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Seed Dispersal by Bats and Birds in Forest and Disturbed Habitats of Chiapas, México[1]

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ABSTRACT

We examined seed dispersal by bats and birds in four habitats of the Selva Lacandona tropical rain forest region, Chiapas, Mexico. The four habitats represented a disturbance gradient: active cornfield, ten-year-old abandoned cornfield, cacao plantation, and forest. Using seed traps examined before sunrise (0400 h) and before sunset (1800 h), we compared volant vertebrate seed dispersal, assuming that seeds found at the end of the night were dispersed by bats and those found at the end of the day were dispersed by birds. We did not find seeds from other frugivores such as monkeys or opossums. In all habitats bats dispersed more seeds than birds. In most months bats also dispersed more seeds than birds, except in December when no seeds were found in the traps. Bats also consistently dispersed more species of seeds than birds, although a χ^2 comparison showed differences not to be significant. Fifty percent of the species represented in the dispersed seeds in all habitats were pioneer species. *Cecropia* seeds represented a high percentage (up to 87% of those dispersed by bats and up to 83% by birds) of dispersed seeds that fell in our traps. The influence of bats and birds on secondary successional processes is likely to be fundamental for the establishment of vegetation. Since bats dispersed more seeds than birds (primarily to disturbed areas and consisting primarily of pioneer species), they are likely to play an important role in successional and restoration processes among habitats as structurally and vegetationally different as cornfields, old fields, cacao plantations, and forest.

RESUMEN

En cuatro habitats del bosque tropical húmedo de la Selva Lacandona, Chiapas, México, estudiamos la dispersión de semillas por murciélagos y por aves. Los cuatro habitats incluyeron un gradiente de perturbación: sembradío activo de maíz, sembradío abandonado de maíz, plantación de cacao, y bosque. Usando trampas de semillas examinadas antes del amanecer (0400 h) y antes del anochecer (1800 h) comparamos la dispersión de semillas por vertebrados voladores, suponiendo que las semillas encontradas al final de la noche fueron dispersadas por murciélagos y las encontradas al final del día fueron dispersadas por aves. En ninguna ocasión encontramos semillas dispersadas por otros dispersores, tales como monos o tlacuaches. En todos los habitats los murciélagos dispersaron más semillas que las aves. En la mayoría de los meses los murciélagos también dispersaron más semillas que las aves, excepto en diciembre, cuando no se encontraron semillas en las trampas. Los murciélagos también dispersaron consistentemente más especies de semillas que las aves, aunque una comparación con χ^2 no fue significativa. El 50 por ciento de las especies representadas en las semillas dispersadas son especies pioneras. Las semillas de *Cecropia* representan un alto porcentaje (hasta el 87% de las dispersadas por murciélagos y hasta el 83% de las dispersadas por aves) del total de semillas dispersadas y recuperadas de las trampas de semillas en cada habitat. La influencia de los murciélagos y las aves sobre los procesos de sucesión secundaria es probablemente fundamental para el establecimiento de la vegetación. Dado que los murciélagos dispersan más semillas que las aves, principalmente hacia sitios perturbados, y en su mayoría de especies pioneras, ese grupo probablemente juega un papel importante en los procesos sucesionales y de restauración en habitats tan distintos desde el punto de vista estructural y de la vegetación como sembradíos de maíz activos y abandonados, plantaciones de cacao, y bosque húmedo tropical.

Key words: bats; birds; cacao plantation; cornfield; old field; seed dispersal; tropical rain forest.

Seed dispersal by vertebrates has been identified as a key reproductive mechanism for many tropical plants. Vertebrates are known to disperse the seeds belonging to a major percentage (50–90%) of tropical trees and shrubs (Howe & Smallwood 1982, Janzen 1983, Van Dorp 1985); those plants produce fruits with specific morphological and nutrient characteristics, such as presentation on the plant, color, smell, size, and chemical constitution that can be grouped into vertebrate-dispersal syndromes (Janzen 1975, Charles-Dominique *et al.* 1981). Birds frequently have been identified as a particularly important group of seed dispersers (Stiles 1985, Murray 1988, Howe 1990). The vagility of birds is only comparable to that of bats, and this intrinsic feature allows birds or bats to cover a greater distance per unit of time than any

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other animal group (McDonnell 1988, Howe 1990). It also has been pointed out that the numerically dominant bird and mammal species in tropical rain forests are frequently frugivores (Terborgh 1983, Levey 1988, Terborgh *et al.* 1990).

Neotropical frugivorous bats are a very abundant component of tropical faunas; several authors consider this group to be more abundant than all other mammal groups and equal to or greater than all frugivorous birds in numbers (Terborgh 1977, 1983; Bonaccorso 1979). Frugivory is the most abundant trophic category among species of Neotropical rain forest mammals (Medellín & Redford 1992). Several authors have stated that birds generally defecate seeds from a perched position (dispersing seeds primarily when not in flight), whereas bats generally defecate in flight (Charles-Dominique 1986: 125; 1991: 244; Gorchov *et al.* 1993: 347). Regeneration of African rain forests depends largely on frugivorous bats of the family Pteropodidae (Thomas 1984). In successional areas in Côte d'Ivoire, 75 percent of the fruits from eight tree species in nearby forest were removed at night, and 95 percent of the seeds from those fruits were dispersed by bats. Birds and primates accounted for the remaining 25 percent of fruits removed and 5 percent of seeds dispersed into successional areas (Thomas 1991). In French Guiana, bats are also responsible for an important percentage of dispersed seeds; virtually all seeds that fell in open areas and treefall gaps did so during the night, whereas most seeds that fell under large, isolated trees were deposited during the day (Charles-Dominique 1991).

It also has been suggested that ornithocory is a key mechanism in the successional processes of tropical habitats, based on evidence indicating that birds move propagules from forests (presumably from the vicinity of a parent tree) to disturbed habitats or isolated forest remnants and thereby help to maintain forest structure and diversity (Howe & Smallwood 1982, Guevara & Laborde 1993). For frugivorous birds, the habitat will be attractive if it has food, perching and nesting sites, and refuges from predators. In early successional patches and disturbed areas such as cornfields, pastures, or gaps in which trees and branches are virtually absent, perching and nesting sites become a major limiting factor for the dispersal role of birds (McDonnell 1986, Gorchov *et al.* 1993, Laborde 1996).

The purpose of this study was to compare seed dispersal by birds to that by bats in different successional (disturbance) stages by examining the contribution of each group to seed shadows in these habitats. Specifically, we asked if bats and birds represented two distinct functional dispersal groups, and examined the relative contribution of each group to seed rain along a disturbance gradient in four habitats.

STUDY SITE AND METHODS

We studied seed dispersal by bats and birds in the Lacandon forest of Chiapas, Mexico. This rain forest has been identified as the most species-rich locality in Mexico, at least for mammals and diurnal butterflies (Medellín 1994a). Details of the study area are given in Medellín (1994a). The logistic base was the Chajul Tropical Biology Station (16°06' N, 90°56' W, 120 m elev.), managed by the National Autonomous University of Mexico. Rainfall data obtained from the International Commission of Borders and Water between Mexico and Guatemala show an average of 2537 mm a year (SE = 516) for the last 11 years, 88 percent of which fell between May and November.

We placed one 1.26 m^2-circular seed trap at ten randomly chosen points 2 m from a trail in each of four habitats: primary forest, a cacao plantation (7 ha surrounded on two sides by forest, on one by the Lacantun River, and on the other by an old field), a ten-year-old abandoned cornfield (3 ha completely surrounded by forest), and an active cornfield (4 ha, bordered on one side by forest, on two sides by other disturbed habitats, and on the other side by the Lacantun River). Traps were separated by at least 10 m and were held 0.9 m above ground by rebars. No trap was placed closer than 30 m from the edge of that habitat. Cacao plantations in the Lacandona (as in other areas) use forest canopy trees as shade, and thus only understory vegetation was removed. Traps were examined twice daily for ten days in each of 12 months, September 1993–August 1994, except for the old field and forest that were not visited during January, February, and March of 1994 when sociopolitical problems in the Lacandona prevented us from visiting the site. We obtained data from the other two habitats during those three months with the help of a field assistant who lived close to the sampling sites and could move about without risk. The shortest distance between the four sites was 1 km. Traps were visited before sunset (1800) and before sunrise (0400). We assume that seeds encountered at 1800 were dispersed by birds and those encountered at 0400 were dispersed by bats. There are other frugivores such as opossums, primates, and carnivores in the area, but their feces and dispersal

TABLE 1. *Results of a generalized linear model applied to test for effects of disperser groups (bats and birds), habitat, and month and their interactions on seed rain generated during one year in the Selva Lacandona, Chiapas, Mexico.*

Source	Deviance	R^2	df	P
Main effects:				
Dispersers (D)	14.08	0.115	1	<0.005
Habitat (H)	24.2	0.199	3	<0.005
Month (M)	16.94	0.139	8	<0.05
Effects of interactions:				
D*H	3.04	0.025	3	NS
D*M	9.62	0.079	8	NS
H*M	25.51	0.209	24	NS
D*H*M	28.09	0.23	24	NS
Total	121.48	—	71	—

mode is different and very easy to identify; they either drop large numbers of seeds in one defecation event (tens of times larger than that of a large bat or bird) or drop pieces of fruit (Medellín 1994b). We collected all seeds, then dried, counted, and identified them to species.

Comparisons of seed dispersal by bats and birds between habitats and months (and interactions among the three variables) were performed with the generalized linear model analysis of deviance (Crawley 1993). We used chi-square tests (Sokal & Rohlf 1981, Zar 1984) to analyze species richness of seeds per functional group and per habitat. In total, our data came from 5544 m^2 sampled over 120 days/nights in the four different habitats. For clarity, seeds dispersed are expressed in number of seeds/m^2/night (bats) or day (birds), except when examining total numbers of seeds dispersed.

RESULTS

We obtained a total of 10,325 seeds, of which 8170 (79.1%) were dispersed by bats and 2155 (20.9%) by birds. No feces from any other frugivore were found. Bats dispersed significantly more seeds than birds, and there are also significant differences by habitat and by month. The greatest differences appeared in the intermediate stages of disturbance; *i.e.,* in the abandoned cornfield and cacao plantation (Table 1; Fig. 1; see below); from two to seven times more seeds were dispersed by bats than by birds.

The old field habitat showed the greatest dispersal by bats with a total of 3641 dispersed seeds (86% of the total dispersed to that habitat) or 3.21 seeds/m^2/night. The greatest dispersal by birds oc-

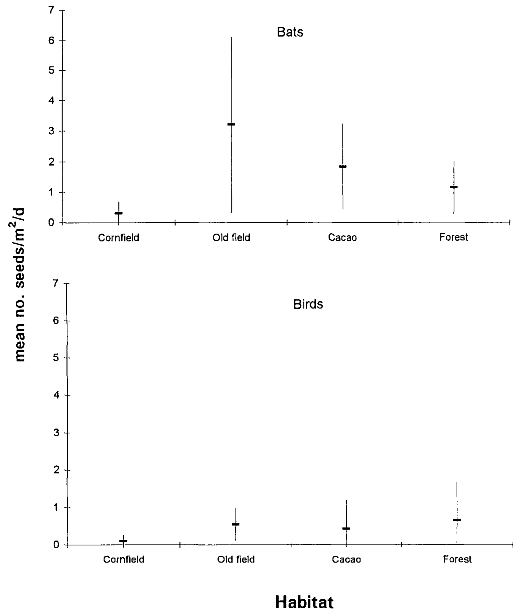

FIGURE 1. Number of seeds dispersed/m^2/night for bats and per day for birds in four habitats of the Selva Lacandona region of Chiapas, Mexico. Horizontal bar indicates mean; vertical line indicates 1 SE.

curred in the forest, with a total of 740 (36%) or 0.65 seeds/m^2/day. The cornfield was the habitat with the smallest incidence of seed dispersal by both groups: 461 seeds or 0.3 seeds/m^2/night dispersed by bats (76%) and 144 or 0.09 seeds/m^2/day by birds (24%). Bats consistently dispersed more seeds than birds per month (Table 2). Only in December were no seeds found either during the day or night. The greatest number of seeds was recorded in August, with 1609 (96%) or 12.8 seeds/m^2/night by bats and 70 (4%) or 0.6 seeds/m^2/day by birds. The greatest seed dispersal by bats occurred during August, September, and June; the greatest seed dispersal by birds was during June and July (Fig. 2).

When examining monthly dispersal by bats within habitats, we found that the greatest seed dispersal occurred during August in the oldfield, with 9.5 seeds/m^2/night. During February and June in the cacao plantation, the maximum was 3.2 seeds/m^2/night. In the forest, the greatest seed dispersal occurred in September when 2.4 seeds/m^2/night was recorded. In the cornfield, we found the greatest seed dispersal by bats during January, February, and March, but never above 1.6 seeds/m^2/night. Bird seed dispersal was highest in the forest during July, with 3.3 seeds/m^2/d. In the ca-

TABLE 2. *Average number of seeds falling per square meter per night (for bats) and per day (for birds) in four habitats. The average was calculated by dividing the total number of seeds collected during the day and the night and dividing by the total surface of traps in each habitat times number of days/nights they were active. The second column under each habitat indicates the total number of seed species dispersed by bats and birds in four habitats of the Selva Lacandona, Chiapas. Numbers in parentheses indicate the number of pioneer species in the total.*

	Cornfield Seeds/m²/no. spp. night-day	Old field Seeds/m²/no. spp. night-day	Cacao Seeds/m²/no. spp. night-day	Forest Seeds/m²/no. spp. night-day	Total No. spp.
Bats	0.31 11 (9)	3.21 12 (5)	1.83 11 (6)	1.14 12 (6)	25 (14)
Birds	0.10 4 (3)	0.54 11 (5)	0.44 10 (6)	0.65 9 (4)	19 (9)

cao plantation it occurred in June with 2.6 seeds/m^2/night. The greatest seed dispersal in open, early successional habitats by birds occurred during October in old field (1.6 seeds/m^2/day) and during February in the cornfield (0.6 seeds/m^2/day).

The number of species dispersed by bats was greater in each habitat than that dispersed by birds (11 vs. 4, 12 vs. 11, 11 vs. 10, and 12 vs. 9 in cornfield, old field, cacao, and forest, respectively), but these differences were not significant ($\chi^2 = 13$; $P = 0.8$). The number of seed species dispersed by bats and birds by month and habitat differed significantly (Kruskall-Wallis ANOVA, $H = 8.45$, df $= 3$, $P = 0.04$), although no paired comparison between the two groups was significantly different. Except in the old field, pioneer species represented over 50 percent of the species dispersed by bats, whereas pioneer species represented in all but one case (cornfield) less than 50 percent of the species dispersed by birds. A high percentage of the seeds dispersed by both groups were *Cecropia* seeds, ranging from 12 percent for bats in cornfield and 6 percent for birds in cornfield to 87 percent for bats in cacao plantation and 83 percent for birds in old field. The small percentages of *Cecropia* seeds in cornfield may be related to the relatively high abundance of another vertebrate-dispersed pioneer in that habitat, *Physalis campanulata,* which in that habitat accounted for 79 percent of bat-dispersed seeds and 77 percent of bird-dispersed seeds.

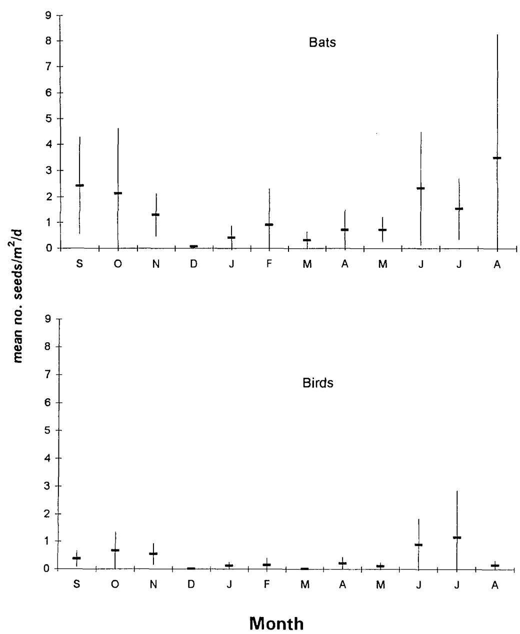

FIGURE 2. Number of seeds/m^2/24 h period dispersed by bats and birds during a 12-month period in Chiapas, Mexico. In December no seeds were found in traps. Horizontal bar indicates mean; vertical line indicates 1 SE.

DISCUSSION

Birds have frequently been indicated as being very important seed dispersers and initiators of successional processes in tropical rain forests around the world, and it is also known that in these ecosystems one can find the largest proportion of frugivorous birds (Karr 1971; Snow 1981; Janzen 1983; Howe 1984, 1986; Van Dorp 1985). Although bats are frequently recognized as important seed dispersers, few studies have shown the relative importance of these two groups compared simultaneously (*e.g.,* Charles-Dominique 1991, Gorchov *et al.* 1993). In this sense, our results clearly indicate that bats are at least as important (numerically) as birds in terms of seed dispersal, particularly in disturbed habitats in which seed dispersal of pioneer trees and shrubs is most important for initiating successional processes. Not only is the seed rain due to bats copious, it also contains at least 50 percent of shrub and tree species identified as key elements in the early stages of succession (Gardner 1977, Humphrey & Bonaccorso 1979, Heithaus 1982, Thomas 1984, Fleming 1988, Charles-Dominique 1991). This is reinforced by the fact that the absolute number of seeds is overwhelmingly composed of seeds belonging to pioneer species; *Cecropia* alone represents up to 87 percent of the bat-dispersed seeds.

It is important to note that our results only apply to that portion of the seed dispersal process related to deposition of the seeds. Successful dispersal depends on a large number of factors, including post-dispersal seed predation, germination, and establishment. The first step, however, is always the removal of seeds from the parent plant and their deposition away from it. Since bats are relatively small in size, they disperse only a few tens of seeds in one defecation event (O. Gaona, pers. obs.), whereas medium-sized mammals such as the brown four-eyed opossum (*Philander opossum*) or the common opossum (*Didelphis marsupialis*) deposit an average of 218 and 501 seeds and up to 2137 and 3225 seeds of *Cecropia* per defecation event, respectively (Medellín 1994b). Because bats and birds are more abundant and smaller than opossums and other frugivores (and thus deposit fewer seeds belonging to a greater number of seed groups), their seed shadows should be spatially more homogeneous than those produced by larger frugivores. This in turn should reduce the chances of post-dispersal seed predation via the location of large deposits of seeds by predators; intraspecific competition of seedlings should also be lower.

We concur with Whittaker and Jones (1994) that bats and birds apparently differ in their tendencies to disperse seeds to open habitats, although the roles of the two groups as dispersers clearly overlap broadly; they probably complement each other in that process. Many shrub and tree species in the tropics and in many other habitats have been shown to depend on birds for their dispersal (*e.g.*, Janson 1983, Howe 1990). This paper presents evidence for only the first step after removal from the parent plant by those two groups of dispersers. Studies on the patterns and processes of seed germination, seedling establishment, and recruitment into sapling stages are under way as a second step in comparing the dispersal efficiency of bats and birds.

It is important to note that the design used here allowed for relatively detailed information and fine-grained differentiation between nocturnal and diurnal seed rain, but the degree of generalization probably suffered by having only one study plot in each habitat. The next step would be to adopt a more general design allowing a larger sample size and replicating it over several tropical areas to increase the possibilities for generalization.

Given their diet of pioneer plant fruits, seed dispersing capabilities (especially in disturbed habitats), and abundance, frugivorous bats in Neotropical rain forests play an essential role in early successional stages; few other groups transport as many seeds in as many dispersal events (relatively few seeds in many events) along the entire disturbance gradient. This is a key piece of information that could yield important insight related to successional processes, the restoration of degraded tropical rain forests, and the conservation of forest fragments.

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APPENDIX 1. *Seed species found to be dispersed by bats and birds, their successional category, habitat where they were found to be dispersed (Cornfield: C; Old field: O; Cacao plantation: A; Forest: F), and life-form.*

Species	Bat dispersed No. seeds	Bird dispersed No. seeds	Successional category	Habitat	Life-form
ANACARDIACEAE					
Spondias radlkoferi	27	5	Late	O, A, F	Tree
BORAGINACEAE					
Cordia sp.	6		Late	O	Tree
CUCURBITACEAE					
Melothria pendula	5		Early	C	Vine
MORACEAE					
Brosimum sp.	41		Late	A	Tree
Castilla elastica	73	7	Early	A, F	Tree
Cecropia peltata	5497	906	Early	C, O, A, F	Tree
C. obtusifolia	28	23	Early	C, O, A, F	Tree
Ficus aurea	111	193	Late	O, F	Tree
F. insipida	621	489	Late	C, O, A, F	Tree
F. pertusa	154	294	Late	C, O, A, F	Tree
MARCGRAVIACEAE					
Souroubea loczyi		1	Late	O	Vine
MELIACEAE					
Guarea excelsa	1	3	Late	O, F	Tree
G. grandifolia	4	8	Late	O, F	Tree
PIPERACEAE					
Piper auritum	1140	40	Early	C, O, A	Shrub
P. hispidum	33		Early	C, F	Shrub
P. nitidum	6	2	Early	O	Shrub
SAPINDACEAE					
Cupania belizensis		3	Late	O	Vine
SOLANACEAE					
Lycianthes nitida	12	1	Early	C, A	Small shrub
Physalis campanulata	357	157	Early	C, A, F	Small shrub
Solanum americanum	6	1	Early	O	Small shrub
S. athurensis	21		Early	A, F	Small shrub
Witheringia nelsonii	11	17	Early	C, O, A, F	Small shrub
sp. 1	2		Early	A	

APPENDIX 1. *Continued.*

Species	Bat dispersed No. seeds	Bird dispersed No. seeds	Successional category	Habitat	Life-form
ULMACEAE					
Ampelocera hottlei	3	2	Late	A, F	Tree
URTICACEAE					
Urera caracasana	4		Early	C	Shrub
UNKNOWN					
sp. 1	1			C	
sp. 2		3		A	
sp. 3	2			O	