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RESEARCH ARTICLES

Tropical Rain Forest Fragmentation, Howler Monkeys (*Alouatta palliata*), and Dung Beetles at Los Tuxtlas, Mexico

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In Neotropical rain forests, fresh mammal dung, especially that of howler monkeys, constitutes an important resource used by dung beetles as food and for oviposition and further feeding by their larvae. Tropical rain forest destruction, fragmentation, and subsequent isolation causing reductions in numbers of and the disappearance of howler moneys may result in decreasing numbers of dung beetles, but this has not been documented. In this study, we present information on the presence of howlers and dung beetles in 38 isolated forest fragments and 15 agricultural habitats. Howler monkeys were censused by visual means, while dung beetles were sampled with traps baited with a mixture of howler, cow, horse, and dog dung. Results indicated that loss of area and isolation of forest fragments result in significant decrements in howlers and dung beetles. However, dung beetle abundance was found to be closely related to the presence of howler monkeys at the sites and habitats investigated. Scenarios of land management designed to reduce isolation among forest fragments may help sustain populations of howler monkeys and dung beetles, which may have positive consequences for rain forest regeneration. Am. J. Primatol. 48:253–262, 1999. © 1999 Wiley-Liss, Inc.

Key words: *Alouatta;* tropical rain forest; Los Tuxtlas; dung beetles; seed dispersal; conservation

INTRODUCTION

In Neotropical rain forests, fresh mammal dung, especially that of howler monkeys, constitutes an important food resource for dung and carrion beetles (Scarabeidae Scarabeinae) [Halffter & Edmonds, 1982; Hanski, 1989; Gill, 1991; Young, 1981; Hanski & Cambefort, 1991; Estrada et al., 1993]. Dung relocation and its rapid burial is a strategy found in dung and carrion beetles to avoid competition with other coprophagous insects for this ephemeral resource [Halffter & Mathews, 1966].

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Dung beetles are ecologically important in the Neotropical habitats in which they occur. By burying the dung and carrion as food for their offspring, they may increase the rate of soil nutrient cycling [Halffter & Mathews, 1966; Bornemissa & Williams, 1970; Nealis, 1977], and they exert an important control over the egg and larvae populations of parasitic flies present in the fresh dung of mammals [Bergstrom et al., 1976]. Recently dung beetles have been suggested to be good indicators for measuring biodiversity in the tropics [Halffter & Favila, 1993]. Depending on the locality, 28–60 species may be represented [Klein, 1989; Hanski & Cambefort, 1991], and as many as 2,000 beetles per hectare may be found in forested areas [Peck & Forsyth, 1982]. Further, dung beetles have been reported to be important secondary seed dispersal agents for several tree species dispersed by howler monkeys [Estrada & Coates-Estrada, 1991].

Dung beetles may be sensitive to fragmentation of the forest because the general abundance of mammals such as howler monkeys sets the level of resources available to them [Klein, 1989; Hanski & Cambefort, 1991]. Such sensitivity needs documentation, especially in view of the dependency of several dung beetle species on howler monkey dung [Estrada et al., 1993] and of the important role these insects play in the seed dispersal ecology of many tree species used by the monkeys as food sources ([Estrada & Coates-Estrada, 1991].

Lowland tropical rain forest and representatives of *Alouatta* reach their northernmost distribution in the American continent, in the mountain region of Los Tuxtlas, in southern Veracruz, Mexico, where currently most of the forest is present in a fragmented condition [Estrada & Coates-Estrada, 1996]. While many forest fragments are still inhabited by *Alouatta,* in many others the monkeys have become extinct. In a few cases, howler monkeys have become isolated in or visit coffee and cacao plantations [Estrada & Coates-Estrada, 1996]. About 50 species of dung beetles have been reported to exist in the region [Halffter et al., 1992; Moron & Blackaller, 1997].

In spite of the ecological importance of the howler monkey–plant–dung beetle interaction [Estrada & Coates-Estrada, 1991], reports on dung beetle richness in relation to the richness of *Alouatta* populations in forest fragments and in anthropogenic vegetation are not existent in the literature [Howden & Nealis, 1975; Nealis, 1977; Peck & Forsyth, 1982; Halffter et al., 1992]. Here we report the results of surveys conducted in a segment of the region of Los Tuxtlas between April and September 1996 of the presence of *A. palliata* and dung beetles in 38 isolated forest fragments and in 15 agricultural habitats represented by three replicates of each of the following types of plantations: cacao. coffee, citrus, allspice, and mixed (cacao and coffee).

The data presented below are a complement to earlier reports of the presence of *Alouatta palliata* in forest fragments and in shaded plantations [Estrada & Coates-Estrada, 1996] and to more recent documentation on dung beetle presence in forest fragments and agricultural habitats at Los Tuxtlas [Estrada et al., 1998]. The data set reported here differs from the above in that a set of sites surveyed for presence of howler monkeys in 1995 was surveyed again in 1996 as part of a long-term program monitoring the howler population in the region. Concurrent with these surveys, dung beetles were also sampled at these sites. Our study is basically descriptive, and we consider the project and results preliminary.

METHODS

Study Area

The landscape of Los Tuxtlas (95°00′ W, 18°25′ N) in southern Veracruz, Mexico, has been severely transformed by human activity in the last 40–50 years. Remaining rain forest vegetation is present in the form of constellations of fragments that vary in size, years of isolation, and isolating distance. While at Los Tuxtlas the landscape is comprised mainly of pastures, in some areas mosaics of different kinds of land uses are interdigitated with rain forest fragments. In these areas, cultivation of arboreal crops constitutes human-made tree islands of vegetation such as citrus (*Citrus sinensis*, Rutaceae), allspice (*Pimienta dioica*, Myrtaceae) and cacao (*Theobroma cacao*, Sterculiaceae). Farmers also cultivate coffee (*Coffea arabica*, Rubiaceae) as a single crop and as a companion crop to cacao. Rain forest trees left by farmers provide shade in the case of cacao, coffee, and mixed plantations. In this region, mean annual rainfall is 4,900 mm, with a drier season ($\bar{X}$ = 111.7 s.d. ± 11.7 mm per month) from March to May and a wetter season ($\bar{X}$ = 486.25 s.d. ± 87.0 mm per month) from June to February. Mean annual temperature is 27°C (range 20–28°C) [Estrada & Coates-Estrada, 1996].

We conducted surveys of howler monkeys and dung beetles in 38 forest fragments within a 32 km^2 landscape in the region of Los Tuxtlas. The sites varied in elevation from sea level to about 300 m above sea level, in time of isolation from 1–20 years, in size from 1–112 ha, and in isolating distance (straight line distance to the edge of the nearest forest fragment) from 0.2–0.8 km.

Howler monkeys and dung beetles were surveyed in three replicates of each of the following human-made habitats: cacao and coffee plantations, mixed crop plantations (cacao and coffee), and citrus groves and allspice. Plantation habitats varied in size from 2–10 ha and in age from 12–15 years and were all fruit-productive. The distance to the nearest forest patch in these cases varied from 200–1,500 m, and the distance to other plantations varied from 200–1,000 m. Tall (>15 m) rain forest trees provided shade at the coffee, cacao, and mixed plantations.

Sampling of Howler Monkeys

We conducted visual censuses of *Alouatta* following procedures described earlier [Estrada & Coates-Estrada, 1996]. These consisted of walking slowly (approximately 1 km/h) through the interior of the forests along existing trails or trails opened by us whose length varied with the size of the patch of vegetation investigated. The lengths of these sampling trails were 400 m for sites <50 ha, 600 m for sites <100 ha, and 800 m for sites ²200 ha. We selected the census routes to avoid overlaps from one day to the next and to minimize the probability of observing the same troop or individuals more than once. With each contact, we recorded the number of individuals observed, their general age (adults, immatures), and, if adults, their sex. We recorded the height at which they were found with the aid of a rangefinder and the general activity of the troop (traveling, resting, feeding, other). We also noted any special markings, such as patches of light hair on the backs, tails, and or feet of the monkeys observed, to improve identification of the troops observed. Trails were transversed twice a day, between 0600 h and 1800 h, in 2 consecutive days at each site. We estimated total howler monkey biomass at the sites surveyed by multiplying the reported average weight of individuals of each age/sex class (adult males, 7.7 kg; adult females, 6.5 kg; juveniles, 2.0 kg; infants, 1.0 kg [Estrada & Coates-Estrada 1996]) by the number of howler monkeys counted of each age/sex class.

Sampling of Dung Beetles

We used dung baited pitfall traps consisting of a cylinder-shaped plastic container with 15 cm of loose soil [Howden & Nealis, 1975]. We placed 35 pitfall traps in the interior of each site investigated. Bait consisted of 60 g of a homogenized mixture of fresh howler monkey, cow, horse, and dog dung. This mixture grossly mimicked the excreta produced by wild herbivores and omnivores in the forest [Estrada et al., 1993]. We placed the traps at 10–15 m intervals along a sinuous route through interior of the forest fragments and plantations investigated. At forest sites >50 ha, we placed two sets of 35 traps, each separated by at least 100 m.

Trapping was carried out under generally similar climatic conditions, avoiding rainy or heavily overcast days. Pitfall traps were baited at 1800 h and retrieved 24 h later at all sites investigated. We kept all dung beetles captured for 12 h before releasing them at the site of capture. Each individual was identified by species through comparison with a reference collection at the biological research station Los Tuxtlas. We carried concurrent surveys of *Alouatta* and dung beetles between April and September 1996, a time when dung beetle populations have been documented to be at their peaks in the study area [Estrada et al., 1993].

We used descriptive statistics (mean ± standard deviation), which for dung beetle capture data were expressed as the average (± standard error) number of individuals and species captured per trap per site in each habitat. Spearman's (r_s) correlation coefficients and the Wilcoxon test were used when contrasting groups of data [Ludwig & Reynolds, 1988; Fitch, 1992].

RESULTS

Howler Monkeys

We detected the presence of 160 individuals of *Alouatta* in 21 of the 38 forest fragments surveyed. At these sites, *Alouatta* numbers ranged from 1–25 individuals distributed in 26 troops. One record in one site consisted of a solitary male. Troop size ranged from three to nine individuals ($\bar{X} = 6.3 \pm 2.0$). Total estimated howler monkey biomass per site ranged from 8–137 kg (Table I).

Forest fragments with *Alouatta* present ranged in size from 2–112 ha (mean 36 ha) and in isolation from 20–800 m (average 166 m). The total number and total biomass of *Alouatta* per site were significantly associated with area of the sites ($r_s = 0.43$, $P = 0.02$; $r_s = 0.42$, $P = 0.02$). We did not detect presence of howlers in 17 of the 39 forest fragments investigated. These sites ranged in size from 1–30 ha (mean 3.2 ha) and in isolation from 220–750 m (mean 462 ± 197) (Table II). The differences in the average area and isolating distance of those forest sites inhabited by howler monkeys and those in which monkeys were absent were significant (area $z = 2.81$, $P = 0.02$; distance $z = 2.43$, $P = 0.01$). We detected a total of 55 *Alouatta* individuals distributed in nine troops in the cacao, coffee, and mixed plantations. Mean troop size was 6.1 ± 1.6. We did not detect any howler monkeys in the citrus and allspice plantations (Table III).

Dung Beetles

We captured 3,730 dung beetles representing 30 species at the forest fragments investigated (Tables I, II). Average captures per site in the forest fragments ranged from 0.06–0.54 species per trap and from 0.09–13.43 individuals per trap. Dung beetle presence was influenced by the area of the forest fragment (species average capture $r_s = 0.54$, $P = 0.001$; individuals' average capture $r_s = 0.56$, $P = 0.0001$) and the isolating distance (species average capture $r_s = -0.64$, $P = 0.0001$; individuals' average capture $r_s = -0.59$, $P = 0.0001$).

TABLE I. Dung Beetles at Forest Fragments With Presence of Howler Monkeys*

Area (ha)	Isolation distance (m)	Dung beetles Species	N	Average per trap Species	Individuals	Howler monkeys M	H	J	I	Total	Troops	Biomass (kg)
3	160	13	45	0.4	1.3	1	1	1		3	1	16
5	100	7	38	0.2	1.1	3	2	1	1	7	1	39
33	160	9	171	0.3	4.9	4	6	3	3	16	4	79
2	400	3	19	0.1	0.5	1	1	2		4	1	18
2	500	6	163	0.2	4.7	3	3	2		8	1	47
2	100	6	123	0.2	3.5	3	3	2		8	1	47
8	100	7	175	0.2	5.0	1	2	2		5	1	25
4	800	8	191	0.2	5.5	1	2	1	1	5	1	24
4	50	10	73	0.3	2.1	1				1	1	8
10	200	6	162	0.2	4.6	4	7	1		12	2	78
66	100	15	95	0.4	2.7	2	3	1	3	9	1	40
50	100	9	108	0.3	3.1	3	2	1		6	1	38
40	75	9	108	0.3	3.1	1	1	2		4	1	18
30	150	9	108	0.3	3.1	2	2			4	1	28
112	100	12	470	0.3	13.4	9	9	2	5	25	3	137
10	80	10	77	0.3	2.2	2	3	2	1	8	1	40
150	50	17	414	0.5	11.8	3	3	1	1	8	1	46
100	70	19	369	0.5	10.5	3	2	1	1	7	1	39
100	20	16	406	0.5	11.6	2	3	2	1	8	1	40
20	160	4	24	0.1	0.7	1	3	1	1	6	1	30
4	20	15	87	0.4	2.5	1	2	1	2	6	1	25
Total		28	3,426			51	60	29	20	160		
Mean 36	166	10	163	0.3	4.7							41
s.d. 44	186	4	135	0.1	3.9							28

*Shown also are the age and sex composition of howler troops at each site. Biomass is an estimate. I, infants; J, juveniles, M, adult males, F, adult females.

At the shaded plantations, we captured 1,446 dung beetles representing 25 species. Species and individual capture averages per trap at these sites ranged from 0.23–0.46 and from 1.1–11.5, respectively (Table III). At the unshaded plantations (citrus and allspice), we captured 139 dung beetles of 13 species. Average captures of species and individuals per trap per site ranged from 0.17–0.34 and from 0.20–1.0, respectively (Table III).

Howlers and Dung Beetles

We captured 90% of the beetles at forest sites in which *Alouatta* was present, and they were represented by 28 species; the remaining 10% of beetles, represented by 24 species, were captured at sites where *Alouatta* was not present (Table II). Average captures of dung beetle species and individuals in the forest fragments with howlers ranged from 0.09–0.54 species per trap per site (average 0.29 ± 0.002) and from 0.54–13.42 individuals per trap per site respectively (average 4.7 ± 0.8) (Table I). At the forest sites where howlers were absent, average captures of dung beetles ranged from 0.06–0.31 species per trap per site (average 0.15 ± .02) and from 0.09–1.17 individuals per trap per site (average 0.51 ± .002) (Table II). Average captures per trap per site of species and individuals were significantly higher at forest sites with *Alouatta* present than in forest fragments that lacked howlers (species $z = 2.9$, $P < 0.001$; individuals $z = 3.6$, $P < 0.0001$).

TABLE II. Dung Beetles at Forest Sites in Which Howler Monkeys Were Absent

	Area (ha)	Isolation distance (m)	Species	N	Average per trap	
					Species	Individuals
	1	250	7	41	0.2	1.2
	1.5	450	2	3	0.1	0.1
	3	330	5	27	0.1	0.8
	2.5	300	3	5	0.1	0.1
	7.5	285	10	23	0.3	0.7
	5.5	550	2	3	0.1	0.1
	4.5	330	5	32	0.1	0.9
	1	410	2	2	0.1	0.1
	1	400	3	5	0.1	0.1
	2	279	6	17	0.2	0.5
	2	250	5	9	0.1	0.3
	2	250	3	4	0.1	0.1
	30	750	6	25	0.2	0.7
	8	220	7	25	0.2	0.7
	2	800	8	26	0.2	0.7
	8	850	7	25	0.2	0.7
	1	340	11	32	0.3	0.9
Total			24	304		
Mean	4.9	414	5.4	17.9	0.2	0.5
s.d.	6.7	197	5.0	66.7	0.1	0.3

At the forest sites where howlers were absent, there were important decrements in the total number of individuals captured for the majority (71%) of the dung beetle species detected at the sites where monkeys were present (Table IV).

At the shaded plantations, average captures of dung beetles per trap per site were 0.34 ± 0.002 species and 4.5 ± 1.1 individuals. At the unshaded plantations (citrus and allspice), average captures per trap per site of dung beetles were 0.19 ± 0.02 species and 0.66 ± 0.13 individuals. These differences were significant (species $z = 2.01$, $P < 0.01$; individuals $z = 2.20$, $P < 0.01$) (Table III).

DISCUSSION

Our study suggests that isolation and loss of habitat area are associated with significant decrements in numbers of *A. palliata* in the tropical landscape, a finding consistent with results from an earlier and broader primate population survey in the region [Estrada & Coates-Estrada, 1996]. Such reduction in habitat area results also in the local extinction of *Alouatta,* as attested by our findings that howlers were absent in 46% of the sites investigated. Shaded plantations were the only human-made habitats in which howler monkeys were present, probably the result of the presence of tall trees of the Moraceae, Leguminosae, Anacardiaceae, and Annonaceae plant families among others, known to be an important source of leaves and fruit and physical substratum for the monkeys [Estrada & Coates-Estrada, 1993]. In contrast, unshaded plantations (citrus and allspice) lack tall tree cover, have a wide interrow space between cultivated trees, and also lack suitable structures for howler locomotion, which may deter howlers from visiting these habitats [Estrada & Coates-Estrada, 1996].

Data indicated that while the total number of dung beetle species detected were similar between forest fragments inhabited by *Alouatta* and forest frag-

TABLE III. Dung Beetles and Howler Monkeys at Shaded and Unshaded Agricultural Habitats*

			Dung beetles				Howler monkeys						
		Isolation			Average per trap								
Vegetation	Area (ha)	distance (m)	Species	N	Species	Individuals	M	H	J	I	Total	Troops	Biomass (kg)
Shaded plantations													
Cacao	10	300	13	401	0.4	11.5	1	3	1	1	6	1	30
Cacao	10	200	10	186	0.3	5.3	1	4	2	1	8	1	39
Cacao	10	300	11	293	0.3	8.4	2	4		1	7	1	42
Mixed	3	200	12	100	0.3	2.9	3	4		1	8	1	50
Mixed	3	100	16	102	0.5	2.9	2	3	1		6	1	37
Mixed	15	900	13	211	0.4	6.0	1	1		1	3	1	15
Coffee	5	600	8	75	0.2	2.1	2	3	1		6	1	37
Coffee	5	500	15	40	0.4	1.1	1	3	1	1	6	1	30
Coffee	5	600	9	38	0.3	1.1	1	3		1	5	1	28
Total			25	1,446			14	28	6	7	55	9	
Mean	7	411	11.9	160.7	0.3	4.6							
s.d.	4	257	2.7	123.8	0.1	3.5							
Unshaded plantations													
Citrus	2	200	6	7	0.2	0.2							
Citrus	8	1,500	5	13	0.1	0.4							
Citrus	4	300	5	35	0.1	1.0							
Allspice	6	200	6	35	0.2	1.0							
Allspice	8	400	13	29	0.4	0.8							
Allspice	10	500	6	20	0.2	0.6							
Total			13	139									
Mean	6	517	6.8	23.2	0.2	0.7							
s.d.	3	496	3.1	11.7	0.1	0.3							

F, adult females; I, infants; J, juveniles; M, adult males. Biomass is an estimate.

TABLE IV. Dung Beetle Species Detected in Forest Fragments in Which Howler Monkeys Were Present (N = 21) and at Those Forest Sites in Which They Were Absent (N = 17)

Species	Dung beetles in forest fragments	
	With howlers	Without howlers
Canthon femoralis Chevrolat[a]	1,238	30
Copris laeviceps Harold[a]	569	121
Deltochilum pseudoparile Paglian[a]	404	21
Canthidium centrale Boucomont[a]	336	61
Onthophagus rhinolophus Harold[a]	258	15
Onthophagus batesi Howden & Cartwright[a]	154	8
Canthon viridis vazquezae Martinez, Halffter & Halffter[a]	127	3
Dichotomius satanas Harold[a]	67	2
Dichotomius carolinus colonicus Say[a]	50	1
Canthon cyanellus cyanellus Harold[a]	33	4
Phanaeus endymion Harold[a]	25	5
Uroxys boneti Pereira & Halffter[a]	24	10
Eurysternus caribaeus Herbst	21	2
Copris lugubris Bohemen	19	1
Eurysternus mexicanus Harold[a]	18	4
Sulcophanaeus chryseicollis Harold[a]	17	1
Deltochilium gibbosum sublaeve Bates	15	2
Coprophaneus telamon corythus Harold	12	5
Canthon (C.) morsei Harold[a]	11	2
Canthon (Gl.) subhyalinus Harold[a]	10	1
Eurysternus angustulatus Harold	5	
Anaides laticollis Harold	3	
Sp. 1	2	
Ateuches illaesum Harold	2	
Onthophagus crinitus Harold	2	1
Sp. 2	2	
Sp. 3	1	
Uroxys sp.	1	1
Onthophagus nasicornis Harold[a]		1
Digitonthophagus gazella Fabricius		2
Total	3,426	304
Species	28	24

[a]Species that display affinity for howler monkey dung (Estrada et al., 1993).

ments with an absence of howlers, average captures of dung beetle species and individuals were significantly higher in those forest fragments and plantations in which howler monkeys were present. Similarly, significantly fewer individuals were captured for 20 dung beetle species at the forest fragment where howlers were absent. Eighty percent of these species are known to display a marked affinity for howler monkey dung [Estrada et al., 1993]. The presence of howlers in shaded plantations was associated with higher average numbers of dung beetles captured per trap than at the unshaded plantations where howlers were absent, further attesting to the close association between howler monkeys and dung beetles.

In general, results suggest that the decline or disappearance of howler monkey populations as a result of fragmentation and isolation may result in major declines in dung beetle numbers. The consequences of these changes on the howler monkey–plant–dung beetle interaction are unknown, but it is reasonable to surmise that the regenerating capacity of isolated plant populations may be gradually or suddenly weakened by the absence of their primary and secondary seed dispersal agents and by the disappearance of the interaction between howlers and dung beetles that modulates the fate of seeds dispersed by the primates [Estrada & Coates-Estrada, 1991; Offerman et al., 1995; Kinzey, 1997].

Marked isolation of forest fragments was associated with the absence of howler monkeys [Estrada et al., 1994] and reduced numbers of dung beetles [Klein, 1989; Estrada et al., in press], suggesting that short interfragment distances may favor the movement of howlers and dung beetles from one habitat island to another [Estrada & Coates-Estrada, 1996]. Although we lack information on the mobility of each of the dung beetle species recorded, distances of up to 1.0 km have been reported to be transversed by these beetles in 2 days in other tropical localities [Peck & Forsyth, 1982].

A landscape arrangement in which arboreal and shaded agricultural habitats occupy some of the pasture separating forest fragments, including forests in the process of regeneration, may reduce isolation, facilitating the movement of primates and dung beetles among isolated habitat islands. In some instances, the agricultural plots could be used to protect the edges of forest fragments from exposure to wind and high temperatures and to increase the area of vegetation available to howlers and dung beetles. In this scenario, the conservation of corridors of residual forest vegetation along streams and rivers could enhance faunal connections between forest and agricultural islands in the landscape [Noss, 1991; Pimentel et al., 1992; Naiman et al., 1993]. Such management of the land may have several important added benefits, including preservation of water resources and retention of soil and soil fertility [Gleissman et al., 1981; Morowitz, 1991; Orr, 1991].

The conservation of the ecological association between howlers and dung beetles may also result in the sustainability of seed movement by howler monkeys and dung beetles and a diverse soil seed bank. Such benefits may help preserve the regenerating capacity of the forest, with obvious benefits for the conservation of the primate and dung beetle fauna and for the subsistence activities of local human inhabitants. Finally, our study suggests that successful conservation of primates in their natural habitats should involve not only the conservation of the species of interest but also the identification and conservation of the ecological links in which the primates participate and which may be of fundamental importance in sustaining the life of their natural habitat.

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