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On the density-dependence of seed predation in *Dipteryx micrantha*, a bat-dispersed rain forest tree

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Abstract We studied the effect of seed density on seed predation by following the fate of bat-dispersed *Dipteryx micrantha* (Leguminosae) seeds deposited under bat feeding roosts. The study was conducted in Cocha Cashu biological station, Amazonian Peru, during the fruiting period of *Dipteryx*. Predation of *Dipteryx* seeds in the area is mainly by large to medium-sized rodents. Seed deposits beneath bat feeding roosts were monitored for a 13-week period in an 18-ha study area. A total of 210 seed deposits were found, and on average, seed predators encountered 22% of them during any one week. About one-third of the seed deposits escaped predation, and those deposits that had relatively few seeds were more likely to go unnoticed by rodents than were deposits with many seeds. The mean seed destruction rate was 8% per week; deposits with many seeds tended to lose a smaller proportion of their seeds to seed predators than did deposits with few seeds. Regression tests for the weekly data showed that, at the beginning of the observation period, seed predation was not density-dependent. Later, when the total seed crop beneath roosts was high, the number of seeds predated per deposit was positively density-dependent, while the proportion of seeds predated was negatively density-dependent, indicating predator satiation. Seed deposits that had been visited by seed predators once had a higher probability of being revisited the week after, especially if they contained many seeds when first encountered. This indicates that the foraging behavior of rodents may be affected by their remembering the location of seed-rich patches.

Keywords Seed predation · Density-dependence · Rodents · Bat feeding roosts · *Dipteryx*

Introduction

Seed predation is one of the important factors that affect recruitment of rain forest trees. The best-known model for spatial patterns in recruitment is the Janzen-Connell model. It proposes that most seeds fall close to the mother tree, where density-dependent mortality kills a high proportion of them. As distance to the mother tree increases, the density of seeds decreases and, hence, the probabilities of seed and seedling survival increase (Janzen 1970; Connell 1971).

In a review of studies that tested the Janzen-Connell model, Hammond and Brown (1998) suggested that one source of confusion for seed predation data (as opposed to herbivory/pathogen data) has been that different kinds of seed predators may give different results. They found that 15 of 19 studies on seed predation by insects supported the model, whereas only 2 of 27 studies on seed predation by vertebrates did so. Different results with different groups of seed predators may be a consequence of the spatial scales at which they perceive their environment, but studies focusing on vertebrate attack generally did not support the model at any scale. Seed predation may be either positively or negatively density-dependent, and the pattern can be expected to vary with the relative abundance of seeds and their predators. When food resources are scarce for a particular seed predator population, predation is likely to be positively density-dependent, but when the resources are abundant, seed predators become satiated and a negatively density-dependent response is expected to occur (Janzen 1970; Connell 1971; Augsburger and Kitajima 1992; Clark and Clark 1994; Hammond and Brown 1998; Manson et al. 1998). Lack of response may occur if factors other than the relative abundance of seeds determine the behavior of seed predators.

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The review of Hammond and Brown (1998) did not differentiate between studies on the basis of whether they tested the effect of distance, density, or both. With many tree species, seed density decreases with increasing distance from the mother tree, and hence it makes little difference whether the Janzen-Connell model is tested using distance to the mother tree or density of seeds as the explanatory factor for intensity of seed predation. However, with large-seeded trees dispersed by canopy bats, the seed shadow may be very different from this simple pattern. This is because canopy bats pick a fruit and take it away to a feeding roost, which is often underneath a palm leaf, between 3.5 m and 5 m above the ground (M. Romo, personal observation). Having eaten the fruit pulp, the bat lets the seed fall to the ground, and gradually seeds accumulate in a small area below the roost. This area will be referred to as a (seed) deposit in the present paper. As a result, a seed shadow is created where seed density is not necessarily related to the distribution of adult trees. High-density patches of seeds may occur at various distances from the mother tree, and seed density may be determined mainly by the availability and popularity of suitable roosting sites. *Dipteryx micrantha* Harms (Leguminosae, Papilionoideae) is an example of a bat-dispersed emergent tree whose seeds seem to be dispersed very efficiently: few seeds of this species have been observed directly under the adult trees around Cocha Cashu biological station, Peru (Cintra 1997a; M. Romo, personal observation). The fruit pulp of *Dipteryx* is consumed by frugivorous bats of the subfamily Stenoderminae, mainly *Artibeus* spp. (Romo 1996).

The large (3–4 cm long) seeds of *Dipteryx* are protected by a heavy endocarp, and they are mainly preyed upon by large to medium-sized rodents. Agoutis (*Dasyprocta*) and squirrels (*Sciurus*), and possibly acouchis (*Myoprocta*) and spiny rats (*Proechimys*) feed on *Dipteryx* seeds (Bonaccorso et al. 1980; Forget 1993; M. Romo, personal observation). However, spiny rats may mostly eat seeds whose endocarp is degraded or open and hence easier to penetrate (Adler 1995). Agoutis and squirrels may also be secondary dispersers. It has been estimated that the seed supply at Cocha Cashu exceeds the energy requirements of the main seed predators even at times of lowest seed availability (Janson and Emmons 1990). Bruchid beetles are not significant predators of *Dipteryx* seeds at Cocha Cashu (M. Romo, personal observation).

Experimental studies testing the Janzen-Connell model on *Dipteryx* species have produced mixed results. Studies on Barro Colorado Island (BCI), Panama, found no evidence of distance effects on the survival of experimentally placed *D. panamensis* seeds that were variously protected from predation (De Steven and Putz 1984; Terborgh and Wright 1994). In Cocha Cashu, the study of Terborgh and Wright (1994) found no evidence of distance-dependent seed mortality in *D. micrantha*, whereas the study of Cintra (1997a) did. Cintra (1997a) also tested experimentally whether seed predation was density-dependent, but found that it was not.

We studied spatial and temporal patterns in the predation of *Dipteryx micrantha* seeds at Cocha Cashu by taking advantage of the natural seed shadow created by canopy bats. We followed bat feeding roosts and the fates of the seeds deposited beneath them for a total of 13 weeks during the *Dipteryx* fruiting season (first week of July to the first week of October) in order to determine whether seed predation was density-dependent, and if so, at what spatial and temporal scales. If seed predation is density-independent, then the probability that seeds beneath a given bat roost are preyed upon should be independent of the number of seeds present in the seed deposit. On the other hand, if seed predation is density-dependent, then the probability of predation in deposits with many seeds should be either higher (in the case of positive density dependence) or lower (in the case of negative density dependence) than expected under the assumption of independence. A seed deposit may also suffer a higher than average probability of predation if it happens to be in the path of a seed predator, or if seed predators learn the locations of seed deposits and show a tendency to return to familiar deposits. Consequently, seed predation is a function of (1) the probability that a given seed deposit is discovered, and (2) once discovered, the probability that a given seed in that particular deposit is consumed. Any of these patterns may change from week to week, because the total availability, and hence mean density of seeds varies as the fruit production of *Dipteryx* first approaches its peak and then dwindles.

Materials and methods

Study site and field work

The study was conducted at Cocha Cashu Biological Station, which is located in Manu National Park in southeastern Peru (11°54'S, 71°18'W), at an elevation of about 400 m above sea level. The mean annual precipitation in the area is about 2,000 mm. Most of the rain falls during the 5-month rainy season (November–May), and the monthly rainfall during the dry season (June–November) is less than 100 mm. The mean annual temperature is 23–24°C, and Cocha Cashu is considered to be near the climatic limit between Tropical and Subtropical Moist Forest. For an extensive description of the site, see Gentry (1990). The study was conducted in old-growth floodplain forest, where *Dipteryx* trees occur at densities of 2–6 individuals per hectare (Cintra 1997a). Due to the relatively high density of *Dipteryx* trees, Cocha Cashu floodplain forest has been characterized as a *Dipteryx-Quararibea* forest (Janson and Emmons 1990).

Dipteryx trees fruit during the dry season, usually from June to September; the present study was carried out in July–October 1991. To find seed deposits beneath bat feeding roosts, a part of the trail system at the Cocha Cashu station was used. At least once a week, the trails and their surroundings were systematically searched during the day by walking in zigzag and checking the ground for piles of *Dipteryx* seeds and other bat-transported fruits. The searches extended 20 m to both sides of the trails, resulting in a 40-m-wide transect and a total sampled area of approximately 18 ha. Seed deposits under bat roosts were checked between 1 and 3 times each week, and new deposits were added as the fruiting of *Dipteryx* approached its peak. For a part of the seed deposits, monitoring ended before the end of the study period, usually because they were accidentally overlooked.

Bats use most feeding roosts for several nights, allowing seeds to accumulate on the ground below them. During each census, we recorded for each roost the number of intact seeds present, the number of seeds that had appeared since the last census, and the number of seeds predated since the last census. Each newly found seed was marked with nigrosin ink, and each seed that had been predated was re-marked in a different way, so that newly dispersed or predated seeds could be distinguished from seeds that had already been observed in the previous censuses. Seed predation was easy to recognize when the empty endocarp was found, as was usually the case. Only 73 seeds disappeared during the study period so that their fate could not be established, so if scatter-hoarding occurred, it was not very common. Seeds that had either germinated or experienced mortality from other causes than predation (i.e., were rotten or dried out) were counted separately and are not included in the present analyses.

Data analysis

An estimate of the total number of seeds available to seed predators beneath a given roost during a given week was calculated as the sum of the number of intact seeds remaining in the deposit at the end of the week and the number of seeds that had been predated since the previous week. We define an active roost as one that has at least one intact seed in the deposit beneath it during a particular week. Most roosts were active for only a part of the observation period; data for those weeks when a seed deposit was empty were not used in the numerical analyses. Therefore, the mean number of seeds present in a given seed deposit over the entire study period was obtained by counting the total number of seeds found in the deposit, and dividing by the number of weeks the corresponding roost was documented to be active. All newly dispersed or predated seeds found during a particular week were summed and counted as one dispersal or predation event. Seeds that disappear without direct evidence of seed predation were not considered as predated.

Regression analysis was used to test whether the amount of seed predation depends on the number of available seeds. Seed predation can be quantified as the number of seeds predated per roost, or as the proportion of seeds predated out of those present in the roost. Both approaches were taken in the present case, as they test different aspects of density dependence. The regressions were computed for each week separately to test whether the situation changed as the fruiting season of *Dipteryx* advanced. Because most seed deposits escaped predation during any given week, the regression tests were run separately for (1) all active deposits and (2) those deposits that had actually experienced seed predation. Because number of seeds has a Poisson distribution, seed counts were square root transformed before analysis.

The behavior of seed predators may depend on variation in seed density at a spatial scale larger than a single seed deposit. Therefore, the seed deposits and the Cocha Cashu trail system were mapped using GIS software (ESRI, ArcInfo, ArcView), and zones of 5 m and 10 m were established around each seed deposit. The deposits were assumed to be 1 m in diameter, so this “buffering” created circular areas of 11 m and 21 m in diameter around each seed deposit. The number of seeds inside each circular area was computed, and the regression tests described above were repeated for the 11-m scale and the 21-m scale. Broader scales were not analyzed, because the transect was only 40 m wide, and larger circles would often have extended beyond this area. Analysis of the 21-m scale was still considered appropriate, because most seed deposits were found close to the trails: only 15 seed deposits out of 210 (7.1%) were located farther than 15 m from the trails. During week 7, which had the highest number of active roosts, the mean distance between a seed deposit and its nearest neighbor was 16.4 m, which means that in many cases the 10-m-wide “buffer zone” around a roost did not contain a second roost. The observed distribution pattern of bat roosts probably reflects their true distribution rather well, because bats have often been observed to concentrate their flying routes into the relatively open canopy space

above trails (e.g., Palmeirim and Etheridge 1985). Seed deposits are usually easy to spot in the forest, but sampling bias may nevertheless have accentuated the concentration of observed deposits close to the trails.

A number of other hypotheses on patterns in seed predation at the single-roost scale were tested using different test statistics. The statistical significance of each test statistic was determined with a Monte Carlo permutation test using 999 permutations. All test statistics were chosen so that high values indicated deviation from the random expectation; i.e. each random value that is at least as high as the observed value provides support for the null hypothesis. In the analyses that involved all observation weeks, data from all weeks were pooled to compute the observed value of the test statistic, but the permutations were restricted in such a way that observations made in different weeks were not mixed when computing the permuted values. This gives more conservative significance values than an unrestricted permutation (see Legendre and Legendre 1998). The permutation tests were run using the Resampling Stats 4.1 software.

We first tested whether the probability of any predation in a seed deposit depends on the number of seeds present. The null hypothesis is that a high number of seeds in the deposit does not increase the probability that seed predation occurs; the alternative hypothesis is that deposits with many seeds experience a higher probability of seed predation than deposits with few seeds. For the analyses, we divided the seed deposits into two categories: high-density and low-density, i.e. those with more versus fewer seeds than the median in a given week. We then tested whether the proportion of the high-density deposits that were preyed upon was higher than expected by chance, given the overall proportion of seed deposits where predation had been observed. These tests were done both for the entire study period to test for the overall trend, and for each week separately, to test whether result changed as the fruiting season of *Dipteryx* advanced. The test statistic was the number of high-density seed deposits that had been subject to predation.

We further tested whether the occurrence of seed predation was locality-dependent. If seed predation at any one deposit is independent between consecutive weeks, this indicates that the seed predators move randomly in the forest and do not learn the location of seed deposits. If, on the other hand, the probability that a deposit is predated during one week increases its risk of also being predated the next week (the alternative hypothesis), this indicates that either some deposits are more prone to be attacked because they are situated along seed predator trails, or that the seed predators learn and return to the deposits they have already visited. As the analyses compared the occurrence of seed predation in consecutive weeks, only those deposits that had seeds in both weeks were included. The test statistic was the number of seed deposits preyed upon during 2 consecutive weeks.

In an attempt to separate the effects of seed deposit location versus learning by seed predators, we combined the two approaches described above and tested whether higher-than-median seed density in a deposit during one week increased the probability that seeds in the deposit were preyed upon both during that week and the next week. If so, it would indicate that seed predators learn the locations of deposits, and return preferentially to those with many seeds. The test statistic was the number of high-density deposits that had newly predated seeds in both the week when the seeds were counted and the next week. In the permutation test, the observed occurrences of seed predation in consecutive weeks were kept fixed, while the seed numbers observed in the first week were permuted.

Results

A total of 210 seed deposits that contained *Dipteryx* seeds were found and mapped during the 13 weeks of the study (Fig. 1). The number of seed-containing deposits varied from week to week as the fruiting season of *Dipteryx* advanced. In the beginning of July, only 15 seed deposits

were found, whereas 200 were found at the peak of the season in the third week of August (Fig. 2a). Only two new seed deposits were found after the beginning of September. Most deposits only contained seeds for a part of the observation period. During the last census week, about 90 seed deposits were documented to be active. About one-third of the other seed deposits had been emptied by seed predators, while for the remainder, the final fate of their seeds is not known. The total seed crop present in the seed deposits showed a similar trend to the number of roosts: about 100 seeds were found in the first weeks and almost 1,500 seeds at the seasonal peak (Fig. 2b). However, the mean number of seeds present beneath the active roosts remained relatively constant during the study period, varying between 6.7 and 9.5 with no obvious temporal trend.

On average, seed predators ate 60 seeds per week in the deposits (range 4–212), which corresponds to a weekly seed destruction rate of about 8% (range 1–20%). Over the study period, a small proportion of the seeds (73 seeds or 3.9%) disappeared entirely from the seed deposits, so their fates are unknown. Squirrels are secondary dispersers and most probably took some of the seeds to consume them in a safer place. There was no clear temporal trend in the amount of predation. Insects were not found to attack the seeds of *Dipteryx*, but fungi were observed on seeds that remained in wet ground for a long time. By the end of

September, some seeds in the seed deposits were already dead (desiccated or rotting), and a few had germinated, after which they were no longer included in the inventories (see Fig. 2c)

The percentage of seed deposits experiencing seed predation during any one week ranged from 7% to 47%; the mean percentage over the entire observation period was 22%. Of the 210 observed seed deposits, 32% experienced no seed predation during the study period and 31% were visited by seed predators during 1 week, 18% in 2 weeks, 10% in 3 weeks, and 9% 4 or more weeks. The mean number of seeds present in the seed deposits (over all active periods) was 2.4 in deposits that were never visited by seed predators and 9.5 in the ones visited; the difference is statistically significant (Mann Whitney $U=7913$, $P<0.00001$; Fig. 3).

For deposits with high seed density (i.e., more seeds than the median in the week in question), the incidence of seed predation increased from a mean of 22% of the deposits per week to 31%; the difference is statistically significant (permutation test, $P<0.001$). When data were analyzed separately by week, high-density seed deposits usually experienced a rate of seed predation as high as or higher than low-density deposits. However, the difference was statistically significant ($P<0.05$) only in the later part of the observation period, from the third week of August onwards.

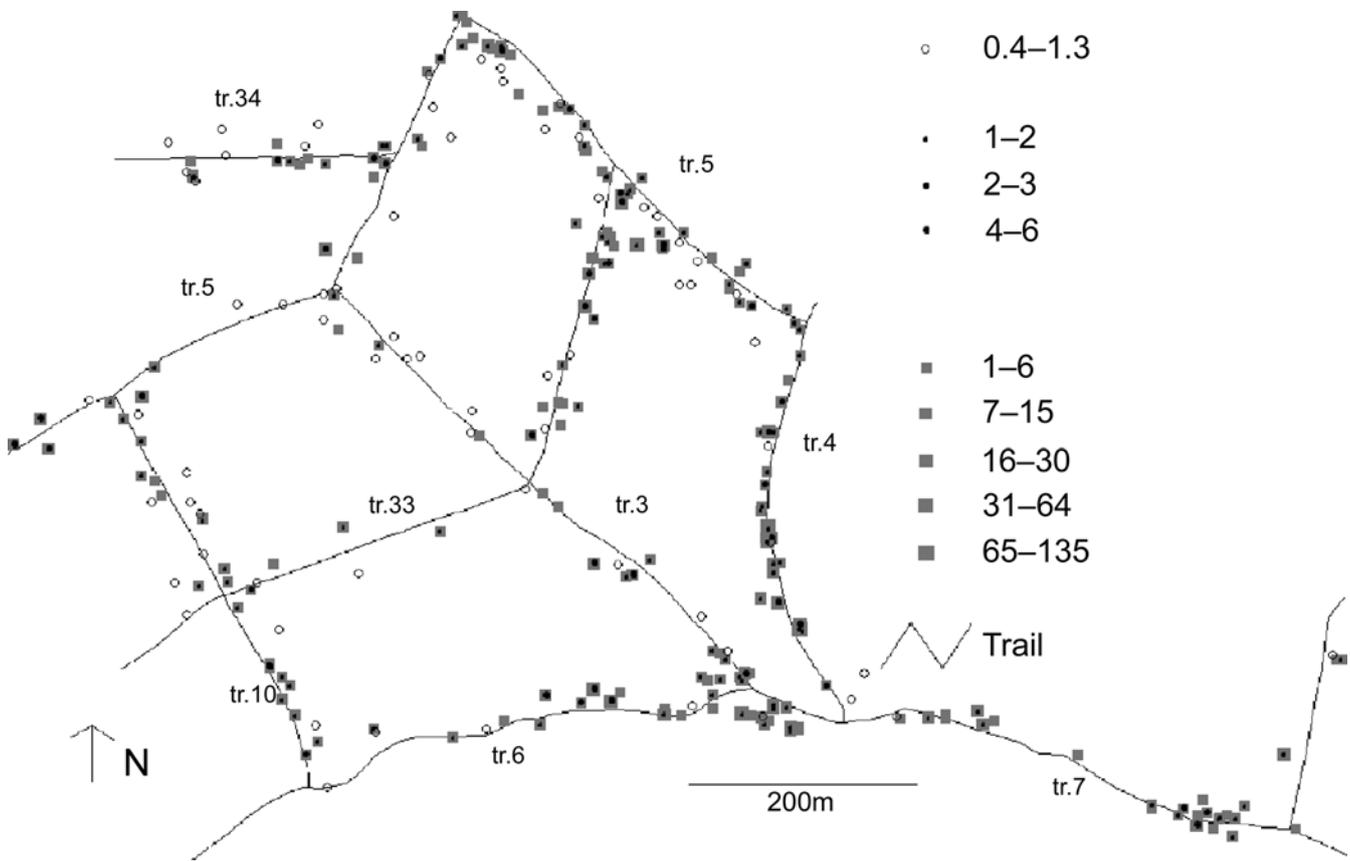
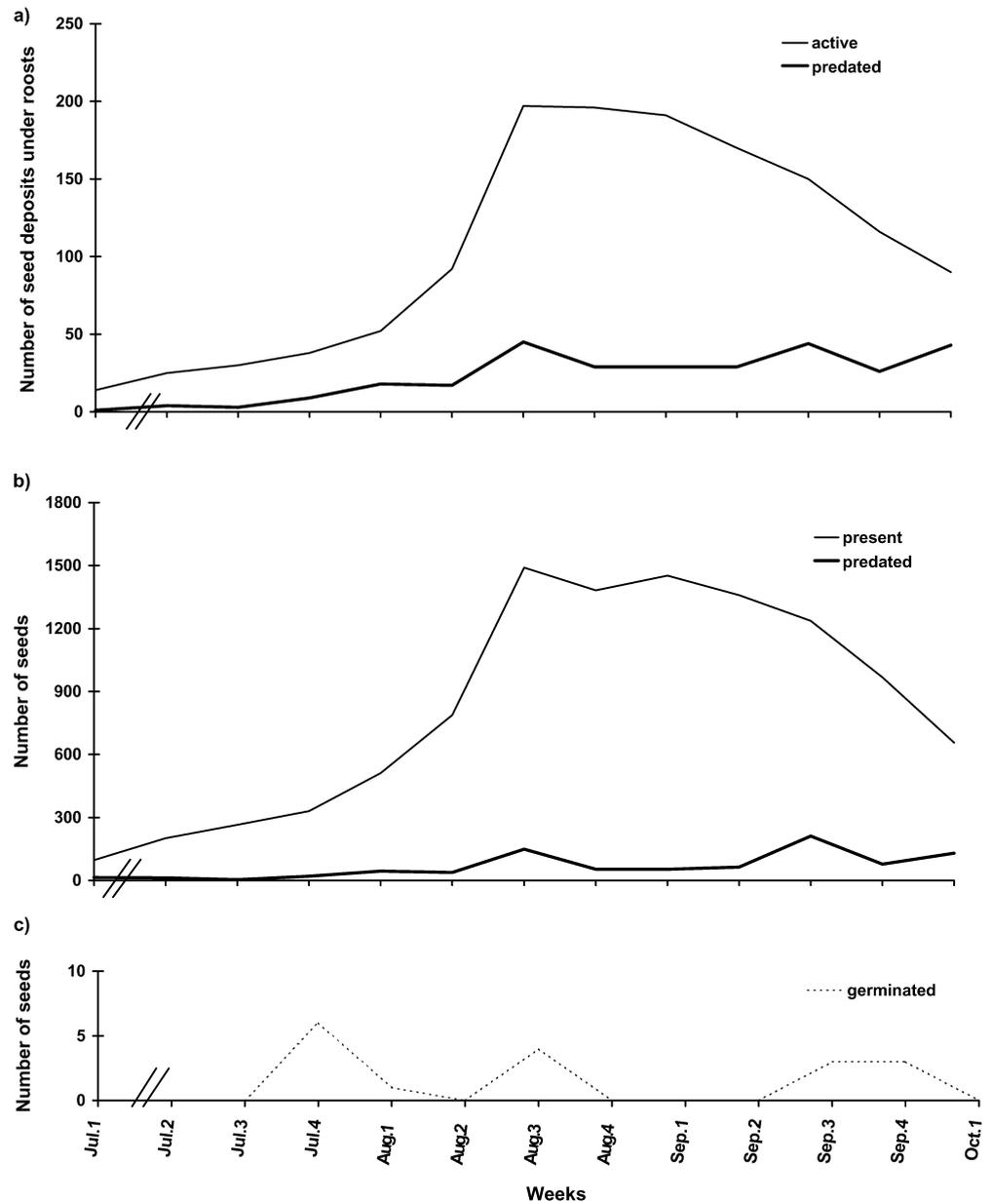


Fig. 1 Map of the study site showing trails, *Dipteryx* trees and deposits of *Dipteryx* seeds beneath bat feeding roosts. Circles indicate *Dipteryx* trees, black dots indicate in how many weeks a

predation event was observed in that particular seed deposit and gray squares indicate the mean number of seeds present in each seed deposit

Fig. 2 Temporal changes during the study period in **a** the number of seed deposits that were active and where a seed predation event occurred, **b** the number of seeds present and predated, **c** the number of seeds that germinated



When only those seed deposits where seed predation had occurred were included in the regression analyses, both the number and the proportion of seeds consumed by seed predators were found to be density-dependent in most weeks (Table 1). When there was significant density-dependence, this was invariably positive for the number of seeds predated and negative for the proportion of seeds predated. The temporal pattern in density-dependence of the number of seeds predated was irregular, whereas the proportion of seeds predated was not density-dependent in the beginning, but became so from the second week of August onward. The patterns at the three spatial scales (single-roost, 11-m and 21-m scales) were highly similar, although the explanatory power of available seed density was generally highest at the single-roost scale. When all active seed deposits were included in the regression analyses, the patterns changed: the number of seeds

predated became systematically density-dependent in the latter part of the study period, whereas the density-dependence of the proportion of seeds predated practically vanished.

The frequency of seeds in roosts when a predation event occurred and the overall pattern of seed predation for the entire study period is shown in Fig. 4. The number of seeds predated in a deposit increased with the number of seeds present ($r^2 = 0.19$, $P < 0.0000$) up to around 30 seeds/roosts when a decrease in the proportion of seeds taken is seen.

Temporal trends in seed predation were also analyzed using paired data where the incidence of seed predation was considered for the same roosts in two consecutive weeks. The data showed clearly that over the entire observation period, deposits with more seeds than the weekly median had a higher probability of being

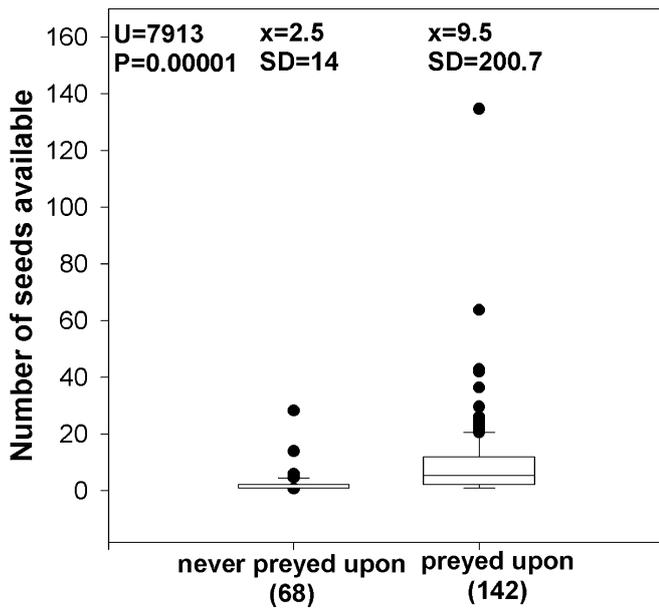


Fig. 3 Mean numbers of seeds present in deposits where seeds were never predated and in deposits where seeds were predated at least once (Mann-Whitney U statistic and P values are shown)

encountered by seed predators than expected by chance ($P < 0.001$). Deposits visited by seed predators in one week had an increased probability of being visited again the next

week ($P < 0.001$). Furthermore, deposits with more seeds than the median were visited more often by seed predators in 2 consecutive weeks than expected by chance ($P < 0.001$).

Taken together, the results show that when the number of seeds present in a deposit increased, the probability that the deposit was encountered by seed predators increased, while the proportion of seeds destroyed by seed predators decreased. The net effect is that deposits with fewer seeds than the median experienced a slightly higher weekly predation rate (8.3%) than did deposits with more seeds than the median (8.0%). The difference is statistically significant at the $P = 0.02$ level (permutation test).

Discussion

Density dependence

Our results do not support the hypothesis that increasing local seed density leads to increasing seed predation rates. At the beginning of the study period, neither the number nor the proportion of *Dipteryx* seeds predated in seed deposits beneath bat feeding roosts was related to local seed density. In the second half of the study period, these relationships did become significant. However, only the absolute number of seeds predated from a deposit was

Fig. 4 a Frequency distribution of the number of seeds present in a deposit when a predation event occurred. **b** number of seeds eaten in a predation event regressed against the number of seeds present in a deposit ($n = 251$ predation events)

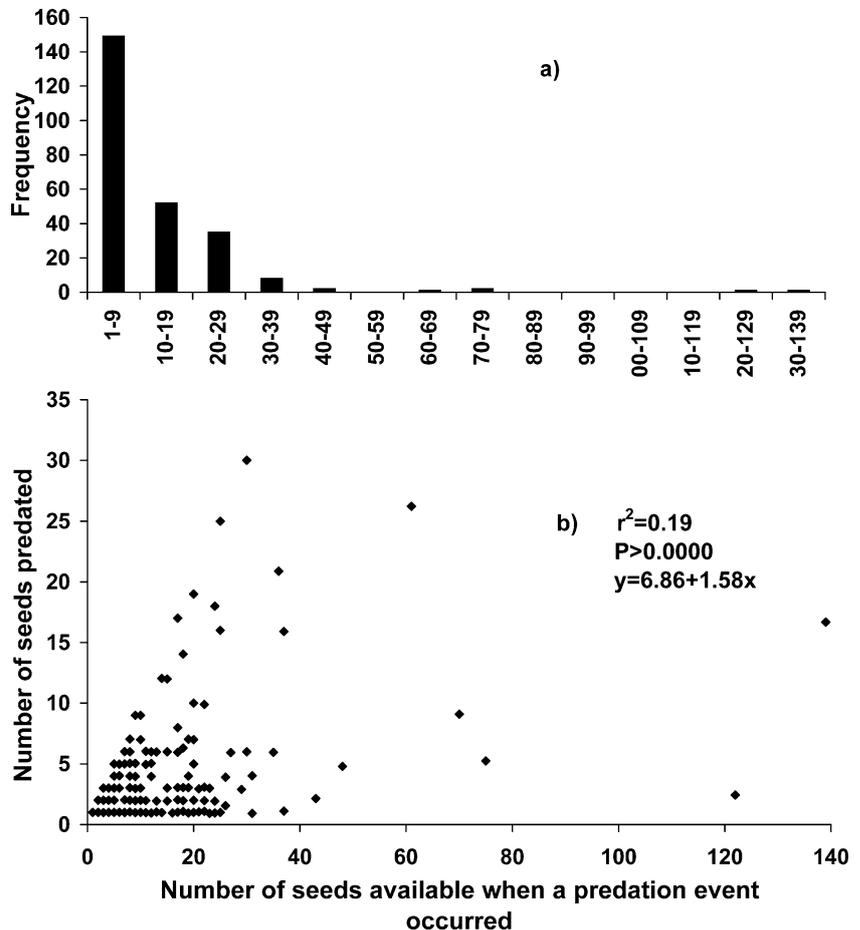


Table 1 Results of regression analyses where the independent variable is the number of seeds present, and the dependent variable is either the number of seeds predated (first part of the table) or the percentage of seeds predated (second part of the table) from a seed deposit beneath a bat feeding roost during the observation week. The analyses were run separately for three spatial scales (roost, roost

+5 m buffer, roost +10 m buffer). Either all deposits (*all deposits*) or only those deposits where a predation event had occurred (*predated deposits*) during the week in question, were included in the analysis. The numbers of seeds present were square root transformed. Statistically significant values ($P < 0.05$) are shown in bold

Week	Preated deposits: single-roost scale		Preated deposits: 11-m scale		Preated deposits: 21-m scale		All deposits: single-roost scale		All deposits: 11-m scale		All deposits: 21-m scale	
	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P
Number of seeds predated versus number of seeds available												
July 1							0.26	0.0624	0.04	0.5019	0.04	0.5019
July 2	0.55	0.2575	0.55	0.2575	0.55	0.2575	0.01	0.5558	0.00	0.9874	0.00	0.9598
July 3	0.04	0.8753	0.15	0.7450	0.15	0.7450	0.05	0.2204	0.04	0.2509	0.04	0.2745
July 4	0.59	0.0150 +	0.59	0.0150 +	0.56	0.0198 +	0.06	0.1155	0.01	0.5061	0.01	0.5517
Aug 1	0.33	0.0093 +	0.12	0.1407	0.07	0.2489	0.07	0.0518	0.03	0.1730	0.02	0.3571
Aug 2	0.17	0.0882	0.17	0.0836	0.04	0.4287	0.03	0.0715	0.04	0.0459 +	0.01	0.2376
Aug 3	0.14	0.0117 +	0.08	0.0587	0.04	0.1846	0.13	0.0000 +	0.09	0.0000 +	0.04	0.0055 +
Aug 4	0.27	0.0037 +	0.27	0.0035 +	0.25	0.0060 +	0.07	0.0001 +	0.03	0.0097 +	0.40	0.0000 +
Sept 1	0.25	0.0055 +	0.17	0.0194 +	0.14	0.0425 +	0.05	0.0011 +	0.03	0.0223 +	0.01	0.1784
Sept 2	0.01	0.5685	0.10	0.0987	0.06	0.2072	0.03	0.0210 +	0.06	0.0009 +	0.03	0.0189 +
Sept 3	0.49	0.0000 +	0.30	0.0001 +	0.22	0.0013 +	0.32	0.0000 +	0.22	0.0000 +	0.14	0.0000 +
Sept 4	0.07	0.1758	0.05	0.2499	0.04	0.3403	0.10	0.0004 +	0.08	0.0022 +	0.05	0.0137 +
Oct 1	0.27	0.0003 +	0.18	0.0036 +	0.19	0.0030 +	0.30	0.0000 +	0.17	0.0000 +	0.13	0.0003 +
Proportion of seeds predated versus number of seeds available												
July 1							0.26	0.062	0.04	0.502	0.04	0.502
July 2	0.13	0.6432	0.13	0.6432	0.13	0.6432	0.00	0.749	0.00	0.832	0.00	0.767
July 3	0.65	0.4028	0.83	0.2725	0.83	0.2725	0.02	0.387	0.00	0.553	0.01	0.600
July 4	0.08	0.4492	0.08	0.4492	0.10	0.3904	0.01	0.682	0.02	0.392	0.02	0.328
Aug 1	0.10	0.1832	0.10	0.1800	0.16	0.0924	0.00	0.990	0.00	0.751	0.01	0.502
Aug 2	0.28	0.0236 -	0.09	0.2314	0.12	0.1540	0.00	0.804	0.00	0.840	0.00	0.871
Aug 3	0.22	0.0013 -	0.16	0.0057 -	0.18	0.0035 -	0.01	0.110	0.01	0.107	0.00	0.648
Aug 4	0.33	0.0011 -	0.32	0.0015 -	0.31	0.0016 -	0.00	0.929	0.00	0.343	0.01	0.107
Sept 1	0.60	0.0000 -	0.56	0.0000 -	0.52	0.0000 -	0.02	0.045 -	0.02	0.036 -	0.03	0.010 -
Sept 2	0.51	0.0000 -	0.23	0.0080 -	0.23	0.0089 -	0.00	0.751	0.00	0.827	0.00	0.777
Sept 3	0.19	0.0033 -	0.16	0.0071 -	0.11	0.0260 -	0.01	0.267	0.00	0.490	0.00	0.405
Sept 4	0.56	0.0000 -	0.27	0.0071 -	0.32	0.0025 -	0.01	0.282	0.00	0.939	0.00	0.685
Oct 1	0.47	0.0000 -	0.51	0.0000 -	0.36	0.0000 -	0.00	0.510	0.02	0.176	0.01	0.253

positively density-dependent, whereas the proportion of seeds predated, a measure more directly related to the probability of seed survival, was negatively density-dependent. This result indicates higher survival of seeds in many-seeded deposits due to satiation of seed predators at and after the peak in *Dipteryx* fruiting. In Fig. 4b, the number of seeds predated in a deposit increases with the number of seeds present in the deposit up to about 30 seeds/deposit. Above that number, an increasing proportion of the seeds were left intact, which indicates the presence of a threshold of seed predator satiation. Satiation has also been suggested by Janson and Emmons (1990), who found that seed biomass supply at Cocha Cashu is higher than required to maintain the seed predator biomass present in the area.

Interpretation of studies on seed predation by rodents is difficult because such investigations often include a diverse assemblage of species. The present study mea-

sured natural seed predation in a community where both seed shadow and seed densities were observed in their natural states. The analysis was done in a large study area and at different spatial scales in an effort to observe seed predation patterns at the scales at which seed predators are operating (Clark and Clark 1984). However, the regression tests at the 11-m and 21-m scales yielded results very similar to those at the single-deposit scale (Table 1). This probably reflects the wide spacing of the bat roosts (see Fig. 1); at the scales analyzed here, a single sampling circle included few roosts. Therefore, seed density values were highly correlated across scales. In other studies, spatial scale has been found to be more important. Manson et al. (1998) found that predation of experimentally placed seeds was not density-dependent at the local scale (piles with different numbers of seeds showed the same predation rate when placed close together), but was positively density-dependent at a wider scale (piles with few seeds

placed in isolation experienced a lower predation rate). The study of Forget (1992), on the other hand, found that the predation rate of *Gustavia* seeds was negatively density-dependent on Barro Colorado Island: seeds that fell in an area where *Gustavia* trees were rare and seed density therefore low, experienced a much higher predation rate than seeds that fell in an area where the species was common.

Unlike invertebrates, rodents are often facultative seed predators, whose impact on the available seed population depends on a multitude of factors, such as foraging behavior, home range, territoriality, habitat or microhabitat preference, predator or competitor avoidance, and the availability of other resources (e.g., Willson and Whelan 1990; Hulme 1994; Manson et al. 1998; Forget et al. 1999; Hammond et al. 1999; Hulme and Hunt 1999). Therefore, rodents may not respond in a consistent manner to a gradient in seed density (Hammond and Brown 1998). For example, Cintra (1997b) found that, irrespective of seed density, *Dipteryx* seeds experimentally placed on bare ground were predated faster than seeds placed on ground covered with leaf litter. Hulme (1994) found that location of experimentally placed seeds by rodents did not depend on overall rodent density in the habitat, but showed a clear relationship with local-scale spatial distribution of rodents. We found evidence that rodents can memorize the location of favorable food supply sites: the probability of seed predation was increased for deposits that had already been discovered by seed predators, especially if they had many seeds when encountered. However, it is also possible that rodents cue on the movement patterns of other rodents either by following their scents, watching their activities, or hearing sounds of their feeding activities.

We have located 17 published studies focusing on density-dependent seed predation by rodents, and these provide 29 independent test cases, since some authors analyzed several plant species separately. About half of the cases showed no density effect, and positive density-dependence was found more often than negative density-dependence (Table 2). In four studies, different outcomes were obtained when study conditions were varied. In the present study, an average of 22% of the roosts was discovered by seed predators during any given week, and 32% of the deposits remained undiscovered for the entire 13-week study period. The undiscovered deposits had important consequences for the results in the regression analyses. When only the visited seed deposits were included in the analysis, a negatively density-dependent response was found in most weeks. However, this relationship practically vanished when the undiscovered roosts were also included in the analyses. This result suggests that both probability of discovery and degree of exploitation need to be taken into account to understand seed predation patterns by rodents. If, for any reason, a seed deposit is not discovered by a predator, it will automatically escape predation as well, but among those seed deposits that are discovered, the degree of exploitation (e.g., proportion of seeds eaten) may vary in a density-dependent manner.

Table 2 Summary of studies on rodent-predated plant species showing positively (+) or negatively (-) density dependent seed predation, or no relationship (*none*). When two outcomes are indicated, results differed depending on exact study conditions, for example between vegetation types, between short-term and long-term monitoring, or when analyzed using different approaches. Parentheses indicate that the statistical significance of the relationship is not clear

Species	Density-dependency	Reference
Temperate		
<i>Acer rubrum</i>	+/none	Manson et al 1998
<i>Acer rubrum</i>	none	Myser and Pickett 1993
<i>Arrhenatherum elatius</i>	+	Edwards and Crawley 1999
<i>Centaurea nigra</i>	+	Edwards and Crawley 1999
<i>Crataegus monogyna</i>	none	Hulme 1997
<i>Festuca rubra</i>	+	Edwards and Crawley 1999
<i>Fraxinus americana</i>	-	Myser and Pickett 1993
<i>Fraxinus excelsior</i>	none	Hulme and Hunt 1999
<i>Helianthus annuus</i>	none	Cummings and Alexander 2002
<i>Lesquerella fendleri</i>	+	Cabin et al. 2000
<i>Olea europaea</i>	none	Alcántara et al. 2000
<i>Prunus mahaleb</i>	(+)	Hulme 1997
<i>Rumex acetosa</i>	+	Edwards and Crawley 1999
<i>Taxus baccata</i>	none	Hulme 1997
<i>Ulmus glabra</i>	none	Hulme and Hunt 1999
Several spp	-	Willson and Whelan 1990
Tropical		
<i>Astrocaryum mexicanum</i>	+	Brewer and Webb 2001
<i>Astrocaryum mexicanum</i>	+	Sánchez-Cordero and Martínez-Gallardo 1998
<i>Astrocaryum murumuru</i>	+	Cintra 1997a
<i>Brosimum alicastrum</i>	-	Burkey 1994
<i>Brosimum alicastrum</i>	none	Sánchez-Cordero and Martínez-Gallardo 1998
<i>Cymbopetalum baillonii</i>	+	Sánchez-Cordero and Martínez-Gallardo 1998
<i>Dipteryx micrantha</i>	none	Cintra 1997a
<i>Dipteryx micrantha</i>	-/none	this study
<i>Erythroxylum havanense</i>	none	Gryj and Domínguez 1996
<i>Ficus yoponensis</i>	(-)	Sánchez-Cordero and Martínez-Gallardo 1998
<i>Gustavia superba</i>	-	Forget 1992
<i>Nectandra ambigens</i>	+	Sánchez-Cordero and Martínez-Gallardo 1998
<i>Tachigali versicolor</i>	-/none	Forget et al. 1999
<i>Virola michelii</i>	-/none	Forget et al. 2000

Some experimental studies have found that the probability that seed piles are discovered by rodents depends on seed density (number of seeds in a pile; Willson and Whelan 1990; Hulme 1994), although others have found this not to be the case (Hulme and Hunt 1999). In our study, deposits with few seeds were less likely to be discovered by seed predators than were deposits with many seeds. Studies that have considered degree of

exploitation in those deposits that have actually been discovered by rodents have shown either no response to density (Hulme and Hunt 1999) or a negative density-dependence (our study). Which of the patterns is more common in nature is still an open question.

The densities of agoutis, squirrels and spiny rats in Cocha Cashu are about 5.2, 25 and 230 individuals/km², respectively (Janson and Emmons 1990), whereas in Barro Colorado Island (BCI, Panama), these animal groups are much more abundant (100, 180, and 190 individuals/km², respectively; Glanz 1982). Also the difference in terrestrial seed-eater biomass is considerable: at Cocha Cashu all rodents and peccaries together reach a biomass of 4.0 kg/ha, whereas at BCI just agoutis and pacas add up to 12 kg/ha (Janson and Emmons 1990; Smythe et al. 1982). However, measured predation levels for experimentally placed seeds exceed 90% at both sites (Cocha Cashu: Cintra 1997a, 1997b; Cintra and Horna 1997; BCI: De Steven and Putz 1984; Forget 1993). Since the abundance of rodents differs between Cocha Cashu and BCI, but seed predation levels do not, some differences in foraging behavior of seed predators at the two sites might be expected. Indeed, secondary seed dispersal is known to be important for *Dipteryx* at BCI, where the percentage of seeds buried by agoutis reach 26% in mid fruiting season (Forget 1993). Food hoarding is associated with a time of food excess followed by a time of food scarcity (Vander Wall 1990). At Cocha Cashu, even the period of apparent seed scarcity (early September) still seems adequate to meet the energy demands of the seed-eaters (Janson and Emmons 1990). This may explain why scatter-hoarding behavior was not observed in either the present study or by Cintra (1997b). Similar differences in foraging behavior have been found when comparing levels of scatter-hoarding at different islands close to BCI. Adler and Kestell (1998) observed that a higher proportion of seeds was scatter-hoarded on islands where the overall seed exploitation rate was high than on islands where many seeds were left intact. Forget (1993) hypothesized that at BCI, a good year of recruitment might be related to a large seed crop that satiates post-dispersal predators and promotes scatter-hoarding by agoutis. At Cocha Cashu, a good year of fruit production may also satiate the predators and enhance seed survival.

The present study included only one fruiting season, so it cannot answer questions related to the importance of seed survival patterns for *Dipteryx* populations in the long term. Forget et al. (2000) found that in the short term (6 weeks), clumped seeds of *Virola michelii* had a higher probability of survival than did scattered seeds, but that no such difference remained after 1 year. Our results indicate that a similar process may be operating in *Dipteryx*. Over the 13-week observation period, there was a slight survival advantage to seeds that had been dispersed beneath bat feeding roosts containing many seeds. This was apparently due to predator satiation when the roost contained more seeds than the predator could eat. However, the data indicated also that in consecutive weeks, predators returned preferentially to seed deposits that had contained

many seeds, so by the end of the fruiting season the predators may learn the locations of the favored deposits. If so, predators might continue to return to these even after seed production ends, until the seed deposits are left empty. This could reverse the pattern favoring seeds deposited in few-seeded deposits, as these were more likely to escape the notice of seed predators entirely. The probability of seedling establishment and future recruitment, of course, also depends on many factors (both biotic and abiotic) other than seed predation.

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