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SEED DISPERSAL PATTERNS IN TWO CLOSELY RELATED HOWLER MONKEY SPECIES (*ALOUATTA PALLIATA* AND *A. PIGRA*): A PRELIMINARY REPORT OF DIFFERENCES IN FRUIT CONSUMPTION, TRAVELING BEHAVIOR, AND ASSOCIATED DUNG BEETLE ASSEMBLAGES

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Abstract

Two-phased seed dispersal by primates and dung beetles is crucial for tropical rainforest regeneration. Two species of howler monkey exist in the tropical rainforests of southern Mexico: the mantled howler monkey (*Alouatta palliata*), and the black howler monkey (*A. pigra*). Differences between these species in foraging and traveling behavior, as well as associated dung beetle assemblages, may influence seed dispersal patterns. In this paper we present the results of a preliminary four-month study comparing the above aspects between a group of *A. palliata* (N = 15) in Los Tuxtlas, Veracruz and a group of *A. pigra* (N = 7) in Palenque National Park, Chiapas, Mexico. We observed each group in alternating months using focal sampling, fecal examination, and trapping of dung beetles. Results showed that the *A. palliata* group consumed more mature fruit, but both groups dispersed similar numbers of seeds over the study period (ca. 13,000 seeds). The total number of seed species collected from the feces of the *A. palliata* group was lower than for the *A. pigra* group (13 vs. 31 species). The *A. palliata* group had a larger home range (33 vs. 6.25 ha) and average day range (202 vs. 126 m). More dung beetles from more species were associated with the *A. palliata* group (357 v. 99 beetles, 16 v. 8 species). The *A. palliata* group attracted more ball-rolling dung beetles (75.1% of total), while the *A. pigra* group attracted more burrowers (80.8% of total). Our results suggest important differences between black and mantled howler monkeys of southern Mexico as seed dispersers and highlight the need to consider foraging and ranging patterns, as well as associated secondary dispersers, when assessing seed dispersal by primates.

Key Words: howler monkeys, seed dispersal, *A. palliata*, *A. pigra*, dung beetles, Mexico

Resumen

La dispersión por primates y cucarrones estercoleros es crucial para la regeneración del bosque tropical. Dos especies de monos aulladores existen en los bosques lluviosos del sur de México: el mono aullador de manto (*Alouatta palliata*), y el mono aullador negro (*A. pigra*). Las diferencias entre estas dos especies en el comportamiento de forrajeo y desplazamiento, así como los ensamblajes de cucarrones estercoleros asociados, pueden influenciar los patrones de dispersión de semillas. En este artículo presentamos los resultados de un estudio preliminar de cuatro meses, comparando estos aspectos entre un grupo de *A. palliata* (N = 15) en Los Tuxtlas, Veracruz, y un grupo de *A. pigra* (N = 7) en el Parque Nacional Palenque, Chiapas, México. Observamos cada grupo durante meses alternos utilizando el muestreo focal, examinando muestras de heces, y coleccionando cucarrones estercoleros. Los resultados mostraron que el grupo de *A. palliata* consumió más frutos maduros, pero los grupos de ambas especies dispersaron un número similar de semillas durante el período de estudio (ca. 13,000 semillas). El número total de especies de semillas coleccionadas de las heces del grupo de *A. palliata* fue más bajo que aquel para el grupo de *A. pigra* (13 vs. 31 especies). El grupo de *A. palliata* tuvo un área de rango vital más grande (33 vs. 6.25 ha) así como un recorrido diario promedio mayor (202 vs. 126 m). Más cucarrones estercoleros de más especies estuvieron asociados con el grupo de *A. palliata* (357 v. 99 cucarrones, 16 v. 8 especies). El grupo de *A. palliata* atrajo más cucarrones estercoleros peloteros (75.1% del total), mientras que el grupo de *A. pigra* atrajo más estercoleros cavadores (80.8% del total). Nuestros resultados sugieren importantes diferencias entre los aulladores negros y aulladores de manto del sur de México como dispersores de semillas y resaltan la necesidad de considerar el forrajeo y los patrones de movimiento, así como los dispersores secundarios asociados, cuando se evalúa la dispersión de semillas por parte de primates.

Palabras Clave: monos aulladores, dispersión de semillas, *A. palliata*, *A. pigra*, cucarrones estercoleros, México

Introduction

Large frugivorous primates are important seed dispersers for many tropical tree species (Link and Di Fiore 2006). Although birds disperse a larger number of seeds, primates disperse the seeds of twice as many plant species as birds via endozoochory (Clark et al. 2001), and their ecological services are critical for recruitment of many medium- and large-seeded plant species (Ponce-Santizo and Andresen 2006; Stevenson and Aldana 2008; Stoner et al. 2007). Additionally, many seeds ingested by primates undergo two-phase dispersal. Dung beetles attracted to primate feces act as secondary dispersal agents by accidentally burying seeds along with feces at the deposition site or, if the beetles are ball-rollers, a short distance away (Vander Wall and Longland 2004; Vulinec et al. 2006). This behavior may allow some seeds to escape post-dispersal predation and may provide ideal microclimatic conditions, increasing the probability of seed germination and establishment (Nichols et al. 2008; Vander Wall and Longland 2004; Vulinec and Lambert 2009; Vulinec et al. 2006).

Two species of howler monkeys exist in the tropical forests of southern Mexico. The mantled howler monkey (*Alouatta palliata*), which is found throughout Central America and into western South America, and the black howler monkey (*A. pigra*), which is endemic to the area shared by Mexico, Belize, and Guatemala (Ford 2006; Rylands et al. 2006). Behavioral studies generally report similar resource use and activity budgets for *A. palliata* and *A. pigra* (Estrada 1984; Pavelka and Knopff 2004), and the reported values of species richness for dung beetle populations associated with each primate species (*A. palliata*: 33 sp.; *A. pigra*: 29 sp.) are also similar (Estrada and Coates-Estrada 2002; Ponce-Santizo and Andresen 2006).

Many seed dispersal studies assume that all primates disperse seeds similarly (Gross-Camp et al. 2009; Nunez-Iturri et al. 2008), and only a few studies compare seed dispersal by closely related primate species in similar habitats (Knogge and Heymann 2003; Stevenson et al. 2002). However, based on differences in average body size (*A. palliata*, males: 4.5–9.8 kg, females: 3.1–7.6 kg; *A. pigra*, males: 11.1–11.6 kg, females: 6.2–6.6 kg, (Ford and Davis 1992) and group size (*A. palliata*, 5–16 indiv., average: 8 indiv.; *A. pigra*, 2–12 indiv., average: 4 individuals, (Di Fiore and Campbell 2007; Van Belle and Estrada 2008), *A. palliata* and *A. pigra* may differ in seed dispersal patterns. In this paper, we report results from a short comparative study of *A. palliata* and *A. pigra* aimed at documenting daily travel patterns, seed species dispersed, and dung beetle species associated with howler monkey feces.

Methods

Data collection

The mantled howler monkey (*A. palliata*) was studied in a 2000 ha segment of the Los Tuxtlas Biosphere Reserve in the region of Los Tuxtlas, Veracruz (18°35'08.63"N, 95°04'26.99"W), and the black howler monkey (*A. pigra*) was studied in Palenque National Park (PNP) (~1800 ha; 17°29'12.02"N, 92°03'01.05"W), Chiapas, both in southeast Mexico (Fig. 1). At both sites vegetation is classified as tall, tropical rainforest, and the altitudinal gradient ranges from 150m to 500m above sea level (Estrada 1984; Estrada et al. 2002). Sampling was conducted in areas of continuous forest at both sites. Focal samples were collected for one group of *A. palliata* (N = 15) in Los Tuxtlas during March and May 2008, and for one group of *A. pigra* (N = 7) in PNP during February and April 2008 for eighteen days each month. We collected 135 and 120 hrs of continuous focal samples on the *A. palliata* group and *A. pigra* group, respectively. To control for differences in group size and observation time, all focal data for each species were pooled across individuals and an average focal observation for each species was calculated. We assumed that by alternating monthly observations for each howler group/species during the dry season (Estrada et al. 2002; Estrada and Coates-Estrada 2002) at both sites that, to a certain extent, we compensated for seasonal effects in the data. Additionally, sampling took place during the high-fruit season in both forests. In Los Tuxtlas, *A. palliata* consumes the most mature fruit between March and October (Estrada 1984; Estrada and Coates-Estrada 1991), and in PNP, *A. pigra* consumes the most mature fruit between March and July (Estrada and Muñoz, unpublished data). Studies of dung beetles in Los Tuxtlas have demonstrated that dung beetle populations during the same months (Estrada et al. 1993). No previous studies have examined the dung beetle population at PNP, but because the annual rainfall profile generally matches that observed at Los Tuxtlas (Estrada and Muñoz, unpublished data), seasonal fluctuations in the dung beetle population are likely similar to those in Los Tuxtlas.

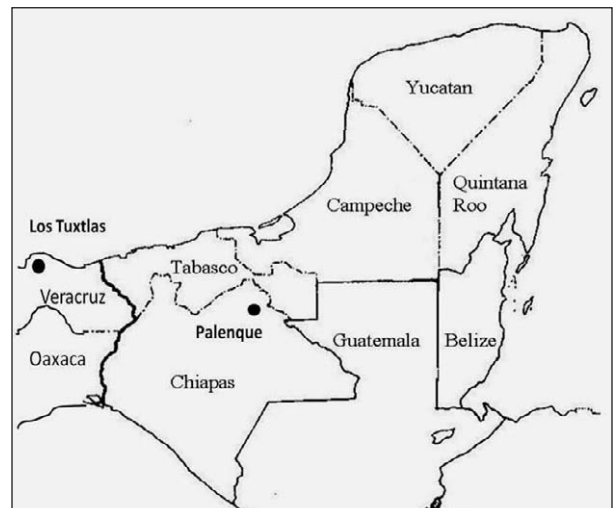


Figure 1. Location of study sites in southeast Mexico.

Focal samples were completed between 06:00 and 15:00 hrs each day to allow time for fecal sample processing. Each sample lasted between five and 15 min (avg.: 14 min ± 3). Focal individuals were chosen in a random order, and sampling was rotated until all individuals in the group were sampled. For each sample, the occurrence and duration of feeding (ingestion of plant material) and travel (group movement from one tree to another) activity was recorded. During feeding observations, the type of plant part ingested was recorded and identified to the species level. A scaled topographic map was used to estimate the distances traversed by the howlers. Total group biomass was estimated using the median body weight for each species (Ford and Davis 1992), and group biomass per hectare was calculated using the home range estimate from each map. Both groups were known to have only one neighboring group, and home range overlap was negligible. Only two *A. palliata* and three *A. pigra* intergroup interactions were observed during the study period.

Fecal samples were collected each day and examined for seeds. Seeds collected from the fecal samples were counted and, when possible, identified to species by comparison to the seed collection at the Los Tuxtlas field station and the National Herbarium housed at the Institute of Biology of the Universidad Nacional Autónoma de México. In the case of seeds < 1 mm in length occurring at high densities, the number of seeds in the sample was estimated by sample volume (seeds/30 mL feces).

Sampling of dung beetles was conducted at each site within the home range of the study groups using 10 pit-fall traps (15 cm in height × 5 cm width) baited with 60 g of feces from the howler species present. Traps were placed at 50 m intervals along a 500 m sinuous transect (Larsen and Forsyth 2005) and remained there for 24 hr. The traps were located about 1 m off of the main trail in ecologically similar locations at each site. Sampling was repeated three times per months at each site, and three distinct transects were used each month in an effort to fully represent each group's home range. Dung beetles encountered in the traps were counted and, when possible, identified to species by

comparison of specimens with the dung beetle collection at the Los Tuxtlas field station.

Data analysis

Because individuals were sampled randomly, and no individual was sampled two times consecutively, focal samples were assumed to be independent. The proportion of time spent traveling and feeding on each resource during a given focal sample were compared between groups using a Kruskal-Wallis test with a Bonferroni correction (R Software). The amount of time dedicated to feeding on each mature fruit species was expressed as a percent of total mature-fruit consumption time. Total average distance traveled per day during the observation period was compared between howler monkey groups using a two-tailed, one-way ANOVA, after log-transformation (JMP 7.0). Since tree crowns as large as 50 m have been measured in the tropical forests of southeastern Mexico (Estrada and Coates-Estrada 1984), only daily movements of 50 m or more were considered as contributions to seed dispersal. Home range was calculated by using a gridded topographic map (50 × 50 m) of the study site to count the number of quadrants in which the group was present during monthly observations.

The number of seeds dispersed per day and the number of seeds per milliliter of fecal sample were compared using a two-tailed, one-way ANOVA (JMP 7.0). A chi-squared test was used to compare the total number of seeds dispersed, the number of large and small seeds dispersed, the total volume of feces produced, and the estimated biomass of each group. Shannon's diversity index (H') and Sorenson's similarity quotient were calculated to compare the dung beetle populations collected at each study site (Estrada and Coates-Estrada 2002).

Results

On average, both howler groups spent a similar percentage of time feeding on fruit during a focal sample (*A. palliata*: 9.27 % ± 5.05, *A. pigra*: 11.21 % ± 4.76; $\chi^2=0.81$, df=1, p=0.37; Table 1). Consumption of mature fruit accounted for 8.54 % ± 4.94 of an average focal sample for the *A. palliata* group and 5.28 % ± 2.96 for the *A. pigra*

Table 1. Average percent time individuals from the *A. palliata* and *A. pigra* groups spent consuming fruit and leaves during any given focal sample (N = 584 and 547 focal samples, respectively). Comparisons between groups were performed using a Kruskal-Wallis test with Bonferroni correction. Asterisks indicate significant p values. All medians = 0%.

	<i>Alouatta palliata</i>		<i>Alouatta pigra</i>		Kruskal-Wallis		
	Average	SD	Average	SD	χ^2	df	p
Fruit	9.27	5.056	11.21	4.76	0.80	1	0.37
Mature fruit	8.54	4.94	5.28	2.96	2.69	1	0.10
Young fruit	0.73	1.29	5.93	3.28	11.53	1	0.00069*
Leaves	2.66	2.06	10.24	4.89	11.31	1	<0.00077*
Mature leaves	0.46	0.72	1.86	2.30	2.75	1	0.097
Young leaves	2.21	1.81	8.38	2.96	11.35	1	<0.00076*

group (Table 1). During the study period the *A. palliata* group consumed the mature fruits of a total of nine species (Table 2), while the *A. pigra* group consumed the mature fruits of four species (Table 3). *A. palliata* group was observed consuming mostly *Ficus* species (Moraceae) (*F. pertusa*: 17.33% of mature-fruit feeding time, *F. colubrinae*: 15.30%, *F. insipida*: 15.65 %) (Table 2), and *A. pigra* group mostly *P. armata* (Moraceae) (43.04%) (Table 3).

Overall, fewer fecal samples were collected from the *A. palliata* group (156 samples=3230 mL) than from the *A. pigra* group (167 samples=4800 ml, $\chi^2=307.0$, $df=1$, $p=0.0001$). More seeds were collected from the fecal samples of the *A. palliata* group (13,756 seeds) than the *A. pigra* group (13,162 seeds; $\chi^2=13.1$, $df=1$, $p=0.0003$), and fecal samples contained seeds from 13 and 31 species, respectively (Tables 2 and 3). Based on both focal and fecal sample data, the *A. palliata* group utilized 18 fruit species during the study period, and the *A. pigra* group utilized 33. The majority of seeds recovered from both groups were from *Ficus* species (*A. palliata*, *F. eugeniaefolia*: 43.7 % of *Ficus* seeds, *A. pigra*, *F. sp. 1*: 43.9 %; Table 2, 3). However, the seeds collected from the two groups varied in size.

The largest seed found in fecal samples of *A. palliata* was 21 mm in length (unknown sp. 10) (Table 2), and the largest seed found in fecal samples of *A. pigra* was 40 mm in length (*Inga* sp. 1) (Table 3). Most seeds measuring <3 mm belonged to the *Ficus* genus, and both howler groups expelled more seeds measuring <3 mm than seeds measuring >3 mm (*A. palliata*: $\chi^2=13022.2$, $df=1$, $p<0.0001$; *A. pigra*: $\chi^2=10831.2$, $df=1$, $p<0.0001$). However, the percent of total seeds deposited that were greater than 3 mm was smaller for the *A. palliata* group (1.3%) than for the *A. pigra* group (4.6%). These seeds belonged to four and 11 plant species, respectively. Feces from *A. palliata* contained slightly more seeds/ml than those from *A. pigra* (4 ± 4 seeds/ml and 2 ± 3 seeds/ml respectively; $F_{1,64}=7.63$, $p=0.007$). However, both groups deposited similar numbers of seeds per day (*A. palliata*: 458 ± 643 (\pm SD), *A. pigra*: 376 ± 1030 (\pm SD); $F_{1,64}=0.15$, $p=0.70$).

The *A. palliata* group used a larger home range (12.5 ha) than the *A. pigra* group (6.25 ha) during the study period. Therefore, despite differences in group size, both groups accounted for similar howler monkey biomass/ha (*A. palliata*: 6.1 kg/ha, *A. pigra*: 7.7 kg/ha, $\chi^2=0.185$, $df=1$, $p=0.33$).

Table 2. List of seed species collected from howler fecal samples and mature fruit species howlers were observed consuming in Los Tuxtlas (*A. palliata*). Quantity of seeds from each plant species is reported using the absolute number and the percent of total seeds collected in each site. Also shown is the percent of mature-fruit feeding time howlers devoted to consuming a particular species. Species recorded from focal samples only are highlighted in bold. Values for seed size marked with an asterisk were estimated in the field. Values without an asterisk were obtained from Croat (1978).

Species/Morphotype	Family	Lifeform	Type of Fruit	Percent Feeding Time	Number Seeds	Percent Total Seeds	Seed Size (mm)
<i>Brosimum alicastrum</i>	Moraceae	Tree	drupe	10.96	-	-	15
<i>Coussapoa purpusii</i>	Moraceae	Tree	drupe	drupe	-	-	-
<i>Ficus pertusa</i>	Moraceae	Tree	syconium	17.33	-	-	<1*
<i>Ficus</i> sp.	Moraceae	Tree	syconium	2.65	-	-	<1*
<i>Ficus tecolutensis</i>	Moraceae	tree	syconium	7.07	-	-	<1*
sp. 1	-	-	-	0.53	-	-	-
<i>Ficus eugeniaefolia</i>	Moraceae	tree	syconium	-	5679	43.70	<1*
<i>Ficus colubrinae</i>	Moraceae	tree (strangler)	syconium	15.30	3925	30.20	1*
<i>Ficus insipida</i>	Moraceae	tree	syconium	15.65	1647	12.67	2*
<i>Ficus petenensis</i>	Moraceae	tree (strangler)	syconium	-	1462	11.25	1*
<i>Cecropia obtusifolia</i>	Cecropiaceae	tree	drupe	0.88	808	6.22	2*
<i>Poulsenia armata</i>	Moraceae	tree	aggregate	15.83	116	0.89	4, 10*
sp. 10	-	-	-	-	37	0.28	21*
sp. 5					33	0.25	
sp. 11	-	-	-	-	26	0.20	3*
<i>Cynometra vetusa</i>	Fabaceae	tree	drupe	8.66	16	0.12	13*
<i>Smilax</i> sp.1	Smilicaceae	vine	berry	-	4	0.03	8*
sp. 13	-	-	-	-	2	0.02	3*
sp. 12					1	0.01	
Total Species = 18 Total Seed					13,756		

The average proportion of time spent traveling also did not differ between groups (*A. palliata*: 0.058 ± 0.055 , *A. pigra*: 0.069 ± 0.018 ; $\chi^2 = 2.23$, $df = 1$, $p = 0.13$). During the study period, the *A. palliata* group traveled less than 50 m on 12 of the 34 days during which it was followed. The *A. pigra* group traveled less than 50 m on 15 of 34 days. Excluding these days, the *A. palliata* group had a marginally significantly larger day range (202 ± 149 m, range:

50–630 m) than the *A. pigra* group (127 ± 66 m, range 50–250m; $F_{1,40} = 4.15$, $p = 0.048$).

At Los Tuxtlas, pit-fall traps captured 357 beetles belonging to 16 species (avg beetles/session = 59.50 ± 78.69), while in Palenque they captured 99 beetles belonging to eight species (avg. beetles/session = 16.50 ± 12.68) (Table 4). There was some evidence for higher dung beetle species

Table 3. List of seed species collected from howler fecal samples and mature fruit species howlers were observed consuming in Palenque (*A. pigra*). Quantity of seeds from each plant species is reported using the absolute number and the percent of total seeds collected in each site. Also shown is the percent of mature-fruit feeding time howlers devoted to consuming a particular species. Species recorded from focal samples only are highlighted in bold. Values for seed size marked with an asterisk were estimated in the field. Values without an asterisk were obtained from Croat (1978).

Species/Morphotype	Family	Lifeform	Type of Fruit	Percent Feeding Time	Number Seeds	Percent Total Seeds	Seed size (mm)
<i>Brosimum alicastrum</i>	Moraceae	tree	drupe	13.92	-	-	15
<i>Ficus</i> sp. 1	Moraceae	-	syconium	-	5599	43.87	<1*
<i>Ficus</i> sp. 9	Moraceae	-	syconium	-	3152	24.70	<1*
<i>Ficus colubrinae</i>	Moraceae	tree (strangler)	syconium	30.87	2670	20.92	1*
<i>Poulsenia armata</i>	Moraceae	tree	aggregate	43.04	459	3.60	4, 10*
<i>Ficus pertusa</i>	Moraceae	tree (strangler)	syconium	-	425	3.33	<1*
<i>Ficus insipid</i>	Moraceae	tree	syconium	-	379	2.97	2*
sp. 2	-	-	-	-	140	1.10	-
<i>Ficus</i> sp. 3	Moraceae	-	syconium	-	69	0.54	1*
<i>Ficus</i> sp. 2	Moraceae	-	syconium	-	40	0.31	1*
<i>Ficus petenensis</i>	Moraceae	tree (strangler)	syconium	-	38	0.30	1*
<i>Cecropia obtusifolia</i>					36	0.28	
sp. 6	-	-	-	-	33	0.26	8*
sp. 3	-	-	-	-	17	0.13	-
<i>Ficus eugeniaefolia</i>	Moraceae	tree	syconium	-	15	0.12	<1*
<i>Ficus</i> sp. 4	Moraceae	-	syconium	-	14	0.11	<1*
sp. 1	-	-	-	-	13	0.10	15*, 34*
<i>Cynometra vetusa</i>	Fabaceae	tree	drupe	12.15	11	0.09	13*
<i>Ficus</i> sp. 7	Moraceae	-	syconium	-	10	0.08	1*
<i>Pseudolmedia oxyphyllaria</i>	Moraceae	tree	drupe	-	10	0.08	10*
<i>Dendropanax arboreus</i>	Araliaceae	tree	berry	-	5	0.04	7, 5*
<i>Ficus</i> sp. 6	Moraceae	-	syconium	-	5	0.04	<1*
sp. 8	-	-	-	-	4	0.03	-
<i>Cissus</i> sp. 1	Vitaceae	vine	berry	-	3	0.02	9*
<i>Ficus</i> sp. 8	Moraceae		syconium	-	3	0.02	4*
sp. 4	-	-	-	-	3	0.02	-
<i>Ocotea</i> sp. 1	Lauraceae	tree	drupe	-	2	0.02	15*
sp. 5	-	-	-	-	2	0.02	-
<i>Coussapoa purpusii</i>	Cercropiaceae	epiphyte	aggregate	-	1	0.01	2*
<i>Ficus</i> sp. 5	Moraceae	-	syconium	-	1	0.01	2*
<i>Inga</i> sp. 1	Fabaceae	tree	legume	-	1	0.01	40
sp. 7	-	-	-	-	1	0.01	2*
<i>Trichostigma octandrum</i>	Phytolaccaceae	vine	drupe	-	1	0.01	5*
Total Species = 33					13,162		
Total Seeds							

diversity at Los Tuxtlas ($H' = 1.59$, $E_H = 0.57$) than in Palenque ($H' = 1.30$, $E_H = 0.63$). Six dung beetle species were associated with both howler monkey groups, and Sorenson's quotient for dung beetles was 0.50. The most common beetle species associated with howler feces at Los Tuxtlas was *Canthon femoralis* (58.3 %; Table 4), and at PNP it was *Copris laeviceps* (56.6 %; Table 4). At Los Tuxtlas, most of the beetles captured were ball-rollers (75.1 %), while at PNP most were burrowers (80.8 %; Table 4). Also, at Los Tuxtlas 21.3 % of the beetles collected were nocturnal and 78.7 % were diurnal, while at PNP 62.6 % were nocturnal and 37.4% were diurnal (Table 4).

Discussion

Our behavioral and fecal samples data suggest that *A. palliata* and *A. pigra* differ somewhat in seed dispersal patterns despite being closely related. Previous studies report that

A. palliata can incorporate between nine and 35 fruit species into its diet depending on the location, and in Los Tuxtlas, a year-long study documented 28 seed species in *A. palliata* feces (Estrada and Coates-Estrada 1991; Whencke et al. 2004). *A. pigra* utilizes 25 fruit species in fragmented forests in Belize, and a five-month study reported ten seed species in *A. pigra* feces in Guatemala (Marsh and Loiselle 2003; Ponce-Santizo and Andresen 2006). These data suggest that *A. palliata* is capable of consuming more seed species than the 18 documented in this study and that *A. pigra* consumes more seed species in PNP than in other locations. However, because this study directly compares the two species in similar forests during the same period of the year, the differences detected between *A. palliata* and *A. pigra* may indicate a potential distinction in plant-primate dynamics. Specifically, *A. palliata* appears to consume more mature fruit and disperse more total seeds while *A. pigra* appears to disperse a greater diversity of seeds.

Table 4. Dung beetle species collected in Los Tuxtlas (*A. palliata*) and Palenque (*A. pigra*). 60 traps were set in each site for 24 hours for a total of 1,440 trap hours at each site. Quantity of each beetle species is reported using the absolute number and the percent of total beetles collected in each site. Activity describes the time of day at which each species is active, and behavior describes fecal treatment.

<i>Alouatta palliata</i>				
Species	Activity	Behavior	Number	Percent
<i>Canthon femoralis</i>	diurnal	ball-roller	208	58.3
<i>Copris laeviceps</i>	nocturnal	burrower	52	14.6
<i>Canthon euryscelis</i>	diurnal	ball-roller	19	5.3
<i>Deltotichilum pseudoparile</i>	nocturnal	ball-roller	12	3.4
<i>Onthophagus batesi</i>	diurnal	burrower	12	3.4
<i>Canthon viridis vazquezi</i>	diurnal	ball-roller	11	3.1
<i>Dichotomius satanis</i>	nocturnal	burrower	11	3.1
<i>Neocanthidium martinezi</i>	diurnal	ball-roller	7	2.0
<i>Onthophagus rhinolophus</i>	diurnal	burrower	7	1.0
<i>Pseudocanthos perplexus</i>	diurnal	ball-roller	5	1.4
<i>Canthidium aff ardens Bates</i>	diurnal	burrower	4	1.1
<i>Canthon subhyalinus</i>	diurnal	ball-roller	3	0.8
<i>Canthidium perceptible</i>	diurnal	burrower	2	0.6
<i>Phanaeus chryseicollis</i>	diurnal	ball-roller	2	0.6
<i>Canthon</i> sp.	diurnal	ball-roller	1	0.3
<i>Copris lubgris</i>	nocturnal	burrower	1	0.3
Total			357	
<i>Alouatta pigra</i>				
Species	Activity	Behavior	Number	Percent
<i>Copris laeviceps</i>	nocturnal	burrower	56	56.6
<i>Onthophagus vatesi</i>	diurnal	burrower	19	19.2
<i>Canthon euryscelis</i>	diurnal	ball-roller	15	15.2
<i>Dichotomius satanis</i>	nocturnal	burrower	4	4.0
<i>Canthon femoralis</i>	diurnal	ball-roller	2	2.0
<i>Copris lubgris</i>	nocturnal	burrower	1	1.0
<i>Deltotichilum gibbosum</i>	nocturnal	ball-roller	1	1.0
<i>Phanaeus endymion</i>	diurnal	ball-roller	1	1.0
Total			99	

Differences in patterns of range-use and daily travel between the two howler groups also likely result in the production of different seed shadows (sensu Clark et al. 2005). Since both groups dispersed similar amounts of seeds per day, but the *A. palliata* group utilized a larger home range and day range than the *A. pigra* group, the seed shadow produced by the *A. palliata* group is likely less dense than that produced by the *A. pigra* group. These behavioral differences are unlikely to be a result of group size since group size in these species appears to be dictated by social constraints and not by food availability (Chapman and Pavelka 2005; Cowlshaw and Dunbar 2000; Van Belle and Estrada 2008). Similarly, because territory overlap among groups was minimal, these patterns are likely to remain constant across the entire territory. During the high-fruit season, seed dispersal patterns also appear to differ between howler species with regard to associated secondary dispersers. Previous research in the continuous forest of Los Tuxtlas described 20 dung beetle species associated with *A. palliata*, and a study of *A. pigra* in Guatemala documented 29 dung beetle species (Estrada and Coates-Estrada 1991; Ponce-Santizo and Andresen 2006). However, our data reveal a larger and more diverse dung beetle population associated with the *A. palliata* group than the *A. pigra* group, which may indicate a higher probability of secondary dispersal for seeds dispersed in *A. palliata* feces between February and May. Furthermore, most seeds dispersed by ball-rollers are less than 3 mm in length (Estrada et al. 1993; Vulinec et al. 2006). The *A. palliata* group was associated with more ball-rollers and dispersed fewer large seeds than the *A. pigra* group, and the *A. pigra* group was associated with more burrowers and dispersed more large seeds than the *A. palliata* group. Therefore, the effectiveness of seed dispersal by each howler species may depend on the interaction of seed size and secondary dispersal by dung beetles. The association of more diurnal dung beetles with the *A. palliata* group and more nocturnal dung beetles with the *A. pigra* group likely also influences patterns of secondary seed dispersal since a large proportion of diurnal dung beetles are ball-rollers which may move seeds up to 5 m from the initial deposit site while a large proportion of nocturnal dung beetles are burrowers which bury seeds on-site (Slade et al. 2007; Vulinec and Lambert 2009).

The subtle differences in howler seed dispersal behavior and associated dung beetle assemblages described in this study suggest an important distinction between black and mantled howler monkeys as seed dispersers. Further investigation of these differences in more groups of each species may broaden our understanding of how closely related primate species differing in associated secondary seed dispersal agents, among other features (e.g. body size and group size), may also differ in their contribution to the maintenance of plant diversity in their habitats. The participation of distinct dung beetle communities in processing the feces produced by each howler group during the high-fruit season also highlights the importance of dung beetles as secondary dispersers (Nichols et al. 2008). Recent studies

have shown that the stability of this interface is altered by human-induced forest fragmentation and habitat isolation, which cause local declines in size or extinctions of primate and dung beetle populations (Andresen 2002; Estrada and Coates-Estrada 2002; Nichols et al. 2008; Ponce-Santizo and Andresen 2006). Such changes may result in significant modifications in patterns of recovery and distribution for many forest plant species. These modifications will have a strong impact on the persistence of primates in fragmented landscapes and on human livelihood and merit further investigation.

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