

## The Bushmeat Harvest Alters Seedling Banks by Favoring Lianas, Large Seeds, and Seeds Dispersed by Bats, Birds, and Wind

S. Joseph Wright<sup>1</sup>, Andrés Hernández, and Richard Condit

Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, República de Panamá

### ABSTRACT

We evaluated predictions that hunters favor lianas, large seeds, and seeds dispersed by bats, small birds, and mechanical means for seedling banks in central Panama. We censused 3201 trees in 20 1-ha plots and 38,250 seedlings in the central 64 m<sup>2</sup> of each plot. We found significant differences in the species composition of the seedling bank between nine protected sites in the Barro Colorado Nature Monument and 11 hunted sites in the contiguous Parque Nacional Soberanía. Lianas, species with large seeds, and species with seeds dispersed by bats, small birds, and mechanical means were all overrepresented at hunted sites. The latter two findings could also be evaluated relative to the species composition of reproductively mature adults for canopy trees. The tree species present in the seedling bank had significantly heavier seeds than the tree species present as adults at hunted sites but not at protected sites. The representation of seed dispersal modes among the species present in the seedling bank did not reflect pre-existing differences in the local species composition of adults. We hypothesize that hunting large seed predators favors large seeds by reducing predation and increasing survival. We also hypothesize that the harvest of large birds and mammals that disperse many seeds favors other species whose seeds are dispersed by bats, small birds, and mechanical means. This process also favors lianas because the seeds of disproportionate numbers of liana species are dispersed by wind.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

*Key words:* anthropogenic disturbance; Barro Colorado Island; poachers; seed dispersal; tropical forest.

HUMANS ARE HUNTING FOREST VERTEBRATES AT UNSUSTAINABLE LEVELS throughout the tropics (Fa *et al.* 2002, Corlett 2007, Peres & Palacios 2007). Most of the preferred game species consume fruit, seeds, and/or leaves. Hunters alter these plant–animal interactions when they remove frugivores, granivores, and browsers (Emmons 1989, Redford 1992). This, in turn, raises the possibility that hunters might indirectly alter the species composition, diversity, and structure of forest plant communities (Dirzo & Miranda 1991, Dirzo 2001, Wright 2003, Muller-Landau 2007). In particular, frugivores disperse and granivores kill seeds, and these interactions largely determine the spatial template for plant recruitment (Janzen 1970). Hunting is known to alter the spatial dynamics of seedling recruitment by removing seed dispersal agents and seed predators for selected plant species in tropical forests (Wright *et al.* 2000, Roldán & Simonetti 2001, Wright & Duber 2001, Galetti *et al.* 2006, Beckman & Muller-Landau 2007, Wang *et al.* 2007). Here, we ask whether hunters also alter the structure, species composition, and diversity of the entire community of the seedling and herbaceous layer along a strong gradient of hunting pressure in central Panama. We focus on three *a priori* predictions, each concerning a particular plant trait.

Our first *a priori* prediction is that hunting will favor plant species with large seeds by removing their seed predators. Seed mass varied over five orders of magnitude (0.04 to 7300 mg) among plant species found in the seedling layer in this study. Each species of granivore consumes seeds from a subset of this range of seed

sizes. Hunters active in the forests of central Panama select only the largest avian granivore, the 1 kg Great Tinamou *Tinamus major*, and mammalian granivores as large as or larger than the 2.8 kg agouti *Dasyprocta agouti*. The next smaller avian and mammalian granivores (pigeons, parrots and red-tailed squirrels *Sciurus granatensis*) are not hunted in central Panama (Méndez 1970, Wright *et al.* 2000). The largest vertebrate granivores preferentially consume large seeds (Dirzo *et al.* 2007). Thus, hunters could differentially increase the survival of larger seeds by removing their vertebrate predators.

Our second *a priori* prediction is that hunting will favor plant species whose seed dispersal agents are not hunted by limiting seed dispersal distances for other species whose seed dispersal agents are hunted. Primary seed dispersal is by animals or by mechanical means (wind, water, or ballistic) for 76 percent and 24 percent of the woody plant species of Barro Colorado Island (BCI), respectively (Muller-Landau & Hardesty 2005). Animal seed dispersal agents include preferred game species as well as many species that are not hunted. Just six of the most highly preferred game species (Great Tinamou, tapir *Tapirus bairdii*, collared peccary *Tayassu tajacu*, paca *Agouti paca*, agouti and red brocket deer *Mazama americana*) consume 53.5 percent of the fleshy fruit consumed by vertebrates on BCI (Muller-Landau & Hardesty 2005). These and other large game species are particularly important seed dispersal agents for many large-seeded plant species (Peres & Roosmalen 2002, Nunez-Iturri & Howe 2007). Thus, our first and second *a priori* predictions are in conflict for species with large seeds whose seed predators and seed dispersal agents are both removed by hunters. The empirical resolution of this conflict will indicate whether the seed predators or seed dispersal agents removed by hunters have the greatest impact

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<sup>1</sup>Corresponding author; Mailing address: Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948 USA; e-mail: [wrightj@si.edu](mailto:wrightj@si.edu)

on seedling establishment in these species. For species with smaller seeds, hunting is predicted to favor species whose seeds are dispersed by mechanical means or by animals that are not hunted.

Our third *a priori* prediction is that hunting will favor climbing species over free-standing species. Hunter-frugivore-seed interactions combined with a strong difference in seed dispersal agents among plant life forms motivates this final prediction. Primary seed dispersal is by wind for 60 percent of liana species and 25 percent of canopy tree species and is exceedingly rare among species that reproduce below the canopy (smaller trees, shrubs, and terrestrial herbs) on BCI (Muller-Landau & Hardesty 2005). This strong difference in seed dispersal modes between lianas and other life forms is characteristic of most tropical forests (Gentry 1983, Chazdon *et al.* 2003). Thus, hunters might favor climbing species as a consequence of the second prediction and the preponderance of wind-dispersed seeds among climbing species.

To evaluate these three predictions, we censused all canopy trees, terrestrial herbs, and woody seedlings at protected and heavily hunted sites. We then used two approaches to test the predictions. The first approach directly compared the distribution of the critical trait (seed mass, seed dispersal agent, or life form) for herbs and woody seedlings from protected and heavily hunted sites. The second approach evaluated the distribution of the critical trait for trees and tree seedlings at each site to control for possible pre-existing site differences. The second approach was limited to trees because other life forms were not mapped as adults. Our findings show that hunters indirectly favor lianas, large-seeded species, and species whose seeds are dispersed by mechanical means and by animals that are not hunted.

## METHODS

**STUDY SITES.**—The nine protected and 11 heavily hunted sites were located within the Barro Colorado Nature Monument (BCNM) and the contiguous Parque Nacional Soberanía (PNS), respectively (Fig. 1). All 20 sites support secondary forests between 90 and perhaps 150-yr old. The levels of hunting 90 to 150 yr ago are unknown, but are likely to have been high. All 20 sites have been protected since 1979 when the BCNM and PNS were created. In addition, the three BCI sites experienced variable levels of protection since 1923 when BCI became a forest reserve (see Discussion). Wright *et al.* (2000) and Wright and Duber (2001) documented levels of poaching, abundances of mammals, and the regeneration of two palm species for the BCNM and PNS in the late 1990s. At that time, poachers were absent from BCI, active at intermediate levels on mainland peninsulas within the BCNM (Fig. 1), and active at much higher levels in the PNS. Since then, the situation has deteriorated in the PNS and improved on the mainland peninsulas within the BCNM. The PNS (225 km<sup>2</sup>) is now patrolled by six (rather than eight) forest guards who are not cooperating with the national police force at this time and who still lack vehicles, most other equipment, and funds to purchase food for field patrols and therefore stay close to their headquarters (A. Hernández, pers. obs.). The BCNM (59 km<sup>2</sup>) is still patrolled by 21 well-provisioned forest

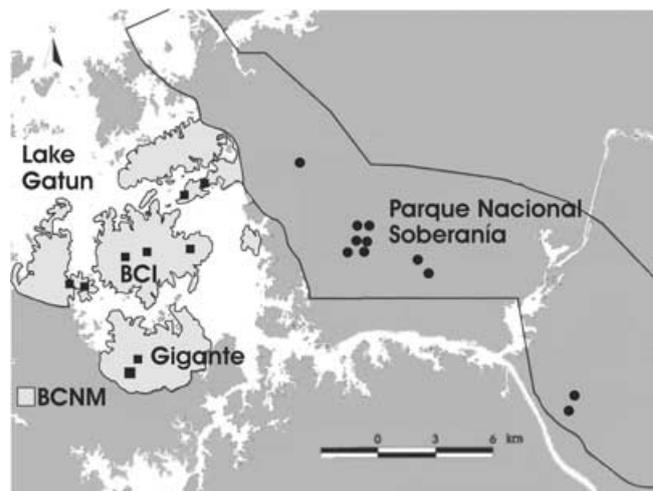


FIGURE 1. Map of the study area showing protected sites (squares) in the Barro Colorado Nature Monument (BCNM) and heavily hunted sites (circles) in the nearby Parque Nacional Soberanía (boundaries delimited by solid line). Land is dark gray, land within the BCNM is light gray, and white represents the open waters of Lake Gatun, the Panama Canal, and the Chagres River.

guards and members of the national police force. Their effectiveness on the mainland peninsulas within the BCNM (Fig. 1) increased markedly in 2000 when a new national law, which was designed to control urban crime, required a license to transport firearms. The BCNM guards capitalized on this new law by extending ambushes outside the BCNM to the principal forest trails used by poachers to approach the BCNM. The number of poachers arrested and firearms confiscated spiked in 2000 and has since declined to very low numbers. The number of shots heard and poachers encountered by scientists working on the remote Gigante Peninsula within the BCNM declined from one or two incidents each month in the late 1990s to zero incidents in the past 4 yr (2002–2006). In contrast, scientists working in the PNS continue to report frequent shots and encounters with poachers. Poachers have been absent from BCI since the late 1980s (see Discussion), virtually absent from other parts of the BCNM since 2000 or 2001, but continue to hunt freely in the PNS.

**PLANT CENSUSES.**—We censused canopy trees, terrestrial herbs, and woody seedlings at all 20 sites. We used methods described by Condit (1998) to map trees larger than 20 cm in diameter at breast height (dbh) in square 1-ha plots. Trees were mapped at 15 sites by Condit *et al.* (2002) and at the five remaining sites for this study.

We censused seedlings and herbs less than 50-cm tall in an 8 × 8 m plot located at the center of each tree plot between June and December 2004. There were recent treefalls in the centers of three tree plots, and their 64 m<sup>2</sup> seedling plots were moved outside the treefall gap but as close to the center of the tree plot as possible. All seedlings less than 20-cm tall were collected, pressed, dried, and identified in the laboratory. Seedlings between 20- and 50-cm tall were identified in the field, or, when field identification was

uncertain, a few leaves were collected, pressed, and dried for later identification. The presence of seed reserves and cotyledons, seedling height (distance from the ground to the terminal meristem along the main stem), leaf number, and the presence of leaf pathogens and holes chewed in leaves by insects were recorded for each seedling.

In a separate study, we censused seedlings less than 50 cm tall for 600 randomly located 1 m<sup>2</sup> plots on BCI between January and March each year since 1994 (Gilbert *et al.* 2006). In 2005, 62 percent of the seedlings were less than 6-yr old and 77 percent were less than 12-yr old. Thus, virtually all seedlings postdate the establishment of the BCNM and PNS 25 yr earlier and 62 percent postdate improvements in protection of mainland peninsulas in the BCNM 5 yr earlier.

**PLANT TRAITS.**—The plant traits evaluated were seed mass, seed dispersal mode, and life form. We determined dry seed mass (endosperm plus embryo after oven drying to constant mass at 60°C) for 261 species from central Panama. Dry seed mass for an additional 52 species encountered in this study were taken from Daws *et al.* (2005).

Wright and associates have recorded seed dispersal agents for plant species from BCI over the past 20 yr. These data are based upon all published records of seed dispersal, unpublished observations made by Bonifacio DeLeon, Osvaldo Calderón and SJW, and large numbers of personal communications from others, notably from Charles Handley for bats. Primary seed dispersal agents are placed in the following seven categories: bats, small birds (< 300 g body mass), larger birds, nonvolant mammals, and mechanical means including explosion, water, and wind. Bats are probably underreported (C. Handley, pers. comm.). Muller-Landau and Hardesty (2005) used these data to characterize seed dispersal on BCI. In central Panama, poachers only hunt dispersal agents from two of these seven categories—large birds and nonvolant mammals. We distinguished seedlings whose seeds are dispersed only by large birds and nonvolant mammals, only by nonhunted dispersal agents (bats, small birds, and mechanical agents), or by both hunted and nonhunted dispersal agents. We predict that species whose seeds are dispersed only by large birds and nonvolant mammals will be underrepresented at heavily hunted sites while species whose dispersal agents are not hunted will be overrepresented at heavily hunted sites.

We used plant life forms in two ways. First, we contrasted free-standing species (herbs, shrubs, understory, midstory, and canopy trees) with climbing species (woody lianas and nonwoody vines). Second, we compared adult and seedling traits for canopy tree species only. We limited this second comparison to canopy tree species because our tree plots excluded stems smaller than 20 cm dbh. The size at reproductive maturity is less than 20 cm dbh for shrubs, understory trees, and midstory trees and 20 cm dbh or slightly larger for canopy tree species on BCI (Wright *et al.* 2005). Thus, we limited comparisons of seedling and adult traits to canopy tree species because our tree plots missed reproductively mature shrubs, understory, and midstory trees.

**ANALYSES.**—We treated each 1-ha tree plot and its central 64-m<sup>2</sup> seedling plot as a replicate ( $N = 20$ ). We always weighted individuals

equally to calculate median trait values for each plot. We repeated all analyses for all seedlings and for older seedlings that lacked cotyledons or seed reserves. We felt this was necessary because germination is concentrated in May and June in central Panama (Garwood 1983), our seedling censuses extended from June through December, and therefore the number of recently germinated seedlings that survived until a plot was censused varied among plots. The presence of cotyledons identified recently germinated seedlings for most species. The text and figures present results for older seedlings that lacked cotyledons. The analysis for all seedlings is reported only when its results were qualitatively different (*i.e.*, significant versus insignificant outcomes are reported).

We performed two analyses of covariance (ANCOVA) to determine whether pre-existing differences in adult trees between protected and hunted sites might explain differences observed among tree seedlings. The ANCOVAs used a trait value calculated for tree seedlings as the response variable, the same trait value calculated for tree adults as a covariate, and the type of site (protected versus hunted) as a grouping factor. One ANCOVA was performed for median seed dry mass. A second ANCOVA was performed for the proportion of trees whose seed dispersal agents are unaffected by poachers (*i.e.*, seed dispersal is by bats, small birds or mechanical means).

We also performed *t*-tests to determine whether trait values differed between protected and hunted sites for seedlings from all life forms (the ANCOVAs were for canopy tree species only). Each *t*-test was preceded by an analysis of variance to determine whether the variance of the trait value was similar for the nine protected and 11 hunted sites, and the appropriate separate or pooled variance *t*-test was then chosen.

We use one-tailed probabilities when there was an *a priori* prediction and two-tailed probabilities otherwise. Each one-tailed probability is clearly identified and exact probabilities are given. Analyses were performed with SYSTAT© 11.0 (Richmond, CA, U.S.A.).

## RESULTS

We recorded 38,170 woody seedlings and 80 herbs less than 50 cm tall in the 20 64 m<sup>2</sup> plots. Henceforth, we will refer to herbs and woody seedlings as seedlings. We identified 94.5 percent of the seedlings to species, 1.54 percent to genus and 1.60 percent to family. We were unable to identify the final 2.36 percent of seedlings to family. The 312 identified species included 279 species among 20,231 established individuals that lacked cotyledons. An additional 33 species were only represented among the 18,019 recently recruited seedlings that retained cotyledons.

The community-level density and diversity of seedlings was similar for protected and hunted sites. The density of individuals (Fig. 2A; pooled variance  $t = 0.37$ ,  $P = 0.71$ ), the density of species (Fig. 2B; pooled variance  $t = -0.95$ ,  $P = 0.35$ ), and the Shannon–Wiener diversity index (Fig. 2C; pooled variance  $t = -0.50$ ,  $P = 0.63$ ) were statistically indistinguishable between protected and hunted sites for established seedlings that lacked cotyledons. The absence of statistically significant differences between protected and

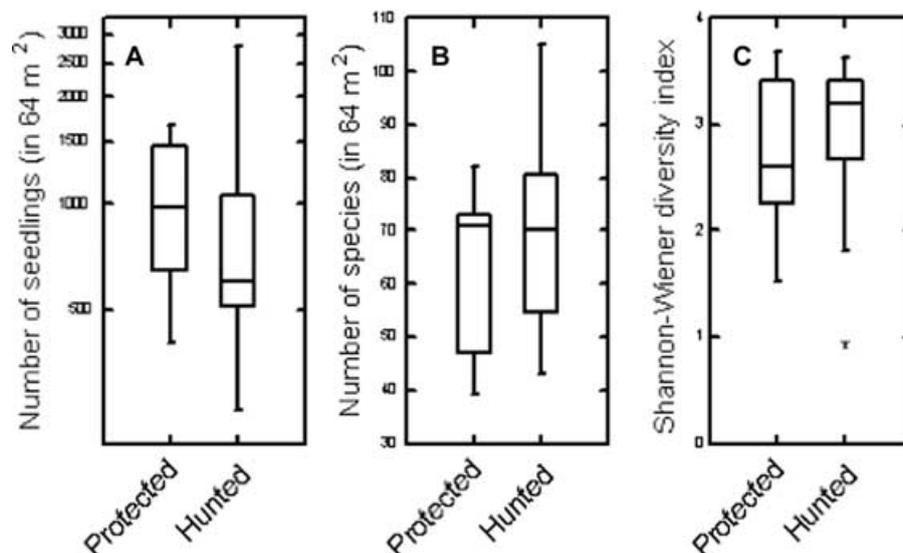


FIGURE 2. The density and diversity of seedlings for nine protected and 11 heavily hunted sites in central Panama. Box plots present the total number of seedlings (panel A), the number of species represented (B) and the Shannon–Wiener diversity index (C) for 64 m<sup>2</sup> plots. None of these community-level metrics differ significantly between protected and hunted sites. Within each box plot, the central horizontal line represents the median; the top and bottom horizontal lines are the first and third quartiles or hinges, respectively; the whiskers are the range of values within 1.5 inter-quartile ranges of the hinges; and the asterisks and open circles are values that fall more than 1.5 and 3 inter-quartile ranges from the hinges, respectively.

hunted sites also held for density and diversity when seedlings that retained cotyledons were included (data not shown).

**SEED MASS.**—Seed dry mass was known for 172 species and 30,222 (79.0%) of 38,250 seedlings overall and for 166 species and 13,363 (66.1%) of 20,231 seedlings that lacked cotyledons.

The outcome of the ANCOVA, which was performed for canopy tree species only, was consistent with the *a priori* prediction that poachers favor large-seeded species. Median seed masses were similar for adult trees and tree seedlings at protected sites, but were larger for tree seedlings than for adult trees for 10 of 11 hunted sites (Fig. 3). The ANCOVA interaction term was insignificant ( $F_{1,16} = 0.47$ ,  $P = 0.50$ ). After removing the interaction term ( $R^2 = 0.39$  for the reduced ANCOVA model), the median mass of tree seeds was significantly correlated with the median mass of tree seedlings ( $F_{1,17} = 6.99$ ,  $P = 0.017$ ) and hunted sites had significantly larger seedling seed masses than did protected sites ( $F_{1,17} = 6.22$ ,  $P = 0.011$ , one-tailed test).

The outcome of the *t*-test, which included seedlings from all life forms, was also consistent with the *a priori* prediction that poachers favor large-seeded species (Fig. 4). Median seed dry mass was marginally significantly greater at hunted sites than at protected sites for seedlings that lacked cotyledons (Fig. 4; pooled variance  $t = 1.71$ ,  $P = 0.052$ , one-tailed test). This final result was significant for all seedlings, including seedlings that retained cotyledons (data not shown, pooled variance  $t = 1.85$ ,  $P = 0.040$ , one-tailed test).

**SEED DISPERSAL AGENTS.**—The seeds of 35,711 (93.4%) of the 38,250 seedlings were known to be dispersed by means of one or more of the seven categories of dispersal agents (see METHODS:

PLANT TRAITS). This included 15 seedlings identified only to genus when all species in the genus were known to share a single combination of the seven seed dispersal categories.

The outcome of the ANCOVA, which was performed for canopy tree species only, did not support the *a priori* prediction that poachers favor species whose seed dispersal agents are not hunted. There was a surprising lack of relationship between the percentages of adult trees and tree seedlings whose seed dispersal agents are not hunted (Fig. 5;  $R^2 = 0.28$  for the full ANCOVA model). In retrospect, we believe seedling microhabitat requirements confounded this relationship. The 20 tree plots included 32 species and 641 individual canopy trees whose seed dispersal agents were unaffected by hunters. We were able to assign 24 of these species and 561 individuals to dichotomous light-demanding versus shade-tolerant guilds. Fully 67.4 percent of these 561 individuals were from the following seven highly light-demanding species: *Luehea seemannii*, *Terminalia amazonia*, *Jacaranda copaia*, *Cordia alliodora*, *Tabebuia guayacan*, *Pachira sessilis*, and *Hura crepitans*. These species cannot persist in our shaded understory seedling plots. We believe this explains why the proportion of tree seedlings of species whose seed dispersal agents are unaffected by hunters was consistently lower than the proportion of canopy trees drawn from those same species (Fig. 5).

The outcome of the *t*-test, which included seedlings from all life forms, was consistent with the *a priori* prediction that poachers favor species whose seed dispersal agents are not hunted (Fig. 6). Those species whose seeds are only dispersed by animals that are hunted comprised a significantly greater proportion of seedling individuals at protected sites relative to hunted sites (Fig. 6A; pooled variance  $t = 1.89$ ,  $P = 0.037$ , one-tailed test). And, those species whose seeds are

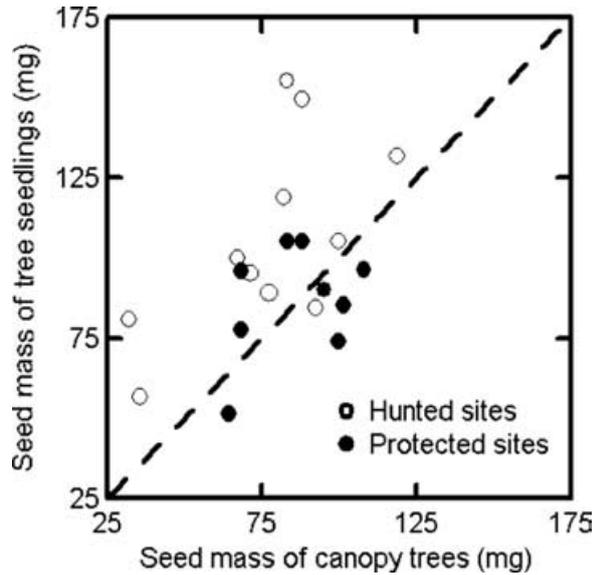


FIGURE 3. The relationship between median seed masses for canopy trees and seedlings of canopy trees for nine protected and 11 heavily hunted sites in central Panama. The dashed 1:1 line represents equal seed masses for trees and tree seedlings. Ten of 11 hunted sites fall above the 1:1 line meaning that seed masses for tree seedlings are larger than seed masses for adult trees. In contrast, protected sites tend to fall around the 1:1 line with four sites above and five sites below the 1:1 line. Two protected sites had nearly identical values, and one was moved slightly to make it visible.

dispersed mechanically or by animals that are never hunted in central Panama comprised a significantly greater proportion of seedling individuals at hunted sites relative to protected sites (Fig. 6C; pooled variance  $t = 1.90$ ,  $P = 0.038$ , one-tailed test). The final group of species whose seeds are dispersed by both hunted and never-hunted animals comprised a similar proportion of seedling individuals at protected and hunted sites (Fig. 6B, analysis not performed because proportions sum to one over the three categories of Figs. 6A, B, and C). We observed similar but marginally significant trends when seedlings that retained cotyledons were included (data not shown,  $0.05 < P < 0.10$ , one-tailed tests).

FREE-STANDING VERSUS CLIMBING SPECIES.—Life form was determined for 35,770 (93.5%) of the 38,250 seedlings. This included 9223 seedlings of climbing species and 6394 seedlings of canopy tree species.

The susceptibility of seed dispersal agents to hunting differed dramatically between species whose adults were free-standing versus climbing. Species whose seed dispersal agents are not hunted comprised 76 percent and 25 percent of all climbing and free-standing species, respectively (Table 1;  $\chi^2 = 56.2$ ,  $P < 1 \times 10^{-6}$ ). The many lianas with wind-dispersed seeds were largely responsible for this difference between life forms. The preponderance of climbing species whose seed dispersal agents are not hunted sets the stage for the final prediction that climbers should be more important at hunted sites.

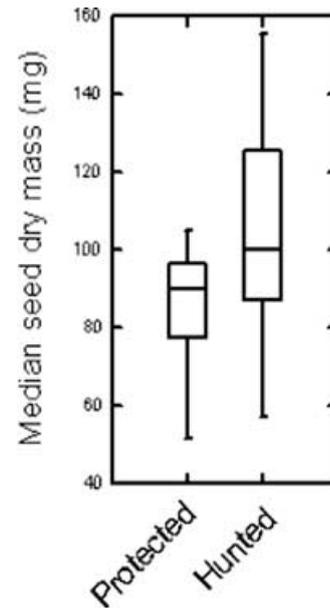


FIGURE 4. Median seed mass for all life forms for nine protected and 11 heavily hunted sites in central Panama. Seed mass was marginally significantly greater at hunted sites than at protected sites (pooled variance  $t = 1.71$ ,  $P = 0.052$ , one-tailed test). The caption to Figure 2 explains the box plots.

The outcome of the  $t$ -test was consistent with this *a priori* prediction. Climbers comprised a significantly larger proportion of seedlings at hunted sites than at protected sites (Fig. 6K, pooled variance  $t = 2.20$ ,  $P = 0.021$ , one-tailed test). This difference between protected and hunted sites was reinforced when seedlings that retained cotyledons were included (data not shown, pooled variance  $t = 2.89$ ,  $P = 0.0049$ , one-tailed test). The parallel analysis was not performed for free-standing species (Fig. 6G) because the proportions in Figures 6G and 6K sum to one. Figure 6 is constructed so that proportions sum over selected panels so that values in panel G equal the sum of the appropriate values in panels D, E, and F; K the sum of H, I, and J; A the sum of D and H; B the sum of E and I; and C the sum of F and J.

We next asked whether the different compositions with respect to seed dispersal agents observed between protected and hunted sites for all life forms (Figs. 6A–C) also held for species with free-standing adults alone (Figs. 6D–F) and species with climbing adults alone (Figs. 6H–J). The answer was a qualified yes, with statistical significance where numbers of seedlings were greatest. Species with free-standing adults whose seed dispersal agents are hunted comprised a median of 42.2 percent of seedlings overall and a significantly larger proportion of seedlings at protected sites than at hunted sites (Fig. 6D; pooled variance  $t = 1.77$ ,  $P = 0.047$ , one-tailed test). Species with climbing adults whose seed dispersal agents are not hunted comprised a median of 21.5 percent of seedlings overall and a significantly larger proportion of seedlings at hunted sites than at protected sites (Fig. 6J; separate variance  $t = 2.79$ ,  $P = 0.0070$ , one-tailed test). Thus, the preponderance of climbing species whose

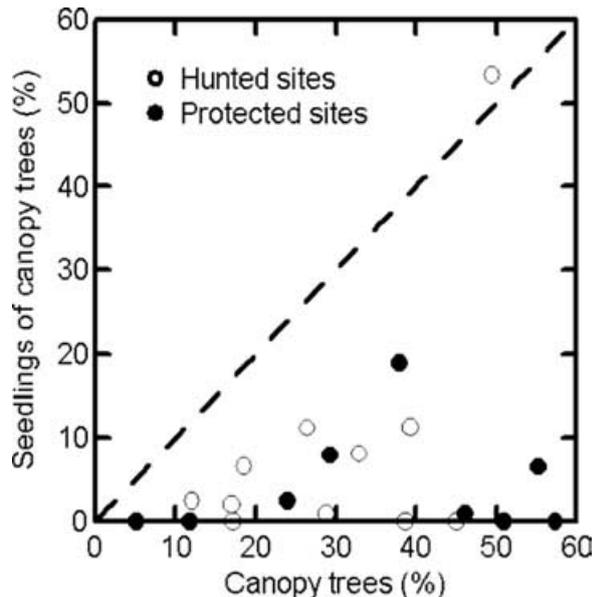


FIGURE 5. The relationship between the percentage of canopy trees and the percentage of seedlings of canopy trees comprised of species whose seed dispersal agents are not hunted for nine protected and 11 heavily hunted sites in central Panama. The dashed 1:1 line represents equal percentages for canopy and seedling individuals. Nineteen of 20 sites fall below the 1:1 line because the tree species whose seed dispersal agents are not hunted tend to have light-demanding seedlings that are poorly represented at our closed-canopy sites. Two hunted sites had nearly identical values, and one was moved slightly to make it visible.

seed dispersal agents are not hunted (largely wind-dispersed lianas) leads to increased success of seedlings of climbing species at hunted sites.

## DISCUSSION

This study demonstrates that hunting alters the species composition of the seedling bank by favoring species with large seeds (Figs. 3 and 4) and species with seeds dispersed by bats, small birds, and mechanical means (Fig. 6). These conclusions are reinforced because we are also able to demonstrate that the composition of the seedling bank diverges from the local composition of adults at hunted sites for seed mass (Fig. 3) and that the composition of the seedling bank does not reflect pre-existing differences in the local composition of adults for seed dispersal modes (Fig. 5). We conclude that hunting altered community-level plant species composition in the seedling layer.

Mechanisms are likely to involve changes in seed predation and dispersal caused by the bushmeat harvest. We hypothesize that hunters favor large seeds by removing large vertebrate seed predators and increasing survival rates for large seeds (Dirzo *et al.* 2007). This has been documented for two large-seeded palm species in central Panama (Wright *et al.* 2000, Wright & Duber 2001). We also hypothesize that hunters reduce seed dispersal and hence seed and

seedling survival for species with seeds dispersed by game species and thereby indirectly favor species with seeds dispersed by bats, small birds, and mechanical means. Game species often disperse and consume the same large seeds. This raises the additional possibility that hunters might reduce both dispersal and predation for the same large-seeded plant species. This added complication was also documented for the same two large seeded palm species, and the decrease in seed predation outweighed effects mediated by seed dispersal such that the seedling densities of these two large-seeded palms were greatest at the most heavily hunted sites (Wright *et al.* 2000, Wright & Duber 2001).

There is probably not a single plant species whose seeds are *only* dispersed by game species in central Panama. Every species with fleshy fruit attracts multiple animal species and several potential seed dispersal agents. Although hunters only take large birds and mammals in central Panama, there are other large birds and relatively large mammals that are not hunted. Examples include toucans, parrots, red-tailed squirrels, and kinkajous (*Potos flavus*; Méndez 1970, Wright *et al.* 2000). Thus, even those plant species whose seed dispersal agents include game species are likely to have other nonhunted seed dispersal agents in this study. This complexity highlights the need for more detailed studies to identify the effects of hunting for seed dispersal versus seed predation.

**LIANAS.**—We also found that climbing species, which are overwhelmingly woody lianas, are more important in the seedling bank at heavily hunted sites than at protected sites (Fig. 6K), and we believe we have identified the likely mechanism. Hunting favors lianas because the seeds of disproportionate numbers of liana species are dispersed by wind (Figs. 6H–J, Table 1; Gentry 1983). Our findings for lianas in the seedling bank cannot be validated against the adult community because the adult liana community was not documented. The absence of any difference between hunted and protected sites for the adult tree community (consider the distribution of sites along the horizontal axes in Figs. 3 and 5) suggests, however, that there is no reason to anticipate differences in the adult liana community. We conclude that hunting favors the many liana species with wind-dispersed seeds.

Large increases in the importance of lianas relative to baseline values from the 1980s have been documented for old-growth forests in the western Amazon from repeated censuses of the largest lianas (>10 cm dbh, Phillips *et al.* 2002) and for old-growth forests on BCI from the species composition of falling leaves and flowers (Wright *et al.* 2004, Wright & Calderón 2006). Prior to this study, speculation about possible causation has focused on a particularly strong response by lianas to fertilization by rising nutrient deposition and/or atmospheric CO<sub>2</sub> concentrations. The widespread disruption of tropical forest mammal communities by hunters must now be added to the mix of possible causes of long-term increases in the importance of the many lianas with wind-dispersed seeds.

The long-term increase of lianas on BCI presents a paradox because BCI is perhaps the most rigorously protected site in the Neotropics today. This has not always been the case, however, and a brief history of poaching on BCI can help to resolve the apparent paradox. BCI became a nature reserve in 1923, but lacked guards.

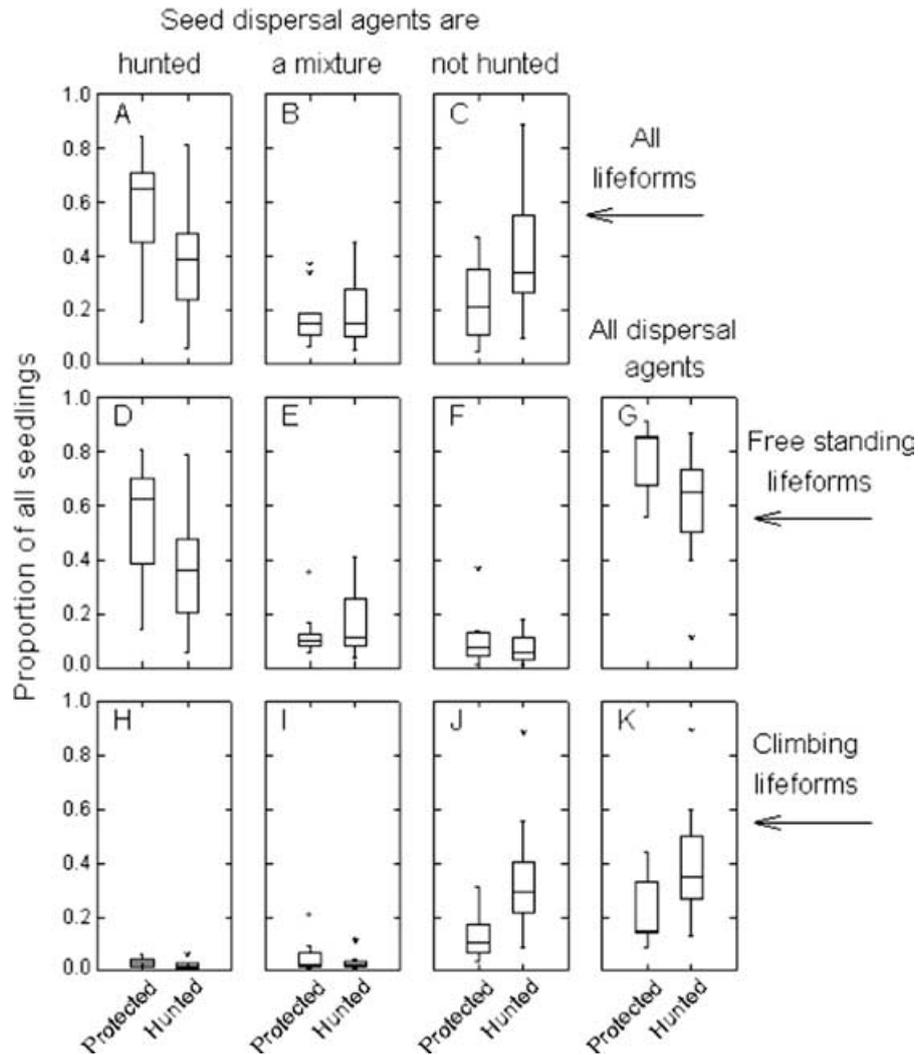


FIGURE 6. The proportion of all seedlings partitioned by the susceptibility of their seed dispersal agents to hunters for all life forms (panels A–C), free-standing life forms (D–G), and climbing life forms (H–K). Seed dispersal agents include hunted species (A, D, H), a mixture of hunted and nonhunted agents (B, E, I), or only nonhunted agents (C, F, J). All primary seed dispersal agents are pooled in panels G and K. Proportions sum over selected panels so that values in panel G equal the sum of the appropriate values in panels D, E, and F; K the sum of H, I, and J; A the sum of D and H; B the sum of E and I; and C the sum of F and J. The caption to Figure 2 explains the box plots.

Poachers discovered BCI in 1932 and quickly eliminated white-lipped peccaries (*Tayassu pecari*), puma (*Puma concolor*) and tapir (Enders 1939). Residents of the former Panama Canal Zone believed members of the Canal Zone Bush Police treated BCI as a private hunting reserve in the 1950s, 1960s, and early 1970s (S. J. Wright, numerous personal conversations from the late 1970s). Six forest guards patrolled BCI by the late 1970s; however, scientists reported frequent gunshots and believed the supervisor of the forest guards suppressed evidence of poaching (S. J. Wright, pers. obs.). Unequivocal evidence of poaching emerged in 1985 and 1986 soon after the suspect supervisor retired. Equipment and methods were improved in response, and the number of guards was doubled over the next 8 yr. The most important change made in the late 1980s might have

been the initiation of ambushes at the fruiting trees that concentrated game animals. This greatly increased the number of poachers captured throughout the BCNM. The last evidence of poachers recorded on BCI was the remains of two cleaned deer discovered after BCI was evacuated during the invasion of Panama by the USA in December 1989. The increase in the importance of lianas documented between 1986 and 2005 for BCI (Wright *et al.* 2004, Wright & Calderón 2006) can now be reconciled with changes in poaching pressure by a lag between the composition of the seedling bank, which was influenced by poachers into the 1980s, and the eventual recruitment of lianas from the seedling bank to the forest canopy whence they contribute to leaf fall and flower production. A role for other regional and global drivers is also likely.

TABLE 1. Numbers of species classified by life form (free-standing vs. climbing) and by the susceptibility of their seed dispersal agents to hunters (hunted vs. nonhunted) among seedlings encountered at 20 sites in central Panama.

Seed dispersal agents	Life form	
	Free-standing	Climbing
Nonhunted (bats, small birds, mechanical means)	46	56
Hunted (large birds, nonvolant mammals)	137	18

IMPLICATIONS FOR DIVERSITY.—We did not observe changes in seedling bank diversity in this study (Fig. 2); however, the changes observed in the species composition of the seedling bank set the stage for future changes in community-level diversity. Tropical forest plants regenerate from seed via the recent seed rain, a soil seedbank of dormant seeds, a seedling bank of suppressed understory seedlings, and/or the advanced regeneration of suppressed understory saplings. The seedling bank and the advanced regeneration grade together seamlessly as seedlings age, grow and become saplings. Light-demanding ‘pioneers’ tend to regenerate from the seed rain and/or the soil seedbank, while shade tolerant ‘climax’ species tend to regenerate from the understory seedling/sapling bank. Most forest species are relatively shade tolerant and regenerate from the seedling/sapling bank in central Panama (Wright *et al.* 2003). Thus, changes in the species composition of the seedling bank have the potential to change future community-level diversity.

The bushmeat harvest impacts several mechanisms that are widely believed to promote the coexistence of plant species in tropical forests (Wright 2003, Muller-Landau 2007). Poachers will increase dispersal and recruitment limitation by reducing dispersal distances for seeds dispersed by game species, which has the potential to reduce local diversity in the short term and also to increase regional diversity in the longer term (Muller-Landau *et al.* 2002). Poachers alter the spatial dynamics of regeneration posited by Janzen (1970) by reducing dispersal distances and altering seed and seedling survival, which also has the potential to reduce local diversity (Wright & Duber 2001, Terborgh *et al.* 2002). Finally, poachers alter competitive interactions, by favoring larger seeds that already develop into larger, more competitive seedlings, and this too has the potential to reduce local diversity (Wright 2003, Dirzo *et al.* 2007, this study). All mechanisms point toward the prediction first enunciated by Emmons (1989) and Dirzo and Miranda (1991) that hunting will eventually lead to declines in the local diversity of tropical forest plants (Muller-Landau 2007).

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## LITERATURE CITED

- BECKMAN, N., AND H. C. MULLER-LANDAU. 2007. Differential effects of hunting on pre-dispersal seed predation, primary dispersal, and secondary seed removal of two tropical tree species. *Biotropica* 39: 328–339.
- CHAZDON, R., S. CAREAGA, C. WEBB, AND O. VARGAS. 2003. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecol. Monogr.* 73: 331–348.
- CONDIT, R. 1998. Tropical forest census plots. Springer-Verlag, Berlin, Germany. 211 pp.
- CONDIT, R., N. PITMAN, E. G. LEIGH, J. CHAVE, J. TERBORGH, R. B. FOSTER, P. NÚÑEZ, S. AGUILAR, R. VALENCIA, G. VILLA, H. C. MULLER-LANDAU, E. LOSOS, AND S. P. HUBBELL. 2002. Beta-diversity in tropical forest trees. *Science* 295: 666–669.
- CORLETT, R. T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* 39: 292–303.
- DAWS, M. I., N. C. GARWOOD, AND H. W. PRITCHARD. 2005. Traits of recalcitrant seeds in a semi-deciduous tropical forest in Panamá: Some ecological implications. *Funct. Ecol.* 19: 874–885.
- DIRZO, R. 2001. Plant-mammal interactions: Lessons for our understanding of nature, and implications for biodiversity conservation. *In* M. C. Press, N. J. Huntly and S. Levin (Eds.). *Ecology: Achievement and challenge*, pp. 319–335. Blackwell Science, Oxford, UK.
- 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. *In* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson (Eds.). *Plant-animal interactions: Evolutionary ecology in tropical and temperate regions*, pp. 273–287. Wiley & Sons, New York, New York.
- DIRZO, R., E. MENDOZA, AND P. ORTÍZ. 2007. Effects of differential mammal defaunation on seed predation patterns in a Mexican tropical rain forest. *Biotropica* 39: 355–362.
- EMMONS, L. H. 1989. Tropical rain forests: Why they have so many species and how we may lose this biodiversity without cutting a single tree. *Orion* 8: 8–14.
- ENDERS, R. K. 1939. Changes observed in the mammal fauna of Barro Colorado Island, 1929–1937. *Ecology* 20: 104–106.
- FA, J. E., C. PERES, AND J. MEEUWIG. 2002. Bushmeat exploitation in tropical forests: An intercontinental comparison. *Conserv. Biol.* 16: 232–237.
- GALETTI, M., C. I. DONATTI, A. S. PIRES, P. R. GUIMARÃES JR, AND P. JORDANO. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: The combined effects of defaunation and forest fragmentation. *Bot. J. Linn. Soc.* 151: 141–149.
- GARWOOD, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: A community study. *Ecol. Monogr.* 53: 159–181.
- GENTRY, A. H. 1983. Dispersal ecology and diversity in Neotropical forest communities. *In* K. Kubitzki (Ed.). *Dispersal and distribution: An international symposium*, pp. 303–314. Paul Parey, Hamburg, Germany.
- GILBERT, B., S. J. WRIGHT, K. KITAJIMA, H. C. MULLER-LANDAU, AND A. HERNÁNDEZ. 2006. Life history trade-offs in tropical trees and lianas. *Ecology* 87: 1281–1288.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501–528.
- MÉNDEZ, E. 1970. Los principales mamíferos silvestres de Panamá. Imprenta Bárcenas, Panamá City, República de Panamá.

- MULLER-LANDAU, H. C. 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica* 39: 372–384.
- MULLER-LANDAU, H. C., AND B. D. HARDESTY. 2005. Seed dispersal of woody plants in tropical forests: Concepts, examples, and future directions. *In* D. F. R. P. Burslem, M. A. Pinard, and S. Hartley (Eds.). *Biotic interactions in the tropics*, pp. 267–309. Cambridge University Press, Cambridge, UK.
- MULLER-LANDAU, H. C., S. J. WRIGHT, O. CALDERÓN, S. P. HUBBELL, AND R. B. FOSTER. 2002. Assessing recruitment limitation: Concepts, methods, and case studies from a tropical forest. *In* D. J. Levey, W. R. Silva, and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 35–53. CABI Publishing, Wallingford, Oxfordshire, UK.
- NUNEZ-ITURRI, G., AND H. F. HOWE. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rainforest in western Amazonia. *Biotropica* 39: 348–354.
- PERES, C. A., AND E. PALACIOS. 2007. Basin-wide effects of game harvest on vertebrate population densities in Neotropical forests: Implications for animal-mediated seed dispersal. *Biotropica* 39: 304–315.
- PERES, C. A., AND M. VAN ROOSMALEN. 2002. Patterns of primate frugivory in Amazonia and the Guianan shield: Implications to the demography of large-seeded plants in overhunted tropical forests. *In* D. Levey, W. Silva, and M. Galetti, (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 407–423. CAB International, Oxford, UK.
- PHILLIPS, O. L., R. VASQUEZ MARTINEZ, L. ARROYO, T. R. BAKER, T. KILLEEN, S. L. LEWIS, Y. MALHI, A. M. MENDOZA, D. NEILL, P. NUNEZ VARGAS, M. ALEXIADES, C. CERON, A. DI FIORE, T. ERWIN, A. JARDIM, W. PALACIOS, M. SALDIAS, AND B. VINCETI. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770–774.
- REDFORD, K. H. 1992. The empty forest. *Bioscience* 42: 412–422.
- ROLDÁN, A. I., AND J. A. SIMONETTI. 2001. Plant-mammal interactions in tropical Bolivian forests with different hunting pressures. *Conserv. Biol.* 15: 617–623.
- TERBORGH, J., N. PITMAN, M. SILMAN, H. SCHICHTER, AND P. NUÑEZ V. 2002. Maintenance of tree diversity in tropical forests. *In* D. J. Levey, W. R. Silva, and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 1–17. CABI Publishing, Wallingford, UK.
- WANG, B. C., M. T. LEONG, T. B. SMITH, AND V. L. SORK. 2007. Hunting of mammals reduces seed removal and dispersal of the Afrotropical tree, *Antrocaryon klaineianum* (Anacardiaceae). *Biotropica* 39: 340–347.
- WRIGHT, S. J. 2003. The myriad effects of hunting for vertebrates and plants in tropical forests. *Perspect. Plant Ecol. Evol. Syst.* 6: 73–86.
- WRIGHT, S. J., AND O. CALDERÓN. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.* 9: 35–44.
- WRIGHT, S. J., AND H. C. DUBER. 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33: 583–595.
- WRIGHT, S. J., O. CALDERÓN, A. HERNÁNDEZ, AND S. PATON. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85: 494–489.
- WRIGHT, S. J., M. A. JARAMILLO, J. PAVON, R. CONDIT, S. P. HUBBELL, AND R. B. FOSTER. 2005. Reproductive size thresholds in tropical trees: Variation among individuals, species and forests. *J. Trop. Ecol.* 21: 307–315.
- WRIGHT, S. J., H. C. MULLER-LANDAU, R. CONDIT, AND S. P. HUBBELL. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84: 3174–3185.
- WRIGHT, S. J., H. ZEBALLOS, I. DOMÍNGUEZ, M. M. GALLARDO, M. C. MORENO, AND R. IBÁÑEZ. 2000. Poachers alter mammal abundance, seed dispersal and seed predation in a Neotropical forest. *Conserv. Biol.* 14: 227–239.