Journal of Tropical Ecology (1991) 7:459–474. With 2 figures

Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico

ALEJANDRO ESTRADA *and* ROSAMOND COATES-ESTRADA

Estación de Biología 'Los Tuxtlas', Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 176, San Andrés Tuxtla, Veracruz, México

ABSTRACT. The dispersal of seeds by howler monkeys (*Alouatta palliata*) and the activity of dung beetles in modulating the fate of the dispersed seed were studied at Los Tuxtlas, Mexico. Howlers consumed the fruits of 35 species of plants. The seeds of 28 of these were dispersed by the monkeys. The majority (≥ 90%) of the seeds dispersed by monkeys were destroyed by rodents. Rapid relocation and burial of dung by dung beetles resulted in accidental relocation and burial of large numbers of seeds shortly after deposition. Faecal clumps (20 mg) remained on the ground for an average of only 2.5 h (range 1–3 h). Ball-rolling beetles transported balls up to 5.0 m from the site of deposition (range 1–5 m). Burrowing and ball-rolling dung beetles buried seeds at depths ranging from 2.5 to > 12.0 cm. The deeper a seed is buried, the less likely it is to be found and eaten by rodents. Eighty percent of the species used by *Alouatta* as sources of fruit at Los Tuxtlas benefited by the dispersal and post dispersal service provided by howlers and dung beetles respectively. Seasonality in dung beetles abundance in the forest may influence the number of seeds per species escaping post-dispersal predation during the year. Dung beetles play not only an important ecological role in the recycling of matter and energy in the ecosystem, but also in the process of rain forest regeneration.

RESUMEN. La dispersión de semillas por monos aulladores (*Alouatta palliata*) y el impacto de la actividad de forrajeo y nidificación de escarabajos coprófagos sobre el destino de las semillas dispersadas fueron estudiados en la selva de Los Tuxtlas, México. La mayoría (≥ 90%) de las semillas (28 especies de plantas) dispersadas por los monos son depredadas por roedores. El aprovechamiento de materia faecal por escarabajos en el suelo de la selva resulta en la relocalización y enterramiento accidental de un gran número de semillas poco después de ser expulsadas por los monos a través de sus heces. Los escarabajos entierran las semillas a profundidades que van desde 2.5 a > 12.0 cm disminuyendo asi la eficiencia con la que los reodores pueden localizarlas. Ochenta porciento de las especies de plantas usadas por lo monos como fuentes de frutos en Los Tuxtlas reciben los beneficios de dispersión y postdispersión aportados por aulladores y escarabajos coprófagos respectivamente. La estacionalidad en la abundancia relativa de escarabajos coprófagos en la selva de Los Tuxtlas podría determinar el número de semillas que escapan a la fuerte depredación postdispersión en el año. Los escarabajos coprófagos son componentes importantes no solo en reciclaje de materia y energía en el ecosistema pero también en el proceso natural de regeneración de la selva.

KEY WORDS: *Alouatta palliata*, dung beetles, howlers, Mexico, Scarabaeidae, seed dispersal, seed predation, tropical rain forest.

INTRODUCTION

In the humid tropics, frugivorous vertebrates ingest seeds as contaminants of fruit pulp and the seeds ingested are expelled from the digestive tract as contaminants of faecal matter at variable times and at variable distances from the parent tree (Charles-Dominique 1986, Coates-Estrada & Estrada 1988). Howler monkeys (*Alouatta palliata* Gray) are ubiquitous canopy dwellers of the Neotropical rain forest consuming leaves and fruit daily to satisfy nutritional and energetic requirements (Nagy & Milton 1979). The daily ingestion of a great number of seeds as contaminants of fruit pulp by howlers in concert with their daily movements has no negative effects on seed viability and may decrease average germination time for the seeds of some species; it also results in movement of the seeds away from the parent tree to distances of up to 1 km, and may reduce predispersal predation risk for certain tree species (Estrada & Coates-Estrada, 1984, 1986).

Rodents

In Neotropical rain forests seeds dispersed on the forest floor are a primary source of food to seed eating rodents which consequently have an important impact on recruitment in plant populations (see papers in Estrada & Fleming 1986, Janzen 1982a,b).

Dung beetles

Coprophagous organisms such as Diptera, Dermaptera, and Coleoptera including dung beetles (Scarabaeidae) are conspicuous in tropical rain forests (Halffter & Matthews 1966, Howden & Nealis 1978, Howden & Young 1981, Peck & Forsyth 1982). Dung beetles use the dung produced by forest vertebrates such as primates, bats, birds, and reptiles (Howden & Young 1981, Young 1981) as food, and as a substrate for oviposition and for feeding by their larvae (Halffter & Edmonds 1982, Moron 1979). Food is detected during search flights or during periods of perching at sites exposed to air currents (Halffter & Edmonds 1982, Halffter & Matthews 1966). Dung beetles process the dung by rolling it away from the site of deposition in the form of spherical pellets which are buried (ball-rollers) or by burying it at the site of deposition (burrowers). Adults extract most of their nutrients from the microorganisms and organic colloids suspended in dung and much of the food supply used by the larvae is derived from the fibre content of excrement, particularly that of herbivores (Halffter & Edmonds 1982). Howler (*Alouatta palliata*) dung is a resource assiduously sought by several dung beetle species in Neotropical rain forest (Halffter & Edmonds 1982, Howden & Young 1981, Peck & Forsyth 1982).

Monkey dung is thus of particular importance in the foraging ecology and reproductive behaviour of dung beetles. Rapid desiccation and intense competition with other coprophagous insects, particularly flies and other dung beetles, can rapidly render dung useless to beetles. Such conditions require that excrement is quickly exploited or that it be protected from drying if it is to be used over an extended period of time (Halffter & Edmonds 1982, Peck & Forsyth 1982). Protection of excrement by burial may also result in the burying of, for example, seeds embedded in the dung.

Seed dispersal

Over their evolutionary history, plants have developed strategies and tactics aimed at repelling potential seed predators before their seeds are dispersed, by means of chemical and mechanical defences and by varying the times of production of seeds. Once the seed is dispersed however, control over its fate by the parent plant is negligible. Dispersed seeds fall victim to physical (inadequate germination sites, desiccation, etc) and biotic (pathogens, fungi, predation by rodents, etc.) accidents which tend to waste the maternal investment (Augspurger 1983, Coates-Estrada & Estrada 1988, Hallwachs 1986, Janzen 1982a, b, 1986, Schupp & Frost 1989, Vázquez-Yanes *et al.* 1975).

Little is known about the biotic or abiotic factors that ultimately may determine the fate of the dispersed seed. Such knowledge is of particular importance for understanding key ecological processes in the tropical rain forest, such as frugivory, seed dispersal and recruitment in plant populations, and for identifying the participating components in the interactions. In this paper we report the dramatic impact of dung processing behaviour by dung beetles in modulating the fate of seeds of plant species dispersed by howlers in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico.

METHODS

Fruit-eating by howlers

Howler frugivory and seed dispersal were studied over six years (1983–1988) in the forest of the Los Tuxtlas biological reserve in southern Veracruz (95° 04′ – 95° 09′ N, 18° 34′ – 18′ 36′ W), Mexico. Troops were followed through the forest on a monthly basis and records were kept of plant species used and of time spent feeding on fruit. Faecal samples collected during observations yielded seeds which were identified to species. These were planted in a screened growing house to assess germination potential (see Estrada & Coates-Estrada 1986 for details of procedures).

Seasonality in fruit/seed production

Phenological data on fruit/seed production in the forest was monitored over a two year period using two methods: (1) seed traps and (2) phenological monitoring. Fifty fruit traps were placed every 20 m along a 1 km long transect and the contents were collected every week. Fruits/seeds collected were identified to species and weighed after drying at 60°C for 48 hours. Additionally bi-weekly records were kept of the fruit phenology of all plants ≥ 25 cm DBH in three 500 m × 20 m belt transects in the forest occupied by three howler troops.

Dung beetles

The processing of howler dung by dung beetles was recorded while making observations on the monkeys. Samples of beetles feeding on howler dung were collected for identification. Seasonality in the population of dung beetles attracted to *Alouatta* dung in the forest was evaluated by conducting monthly censuses of dung beetles within the area occupied by the three howler troops. These censuses were conducted along a 500 m long × 20 m wide transect by placing a pit trap baited with fresh monkey dung at intervals of 20 m over a 24-hour cycle once a month, for 12 months. Fresh bait was placed at 0600 h and beetles were collected from the traps at 1800 h at which time the bait was replaced; beetles were retrieved from the traps again at 0600 h the next morning. All beetles collected in the censuses were identified to species, measured (length) and weighed.

Predation of howler dispersed seeds by rodents

Predation by small rodents of the seeds dispersed by howlers was quantified as follows: about 20 g of howler dung with a known number of seeds (range 3–4) of monkey dispersed species were placed at random locations on the forest floor. A replicate dung clump with the same number of seeds and surrounded by a wire mesh cage (exclosure) covered with mosquito netting that impeded access by rodents and beetles was placed adjacent to the clump with no exclosure. Seeds remaining in each case were counted at each of two 12-hour intervals in a 24-hour cycle. Eight replicates of this experiment for each of eight plant species dispersed by *Alouatta* were conducted in the forest at the times when each of the plant species were fruiting. Potential seed predators were determined by placing Sherman traps baited with seeds of the plants of interest in the same locations where the exclosure experiments had been conducted.

Detection of seeds by rodents in experimental wooden boxes

Field experiments designed to estimate the ability of rodents to detect seeds buried in the soil were conducted in a wooden box (1.5 × 1.5 × 0.40 m) placed on the forest floor. The box was filled with 20 cm of forest soil covered with a 2 cm layer of leaf litter. The top of the box consisted of a mosquito net and wire mesh frame which we could lift for exploration of the box and which prevented escape by the experimental rodent placed in the box and access into the box by other animals. In one corner of the box a 20 cm long PVC pipe was half buried horizontally to serve as a burrow for individual mice, *Peromyscus mexicanus* Osgood or *Heteromys desmarestianus* Goldman. Experiments commenced after a three-day habituation of the mouse to the experimental cage. Seeds of six plant species dispersed by howlers were buried at different depths. The detection ability of rodents was observed by counting the seeds remaining at each of six depth intervals: 0 cm, 1–2.5 cm, 2.6–5.0 cm, 5.1–8.0 cm, 8.1–12 cm and > 12.0 cm. Seeds were buried in the afternoon and their presence was checked early the next morning. Marbles of a size similar to that of the seeds were used as controls by burying them at the same depths as the experimental seeds.

Dung beetles

The processing of howler dung by dung beetles was recorded while making observations on the monkeys. Samples of beetles feeding on howler dung were collected for identification. Seasonality in the population of dung beetles attracted to *Alouatta* dung in the forest was evaluated by conducting monthly censuses of dung beetles within the area occupied by the three howler troops. These censuses were conducted along a 500 m long × 20 m wide transect by placing a pit trap baited with fresh monkey dung at intervals of 20 m over a 24-hour cycle once a month, for 12 months. Fresh bait was placed at 0600 h and beetles were collected from the traps at 1800 h at which time the bait was replaced; beetles were retrieved from the traps again at 0600 h the next morning. All beetles collected in the censuses were identified to species, measured (length) and weighed.

Predation of howler dispersed seeds by rodents

Predation by small rodents of the seeds dispersed by howlers was quantified as follows: about 20 g of howler dung with a known number of seeds (range 3–4) of monkey dispersed species were placed at random locations on the forest floor. A replicate dung clump with the same number of seeds and surrounded by a wire mesh cage (exclosure) covered with mosquito netting that impeded access by rodents and beetles was placed adjacent to the clump with no exclosure. Seeds remaining in each case were counted at each of two 12-hour intervals in a 24-hour cycle. Eight replicates of this experiment for each of eight plant species dispersed by *Alouatta* were conducted in the forest at the times when each of the plant species were fruiting. Potential seed predators were determined by placing Sherman traps baited with seeds of the plants of interest in the same locations where the exclosure experiments had been conducted.

Detection of seeds by rodents in experimental wooden boxes

Field experiments designed to estimate the ability of rodents to detect seeds buried in the soil were conducted in a wooden box (1.5 × 1.5 × 0.40 m) placed on the forest floor. The box was filled with 20 cm of forest soil covered with a 2 cm layer of leaf litter. The top of the box consisted of a mosquito net and wire mesh frame which we could lift for exploration of the box and which prevented escape by the experimental rodent placed in the box and access into the box by other animals. In one corner of the box a 20 cm long PVC pipe was half buried horizontally to serve as a burrow for individual mice, *Peromyscus mexicanus* Osgood or *Heteromys desmarestianus* Goldman. Experiments commenced after a three-day habituation of the mouse to the experimental cage. Seeds of six plant species dispersed by howlers were buried at different depths. The detection ability of rodents was observed by counting the seeds remaining at each of six depth intervals: 0 cm, 1–2.5 cm, 2.6–5.0 cm, 5.1–8.0 cm, 8.1–12 cm and > 12.0 cm. Seeds were buried in the afternoon and their presence was checked early the next morning. Marbles of a size similar to that of the seeds were used as controls by burying them at the same depths as the experimental seeds.

Dung/seed processing by dung beetles

The rate at which howler dung was removed by dung beetles and other coprophagous insects was quantified by placing a pile of dung (20 g) on the forest floor and monitoring its presence every 30 minutes. In this case 10 diurnal and 10 nocturnal samples were placed on the ground in random locations throughout the forest on different days and each was observed as above.

The distance ball-rolling dung beetles relocated dung away from the site of deposition was determined by following the progess of these beetles and by measuring the distance moved. Also measured was the depth at which ball-rolling and burrowing dung beetles buried the dung. In this latter case complementary information was obtained from the experiments described below.

Response of dung beetles to seeds in monkey dung

In a set of experiments dung clumps (20 g) with a known number of seeds (2–3) of eight plant species dispersed by *Alouatta* were placed on the forest floor at random locations. A control clump enclosed in a cage whose mesh permitted access by dung beetles, but not by rodents, and with the same number of seeds was placed adjacent to each experimental clump. All clumps were checked 24 h later to determine the presence of seeds. Eight replicates of this experiment were conducted in the field for each of eight plant species.

To determine with more precision the responses of beetles to seeds as contaminants of monkey dung, individuals of five species of ball rollers and five species of burrowers varying in length from 3.5–18.0 mm were presented with clumps of monkey dung (c. 20 g) in which a known number of seeds (2–3) of each of 20 plant species dispersed by *Alouatta* were placed. The beetles and the dung/seed clumps were placed in polyvinylchloride (PVC) cylinders 40 cm high by 20 cm in diameter filled with 30 cm of forest soil. The cylinders had each been split in half longitudinally, and the two halves were held together with tape. After 24 h the cylinder was opened to determine the depth at which dung was buried. The experiment yielded 10 replicates per species of seed, five with ball rollers and five with burrowers, i.e. a total of 100 replications with ball rollers and 100 replications with burrowers.

RESULTS

Fruit-eating by howlers

At Los Tuxtlas, howlers exploited the fruits of 35 plant species (94% were trees) of 14 plant families (names follow Ibarra & Sinaca (1987)). Mature fruit accounted for > 90% of their feeding time on fruit. Fruit eating by *Alouatta* had a seasonal component. Significantly more fruit species were exploited per month between April and October (mean = 8.5, SD = 1.5; range 6–11) than in the other five months (mean = 2.6, SD = 0.83; range 2–4; $t = 7.17$, $DF = 10$, $P < 0.0001$).

Fruit phenology and use of fruit by howlers

Data collected on fruit phenology showed that fruit is produced in the forest throughout the year but that more species fruit between March and October than at other times of the year. The use of fruit species by howlers corresponded quite well with the plant species' patterns of fruiting (Figure 1). The number of months in which the top ranking 14 species on the monkeys' fruit diet were used was correlated with the number of months each species was in fruit ($r_s = 0.52$, $P < 0.05$).

Seed dispersal by howlers

The seeds of 28 of the species used as sources of fruit by howlers were found in their faeces in a viable condition about 18–20 hours after ingestion and at distances ranging from 10–1000 m from their source of origin. Seeds of seven species used by *Alouatta* as fruit sources were dropped under the tree and were not ingested presumably as a result of their large size (length ≥ 35 mm). Eighty percent of the species dispersed by howlers had high germination success after gut passage (see Estrada & Coates-Estrada, 1984, 1986 for further details).

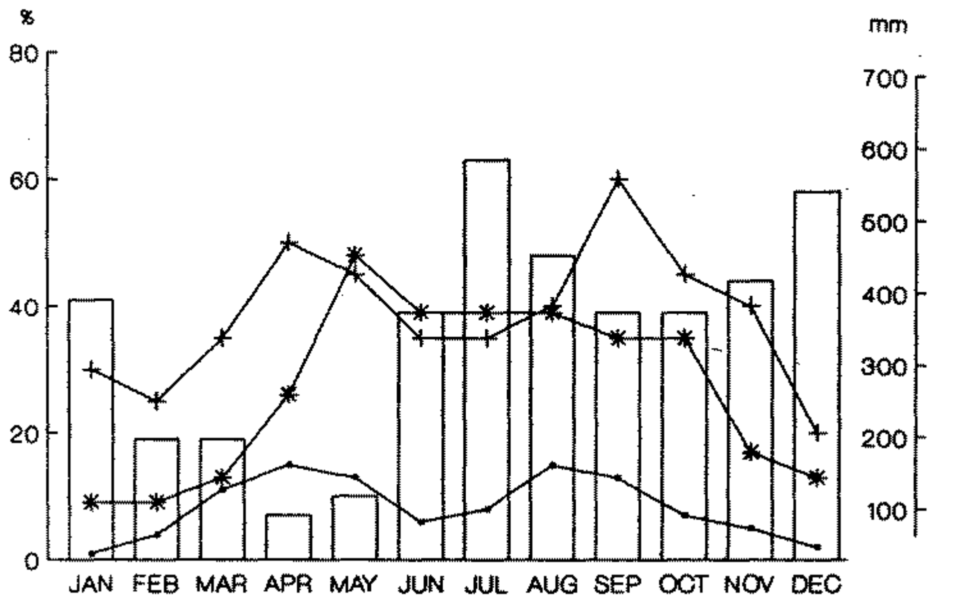

Figure 1. Seasonal variation in fruiting (+ precentage of tree species in fruit, N = 63), *Alouatta* fruit feeding (* percentage of tree species used per month), dung beetle abundance (— percentage of individuals captured in the 24 hour/month pit traps) and rainfall (histogram) at Los Tuxtlas.

Dung beetles

Field observations and sampling with pit traps baited with howler dung showed that 20 species of dung beetles (Scarabaeinae), four Diptera (Micropezidae, Sphaeroceridae, Calliphoridae, Sepsidae), one Dermaptera (Chelisochidae) and one unidentified Coleoptera (Staphylinidae) were attracted to dung. Seven dung beetle species attracted to howler dung are ball rollers, three species of the genus *Eurysternus* consume the dung on the ground surface, and the remaining 10 species bury the dung at the site of deposition (Table 1).

Table 1. Species of dung beetles attracted to howler dung at Los Tuxtlas. Mean body length based on 80–100 individuals per species.

Species	Mean body length (mm)
Burrowers	
Dichotomius satanas Harold	18.2
Dichotomius carolinus (Say)	20.9
Phanaeus endymion Harold	17.6
Phanaeus chryseicollis Harold	16.7
Sulcophanaeus chryseicollis Harold	17.5
Copris laeviceps Harold	10.5
Canthidium martinezi Halffter & Halffter	9.5
Onthophagus batesi Howden & Cartwright	7.7
Onthophagus nasiricornis Harold	9.3
Onthophagus rhinolophus Harold	8.9
Ball rollers	
Deltochilum pseudoparile Paulian	11.4
Canthon viridis Martinez, Halffter & Halffter	7.2
Canthon femoralis Chevrolat	7.1
Canthon subyalinus Harold	4.8
Canthon cyanellus LeC.	9.9
Canthon sp. # 1	5.3
Canthon sp. # 2	5.9
Non ball rolling/non burrowers	
Eurysternus caribaeus (Herbst)	13.8
Eurysternus mexicanus Harold	11.4
Eurysternus angustulus Harold	8.7

Monthly sampling of dung beetles with pit fall traps baited with fresh howler dung captured a total of 654 dung beetles representing 17 species; the mean number of species caught per month was 9.8 (SD $\pm$ 2.7). The 24 h/month traps showed that dung beetles attracted to *Alouatta* dung were present and active in all months of the year, but more numerous between March and October (range 42–105 individuals; 8–14 species) than in the rest of the months (range 4–24 individuals; 2–7 species) (Figure 1).

Predation of howler-dispersed seeds by rodents

Exclosure experiments in the forest showed that unexclosed seeds were consistently removed, possibly by rodents, from the faecal samples. On average 59% of the seeds disappeared from the forest floor in 24 hours (range per species 13–100%). The protected faecal samples lost no seeds (Table 2). Sherman traps baited with seeds of the species at the same locations captured *Heteromys desmarestianus* Goldman and *Peromyscus mexicanus* Osgood rodents.

Table 2. Removal of seeds by rodents from exclosed (no access to rodents or beetles) and unexclosed positions for eight species dispersed by howler monkeys. Data based on eight replicates per species. N: number of seeds removed. Plant names follow Ibarra & Sinaca (1987).

Species	No exclosure Number of seeds	Seeds removed N	Seeds removed %	Exclosure Number of seeds	Seeds removed %
Brosimum alicastrum	24	21	88	24	0
Poulsenia armata	32	17	53	32	0
Pseudolmedia oxyphyllaria	24	13	54	24	0
Dialium quianensis	24	24	100	24	0
Dipholis minutiflora	24	24	100	24	0
Cordia stellifera	32	18	56	32	0
Spondias mombin	24	3	13	24	0
Rollinia jimenezii	32	24	75	32	0
TOTAL	246	144	59	246	0

Detection of seeds by rodents in experimental wooden boxes

Rodents of both species were able to locate 90–100% of the seeds of each of the six plant species left on the soil surface in the wooden box. Rodents were also efficient at locating seeds buried to 2.5 cm. At depths greater than 2.5 cm the locating ability of both species of rodents decreased and only a very small number of seeds were located at 2.5 cm (average 56%), 5.0 cm (average (17%), and > 8.0 cm (average (2%) depths (Table 3). Marbles buried at the various depths were never detected by rodents.

Table 3. Percentage of seeds detected by the rodents (*Peromyscus mexicanus* (PM) and *Heteromys desmarestianus* (HD) for six plant species dispersed by howler monkeys. N: number of seeds at each depth for all experiments at that depth.

Depth		Percentage of seeds detected									
		P.o.		P.a.		B.a.		E.sp.	A.h.	R.j.	
cm	N	PM	HD	PM	HD	PM	HD	PM	PM	PM	Mean
0	20	100	100	100	100	85	85	55	100	100	92
1–2.5	40	95	95	98	90	53	60	55	100	100	83
2.5–5	20	80	20	50	80	40	55	50	65	65	56
5.1–8	20	0	10	0	75	40	30	0	0	0	17
> 12.0	20	0	0	0	0	15	0	0	0	0	2

P.o. *Pseudolmedia oxyphllaria* (Moraceae), P.a. *Poulsenia armata* (Moraceae), B.a. *Brosimum alicastrum*, (Moraceae), E.sp. *Eugenia* sp. (Myrtaceae), A.h. *Ampelocera hottlei* (Ulmaceae), R.j. *Rollinia jimenezii* (Annonaceae). (Names follow Ibarra & Sinaca (1987).)

Dung processing by dung beetles

Monkey dung was rapidly relocated and buried by dung beetles. Faecal clumps (20 g) remained on the ground for an average of only 2.5 hours (range 1–3 h; 10 diurnal and 10 nocturnal samples). Ball-rolling beetles (genera *Canthon*, *Geocanthon* and *Deltochilum*) transported balls up to 5.0 m from the site of deposition (range 0.10–5 m; mean = 1.2 m).

Response of dung beetles to seeds in monkey dung: exclosure experiments

Experiments showed that seeds were lost both from the unexclosed and from the exclosed dung/seed clumps. Careful examination of the soil underneath revealed the presence of dung beetles and that some seeds were buried at depths ranging from 1–10 cm in both situations. On average more seeds were buried in the exclosed (39%) than in the unexclosed (13%) conditions. In the exclosed condition, and depending on the species, from 4–79% of seeds were buried, the rest were found on the soil surface (Table 4). In contrast, in the unexclosed condition only buried seeds were detected at the site of deposition; the rest disappeared, probably removed by rodents.

Table 4. Seeds of eight *Alouatta*-dispersed species buried by dung beetles in field experiments using exclosures (access to dung bettles but not to rodents). Control set was run without exclosure. N: number of seeds used in each experiment. Also shown are the number of seeds germinating and becoming established as seedlings ≥ 3.0 cm and ≤ 30 cm in height in the unexclosed and exclosed conditions for six species.

		Unexclosure		Exclosed		Seeds established	
Species	N	Seeds buried	%	Seeds buried	%	Unexclosed	Exclosed
Brosimum alicastrum	24	3	13	3	13	3	3
Poulsenia armata	32	7	22	16	50	7	16
Pseudolmedia oxyphyllaria	24	4	17	19	79	4	19
Dialium quianensis	24	0	0	9	38		
Dipholis minutiflora	24	0	0	1	4	—	10
Cordia stellifera	32	4	13	15	47	4	15
Spondias mombin	32	0	0	0	0		
Rollinia jimenezii	24	6	25	11	46	6	11
Total		24	13*	74	39*	24 (14%)	74 (44%)

*Overall percentage.

Response of dung beetles to seeds in monkey dung: PVC cylinder experiments

Relocation of monkey dung from the experiments conducted in the PVC cylinders showed that 689 (41%) of a total of 1667 experimental seeds were buried by dung beetles (30% by burrowers and 11% by ball rollers) at depths ranging from 1.0 cm to > 12.0 cm beneath the soil surface. Of the 689 buried seeds, 83% were at depths > 2.5 cm and 54% were buried at depths > 5.0 cm, (Table 5). At these depths location of seeds by rodents is less efficient (see above).

Burrowing and ball rolling dung beetles buried 60% and 22% respectively of the seeds they processed (856 by burrowers and 811 by ball rollers). Burrowing dung beetles buried seeds of all 20 species (range 1–18 mm in length) presented to them in faecal clumps, but ball rollers buried the seeds of only 11 of the 20 species (Table 5, Appendix I).

Table 5. Burial of seeds of 20 *Alouatta*-dispersed species by dung beetles in experimental PVC cylinders. Percentages are of the total number of seeds buried. (More details in Appendix 1).

	Dung Beetles					
	Burrowers			Ball rollers		
Depth (cm)	Seeds buried No.	Seeds buried %	No. of species buried	Seeds buried No.	Seeds buried %	No. of species buried
≤ 2.5	82	16	20	35	20	11
2.6–5.0	144	28	13	59	33	8
5.1–8.0	144	28	12	63	36	3
8.1–12.0	132	26	8	20	11	1
> 12.0	10	2	1	0	0	0
Total no. buried	512			177		
% buried	60			22		

Seed size (length) and depth at which seeds were buried by dung beetles

The seed species used in the burying experiments ranged in weight from 0.05 (*Cithraxylum affine*) to 2.5 g (*Brosimum alicastrum*) and in maximum length (mm) from 1.5 (*Cecropia obtusifolia*) to 17.5 (*Brosimum alicastrum*). Seed length was correlated with percentage of seeds buried by dung beetles (r_s burrowers = 0.95, $P < 0.05$; r_s ball rollers = 0.65, $P < 0.05$) (Figure 2).

Germination of seeds and establishment of seeds buried by dung beetles

The germination and establishment as seedlings of the seeds buried by dung beetles in the control and treatment clumps in the exclosure experiments in which access by rodents was not permitted, were followed for six species until seedlings were at least 30 cm tall. While 44% of the seeds in the protected samples germinated and became established (range of seeds per species = 3–19), in the unprotected samples only 14% of the seeds became established (range of seeds per species = 3–7) (Table 4).

Relationship between dung beetle relative abundance, fruit/seed production and fruit eating by howlers

At Los Tuxtlas, fruiting by tree species, presence of dung beetles, and howler fruit-eating occurred throughout all months of the year. However, two clear peaks in fruiting species, matched by two peaks in dung beetle relative abundance and by a more diverse fruit diet of the monkeys were evident in the data (Figure 1).

DISCUSSION

Clearly rodents have an important impact on seed survivorship after dispersal and they may destroy, if the seeds are not relocated by biotic and/or physical

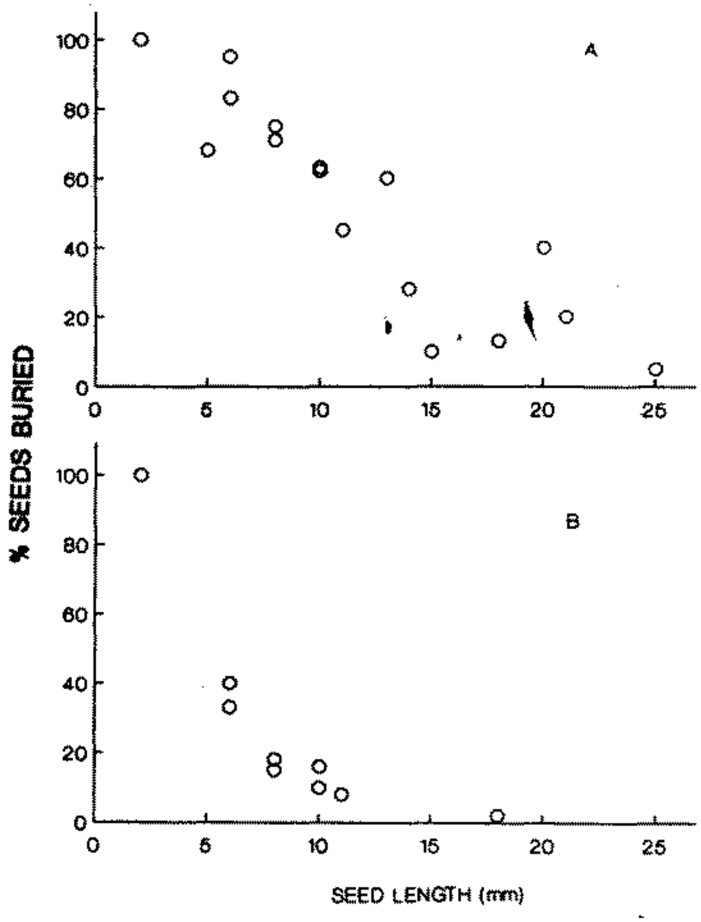

Figure 2. Relationship between seed size and percentage of seeds buried by dung beetles: A burrowers, B ball rollers.

factors, up to 100% of the seeds dispersed by frugivores (Coates-Estrada & Estrada 1988, Estrada & Coates-Estrada 1986, Janzen 1982a,b 1983, 1986). This study has shown that the accidental removal and burial of seeds by dung beetles significantly reduces the ability of rodents to locate the dispersed seeds. Dung beetles reduce clumping of seeds in three dimensions through fragmentation and relocation of dung both horizontally and vertically down into the soil profile. In addition to reducing clumping, burial also makes seeds less detectable to seed predators. The speed with which dung is fragmented, relocated and buried by dung beetles reduces the length of time the seed is exposed to seed predators on the ground. It also reduces the length of time the seed is covered with faecal matter whose odour may cue predators to the seed (Janzen 1982a, Estrada & Coates-Estrada 1986).

Dung beetles in tropical rain forests are an important component of the community. The density of dung beetles in an Ecuadorian forest was estimated at 2000 beetles ha^{-1} and individuals moved distances ranging from 50 m to 1 km (Peck & Forsyth 1982). In Panama as many as 22 species have been captured in one locality at traps baited with human faeces (Howden & Young 1981). At Los Tuxtlas, a 24-hour sampling of dung beetles at 20 trapping stations in the forest using howler dung as bait captured 144 beetles of 13 species (A. E., unpublished data). As a result of their flying ability, beetles can easily locate monkey dung in the forest either on the ground or on the vegetation. Discovery times are short, with beetles arriving at the dung within 1 min during the day, and dung burial rates have been documented to be extremely fast (< 2 hrs) (Peck & Forsyth 1982, this study). The presence of diurnal, crepuscular and nocturnal species of beetles at Los Tuxtlas (Moron 1979) means that seeds defecated by monkeys at any time during the day or night should be rapidly relocated, cleaned and buried by dung beetles as a result of their feeding and nesting activities.

Our study showed that both large and small ball rolling and burrowing dung beetles buried seeds as contaminants of faecal matter. The number of plant species whose seeds were buried by dung beetles was limited by the size of the seed, but in both ball rollers and burrowers, rapid relocation of food resulted in rapid relocation and burial of large and small seeds.

Many seeds were also left accidentally on the ground as a result of dung beetle feeding, nesting behaviour and maintenance of nesting tunnels and galleries. Exclosure experiments showed, for example, that at the species level 7–79% of the seeds processed by dung beetles were left on the surface of the soil; and experiments with PVC cylinders showed that while 42% of the experimental seeds (N = 1667) were buried at depths ranging from 1.0 to > 12.0 cm, 58% of the seeds were left exposed on the surface. Although a positive relationship was found between seed size and the proportion of seeds left on the surface, both large (e.g. 20.2 mm) and small (e.g. 1.5 mm) seeds were buried by dung beetles.

Seed size may have important consequences in the survival of those seeds buried by dung beetles. It is possible that for small seeds (e.g. *Ficus*, *Cecropia*) burial to 12 cm would make germination impossible, a depth, perhaps, not so critical to large seeds (e.g. *Brosimum alicastrum*). Our experiments showed however, that dung beetles buried few seeds at 12 cm, and that the majority were buried at 2–5 cm; a depth perhaps less obstructing to small seed germination and sufficient to reduce detection by rodents. Be this as it may, seeds buried by dung beetles do become more rapidly incorporated into the soil seed bank thus avoiding physical and biotic hazards, and some may even germinate and grow.

Our study indicated that howlers were dispersing the seeds of many more species in their faeces between April and October than in the other months of the year and that dung beetles were also more abundant in the forest at that time of the year. These aspects suggest a possible scenario in which, as a result of intense competition among dung beetles for monkey dung (Peck & Forsyth 1982), seeds of many species escape post dispersal predation at the time of year when dung beetles are more abundant.

Virtually no quantitative data exist on the role of dung beetles in tropical rain forest communities (Peck & Forsyth 1982). Dung beetles are known to be ecologically important in terrestrial habitats with populations of large vertebrates (Heinrich & Bartholomew 1979). By burying and eating dung, beetles increase the rate of soil nutrient recycling, decrease helminth and pest Diptera population and act as a vector for vertebrate parasites and diseases (Bornemissza 1960, Fincher *et al.* 1969, Gillard 1967, Halffter & Matthews 1966, Klemperer & Boulton 1976, Lindquist 1933, Miller 1954, Nealis 1977). However, their role in modulating the fate of seeds dispersed by vertebrates and the contribution they make, at this level, to the process of forest regeneration had not, until now, been quantitatively documented for tropical rain forests.

Preliminary observations indicate that clearing of the forest can reduce the diversity and abundance of dung beetles by a factor of 10 (Howden & Nealis 1975) and substitution of the forest by plantations substantially reduces species richness (Nummelin & Hanski 1989). The important ecological role dung beetles play not only in the recycling of nutrients and energy in the ecosystem, but also in the process of rain forest regeneration suggest that more studies of these insects are needed. With the rapid destruction of the rain forests in the Neotropics we are losing not only a great number of species but also delicate ecological links relevant to our understanding of the self-sustaining capacity of the ecosystem.

ACKNOWLEDGEMENTS

We are grateful to Dr G. Halffter for identification of the dung beetles collected at Los Tuxtlas and to Dr E. W. Schupp and A. Marshall for valuable editorial assistance.

LITERATURE CITED

AUGSPURGER, C. 1983. Seed dispersal of the tropical tree *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 7:759–771.

BORNEMISSZA, G. F. 1960. Could dung eating insects improve our pastures? *Journal of the Australian Institute of Agricultural Sciences* 26:54–56.

CHARLES-DOMINIQUE, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana. Pp. 122–135 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.

COATES-ESTRADA, R. & ESTRADA, A. 1988. Frugivory and seed dispersal in *Cymbopetalum baillonii* (Annonaceae) at Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 4:157–171.

ESTRADA, A. & COATES-ESTRADA, R. 1984. Fruit eating and seed dispersal by howlers (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. *American Journal of Primatology* 6:77–91.

ESTRADA, A. & COATES-ESTRADA, R. 1986. Frugivory by howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: dispersal and fate of seeds. Pp. 93–104 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.

ESTRADA, A. & FLEMING, T. H. 1986. *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.

FINCHER, G. T., STEWARD, T. B. & DAVIS, R. 1969. Beetle intermediate hosts for swine spirurids in southern Georgia. *Journal of Parasitology* 56:378–383.

GILLARD, P. 1967. Coprophagous beetles in pasture ecosystems. *Journal of the Australian Institute of Agricultural Sciences* 33:30–34.

HALFFTER, G. & EDMONDS, W. D. 1982. *The nesting behaviour of dung beetles (Scarabaeinae): an ecological and evolutive approach*. Publicaciones del Instituto de Ecologia. Mexico City, 175 pp.

HALFFTER, G. & MATTHEWS, E. G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologica Mexicana* 38:29–107.

HALLWACHS, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymanea courbaril*: Leguminosae). Pp. 285–303 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.

HEINRICH, B. & BARTHOLOMEW, G. A. 1979. The ecology of the African dung beetle. *Scientific American* 241:146–156.

HOWDEN, H. F. & NEALIS, V. G. 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica* 7:77–85.

HOWDEN, H. F. & NEALIS, V. G. 1978. Observations on height of perching in some tropical dung beetles (Scarabaeidae). *Biotropica* 10:43–46.

HOWDEN, H. F. & YOUNG, O. P. 1981. Panamanian Scarabaeidae. *Contributions to the American Entomological Institute* (Ann Arbor) 18:1–204.

JANZEN, D. H. 1982a. Removal of seeds from horse dung by tropical rodents: influence of habitat and amount of dung. *Ecology* 63:1887–1900.

JANZEN, D. H. 1982b. Attraction of *Lyomis* mice to horse dung and the extinction of this response. *Animal Behaviour* 30:483–489.

JANZEN, D. H. 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.

JANZEN, D. H. 1986. Mice, big mammals, and seeds: it matters who defecates what where. Pp. 251–271 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.

KLEMPERER, H. G. & BOULTON, R. 1976. Brood burrow construction and brood care by *Heliocopris japetus* (Klug) and *Heliocopris hamadryas* (Fabrines) (Coleoptera, Scarabaeidae). *Ecological Entomology* 1: 19–29.

LINDQUIST, A. W. 1933. Amount of dung buried and soil excavated by certain Coprini (Scarabaeidae). *Journal of the Kansas Entomological Society* 6:109–125.

MILLER, A. 1954. Dung beetles (Coleoptera, Scarabaeidae) and other insects in relation to human feces in a hook-worm area of southern Georgia. *American Journal of Tropical Hygiene* 3:372–388.

MORON, A. 1979. Fauna de coleopteros lamelicornios de la Estacion de Biologia Tropical 'Los Tuxtlas', Veracruz, UNAM, Mexico. *Anales del Instituto de Biologia, UNAM, Mexico*. 50:375–454.

NAGY, K. & MILTON, K. 1979. Energy metabolism and food consumption by wild howler monkeys. *Ecology* 60:475–480.

NEALIS, V. G. 1977. Habitat association and community analysis of south Texas dung beetles (Coleoptera: Scarabaeidae). *Canadian Journal of Zoology* 55:138–147.

NUMMELIN, N. & HANSKI, I. 1989. Dung beetles of the Kibale forest, Uganda; comparison between virgin and managed forests. *Journal of Tropical Ecology* 5:349–352.

PECK, B. S. & FORSYTH, A. 1982. Composition, structure and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera, Scarabaeidae). *Canadian Journal of Zoology* 60:1624–1634

SCHUPP, E. W. & FROST, E. 1989. Differential predation of *Welfia georgii* seeds in treefall gaps and the forest understorey. *Biotropica* 21:200–203.

VAZQUEZ-YANES, C., OROZCO, A., FRANCISCO, G. & TREJO, L. 1975. Observations of seed dispersal by bats in a tropical humid region in Veracruz, Mexico. *Biotropica* 7:73–76.

YOUNG, O. P. 1981. The attraction of neotropical Scarabaeinae (Coleoptera, Scarabaeinae) to reptile and amphibian faecal material. *The Coleopterist Bulletin* 35:345–348.

Accepted 16 October 1990

Appendix I. Number (N) and percentage of seeds buried by dung beetles in experimental PVC cylinders for 20 species of plants dispersed by *Alouatta*. Plant names follow Ibarra & Sinaca (1987).

Seed Species	Mean seed length mm	BURROWERS SEEDS BURIED Seeds used	> 0 cm N	> 0 cm %	> 2.5 cm N	> 2.5 cm %	> 5 cm N	> 5 cm %	BALL ROLLERS SEES BURIED Seeds used	> 0 cm N	> 0 cm %	> 2.5 cm N	> 2.5 cm %	> 5 cm N	> 5 cm %
Abuta panamensis (Menispermeaceae)	25	20	1	5	0	0	0	0	20	0	0	0	0	0	0
Ampelocera hottlei (Ulmaceae)	14	25	7	28	3	12	0	0	25	0	0	0	0	0	0
Brosimum alicastrum (Moraceae)	18	48	6	13	4	8	1	2	42	1	2	0	0	0	0
Bursera simaruba (Burseraceae)	8	40	30	75	30	75	30	75	4	6	15	6	15	0	0
Cecropia obtusifolia (Moraceae)	2	50	50	100	50	100	50	100	50	50	100	50	100	30	60
Cissus sp. (Vitaceae)	10	50	31	62	18	36	5	10	50	8	16	4	8	0	0
Cithraxylum affine (Verbenaceae)	6	40	33	83	32	80	20	50	40	16	40	7	18	0	0
Clarisia biflora (Moraceae)	21	20	4	20	0	0	0	0	20	0	0	0	0	0	0
Cordia stelifera (Boraginaceae)	6	40	38	95	30	75	11	28	40	13	33	6	15	0	0
Dialium quianensis (Ulmaceae)	10	60	38	63	26	43	10	17	60	6	10	0	0	0	0
Dipholis minutiflora (Sapotaceae)	15	20	2	10	0	0	0	0	20	0	0	0	0	0	0

Appendix I. *Continued.*

Seed Species	Mean seed length mm	BURROWERS SEEDS BURIED							BALL ROLLERS SEES BURIED						
		Seeds used	> 0 cm		> 2.5 cm		> 5 cm		Seeds used	> 0 cm		> 2.5 cm		> 5 cm	
			N	%	N	%	N	%		N	%	N	%	N	%
Eugenia sp. (Myrtaceae)	20	20	8	40	4	20	0	0	20	0	0	0	0	0	0
Ficus spp. (Moraceae)	2	50	50	100	50	100	50	100	50	50	100	50	100	50	100
Inga sp. (Leguminosae)	25	20	6	30	4	20	0	0	20	0	0	0	0	0	0
Poulsenia armata (Moraceae)	8	112	79	71	79	71	55	49	89	16	18	13	15	3	3
Pseudolmedia oxyphyllaria (Moraceae)	11	96	43	45	41	43	31	32	80	6	8	4	5	0	0
Rollinia jimenezii (Annonaceae)	13	25	15	60	9	36	5	20	25	0	0	0	0	0	0
Smilax sp. (Smilaceae)	7	50	35	70	24	48	6	12	50	5	10	2	4	0	0
Spondias mombin (Anacardiaceae)	15	20	2	10	0	0	0	0	20	0	0	0	0	0	0
Trichostigma octandrum (Phytolacceae)	5	50	34	68	26	52	12	24	50	0	0	0	0	0	0
Total		856	512		430		286		811	177		142		83	