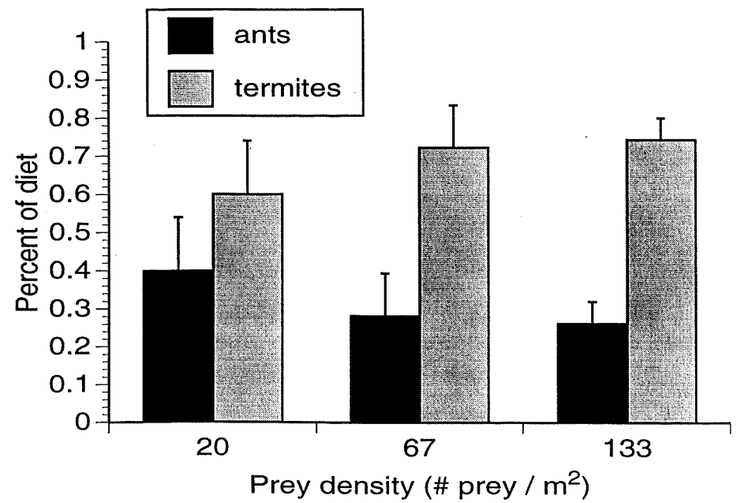

Fig 1. The proportion of *D. pumilio* diet consisting of ants and termites at different prey densities (n=7 replicate trials at each level of prey density).

At low prey density, frogs consumed 40% ants and 60% termites; at medium prey density, 28% ants and 72% termites; at high prey density, 26% ants and 74% termites.

In the control trials the mean escape rate for ants was 0.3/trial, and for termites was 0.14/trial.

Discussion

Optimal foraging theory predicts that the density of a preferred prey species will determine whether or not a less preferred prey species is consumed. (Begon, et al. 1990). We found that *D. pumilio* consumed higher proportions of preferred termites at high termite density (small search time) and lower proportions of less preferred ants at higher prey densities. Yet the number of ants consumed did not decrease as termite density increased, as the model of optimal foraging theory would predict. Perhaps termite density is not high enough in these treatments to cause the frogs to exclude ants from their diet, or perhaps the ants remain an essential part of the diet for other reasons, and this is why we witnessed no significant change in the number of ants consumed across the density treatments. Although a significant decrease in the number of ants consumed at increasing prey densities was not found, a look at the relative proportions of prey species consumed suggests that poison-dart frog prey selection is dependent on the abundances of prey items in a particular habitat. The finding that ants are eaten by poison-dart frogs, even in instances of abundant termite densities, suggests that ants may be important in the diet of frogs at some constant level of consumption.

Literature Cited

Begon, M., J. Harper and C. Townsend. 1990. Ecology, Individuals, Populations and Communities. Blackwell Scientific Publications. Cambridge, MA.

Crump, M.L. 1983. Dendrobates pumilio pp. 688-691 in D.H. Janzen. Costa Rican Natural History. University of Chicago Press. Chicago IL.

Donnelly, M.A. 1991 Feeding patterns of strawberry poison dart frogs, Dendrobates pumilio. Copeia 3: 723-730

DISTANCE AND DENSITY DEPENDENCE OF POST-DISPERSAL SEED PREDATION IN *DIPTERYX PANAMENSIS*

Grace S. Chen, Chris I. Dums, Phuong T. X. Hang

Abstract. This study examined the effect of density and distance on post-dispersal seed predation of a rain forest tree. Seeds of *Dipteryx panamensis* were laid out in different patch densities (1 seed and 5 seeds) and different distances from each other (1 m, 5 m, 15 m and 30 m) in primary forest plots at La Selva Biological Station, Costa Rica. There was no difference in percentages of seeds taken between high density patches (5 seeds) and low density patches (1 seed). However, seed predators ate more seeds from the patches located closer together than those located further apart. For every 10 m increase between patches, seed predators ate 20 % fewer seeds. Our results are in accordance with the Janzen-Conell hypothesis and show the importance of seed dispersal distance in the survival of seeds.

Introduction

Seed predation is detrimental to most plants because it reduces the number of propagules available for recruitment to subsequent generations (Marquis and Braker 1994). For this reason, the assessment of seed predation rates can provide important information on the population dynamics of plants. In this study, we focused on the rate of post-dispersal seed predation on *Dipteryx panamensis* (hereafter referred to as *Dipteryx*) a neotropical canopy tree species of primary lowland wet forest. We hypothesized that the rate of seed predation would increase with seed-patch density because it would be easier for predators to detect high-density patches than low-density patches. For the same reason, we further predicted that seed predation rate would decrease with increasing distance between patches. Clark and Clark (1984) cited 7 of 8 studies supporting density dependent seed/seedling mortality, and 8 of 10 studies supporting distance dependent seed/seedling mortality. By testing both density and distance effects on predation rates, we hoped to distinguish between these two processes. In addition, by testing predation on patches of seeds separated by several different distances, we bring new insights into the scale at which predators forage for Dipteryx seeds and their impact on plant populations.

Methods

On 14 - 16 February 1997 we collected freshly fallen *Dipteryx* seeds from below two trees within the primary forest at La Selva Biological Station, Costa Rica. We set the seeds on the ground within the primary forest along the CES trail in 10 replicate arrays. One array was set out on 14 February, six on 15 February, and three on 16 February.

Each replicate had five patches of one seed separated by 1 m, by 5 m, and by 15 m, as well as five patches of five seeds separated by 1 m, by 5 m, and by 15 m. Each of the six treatments within each array was separated from the others by at least 30 m (Fig. 1). In addition to these arrays, on 16 February we set up three additional replicates of five patches of one seed separated by 30 m, and three replicates of five patches of five seeds separated by 30 m. In the patches of five seeds all seeds were placed within a 0.25 m2 area. A total of 990 seeds was used during the experiment.

The seeds were set out in the forest between 15:00 and 17:00 each day, left overnight, and then checked for evidence of predation the next morning between 07:00 and 09:00. In all cases predation observed was in the form of seed removal (i.e. the number of seeds disappearing over one night). After checking each array, we removed any remaining seeds from the area.

Results

Overall, 75 % of treatments within the arrays had at least one seed taken. Since we were testing foraging scale and because the probability of a predator finding the first seed in an array is random, we excluded from our analysis all treatments in which none of the seeds were found.

In two-way analysis of variance, we found no interaction between patch size and patch spacing influencing percentage of seeds taken ($F=0.27$, $df=47$, $P=0.85$). Furthermore, there was no relationship

between the mean percentage of seeds taken from patches of one seed and from patches of five seeds (t-test, t=0.32, df=48, P=0.747). However, there was a strong negative relationship between patch spacing and percentage of seeds taken (one-way Anova, F=6.42, df=46, P=0.001; Fig. 2). In this case, the percentage of seeds taken decreased by approximately 20 % for every additional 10 m of spacing between patches (r2=0.22, F=13.54, df=48, P<0.001). There were significant differences in seeds found between the 1 m patches and both the 15 m and 30 m patches (Tukey Kramer H.S.D., P<0.05; Fig. 2).

DISCUSSION

We found that the percentage of seeds taken decreased with increasing seed spacing. This supports previous studies which have shown an inverse relationship between seed predation and distance from the parent tree (Clark and Clark 1984). Our study was different from many in that we measured seed predation in relation to distance between individual seeds or groups of seeds at four different spacings in areas where fruiting parent trees were not present. By measuring seed removal at four different distances, we not only measured the effect of spacing upon seed predation, but we also obtained some measure of the scale at which seed predators forage. Presumably, upon finding a patch of seeds the predator will begin a search for more seeds in the general area. With increasing distance between seeds, the efficiency of foraging must decrease. We attempted to obtain the background seed predation rates in the forest by spacing some seeds at 30 m to determine at what inter-seed distance predation attains a constant level. It would be at this level where seed removal would in effect be random and not directly related to active searching by the seed predators. However, because predation was higher in our 15 m than in our 30 m plots, all we can conclude is that the predation at 15 m is not the background rate. To determine background predation rates patches spaced further apart are needed.

We found no difference in percent seed removal between treatments having individual seed patches and those having patches of five seeds. Because all seeds in the patches of five were located within 0.5 m of each other, the probability of a predator finding seeds from a group of five, or an individual seed appeared to be similar.

Although our study found no difference in predation on patches of individual seeds versus patches of five seeds, it did, in effect, find a correlation with seed density. The patches with 1 m spacing imparted a higher seed density to a portion of the forest than did the patches with 5 m spacing. Thus, because there was a trend towards decreasing predation with increasing inter-patch distance, there was also a trend of decreasing predation with decreasing seed density.

Our study is consistent with Janzen-Connell hypothesis (Clark and Clark 1984) which predicts a disproportionally high mortality of young trees close to adults due to natural predation from host-specific seed predators, herbivores or pathogens. Because our study measured seed predation as seed removal, and removal was tested over a relatively short period, it was impossible to document any effect of smaller seed predators such as weevils or pathogens. Thus, the major seed predators influencing our results were probably large rodents, or other large seed eating mammals. Possible predators removing seeds from our experiment were squirrels (*Sciurus* spp.), coatis (*Nasua narica*), collared peccaries (*Tayussa tajucu*), and agoutis (*Dasyprocta punctata*) (Kauffman 1962, Smythe 1978, Clark and Clark 1984). The majority of seed removal was probably done by agoutis. We observed agoutis foraging in the area of our study and actually carrying *Dipteryx* seeds in their mouths. In addition, several of our seeds had bite marks in them, characteristic of agoutis. It is important to note that agoutis bury a large percentage of the seeds they collect for later use, and since these seeds are sometimes not retrieved, by recording seed removal as our measure of predation, we may have overestimated predation rates. Finally, in addition to seed predation by pathogens, insects and mammals, a large portion (50%) of *Dipteryx* seeds are eaten by large frugivorous birds before falling to the ground (Dunn et al. 1993). Thus, burial and dispersion of seeds by mammals like agoutis are important in maintaining *Dipteryx* levels. Because such a large percentage of *Dipteryx* seeds are preyed upon, and because a low percentage of seedlings survive (Clark and Clark 1984), it is necessary for *Dipteryx* to produce a large seed crop. As evidence of this, we collected over 1200 seeds from the base of two trees, and upon returning to the trees on subsequent days, the seeds on the ground had been largely replenished.

Past studies testing seed predation of *Dipteryx* have found much lower predation rates than we obtained (R. T. Holmes, pers. comm.). The high rates in our study may be due to our collecting freshly fallen seeds upon which predators were known to be currently foraging. Once seeds have been left on the ground for any period of time, they often become host to pathogens or insects (pers. obs.). Thus, seeds used in removal experiments must be fresh seeds if they are to show representative predation levels.

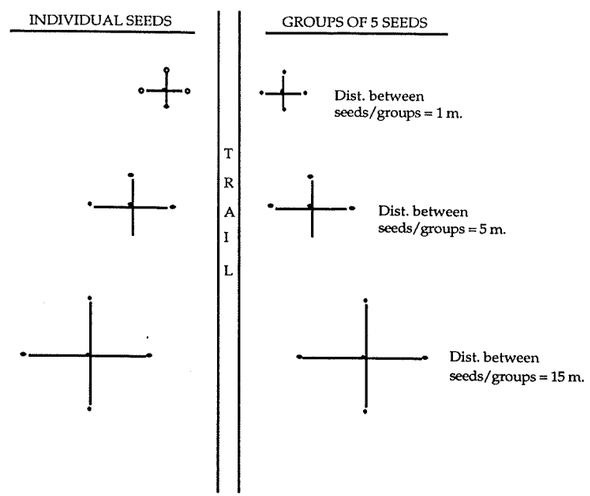

FIG. 1. One sample array. A total of 10 such arrays was used in the experiment. Three additional sets of five individual seeds separated by 30 m, and three sets of five patches of 5 seeds separated by 30 m, were also used. The four corners of the crosses and the center represent areas of seed placement.

LITERATURE CITED

Dunn, H. A., K. K. Ingram, and L. M. Mizak. 1993. Seed predation on *Dipteryx panamensis*.. Pp. 106 - 109 in S. Bansak and M. Seandel, eds. Dartmouth Studies in Tropical Ecology. Hanover, NH.

Kauffman, J.H. 1983. Nasua narica. Pp. 478 - 480 in D. H., Janzen, Daniel H., ed., Costa Rican Natural History. University of Chicago Press

Marquis, R. J., and H. E. Braker. 1994. Plant-herbivore interaction; diversity, specificities, and impact. Pp. 261-281 in L.A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds. La Selva - Ecology and Natural History of a Neotropical Rainforest. University of Chicago Press.

Smythe, N. 1983. *Dasyprocta punctata*. Pp. 463 - 465 in D.H. Janzen, ed. Costa Rican Natural History. University of Chicago Press.

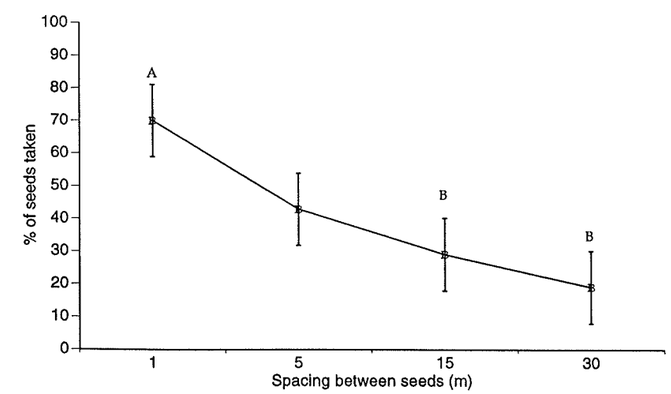

FIG. 2. Percentage (Mean ± S.E.) of seeds taken at different seed spacings. Data from individual seed treatments and group of five seed treatments combined. Spacings labelled with different letters are significantly different from one another (Tukey Kramer, P < 0.05).