at each trap station. Traps remained open for four consecutive nights and were checked each morning. Upon first capture, spiny rats were toe-clipped for permanent identification. Age class (young or adult, determined by pelage, Adler 1994), sex, weight, reproductive condition, and identification number were recorded for all captured individuals.

During both months, faecal pellets were collected from the bottom of the traps and placed into vials containing 70% ethanol. Dark solid pellets (one to five pellets, depending on availability) were selected to avoid samples contaminated with bait (contaminated pellets were lighter in colour and of a softer consistency). Faecal samples were collected only from individuals upon their first capture during a sampling period to prevent bias due to trapping effects (i.e. foraging duration and behaviour for individuals caught previously that sampling period may have been affected).

Faecal pellets were placed in a gridded Petri dish containing distilled water and lightly crushed into a fine debris. The contents were examined under a dissecting microscope at 40×, and AMF spores were grouped into morphotypes. The presence or absence of each spore morphotype was recorded for samples from each individual rodent. Representative spores from each morphotype were mounted permanently in PVLG (polvinyl-lacto-glycerol) and Meltzer's reagent on slides and examined at high magnification for identification to at least genus. Where species names could not be assigned, letters representing different morphospecies were assigned to a genus. Different morphospecies were distinguished by spore size, colour, shape and colour change in Meltzer's reagent.

Statistical analysis

We began the analysis by estimating spiny rat density for each island and month as the minimum number of individuals known to be alive (see Adler 1994). Although we collected faecal pellets in only 2 mo, spiny rat censuses were conducted from January 1991 through January 1996, in July 1996, and from January 1997 through May 1999. Thus, density estimates were greatly enhanced by prolonged regular sampling before and after the study period (Adler & Lambert 1997).

We then tabulated the proportion of faecal samples that contained spores

for each island and month. Proportions were computed for all AMF species combined and separately for each species (or morphospecies). Proportions of samples containing spores were compared by constructing linear models for repeated-measures categorical data. We first compared the proportion of samples (all islands combined) that contained spores of at least one AMF species between seasons by including month as the main effect. We then compared AMF species composition among islands by constructing a saturated model consisting of two main effects (species and island) and the interaction term. Seasonal differences within AMF species were compared by constructing separate models for each species.

The number of AMF species found in each faecal sample was tabulated and compared among islands by Kruskal–Wallis non-parametric ANOVA. Separate ANOVAs were conducted for both months.

We used multiple logistic regression analysis to examine factors related to the probability of spore occurrence (any AMF species) in faecal samples. The binomial dependent variable (presence or absence of spores in a sample) was related to four explanatory variables (island area and *P. semispinosus* density, age and sex) to identify those variables that best predicted spore occurrence. Full models with all four variables were constructed separately for January and July samples because of problems associated with sample dependence (i.e. many of the same individual *P. semispinosus* were captured in both months). Each spiny rat's faecal sample represented a single observation. We then used simple linear regression analysis to investigate the importance of island area and *P. semispinosus* density in determining the proportion of samples containing spores (with all species combined) for each island. Regression models again were constructed separately for January and July samples.

RESULTS

Proechimys semispinosus was the only rodent captured during the 2-mo of this study. Densities were highest during July on seven of the eight islands, with a two-fold increase on islands 8 and 12. Density was lowest on island 5 and highest on island 8 during both months (Table 1). Rodent density and island area

Table 1. Island area and densities of *Proechimys semispinosus* on each of the eight study islands located in Gatun Lake, Panama, for two months sampled in 1996.

		Density (individuals/ha)	
Area (ha)	Island number	January	July
1.7	5	2.9	2.4
1.8	12	10.6	20.6
1.8	55	6.1	10.6
2.5	52	7.2	9.2
2.7	8	14.4	28.1
3.2	53	9.7	15.0
3.5	51	13.1	13.7
3.7	54	5.4	8.4

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Table 2. Spore characteristics of the four *Glomus* morphospecies collected in faecal samples of *Proechimys semispinosus*.

Morpho-species	Mean spore diameter (SE)*	Colour	Shape	Colour change in Meltzer's	Notes
A	106.4 (2.06)	red–brown	globose	no colour change	clusters common, thick-walled
B	79.6 (0.84)	light yellow	globose	red	clusters common
C	57.2 (0.57)	light yellow	globose	dark red	extremely thick-walled relative to spore diameter, similar to *Glomus fasiculatum* (Thaxter) Gerd. & Trappe
D	73.3 (1.87)	white to yellow	ellipsoid	no colour change	thin-walled, similar to *Glomus fulvum* (Berk. & Broome) Trappe & Gerd.

* Diameters (μm) were computed for 100 spores.

were not related in either month (January: Pearson's $r = 0.334$, $n = 8$, $P = 0.418$; July: $r = 0.090$, $n = 8$, $P = 0.833$).

We collected a total of 231 faecal samples from the eight study islands, comprising 119 samples during January and 112 samples during July. Spores found in the faecal samples were of two genera, *Glomus* and *Sclerocystis* from the order Glomales. We did not attempt to assign species names to members of the genus *Glomus*. Instead, spores from *Glomus* were grouped into four morphospecies (referred to hereafter as species) (Table 2). Although spores that occurred in each faecal sample were not counted, faecal samples were estimated to commonly contain hundreds and sometimes several thousand spores from each of the four species. The large number of spores in each faecal sample, along with spores often found in clusters (especially *Glomus* A and *Glomus* B), suggest that all four species probably produce their spores in sporocarps.

We identified *Sclerocystis coremioides* Berk. & Broome based on morphology of sporocarps that remained intact. Sporocarps of *S. coremioides* are unique in that spores are arranged side-by-side in a single near-spherical layer and are covered by a thick peridium (Almeida & Schenck 1990). Both loose spores and whole sporocarps of *S. coremioides* were found in the faecal samples.

When faecal samples from all islands were combined, the proportion of samples containing spores from at least one species of AMF did not differ between months (January, 0.773; July, 0.768: $\chi^2 = 0.01$, $df = 1$, $P = 0.924$). The proportion of faecal samples containing spores did differ in AMF species composition ($\chi^2 = 180$, $df = 4$, $P = 0.0001$) and among islands ($\chi^2 = 154$, $df = 7$, $P = 0.0001$). The significant island-by-species interaction ($\chi^2 = 212$, $df = 28$, $P = 0.0001$) reflected the unequal proportions of species found in the diets of individuals residing on each island (Figure 2). The number of AMF species varied from only one species found in faecal samples in July on island 5 to all five species present in the diets of individuals on island 51 during both months. *Glomus* C was the most frequent species and was found in samples from all islands in July and from seven of the eight islands in January. *S. coremioides* was

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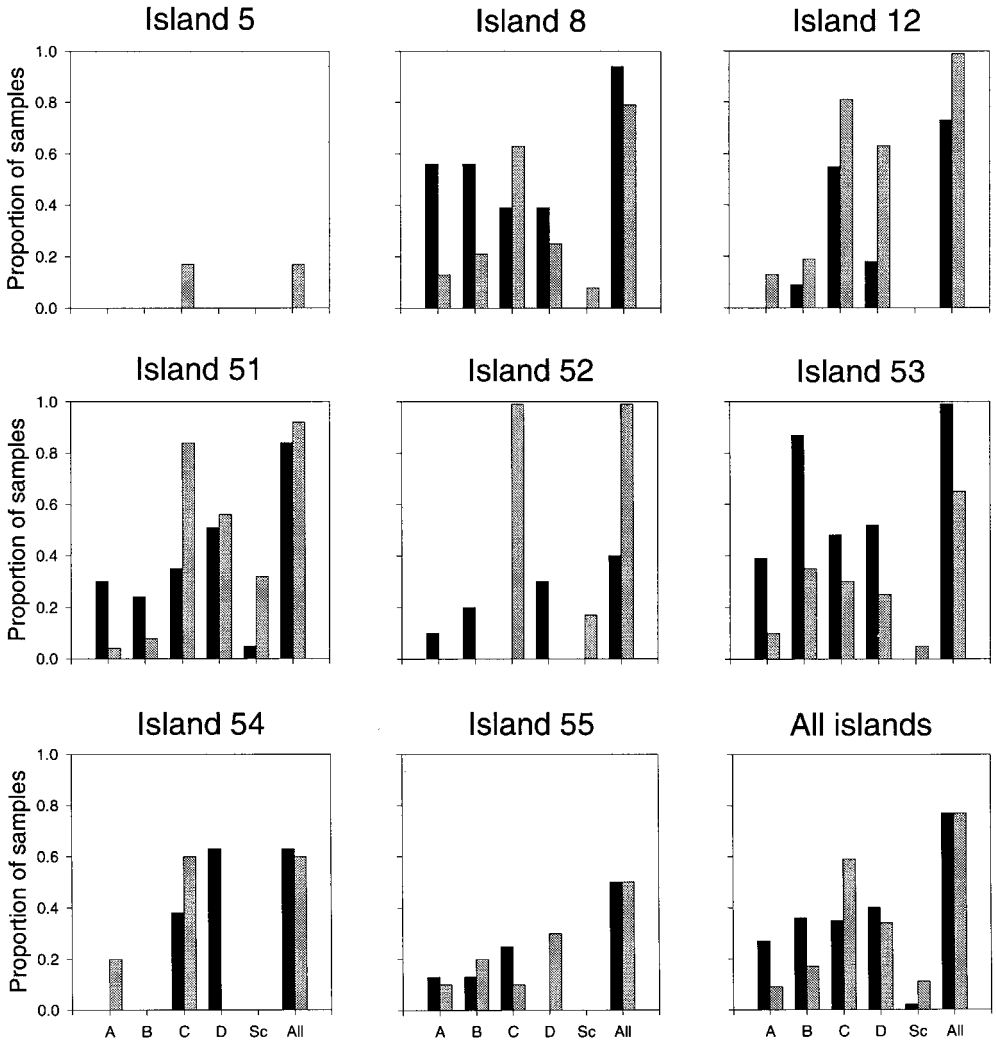

Figure 2. Proportion of samples containing each species separately and all species combined of glomalean fungus for each island in Gatun Lake and month in 1996; black = January, grey = July. A–D are the four morphospecies (Table 2), SC = *Sclerocystis coremoides*.

the least frequent species and was found in samples from five of the eight islands in July and from only one island in January (Figure 2). When samples from all islands were combined, there were significant seasonal differences for four of the five AMF species (Figure 2). *Glomus* A and *Glomus* B were found in higher proportions during January ($\chi^2 = 13.6$, df = 1, P = 0.0002; $\chi^2 = 11.6$, df = 1, P = 0.0007, respectively), whereas *Glomus* C and *S. coremioides* were significantly more prevalent in samples in July ($\chi^2 = 13.7$, df = 1, P = 0.0002; $\chi^2 = 13.7$, df = 1, P = 0.0041, respectively). *Glomus* D did not exhibit a seasonal difference ($\chi^2 = 1.02$, df = 1, P = 0.312).

The number of AMF species in the faecal pellets of individual spiny rats

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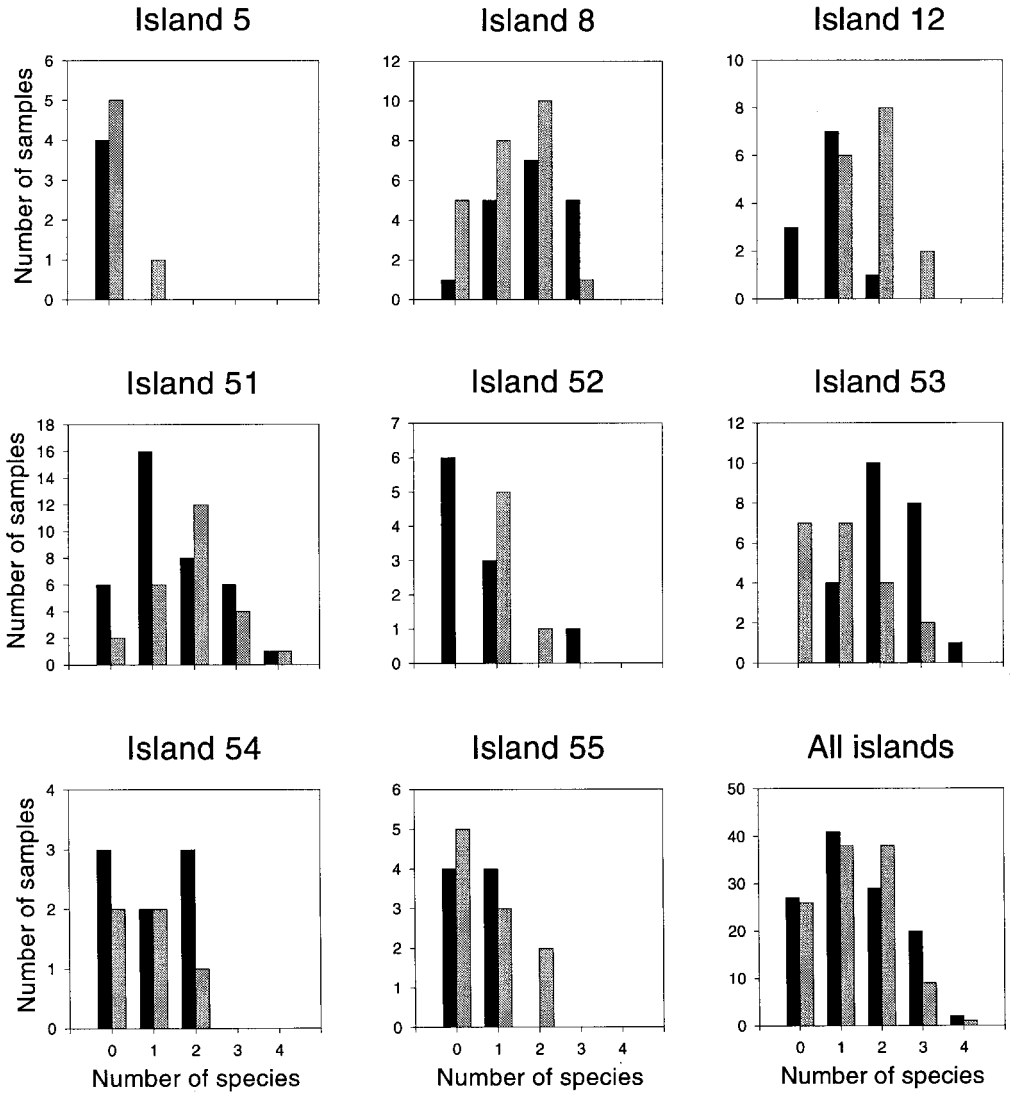

Figure 3. Number of glomalean fungus species found in faecal samples of *Proechimys semispinosus*; black = January, grey = July, 1996.

ranged from zero to four (Figure 3). Mean ranks of the number of species per individual significantly differed among islands during both months (January: $\chi^2 = 43.9$, df = 7, P = 0.0001; July: $\chi^2 = 27.6$, df = 7, P = 0.0003; Kruskal–Wallis test). The lowest mean number of species was in samples from island 5 in January, whereas island 53 had the highest mean (Table 3). During July, island 5 had the lowest mean number of species, whereas samples from island 51 had the highest mean (Table 3).

Only one variable significantly predicted the probability of spore occurrence in faecal pellets. With all variables in the model, spore occurrence was related

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Table 3. Mean (± SD) number of AMF species found in faecal samples collected from individuals of each population of *Proechimys semispinosus* during the study, for two months sampled in 1996.

Island number	n	January	n	July
5	4	no spores	6	0.17 ± 0.41
8	18	1.89 ± 0.90	24	1.29 ± 0.86
12	11	0.82 ± 0.60	16	1.75 ± 0.68
51	37	1.46 ± 1.04	25	1.84 ± 0.94
52	10	0.60 ± 0.97	6	1.17 ± 0.41
53	23	2.26 ± 0.81	20	1.05 ± 1.00
54	8	1.00 ± 0.93	5	0.80 ± 0.84
55	8	0.50 ± 0.53	10	0.70 ± 0.82

positively to *P. semispinosus* density during January ($\beta = 0.26$, $\chi^2 = 10.6$, $P = 0.001$). Spiny rat density also showed a marginally significant positive trend during July ($\beta = 0.07$, $\chi^2 = 3.40$, $P = 0.065$). Island area, age and sex were not significant during either month.

When the proportion of samples containing AMF spores was regressed on spiny rat density, a positive relationship occurred only in January (January: $\beta = 6.90$, $F = 13.6$, $P = 0.003$; July: $\beta = 2.058$, $F = 2.94$, $P = 0.138$). No significant relationship was found between the proportion of samples containing spores and island area in either month (January: $\beta = 23.54$, $F = 2.49$, $P = 0.137$; July: $\beta = 9.66$, $F = 0.48$, $P = 0.516$).

DISCUSSION

The high proportion of faecal samples that contain spores (77%) suggests that glomalean fungi are an important food resource for *P. semispinosus* within the study populations. Moreover, the lack of a significant relationship between spore occurrence and sex or age class suggests that mycophagy is a general foraging strategy utilized by most *P. semispinosus* individuals. The broadening of diets by including glomalean fungi may contribute to the ubiquity and generalist behaviour often reported for species of this genus (Adler 1996, Emmons & Feer 1990, Tomblin & Adler 1998).

The frequency with which spiny rats consume AMF depends undoubtedly not only on the availability of sporocarps in their habitat but also on the relative importance of fungi as a nutrient source when compared to other dietary items. AMF could be (1) preferentially consumed over other available food resources (fruits and seeds), (2) included in the diet as a supplement to primary resources, or (3) only consumed as an alternative resource when primary resources are scarce. Janos *et al*. (1995) reported that AMF consumption by rodents of two genera (*Proechimys* and *Oryzomys*) in Peru was not related to fruit and seed availability. They concluded that rodents in their study exploited AMF when sporocarps were available and not in response to the low availability of other food resources. On our study islands, fleshy fruits and seeds eaten by *P. semispinosus* (Adler 1995) were scarcest at the end of the rainy season and beginning of the dry season (i.e. November to January; Adler 1998). If spiny rats

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were consuming AMF only as an alternative resource, mycophagy should have occurred more frequently during January than during July. However, mycophagy by *P. semispinosus*, as indicated by the presence or absence of AMF spores in faecal pellets, was equally common during both months of this study.

Mycorrhizal fungus consumption was most frequent on islands that supported higher spiny rat densities during the period of low fruit availability. *P. semispinosus* may increase their consumption of AMF sporocarps as a result of competition for primary resources when rodent densities are high. Alternatively, higher rodent densities may be supported in habitats in which AMF sporocarp production is more frequent. A positive relationship between body condition and fungus consumption has been reported for other species of small mammals (Johnson 1994, Tevis 1952, Ure & Maser 1982). Despite our data on frequent mycophagy by *P. semispinosus* during January, mean body weight generally begins to decrease in late November and does not recover until the end of the dry season (Adler 1996). It is therefore unlikely that consumption of AMF alone results in increased spiny rat densities. Instead, the availability of native fruits and seeds has been demonstrated rigorously by fruit-provisioning experiments to be an important determinant of reproductive output and density within *P. semispinosus* populations (Adler 1998). Because of the frequent occurrence of spores in faeces during both seasons, we suggest that AMF probably serve a more important role than simply as an emergency resource when fruits and seeds are scarce. Fogel & Trappe (1978) note that fungi are rich in vitamins and steroids. AMF therefore may function as a supplement, supplying essential nutrients that fruits and seeds lack. Mycophagy by *P. semispinosus* probably occurs throughout the period in which sporocarps are available (Janos *et al*. 1995), but AMF may become especially critical when competition for primary resources is elevated. Studies elucidating the nutritional benefits of AMF to *P. semispinosus* are essential to understand fully rodent mycophagy.

P. semispinosus is often the most abundant terrestrial mammal species in its range. Because of the ubiquity of *P. semispinosus*, interactions of this species with seeds and AMF may have important implications for forest regeneration. Studies have shown that the growth response of the host plant as a result of the formation of arbuscular mycorrhizae is dependent on the species of fungus involved (Streitwolf-Engel *et al*. 1997, Van der Heijden *et al*. 1998). In the present study, we have found that *P. semispinosus* may disperse spores from several species of AMF, and a single faecal sample may include more than one species. Besides introducing AMF inocula (spores) to disturbed habitats, *P. semispinosus* therefore may play an equally important role in intact forests by moving and making available spores of different species of AMF to germinating seedlings. Furthermore, because *P. semispinosus* also scatterhoards seeds (Adler & Kestell 1998), AMF spores and tree seeds may be concentrated together in areas that *P. semispinosus* frequently occupies, thus increasing the chance of successful tree establishment.

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