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Notes and Comments

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EFFECTS OF MAMMALIAN HERBIVORES ON PLANT RECRUITMENT IN TWO NEOTROPICAL FORESTS

John Terborgh¹ and S. Joseph Wright²

Major changes in seed or seedling survivorship could alter the recruitment dynamics of tropical forest trees. One mechanism that could cause altered survival is modified herbivore pressure, in our context, by mammals. Clear differences in seed and seedling survivorship result when human hunters and/or habitat fragmentation extirpate mammalian herbivores or greatly reduce their abundances (DeSteven and Putz 1984, Sork 1987, Dirzo and Miranda 1991, Leigh et al. 1993). Increases in mammalian herbivore abundances may also influence tree recruitment. In particular, Terborgh (1992) hypothesized that absent carnivores contribute to high abundances of medium-sized mammalian herbivores on Barro Colorado Island (BCI), Panama and that this may in turn alter tree recruitment.

We tested the second part of this hypothesis. We compared seed and seedling dynamics for BCI and for Cocha Cashu (CC), Peru, where the apparent population densities of medium-sized mammalian herbivores are much lower. We studied trees in the genus *Dipteryx* (Leguminosae, Papilionoidae) because their seeds are consumed by terrestrial mammals, closely related species producing almost identical seeds occur in Panama and Peru, and the seed and seedling demography of *D. panamensis* have been studied in Panama and Costa Rica (DeSteven and Putz 1984, Clark and Clark 1987, DeSteven 1988). To examine the implications of high vs. low numbers of mammalian herbivores, we followed the fates of *Dipteryx* seeds and seedlings in impermeable and semipermeable mammal exclosures and in open controls at both sites. We also monitored the survival and recruitment of all plants (mostly tree seedlings) growing in the experimental and control plots.

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Study Sites

The Cocha Cashu Biological Station is set in mature Amazonian floodplain forest in Peru's Manu National Park (11°54' S, 71°19' W). BCI is an emergent forested hilltop in Gatun Lake, Panama (9°10' N, 79°51' W). Key aspects of the environment are similar at the two sites (Terborgh 1983, Windsor 1990). Annual rainfall is ≈2100 mm at CC vs. 2600 mm at BCI. The vegetation at both sites is tall evergreen forest with increasing canopy deciduousness as the 4–5-mo dry season progresses.

The floras and mammal faunas of BCI and CC are strikingly similar, except for a higher species richness at CC (Gentry 1990). With the exception only of some small rodents, every nonflying mammal inhabiting BCI is represented at CC, either by the same species or by a geographical replacement (Glanz 1990, Janson and Emmons 1990). Three large carnivores (jaguar, puma, and harpy eagle) are no longer resident on BCI, although jaguar is a regular visitor (BCI sightings in 1983, 1985, 1988, and 1993).

Despite similar mammal faunas, the sites differ in mammal abundances, especially medium-sized prey of jaguar, puma and to a lesser degree, ocelot (Janson and Emmons 1990, Terborgh 1992). Particularly relevant to the question of seed and seedling survival are higher densities (by roughly an order of magnitude) of agoutis (*Dasyprocta* sp.) and pacas (*Agouti paca*) on BCI. Agoutis are major seed predators in neotropical forests, and pacas consume many seedlings, as well as seeds (Smythe et al. 1982, Hallwachs 1986). Smaller seed-eating rodents, such as squirrels (*Sciurus* spp.), spiny rats (*Proechimys* spp.), and rice rats (*Oryzomys* spp.), are equally abundant at the two sites, as are two large herbivores, brocket deer (*Mazama* sp.) and tapir (*Tapirus* sp.). Collared peccaries (*Tayassu tajacu*), large granivores, are ≈50% more abundant on BCI, but the difference is offset by the presence of a second species (*T. pecari*) at CC (Glanz 1990, Janson and Emmons 1990).

Dipteryx

D. panamensis (Pitt.) Record & Mell occurs in southern Central America, and *D. micrantha* (Harms) occurs in western Amazonia. The two are very similar in stature (to 50–60 m tall) and general appearance. We estimate population densities at BCI and CC to range from 0 to 5 adults per hectare. Adults flower at the beginning of the rainy season and ripen fruits ≈6 mo later (Perry and Starrett 1980). The single-seeded legumes (5–6 cm long; 2–2.5 cm wide) have a hard, thick-walled endocarp. Rodents are the most important seed

TABLE 1. Seed fates and distance from focal *Dipteryx* trees at Cocha Cashu, Peru and Barro Colorado Island, Panama.

Site	Caging treatment									
	Impermeable			Semipermeable			Control with seeds			
	Distance	Alive	Dead	Missing	Alive	Dead	Missing	Alive	Dead	Missing
Cocha Cashu										
10 m	12	24	0	3	33	0	1	31	4	
50 m	14	22	0	4	22	10	1	28	7	
Barro Colorado Island										
10 m	8	23	5	2	30	4	0	14	22	
50 m	10	24	2	2	31	3	0	11	25	

predators, and seeds of *D. panamensis* are a major food resource for squirrels and agoutis in Panama (Glanz et al. 1982, Smythe et al. 1982). Pacas and spiny rats also open *D. panamensis* seeds on BCI (N. Smythe, *personal communication*). Primary dispersal is by bats, especially *Artibeus* spp., which carry the fruits to feeding roosts. Toward the end of the fruiting period, one finds scattered heaps of seeds on the ground under feeding roosts (Bonaccorso et al. 1980). The heaps gradually dwindle as rodents remove the seeds (Forget 1993).

Experimental Design

Our goal was to assess the impact of mammalian seed predators on the survival of *Dipteryx* seeds and seedlings, and concurrently, to compare rates of recruitment and mortality of plants of all species in plots protected from vertebrate herbivores. We excluded mammals from 2 × 1 m plots that had been stocked with intact and apparently viable *Dipteryx* seeds. The enclosures were constructed of galvanized wire cloth (17 mm mesh; 85 cm tall at CC, 100 cm at BCI) supported by stakes at the four corners and in the middle of the long sides. The wire was pressed tightly against the soil to preclude passage of small mammals underneath. The enclosures were open at the top, ensuring normal exposure to rain and sunlight and also access to squirrels and other climbing mammals.

There were two types of enclosures. "Impermeable" enclosures described above were intended to exclude all nonclimbing terrestrial mammals. "Semiperme-

able" enclosures were identical except that the wire around the bottom perimeter contained gates (6 cm wide, 7.5 cm tall) at 8 cm intervals. The gates provided access to small rodents (*Oryzomys*, *Proechimys*, etc.) but not to larger mammals. Open control plots of two kinds were marked by stakes at the corners. One set of control plots received seeds, the other did not. The latter served to control for the possibility that *Dipteryx* seeds present in the first type of control plot could attract mammals which might then browse plants within the plot.

Nine *Dipteryx* seeds were set out in evenly spaced arrays in half of each plot; the adjacent half served to measure the natural rain of *Dipteryx* seeds. The seeds were collected from bat roosts in the surrounding forest and pooled. All seeds used in the experiment were examined for any damage, especially insect infestation, and were rejected if hollow, lighter than normal, or with visible entrance/exit holes.

The enclosures and control plots were installed in sets of eight, centered around each of four large adult *Dipteryx* trees, for a total of 32 plots at each site. The four types of plots—impermeable, semipermeable, controls with seeds, and controls without seeds—were set out at random along the four cardinal directions, one plot of each type at 10 and 50 m from the focal trees. Because the focal trees had broad crowns, plots at 10 m were well inside the crown perimeters. Plots at 50 m were intended to be outside the tree's zone of influence on seed predators (e.g., Howe et al. 1985). Focal trees were at least 150 m apart except for two at CC with conspecific neighbors within 100 m.

Identical experiments were established at the end of the dry season when the current year's fruit fall was complete (October 1988 at CC, March 1989 at BCI). We scored the results 1 and 2 yr later, carefully sifting through the leaf litter of all plots to uncover all *Dipteryx* seeds. More than 80% of the seeds that had been set out initially were recovered in the impermeable enclosures. Seeds that fell into the plots naturally in subsequent years were easily identifiable by the condition of the endocarp and were excluded from analyses.

TABLE 2. Analysis of 1st-yr survivorship of *Dipteryx* seeds.

The analysis was performed on the arcsine transformation of the proportion of seeds that survived.

Source	Sum of squares	df	MS	F
Treatment	3.69	2	1.85	28.06***
Site	0.19	1	0.19	2.84
Tree (Site)	0.98	6	0.16	2.47*
Treatment × Site	0.07	2	0.04	0.53
Error	2.37	36	0.07	

* $P < 0.05$; *** $P < 0.001$.

TABLE 3. Initial number, recruitment, mortality, and final number of plants in the 2-m² plots over 2 yr. Values are numbers of individuals per 2 m².

Locality	Initial		1st yr		2nd yr		Final	
	Mean	SE	Recr.	Mort.	Recr.	Mort.	Mean	SE
Barro Colorado Island								
Control without seed add'n.	11.1	2.8	14.8	2.8	13.5	7.4	29.3	8.4
Control with seed add'n.	16.6	3.8	9.9	5.5	3.7	5.7	19.4	5.6
Semipermeable	21.1	4.1	20.8	3.8	19.1	10.0	47.3	11.1
Impermeable	21.4	7.4	18.8	5.6	12.6	12.0	35.1	7.4
Cocha Cashu								
Control without seed add'n.	35.8	5.1	9.3	7.9	9.3	6.7	38.3	6.5
Control with seed add'n.	40.9	3.3	7.1	8.3	10.1	7.9	42.0	4.3
Semipermeable	36.1	6.6	14.8	7.8	10.4	9.1	43.0	6.1
Impermeable	35.5	4.9	14.1	6.5	11.6	8.3	46.5	5.0

Experimental seeds were classified according to their condition after 1 yr: alive (germinated with live seedling present), dead (germinated with remains of dead seedling evident, or one or both valves present but seed missing), or missing (entire fruit missing). After 1 yr, no *Dipteryx* fruits remained intact and potentially viable. We observed no evidence of attack by arthropods in either *Dipteryx* species.

The second component of the experiment entailed following the recruitment and mortality of understory vegetation. At the initiation of the experiment, all plants in each plot were mapped, measured (height only), identified (if possible), and marked by inserting a colored plastic toothpick into the ground beside the stem. Most of these plants were either young tree seedlings or understory herbs: a few were older seedlings/saplings or vines. At annual recensuses, we tallied all mortality, remeasured survivors, and marked, measured, and mapped all new plants. The plastic toothpicks were reliable markers, even of plants that had died.

Analyses

Log-linear models were first used to determine whether distance to focal tree (10 or 50 m) influenced in situ *Dipteryx* survivorship. Two log-linear models were compared. The first involved site (BCI or CC), treatment, and their interaction. The second added distance and all interactions involving distance. Treatments were impermeable exclosures, semipermeable exclosures, and controls with added seeds. Trees were pooled within sites because there was just one distance-treatment replicate for each tree. First-year *Dipteryx* survivorship was analyzed throughout because too few seedlings survived to the 2nd yr in some treatments.

Analyses of variance were then performed for *Dipteryx* survivorship and community-level mortality and recruitment in which site and treatment were fixed main effects and replicate trees were a random effect nested within site. The fourth treatment, controls without added seeds, was included in the community-level

analyses. Year was treated as a repeated measure for the community-level analyses. When a main effect was significant, post hoc tests based on the full ANOVA model were used to evaluate differences among treatments. Variances were stabilized by logarithms of numbers of recruits and arcsine square root transformations of proportions of understory plants dying and *Dipteryx* seeds surviving.

Results

Table 1 presents the fates of *Dipteryx* seeds after 1 yr. The inclusion of distance and interactions involving distance did not improve the log likelihood ratio chi-square obtained for a simpler model involving just site, treatment, and their interaction ($\chi^2 = 0.60$, $df = 6$). First-year *Dipteryx* survivorship did not show a distance effect.

Treatment affected the proportion of *Dipteryx* seeds that survived 1 yr (Tables 1 and 2). Survivorship was greatest in impermeable exclosures (Fisher's least significant difference test, $P < 0.001$) and did not differ between semipermeable exclosures and controls ($P = 0.14$). The significance of the nested tree effect was caused by high survivorship at one CC tree.

Community-level mortality of understory plants was greater at BCI than at CC (Tables 3 and 4). This site effect held over treatments and years. Community-level recruitment differed among treatments (Tables 3 and 4). Post hoc tests demonstrated that community-level recruitment differed between pooled exclosures and pooled controls ($F_{2,28} = 7.50$, $P < 0.01$), but not between the two types of exclosures ($F_{2,28} = 0.03$, NS), nor between the two types of controls ($F_{2,28} = 2.80$, NS).

Discussion

No evidence of a distance effect on the survival of *Dipteryx* seeds was noted either at BCI or CC. Similarly, there was no evidence for distance effects with seedlings for six of seven additional tree species pro-

TABLE 4. Analyses of recruitment and mortality of understory plants.† Repeated measures occur on Year.

Source	df	Mortality			Recruitment		
		SS	MS	F	SS	MS	F
Between-subjects effects							
Treatment (Tmt)	3	0.13	0.04	0.40	9.94	3.31	5.67**
Site	1	1.54	1.54	38.50***	0.14	0.14	0.15
Tree (Site)	6	0.24	0.04	0.36	5.57	0.93	1.59
Tmt × Site	3	0.43	0.14	1.17	2.56	0.85	0.91
Tmt × Tree (Site)	18	2.12	0.12	1.06	16.68	0.93	1.58
Error	29	3.21	0.11		16.95	0.59	
Within-subjects effects							
Year	1	0.05	0.05	1.17	1.02	1.02	3.49
Treatment	3	0.08	0.03	0.65	0.84	0.28	0.95
Site	1	0.03	0.03	0.64	0.95	0.95	3.24
Tree (Site)	6	0.58	0.10	2.35	1.61	0.27	0.91
Tmt × Site	3	0.12	0.04	0.94	0.60	0.20	0.68
Tmt × Tree (Site)	18	0.92	0.05	1.25	3.62	0.20	0.68
Error	29	1.19	0.04		8.52	0.29	

** $P < 0.01$; *** $P < 0.001$.

† Analyses were performed on the arcsine transformation of the proportion of plants that died and on the natural logarithm of numbers of recruits.

tected from mammals (Molofsky and Fisher 1993, Terborgh et al. 1993). The one exception, *Astrocaryum macrocalyx*, showed heavy damage by bruchid beetles under crowns of adult trees but not at 25 m (Terborgh et al. 1993). Thus, exclosure studies conducted on eight species of large-seeded neotropical trees have revealed no distance effect attributable to mammals. One could conclude from this that distance effects are largely due to invertebrates and/or pathogens which often complete their life cycles within the space occupied by a large tree (e.g., Wright 1983). Mammals, in contrast, must roam over considerably greater areas in the course of an annual cycle. Their impact may therefore be spread more uniformly over the forest floor.

Mammal exclusion from 2-m² experimental plots had almost identical effects on the survivorship of *Dipteryx* seeds at BCI, Panama and CC, Peru. This result disproved our initial expectation, which was that unprotected *Dipteryx* seeds would survive in greater numbers at CC than at BCI, due to the lower densities of agoutis and pacas at CC. *Dipteryx* seeds are a preferred item in agouti diets, and the seeds are entirely consumed (Smythe et al. 1982). Either an order of magnitude difference in agouti abundances between CC and BCI did not result in different levels of predation on *Dipteryx* seeds, or there were other compensatory sources of mortality.

The consistent removal of seeds from semipermeable exclosures implies that small rodents (e.g., *Proechimys*, *Oryzomys*) are important consumers of *Dipteryx* seeds in both localities and a possible source of compensatory mortality. The true importance of small rodents cannot be extrapolated from semipermeable

exclosures, however. By excluding larger mammals, the semipermeable exclosures may become privileged foraging grounds for small rodents, and the true impact of small rodents may have been overestimated.

It should be noted that squirrels might have raided some of the exclosures through their open tops, thereby accounting for a low level of uncontrolled *Dipteryx* seed loss from impermeable exclosures. The low level of uncontrolled loss, however, did not alter the qualitative outcome of the experiments.

Finally, both types of exclosures enhanced community-level seedling recruitment, and, once again the effect was similar at BCI and CC. We can only surmise that seed and/or seedling predation by larger mammals (e.g., agouti, paca, peccary, deer, and tapir) was responsible for this effect. Except for the agouti and paca, these larger mammals are present at CC and BCI in similar numbers, perhaps accounting for the parallel findings at the two localities. We conclude that mammalian herbivores have similar important effects on tree regeneration at BCI and CC. Similar experiments on a larger scale will be required for a more detailed, species-by-species assessment of the impact of vertebrate herbivores on seedling survival in neotropical forests.

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Literature Cited

- Bonaccorso, F. J., W. E. Glanz, and C. M. Sanford. 1980. Feeding assemblages of mammals at fruiting *Dipteryx panamensis* (Papilionaceae) trees in Panama: seed predation, dispersal, and parasitism. *Revista Biologica Tropical* **28**: 61-72.
- Clark, D. B., and D. A. Clark. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. *Biotropica* **19**:236-244.
- DeSteven, D. 1988. Light gaps and long-term seedling performance of a Neotropical canopy tree (*Dipteryx panamensis*, Leguminosae). *Journal of Tropical Ecology* **4**:407-411.
- DeSteven, D., and F. E. Putz. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* **43**:207-216.
- Dirzo, R., and A. Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. Pages 273-287 in P. W. Price, P. W. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. John Wiley & Sons, New York, New York, USA.
- Forget, P. M. 1993. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia (Berlin)* **94**:255-261.
- Gentry, A. H., editor. 1990. *Four neotropical rainforests*. Yale University Press, New Haven, Connecticut, USA.
- Glanz, W. E. 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama? Pages 287-311 in A. H. Gentry, editor. *Four neotropical rainforests*. Yale University Press, New Haven, Connecticut, USA.
- Glanz, W. E., R. W. Thorington, Jr., J. Giacalone-Madden, and L. R. Heaney. 1982. Seasonal food use and demographic trends in *Sciurus granatensis*. Pages 239-252 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C., USA.
- Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). Pages 285-304 in A. Estrada and T. H. Fleming, editors. *Frugivores and seed dispersal*. Dr. W. Junk, Dordrecht, The Netherlands.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Viola surinamensis*). *Ecology* **66**:781-791.
- Janson, C. H., and L. H. Emmons. 1990. Ecological structure of the nonflying mammal community at Cocha Cashu Biological Station, Manu National Park, Perú. Pages 314-338 in A. H. Gentry, editor. *Four neotropical rainforests*. Yale University Press, New Haven, Connecticut, USA.
- Leigh, E. G., Jr., S. J. Wright, F. E. Putz, and E. A. Herre. 1993. The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evolutionary Ecology* **7**:76-102.
- Molofsky, J., and B. L. Fisher. 1993. The effect of habitat and predation on seedling survival and growth of three shade-tolerant tree species in Panama. *Ecology* **74**:261-265.
- Perry, E. R., and A. Starrett. 1980. The pollination ecology and blooming strategy of a neotropical emergent tree, *Dipteryx panamensis*. *Biotropica* **12**:307-313.
- Smythe, N., W. E. Glanz, and E. G. Leigh, Jr. 1982. Population regulation in some terrestrial frugivores. Pages 227-238 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C., USA.
- Sork, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* **68**:1341-1350.
- Terborgh, J. 1983. *Five Neotropical primates: a study in comparative ecology*. Princeton University Press, Princeton, New Jersey, USA.
- . 1992. Maintenance of diversity in tropical forests. *Biotropica* **24**:283-292.
- Terborgh, J., E. Losos, M. P. Riley, and M. Bolaños Riley. 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. *Vegetatio* **108**:375-386.
- Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Smithsonian Contributions to the Earth Sciences* **29**:1-145.
- Wright, S. J. 1983. The dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds, and the effect of distance to the parent palm. *Ecology* **65**:1016-1021.

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