
Poachers Alter Mammal Abundance, Seed Dispersal, and Seed Predation in a Neotropical Forest

S. JOSEPH WRIGHT,*§ HORACIO ZEBALLOS,†‡ IVÁN DOMÍNGUEZ,‡
MARINA M. GALLARDO,‡ MARTA C. MORENO,‡ AND ROBERTO IBÁÑEZ*‡

*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancón, República de Panamá

†Prodefensa de la Naturaleza-Arequipa, Jorge Polar N. 308, Miraflores, Arequipa, Perú

‡Instituto Nacional de Recursos Naturales Renovables, Dirección Nacional de Cuencas Hidrográficas, Apartado 2016, Panamá, República de Panamá

Abstract: *We evaluated the hypothesis that poachers reduce the abundance of herbivorous mammals, and that this, in turn, alters seed dispersal, seed predation, and seedling recruitment for two palms (*Attalea butyraceae* and *Astrocaryum standleyanum*) in central Panama. Using physical evidence left by poachers and interviews with forest guards, we quantified poaching intensity for eight forest sites. We quantified mammal abundance using transect counts and small-mammal traps. Abundance was inversely related to poaching intensity for 9 of 11 mammal species (significantly so for 5 species), confirming the first component of the hypothesis. The outcome of interactions among seeds, mammals, and beetles also varied with poaching intensity. Nonvolant mammals were the only seed-dispersal agents, and rodents and beetles were the only seed predators. We quantified seed fate by examining the stony endocarps that encase the seeds of both palms. The large, durable endocarps were located easily on the forest floor and bear characteristic scars when a rodent or beetle eats the enclosed seed. The proportion of seeds dispersed away from beneath fruiting conspecifics was inversely related to poaching intensity, ranging from 85% to 99% at protected sites where mammals were abundant and from 3% to 40% at unprotected sites where poachers were most active. The proportion of dispersed seeds destroyed by beetles was directly related to poaching intensity, ranging from 0% to 10% at protected sites and from 30% to 50% at unprotected sites. The proportion of dispersed seeds destroyed by rodents was inversely related to poaching intensity, ranging from 85% to 99% at protected sites and from 4% to 50% at unprotected sites. Finally, seedling densities were directly related to poaching intensity. There was no single relationship between poaching intensity and the biotic interactions that determine seedling recruitment. The net effect of poaching on seedling recruitment can be determined only empirically. For these palms, seedling densities were directly related to poaching intensity.*

Los Cazadores Alteran la Abundancia, Dispersión de Semillas y Depredación de Semillas en un Bosque Neotropical

Resumen: *Evaluamos la hipótesis que los cazadores reducen la abundancia de mamíferos herbívoros y que esto, a su vez, altera la dispersión de semillas, la depredación de semillas y el reclutamiento de plántulas de dos palmeras (*Attalea butyraceae* y *Astrocaryum standleyanum*) en Panamá central. La intensidad de cacería fue cuantificada para ocho sitios dentro de bosque, utilizando la evidencia física dejada por los cazadores y entrevistas con los guardaparques. La abundancia de mamíferos fue cuantificada usando conteos a lo largo de transectos y trampas para los mamíferos pequeños. La abundancia estuvo inversamente relacionada a la intensidad de cacería para nueve de 11 especies de mamíferos (significativamente en cinco especies), confirmando el primer componente de la hipótesis. El resultado de las interacciones entre semillas, mamíferos y escarabajos, también varió con la intensidad de cacería. La suerte de las semillas fue cuantificada utilizando el endocarpo duro que recubre a las semillas de ambas palmeras. Estos endocarpos grandes y durables son fácilmente encontrados sobre el suelo del bosque, y tienen cicatrices características cuando un roedor o es-*

§Address correspondence to Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, U.S.A.
Paper submitted July 6, 1998; revised manuscript accepted June 9, 1999.

carabajo comió la semilla dentro de éste. Los mamíferos no voladores son los únicos agentes que dispersan estas semillas, y los roedores y escarabajos son los únicos depredadores de las mismas. La proporción de las semillas dispersadas, lejos de abajo de los coespecificos en fructificación, estuvo inversamente relacionada a la intensidad de cacería (dentro de un rango desde 85% hasta 99% en los sitios protegidos donde los mamíferos eran abundantes, y desde 3% hasta 40% en los sitios desprotegidos donde los cazadores estaban más activos). La proporción de semillas dispersadas exterminadas por escarabajos estuvo directamente relacionada a la intensidad de cacería (dentro de un rango desde 0% hasta 10% en los sitios protegidos, y desde 30% hasta 50% en los sitios desprotegidos). La proporción de semillas dispersadas exterminadas por roedores estuvo inversamente relacionada a la intensidad de cacería (dentro de un rango desde 85% hasta 99% en los sitios protegidos, y desde 4% hasta 50% en los sitios desprotegidos). Finalmente, las densidades de plántulas estuvieron directamente relacionadas a la intensidad de cacería. No se encontró una relación única entre la intensidad de cacería y las interacciones bióticas que determinan el reclutamiento de plántulas. El efecto neto de la cacería sobre el reclutamiento de plántulas solamente puede ser determinado empíricamente.

Introduction

Hunters kill and maim some 60 million animals in Neotropical forests each year (Redford 1992). Preferred game species include monkeys, peccaries, tapir, deer, and caviomorph rodents (Redford & Robinson 1987). These herbivores disperse seeds, eat seeds, and/or browse seedlings. Their removal may directly alter plant regeneration and may also have indirect effects on plant regeneration if competitive release favors other herbivores. Nonindigenous peoples rarely hunt squirrels, other small rodents, or nocturnal, arboreal mammals in the Neotropics (Redford & Robinson 1987). These species also disperse and eat seeds, and their numbers may increase after game species are removed. Insects and microbes that attack seeds and seedlings may also multiply if seed and seedling densities increase. A range of direct and indirect effects may follow when poachers remove herbivores, but the net effect on plant regeneration is unclear.

Two case studies illustrate the possibilities. Dirzo and Miranda (1991) compared plant regeneration at Montes Azules and Los Tuxtlas, Mexico. The mammal fauna of Montes Azules is intact, whereas poachers and habitat fragmentation have combined to reduce populations of caviomorph rodents and to extirpate tapir, peccaries, and deer from Los Tuxtlas. Dense carpets of seedlings covered the forest floor at Los Tuxtlas, but not at Montes Azules. Partial mammal defaunation *increased* seedling recruitment. The opposite occurred in central Panama (Asquith et al. 1997). Experimental fences protected seedlings at sites with four nested mammal communities. Survival of protected seedlings was similar at all sites. Survival of unprotected seedlings was lowest where the spiny rat (*Proechimys semispinosus*) was the only nonvolant mammal, intermediate where an opossum and a larger caviomorph rodent were also resident, and greatest where the fauna of herbivorous mammals was complete. Partial mammal defaunation *decreased* seedling recruitment.

Why did partial mammal defaunation have opposite effects in Mexico and Panama? The intricate web of direct and indirect effects of mammal defaunation makes this question difficult to answer without documenting the processes that determine seedling recruitment. We evaluated seed dispersal, seed predation, and seedling recruitment for two species of palms at eight sites with different levels of poaching. We sought to answer six questions: (1) Does poaching reduce mammal abundance? (2) Is seed dispersal affected? (3) Is seed predation by mammals and insects affected? (4) Does this affect seedling recruitment? (5) Is the density and diversity of plants in the herbaceous layer affected? and (6) Does poaching alter plant species composition?

Study Species

The palms *Astrocaryum standleyanum* L. H. Bailey and *Attalea butyraceae* (Mutis ex. L.f.) Wess. Boer are abundant in central Panama. Falling fronds, spathes, and pedicels doom seedlings that germinate beneath adults (S.J.W., personal observation). Seedlings that germinate away from adults produce entire leaves for several years before developing into a basal rosette of complex fronds. This latter stage may persist for 20 years or more before trunk growth begins (S.J.W., personal observation). The monoecious trees are 15 m and 30 m tall, respectively, and produce from one to three (rarely four) infructescences each year (De Steven et al. 1987). The number of seeds per infructescence ranges from 20 to 400 for *Astrocaryum* and from 100 to 600 for *Attalea* (Smythe 1989; Wright 1990). The stony endocarps are large (3–5 cm long) and easy to locate on the forest floor. Germination may occur up to 3 years after seed dispersal (Smythe 1989; Harms & Dalling 1995). Endocarps persist on the forest floor for several years (Wright 1983, 1990; Smythe 1989). These traits permit quantification of seed dispersal and seed fate.

Mammals disperse and eat the seeds of both species. Red-tailed squirrels (*Sciurus granatensis*), agoutis (*Dasyprocta punctata*), and spiny rats gnaw through the stony endocarps to eat the seed (Smythe et al. 1982; Giacalone-Madden et al. 1990; Adler 1995; Hoch & Adler 1997). This leaves persistent and unmistakable tooth scars on the endocarp. Bruchid beetles are the only other predators of mature seeds, and bruchids leave equally persistent and unmistakable emergence holes (Smythe 1989; Wright 1990; Johnson et al. 1995). White-faced monkeys (*Cebus capucinus*), spider monkeys (*Ateles geoffroyi*), howler monkeys (*Alouatta palliata*), kinkajous (*Potos flavus*), coatis (*Nasua narica*), red-tailed squirrels, agoutis, pacas (*Agouti paca*), and spiny rats disperse the seeds of one or both species (Enders 1935; Smythe et al. 1982; Giacalone-Madden et al. 1990; Gompper 1996; Kays 1999). Several species of opossum, olingos (*Bassaricyon gabbii*), tayras (*Eira barbara*), armored rats (*Hopломys gymnurus*), collared peccaries (*Tayassu tajacu*), and tapir (*Tapirus bairdii*) may also disperse the seeds (Charles-Dominique et al. 1981; Kiltie 1981). Neither bats nor birds disperse the seeds of either species (E. Kalko and C. O. Handley, personal communication; S.J.W., personal observation).

Study Sites

The eight study sites support secondary evergreen forests with 20 to 30-m tall canopies (Fig. 1). Forest age ranges from 80 to 150 years, with a few more recent openings (Foster & Brokaw 1982). Annual rainfall averages 2188 mm to the southeast at Gamboa and 2612 mm to the northwest at Barro Colorado Island (BCI; Windsor 1990). This gradient reflects heavier wet-season rainfall to the northwest and has little effect on the vegetation. The entire area would be classified as lowland rain forest in a wet climate under Walsh's (1996) scheme. Tree species composition is strikingly similar at all sites, with the exception of Rio Macho, where the bedrock is distinctive (R. Condit, unpublished data).

Levels of protection from poaching differ widely among sites. Eighteen forest guards protect BCI and Gigante (GIG) within the Barro Colorado Nature Monument (BCNM). Twelve forest guards protect Rio Macho (MAC), Limite (LIM), Plantation Road (PLA), Sendero Las Cruces (SLC), and Carretera C25 (C25) within the much larger Parques Nacionales Soberanía and Camino de Cruces (Fig. 1). Rio Mandinga (MAN) is unprotected. The level of protection changed for the six sites outside the BCNM when the Canal Zone Government ended in 1979. Before 1979, hunters from Panama were excluded, and hunters from the Canal Zone were encouraged. Adult palms and older juveniles probably became established under the pre-1979 hunting regime. For this reason, we evaluated the performance only of seeds and seedlings (plants with entire leaves only) under the current hunting regime.

Methods

Poaching Intensity

Most hunting is illegal in Panama, and it was necessary to use indirect methods to assess poaching intensity. We recorded evidence of poaching during mammal transect censuses, including structures (blinds and camps), tracks of poachers and their dogs, shotgun shells, hunting implements, gunshots heard, and encounters with armed poachers. Forest guards and records of poachers captured (available only for the BCNM) provided a second independent assessment for the seven protected sites. Of the 12 national park guards, 8 were asked as a group to rank poaching pressure for the five sites within their jurisdiction. The national park and BCNM guards were also asked to compare levels of poaching between the national parks and the BCNM.

We used three methods to assess poaching intensity for different mammal species. First, we compiled records of mammals confiscated from poachers within the BCNM (BCNM Security Forces, unpublished data). Second, the eight national park guards independently scored 28 mammal species from most (1) to least (5) preferred. No score was assigned when a guard believed a species was never hunted within the national parks. Finally, based on 40 years of experience throughout Panama, Méndez (1970, 1993) assessed poaching intensity for many mammal species.

Mammal Abundance

A 5-km trail was chosen at each site by technicians who were unfamiliar with our research objectives (Fig. 1). Pre-existing trails were selected at BCI, GIG, LIM, and SLC. New loop trails were opened at MAC, MAN, PLA, and C25. All measurements took place along these trails.

A transect count was conducted along each 5-km trail once each week from 18 August through 11 December 1997. Censuses were conducted between 0615 and 1130 hours when it was not raining. The observer covered 1.2 km/hour and noted the species, sex, age (juvenile or adult), and initial detection distance between mammal and observer. Detection distances were measured with a range finder (Bushnell 71-0075, E. Bloomfield, New York).

The King estimator was used to estimate population densities from transect counts (Freese et al. 1982; Glanz 1982; Wright et al. 1994; Peres 1996). The King estimator is $D = N/(2LR)$, where D is the estimated population density, N is the number of individuals encountered, L is the length of transect, and R is the mean detection distance. For social species, N is often estimated by multiplying the number of social groups encountered by mean group size (Freese et al. 1982; Glanz 1982). We avoided this convention because group size may vary

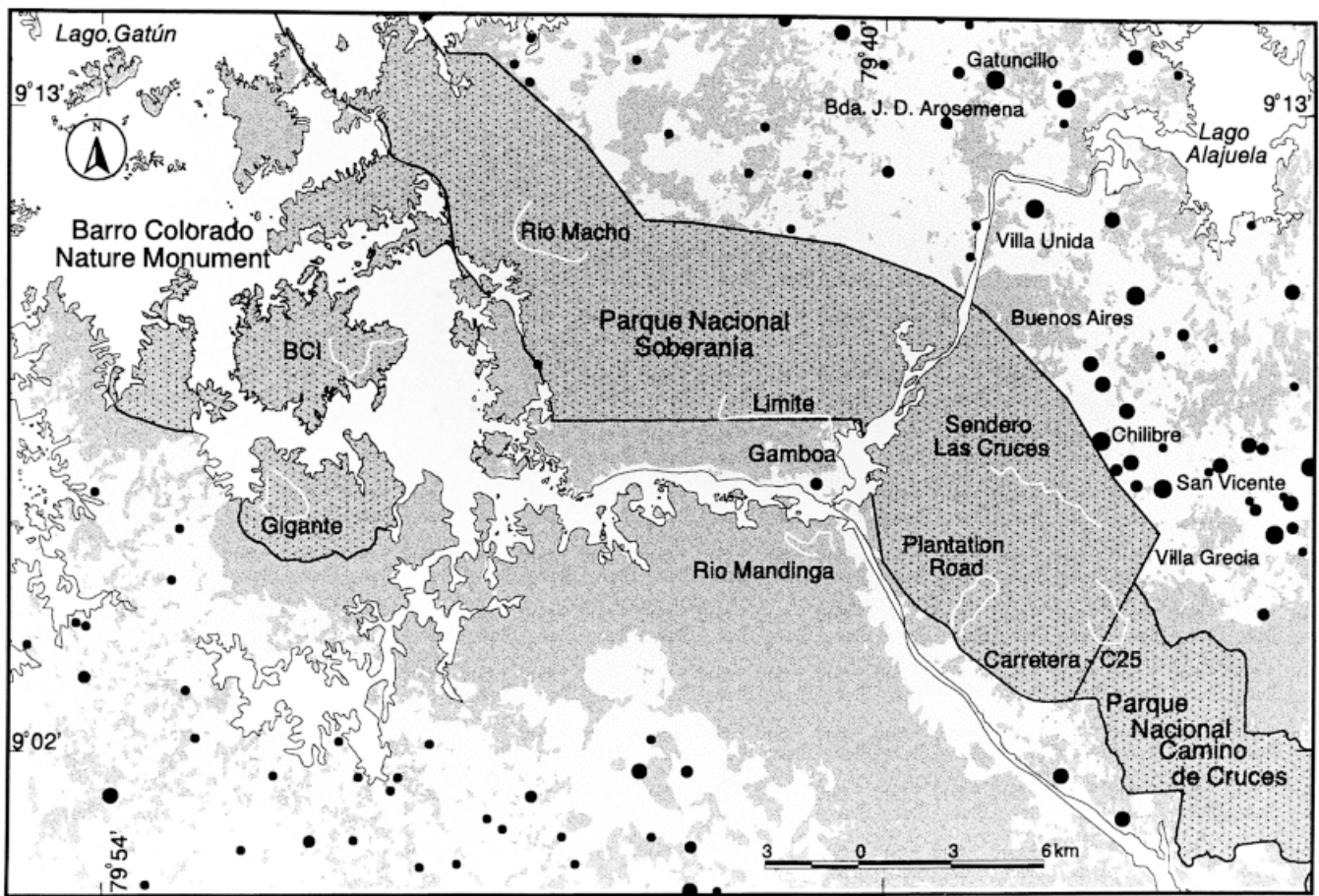


Figure 1. Map of central Panama. Gray shading represents forest cover in 1998 as determined from Landsat images. White lines represent the eight 5-km transects. Solid lines and speckling represent the Barro Colorado Nature Monument and the Parques Nacionales Soberanía and Camino de Cruces. Solid circles represent villages. The size of the circle represents the number of inhabitants in 1990 (small, <250 inhabitants; intermediate ≥ 250 and <2000; large ≥ 2000 ; Censo Nacional de 1990, Contraloría General de la República de Panamá). Landsat images were Thematic Mapper, path 12, row 54 for 19 March 1996, 3 March 1997, and 18 February 1998.

with poaching. Instead, for coatis and collared peccaries, we estimated N directly by counting each animal in each group. For primates, the time required to count the individuals in a troop precluded an ongoing census, so primate abundance was reported as the number of groups encountered per kilometer.

There have been several discussions of the reliability of transect censuses for central Panama (Eisenberg & Thorington 1973; Glanz 1982; Gompper 1996). Abundance estimates from transect censuses and more intensive methods are similar for agoutis, coatis, collared peccaries, and diurnal primates. Transect efficiency cannot be assessed for deer because more intensive methods have not been used. Transect censuses consistently underestimate squirrel densities, and squirrel density is best regarded as an estimate of relative abundance.

Two bouts of small-mammal trapping were conducted at each site. The first occurred between 17 September and 26 November 1997 and the second between 1 De-

cember 1997 and 30 January 1998. During each bout, 28–30 Sherman and 112–116 Tomahawk traps were operated for 5 consecutive nights along two randomly chosen 1.4-km sections of each 5-km trail. Traps were separated by 15–20 m and were placed near a fallen tree or branch, or, where fallen debris were absent, near the base of a large tree. A claw was clipped on captured animals, and recaptures were not counted within trapping bouts. We reported relative abundance as the number of animals captured per 100 trap nights, averaged over the two trapping bouts.

Two predictions will hold if poachers reduce mammal abundance. First, poaching intensity and the abundance of game species should be negatively correlated in intersite comparisons. Second, poaching intensity and spatial variation in abundance should be positively correlated in interspecific comparisons, because poaching has a disproportionate effect on preferred game species, whereas other sources of variation (measurement error, physical

differences among sites) affect all species. The intersite coefficient of variation quantified spatial variation in abundance. Spearman rank tests were used to evaluate correlations. All analyses were performed with SYSTAT 5.0 (Wilkinson 1990).

Early Palm Regeneration

Seeds fail to arrive in most appropriate habitats because reproductive plants are patchily distributed and seed dispersal is limited (Hubbell et al. 1999). Seedling regeneration was therefore characterized where reproductive conspecifics were present. Visible trees were noted from each 100-m segment of each 5-km trail. The trunks and crowns of both palms are distinctive, and foot surveys confirmed that virtually all trees were visible up to 22 m from a trail. Four or five trail segments with visible trees were selected at random for each site for subsequent measurements.

The proportion of seeds dispersed from beneath conspecific trees (P) was quantified as

$$P = S_d / (S_d + T \times S_t \times A), \quad (1)$$

where T is the density of reproductive conspecifics (trees m^{-2}), S_d is the density of seeds dispersed away from reproductive conspecifics (seeds m^{-2}), S_t is the density of seeds directly under reproductive conspecifics (seeds m^{-2}), and A is the horizontal projection of the crown onto the ground ($\text{m}^2 \text{ tree}^{-1}$). The quantities $S_t \times A$ and $T \times S_t \times A$ equal the number of seeds beneath a conspecific tree (seeds tree^{-1}) and the density of seeds beneath conspecific trees (seeds m^{-2}), respectively.

We determined S_t and A for one (or two) randomly chosen tree(s) of each species near each trail segment (five trees for each species and site). We determined A by carefully measuring the area influenced by fallen fronds, spathes, and pedicels. We determined S_t for two 1-m² plots located randomly beneath each tree. Endocarps were raked from the litter and from the upper few centimeters of soil to determine S_t and S_d .

Seedling density (J) and T were determined for one randomly located transect for each trail segment. Seedlings had entire leaves only and lacked complex fronds. Reproductive trees had spathes and/or pedicels. Both structures decompose over several years. Transects were 70 m long and 2 m wide for seedlings and 44 m wide for trees. The latter width was determined by the visibility of trees in preliminary surveys. Foot surveys of each transect insured that all reproductive trees were detected.

Seed fate and S_d were determined for five 1-m² plots located randomly along each 70-m transect. To ensure random locations, a 70-m tape was laid on the ground and plots were centered at 5, 20, 35, 50 and 65 m. When a 1-m² plot fell beneath a focal tree species, seed fates

and S_d were not determined for that species. Three fates were distinguished for all recent endocarps: seeds were (1) destroyed by a rodent, (2) destroyed by a beetle, or (3) not obviously destroyed. Category 3 included viable seeds, seeds destroyed by microbes, and seeds that germinated and then died as seedlings. Recent endocarps could not be crushed by hand (by S.J.W.). Older endocarps were excluded to preclude the possibility that decomposition erased rodent tooth scars or bruchid emergence holes. Seed predation was defined as the proportion of dispersed endocarps opened by rodents or beetles.

We performed one-way analyses of variance (ANOVA) to determine whether S_d , S_p , T , and A differed among sites. Homogeneous residuals were obtained with logarithmic transformations of $S_d + 1$, $S_t + 1$, and $T + 1$ and untransformed values of A . Spearman rank tests were performed to evaluate relationships between poaching intensity and the proportion of seeds dispersed (P), rodent seed predation, beetle seed predation, seedling density (J), and per capita recruitment, which was defined as the ratio of densities of seedlings to reproductive adults (J/T). Variable levels of seed production may satiate mammals and complicate the interaction between seeds and mammals. Spearman rank tests were therefore performed to evaluate relationships between seed production, P , and rodent seed predation. The density of reproductive trees served as a proxy for seed production.

Density and Diversity of Plants in the Herbaceous Layer

One of us (S.J.W.) determined the density and diversity of all plants in the herbaceous layer for the 1-m² plots described above. The herbaceous layer was defined to include woody plants <50 cm tall as well as all herbs. Plants that could not be identified to species were sorted to morphospecies. Morphospecies with only cotyledons could not be distinguished from morphospecies lacking cotyledons. Analyses of species densities were therefore repeated for all plants and after removing unidentified morphospecies with cotyledons only. A single individual was recorded for species with vegetative reproduction (*Selaginella*, many ferns, several Marantaceae, *Piper dariense*, *Geophila*, several *Psychotria*).

A one-way ANOVA was performed to determine whether the density of individuals differed among sites. Homogeneous residuals were obtained with the logarithmic transformation of density. An analysis of covariance (ANCOVA) was performed to determine whether the density of species differed among sites. The covariate was the density of individuals, because the number of species increases linearly with the number of individuals for small plots in these forests (Condit et al. 1996). Homogeneous residuals were obtained with logarithmic

transformations of both the density of species and the density of individuals.

Results

Poaching Intensity

The two independent assessments of poaching intensity were identical among sites. Evidence of poaching encountered during transect censuses included shotgun shells ($n = 14$), tracks of poachers and dogs (6), camps and blinds (4), gunshots and poachers encountered (3), and other hunting implements (3). These items were encountered at MAN ($n = 7$), C25 (7), SLC (6), LIM (5), PLA (3), MAC (1), and GIG (1), but not on BCI. The park guards provided the following ranking of poaching intensity for the five sites within their jurisdiction (most to least severe): C25, SLC, LIM, MAC, and PLA. Only the relative rankings of MAC and PLA differed from our own experience. The park guards stated that poaching was recently severe at PLA and that poachers now traversed PLA to reach more isolated areas. This is consistent with a higher ranking for recent poaching pressure for PLA than for MAC. The park and BCNM guards concurred that poaching intensity was lowest in the BCNM. The

distribution of the Crested Guan (*Penelope purpurascens*) confirms this. This prized game species is abundant within the BCNM and rare to locally extirpated elsewhere (S.J.W., personal observation). Within the BCNM, poachers are apprehended on GIG several times each year but were last detected on BCI in 1989, when security lapsed during a brief war. In summary, forest guards and physical evidence of poaching provided precisely the same ranking of poaching intensity for the seven protected sites. Permanent blinds and camps were found only at the unprotected site (MAN), where poachers were less secretive. We used the following ranking of poaching intensity (most to least severe): MAN, SLC, and C25 tied; PLA and LIM tied; MAC; GIG; and BCI. Ties were introduced conservatively when we believed that the available evidence failed to discriminate poaching intensity. Only ties prevented a perfect correlation with the number of records of active poaching encountered during transect censuses ($r_s = 0.97, p < 0.01$).

The three independent assessments of poaching intensity were similar for the 12 mammal species encountered regularly (Table 1). Agouti, collared peccary, and white-tailed and brocket deer were highly preferred game species in all three assessments. Coatis were consistently described as less preferred but regularly taken. The seven remaining species have never been confis-

Table 1. Poaching intensity in central Panama evaluated by three independent means for the 12 mammal species encountered regularly during transect censuses or captured regularly in small-mammal traps.

Common name and scientific name	National parks mean score (N) ^a	Gigante ^b	Elsewhere in Panama ^c
Common opossum <i>Didelphis marsupialis</i>	5.0 (1)	never	rarely
Anteater <i>Tamandua mexicana</i>	5.0 (1)	never	rarely/never
Geoffroy's tamarin <i>Saguinus geoffroyi</i>	4.0 (2)	never	rarely
Howler monkey <i>Alouatta palliata</i>	3.5 (2)	never	rarely
White-faced monkey <i>Cebus capucinus</i>	4.0 (1)	never	rarely
Coati <i>Nasua narica</i>	3.4 (7)	rarely	often
Collared peccary <i>Tayassu tajacu</i>	1.4 (8)	preferred	preferred
Brocket deer <i>Mazama americana</i>	1.4 (7)	—	preferred
White-tailed deer <i>Odocoileus virginianus</i>	1.0 (8)	preferred	preferred
Red-tailed squirrel <i>Sciurus granatensis</i>	— (0)	never	rarely/never
Agouti <i>Dasyprocta punctata</i>	1.6 (7)	preferred	preferred
Spiny rat <i>Proechimys semispinosus</i>	— (0)	never	rarely

^aEight national park guards rated species from most (1) to least (5) preferred. Mean scores are for the N guards that scored each species. The remaining 8-N guards believed that the species was not hunted within the national parks.

^bAnimals confiscated from poachers between 1979 and 1998 were compiled (BCNM Security Forces, unpublished data).

^cMéndez (1970, 1993) provided a qualitative assessment of poaching intensity by nonindigenous peoples based on 40 years of study in Panama.

cated from a poacher on GIG, were listed as not being hunted by six or more of the eight park guards, and are rarely or never hunted elsewhere in Panama (Méndez 1970, 1993). We used the number of park guards that listed each species as being hunted as the most relevant, objective, and quantitative index of poaching intensity by species (Table 1).

Mammal Abundance

Ten species of mammals were regularly encountered in 634 km of diurnal transect censuses (Table 2). The two deer species were pooled for several analyses because the brocket deer was recorded only on BCI, whereas the white-tailed deer was recorded only off BCI (Table 2). One or two individuals of the following species were also encountered during transect censuses: armadillo (*Dasyus novemcinctus*), two-toed sloth (*Choloepus hoffmanni*), three-toed sloth (*Bradypus variegatus*), tayra, river otter (*Lontra longicaudis*), paca, and capybara (*Hydrochaeris hydrochaeris*). The following animals were captured in 11,185 trap nights: 1 Philander opossum, 66 common opossums (*Didelphis marsupialis*), 4 *Marmosa robinsoni*, 7 *Heteromys desmarestianus*, 1 *Oryzomys tala-mancae*, 2 armored rats, and 142 spiny rats.

Population densities were greatest on BCI, intermediate on Gigante, and lowest at sites with greater poaching inten-

sities for the preferred game species (Fig. 2). Negative correlations between population density and poaching intensity were significant for agouti, deer pooling brocket and white-tailed deer, and white-tailed deer alone (Table 2). Negative correlations between abundance and poaching intensity were also significant for white-faced monkeys, howler monkeys, and spiny rats (Table 2, Figs. 2 & 3; $r_s = -0.749$, $p < 0.05$ for spiny rat). The final three significant correlations were unexpected because these species are rarely hunted in Panama (Table 1). Correlations between abundance and poaching intensity were not significant for the five remaining species (Table 2; $r_s = 0.565$, $p > 0.10$ for common opossum). The index of poaching intensity for a species and the coefficient of variation of its abundance were positively correlated (Fig. 4, $r_s = 0.78$, $p < 0.01$, $n = 11$ species with two deer species pooled).

Early Palm Regeneration

Site differences were evaluated for the four quantities used to estimate the proportion of seeds dispersed (equation 1). As expected, the horizontal projection of the crowns of reproductive trees (*A*) did not differ among sites (data not shown; $F_{7,32} = 0.421$, $p = 0.88$, for *Astrocaryum* and $F_{7,32} = 1.62$, $p = 0.16$, for *Attalea*). Reproductive trees were patchily distributed, and their densities were indistinguishable or differed marginally among

Table 2. Kilometers of transect censuses, numbers of groups encountered for primates, and numbers of individuals encountered for other species.^a

Common name and scientific name	Site ^b								r_s^c
	BCI	GIG	MAC	PLA	LIM	MAN	SLC	C25	
Anteater									
<i>Tamandua mexicana</i>	6	4	3	0	7	4	2	0	-0.54
Tamarin									
<i>Saguinus geoffroyi</i>	2	7	1	28	1	25	17	17	0.61
Howler monkey									
<i>Alouatta palliata</i>	65	70	29	36	50	3	24	15	-0.77*
White-faced monkey									
<i>Cebus capucinus</i>	21	17	10	11	16	4	2	1	-0.87**
Coati									
<i>Nasua narica</i>	102	26	4	6	40	41	2	10	-0.39
Collared peccary									
<i>Tayassu tajacu</i>	14	4	1	3	3	2	3	0	-0.58
Brocket deer									
<i>Mazama americana</i>	7	0	0	0	0	0	0	0	-0.94**+
White-tailed deer									
<i>Odocoileus virginianus</i>	0	3	2	2	2	0	1	0	-0.91**-
Red-tailed squirrel									
<i>Sciurus granatensis</i>	53	26	29	19	41	36	9	7	-0.59
Agouti									
<i>Dasyprocta punctata</i>	192	53	46	28	23	34	12	31	-0.72*
Kilometers of transect	87	60	87	89	82	73	71	85	

^aSpearman rank correlations compare mammal abundance and poaching intensity.

^bBCI, Barro Colorado Island; GIG, Gigante; MAC, Rio Macho; PLA, Plantation Road; LIM, Limite; MAN, Rio Mandinga; SLC, Sendero Las Cruces; and C25, Carretera C25.

^c* $p < 0.05$; ** $p < 0.01$; +, rank correlation combines the two deer species; -, rank correlation for the white-tailed deer only, excluding BCI.

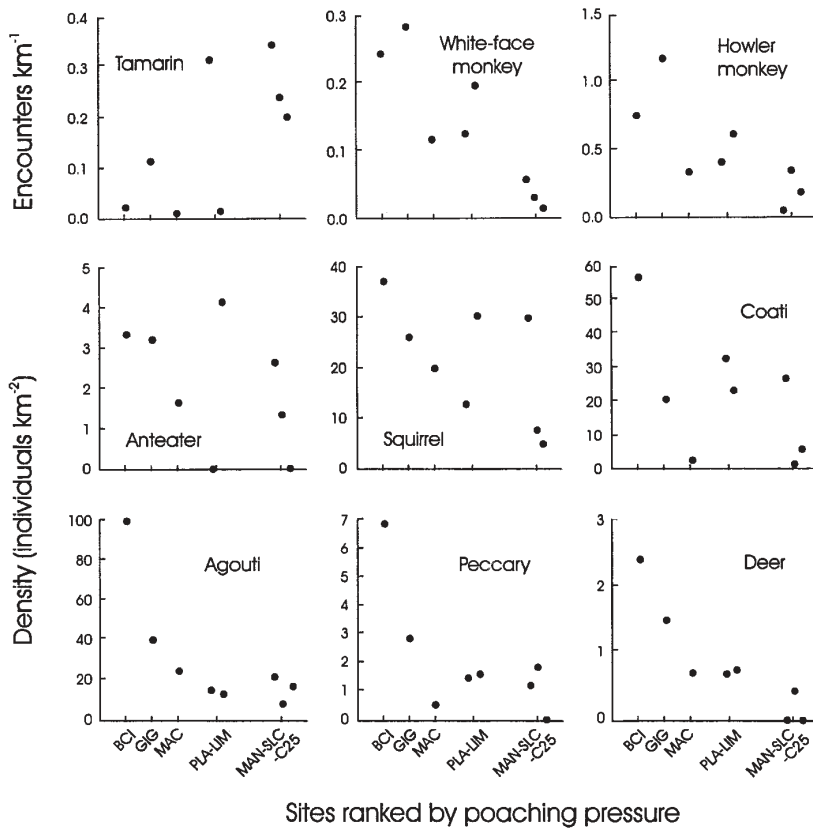


Figure 2. Mammal population estimates from transect censuses for eight sites in central Panama. Population estimates equal the number of groups encountered per kilometer for primates and the number of individuals per square kilometer for other species. The lower right panel pools two deer species. Sites are ordered from least to greatest poaching intensity along the abscissa (for site abbreviations see Table 2, footnote b). Where site abbreviations are connected by hyphens, poaching intensity was indistinguishable (i.e., PLA-LIM and C25-MAN-SLC).

sites (Fig. 5a & 5b; $F_{7,28} = 2.37, p = 0.049$, for *Astrocaryum*; $F_{7,28} = 1.22, p = 0.325$, for *Attalea*). More interestingly, the mean density of seeds under reproductive conspecifics (S_r) and the mean density of seeds dispersed away from conspecifics (S_d) both differed significantly among sites (for S_r $F_{7,32} = 10.5, p < 0.001$, and $F_{7,32} = 15.9, p < 0.001$; for S_d $F_{7,172} = 6.29, p < 0.001$, and $F_{7,170} = 2.77, p < 0.01$, for *Astrocaryum* and *Attalea*,

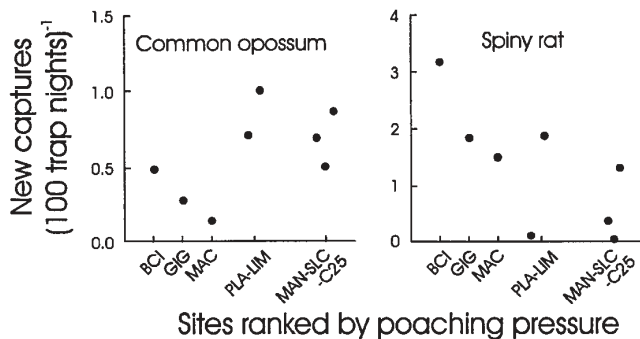


Figure 3. Numbers of common opossums and spiny rats captured per 100 trap nights for eight sites in central Panama. Sites are ordered from least to greatest poaching intensity along the abscissa (for site abbreviations see Table 2, footnote b). Where site abbreviations are connected by hyphens, poaching intensity was indistinguishable (i.e., PLA-LIM and C25-MAN-SLC).

respectively). The numbers of seeds under conspecific adults (or $S_r \times A$, where A is the mean over all sites for each species) increased with poaching intensity (Fig. 5c & 5d). The density of dispersed seeds (S_d) decreased with poaching intensity (Fig. 5e & 5f).

Site means for S_r, S_d, T , and the overall mean for A were substituted into equation 1 to estimate the proportion of seeds dispersed (P) for each site and species. This proportion ranged from 0.03 for *Attalea* at C25 to 0.99 for *Astrocaryum* at MAC (Fig. 5g & 5h). The proportion of seeds dispersed declined as poaching intensity increased for both species ($r_s = -0.896$ and $r_s = -0.884, p < 0.01$, for *Astrocaryum* and *Attalea*, respectively).

The fates of dispersed seeds also varied with poaching intensity (Fig. 6). The proportion of dispersed seeds that were destroyed by rodents declined from around 90% at sites with low poaching intensity to 5–50% at sites with high poaching intensity (Figs. 6a & 6b; $r_s = -0.651, p < 0.05$, for both species). There was a compensatory trend for a greater proportion of dispersed seeds to be destroyed by beetles at heavily poached sites (Fig. 6c & 6d). This trend was significant for *Attalea* ($r_s = 0.81, p < 0.02$) but not for *Astrocaryum* ($r_s = 0.30, p > 0.10$). Seedling density increased with poaching intensity (Fig. 6e & 6f; $r_s = 0.643, p < 0.05$, for both species). Per capita recruitment increased with poaching intensity for *Astrocaryum* (Fig. 6g; $r_s = 0.749, p < 0.05$) but not for *Attalea* (Fig. 6h; $r_s = 0.172, p > 0.05$).

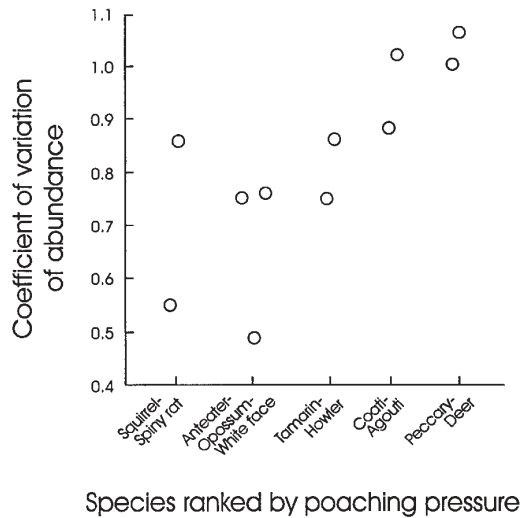


Figure 4. The relationship between poaching intensity and the coefficient of variation in abundance among eight sites in central Panama for 11 species of mammals (brocket and white-tailed deer pooled). Species are ordered from least to greatest poaching intensity along the abscissa according to the number of park guards that believed each species was hunted within the Parques Nacionales Soberanía and Camino de Cruces (Table 1). Where species names are connected by hyphens, poaching intensity was indistinguishable.

The alternative hypothesis that variable seed production controls seed dispersal and rodent seed predation was discounted for *Astrocaryum* but not for *Attalea*. The local density of reproductive *Astrocaryum* was unrelated to the proportion of seeds dispersed and the proportion of dispersed seeds eaten by rodents ($r_s = -0.096$ and $r_s = -0.263$, $p > 0.50$, respectively). In contrast, the local density of reproductive *Attalea* was negatively correlated with both proportions ($r_s = -0.81$, $p < 0.05$, and $r_s = -0.62$, $p < 0.10$, respectively).

Density and Diversity of Plants in the Herbaceous Layer

The density of plants in the herbaceous layer averaged 21.5 individuals m^{-2} and was indistinguishable among sites ($F_{7,172} = 1.96$, $p = 0.063$). High spatial variation within sites (mean coefficient of variation = 96) limited the power of this ANOVA. Mean densities would have had to differ by 88% among sites for there to have been a 90% chance of detection (Sokal & Rohlf 1981).

The mean density of species in the herbaceous layer was 9.9 species m^{-2} . The interaction between site and number of individuals (the covariate) had no effect on number of species ($F_{7,163} = 1.60$, $p = 0.14$). After the interaction was removed, the number of individuals largely determined the number of species ($F_{1,170} = 250.0$, $p < 0.0001$), and site was insignificant ($F_{7,170} = 0.85$, $p = 0.55$). The ANCOVA had acceptable power be-

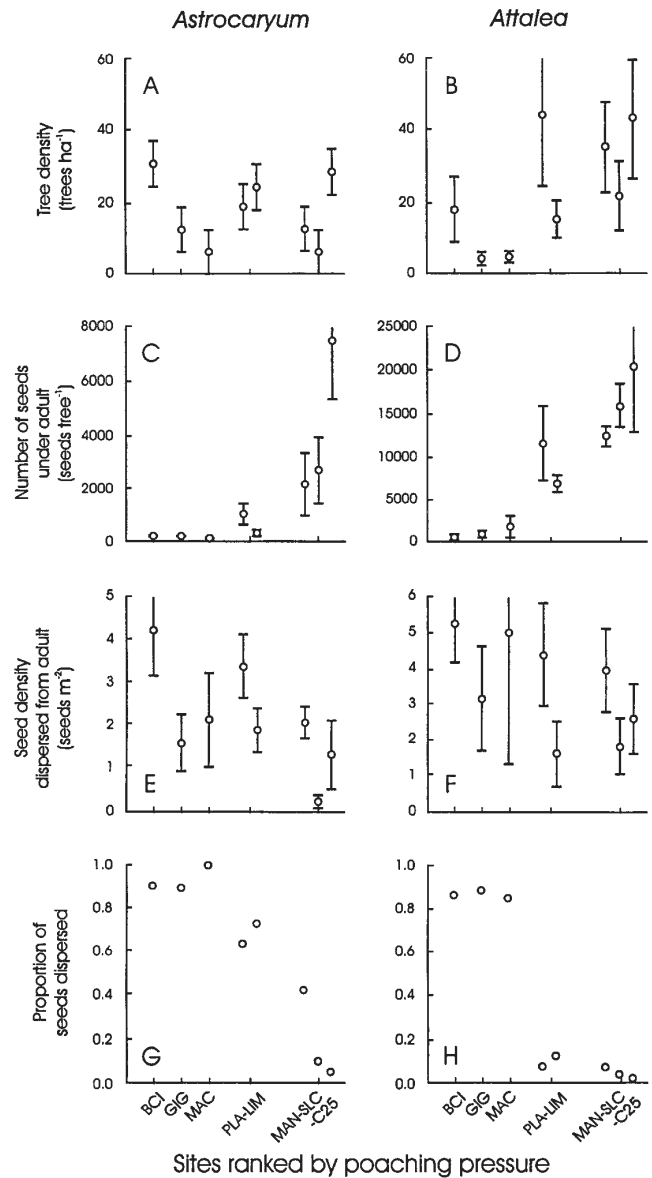


Figure 5. Elements of equation 1 for *Astrocaryum standleyanum* and *Attalea butyraceae*. Panels a through f present mean values (± 1 SE) for the parameters in equation 1 that were measured directly and that differed significantly among sites. Panels a and b present the densities of reproductive adults. Panels c and d present the numbers of seeds that remained beneath reproductive adults. Panels e and f present the densities of seeds dispersed away from beneath conspecific adults. Panels g and h present the proportion of seeds dispersed (see equation 1). Sites are ordered from least to greatest poaching intensity along the abscissa (for site abbreviations see Table 2, footnote b). Where site abbreviations are connected by hyphens, poaching intensity was indistinguishable (i.e., PLA-LIM and C25-MAN-SLC).

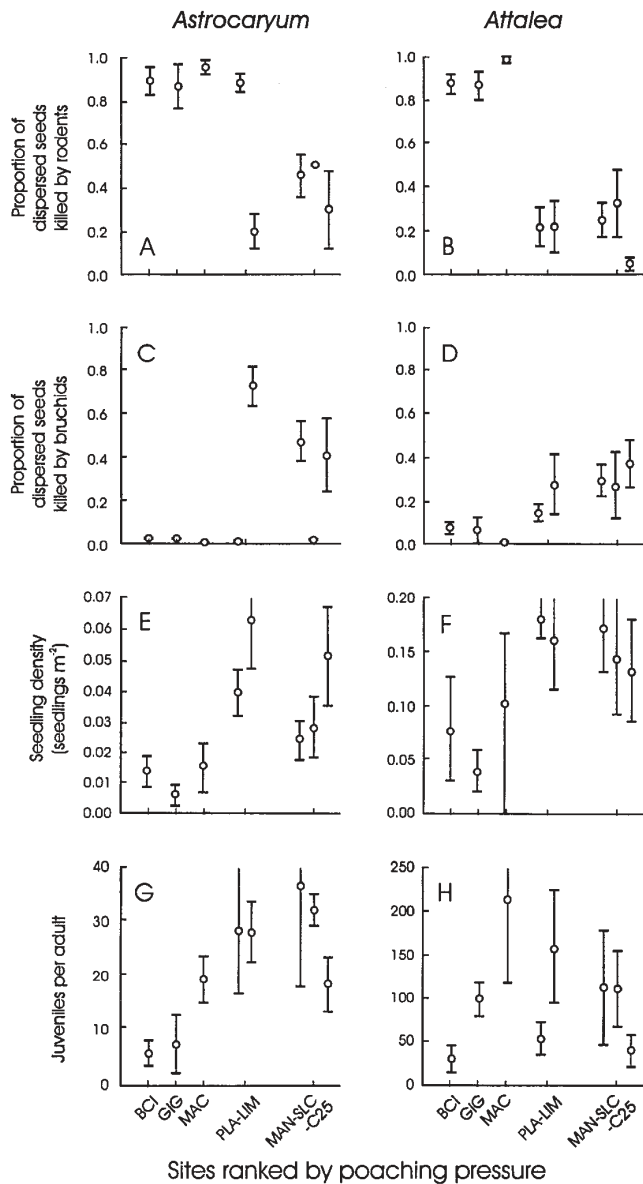


Figure 6. The fate of dispersed seeds of *Astrocarylum standleyanum* and *Attalea butyraceae*. Symbols represent mean values ± 1 SE. Panels a and b present the proportion of dispersed seeds destroyed by rodents. Panels C and D present the proportion of dispersed seeds destroyed by bruchid beetles. Panels E and F present seedling densities. Panels G and H present the ratio of seedling density to reproductive adult density. Sites are ordered from least to greatest poaching intensity along the abscissa (for site abbreviations see Table 2, footnote b). Where site abbreviations are connected by hyphens, poaching intensity was indistinguishable (i.e., PLA-LIM and C25-MAN-SLC).

cause the covariate explained most of the variation in species densities ($R^2 = 0.80$). Residual species densities (from the common relationship between species and individuals) that differed by just 12% among sites had a 90% chance of detection. The results of the ANCOVA were nearly identical when unidentified morphospecies with just cotyledons were excluded (not shown).

Discussion

Poaching Intensity and Mammal Abundance

Three observations are consistent with the hypothesis that poachers reduce the abundance of forest mammals in central Panama. First, interviews with forest guards and physical evidence left by poachers confirmed different levels of poaching intensity for eight forest sites. Second, the abundance of 9 of 11 mammal species declined where poachers were active (Figs. 2 & 3). Third, these declines were larger and spatial variation in abundance was greater for preferred game species (Fig. 4). An alternative explanation for these observations is lacking. Climate, tree-species composition, and forest age were similar among sites. Forest age can also be discounted because the declines affected species associated with both mature forest (white-faced monkeys, collared peccaries) and secondary forest (white-tailed deer, spiny rat). Poaching is the most parsimonious explanation for low mammal abundance where poachers were active and for the disproportionately large increases in abundance among preferred game species at protected sites.

Poachers reduce the abundance of preferred game species in other Neotropical forests (Freese et al. 1982; Peres 1990, 1996; Glanz 1991). Less preferred species, including white-faced monkeys, howler monkeys, and spiny rats, also appear to be affected in central Panama (Table 1, Figs. 2 & 3). Artifact may contribute to the apparent inverse relationship between poaching intensity and spiny rat abundance. The removal of competing herbivores may increase food supplies for spiny rats, making them less likely to enter traps where poachers are active (G. Adler, personal communication). More generally, snares set by poachers kill indiscriminately (BCNM Security Forces, unpublished data), and, where preferred game species are rare, poachers hunt less preferred species. Chilibre and San Vicente are among the most rapidly growing urban centers in Panama (Fig. 1). Poaching is particularly intense at nearby sites (C25 and SLC) and at unprotected sites (MAN). The empty forest anticipated by Redford (1992) is becoming a reality at these sites.

Depleted Mammal Communities and Early Palm Regeneration

The removal of mammals has both direct and indirect effects on palm regeneration. Direct effects include seed dispersal and the destruction of dispersed seeds by ro-

dents. Where mammal abundance was high, most seeds were dispersed away from reproductive palms and then eaten by rodents. Where mammal abundance was low, most seeds accumulated beneath reproductive palms and the few dispersed seeds largely escaped rodents (Figs. 5g, 5h, 6a, & 6b). We conclude that depleted mammal communities alter seed dispersal and rodent seed predation.

An indirect effect of the removal of mammals is mediated by the interaction among rodents, bruchid beetles, and palm seeds. Rodents remove beetle eggs from seeds, eat larval beetles together with seeds, and bury seeds, making them unavailable to ovipositing beetles (Wright 1983, 1990; Smythe 1989). Not surprisingly, seed predation by beetles was greatest where rodent abundance was lowest (Fig. 6c & 6d). This creates opposing effects on seedling regeneration. Where poachers reduce mammal abundance, seedling regeneration will be enhanced by low rodent seed predation and will be reduced by both high bruchid seed predation and low seed dispersal (Fig. 6). These opposing effects preclude an unequivocal prediction about the relationship between early palm regeneration and the integrity of the local mammal community. Poaching could increase, decrease, or have no net effect on palm regeneration, depending on the relative importance of seed dispersal and bruchid and rodent seed predation.

The net effect of poaching can be resolved only empirically. Seedling densities of *Attalea* and *Astrocaryum* and per capita recruitment of *Astrocaryum* increased with poaching intensity (Fig. 6e, 6f, & 6g). We conclude that poaching favors seedling regeneration in these palms. Most tropical-forest trees recruit from the advanced regeneration of seedlings (Uhl et al. 1988). We predict that greater seedling densities will increase recruitment of reproductive adults. Long-term data are required to test this prediction.

Consequences for Plant Species Composition, Plant Density, and Plant Diversity

Poachers are likely to affect plant species composition. In this study, for example, seedling densities of *Astrocaryum* and *Attalea* increased by 300–500% at heavily poached sites (Fig. 6e & 6f), whereas the density of all plants was indistinguishable among sites. Poachers altered plant species composition by favoring the two palms. Generally, poachers are likely to alter plant species composition because the strength of interaction varies between game species and plant species. Each game species interacts strongly with some plant species, weakly with other plant species, and not at all with still others. The net effect of removal of game species therefore varies among plant species, and altered plant species composition is likely to be a widespread consequence of poaching.

Other studies indicate that poachers also affect plant density and diversity. Experiments that exclude all terrestrial vertebrates consistently document increased seedling densities (Terborgh & Wright 1994; J. Connell & W. Carson, unpublished data). These experiments demonstrate the potential effect of vertebrates, but their relevance is limited because terrestrial nongame species are excluded, whereas arboreal and volant game species are present. Comparisons of forests with different levels of anthropogenic disturbance are more germane. Three such comparisons have had very different outcomes. Seedling density was greater, lower, and indistinguishable for disturbed and protected forests in Mexico, Uganda, and Panama, respectively (Dirzo & Miranda 1991; Chapman & Onderdonk 1998; this study). Different game species were removed from each forest, while different nongame species remained and possibly increased in abundance. For these reasons, the net effect of anthropogenic disturbance on plant density and diversity is unpredictable.

Anthropogenic Effects on Higher Trophic Levels

Terborgh (1992) hypothesized that large predators exert top-down control of plant regeneration in tropical forests. This hypothesis presumes that large felids and raptors limit herbivorous mammals (cf. Glanz 1991; Wright et al. 1994), and, where these predators are absent, that an overabundance of herbivores alters plant regeneration. Terborgh (1992) suggested that BCI could be used to test this hypothesis because the jaguar (*Panthera onca*), puma (*Puma concolor*), Harpy Eagle (*Harpia harpyja*), and Crested Eagle (*Morphnus guianensis*) are no longer resident. We therefore compared early palm regeneration for BCI and nearby sites where puma and jaguar are present (MAC) and where poachers reduce herbivore abundance (MAC and GIG). The comparison was restricted to BCI, GIG, and MAC because mammal abundance declined from high levels on BCI to intermediate levels for GIG and MAC (Figs. 2 & 3). Other sites were excluded because intense poaching reduced mammal abundance to low levels. The proportion of seeds dispersed, the proportion of dispersed seeds killed by rodents and by beetles, and seedling density were indistinguishable among BCI, GIG, and MAC (Figs. 5 & 6). Early palm regeneration was not unusual on BCI. Similar results were obtained from experiments conducted at BCI, the adjacent mainland, and the pristine Manu National Park, Peru (Terborgh & Wright 1994; Asquith et al. 1997). In these experiments, herbivorous mammals were excluded and seed and seedling survival increased by virtually identical amounts at sites with and without large predators. The hypothesis that large felids and raptors indirectly control plant regeneration lacks empirical support (Brewer et al. 1997).

Conservation Implications

Dirzo and Miranda (1991) and Redford (1992) first raised the possibility that anthropogenic effects on herbivorous mammals could indirectly alter plant regeneration in tropical forests. We believe that this is happening for two abundant palm species in the forests of central Panama. Both seed dispersal by mammals and seed predation by rodents fell to low levels where poachers were most active (Figs. 5g, 5h, 6a, & 6b). Poachers have indirectly altered the early regeneration of these palms. Many of the same mammal species, *Attalea butyraceae*, and similar *Astrocaryum* species are widely distributed throughout the Neotropics (Henderson et al. 1995; Emmons 1997). Early palm regeneration is likely to change wherever these species co-occur with poachers. Densities of seeds of *Attalea butyraceae* beneath reproductive conspecifics may provide a useful proxy for the integrity of local mammal communities (Fig. 5d). Game species disperse and eat the seeds of many additional plant species, and poachers may also alter their early regeneration. The conservation of forests with natural patterns of early plant regeneration must include measures to protect herbivorous mammals from poachers.

Acknowledgments

The Autoridad Nacional del Ambiente and the directors of the Parques Nacionales Soberanía and Camino de Cruces, Téc. S. Batista, V. Bethancour, and O. Bosques made this study possible. R. Martínez and J. Guevara prepared Fig. 1. E. Leigh, K. Redford, and two anonymous reviewers provided constructive criticism. The Smithsonian Tropical Research Institute and the U.S. Agency for International Development (award no. 525-0308-G-00-6121-00) provided funding for plant and mammal studies, respectively.

Literature Cited

- Adler, G. H. 1995. Fruit and seed exploitation by Central American spiny rats, *Proechimys semispinosus*. *Studies on Neotropical Fauna and Environment* 30:237-244.
- Asquith, N. M., S. J. Wright, and M. J. Claus. 1997. Does mammal community composition control seedling recruitment in Neotropical forests? Evidence from islands in central Panama. *Ecology* 78:941-946.
- Brewer, S.W., M. Rejmanek, E. E. Johnstone, and T. M. Caro. 1997. Top-down control in tropical forests. *Biotropica* 20:364-367.
- Chapman, C. A., and D. A. Onderdonk. 1998. Forests without primates: primate/plant codependency. *American Journal of Primatology* 45:127-141.
- Charles-Dominique, P., M. Atramentowicz, M. Charles-Dominique, H. Gerard, A. Hladik, C. M. Hladik, and M. F. Prevost. 1981. Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: inter-relations plantes-animaux. *Terre et Vie* 35:341-435.
- Condit, R., S. P. Hubbell, J. V. LaFrankie, R. Sukumar, N. Manokaran, R. B. Foster, and P. S. Ashton. 1996. Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *Journal of Ecology* 84:549-562.
- De Steven, D., D. M. Windsor, F. E. Putz, and B. de León. 1987. Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica* 19:342-356.
- 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, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley, New York.
- Eisenberg, J. F., and R. W. Thorington Jr. 1973. A preliminary analysis of a Neotropical mammal fauna. *Biotropica* 5:150-161.
- Emmons, L. H. 1997. *Neotropical rainforest mammals*. 2nd edition. University of Chicago Press, Chicago.
- Enders, R. K. 1935. Mammalian life histories from Barro Colorado Island, Panamá. *Bulletin of the Museum of Comparative Zoology* 78:385-502.
- Foster, R. B., and N. V. L. Brokaw. 1982. Structure and history of the vegetation of Barro Colorado Island. Pages 67-82 in E. G. Leigh Jr., A. S. Rand, and D. M. Windsor, editors. *Ecology of a tropical forest*. Smithsonian Institution Press, Washington, D.C.
- Freese, C. H., P. G. Heltne, N. Castro R., and G. Whitesides. 1982. Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *International Journal of Primatology* 3:53-90.
- Giacalone-Madden, J., W. E. Glanz, and E. G. Leigh Jr. 1990. Fluctuaciones poblacionales a largo plazo de *Sciurus granatensis* en relación con la disponibilidad de frutos. Pages 331-336 in E. G. Leigh Jr., A. S. Rand, and D. M. Windsor, editors. *Ecología de un bosque tropical*. Smithsonian Institution Press, Washington, D.C.
- Glanz, W. E. 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. Pages 455-468 in E. G. Leigh Jr., A. S. Rand, and D. M. Windsor, editors. *Ecology of a tropical forest*. Smithsonian Institution Press, Washington, D.C.
- Glanz, W. E. 1991. Mammalian densities at protected versus hunted sites in central Panamá. Pages 163-173 in J. G. Robinson and K. H. Redford, editors. *Neotropical wildlife use and conservation*. University of Chicago Press, Chicago.
- Gompper, M. E. 1996. Population ecology of the white-nosed coati (*Nasua narica*) on Barro Colorado Island, Panamá. *Journal of Zoology*, London 241:441-455.
- Harms, K. E., and J. W. Dalling. 1995. Observations on the seasonal consistency in germination timing for *Scheelea zonensis*. *Principes* 39:104-106.
- Henderson, A., G. Galeano, and R. Bernal. 1995. *Field guide to the palms of the Americas*. Princeton University Press, Princeton, New Jersey.
- Hoch, G. A., and G. H. Adler. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology* 13:51-58.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light gaps, recruitment limitation, and tree diversity in a Neotropical forest. *Science* 283:554-557.
- Johnson, C. D., S. Zona, and J. A. Nilsson. 1995. Bruchid beetles and palm seeds: recorded relationships. *Principes* 39:25-35.
- Kays, R. W. 1999. The diet of the most frugivorous carnivore: food preference in kinkajou (*Potos flavus*). *Journal of Mammalogy* 80:589-599.
- Kiltie, R. A. 1981. Stomach contents of rain forest peccaries (*Tayassu tajacu* and *T. pecari*). *Biotropica* 13:234-236.
- Méndez, E. 1970. *Los principales mamíferos silvestres de Panamá*. Imprenta Bárcenas, Panama City.
- Méndez, E. 1993. *Los roedores de Panamá*. Impresora Pacifico, Panama City.
- Peres, C. A. 1990. Effects of hunting on western Amazonian primate communities. *Biological Conservation* 54:47-59.
- Peres, C. A. 1996. Population status of white-lipped *Tayassu pecari* and collared peccaries *T. tajacu* in hunted and unhunted Amazonian forests. *Biological Conservation* 77:115-123.

- Redford, K. H. 1992. The empty forest. *BioScience* **42**:412-422.
- Redford, K. H., and J. G. Robinson. 1987. The game of choice: patterns of Indian and colonist hunting in the Neotropics. *American Anthropologist* **89**:650-667.
- Smythe, N. 1989. Seed survival in the palm *Astrocaryum standleyanum*: evidence for dependence upon its seed dispersers. *Biotropica* **21**:50-56.
- 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.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. 2nd edition. W. H. Freeman, San Francisco.
- Terborgh, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* **24**:283-292.
- Terborgh, J., and S. J. Wright. 1994. Effects of mammalian herbivores on plant recruitment in two Neotropical forests. *Ecology* **75**:1829-1833.
- Uhl, C., K. Clark, N. Dezzio, and P. Maquirino. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* **69**:751-763.
- Walsh, R. P. D. 1996. Climate. Pages 159-205 in P. W. Richards, editor. *The tropical rain forest*. 2nd edition. Cambridge University Press, Cambridge, United Kingdom.
- Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT, Evanston, Illinois.
- Windsor, D.M. 1990. Climate and moisture variability in a tropical forest, long-term records for Barro Colorado Island, Panamá. *Smithsonian Contributions to Earth Sciences* **29**:1-145.
- Wright, S. J. 1983. The distribution of eggs by a bruchid beetle among *Scheelea* palm seeds and the effect of distance to the parent palm. *Ecology* **64**:1016-1021.
- Wright, S. J. 1990. Cumulative satiation of a seed predator over the fruiting season of its host. *Oikos* **58**:272-276.
- Wright, S. J., M. E. Gomper, and B. DeLeon. 1994. Are large predators keystone species in Neotropical forests? The evidence from Barro Colorado Island. *Oikos* **71**:279-294.

