

## Primary Seed Dispersal by Red Howler Monkeys and the Effect of Defecation Patterns on the Fate of Dispersed Seeds<sup>1</sup>

Ellen Andresen

Departamento de Ecología de los Recursos Naturales Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM), Antigua Carretera a Pátzcuaro No. 8701, Col. Ex-Hacienda de San José de la Huerta, Morelia, Michoacán, C.P. 58190, Mexico

---

### ABSTRACT

The effectiveness of a seed disperser depends on the quantity and quality of dispersal. The quality of dispersal depends in large part on factors that affect the post-dispersal fate of seeds, and yet this aspect of dispersal quality is rarely assessed. In the particular case of seed dispersal through endozoochory, the defecation pattern produced has the potential of affecting the fate of dispersed seeds and consequently, dispersal quality and effectiveness. In this study, I assessed the effects of dung presence and dung/seed densities on seed predation by rodents and secondary dispersal by dung beetles. In particular, I compared seed fates in clumped defecation patterns, as those produced by howler monkeys, with seed fates in scattered defecation patterns, as those produced by other frugivores. I also determined the prevalence of red howler monkeys (*Alouatta seniculus*) as seed dispersers at the plant community level in Central Amazonia by determining the number of species they dispersed in a 25-month period. I found that dung presence and amount affected rodent and dung beetle behavior. Seed predation rates were higher when dung was present, and when it was in higher densities. The same number of seeds was buried by dung beetles, in clumped versus scattered defecation patterns, but more seeds were buried when they were inside large dung-piles versus small piles. Seed density had no effect on rodent or dung beetle behavior. Results indicate that caution should be taken when categorizing an animal as a high or low quality seed disperser before carefully examining the factors that affect the fate of dispersed seeds. Red howler monkeys dispersed the seeds of 137 species during the study period, which is the highest yet reported number for an *Alouatta* species, and should thus be considered highly prevalent seed dispersers at the plant community level in Central Amazonian terra firme rain forests.

---

### RESUMO

A efetividade da dispersão de sementes depende da quantidade e qualidade da dispersão. A qualidade da dispersão, por sua vez, depende em grande parte dos fatores pós-dispersão que afetam o destino das sementes—um aspecto pouco explorado na literatura. No caso especial de dispersão de sementes por endozoocoria, o padrão de defecação tem potencial de afetar o destino das sementes dispersas e consequentemente a qualidade da dispersão. Neste estudo, eu investiguei os efeitos da presença de fezes e da densidade de sementes e de fezes sobre a predação de sementes por roedores, e sobre a dispersão secundária por besouros coprófagos. Em particular, eu comparei o destino das sementes em padrões de defecação agregada, como as produzidas por macacos guaribas, e em padrões de defecação dispersa, como as produzidas por outros frugívoros. Eu também determinei a prevalência dos guaribas vermelhos (*Alouatta seniculus*) como dispersores de sementes da comunidade de plantas na Amazônia Central, por meio da determinação do número de espécies vegetais que eles dispersaram durante um período de 25 meses. Eu encontrei que a presença e quantidade de fezes afetaram tanto o comportamento de roedores, como o comportamento dos besouros coprófagos. A taxa de predação de sementes foi elevada quando estas estavam associadas à presença e à maior densidade de fezes. O mesmo número de sementes foi enterrado pelos besouros coprófagos de fezes defecadas de forma agregada e de forma dispersa. No entanto, um número maior de sementes foi enterrado por besouros quando estavam dentro de uma pilha grande de fezes, do que em pilhas menores. A densidade de sementes não teve efeito no comportamento dos roedores, nem no comportamento dos besouros. Os resultados indicam que cuidado deve ser tomado ao se categorizar animais como dispersores de sementes de alta ou baixa qualidade, antes de um exame cuidadoso dos fatores que afetam o destino das sementes dispersas seja feito. Os guaribas dispersaram as sementes de 137 espécies durante o período deste estudo. Este é o maior número já reportado para uma espécie de *Alouatta* e, por esta razão, os guaribas devem ser considerados como dispersores muito prevalentes na comunidade vegetal da floresta de terra firme da Amazônia Central.

*Key words:* Alouatta; Central Amazonia; defecation pattern; dung beetles; howler monkeys; primary seed dispersal; secondary seed dispersal; seed fate; tropical moist forest.

THE MAJORITY OF TREE SPECIES IN TROPICAL FORESTS produce fruits that are adapted for consumption

and seed dispersal by frugivorous vertebrates (Howe 1990). The fruits of most of these plant species are eaten by more than one species of frugivore, and consequently, the seeds of these plants are also usually dispersed by more than one species

<sup>1</sup> Received 16 November 2000; revision accepted 26 May 2001.

of animal (Andresen 2000a). What is important from the plant's perspective, however, is the effectiveness of a given disperser species. The effectiveness of a seed disperser is defined by the quantity of seeds dispersed and the quality of dispersal (Schupp 1993). Relatively, animals can be easily compared in terms of dispersal quantity. In terms of dispersal quality, most studies have focused on issues such as fruit handling, effect of gut passage, and dispersal distance (Dew & Wright 1998, Kaplan & Moermond 1998, McConkey 2000, Stevenson 2000). Dispersal quality, however, is also affected by many biotic and abiotic factors that are encountered by the seed after deposition. This post-dispersal fate of seeds is far more difficult to assess, but it will ultimately determine if the plants fitness is affected by the primary dispersal event (Coates-Estrada & Estrada 1988, Chapman 1989, Chambers & MacMahon 1994, Andresen 1999).

One aspect that can greatly affect the post-dispersal fate of seeds dispersed through endozoochory by frugivorous animals is the pattern of defecation; however, this aspect of seed dispersal has received relatively little attention. Defecation patterns determine the spatial distribution of dung and seeds, and may vary greatly among different species of frugivores, according to features such as the size of the animal, its social/ranging behavior, and digestive physiology (Zhang & Wang 1995, Andresen 1999).

In the particular case of dispersal through defecation by mammals, the fecal material is known to attract dung beetles, which act as secondary seed dispersers when they accidentally bury seeds present in the dung, and rodents, which in tropical forests act mostly as seed predators (Janzen 1982a, 1986; Andresen 1999). Seeds buried by dung beetles have a high probability of avoiding rodent predation but may also suffer decreased seedling emergence when they are buried too deeply (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Feer 1999; Andresen 2000b, 2001). In addition to the presence of dung, the amount of dung and the spatial pattern of dung/seed deposition may also affect the behavior of rodents and dung beetles, and consequently seed fate (Janzen 1982a; Andresen 2001, in press).

The role that a seed-dispersing animal plays in plant regeneration, cannot be assessed only in terms of its dispersal effectiveness at the plant population level, but also must be evaluated in terms of its prevalence at the plant community level. Here I define a prevalent disperser as one that disperses the seeds of many species in the plant community.

This aspect of seed dispersal may have practical implications for forest conservation and management. For example, it is sometimes necessary to determine which seed-dispersing species should become the focus of conservation efforts when the overall goal is to maintain the regeneration ability of a forest patch (Howe 1984). An animal that disperses the seeds of many species but with low effectiveness for each of the plant species will be of little interest in terms of forest regeneration. On the other hand, a species that is a very effective disperser for only a few plant species may not be the optimal disperser either. Ideally one would want to maintain healthy populations of animal species that are both prevalent and effective dispersers.

One mammal genus that has been recognized as dispersing seeds in many Neotropical forests is *Alouatta*, which includes all species of howler monkeys (Mittermeier & van Roosmalen 1981, Estrada & Coates-Estrada 1984, Galetti *et al.* 1994, Julliot 1996a). Howler monkeys, however, have sometimes been regarded both as less prevalent and less effective seed dispersers than other primary dispersers (Howe 1980, Mittermeier & van Roosmalen 1981, Andresen 1999). In terms of prevalence, howler monkeys in several forests have been reported to consume the fruits of less than 40 species of plants (Milton 1980, Gaulin & Gaulin 1982, Estrada & Coates-Estrada 1984, Galetti *et al.* 1994, Andresen 1999), which is low compared to the fruit diet of other primates such as spider monkeys, capuchin monkeys, or woolly monkeys (van Roosmalen 1985, Guillotin *et al.* 1994, Simmen & Sabatier 1996, Andresen 1999, Stevenson 2000); however, there are sites in which howler monkeys consume the fruits of many more plant species. In French Guiana, for example, howler monkeys disperse the seeds of over 100 species of plants (Julliot & Sabatier 1993, Julliot 1996b).

Howler monkeys have also been regarded as low quality, and consequently less effective, seed dispersers because their defecations result in large aggregations of seeds and dung on the forest floor (Howe 1980, 1986; de Figueiredo 1993). Such spatial distribution of seeds has been argued to be disadvantageous for plants due to density-dependent seed/seedling mortality in defecation sites. The fate of seeds dispersed in clumped defecations, however, such as those produced by howler monkeys, has not been compared to the fate of seeds dispersed in scattered defecations, such as those produced by most other Neotropical arboreal mammals (Estrada *et al.* 1993, Guillotin *et al.* 1994, Andresen 1999). Further, the effect of dung

on the fate of seeds dispersed by mammals has been considered only in a few studies (Janzen 1982a, b; Chapman 1989; Bermejo *et al.* 1998; Pizo & Oliveira 1999), and only recently has the effect of dung beetles as secondary seed dispersers started to be assessed (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Andresen 1999; Feer 1999; Vulinec 2000; Andresen 2001, in press).

The objectives of this study were to determine the prevalence of red howler monkeys (*Alouatta seniculus*) as seed dispersers in a Central Amazonian rain forest, and to examine how the pattern of defecation influences the fate of dispersed seeds and, consequently, the quality and effectiveness of dispersal. Specific questions were: (1) How many species do howler monkeys disperse? (2) What are the patterns of dung- and seed depositions produced by howler monkeys? and (3) What is the effect of presence of dung and defecation pattern (scattered vs. clumped dung/seed densities) on seed predation by rodents and seed dispersal by dung beetles?

## MATERIALS AND METHODS

**STUDY SITE.**—This study was conducted in an 800 ha forest reserve embedded in an expanse of continuous primary forest greater than 10,000 ha in size. This site is reserve no. 1501 (also known as “km 41”) of the Biological Dynamics of Forest Fragments Project (BDFFP), formerly known as the Minimum Critical Size of Ecosystems Project (Lovejoy & Bierregaard 1990) located *ca* 90 km north of the city of Manaus (2°30’S, 60°W) in the Brazilian state of Amazonas. The area is covered by primary *terra firme* forest classified as Tropical Moist Forest by Holdridge (1967). Mean annual temperature in Manaus is 26.7°C, with monthly means fluctuating *ca* 2°C. A thirty-year average for annual precipitation in Manaus is 2186 mm (Lovejoy & Bierregaard 1990). A relatively drier season occurs from June through October, with the driest months (July, August, and September) usually receiving less than 100 mm of rain each (Lovejoy & Bierregaard 1990); however, both annual precipitation and the severity of the dry season may change substantially from year to year. At reserve no. 1501, annual precipitation was 2935 mm and 2245 mm during 1996 and 1997, respectively. During the dry season (June–October), 35 and 10 percent of the annual precipitation were recorded in 1996 and 1997, respectively.

**PRIMARY SEED DISPERSAL BY RED HOWLER MONKEYS AND THEIR DEFECACTION PATTERN.**—I located howler

monkey troops when they vocalized at dawn. Defecation typically occurs later in the morning, usually between 0700 and 1000 h, at which time I visited the site again and collected all seeds and dung I could find on the forest floor. Between May 1996 and May 1998, I collected 263 defecation samples. While in other studies authors have used the term defecation for one single fecal pile, here I define defecation sample as all the dung found on the forest floor produced after one or more howler monkeys had defecated and the whole troop had moved to a different area.

Red howler monkeys have a bimodal defecation pattern in which all or most of the individuals defecate more or less simultaneously, once in the morning before beginning the day's activities and once in the afternoon at the end of a long resting period in the middle of the day (Andresen 1994, Julliot 1996a). As a consequence, 61 percent of all defecation occurs near resting areas (Julliot 1996b, Gilbert 1997), which generally do not coincide with fruiting trees (E. Andresen, pers. obs.). Therefore, although I only collected defecation samples in the morning, I consider these samples to be representative of the defecation pattern produced by red howler monkeys.

Most defecation samples were collected from five howler monkey troops (four to nine individuals in each) with home areas closest to the research station. Defecation samples were taken to the research station and all seeds greater than 3 mm in length were removed. Seeds 3 mm or less in length were left in the dung, except for a small sample taken for identification. Seeds of this size were not common in defecation samples (8% of defecation samples contained seeds  $\leq$  3 mm), their removal was not practical, and they were considered unlikely to affect the interaction of experimental seeds with dung beetles and rodents. Seeds more than 3 mm in length were washed and counted and a random sample was measured (length, width, and thickness/height). Seed samples were placed in plastic bags with alcohol (70%) and taken to M. G. M. van Roosmalen at INPA's (National Institute for Research in Amazonia) Botany Department (Manaus) for identification. Seedless dung (or dung with seeds  $\leq$  3 mm) was stored in plastic bags and either placed in the shade and used for experiments the same day or placed in an insulated box with ice and used the following day.

Total fresh weight of the defecation samples was recorded for 205 of the samples. One hundred thirty defecation samples that only had seeds greater than 3 mm long were weighed before and after

removal of all the seeds to estimate the proportion of the total defecation-sample weight that was due to seed weight. For 34 defecation samples, I estimated the total area of forest floor in which dung and seeds had fallen. For 30 defecation samples that contained few or no seeds, I counted the total number of individual dung piles that constituted the whole sample of known weight and for 13 of these defecation samples, I weighed individual dung piles. Finally, for 19 defecation samples that contained seeds more than 3 mm long, I counted by species the seeds that fell on the ground surrounded by dung and the seeds that had been separated from the dung while falling to the ground.

EFFECT OF DEFECATION PATTERN ON RODENT AND DUNG BEETLE BEHAVIOR.—Seed predation by rodents: The effect of presence of dung and of dung/seed density. To assess seed predation pressures, I placed raw sunflower seeds in piles of five seeds each. I used sunflower seeds because they could easily be bought in the market, they could be stored, and rodents are known to feed on them. Because I only wanted to assess the relative predation pressures in the different treatments, it was not important what kind of seed I used as long as it was consumed by rodents. Also, seeds dispersed by howler monkeys and other frugivorous animals can vary tremendously in their palatability to seed predators and consequently in the predation pressures they suffer (Andresen 1999, 2000b). Thus, predation rates on sunflower seeds is very likely similar to predation pressures of some forest seeds, and different from others. In this regard, sunflower seeds can be considered equivalent to having used some of the forest seeds with similar predation rates. I used five seeds per pile to increase probability of detection by seed predators.

Seed piles were placed in four treatments representing different defecation patterns: (A) high seed and dung densities in howler monkey defecation sites: Immediately after a troop of monkeys had defecated, I removed all dung and seeds, and placed five experimental sunflower seed piles spaced evenly in a 2 x 2 m area. Next to each seed pile I placed 10 g of dung, and *ca* 50 additional grams of dung were scattered on the surface (approximate dung density: 25 g/m<sup>2</sup>, which is similar to the median dung density observed in howler monkey defecation samples of 31 g/m<sup>2</sup>); (B) high seed density without dung: five seed piles spaced evenly in a 2 x 2 m area, with no dung; (C) low seed and dung densities: a single seed pile placed on the forest floor next to 10 g of howler monkey dung; and

(D) low seed density without dung: a single seed pile without dung.

Only treatment A was placed in a howler monkey defecation site. Treatments A and B were placed simultaneously, *ca* 30 m apart. Treatments C and D were placed on a transect *ca* 30 m away from treatment A, two to three days after treatments A and B had been placed. Treatments C and D were set out simultaneously on the transect, one pile of seeds every 10 m, alternating treatments and using a total of ten seed piles/transect (five each for C and D; 100 m total transect length). Each of the four treatments was replicated 13 times, with one experimental unit consisting of a group formed by five seed piles (placed together in a 2 x 2 m area in the case of treatments A and B, and placed singly along transects for treatments C and D). The number of seeds preyed upon/removed in each seed pile was recorded after one day. A single day was used because it is during the first 24 hours that the difference among treatments in terms of presence of dung is most pronounced (Andresen 1999). It is important to realize, however, that for some plant species the effect of dung on predation disappears with time (Andresen 1999, 2001); this issue will be discussed further.

Bead burial by dung beetles: Scattered vs. clumped dung piles. To assess the activity of dung beetles in scattered versus clumped defecations, round plastic beads (8 mm diam.) were used as seed mimics. Beads were used instead of seeds because at the beginning of this experiment, no howler monkey-dispersed seeds were available in large quantities. For the experiment described in the next section, I used *Byrrsonima crispera* seeds, which are very similar in shape and size to the beads used in this experiment. I found that dung beetles bury similar numbers of both the beads used in this experiment and *B. crispera* seeds ( $\chi^2 = 0.073$ ,  $df = 1$ ,  $P = 0.79$ ,  $N = 179$ ), and bury them at similar depths (*t*-test with log-transformed data,  $t = -0.43$ ,  $df = 76$ ,  $P = 0.67$ ).

I used 10 g dung piles, and placed one bead inside each of the piles. I chose 10 g dung piles because it is a representative dung pile size for howler monkeys and other frugivorous mammals. I placed bead-containing dung piles in two treatments, simulating two defecation patterns: (i) a clumped pattern, with 10 dung/bead piles in a 2 x 2 m area (total dung density: 25 g/m<sup>2</sup>;  $N = 16$ ); and (ii) a scattered pattern with individual dung/bead piles along transects, one pile every 10 m (80 single dung/bead piles were used). Although treatments were not set out simultaneously, they were

done so during the dry season and in the same general area of the forest.

A 50 cm long piece of white nylon thread was attached to each bead to find the beads that were buried by dung beetles. After two days, locations were checked and it was recorded whether or not the bead had been buried by dung beetles. Buried beads were carefully unburied and burial depth was measured to the nearest centimeter (when beads were slightly covered by soil, a burial depth of 0.5 cm was assigned). For the clumped treatment, all beads were recovered; in the case of the scattered treatment, 8 out of 88 (9%) beads placed were not recovered (they were probably buried with the string by dung beetles) and consequently not included in the analyses.

Seed burial by dung beetles: Effect of seed density and amount of dung in scattered dung piles. To assess the effects of seed density and amount of dung in individual dung piles, I used two states of each of these variables, placing experimental seeds in each of the following combinations: (i) one seed in a 10 g dung pile; (ii) four seeds in a 10 g dung pile; (iii) one seed in a 25 g dung pile; and (iv) four seeds in a 25 g dung pile. The amounts of dung used are within the range of sizes produced by howler monkeys as well as other fruit-eating mammals, without representing extremes (Estrada *et al.* 1993, Andresen 1999). One dung pile with seed(s) was placed on the forest floor every 10 m, along transects. Transects contained between 10 and 40 experimental dung/seed piles. When different treatments were set out on the same day, they were interspersed regularly along the same transect. When two or more transects were set out on the same day, they were separated by at least 100 m. All transects were set out during the same season. For the 10 g dung treatment, I used 154 piles with single seeds and 61 with groups of four seeds; for the 25 g dung treatment, I used 123 piles with single seeds and 93 with groups of four seeds.

Seeds of *B. crispa* (Malpighiaceae), a fruit consumed by howler monkeys, were used (spherical seeds  $8.1 \pm 0.2$  mm diam.,  $N = 15$ ; henceforth, mean  $\pm$  one standard error are reported). All seeds were marked with a 50 cm long nylon thread glued to them. After two days, I counted the number of seeds buried by beetles, and burial depths were measured as in the previous experiment. In this case, only 3 percent of seeds were not recovered and thus excluded from analyses.

STATISTICAL ANALYSES.—Results on primary dispersal and defecation pattern are expressed as mean

numbers and mean percentages in the case of normally distributed variables and as median numbers and median percentages in the case of non-normally distributed variables. Data on seed predation/removal of sunflower seeds were analyzed with a one-way ANOVA and pairwise multiple comparisons among the treatments were performed using Bonferroni-adjusted probabilities.

To analyze bead burial by dung beetles in scattered (single) dung piles versus clumped (groups of ten) dung piles, scattered piles were pooled in groups of ten consecutive piles to allow comparison with the "clumped" treatment. The percentage of beads buried in each group of ten piles was calculated and differences among treatments were tested with a two-tailed *t*-test. No data transformation yielded a normal distribution of burial depth; thus, differences in this variable among treatments were tested with a two-tailed Mann-Whitney *U*-test. In this case, sampling units were individual piles.

Two two-way ANOVAs were performed to test for the effect of seed density, dung amount, and their interaction on the percentage of seeds buried (transformed as the arcsine square root of the proportion of seeds buried) and on the depth of burial (square root transformed). To perform the ANOVA on percentage of seed burial, seed/dung piles were pooled so that each sample for analysis had eight seeds; *i.e.*, in the treatment with one seed per dung pile, eight piles were pooled, while in the treatment with four seeds per dung pile, two piles were pooled. Such pooling yielded a normal distribution of the variable.

## RESULTS

PRIMARY SEED DISPERSAL.—One hundred and thirty-seven different species of seeds (including seeds  $<3$  mm) were found in the defecation samples of howler monkeys during the 25-month study period (Table 1). Sixty-four percent of all defecation samples ( $N = 263$ ) contained seeds, while 36 percent had no seeds. In the case of howler monkeys, the absence of seeds in the dung is generally indicative of no fruit in the diet, rather than seeds being spit or dropped (Julliot 1996a, Andresen 1999). Seasonal variation existed in the amount of fruit eaten and seeds dispersed, with a tendency toward higher seed densities at the end of the dry season and beginning of the rainy season, but large variability also existed between the first and the second year (Fig. 1). Sixty-one percent of defecation samples collected during the first year (May 1996–April



TABLE 1. Characteristics of the dung- and seed depositions produced by howler monkeys (one or more monkeys defecating simultaneously).

Variable	Total	$\bar{x} \pm 1$ SE, or median	Range	N
Seed species defecated	137			263
Weight of defecation samples		408 $\pm$ 17.7 g	30–1140 g	205
Dung weight/m <sup>2</sup>		31 g	1–211 g	34
Forest area of defecation sample		17 m <sup>2</sup>	1–63 m <sup>2</sup>	34
Dung piles/defecation sample		62 $\pm$ 5.4	8–112	30
Dung piles/m <sup>2</sup>		6	0.3–28	30
When seeds >3 mm were present in defecation samples:				
Seed weight in a defecation		37 $\pm$ 1.7%	0.3–77%	130
Seed species/defecation sample		4	1–12	154
Seeds/defecation sample		67	1–560	154
Seeds/100 g dung		23	0.2–137	154
Seeds that separate from dung		19 $\pm$ 2.4%	0–35%	19

1997,  $N = 137$  defecation samples) had no seeds in them; in the second year, (May 1997–May 1998,  $N = 126$  defecation samples) only 9 percent of the defecation samples contained no seeds.

Of the 92 seed species that were identified at least to the family level, 61 percent belonged to the Sapotaceae, 14 percent to the Moraceae, and 7 percent to Leguminosae. The rest were distributed among 13 other plant families. Measures of seeds were taken for 112 of the species. The mean length of seeds swallowed by howler monkeys (excluding seeds <3 mm) was  $15.5 \pm 0.6$  mm and the mean width was  $9.9 \pm 0.3$  mm; the maxima were 32.5 and 17.8 mm for length and width, respectively. The average size of the 47 species of Sapotaceae seeds measured (length:  $19.6 \pm 0.7$  mm, width:  $11.2 \pm 0.4$  mm) was above the average of all the species measured.

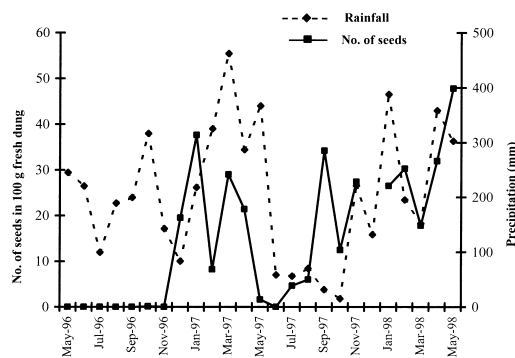


FIGURE 1. Monthly rainfall and abundance of seeds found in howler monkey defecations during the study period (no defecations were collected during December 1997).

DEFECATION PATTERN.—Results concerning the defecation patterns produced by howler monkeys are given in Table 1. Howler monkey defecation samples weighed on average over 400 g, but showed much variation. Most of this variation was probably due to differences in troop size and the fact that although most often (*ca* 75% of the time) all or most of the members of a troop defecate at approximately the same time, it was not uncommon for only one or a few individuals to defecate in a given area (E. Andresen, pers. obs.). As a consequence, the area in which the defecation samples fell also varied greatly (Table 1). The median weight of individual dung piles was only 2.5 g due to many very small pieces of dung being scattered while falling through the vegetation layers; however, 48 percent of all dung collected in the 13 defecations for which individual fecal clumps were weighed (total of 4772 g of dung) was in piles that weighed 5–30 g, 29 percent was in piles of more than 30 g, and 23 percent was in piles of less than 5 g.

In defecation samples in which seeds greater than 3 mm long were present, almost 20 percent of the seeds was separated from the dung in the process of falling to the ground (Table 1). Larger seeds ( $\geq 15$  mm long) were separated from the non-seed fecal material more often than smaller seeds ( $\chi^2 = 22.26$ ,  $df = 1$ ,  $P < 0.01$ ). The percentage of seeds that separated from the fecal material did not depend on the density of seeds in defecation samples (linear regression:  $F_{1,17} = 0.00$ ,  $P = 0.99$ ).

EFFECT OF DEFECATION PATTERN ON RODENT AND DUNG BEETLE BEHAVIOR.—Seed predation by ro-

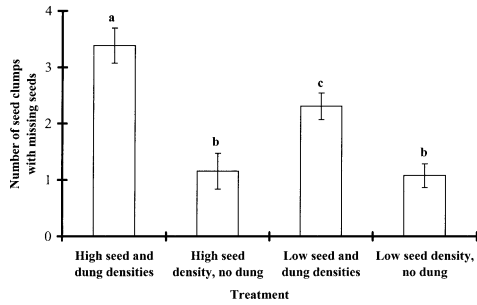


FIGURE 2. Mean number of sunflower seed clumps (out of five seed clumps) with at least one seed missing in four treatments of seed and dung deposition patterns (see text for a more detailed explanation of treatments). Error bars indicate standard error;  $N = 13$  for each treatment. Matching letters above bars indicate statistically homogeneous samples ( $P > 0.05$ ).

dents: The effect of presence of dung and of dung/seed pile density. Significant differences were observed in the amount of seed predation among the four dung/seed deposition patterns (one-way ANOVA:  $F_{3,48} = 16.02$ ,  $P < 0.01$ ). Predation was highest in high seed/dung densities, followed by single seed piles placed next to 10 g of dung, and was lowest for seed piles with no dung, regardless of seed density (Fig. 2).

Bead burial by dung beetles: Scattered vs. clumped dung piles. No significant difference was found in the percentage of beads buried by dung beetles in scattered (53%) versus clumped (46%) dung piles or in burial depth of beads in scattered (34 mm) versus clumped (38 mm) piles (percentage of beads buried:  $t$ -test,  $t = -0.82$ ,  $df = 22$ ,  $P = 0.42$ ; burial depth: Mann-Whitney  $U$ -test,  $U = 1482.50$ ,  $N = 69$  for clumped and 41 for scattered piles,  $P = 0.67$ ).

Seed burial by dung beetles: Effect of seed density and amount of dung in scattered dung piles. No effect of seed density was found for either percentage of seeds buried or burial depth; similarly, the interactions between seed density and dung amount were not significant. Dung amount, however, had a significant effect on both variables with seeds being buried more often and deeper when deposited inside larger dung piles (Fig. 3; two-way ANOVA for percentage of seeds buried: density,  $F_{1,109} = 0.02$ ,  $P = 0.88$ ; dung amount:  $F_{1,129} = 11.86$ ,  $P < 0.01$ ; density  $\times$  dung amount:  $F_{1,129} = 0.28$ ,  $P = 0.60$ ; two-way ANOVA for burial depth: density,  $F_{1,298} = 0.81$ ,  $P = 0.37$ ; dung amount:  $F_{1,298} = 10.43$ ,  $P < 0.01$ ; density  $\times$  dung amount:  $F_{1,298} = 0.30$ ,  $P = 0.58$ ).

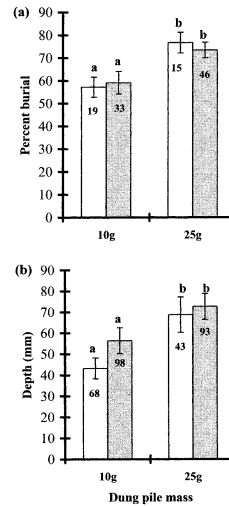


FIGURE 3. Percentage of (a) seeds buried and (b) burial depth for seeds placed in (a) groups of four (gray bars) and singly (white bars), inside individual 10 g and 25 g dung piles. Error bars indicate standard error. Numbers inside bars are sample sizes, which are groups of eight seeds pooled in the case of percentage of seeds buried, and single seeds in the case of burial depth. Matching letters above bars indicate statistically homogeneous samples ( $P > 0.05$ ).

## DISCUSSION

PRIMARY SEED DISPERSAL BY HOWLER MONKEYS: DISPERSAL PREVALENCE AT THE PLANT COMMUNITY LEVEL.—Similar to what has been reported for howler monkeys in other regions (Milton 1980, Mittermeier & van Roosmalen 1981, Estrada & Coates-Estrada 1984, Galetti *et al.* 1994, Julliot 1996a), great variability was observed in the amount of seeds found in the feces during different months, with long periods of time in which leaves constituted the main source of food. Yet, what is unusual in this study site in Central Amazonia is the extremely high number of different seed species that are swallowed, defecated, and thus dispersed by howler monkeys. I found 137 seed species in howler monkey defecation samples over a 25-month period. Most studies on the diet of howler monkeys have reported fruit diets consisting of less than 35 species (Milton 1980, Gaulin & Gaulin 1982, Estrada & Coates-Estrada 1984, Galetti *et al.* 1994, Andresen 1999). Only in French Guiana have howler monkeys been reported to disperse (through defecation) a number of plant species similar to the one observed in this study: 110 species (Julliot & Sabatier 1993, Julliot 1996a). I conclude upon this result that howler monkeys in Central Amazonia

are highly prevalent seed dispersers at the plant community level.

Differences in fruit consumption by howler monkeys are no doubt due in part to differences in forest composition and seasonality among study sites, which will both affect the average year-round fruit availability. Forests in Central Amazonia are more similar in composition to forests in Eastern Amazonia and the Guianas than to forests in Western Amazonia or Central America (Terborgh & Andresen 1998). Thus, it is not surprising to find similar diets for the howler monkeys in the Manaus area and in French Guiana.

Differences in fruit consumption may also occur due to differences in diet preferences among howler monkey species, or even howler monkey populations. Since howler monkeys form cohesive troops, they mostly feed on items that are abundant enough for the whole troop to forage together. Thus, since fruit has a more patchy spatial and temporal distribution than leaves, it may be that species or populations with larger group sizes eat on average more leaves than fruit, and/or eat only fruit that is available in large crops. Group size may vary greatly among and within *Alouatta* species (Chapman & Balcom 1998 and references therein); however, it is more likely that food availability is determining group size and diet (Chapman & Balcom 1998) rather than group size affecting diet preferences.

Another factor that may cause differences in diets among sites is the presence and abundance of competing species of arboreal mammals. Howler monkeys are easily displaced from fruiting trees by other species, such as the spider monkey (E. Andresen, pers. obs.), and probably exploit some fruit species less frequently in sites where competitors are in high densities. In my study site, spider monkeys are extremely rare (Rylands & Keuroghlian 1988; EA, pers. obs.) and this may favor fruit consumption by howler monkeys. Finally, fruit availability can vary tremendously among months and from one year to another, and even when fruit availability is similar in different years, primates may still show considerable variation in the species of fruits eaten and the proportion of the diet constituted by fruit (Chapman 1989). Thus, studies that examine the diet of a primate species during periods of one year or less are likely to show a diet consisting of considerably fewer plant species than longer studies. In my study, for example, howler monkeys only dispersed the seeds of 47 plant species during the first year (May 1996–April 1997), and 90 new species were added to the fruit diet in

the second year (May 1997–May 1998). Similarly, Santamaría-Gómez (1999), who studied the diet of howler monkeys in my study site between July and December 1998, reported that only 17 species of fruits were consumed during that period.

Howler monkeys are able to swallow large seeds (in this study, maximum length: 33 mm and maximum width: 18 mm). Similarly, in French Guiana, howlers swallowed seeds that were 40 x 25 mm in size (Julliot 1996a). Seeds of this size are likely to be swallowed only by large frugivorous animals. Moreover, while on the parent tree, large fruits with hard indehiscent husks are likely to be eaten only by arboreal mammals, since only they have the manipulative and biting ability to open such fruits (except for parrots that are seed predators). For example, most tree species of the family Sapotaceae have these characteristics: large fruits with large seeds (>10 mm long) and hard, indehiscent husks. Consequently, as already noted by Julliot (1996a), howler monkeys and other large primates are probably the main seed dispersers of many Sapotaceae species and thus may be of particular importance for the regeneration of species in this plant family. Both in French Guiana and my study site in Central Amazonia, Sapotaceae is one of the most important families of trees in terms of species numbers and density of trees, and it is the most important family in the fruit diet of howler monkeys (Rankin-de-Merona *et al.* 1992, Julliot 1996a, this study).

DEFECATION PATTERN AND ITS EFFECTS ON THE SHORT-TERM FATE OF DISPERSED SEEDS: DISPERSAL EFFECTIVENESS AT THE PLANT POPULATION LEVEL.—The effectiveness of a seed disperser at the plant population level depends on the quantity and the quality of dispersal (Schupp 1993). In terms of quantity of seeds dispersed, this and other studies have clearly shown that howler monkeys are able to disperse large amounts of seeds (Milton 1980; Mittermeier & van Roosmalen 1981; Estrada & Coates-Estrada 1984; Julliot 1996a; Table 1). In terms of aspects related to dispersal quality such as fruit handling, effect of gut passage, and dispersal distance, researchers also agree on the high quality of howler monkeys. Howler monkeys rarely prey on or spit out seeds; gut passage has in most cases a positive or a neutral effect on germination; most seeds are dispersed away from fruiting trees; and dispersal distances can be 500 m or more (Milton 1980, Estrada & Coates-Estrada 1984, de Figueiredo 1993, Andresen 1994, Julliot 1996a, Santamaría-Gómez 1999). But what is the dispersal quality of



howler monkeys in terms of post-dispersal seed fate?

Defecation by howler monkeys often produces one of the largest aggregations of dung observed among Neotropical arboreal mammals. The experiment with sunflower seeds clearly showed that dung attracts rodents, and further, that predation of seeds is higher in sites with more dung than in sites with less dung. This coincides with previous studies in tropical forests that also showed the effect of fecal material in attracting seed-eating rodents (Janzen 1982a, 1986; Chapman 1989; Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Andresen 1999, 2001); however, it is important to remember that in this experiment, sunflower seeds were placed next to the dung rather than inside it. Consequently, the observed predation rates were higher than would be expected from seeds surrounded by dung, which have a chance of being buried by beetles and thus a high probability of avoiding predation (Estrada & Coates-Estrada 1991, Shepherd & Chapman 1998, Feer 1999, Andresen 2001). It is also important to keep in mind that this experiment only measured the effect of dung during the first day of dung/seed deposition. As dung quickly disappears due to the activity of dung beetles (and also rain during the rainy season), the effect of dung itself is likely to disappear with time as well (Andresen 2001). In an experiment in Perú, for example, I found that the negative effect of the presence of dung on seed predation was still significant after 7 days, but not after 30 days (Andresen 1999). Considering this, the results presented here regarding predation after 1 day for seeds with and without dung, may not be biologically important for seed species with long germination times that are in areas with an abundant dung beetle community. For species that germinate quickly, however, the effect of dung presence on seed predation may still be substantial by the time seeds germinate. Also, the effect of dung presence after the first few days may still be important in forests in which dung beetles are rare or absent (*e.g.*, small forest fragments; Andresen 2000b) or only seasonally abundant (*e.g.*, seasonally dry forests; Janzen 1983).

Regarding howler monkey defecation patterns, it is also important to note that although most of the defecations are large and clumped in space, some are not. It is not rare that only a single or a few individuals will defecate at the same time, producing a much smaller defecation sample than usual. I found, for example, that 26 percent of the defecation samples weighed less than 200 g and

were thus probably produced by one or two individuals (estimated from Julliot 1996a).

Defecation by howler monkeys also often produces large aggregations of seeds. It is important to mention, however, that again, this is not always the case. Low seed densities may occur in the scenario mentioned above, when only one or two monkeys defecate. But low seed density may also occur when howler monkeys are eating a large amount of leaves relative to fruit, even though large defecation samples are produced. I found, for example, that although up to 560 seeds greater than 3 mm long could be found in a defecation sample, 20 percent of the defecation samples that contained seeds had fewer than 30 seeds.

In terms of the effect of seed density on seed predation, I found that sunflower seeds placed without dung suffered similar predation rates regardless of seed density. Results from other studies assessing the effect of seed density on seed predation rates show little consistency. Some studies have shown increased seed removal by predators with increasing seed density (Janzen 1982a, Hulme 1994, Hammond 1995, Cintra 1997, Sánchez-Cordero & Martínez-Gallardo 1998), while others have found no effect of seed density (Heithaus 1981, Webb & Willson 1985, Chapman 1989, Gryj & Domínguez 1996, Cintra 1997, Harrington *et al.* 1997, Sánchez-Cordero & Martínez-Gallardo 1998) and still others have reported higher survival probabilities for seeds in high densities (Janzen 1982b, Willson & Whelan 1990). These differences in results are likely due to differences in rodent behavior, which in turn are a consequence of many factors, such as rodent species, seed species, habitat, season, and overall fruit availability (Price & Jenkins 1986, Forget *et al.* 1998).

Unlike the case of rodent behavior, the density of dung clumps did not have an effect on the behavior of dung beetles. It seems possible that in defecation samples composed of more than one fecal clump, while more beetles are attracted to larger defecation samples, the relative number and composition of dung beetles attracted per unit of dung is the same as in smaller defecation samples. This would also be consistent with results obtained in French Guiana by Feer (1999), who observed similar dung removal rates for large quantities of dung (300–800 g) under howler monkey resting areas, and for individual 50 g dung piles.

Seed density in individual dung piles also had no effect on percentage of seeds buried, or on burial depth; however, a significant effect was observed due to the size of individual dung clumps. Thus,

although dung beetle activity in terms of seed burial was the same for single 10 g dung piles and for groups of ten such piles, seeds were buried more often and more deeply when surrounded by 25 g of dung than by 10 g of dung. The same result was obtained for other seed species in a separate experiment (Andresen 2000b, 2001). This was probably due to the fact that larger individual dung piles attract more dung beetles than smaller dung piles (Peck & Howden 1984, Andresen in press). A possible explanation for the greater burial depths observed for seeds embedded in larger dung piles is that beetles make deeper burrows in order to diminish competition for nesting sites (Andresen in press). Thus, since larger dung piles attract more dung beetles, competition will be more intense; as a consequence, an increase in burial depth may provide a more adequate partitioning of the vertical space beneath the dung source (Hanski & Camberfort 1991).

In terms of the size of individual dung piles, it is probable that howler monkeys, due to their large body size (7–9 kg), the large amount of leaves in their diet, and their habit of defecating from lower branches and in areas free of underlying vegetation, produce the largest individual dung piles compared to other arboreal frugivorous mammals in the Neotropics (Estrada & Coates-Estrada 1991, Gilbert 1997, Andresen 1999). It follows that while howler monkey defecations probably attract more seed predators than the more scattered defecations of other arboreal mammals, seeds in howler defecations also have a higher probability of being buried by dung beetles and thus a higher probability of seedling establishment (Andresen 2000b, 2001). Furthermore, just by being inside a large dung pile, some seeds may avoid predation by remaining “hidden” from predators (Janzen 1982a).

Seeds that separate from the dung while falling through vegetation layers probably suffer the highest rates of predation when compared to seeds that are inside dung clumps and seeds that are not defecated. Seeds that separate from the fecal material will have the disadvantage of being deposited on the forest floor in close proximity to dung. As we

have seen, the odor of dung attracts rodents, which will then easily find seeds lying next to the dung. In this regard, it appears that defecation patterns that produce more coherent feces, and thus with a smaller probability of seeds to separate from dung, could be advantageous from the plant’s perspective. When compared to seeds defecated by arboreal frugivores that have a more scattered defecation pattern such as spider monkeys (Andresen 1999), seeds defecated by howler monkeys probably have a much higher chance of being deposited inside a fecal clump.

**CONCLUDING REMARKS.**—This study has shown that aspects related to the defecation pattern of a frugivorous animal can greatly affect the post-dispersal fate of the seeds it disperses and consequently, its quality as a seed disperser. Thus, caution should be taken to not prematurely categorize an animal as a low quality seed disperser at the plant population level.

At the plant community level, studies on seed dispersal should encompass, when possible, data for more than one year. And it is also important to keep in mind that seed dispersal studies, in particular those performed for management and conservation purposes, should be site specific, since the same species of animal may be a prevalent seed disperser in one site but not in another.

## ACKNOWLEDGMENTS

I thank D. Levey for his helpful advice and support during the development of this research and invaluable comments on an earlier version of the manuscript. I thank R. Bodmer, J. Brockmann, C. Chapman, D. Pérez-Salicrup, F. Putz, M. Verdú, and an anonymous reviewer for their comments on this manuscript. Financial and logistic support were provided by the University of Florida—Department of Zoology, the University of Florida—College of Liberal Arts and Sciences, the Biological Dynamics of Forest Fragments Project (BDFFP), Instituto Nacional de Pesquisas da Amazônia (INPA), the Smithsonian Institution, the Lincoln Park Zoo, and the Wildlife Conservation Society. This research was part of dissertation work conducted at the Department of Zoology, University of Florida. This is contribution number 348 in the INPA–Smithsonian–BDFFP technical series.

---

## LITERATURE CITED

- ANDRESEN, E. 1994. Frugivory and primary seed dispersal by spider monkeys (*Ateles paniscus*) and howler monkeys (*Alouatta seniculus*), and the fate of dispersed seeds at Manu National Park, Perú. M.S. thesis. Duke University, Durham, North Carolina.
- . 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. *Biotropica* 31: 145–158.
- . 2000a. Ecological roles of mammals: the case of seed dispersal. *In* A. Entwistle and N. Dunstone (Eds.).

- Future priorities for the conservation of mammalian diversity: Has the panda had its day?, pp. 11–25. Cambridge University Press, Cambridge, England.
- . 2000b. The role of dung beetles in the regeneration of rainforest plants in Central Amazonia. Ph.D. dissertation. University of Florida, Gainesville, Florida.
- . 2001. Effects of dung presence, dung amount, and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. *J. Trop. Ecol.* 17: 61–78.
- . Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecol. Entomol.* In press.
- BERMEJO, T., A. TRAVESET, AND M. F. WILLSON. 1998. Post-dispersal seed predation in the temperate rainforest of southeast Alaska. *Can. Field Nat.* 112: 510–512.
- CHAMBERS, J. C., AND J. A. MACMAHON. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annu. Rev. Ecol. Syst.* 25: 263–292.
- CHAPMAN, C. A. 1989. Primate seed dispersal: The fate of dispersed seeds. *Biotropica* 21: 148–154.
- , AND S. R. BALCOM. 1998. Population characteristics of howlers: ecological conditions or group history. *Int. J. Primatol.* 19: 385–403.
- CINTRA, R. 1997. A test of the Janzen–Connell model with two common tree species in Amazonian forest. *J. Trop. Ecol.* 13: 641–658.
- COATES-ESTRADA, R., AND A. ESTRADA. 1988. Frugivory and seed dispersal in *Cymbopetalum baillonii* (Annonaceae) at Los Tuxtlas, Mexico. *J. Trop. Ecol.* 4: 157–172.
- DE FIGUEIREDO, R. A. 1993. Ingestion of *Ficus enormis* seeds by howler monkeys (*Alouatta fusca*) in Brazil: effects on seed germination. *J. Trop. Ecol.* 9: 541–543.
- DEW, L. J., AND P. WRIGHT. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* 30: 425–437.
- ESTRADA, A., AND R. COATES-ESTRADA. 1984. Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *Am. J. Primatol.* 6: 77–91.
- , AND ———. 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *J. Trop. Ecol.* 7: 459–474.
- , G. HALFFTER, R. COATES-ESTRADA, AND D. A. MERITT JR. 1993. Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical rain forest of Los Tuxtlas, Mexico. *J. Trop. Ecol.* 9: 45–54.
- FEER, F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. *J. Trop. Ecol.* 15: 129–142.
- FORGET, P.-M., T. MILLERON, AND F. FEER. 1998. Patterns in post-dispersal seed removal by Neotropical rodents and seed fate in relation to seed size. In D. M. Newbery, H. H. T. Prins, and N. D. Brown (Eds.). *Dynamics of tropical communities*, pp. 25–49. Blackwell Science Ltd., Oxford, England.
- GALETTI, M., F. PEDRONI, AND L. P. C. MORELLATO. 1994. Diet of the brown howler monkey *Alouatta fusca* in a forest fragment in southeastern Brazil. *Mammalia* 58: 111–118.
- GAULIN, S. J. K., AND C. K. GAULIN. 1982. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. *Int. J. Primatol.* 3: 1–32.
- GILBERT, K. A. 1997. Red howling monkey use of specific defecation sites as a parasite avoidance strategy. *Anim. Behav.* 54: 451–455.
- GRYJ, E. O., AND C. A. DOMÍNGUEZ. 1996. Fruit removal and postdispersal survivorship in the tropical dry forest shrub *Erythroxylum havanense*: ecological and evolutionary implications. *Oecologia* 108: 368–374.
- GUILLOTIN, M., G. DUBOST, AND D. SABATIER. 1994. Food choice and food competition among the three major primate species of French Guiana. *J. Zool.* 233: 551–579.
- HAMMOND, D. S. 1995. Post-dispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexico. *J. Trop. Ecol.* 11: 295–313.
- HANSKI, I., AND Y. CAMBEFORT. 1991. Competition in dung beetles. In I. Hanski and Y. Cambefort (Eds.). *Dung beetle ecology*, pp. 305–329. Princeton University Press, Princeton, New Jersey.
- HARRINGTON, G. N., A. K. IRVINE, F. H. J. CROME, AND L. A. MOORE. 1997. Regeneration of large-seeded trees in Australian rainforest fragments: a study of higher-order interactions. In W. F. Laurance and R. O. Bierregaard Jr. (Eds.). *Tropical forest remnants. Ecology, management, and conservation of fragmented communities*, pp. 292–303. The University of Chicago Press, Chicago, Illinois.
- HEITHAUS, E. R. 1981. Seed predation by rodents on three ant-dispersed plants. *Ecology* 62: 136–145.
- HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.
- HOWE, H. F. 1980. Monkey dispersal and waste of a Neotropical fruit. *Ecology* 61: 944–959.
- . 1984. Implications of seed dispersal by animals for tropical reserve management. *Biol. Conserv.* 30: 261–281.
- . 1986. Seed dispersal by fruit-eating birds and mammals. In D. R. Murray (Ed.) *Seed dispersal*, pp. 123–189. Academic Press, Sydney, New South Wales, Australia.
- . 1990. Seed dispersal by birds and mammals: implications for seedling demography. In K. S. Bawa and M. Hadley (Eds.). *Reproductive ecology of tropical forest plants*, pp. 191–218. UNESCO and the Parthenon Publishing Group, Paris, France.
- HULME, P. E. 1994. Post-dispersal seed predation in grassland: its magnitude and sources of variation. *J. Ecol.* 82: 645–652.

- JANZEN, D. H. 1982a. Removal of seeds from horse dung by tropical rodents: influence of habitat and amount of dung. *Ecology* 63: 1887–1900.
- . 1982b. Attraction of *Liomys* mice to horse dung and the extinction of this response. *Anim. Behav.* 30: 483–489.
- . 1983. Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican deciduous forest and adjacent horse pasture. *Oikos* 41: 274–283.
- . 1986. Mice, big mammals and seeds: It matters who defecates what where. In A. Estrada and T. H. Fleming (Eds.), *Frugivores and seed dispersal*, pp. 314–338. Dr W. Junk, Dordrecht, The Netherlands.
- JULLIOT, C. 1996a. Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *Int. J. Primatol.* 17: 239–258.
- . 1996b. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. *Am. J. Primatol.* 40: 262–282.
- , AND D. SABATIER. 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. *Int. J. Primatol.* 14: 527–550.
- KAPLIN, B. A., AND T. C. MOERMOND. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. *Am. J. Primatol.* 45: 83–101.
- LOVEJOY, T. E., AND R. O. BIERREGAARD. 1990. Central Amazonian forests and the Minimum Critical Size of Ecosystems Project. In A. Gentry (Ed.), *Four Neotropical rainforests*, pp. 60–71. Yale University Press, New Haven, Connecticut.
- MCCONKEY, K. R. 2000. Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, Central Borneo. *Am. J. Primatol.* 52: 13–29.
- MILTON, K. 1980. The foraging strategy of howler monkeys. A study in primate economics. Columbia University Press, New York, New York.
- MITTERMEIER, R. A., AND M. G. M. VAN ROOSMALEN. 1981. Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia Primatol.* 36: 1–39.
- PECK, S. B., AND H. F. HOWDEN. 1984. Response of a dung beetle guild to different sizes of dung bait in a Panamanian rain forest. *Biotropica* 16: 235–238.
- PIZO, M. A., AND P. S. OLIVEIRA. 1999. Removal of seeds from vertebrate faeces by ants: effects of seed species and deposition site. *Can. J. Zool.* 77: 1595–1602.
- PRICE, M. V., AND S. H. JENKINS. 1986. Rodents as seed consumers and dispersers. In D. R. Murray (Ed.), *Seed dispersal*, pp. 191–235. Academic Press, Sydney, New South Wales, Australia.
- RANKIN-DE-MERONA, J. M., G. T. PRANCE, R. W. HUTCHINGS, M. FREITAS DA SILVA, W. A. RODRIGUES, AND M. E. UEHLING. 1992. Preliminary results of a large-scale tree inventory of upland rain forest in the Central Amazon. *Acta Amazon.* 22: 493–534.
- RYLANDS, A. B., AND A. KEUROGHLIAN. 1988. Primate populations in continuous forest and forest fragments in Central Amazonia. *Acta Amazon.* 18: 291–307.
- SÁNCHEZ-CORDERO, V., AND R. MARTÍNEZ-GALLARDO. 1998. Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. *J. Trop. Ecol.* 14: 139–151.
- SANTAMARÍA-GÓMEZ, A. M. 1999. Ecologia e comportamento de *Alouatta seniculus* em uma mata de *terra firme* na Amazônia Central. M.S. tesis. Universidade Federal de Minas Gerais, Belo Horizonte, Brasil.
- SCHUPP, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/ 108: 15–29.
- SHEPHERD, V. E., AND C. A. CHAPMAN. 1998. Dung beetles as secondary seed dispersers: impact on seed predation and germination. *J. Trop. Ecol.* 14: 199–215.
- SIMMEN, B., AND D. SABATIER. 1996. Diets of some French Guianan primates: food composition and food choices. *Int. J. Primatol.* 17: 661–693.
- STEVENSON, P. R. 2000. Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: Dispersal distance, germination rates, and dispersal quantity. *Am. J. Primatol.* 50: 275–289.
- TERBORGH, J., AND E. ANDRESEN. 1998. The composition of Amazonian forests: patterns at local and regional scales. *J. Trop. Ecol.* 14: 645–664.
- VAN ROOSMALEN, M. G. M., 1985. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazon.* 15(suppl.): 1–238.
- VULINEC, K. 2000. Dung beetles (Coleoptera: Scarabaeidae), monkeys, and conservation in Amazonia. *Fla. Entomol.* 83: 229–241.
- WEBB, S. L., AND M. F. WILLSON. 1985. Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia* 67: 150–153.
- WILLSON, M. F., AND C. J. WHELAN. 1990. Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season, and species. *Oikos* 57: 191–198.
- ZHANG, S. Y., AND L.-X. WANG. 1995. Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. *Biotropica* 27: 397–401.