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Seasonal dispersal of arbuscular mycorrhizal fungi by spiny rats in a neotropical forest

Abstract Many species of neotropical rodents consume and subsequently disperse viable spores of arbuscular mycorrhizal fungi (AMF). Consequently, rodents may be important determinants of both AMF and tree community composition in neotropical forests. We examined the influence of both availability of other food resources and season on the consumption and subsequent dispersal of AMF spores by *Proechimys semispinosus* (the Central American spiny rat) from seven island populations located in Gatun Lake, Panama over a 13-month period. For each island population, we examined the relationship between monthly spore occurrence in fecal pellets and monthly density of trees and lianas producing ripe fruit. During the last 3 months of this study, five islands were provisioned with extra food, while two islands remained unmanipulated to test experimentally whether spiny rats consumed AMF only as an alternative resource when primary resources (fruit) were scarce. Consumption of AMF was highly seasonal, with spores being most common in fecal samples at the end of the rainy season and least common at the end of the dry season. Cross-correlation analysis and logistic regression analysis indicated that spore occurrence in feces varied synchronously among islands and was related positively to soil moisture and unrelated to natural fruit availability. After inoculation with AMF spores isolated from feces, AMF colonized roots of *Paspalum notatum* (bahia grass) grown in sterilized soil, and total dry weights of host plants increased, confirming the viability of AMF spores passed by spiny rats. The ubiquity of viable spores from several species of AMF occurring in feces of *P. semispinosus* implicates this rodent as an important AMF disperser. Furthermore, dispersal of AMF spores by spiny rats was not limited to ephemeral periods of primary resource scarcity, thus suggesting that *P. semispinosus* may influence tree seedling survival by making spores of their mutualistic fungi available throughout the rainy season, a period critical to the establishment of newly germinated seedlings.

Keywords *Proechimys semispinosus* · Resource abundance · Seasonality · Spore dispersal · Tropics

Introduction

Identifying complex interactions important to the integrity of tropical forests has become a priority because of the ever-increasing rates of deforestation. Tropical forests harbor diverse faunas whose members are often integral participants in forest regeneration and maintenance. For example, the probability of tree seedling establishment and the subsequent distribution of adult trees are thought to depend largely on the inter-relationship between organisms that function as seed dispersers and those that serve as mortality agents (Janzen 1970; Connell 1971). Rodents are especially important in this regard because many species function as both seed dispersers (Smythe 1989; Forget and Milleron 1991; Adler and Kestell 1998) and as mortality agents via seed predation (Forget et al. 1994; Hoch and Adler 1997; Adler and Kestell 1998). Such opposing roles exhibited by tropical rodents have been demonstrated experimentally to influence seed and seedling survival (DeSteven and Putz 1984; Smythe 1989; Terborgh and Wright 1994; Asquith et al. 1997).

Not unlike rodent communities, fungal communities also are composed of members that have opposing influences that are critical to the establishment of tropical trees. Although trees benefit by having their seeds removed from fungal pathogens (Augspurger 1983, 1984; Augspurger and Kelly 1984; Gilbert et al. 1994), trees likewise benefit by having their seeds placed in the vicinity of fungal mutualists (Janos 1980; Siqueira et al.

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1998). The root systems of most Neotropical tree species form mutualistic relationships with arbuscular mycorrhizal fungi (AMF) from the order Glomales. AMF are critical to the establishment and survival of plant seedlings because fungal mycelia growing in association with host plants increase the absorbent area of the root system, allowing for increased uptake of scarce and immobile nutrients (Stanley et al. 1993; Sanders and Koide 1994; Merryweather and Fitter 1996). Plants that host AMF often exhibit increased growth and improved competitive abilities (Allen and Allen 1984; Moora and Zobel 1996), which subsequently may be important in structuring plant communities (Gange et al. 1993; van der Heijden et al. 1998a, b; Hartnett and Wilson 1999).

The dispersal of tree seeds to soils rich in AMF inocula should improve the probability of seedling establishment; however, if seeds are placed at micro-sites where suitable AMF species are scarce, the dispersal of inocula to such sites then is required. The ubiquity of AMF spores in the feces of several species of tropical rodents (Emmons 1982; Janos et al. 1995; Reddell et al. 1997; Mangan and Adler 1999, 2000) and the viability of spores after passage through rodent digestive systems (Trappe and Maser 1976; Rothwell and Holt 1978; Reddell et al. 1997) suggest that the influence of these animals on seedling establishment is not restricted exclusively to seed dispersal and predation. Rodents that consume AMF may be important in dispersing spores to micro-sites of low AMF inoculum potential (Janos 1992) or to seedlings colonized by AMF less suited to promote maximum growth (Heijden 1998a).

Despite the importance of AMF to the ecology of tropical forests, studies examining spore dispersal by neotropical rodents have been restricted simply to documenting the presence of spores in rodent feces, and no attempt has been made to examine rigorously the ecological factors that influence the consumption of AMF and subsequent dispersal. Of particular interest is whether AMF sporocarps are sought as a primary dietary resource or whether rodents consume AMF only as an alternative food source when primary resources are scarce. In the former case, spore dispersal may be linked more strongly to abiotic factors promoting sporocarp availability in the soil, whereas in the latter case spore dispersal will be limited largely to ephemeral periods of primary resource scarcity. Elucidating ecological determinants of the intensity and timing of AMF consumption is essential for determining the importance of spore dispersal in tropical forests.

Janos et al. (1995) examined AMF consumption by members of two rodent genera (*Proechimys* and *Oryzomys*) over a 1-year period in Peru. They suggested that AMF probably were consumed preferentially when fungal sporocarps were available in the soil and not only when primary food resources were scarce. In a study in Panama, Mangan and Adler (1999) compared AMF consumption by *Proechimys semispinosus* (Tomes) (Central American spiny rat) residing on eight small islands in the Panama Canal. They found a positive relationship between spore occurrence in feces and density of spiny rats. Spiny rats in high-density populations consumed AMF more frequently than spiny rats within low-density populations. This relationship was strongest during the month when fruit availability was generally the lowest. Mangan and Adler (1999) suggested that spiny rats may have consumed AMF more frequently when competition for primary resources was elevated on higher-density islands.

In both aforementioned studies, primary food resources available to rodents were not assessed directly, and therefore the importance of such resources in influencing AMF spore dispersal was not adequately addressed. Accordingly, we conducted a 13-month study that examined monthly diets of *P. semispinosus* from seven island populations for the presence and abundance of AMF spores. To determine the effectiveness of spiny rats as spore dispersers, a green-house experiment was conducted to test the viability of AMF spores found in feces of spiny rats. In addition, we recorded monthly fruit production by trees and lianas on each island to assess the availability of primary resources for spiny rats. We were interested specifically in whether seasonal fluctuations in fruit production and soil moisture influenced the dispersal of AMF spores by spiny rats. Finally, to examine experimentally the influence of alternative food resources on spore dispersal, food availability was manipulated on five islands during the last 3 months of this study, while the remaining two islands were not manipulated.

Materials and methods

Study sites

The study was conducted from January 1997 through January 1998 on small islands in Gatun Lake, central Panama. During construction of the Panama Canal, over 200 hilltops were isolated as islands upon damming of the Chagres River. These islands range from <1 ha to 1,500 ha and are covered mostly with tropical moist forest. *Proechimys semispinosus* is the only rodent that maintains persistent populations on islands <17 ha (Adler and Seamon 1991; Adler 1996). *P. semispinosus* is a primarily frugivorous and granivorous echimyid rodent (Adler 1995) and serves as an excellent subject to examine ecological influences on mycophagy because it is abundant throughout its range (Adler and Seamon 1991; Emmons and Feer 1997) and, along with other species within the genus, commonly includes AMF in its diet (Emmons 1982; Janos et al. 1995; Mangan and Adler 1999). Because we were interested in examining biotic and abiotic influences on AMF consumption by *P. semispinosus*, seven islands ranging in size from 1.7 to 3.7 ha (see Fig. 1 in Mangan and Adler 1999) were selected to minimize foraging competition with other species of rodents.

Precipitation at the study site is highly seasonal, with annual rainfall averaging approximately 2,600 mm year^{-1} on centrally located Barro Colorado Island (Windsor 1990). Over 90% of annual precipitation falls during an 8-month rainy season (May through December) and is followed by a pronounced dry season (Windsor 1990). Fruit production by most tree species on the islands is related to rainfall, with the majority of trees fruiting at the end of the dry season and through most of the rainy season (Adler 1998).

Rodent sampling and fecal pellet collection

On each of the study islands, rodents were censused monthly by live-trapping. The entire area of each island was sampled by placing Tomahawk live-traps (38.4×12.0×12.0 cm) on the ground in a permanent grid arrangement, with each trap spaced 20 m apart. Traps baited with cut ripe banana were set for four consecutive nights and checked each morning. Newly captured individuals were uniquely toe-clipped for permanent identification. Upon first capture each month, each *P. semispinosus* was sexed and weighed, and reproductive condition was determined. Each individual was assigned to one of three age classes (juvenile, subadult, or adult) based on pelage (Adler 1994). All individuals were released at their station of capture after data collection.

Spiny rat density for each island and month was estimated as the minimum number of individuals known to be alive ha^{-1}. For this purpose, monthly lists of all *P. semispinosus* individuals residing on each study island were compiled from data collected from January 1991 through January 1996, in July 1996, and from January 1997 through January 1999. Data collected before and after the current study period (January 1997–January 1998) allowed for more accurate estimates of densities because individuals may not have been captured for several consecutive months (Adler and Lambert 1997). Individuals known to be alive included those that were (1) captured during a given month, (2) previously marked and not captured during that month but subsequently captured afterwards, and (3) not previously marked but whose estimated birth dates (Adler 1996) fell during or before that month.

Fecal pellets were collected from the bottom of each trap and placed into vials containing 70% ethanol. To avoid problems associated with dietary bias due to trapping effects, fecal samples were collected only from individuals upon their first capture during a month.

Assessing fruit availability

The density of trees and lianas producing ripe fruits known to be eaten by spiny rats (Adler 1995) was used to estimate natural fruit availability on each island. For animals with small home ranges such as spiny rats, this measure is a more accurate index of fruit availability than other estimates based on fruit traps or transects, which may yield biased estimates of fruit availability (Chapman et al. 1994). We inferred that the density of fruiting trees and lianas was a reliable estimate of fruit availability because Adler and Lambert (1997) found that trappability of *P. semispinosus* within a population was correlated negatively with this index. Furthermore, mean density of spiny rats on an island was related positively to the yearly mean density of fruiting trees and lianas (Adler and Beatty 1997).

Monthly fruit censuses were conducted by walking the total area of each island and recording all trees and lianas producing ripe fruits. To facilitate these censuses, all trees ≥10 cm d.b.h. (diameter at breast height, 1.3 m above ground) on each island were previously identified, measured, and uniquely marked with a numbered metal tag (Adler 2000). To ensure full coverage of each island, observations were made by walking a zig-zag pattern between each 20-m wide strip of forest located between the lines of the trapping grid, and the presence of ripe fruits was recorded for each fruiting tree and liana.

We tallied the total number of individual trees and lianas that produced ripe fruits known to be eaten by *P. semispinosus* and estimated fruit density as the number of such trees and lianas per hectare (Adler 1998). Because fruit availability was dependent not only on the number of trees producing fruit but also on the number of potentially competing spiny rats, an index of per capita fruit availability for each island and month was computed by dividing fruit density by *P. semispinosus* density.

Microscopic examination of fecal pellets

Fungus consumption by *P. semispinosus* was assessed by examining fecal pellets for the presence and abundance of AMF spores. Three randomly selected fecal pellets from each individual rodent were sectioned into thirds, and a single section from each pellet was combined to form a composite sample. Composite samples (hereafter referred to as a single sample) were air-dried and weighed to the nearest 0.001 g and placed in a gridded petri dish containing distilled water. The sample was lightly crushed into a fine debris, and the contents were swirled to obtain a thin, even distribution. The entire petri dish then was scanned under 40× magnification. All AMF spores were counted and classified into morphotypes. Representative spores from each morphotype were mounted on slides and examined under higher magnification for identification to at least genus. Where species names could not be given to a genus, letters representing different morphospecies were assigned.

Spore viability

To determine viability of AMF spores consumed and subsequently passed by spiny rats, we compared AMF colonization and growth of host plants grown with and without spores. Because the addition of nutrients can retard root colonization by AMF and potentially confound our assessment of spore viability, we used isolated spores rather than whole fecal pellets as inocula. Although the experimental design did not address formation of mycorrhiza by spores in intact fecal pellets, such pellets are quickly dissolved by heavy wet-season rains (Mangan, personal observation), and spores are probably washed free from fecal material. Spores of three morphospecies (*Glomus* A, C, and D; see Results) were isolated from feces of three spiny rat individuals by wet sieving, and spores were thoroughly mixed. Ten seedlings of 2-week-old bahia grass (*Paspalum notatum* Flugge) grown in sterilized soil were transplanted into a D40 pot containing a 1:1 mixture of autoclaved (120°C for 1 h) field soil and sand. The fungal treatment consisted of approximately 500 spores of the three AMF morphospecies pipetted directly onto roots of the host, whereas the control treatment received no spores. Both treatments were replicated 10 times, and plants were allowed to grow for 16 weeks in a shade house at ambient temperature and exposed to 70% full sunlight. Upon final harvest, wet and dry weights (shoot, roots, and total) were determined. A subset of each root system was cleared in 5% KOH and stained with trypan blue (Phillips and Haymann 1970), and percent AMF colonization was estimated by the gridline-intercept method (Giovannetti and Mosse 1980). Roots were examined under 60× magnification, and the presence of arbuscules, vesicles, or intraradical hyphae was recorded for each gridline intersection with roots.

Experimental food provisioning

To examine experimentally the influence of fruit availability on spore dispersal, we compared fungus consumption by rodents residing on islands that were provisioned with extra food with those residing on islands receiving no provisioned food. As part of a long-term study on population limitation (Adler 1998), eight island populations of *P. semispinosus* were provisioned experimentally with additional food, while four islands were designated as controls and remained unprovisioned (see Adler 1998 for island selection criteria). However, we included five experimental and two control islands in the present study because of insufficient numbers of *P. semispinosus* on three experimental and two control islands during the 13 months of this study. An island population was excluded if we were unable to collect a minimum of five fecal samples during at least 9 of the 13 study months.

Experimental islands were supplied with extra food during November and December 1997 and January 1998, typically the period of lowest natural fruit availability on these islands (Adler 1998).

Ten provisioning stations per hectare were established uniformly on each experimental island, and a single wire mesh cage (40×33×33 cm, with a mesh size of 1 cm) was staked to the ground at each station. Each cage contained two opposing 6.5×7.6-cm openings to provide access to the food by *P. semispinosus* and to exclude larger mammals such as agoutis (*Dasyprocta punctata* Gray) that may have occurred periodically on the islands. Provisioning stations were distributed such that all spiny rats on an island had access to a predictable and reliable resource. Because of inadequate availability during the experimental period, natural fruits and seeds could not be used as the provisioned resource. Instead, cracked corn was placed at the rate of 5 kg month^{-1} into each cage. Thus, individuals residing on experimental islands had access to 50 kg ha^{-1} month^{-1} of the provisioned resource (in addition to any naturally occurring resources) as an alternative to AMF. This resource apparently was used by *P. semispinosus* because most of the corn was consumed each month. Although other organisms such as birds or invertebrates may have consumed some of the corn, the experimental provisioning resulted in an increase in densities of *P. semispinosus* (unpublished data).

Statistical analysis

The proportion of fecal samples that contained AMF spores (all species combined) for each island and month was tabulated. The proportion of fecal samples containing spores was then plotted over time separately with the index of per capita fruit availability and monthly soil moisture. Soil moisture data (0- to 10-cm soil depth) collected at 10 sites on Barro Colorado Island (BCI, centrally located in the study area) during the study period were obtained from the Smithsonian Tropical Research Institute (see Windsor 1990 for methods). Although soil moisture may vary locally, overall seasonal trends between BCI and the islands were similar because they experienced the same climatic patterns. Soil moisture of all sampling sites on BCI was expressed as percent wet weight, and monthly means of the 10 sampling sites on BCI were calculated.

We used time-series analysis to examine the relationships between seasonal fluctuations in spiny rat mycophagy and per capita fruit availability and mean monthly soil moisture. For each island, cross-correlation functions (PROC ARIMA, SAS 1996) were computed between the proportion of samples containing AMF spores and per capita fruit availability and between the proportion of samples containing spores and soil moisture. Only months with fecal samples from at least three individuals on an island were included in the analysis.

Multiple logistic regression analysis (PROC LOGISTIC, SAS 1996) was used to build the best predictive model of spore occurrence in fecal samples. Each spiny rat's fecal sample represented a single observation. We constructed a full model that included observations from all islands and months, with island area, spiny rat body mass, sex, soil moisture, and per capita fruit availability as explanatory variables and the presence or absence of spores as the dependent variable. Data from the experimental period (November 1997 through January 1998) were excluded from the model. Separate models also were constructed in which we grouped observations collected during the first dry season (January–April) and those collected during the wet season (May–October), again excluding data from the experimental period. For these models, only significant variables from the preceding model (other than soil moisture) were included.

Repeated-measures analysis of covariance (PROC GLM, SAS 1996) was used to compare log$_{10}$+1-transformed mean density of AMF spores (all species combined) per 0.05 g of fecal material between control and experimental treatments. Treatment group, period (pretreatment and treatment samples), and population nested within treatment group were included as main effects. Period×treatment and period×population nested within treatment group were included as interactions, with period as the repeated factor. We controlled for natural fruit production by including per capita fruit availability as the covariate.

We also constructed a linear model for repeated-measures count data (PROC CATMOD, SAS 1996) to compare the proportion of samples containing AMF spores between treatment groups. A saturated model including three main effects (treatment, period, and spiny rat population nested within treatment group) and two interaction terms (period × treatment and period × spiny rat population nested within treatment group) was constructed.

Results

Density of spiny rats and fruiting trees

P. semispinosus was the only species of rodent that was captured on the seven study islands during the 13-month period. We captured 643 individual spiny rats (321 males and 322 females) 3,351 times during 26,364 trap-nights. *P. semispinosus* densities on all islands increased throughout the 13-month study (Fig. 1). Lowest density (8.9 individuals ha^{-1}) was recorded on island 55 in January 1997 and highest density (50 individuals ha^{-1}) was recorded on island 8 in January 1998 (Fig. 1).

The density of trees producing ripe fruit exhibited both temporal variation across months on each island and spatial variation among islands during a given month (Fig. 1). The lowest density of fruiting trees (1.1 individuals ha^{-1}) was recorded on island 55 in November, and the highest density of fruiting trees (82.2 individuals ha^{-1}) was recorded on island 8 in June (Fig. 1). All islands had low densities of fruiting trees during the first
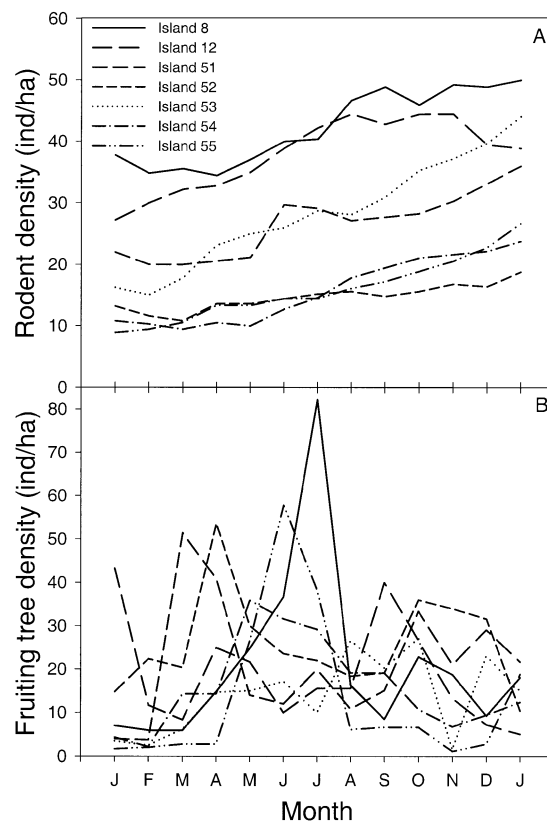

Fig. 1 Rodent density (**A**) and the density of fruiting trees (**B**) for each island and month of the study
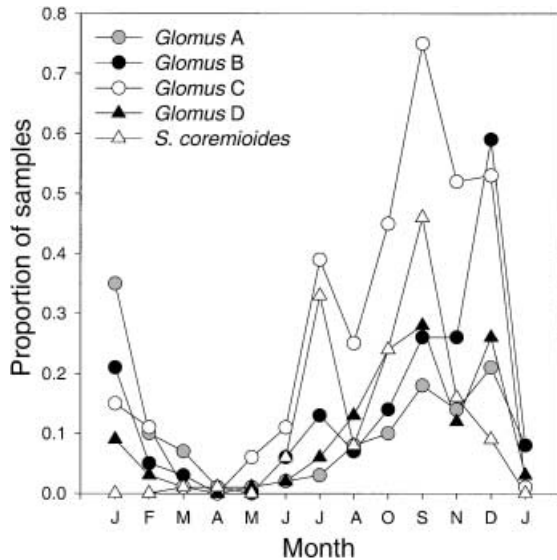
Fig. 2 Proportion of fecal samples containing spores of each AMF species or morphospecies (all islands combined) for each month. Numbers for each month indicate the total number of fecal samples examined

2 months of this study, with the exception of island 12. Elevated fruit production on island 12 during this period was due to the abundance of *Cryosophila warsciewiczii* (H. Wendl.) Bartl., a palm that exhibits high fruit production at the beginning of the dry season (Adler et al. 1998). For most islands, fruit production generally increased during April and peaked asynchronously throughout the rainy season (Fig. 1).

Fungal taxa

We collected fecal samples from 448 individual spiny rats, comprising 521 samples collected from 206 males and 651 samples collected from 242 females. Spores found in fecal samples were of two genera, *Glomus* and *Sclerocystis*. Spores from four morphospecies of *Glomus* (*Glomus* A, B, C, and D; as described in Mangan and Adler 1999) and spores and sporocarps of *Sclerocystis coremioides* Berk. and Broome were encountered commonly during most of the 13-mo study, particularly during the rainy season (Fig. 2, Table 1). The most frequently encountered morphospecies was *Glomus* C, which also had the highest mean spore abundance per sample (Fig. 2,

Table 1). Spores of *Glomus* C were encountered commonly in clusters, and spore morphology of *Glomus* C was very similar to the sporocarpic species *Glomus fasciculatum* (Thaxter) Gerd. and Trappe. *Glomus* A, *Glomus* B, and *Glomus* D also were most likely sporocarpic because of the large number of spores found in spiny rat feces (Table 1). Furthermore, spores of *Glomus* A and *Glomus* B were encountered frequently in clusters. Although spores of *Glomus* D rarely were encountered in clusters, spore morphology was very similar to the sporocarpic species *Glomus fulvum* (Berk. and Broome) Trappe and Gerd. Like *Glomus* D, *G. fulvum* is a thin-walled species with fragile attachment hyphae (Gerdemann and Trappe 1974), which probably break when passed through rodent digestive tracts. The sporocarpic species *Glomus rubiforme* (Gerd. and Trappe) Almeida and Schenck, was found in only 2 fecal samples, while the only non-sporocarpic species, *Glomus geosporum* (Nicol. and Gerd.) Walker, was found in only 18 fecal samples.

Spore viability

AMF spores isolated from feces of spiny rats successfully established mycorrhizae following inoculation of grass seedlings. Vesicles, arbuscules, and hyphae were all common in colonized roots. Mean-percent-fungal colonization of inoculated seedlings was 32.10 (n=10, SD=3.28), whereas uninoculated seedlings remained uncolonized. Moreover, seedlings colonized by AMF had over twice the total dry biomass as those seedlings grown in only sterile soil (sterile+AMF: n=10, 0=0.799 g, SD=0.069 g; sterile: n=10, 0=0.357 g, SD=0.068 g; t=14.436, df=18, P=0.0001).

Influence of per capita fruit availability and soil moisture on fungus consumption

When the proportion of samples containing spores (all AMF species combined) was plotted over time, a consistent seasonal pattern of fungus consumption among the study islands was evident (Fig. 3). Nineteen of the 21 pair-wise cross-correlation functions were significant, suggesting that patterns of mycophagy were highly synchronous among island populations (Table 2). Furthermore, cross-correlation functions between the proportion of samples containing spores and soil moisture were all

Table 1 Number of fecal samples (of the 1,172 total samples) containing spores of each AMF species common in feces, including each respective mean number of *Glomus* spores and spores and sporocarps of *Sclerocystis coremioides* per 0.05 g of fecal material

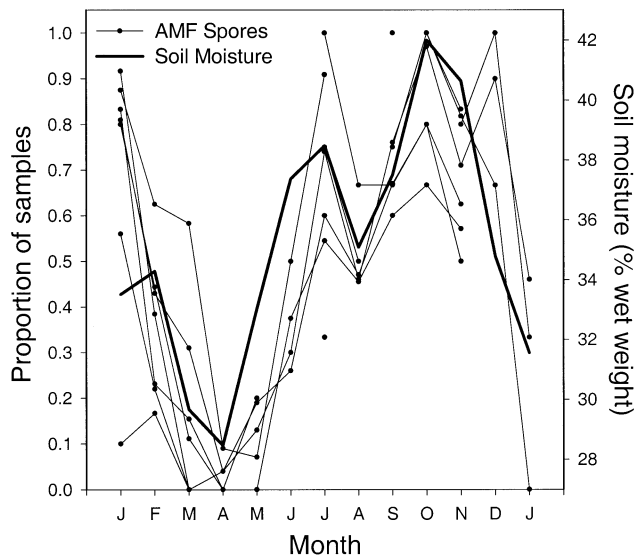| Morphospecies	No. of samples	Mean	SE	Range
Glomus A	103	193.6	50.8	6–4,495
Glomus B	134	373.3	63.3	7–4,144
Glomus C	251	798.5	119.6	6–14,221
Glomus D	94	610.1	99.6	10–6,625
S. coremioides (spores)	55	34.1	2.5	6–416
S. coremioides (sporocarps)	39	19.1	7.8	6–59

Fig. 3 Proportion of fecal samples in which spores were present (all AMF species combined) for each island and month along with mean monthly soil moisture (% wet weight) on Barro Colorado Island. Breaks in time-series lines for some populations result from exclusion of months containing fewer than 3 fecal samples
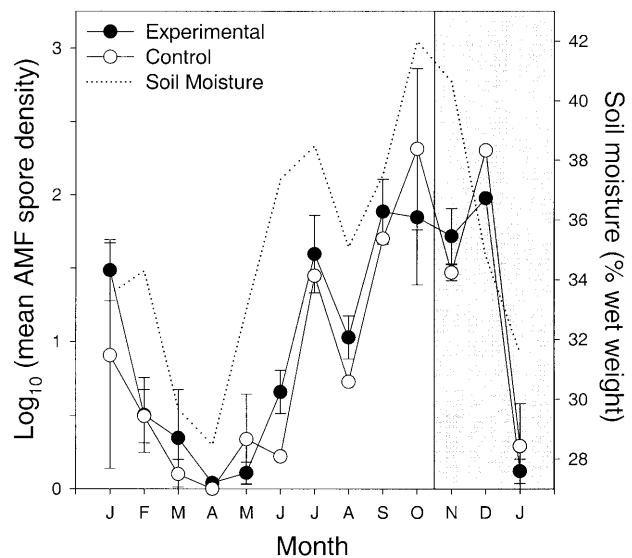
Fig. 4 Treatment group means of $\log_{10}$ density of AMF spores (all species combined) for each month. The shaded area indicates the experimental period. The seasonal trend in soil moisture (% wet weight) on Barro Colorado Island is also presented

Table 2 Cross-correlation functions of each pair-wise island combination for the density of fruiting trees (above the diagonal) and the proportion of samples containing AMF spores (below the diagonal). The *asterisks* indicate functions significant at the 95% tolerance limit (±0.6149; Diggle 1990)

Island	8	12	51	52	53	54	55
8		−0.1924	−0.1122	−0.0419	0.0179	0.5126	0.7297*
12	0.8046*		−0.1731	0.0664	−0.0396	−0.0815	−0.2203
51	0.7219*	0.6676*		0.5730	0.0894	0.1096	−0.2465
52	0.7089*	0.5325	0.8352*		0.1454	0.1651	−0.1365
53	0.8453*	0.6925*	0.5101	0.6324*		0.33358	0.1746
54	0.8646*	0.8433*	0.8870*	0.8913*	0.6307*		0.7412*
55	0.9412*	0.8116*	0.7770*	0.7173*	0.8721*	0.7972*	

significantly positive (>0.6149; Diggle 1990) for all islands, indicating a positive relationship between mycophagy and soil moisture (Fig. 3). Spores occurred frequently in fecal samples collected during January 1997 except on island 52. Proportions of spore occurrence then decreased and reached lows during the end of the dry season and subsequently increased with the onset of the rainy season (Fig. 3). The occurrence of AMF spores in fecal samples peaked in July and again in October, followed by a distinct decline in January 1998 (Fig. 4).

Despite a highly synchronous pattern of fungus consumption, per-capita fruit availability among islands was asynchronous over the course of the study, as only two of the 21 possible pair-wise island crosses produced significant cross-correlation functions (Table 2). With all independent variables in the logistic regression model, soil moisture and per capita fruit availability significantly predicted the probability of AMF spore occurrence. There was no relationship between spore occurrence and island area, sex, age, or body mass. Soil moisture was the best explanatory variable (β=0.335, χ^2=151.26, P=0.0001). Thus, fecal samples had a higher probability of containing AMF spores during months of high soil moisture. Furthermore, there was a negative relationship between spore occurrence and per capita fruit availability (β=−0.46, χ^2=11.85, P=0.0006). On islands and during months of high fruit availability, fecal samples had a lower probability of containing spores. However, when separate models were constructed based on rainfall, this relationship was restricted to months of the dry season (β=−1.33, χ^2=22.93, P=0.0001), while there was no relationship between spore occurrence and per capita fruit availability during the wet season (β=0.01, χ^2=0.04, P=0.9506).

Experimental period

Seasonal fluctuations of $\log_{10}$+1 mean AMF spore densities were similar between control and experimental islands during both pretreatment and treatment periods (Fig. 4). There was no treatment effect, thus suggesting that the addition of extra food did not affect the density of AMF spores in fecal samples (Table 3). Likewise, there was no treatment effect when the proportion of samples containing AMF spores was examined. Spiny-rat popula-

Table 3 Effects of experimental food provisioning on the mean density of AMF spores (ANCOVA) and on the proportion of fecal samples containing AMF spores (linear model)

Source	ANCOVA			Linear model		
	df	F	P	df	χ²	P
Treatment group	1	0.01	0.9156	1	0.20	0.6553
Period	1	0.70	0.6250	1	0.56	0.4548
Population (Treatment group)	5	0.26	0.6113	5	19.49	0.0016
Treatment group × Period	1	0.15	0.7036	1	0.58	0.4467
Period × Population (Treatment group)	5	0.12	0.9881	5	2.21	0.8189
Per capita fruit availability	1	0.10	0.7528	–	–	–

tion nested within treatment group was significant, indicating a high variation in proportions among populations within each treatment group (Table 3). Thus, there was high inter-island variation in the proportion of spiny rats that had spores in their diets, but increased availability of alternative food did not explain this variation.

Discussion

In this study, we show that *P. semispinosus* deposits large quantities of AMF spores in its feces and that spore deposition is highly seasonal and largely independent of primary resource (fruits and seeds) availability. Janos et al. (1995) also suggest that rodents in Peru pass spores independently of primary resources. Although Janos et al.'s (1995) data provide insight to the importance of primary resources to AMF consumption, their suggestion is based on the occurrence of spores in relatively few fecal samples correlated with their site's general pattern of fruit and seed availability, a pattern derived from data collected several years prior to their study (Janson and Emmons 1990). However, the amount of fruit available to neotropical rodents at a given site can vary widely among years, and fruit availability can be extremely patchy within a forest (Adler 1998; Wright et al. 1999). In light of the important consequences that primary food resources could have in determining the importance of AMF spore dispersal by rodents, we sought to verify experimentally the suggestions of both Janos et al. (1995) and Mangan and Adler (1999). In this study, we examine not only the influence of food resources on spore deposition by estimating the amount of fruit *directly* available to *multiple* rodent populations, but we are also the first to examine experimentally whether spore dispersal is influenced by primary resources through food provisioning. Results of this study indicate conclusively that dispersal of viable AMF spores by *P. semispinosus* occurs throughout much of the year and is not restricted simply to periods of primary resource scarcity.

Active versus incidental fungus consumption

AMF spores are ubiquitous in feces of spiny rats during much of the rainy season and the beginning of the dry season. However, the presence of spores in feces alone does not indicate that spiny rats actively consume fungi because spore occurrence in feces could be simply a result of incidental consumption. Our data provide indirect evidence that the presence of AMF spores in feces may be a result of active rather than incidental consumption. We found that only AMF species that produce their spores in clusters or sporocarps occurred in spiny-rat feces despite the ubiquity of several non-sporocarpic AMF species that produce their spores singly from hyphae in soils of our study sites (Mangan, Eom, and Herre, unpublished data). The presence of spores of sporocarpic AMF species and the absence or rarity of non-sporocarpic species in rodent feces and stomach contents have been reported previously and has been interpreted to indicate active consumption (Fogel and Trappe 1978; Maser et al. 1978; McGee and Baczocha 1994; Janos et al. 1995; Mangan and Adler 2000). Furthermore, mean densities of spores in feces are several hundred-fold higher than densities of spores in equivalent volume of soil from our study sites (3.2 spores per 0.05 g soil, unpublished data; Table 1). If spiny rats acquire spores incidentally while consuming other resources (e.g., fruits or seeds), such high densities of spore would not be expected.

While presence of large numbers of spores from only a subset of species found in the AMF soil community suggests that it is unlikely that spores are ingested incidentally while consuming other resources, it does not preclude the possibility of spiny rats consuming other organisms actively associated with AMF spores. For example, spiny rats could obtain spores by directly consuming roots with attached spores or by consuming mycophagous invertebrates that might concentrate AMF spores in their bodies. Although the consumption of these intermediate organisms could explain large numbers of spores in spiny-rat feces, it is unlikely that such consumption accounts for the presence of only a subset of species in feces unless spiny rats differentially digest AMF species with thinner spore walls.

Our data therefore suggest that spore dispersal by *P. semispinosus* is not a result of incidental consumption but instead occurs as a result of active consumption of AMF directly or possibly through the consumption of intermediate organisms. Furthermore, our data corroborate other reports that suggest that only a subset of AMF species has the ability to be dispersed by rodents. Because spore dispersal is most likely not a result of ran-

dom encounters with spores (i.e., incidental consumption), spore dispersal is predictable and under the control of biotic and abiotic factors that influence the consumption of such fungi.

Influence of soil moisture and fruit availability on fungus consumption

Neotropical forests support high numbers of tree species in which most members are patchily distributed (Hubbell 1979; Faber-Langendoen and Gentry 1991). Tree species composition differs markedly among the study islands. Of the 243 tree species represented by 13,336 marked individuals on the study islands, only seven species are located on all islands, and 101 species are confined to a single island (Adler 2000). Furthermore, timing of fruit production differs among tree species and also may be asynchronous within many species that occur on the study islands (Croat 1978; Adler 1998). Differences in the spatial distributions of tree species among islands and temporal variation in fruiting phenologies may explain the observed asynchrony in monthly fruit production (Adler 1994). Despite this asynchrony among islands, the presence of AMF spores in the feces of *P. semispinosus* is highly synchronous among island populations. This synchrony is contrary to what would be expected if *P. semispinosus* consumes AMF only when competition for primary resources is elevated. Instead, AMF consumption is correlated positively with soil moisture, suggesting that AMF spore availability also may be related positively to soil moisture.

In Peru, occurrence of *Glomus* spp. spores in rodent feces was correlated negatively with rainfall, indicating that sporulation by those species may have been more frequent during the dry season (Janos et al. 1995). If *P. semispinosus* indeed consumed AMF when sporocarps were present in soils of our study site, then sporulation of rodent-dispersed *Glomus* spp. was related positively to soil moisture, with spores occurring more commonly during the rainy season rather than the dry season as demonstrated by Janos et al. (1995).

Studies that examined seasonal AMF sporulation in forests did not show consistent patterns in spore production with respect to seasonal rainfall. For example, fluctuation in total spore number in a lowland tropical forest in Singapore was not related to rainfall (Louis and Lim 1987). However, total spore number in a tropical deciduous forest in Mexico was highest at the beginning of the rainy season (Allen et al. 1998), but spore number was highest at the beginning of the dry season in a forest in Argentina (Fontenla et al. 1998). Further, the relationship between precipitation and spore abundance within a site can vary among AMF species (Musoko et al. 1994; Picone 2000). Thus, the inconsistency in timing of spore dispersal of *Glomus* spp. by rodents in our study and those in Peru (Janos et al. 1995) may be explained partly by differences in species compositions of rodent-dispersed AMF of the two sites. Indeed, only one species of *Glomus* (*G. geosporum*) occurred in rodent feces at both sites.

In addition to directly affecting sporulation by AMF, soil moisture indirectly may influence the availability of sporocarps to rodents. Although some species of AMF such as *S. coremioides* may produce sporocarps on the soil surface, most species of AMF produce their spores in the soil (Gerdemann and Trappe 1974). Soils of the study area are mostly rich in clay (Dietrich et al. 1996) and become extremely hard during the dry season. Even though some species of AMF capable of being dispersed by rodents may sporulate in soils during the dry season, the availability of such species would decrease drastically as the dry season progresses because of energetic costs for *P. semispinosus* to excavate the hardened soil. Furthermore, increased moisture has been shown to influence olfactory cues and facilitate detection of seeds by rodents (van der Wall 1995). If spiny rats depend on olfactory cues to find AMF, then drying of the soil may hinder detection of such fungi. Therefore, access to some species of AMF may be determined in part by edaphic properties serving as physical or chemical barriers during the dry season. Concomitant sampling to determine AMF availability in the soil and spore occurrence in feces is required to gain more insight into the mechanism causing the observed patterns of seasonal spore dispersal by spiny rats at our study site.

Although we found a negative relationship between AMF spore occurrence in feces and fruit availability when compared among islands and months, this relationship was restricted to the dry season and was consistent with Mangan and Adler's (1999) finding of a positive relationship between spore occurrence in feces and spiny-rat density only during the dry season. If soil moisture is indeed indicative of sporocarp availability, spiny rats may consume AMF regardless of fruit abundance during the wet season because sporocarps are obtained easily. During the dry season, *P. semispinosus* may be forced to search more intensively for AMF sporocarps and only do so more frequently when fruits and seeds are scarce. The lack of a treatment effect during the experimental period may be explained partly by the relatively high soil moisture content and consequent availability of AMF spores during the first 2 months of the experiment. These results suggest that resource availability influences the dispersal of AMF spores only when primary resources are scarce and AMF are not readily available because of soil conditions. Hence, soil moisture is the primary determinant of AMF consumption and subsequent spore dispersal, while abundance of primary resources influences spore dispersal only when foraging for underground sporocarps becomes energetically costly. However, the overall importance of the interaction between primary resources and spore dispersal is minimal because of the low occurrence of spores in feces during the dry season.

Implications of spore dispersal for forest dynamics

The transition from the wet to dry season is critical in tropical communities because life processes of many organisms are timed with seasonal fluctuations in precipi-

tation (Leigh 1999). For example, flowering, seed germination, and leaf flush by many trees species are correlated with rainfall (Augspurger 1996; Garwood 1983; Wright and Cornejo 1990). Likewise, fluctuations in the presence of AMF spores in feces of *P. semispinosus* appear to be influenced primarily by seasonal change, with the time of greatest spore dispersal coinciding with the rainy season, a period critical for seedling establishment following seed germination (Garwood 1983).

Our experimental results, in concert with seasonal patterns of AMF consumption prior to food provisioning, indicate that *P. semispinosus* disperses large quantities of viable AMF spores independent of primary resources. Furthermore, only a subset of AMF species apparently has the capacity for long-distance dispersal, and such movement of spores across the landscape is not random but instead may be largely dependent on activity patterns of animal dispersers (Allen 1988; Emmons 1982). *P. semispinosus* is a forest-dwelling rodent that is ubiquitous in both primary and second-growth forests (Tomblin and Adler 1998; Adler 2000; Lambert and Adler 2000). Within these forests, spiny rats are associated with treefall gaps and forest edge (Lambert and Adler 2000; Endries 2000), which commonly are characterized by areas of dense vegetation that are used as nesting sites (Emmons 1982; Seamon and Adler 1999; Endries 2000). Increased rodent activity at these sites may result in the concentration of spores of AMF species passed by spiny rats (Emmons 1982).

In tree-fall gaps and forest edge at our study site, tree species that most commonly germinate and establish are small-seeded pioneers (Brokaw 1985; Dalling et al. 1998), some of which have been demonstrated to be highly dependent on AMF for survival and growth (Siqueira et al. 1998; Kiers et al. 2000). Soils of treefall gaps and forest edge most likely contain sufficient amounts of AMF inocula (e.g., fungal hyphae, roots colonized by AMF, and spores) for the colonization of newly emerging tree seedlings (Allen et al. 1998). Thus, the primary importance of rodent-mediated spore dispersal within intact forest is probably not the reintroduction of AMF inocula to inocula-poor sites. Instead, rodents may be important in altering AMF-species compositions in soils exposed to high rodent activity, with vegetation rooted in soils surrounding rodent nests having a higher probability of being colonized by rodent-dispersed AMF. Numerous studies have shown that growth response in plant hosts often is determined by the AMF species (or combination of AMF species) that colonize their root systems (Mosse 1972; Schenck and Smith 1982; Streitwolf-Engel et al. 1997; van der Heijden et al. 1998a; Bever et al. 2001). Such differential growth effects caused by different species of AMF suggest that the fungal community may be especially important in determining the structure of the host community (van der Heijden et al. 1998b; Bever et al. 2001). Thus, if rodents indeed play a role in dispersing AMF spores to areas of high rodent activity, the resulting shift in AMF community structure following forest

gap or edge formation may have a substantial impact on recruitment patterns of the regenerating tree-seedling community.

In conclusion, tropical rodents are increasingly being implicated as important determinants of tree community structure through both seed dispersal and seed and seedling predation (Forget and Milleron 1991; Forget et al. 1994; Adler and Kestell 1998). Likewise, small rodents such as *P. semispinosus* are common consumers of AMF and therefore deposit large quantities of viable spores in areas that they frequent. Consequently, species composition of the AMF community may be altered, thereby influencing seedling establishment and species composition of tropical forests.

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