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IMPACTS OF RESOURCE ABUNDANCE ON POPULATIONS OF A TROPICAL FOREST RODENT

GREGORY H. ADLER

Department of Biology, University of Wisconsin, Oshkosh, Wisconsin 54901 USA

Abstract. Populations of *Proechimys semispinosus* (Central American spiny rat) were provisioned with fresh native fruits for 6 mo to test the hypothesis that populations of frugivorous rodents in seasonal Neotropical forests are not limited by food during the season of greatest resource abundance. Islands in the Panama Canal were used as experimental systems so that results would not be confounded by individuals commuting from the fringes of the study areas. Populations isolated on four islands were censused by monthly live-trapping and served as unmanipulated controls, while populations isolated on four additional islands were provisioned with fruit at 315.2 kg/ha and censused by similar methods. Natural fruit abundance was concurrently censused by counting numbers of fruiting trees and lianas to account for naturally available resources. Means of overall spiny rat density and density of known births were compared between treatment groups using repeated-measures analysis of covariance, with the density of fruiting trees and lianas as the covariate. Both variables showed a treatment effect, with higher-than-expected densities and densities of births within experimental populations based on natural resource abundance. Numbers of known births per adult female were compared between treatment groups by constructing a log-linear model. This model also revealed a treatment effect, with per capita production of young being higher within all experimental populations. Monthly survival rates of young and adults were compared between treatment groups by constructing separate linear models for young and adults, and no treatment effect was evident. Adult male body mass was compared among islands by analysis of variance and similarly showed no treatment effect. Results showed that these spiny rat populations were limited by food even during the period of high resource abundance, and increased densities were due to increased production and recruitment of young rather than to increased immigration or survival.

Key words: *demography; Neotropics; Panama; Proechimys semispinosus; resource limitation; rodents; spiny rats.*

INTRODUCTION

Throughout much of the Neotropics, populations of frugivorous mammals appear to be influenced by seasonal shortages of fruit. In tropical forests with a pronounced dry season, overall fruit production is highly seasonal (e.g., Fleming 1979, Foster 1982), and during the season of lowest fruit production, measured fruitfall may be insufficient to support the biomass of terrestrial frugivores (Smythe et al. 1982, Terborgh 1986). Frugivore demography consequently reflects the impact of seasonal fruit production (Fleming 1992). Body mass often declines during the season of resource scarcity, and reproductive activity may be curtailed (e.g., Fleming 1971, Gliwicz 1984, Smythe 1986, Adler 1996). By contrast, fruit production during the season of resource abundance is often so great that much of the available fruit is unexploited by terrestrial frugivores and decomposes where it falls (Hladik and Hladik 1969). Many frugivorous mammals time their reproductive activity and produce young during the period when fruit is most abundant (Fleming 1971, 1992, Bon-

accorso 1979, Glanz et al. 1982, Milton 1982, Russell 1982, Gliwicz 1984, Mitchell 1989, Henry 1994). Because of uneven birth and survival rates within a single year, overall population density generally follows an annual cycle (Fleming 1971, Gliwicz 1984, Adler 1994). Density reaches a peak at the end of the season of resource abundance and declines during the season of resource scarcity when mortality exceeds fecundity.

Based upon these seasonal population trends, it may be hypothesized that populations of frugivorous mammals in seasonal Neotropical forests are limited by food during the season of resource scarcity but are not so limited during the season of greatest resource abundance. However, there is no experimental evidence to support this hypothesis for any Neotropical mammal. Rodents are excellent model organisms for testing such general hypotheses of food limitation because population-level patterns are well established for several Neotropical species such as agoutis (particularly *Dasyprocta punctata* [Smythe 1978, Henry 1994]) and spiny rats (particularly *Proechimys semispinosus* [Fleming 1971, Gliwicz 1984, Adler 1994], *P. cuvieri* [Henry 1994, Guillotin 1982], and *P. trinitatis* [Everard and Tikasingh 1973]) and because they are often abun-

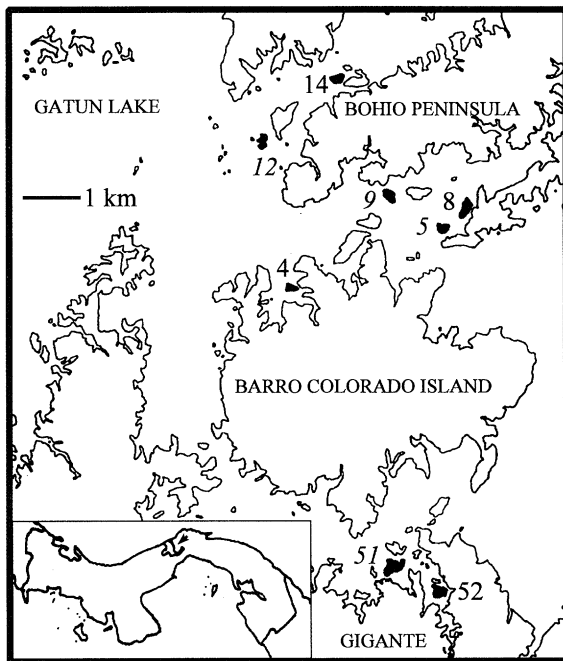


FIG. 1. Locations of the eight study islands (shaded) in Gatun Lake, central Panama. Numbers designating the experimental islands (5, 9, 12, and 51) are italicized. The inset shows the location of Gatun Lake in central Panama.

dant and easily sampled. Several species of frugivorous rodents that have been studied in detail show typical seasonality in population trends (e.g., Fleming 1971, Smythe 1978, Gliwicz 1984) and therefore may conform to this hypothesis of food limitation. Furthermore, rodents have often been used to experimentally test hypotheses of food limitation in temperate regions and therefore provide a basis for temperate-tropical comparisons (Boutin 1990).

In this report, I present results of a field experiment that was designed to test the hypothesis that Central American spiny rats (*Proechimys semispinosus*) are not limited by food during the season of greatest resource abundance. *P. semispinosus* are often the most abundant rodent in lowland forests within their geographic ranges (Fleming 1971, Adler 1995). These large echimyids exploit a wide variety of fruits and seeds (Adler 1995) and generally show annual fluctuations in abundance, reproductive activity, and recruitment that are coincident with annual fluctuations in fruiting phenology of seasonally dry areas (Fleming 1971, Gliwicz 1984, Adler 1994). This species is also more difficult to capture in live-traps when fruit is abundant (Fleming 1971, Gliwicz 1984, Adler and Lambert 1997). Populations of *P. semispinosus* isolated on small islands in the Panama Canal provide an experimental system for hypothesis testing. Using isolated populations as experimental systems eliminated immigration from the fringes of sampling areas, an effect that has frequently confounded results derived from temperate studies.

TABLE 1. Characteristics of each island and population included in this study of food limitation in a neotropical forest rodent, *Proechimys semispinosus*. Density estimates from 1991 represent values from May through October. Density data are means \pm 1 SE.

| Island | Area (ha) | 1991 density (inds./ha) | 1991 density of births (inds./ha) | 1991 density class |
|--------------------------------------|-----------|-------------------------|-----------------------------------|--------------------|
| Control islands and populations | | | | |
| 4 | 1.9 | 13.1 \pm 1.2 | 0.7 \pm 0.5 | Low |
| 8 | 2.7 | 27.9 \pm 2.9 | 4.7 \pm 0.5 | High |
| 14 | 2.4 | 15.8 \pm 0.9 | 1.4 \pm 0.7 | Low |
| 52 | 2.5 | 21.6 \pm 0.4 | 1.7 \pm 0.5 | Medium |
| Experimental islands and populations | | | | |
| 5 | 1.7 | 22.5 \pm 1.9 | 2.5 \pm 0.6 | Medium |
| 9 | 2.1 | 19.1 \pm 0.9 | 2.1 \pm 0.8 | Low |
| 12 | 1.8 | 46.2 \pm 4.2 | 1.1 \pm 0.5 | High |
| 51 | 3.5 | 23.9 \pm 0.9 | 1.1 \pm 0.5 | Medium |

Thus, much of the density increases observed in such studies results from individuals that simply commute into study areas (Boutin 1990).

MATERIALS AND METHODS

Study area

The study area consists of small forested islands in Gatun Lake, central Panama (Adler and Seamon 1991). These islands are former hilltops that were isolated when the Chagres River was impounded to form part of the Panama Canal. Over 200 such islands are covered now with tropical moist forest and range in size from tiny unnamed islets of <0.1 ha to Barro Colorado Island, which is >1500 ha. The climate of the study area is strongly seasonal, with an 8-mo rainy season and a severe dry season that generally lasts from mid-December through April. Annual rainfall on Barro Colorado Island (which is centrally located in the study area) averages 2612 \pm 446 mm (mean \pm 1 SD), of which 90% falls during the rainy season (Windsor 1990).

Community-wide fruiting phenology within forests of the study area is also strongly seasonal and is closely tied with seasonality in rainfall (Foster 1982). Greatest production of fruits exploitable by frugivorous mammals generally occurs during the late dry season and in the first several months of the rainy season (i.e., from April or May through September or October). In general, very little fruit is produced from November through February or March.

Sampling procedures

Proechimys semispinosus are widely distributed and are by far the most abundant terrestrial mammal on the forested islands (Adler and Seamon 1991). I selected for study eight small islands ranging in size from 1.7 to 3.5 ha (Fig. 1, Table 1) and in isolation from 30 to 152 m from other bodies of land known to contain populations of *P. semispinosus*. These islands were se-

lected for this study because they had dense populations of *P. semispinosus* that had been sampled monthly for >1 yr (from January 1991 through April 1992) immediately prior to the study period and were of a size to permit regular and intensive sampling of *P. semispinosus* (Adler 1994, 1996). In the present study, *P. semispinosus* were again sampled by monthly live-trapping. During the previous sampling, a grid of permanent trap stations covering the whole of each island was established, and these sampling grids were maintained throughout the present study. Sampling stations were located 20 m apart, and each station was occupied by a single Taiwan live-trap (a wire mesh trap of dimensions $26.5 \times 17 \times 13$ cm and manufactured in Taichung, Taiwan). Traps were baited with cut ripe banana and set on the ground (*P. semispinosus* are strictly terrestrial) for five consecutive days and four nights each month. Traps were checked on each subsequent morning, and all captured *P. semispinosus* were toe-clipped for permanent identification, sexed, weighed, and aged as juveniles, subadults, or adults based upon pelage characteristics (Adler 1994). Reproductive data consisted of testes position in males and vaginal patency, presence or absence of enlarged lactation tissue, and presence or absence of palpable embryos in females. Following data collection, all individuals were immediately released at their sampling station of capture.

Since fruit production may vary not only temporally but also spatially among tropical forest patches (Fleming 1992), natural fruit abundance was evaluated on each island. For this purpose, I censused fruit abundance each month by walking the whole of each island at the time I sampled its *P. semispinosus* population. I recorded the numbers and species of all trees and lianas that were producing ripe fruit known to be eaten by *P. semispinosus* (Adler 1995). These censuses were facilitated since all trees ≥ 10 cm dbh had been previously marked and identified (Adler, unpublished data). In measuring resource abundance, Chapman et al. (1994) recommended that, for animals with small home ranges, all trees within an animal's home range be censused for fruit production because other methods (e.g., fruit traps and transects) may be biased. I inferred that the density of fruiting trees and lianas provided a reliable index of natural resource abundance since capture efficiency of spiny rats was strongly correlated with this index (Adler and Lambert 1997). In particular, trappability within a population was negatively correlated with the density of fruiting trees and lianas. Lacher and Mares (1996) used a similar methodology, whereby mast-producing trees were censused to quantify resources available to *Tamias striatus* (eastern chipmunk).

Experimental design

I divided the eight island populations into two treatment groups, one of which served as unmanipulated

controls and the other as food-provisioned experimental (Table 1). Because islands were not of identical size and did not have *Proechimys semispinosus* populations of equal density (i.e., islands were not identical replicates), I did not randomly place populations into control and experimental treatment groups. Rather, I used information on island sizes and *P. semispinosus* densities prior to the experimental period (from January 1991 through April 1992) to achieve a distribution such that (1) control and experimental islands were geographically paired to avoid pseudoreplication associated with potential differences in climate (i.e., islands 5 and 8 were located to the east, 4 and 9 were centrally located, 12 and 14 lay to the northwest, and 51 and 52 lay to the south), (2) aggregate area within the two groups of islands was approximately the same (9.5 ha for control islands and 9.1 ha for experimental islands), and (3) both groups contained low-, medium-, and high-density populations (Table 1). Islands were placed into low (mean density of *P. semispinosus* <20 individuals/ha), medium (mean density 20–25 inds./ha), and high (mean density >25 inds./ha) density classes based upon mean densities derived from the monthly samples in 1991 that corresponded with the 1992 study period.

The experimental period of food provisioning extended from May through October 1992. During that period, I provisioned fresh fruit to each experimental population each week except during the week each month in which I sampled *P. semispinosus*. Thus, each treatment population was provisioned three times per month. For the provisioned resources, I collected native ripe fruit from nearby mainland areas. I used only fruits from trees that occurred on the islands and that were known to be heavily exploited by *P. semispinosus* (Adler 1995). Species of provisioned fruits included the palms *Astrocaryum standleyanum*, *Bactris major*, and *Scheelea zonensis*, and the fig *Ficus insipida*. All provisioned fruits except those of *F. insipida* were fairly durable, remained exploitable for at least 1 wk, and contained large seeds that could also be consumed. Identical quantities of fruit of a particular species were provisioned each week within each population.

I established regularly spaced permanent provisioning stations at 10 sampling stations/ha on each experimental island. To ensure that larger frugivorous mammals such as agoutis and pacas (if present) did not gain access to fruits, I placed fruits into rectangular wire mesh cages ($40 \times 33 \times 33$ cm, with a mesh size of 1 cm). Each cage had a 6.3×7.5 cm portal at the base on the two long sides to admit *Proechimys semispinosus*. Another 9×9 cm portal was located on the top of the cage, through which fruits were admitted, and cages were firmly staked into the ground. Thus, I provided *P. semispinosus* with exploitable, reliable, and predictable resources that were within the home range of virtually every individual (mean home range size of adult *P. semispinosus* on the islands is 0.19 ha for males

and 0.13 ha for females, Adler et al. 1997) and that were naturally available at the time of provisioning.

Data analysis

I first calculated monthly densities of fruiting trees and lianas on each island to serve as an index of resource abundance. I next compiled monthly lists of all individuals known to be alive on each island. I considered each island to be a closed system in which there was no immigration and in which all individuals present on an island were born on that island. While distributional patterns on small islands indicated that some immigration may occasionally occur (Adler and Seamon 1991), such events were apparently rare (Adler 1996). I have not recorded any such movements in >6 yr of monthly censuses on these and other islands in the study area, and Gliwicz (1984) also recorded no movements of *P. semispinosus* across 100 m of water in a year of intensive sampling. The monthly lists therefore included (1) all individuals that were captured during a monthly census, (2) all marked individuals that were captured both previous and subsequent to a monthly census, and (3) all individuals whose estimated birth dates fell before a particular monthly census. For these latter-most individuals, I estimated their months of birth based upon growth rates of individuals that were captured shortly after birth (mean mass at birth is 16.5 g [Gliwicz 1983]) and were frequently captured for at least a year (sensu Gliwicz 1984, Adler 1994, 1996). Density estimates were improved on all islands by monthly sampling that extended beyond the study period (i.e., until January 1996) since some individuals were not captured for several consecutive months (Adler and Lambert 1997).

Based upon these monthly lists, I compiled statistics on five population-level characteristics, including total monthly density, monthly density of known births, the total number of known births per adult female, survival, and adult male body mass. Monthly density was calculated as the total number of *P. semispinosus* known to be alive per hectare, and monthly density of known births was calculated as the number of known births per hectare. The total number of known births per adult female was a measure of reproductive effort and recruitment; in calculating this variable, females that were born during the year of the study and matured to adulthood were excluded from the compilation of adult females since they did not produce young (Adler and Beatty 1997). Survival was calculated separately for young and adults and males and females as the percentage of individuals in a given age and sex class that survived from month t to month $t+1$, and a weighted mean was calculated for each age and sex class. Adult male body mass was described as the maximum body mass reached by each adult male during the study period, excluding those males born during the year of the study; adult females were excluded since undetected pregnancies may have biased body mass estimates.

I searched for effects of the experimental manipulation by comparing population variables from the May–October monthly censuses of the experimental populations with those of the control populations during 1992. Population characteristics in the analysis included mean density of all individuals, mean density of all known births, number of known births per adult female, weighted mean monthly survival rates of age and sex classes, and mean maximum adult male body mass.

Mean densities were compared between control and experimental treatment groups using repeated-measures analysis of covariance (ANCOVA). The model included treatment group, population nested within treatment group, month, and the treatment \times month interaction, with the density of fruiting trees and lianas as the covariate. The ANCOVA model therefore compared densities of populations both within and between treatment groups while controlling for natural resource availability. Mean densities of births were compared between control and experimental treatment groups in an identical manner.

Numbers of known births per adult female were compared between treatment groups by constructing a log-linear model with treatment group and population nested within treatment group as terms in the model. Individuals were included in this analysis only once, and the log-linear model therefore tested the hypothesis of cell independence rather than cell homogeneity (Kleinbaum and Kupper 1978). Monthly survival rates summed over the study period were compared between treatment groups separately for young (juveniles and subadults) and adults. Terms in the models included treatment group, population nested within treatment group, sex, and the treatment group \times sex interaction. Since individuals could have been included in the analysis more than once, the linear model was appropriate for repeated measures (i.e., count rather than frequency data [Lindsey 1995]) and tested the hypothesis of cell homogeneity rather than cell independence (Kleinbaum and Kupper 1978).

Mean maximum body masses reached by adult males born before 1992 were compared between treatment groups using analysis of variance (ANOVA), with treatment group and population nested within treatment group as the terms in the model.

RESULTS

Natural and provisioned resources

I recorded 2199 monthly observations of 76 species of trees and lianas that produced fruits exploitable by *Proechimys semispinosus* during the May through October 1992 study period (Appendix). *Trichilia tuberculata* was the only species that produced fruit on all eight islands (Appendix). Several other species (notably the palms *Astrocaryum standleyanum*, *Oenocarpus mapora*, and *Scheelea zonensis*, and the trees *Gus-*

TABLE 2. Natural fruit production on the eight islands studied in this investigation of food limitation in the forest rodent *Proechimys semispinosus*. Data (means \pm 1 SE) are from the 6-mo study period (May through October 1992) and the succeeding 5 mo (November 1992 through March 1993, typically a period of low fruit production).

| Island | Mean density of fruiting trees (individuals/ha) | | Number of species fruiting | |
|-----------------------------|---|---------------------------|----------------------------|-----------------|
| | Study period | Succeeding 5 mo | Study period | Succeeding 5 mo |
| Control islands | | | | |
| 4 | 11.3 \pm 2.1 | 5.6 \pm 0.4 | 19 | 14 |
| 8 | 21.0 \pm 3.6 | 7.0 \pm 2.1 | 31 | 18 |
| 14 | 12.2 \pm 1.3 | 5.1 \pm 0.8 | 24 | 16 |
| 52 | 19.6 \pm 4.4 | 6.1 \pm 1.4 | 30 | 12 |
| All | 16.0 \pm 2.5 | 6.0 \pm 0.4 | 23.5 \pm 2.7 | 15.0 \pm 1.3 |
| Experimental islands | | | | |
| 5 | 15.6 \pm 3.3 | 3.4 \pm 2.0 | 14 | 9 |
| 9 | 19.6 \pm 4.5 | 3.7 \pm 0.8 | 23 | 18 |
| 12 | 19.7 \pm 3.6 | 11.6 \pm 3.5 | 22 | 15 |
| 51 | 15.9 \pm 2.1 | 19.7 \ddagger \pm 5.2 | 26 | 14 |
| All | 17.7 \pm 1.1 | 9.6 \ddagger \pm 3.9 | 21.3 \pm 2.6 | 14.0 \pm 1.9 |

\dagger Density = 1.7 \pm 0.2 individuals/ha excluding *Swartzia simplex*.

\ddagger Density for all experimental islands = 5.1 \pm 2.2 individuals/ha excluding *S. simplex*.

tavia superba, *Protium panamense*, and *Spondias mombin*) were widely distributed and produced large fruit crops during the study period. Mean densities of fruiting trees and lianas varied from 11.3 individuals/ha on island 4 to 21.0 individuals/ha on island 8 (Table 2). Fruit production varied over time and among islands (Fig. 2). Fruit production was generally greatest in May and least in July and August, but several islands (notably islands 12 and 14) did not conform to this trend. Fruit production during the study period (presumably a period of high fruit abundance) did indeed contrast sharply with fruit production during the succeeding 5

mo (presumably a period of fruit scarcity) (Table 2). All islands but one showed a dramatic decline in numbers of both individuals and species of trees and lianas that were fruiting subsequent to the study period. The lone exception (island 51) experienced an extraordinary mass fruiting event of *Swartzia simplex*, which I have not observed fruiting in such numbers on any islands in four subsequent years of fruit censuses. With *S. simplex* excluded, mean density of fruiting trees and lianas on island 51 was only 1.7 individuals/ha (Table 2).

During the 6-mo study period, I provisioned the four experimental populations with 2868.3 kg (315.2 kg/ha) of fresh fruit (Table 3). Monthly provisioning ranged from 23.3 kg/ha in October to 75.9 kg/ha in July. Fruits from *Scheelea zonenis* provided >88% of the provisioned resources since such fruits were abundant and easily collected throughout the study period. Virtually all provisioned fruits (and many seeds) were eaten by *Proechimys semispinosus* each week on islands 5 and 12, while smaller numbers were exploited on islands 9 and 51.

Density

I recorded 1203 captures of 704 individual *P. semispinosus* in 10 704 trapnights during the 6-mo study period. This rat was the only species of rodent captured on any island during the study period. Other rodents sighted during the study period were *Dasyprocta punctata* (Central American agouti) on islands 4, 5, 8, and 14, *Agouti paca* (paca) on island 9, and *Coendu rothschildi* (Rothschild's porcupine) on islands 5 and 12. These three species, although frugivorous to varying degrees (e.g., Eisenberg 1989, Emmons 1990), were excluded from the provisioned food by the wire cages.

Among control populations in 1992, mean density varied from 6.9 individuals/ha on island 4 to 47.2 in-

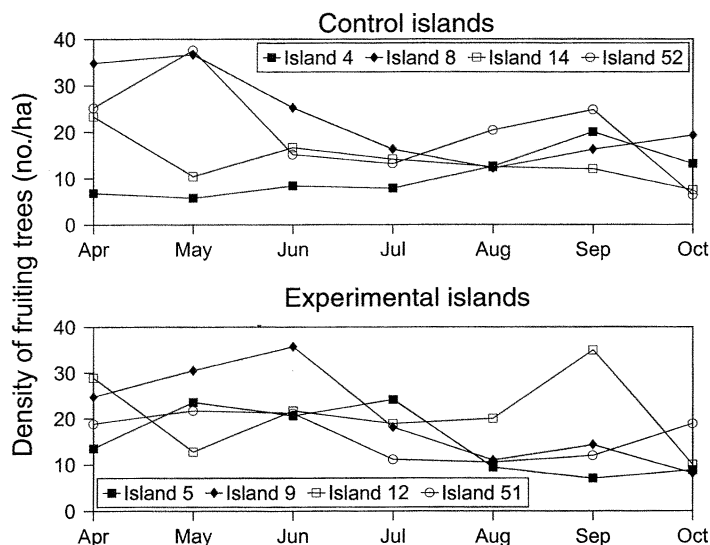


FIG. 2. Changes in densities of fruiting trees and lianas on control and experimental islands, with data from April (the month prior to the experimental period) also shown.

TABLE 3. Monthly and total amounts of fruit provisioned to four experimental populations of the forest rodent *Proechimys semispinosus* in a study of food limitation.

| Fruit species | Mass of fruit provisioned (kg/ha) | | | | | | Total |
|---------------------------------|-----------------------------------|------|------|------|------|------|-------|
| | May | Jun | Jul | Aug | Sep | Oct | |
| <i>Astrocaryum standleyanum</i> | 11.6 | 2.5 | 13.5 | ... | ... | ... | 27.6 |
| <i>Bactris major</i> | 3.4 | ... | ... | ... | ... | ... | 3.4 |
| <i>Scheelea zonensis</i> | 22.5 | 50.0 | 62.4 | 60.0 | 60.0 | 23.3 | 278.2 |
| <i>Ficus insipida</i> | ... | 6.0 | ... | ... | ... | ... | 6.0 |
| Total | 37.5 | 58.5 | 75.9 | 60.0 | 60.0 | 23.3 | 315.2 |

dividuals/ha on island 8 (Table 4). Among experimental populations, mean density varied from 22.5 individuals/ha on island 9 to 70.5 individuals/ha on island 12. The maximum density of 74.4 individuals/ha reached on island 12 was by far the highest density yet recorded for this species; the previously recorded high density was 58.3 individuals/ha on this same island in 1991, when no manipulations were conducted (Adler 1996). Densities were quite stable throughout the 6-mo study period and increased slightly on most islands. Populations on islands 8 and 12 maintained much higher densities than did the other populations. Visual inspection of density trends revealed no discernible effects of food provisioning. However, densities were lower during the 1992 study period relative to the comparable period in 1991 in three of the four control populations; only the population on island 8 had higher densities in 1992 (compare with Table 1). By contrast, all experimental populations had a higher mean density in 1992.

Mean densities in 1992 varied greatly among populations both within ($F_{6,29} = 573.12$, $P = 0.0001$) and between ($F_{1,29} = 474.97$, $P = 0.0001$) treatment groups based on the ANCOVA. Densities varied according to month ($F_{5,29} = 3.48$, $P = 0.0138$), but the treatment \times month interaction term was not statistically significant ($F_{5,29} = 0.14$, $P = 0.9827$). While experimental populations had slightly higher densities than control populations in April before the food provisioning began, the regression line for the experimental populations lay

above that of the control populations (Fig. 3). Thus, there was indeed an experimental increase in *Proechimys semispinosus* density relative to the amount of resources naturally available. Much of the difference between control and experimental populations was caused by the extremely high densities on island 12 relative to the amount of naturally available fruit. Populations on islands 5 and 51 had only slightly higher densities than expected based on the amount of naturally available fruit, while the population on island 9 had densities lower than expected.

Reproduction

The density of known births varied from a mean of <1 births/ha on island 4 to nearly 6 births/ha on island 12 (Table 4). Among control populations, this variable decreased on islands 4 and 14 and increased on islands 8 and 52 from 1991 to 1992 (compare with Table 1). All experimental populations showed an increase in density of known births from 1991 to 1992. ANCOVA revealed a difference in mean densities of births between treatment groups in 1992 ($F_{1,29} = 6.50$, $P = 0.0163$), but no other terms in the ANCOVA model were statistically significant. The regression line for the experimental populations lay above that of the control populations (Fig. 4), again illustrating a treatment effect. Relative positions of each island were similar to those of overall densities, but all experimental populations lay above the regression line for control populations. The known birth rate per adult female varied

TABLE 4. Densities of *Proechimys semispinosus* and of known births per adult female on the eight study islands during the 6-mo experimental period. Data are means \pm 1 SE.

| Island | Density (individuals/ha) | | | Density of births (no./ha) | Number of births per adult female |
|--------------------------|--------------------------|-----------------|-----------------|----------------------------|-----------------------------------|
| | Mean | Minimum | Maximum | | |
| Control populations | | | | | |
| 4 | 6.8 \pm 0.5 | 5.3 | 8.4 | 0.8 \pm 0.2 | 2.25 |
| 8 | 47.2 \pm 1.2 | 43.0 | 50.0 | 3.6 \pm 0.8 | 1.90 |
| 14 | 19.9 \pm 0.5 | 17.9 | 21.7 | 2.0 \pm 0.6 | 2.23 |
| 52 | 16.1 \pm 0.2 | 15.6 | 16.8 | 1.1 \pm 0.4 | 1.42 |
| All | 22.5 \pm 8.7 | 20.5 \pm 8.0 | 24.2 \pm 9.0 | 1.9 \pm 0.6 | 1.95 \pm 0.19 |
| Experimental populations | | | | | |
| 5 | 26.3 \pm 0.9 | 23.5 | 30.0 | 2.9 \pm 0.8 | 2.73 |
| 9 | 22.5 \pm 0.6 | 20.0 | 24.3 | 2.8 \pm 0.8 | 4.38 |
| 12 | 70.5 \pm 1.2 | 66.7 | 74.4 | 5.7 \pm 1.8 | 3.21 |
| 51 | 23.7 \pm 1.5 | 19.4 | 28.9 | 2.7 \pm 0.3 | 4.75 |
| All | 35.8 \pm 11.6 | 32.4 \pm 11.5 | 39.4 \pm 11.7 | 3.5 \pm 0.7 | 3.77 \pm 0.48 |

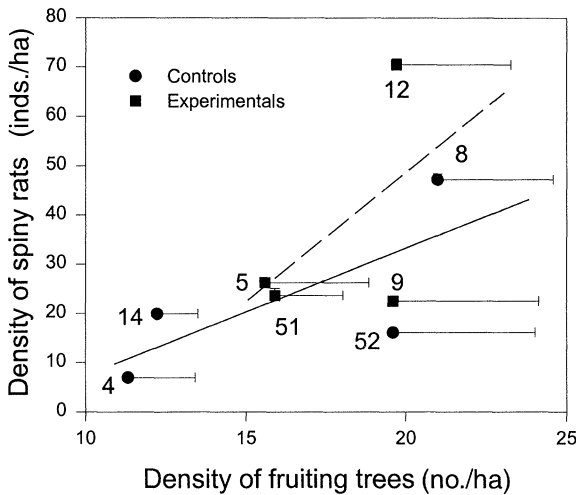


FIG. 3. Mean densities of spiny rats (+1 SE, mostly obscured by the symbols) as a function of mean densities of fruiting trees and lianas (+1 SE) on control and experimental islands in a food-provisioning experiment in Panama. Regression lines are plotted for control (—) and experimental (---) populations.

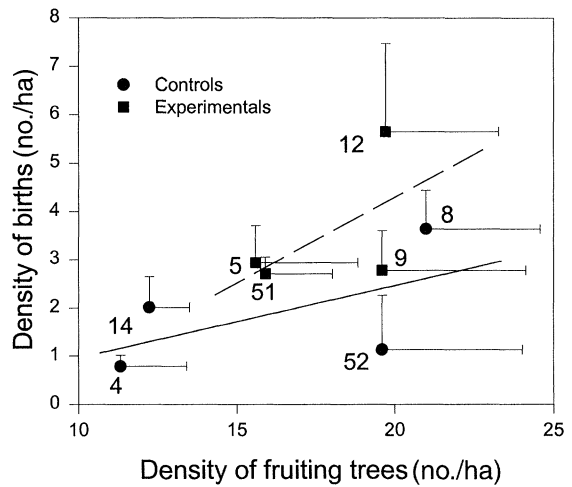


FIG. 4. Mean densities of known births (+1 SE) of *Proechimys semispinosus* as a function of mean densities of fruiting trees and lianas (+1 SE) on control and experimental islands in Gatun Lake, Panama. Regression lines are plotted for control (—) and experimental (---) populations.

from 1.42 births on island 52 to 4.75 births on island 51 (Table 4). All experimental populations had higher values than did the control populations for this index, and the log-linear analysis correspondingly revealed a treatment effect ($\chi^2 = 6.08$, $df = 1$, $P = 0.0137$). There were no differences among populations nested within treatment group ($\chi^2 = 2.74$, $df = 6$, $P = 0.8412$). Thus, reproduction was increased by the experimental food provisioning.

Survival

Summed monthly survival rates of young during the 6-mo study period varied from 85.7% (males on island 4) to 100.0% (females on island 4) (Table 5). Adult survival rates varied from 90.2% (females on islands 5 and 8 and males on island 9) to 100.0% (males on island 4) (Table 5). Linear analysis of survival rates of young showed no treatment effect ($\chi^2 = 0.15$, $df = 1$, $P = 0.7008$), but young females had higher survival rates than did males on all islands ($\chi^2 = 10.96$, $df = 1$, $P = 0.0001$). Adult survival rates did not vary according to treatment ($\chi^2 = 0.56$, $df = 1$, $P = 0.4527$) or sex ($\chi^2 = 1.76$, $df = 1$, $P = 0.1849$). Thus, food provisioning did not improve survival rates of any age or sex class.

Body mass

Mean maximum body mass reached by adult males varied from 440 g on island 12 to 522 g on island 14. Island 4 was excluded from this analysis due to an insufficient sample size of adult males. All islands contained males that reached immense proportions of >600 g. There were no differences between treatment groups ($F_{1,100} = 0.04$, $P = 0.8492$) or among popula-

tions nested within treatment group ($F_{5,100}$, $P = 0.1023$). Thus, food provisioning did not increase body masses of adult males relative to those in the control populations.

DISCUSSION

Numerous food-provisioning experiments have been conducted with temperate forest and grassland rodents in the genera *Apodemus*, *Clethrionomys*, *Microtus*, *Neozapus*, *Neotoma*, *Peromyscus*, *Sciurus*, *Sigmodon*,

TABLE 5. Weighted mean monthly survival rates (expressed as percentage of known individuals surviving) of young and adult *Proechimys semispinosus* on the eight study islands in Gatun Lake in central Panama.

| Island | Sex | Young | | Adult | |
|--------------------------|-----|------------|-----|------------|-----|
| | | % survival | n | % survival | n |
| Control populations | | | | | |
| 4 | ♂ | 85.7 | 14 | 100.0 | 6 |
| | ♀ | 100.0 | 22 | 96.8 | 31 |
| 8 | ♂ | 93.4 | 166 | 95.9 | 196 |
| | ♀ | 95.1 | 203 | 90.2 | 183 |
| 14 | ♂ | 93.1 | 58 | 98.3 | 60 |
| | ♀ | 98.6 | 49 | 97.3 | 75 |
| 52 | ♂ | 91.8 | 49 | 93.5 | 46 |
| | ♀ | 96.9 | 114 | 95.4 | 65 |
| Experimental populations | | | | | |
| 5 | ♂ | 93.9 | 49 | 90.0 | 100 |
| | ♀ | 95.8 | 48 | 90.2 | 51 |
| 9 | ♂ | 94.7 | 95 | 90.2 | 41 |
| | ♀ | 98.5 | 65 | 91.9 | 62 |
| 12 | ♂ | 86.8 | 219 | 97.5 | 120 |
| | ♀ | 94.6 | 202 | 96.6 | 208 |
| 51 | ♂ | 94.4 | 124 | 95.9 | 123 |
| | ♀ | 96.0 | 100 | 96.4 | 110 |

Note: n = total number of individuals summed over the entire 6-mo study period.

Spermophilus, *Tamias*, and *Tamiasciurus*. In a review of these studies, Boutin (1990) concluded that populations provisioned with extra food generally increased in density, individuals within such populations showed greater breeding activity and increased in body mass, young had higher survival rates, and immigration to food-provisioned areas dramatically increased relative to control areas and usually accounted for most of the density increase. In the present study, such immigration was largely eliminated by studying essentially closed populations (i.e., populations isolated on islands). Since between-island immigration appeared to be rare within the ecological time scale of this study, any effects of food provisioning would have resulted from processes other than immigration.

Results of this study showed that, while there was generally much variability in density among populations within treatment groups, there was also a strong treatment effect on density. The presence of other frugivorous rodents on the study islands had an unknown effect on *Proechimys semispinosus* via competitive interactions. While some of the variability among the study populations may have been due to the presence of such species, I suggest that the impact of these species on the experimental results of the study were minimal. These species were generally limited to one individual on an island, and island 52 did not contain any other species of rodent, yet the density of *P. semispinosus* was lower than expected on that island. By contrast, island 8 contained one adult agouti, yet the density of spiny rats was higher than expected. Furthermore, *P. semispinosus* had exclusive access to the 2868.3 kg of provisioned resources.

During the 6-mo study period, an average of 302 individual spiny rats were alive at any given time on all four experimental islands combined. Over the entire study, I provisioned extra resources at the rate of 9.50 kg/rat, or 1.58 kg per rat per month. The mean body mass of all individuals captured on the experimental islands during the study period was 295 g (including young and females), so each spiny rat was provisioned every month with an average of 5.4 times its body mass in exploitable resources that would otherwise not have been available. This level of provisioning was sufficient to increase densities above the level expected based on the amount of available resources. A repeated-measures analysis of variance of density estimates from both 1991 and 1992 (natural fruit abundance could not be included as a covariate since such data were unavailable from 1991) similarly showed a strong difference between treatment groups ($F_{1,76} = 60.73$, $P = 0.0001$). Thus, increasing resource abundance increased densities.

Since immigration in this study was apparently negligible and could be excluded as a substantial contributor to increased densities, the density response could have been due to either increased reproduction or survival. The mean density of known births was higher

within experimental populations, but this increased number of known births may simply have been due to the higher densities within experimental populations. Of greater interest was the per capita increase of known births within the experimental populations, which was nearly double that of the control populations. This per capita increase indicated that either female reproductive effort was increased or early juvenile survival was improved by the experimental provisioning. By contrast, survival rates of neither young nor adults were improved by the provisioning. While it is currently unknown if the index of reproductive effort (number of known births per adult female) was simply a measure of early juvenile survival, the lack of an effect on survival of known young suggests that the index reflected reproduction and subsequent recruitment rather than strictly juvenile survival. This claim is bolstered by the fact that I captured many juveniles shortly after birth and well before weaning; *Proechimys semispinosus* are born precocial at a mean body mass of 16.5 g (Gliwicz 1983), and I captured many individuals as small as 30 g during the study period and as small as 22 g before and after the study period. These smallest individuals were only a few days old at first capture.

Results therefore suggest that the food-provisioning density response was due to increased reproduction (and subsequent recruitment) rather than to increased survival and that these populations (except that on island 9) were indeed food-limited, even when resources were abundant. In fact, fruit production on Barro Colorado Island was greater in 1992 than in any year from 1984 through 1994 (S. J. Wright, unpublished data). While fruit production may at times be so great that much of the fruit remains unexploited, I suggest that this period of superabundant resources is generally very brief during any given year. This period of abundance may occur at different times on different islands or in different forest patches, depending upon local floral composition. However, this period may most often occur late in the dry season and early in the rainy season (i.e., April, May, and June) when spiny rat densities are typically lowest, allowing more resources on a per capita basis. The apparent reproductive response and resulting density increase were particularly pronounced on island 12, where mean density was over twice that predicted based on natural fruit production (predicted mean density = 31.7 individuals/ha).

The pronounced population-level response on island 12 relative to the other provisioned populations may have been related to the overall fruiting phenology on that island. While resources were abundant in May and June on the other experimental islands, overall fruit production declined dramatically from April to May on island 12 and remained low until September (Fig. 2). I therefore provisioned that spiny rat population partially during a season of relative resource scarcity. While data on natural fruit production were unavailable from 1991, a trend of earlier population increase and

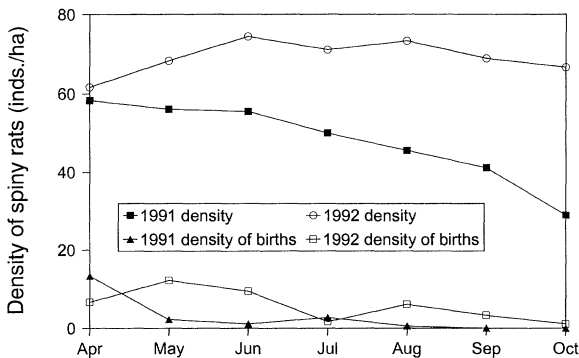


FIG. 5. Densities of spiny rats (*Proechimys semispinosus*) and known births on island 12, with data from April also shown. Note that (1) overall density in April was very similar in the two years but that (2) densities during the experimental period remained high throughout the experimental period, and (3) densities of known births were higher throughout most of the experimental period.

decline on island 12 relative to the other island populations in 1991 was apparent (Adler 1994). The population on island 12 maintained very high densities through the entire food-provisioning period in 1992 (Fig. 5) and did not substantially decline until after the experimental period. This population also sustained a higher level of reproductive activity through the study period relative to 1991 (Fig. 5); more young were known to have been born on island 12 later in the breeding season in 1992 than in 1991 (Fig. 5). By contrast, during 1991 the population reached a peak in April and declined steadily through the remainder of the year, with reproduction ceasing after August.

In the only previous experimental study of resource limitation in a tropical rodent, Duquette and Millar (1995) found no clear effect of experimental food provisioning on densities within three populations of *Peromyscus mexicanus* in Veracruz, Mexico, and immigration to provisioned populations did not increase. However, female reproductive activity and juvenile recruitment increased and age at first reproduction in females decreased within provisioned populations. Thus, food provisioning in *Peromyscus mexicanus* increased reproduction, but the modest increase in reproduction did not increase densities. Duquette and Millar (1995) attributed the lack of a density response to an earlier age of disappearance by reproductive females in provisioned populations relative to control populations. In *Proechimys semispinosus*, increased reproduction led to higher densities, presumably because survival was not affected and emigration was restrained.

The use of closed populations as experimental systems controls for immigration and emigration and illustrates the mechanism by which resources affect population-level processes of *Proechimys semispinosus* (i.e., via increased reproduction). However, restraining movements of individuals may in itself confound interpretations. In the open populations of *Peromyscus*

mexicanus studied by Duquette and Millar (1995), effects on reproduction were similar to my study but did not result in higher densities. Impacts of resource abundance on populations of *Proechimys semispinosus* in contiguous forest are currently unknown but may be similar to effects on *Peromyscus mexicanus*. Such populations may also be strongly limited by predators because of more diverse predator assemblages in larger forest tracts. However, since interspecific competition for resources in more intact mainland frugivore communities may also be more intense than in depauperate island systems, resource limitation may similarly occur. While tree diversity is also higher in larger forest tracts (e.g., Leigh et al. 1993), fruit production is nonetheless highly seasonal (e.g., Foster 1982). If mainland populations are provisioned with extra resources over a larger area or longer time frame, increased reproduction may eventually result in higher densities. Regardless of such effects, it is clear that at least some species of frugivorous rodents in Neotropical forests, particularly those rodents that are generally abundant, are often limited by food. Food limitation may occur not only when resources are extremely scarce and have obvious impacts on the vitality of individuals but also when resources are abundant and individuals and populations are increasing in size.

In conclusion, population limitation of Neotropical frugivorous mammals by seasonal changes in resource abundance explains at least in part the observed seasonal changes in behavior and demography (Leigh et al. 1982). However, intensive research on a wide variety of temperate herbivores and frugivores strongly suggests an important role for intrinsic density-dependent regulating mechanisms in addition to resource limitation (e.g., Ostfeld et al. 1993, Dennis and Taper 1994, Ostfeld and Canham 1995). If tropical organisms sometimes behave in a manner similar to their temperate counterparts, then intrinsic regulating mechanisms may also partly explain seasonal changes in behavior and demography of such populations. Indeed, Duquette and Millar (1995) suggested that increased immigration into their food-provisioned populations of *Peromyscus mexicanus* did not occur because population densities were already high, and social behavior may have prevented such immigration. Doonan and Slade (1995) provisioned populations of *Sigmodon hispidus* (hispid cotton rat) with extra food and similarly suggested that social interactions may have limited numbers of adults in the provisioned populations. Extensive studies on temperate rodents such as *Tamias striatus* suggest a complex interaction among resource abundance, population density, and social spacing (e.g., Mares et al. 1976, 1982, Getty 1981, Mares and Lacher 1987, Bowers et al. 1990). Future studies that concurrently examine resource limitation and density-dependent regulation in relation to natural resource abundance will undoubtedly offer rich insights into the dynamics of tropical populations.

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APPENDIX

List of all trees and lianas found fruiting on the eight study islands during the 6-mo study period.

| Family and species | Number of observations | Islands where fruiting |
|---------------------------------|------------------------|----------------------------|
| Palmae | | |
| <i>Astrocaryum standleyanum</i> | 111 | 8, 9, 12, 14, 51, 52 |
| <i>Bactris</i> sp. | 7 | 4, 8 |
| <i>Elaeis oleifera</i> | 115 | 8, 51, 52 |
| <i>Oenocarpus mapora</i> | 128 | 5, 8, 9, 14, 52 |
| <i>Scheelea zonensis</i> | 149 | 4, 8, 9, 12, 14, 51, 52 |
| Moraceae | | |
| <i>Cecropia peltata</i> | 1 | 14 |
| <i>Ficus bullenei</i> | 5 | 8, 12, 14 |
| <i>F. citrifolia</i> | 2 | 12, 51 |
| <i>F. obtusifolia</i> | 2 | 8, 9 |
| <i>F. popenoei</i> | 9 | 52 |
| <i>F. trigonata</i> | 6 | 5, 8, 12 |
| Olacaceae | | |
| <i>Heisteria concinna</i> | 1 | 14 |
| <i>H. longipes</i> | 3 | 14 |
| Polygonaceae | | |
| <i>Coccoloba manzanillensis</i> | 22 | 5, 8, 9, 12 |
| Nyctaginaceae | | |
| <i>Guapira standleyanum</i> | 13 | 9, 12, 51 |
| Annonaceae | | |
| <i>Annona glabra</i> | 9 | 8, 51, 52 |
| <i>A. spraguei</i> | 1 | 51 |
| <i>Unonopsis pittieri</i> | 1 | 14 |
| <i>Xylopia macrantha</i> | 1 | 14 |
| Myristicaceae | | |
| <i>Virola nobilis</i> | 4 | 14 |
| Lauraceae | | |
| <i>Nectandra purpurascens</i> | 18 | 4, 8, 9, 14, 52 |
| <i>Ocotea pyramidata</i> | 1 | 51 |
| <i>Phoebe cinnamomifolia</i> | 2 | 4, 51 |
| Chrysobalanaceae | | |
| <i>Hirtella americana</i> | 22 | 8, 9, 52 |
| Connaraceae | | |
| <i>Connarus panamensis</i> | 23 | 5, 8, 9, 51 |
| Leguminosae | | |
| <i>Inga fagifolia</i> | 74 | 9, 51, 52 |
| <i>I. quarternata</i> | 2 | 9 |
| <i>Pithecellobium rufescens</i> | 23 | 4, 8, 12 |
| <i>Prioria copaifera</i> | 77 | 9, 12, 14, 51 |
| <i>Ormosia coccinea</i> | 12 | 5, 9, 14 |
| Erythroxylaceae | | |
| <i>Erythroxylum panamense</i> | 1 | 4 |
| Simaroubaceae | | |
| <i>Quassia amara</i> | 4 | 4 |
| Burseraceae | | |
| <i>Bursera simaruba</i> | 1 | 9 |
| <i>Protium panamense</i> | 169 | 4, 5, 8, 14, 52 |
| <i>P. tenuifolium</i> | 11 | 4, 12, 14 |
| <i>Tetragastris panamensis</i> | 13 | 4, 14 |
| Meliaceae | | |
| <i>Guarea guidonia</i> | 1 | 52 |
| <i>Trichilia pleeana</i> | 3 | 4, 12, 14 |
| <i>T. tuberculata</i> | 153 | 4, 5, 8, 9, 12, 14, 51, 52 |
| Malpighiaceae | | |
| <i>Byrsonima crassifolia</i> | 34 | 5, 8, 12, 51, 52 |
| <i>B. spicata</i> | 1 | 8 |
| <i>Spachea membranacea</i> | 3 | 4 |

APPENDIX. Continued.

| Family and species | Number of observations | Islands where fruiting |
|----------------------------------|------------------------|-------------------------|
| Euphorbiaceae | | |
| <i>Alchornea latifolia</i> | 1 | 5 |
| Anacardiaceae | | |
| <i>Anacardium excelsum</i> | 4 | 9, 52 |
| <i>Astronium graveolens</i> | 2 | 9 |
| <i>Mangifera indica</i> | 8 | 51 |
| <i>Spondias mombin</i> | 168 | 4, 8, 9, 12, 14, 51, 52 |
| <i>S. radlkoferi</i> | 2 | 12, 51 |
| Sapindaceae | | |
| <i>Cupania latifolia</i> | 2 | 51 |
| <i>C. rufescens</i> | 7 | 8, 52 |
| <i>C. sylvatica</i> | 71 | 5, 8, 9, 12, 14, 51, 52 |
| <i>Talisia princeps</i> | 4 | 9, 12 |
| Tiliaceae | | |
| <i>Apeiba membranacea</i> | 1 | 8 |
| <i>A. tibourbou</i> | 7 | 8 |
| Bombacaceae | | |
| <i>Quararibea pterocalyx</i> | 1 | 4 |
| Guttiferae | | |
| <i>Calphyllum longifolium</i> | 15 | 14, 51 |
| <i>Vismia macrophylla</i> | 1 | 9 |
| Flacourtiaceae | | |
| <i>Casearia commersoniana</i> | 13 | 51 |
| <i>Lindackeria laurina</i> | 6 | 8 |
| <i>Tetrathylacium johansenii</i> | 1 | 51 |
| <i>Zuelania guidonia</i> | 5 | 4, 8, 12, 51 |
| Lecythidaceae | | |
| <i>Gustavia superba</i> | 194 | 4, 8, 9, 12, 14, 51, 52 |
| Rhizophoraceae | | |
| <i>Cassipourea elliptica</i> | 1 | 5 |
| Myrtaceae | | |
| <i>Eugenia coloradensis</i> | 3 | 4, 9 |
| <i>E. galalonensis</i> | 3 | 8 |
| <i>E. nesiotica</i> | 2 | 5 |
| <i>E. principium</i> | 7 | 4, 12 |
| <i>E. venezuelensis</i> | 3 | 5, 8 |
| <i>Myrcia gatunensis</i> | 350 | 5, 8 |
| <i>Psidium guajava</i> | 11 | 51, 52 |
| Araliaceae | | |
| <i>Didymopanax morototoni</i> | 1 | 52 |
| Sapotaceae | | |
| <i>Chrysophyllum cainito</i> | 1 | 12 |
| Apocynaceae | | |
| <i>Aspidosperma cruenta</i> | 1 | 14 |
| Boraginaceae | | |
| <i>Cordia bicolor</i> | 5 | 8 |
| Rubiaceae | | |
| <i>Faramea occidentalis</i> | 37 | 8, 51 |
| <i>Genipa americana</i> | 13 | 12, 14 |