SEASONAL VARIATION IN FRUIT CONSUMPTION AND SEED DISPERSAL BY CANOPY BATS (*Artibeus* spp.) IN A LOWLAND FOREST IN PERU

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ABSTRACT

Changes in the abundance of frugivorous bats, fruit consumption, and seed dispersal were studied in mature and successional forests in Manu National Park, Peru. Bat abundance, as evaluated by mist-net captures in 1989 and 1991, was similar in both mature and successional forest only during times when *Cecropia* (a major fruit species of successional forest) was fruiting. During the rest of the year, canopy frugivorous bats were significantly more abundant in mature forest where they fed mostly on *Ficus* spp. (Moraceae), *Dipteryx alata* (Leguminosae), and *Clarisia biflora* (Moraceae). Figs were more abundant during the first half of the year and dominated the diet of canopy bats during this time, whereas two large-seeded species (*D. alata* and *C. biflora*) became more important food items during the latter half of the year. Yearly differences in fruit abundance and phenology undoubtedly occur, and this variation affects movement patterns, habitat use, fruit consumption by bats, and consequently, the patterns of seed dissemination between forest habitats in the same season, and within habitats between years.

KEY WORDS: *Artibeus* spp., canopy bats, frugivory, fruit phenology, movement patterns, seed dispersal, Peru

RESUMEN

En este trabajo se estudian los cambios en la abundancia de murciélagos frugívoros, consumo de frutos y dispersión de semillas durante las diferentes estaciones de frutos en bosque maduro y succesional en el Parque Nacional del Manú, Perú. La abundancia de murciélagos, según indica el muestreo con redes de niebla, fue similar en bosque maduro y succesional solamente durante el tiempo en que *Cecropia*, una especie muy abundante en el bosque succesional, estaba fructificando. Durante el resto del año, los murciélagos frugívoros del dosel fueron significativamente más abundantes en el bosque maduro, donde se alimentan de higos (*Ficus* spp.), *Dipteryx alata* (Leguminosae) y *Clarisia biflora* (Moraceae). Los higos, un recurso muy abundante durante la primera mitad del año, dominaron la dieta de los murciélagos durante este tiempo, mientras que *D. alata* y *C. biflora*, dos especies de semillas comparativamente grandes, fueron los alimentos importantes durante la segunda mitad del año. Diferencias anuales en la abundancia y fenología de frutos, indudablemente ocurren. Se hipotiza sobre el grado en que estos cambios afectarían los patrones de movimiento, uso de hábitat y consumo de frutos por murciélagos, así como los efectos sobre los patrones de diseminación de semillas entre hábitats durante la misma estación, y en el mismo hábitat en diferentes años.

PALABRAS CLAVE: *Artibeus* spp., dispersión de semillas, fenología de frutos, frugivorismo, murciélagos de dosel, patrones de movimiento, Perú

RESUMO

Em este trabalho se estudam as mudanças na abundância de morcegos frugívoros, consumo de frutas e dispersão de sementes durante as diferentes estações de frutificação em floresta madura e em sucessão no Parque Nacional de Manú, Peru. A abundância de morcegos, segundo indica a captura com redes, foi similar em floresta madura e em sucessão somente durante o tempo em que a *Cecropia*, uma espécie muito abundante em floresta em sucessão, estava frutificando. Durante o resto do ano, os morcegos frugívoros do dossel foram significativamente mais abundantes que na floresta madura, onde se alimentam de fígados (*Ficus* spp.), *Dipteryx alata* (Leguminosae) e *Clarisia biflora* (Moraceae). Os fígados, um recurso muito abundante durante a primeira metade do ano, dominaram a dieta dos morcegos durante este tempo, enquanto que *D. alata* e *C. biflora*, duas espécies de sementes comparativamente grandes, foram os alimentos importantes durante a segunda metade do ano. Sem dúvida existem diferenças na abundância e fenologia dos frutos em diferentes anos. Hipotetiza-se sobre o grau em que estas mudanças afetariam os padrões de movimento, uso de hábitat e consumo de frutas por morcegos, assim como os efeitos sobre os padrões de disseminação de sementes entre hábitats durante a mesma estação e no mesmo hábitat em diferentes anos.

PALAVRAS-CHAVE: *Artibeus* spp., dispersão de sementes, fenologia de frutos, frugivorismo, morcegos de dossel, padrões de movimento, Peru

***VIDA SILVESTRE NEOTROPICAL* 5(2):110-119**

Availability of fruits in the tropics can be quite variable in both space (Denslow *et al.* 1986, Levey 1988, Terborgh 1983) and time (Foster 1982, Smythe 1970, Wheelwright 1986) compared with availability of other food resources consumed by vertebrates (Fleming 1992, Martin and Karr 1986). Given such spatial and temporal variation in fruit resources, together with the fact that frugivorous vertebrates differ markedly in morphology, behavior, and degree of frugivory, it is not surprising that frugivore populations are often reported to be extremely dynamic (Loiselle and Blake 1993, Terborgh 1983). The differential response of frugivorous vertebrates to changing resource availability may have important consequences for seed dispersal and thus, may potentially affect the reproductive success of plants.

Bats differ from most birds and all primates in that their morphology restricts the number of fruits that can be eaten during a single visit to a fruiting tree. A bat picks a fruit while in flight and carries it to a roost site to eat (Bonaccorso and Gush 1987). In general, bats may dissiminate seeds over a wider area than do the more sedentary birds

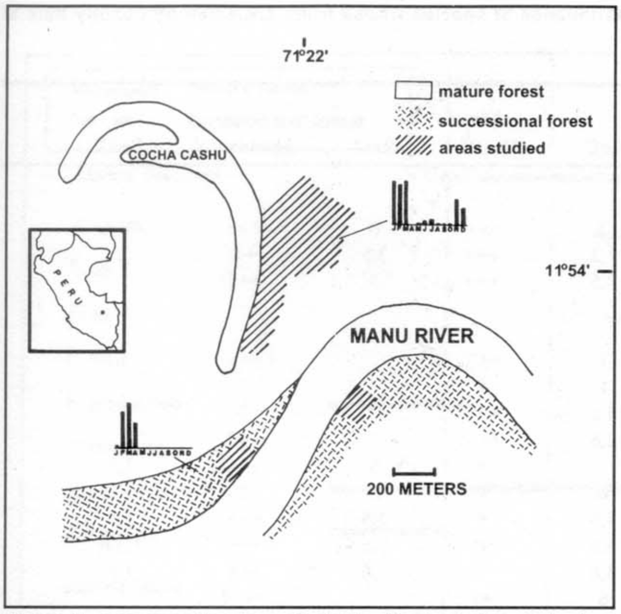

Figure 1. Diagramatic view of study site including extent of mature and successional forest in the Cocha Cashu area. Bar graphs show relative availability of fruits consumed by frugivorous vertebrates by month in each habitat (based on Janson and Emmons 1990.)

and primates (August 1981, Estrada *et al.* 1984, Fleming *et al.* 1985, Janzen *et al.* 1976, Thomas 1988). The fact that bats rely on fewer fruiting species and tend to visit only a few trees in any night likely results in daily and seasonal patterns of foraging that differ from those of birds in the same forest. Yet, despite differences in fruit foraging between bats and other vertebrate frugivores, few studies have determined how bats as obligate frugivores respond to seasonal changes in fruit abundance (see Dinerstein 1986 and Handley *et al.* 1991 for discussions of the effects of variation in fruit abundance on bat reproductive patterns).

Here I describe seasonal variation in fruit consumption and seed dispersal by the three most abundant species of tropical, canopy frugivorous bats, *Artibeus jamaicensis*, *A. obscurus* and *A. lituratus*, in two adjacent forest types at Cocha Cashu, Perú. I provide an analysis of the influence of spatio-temporal changes in fruit availability on these species. I address the following questions: a) what species of fruits are available for bats in two adjacent, different-aged forests? b) does presence or absence of specific fruits in a habitat influence *Artibeus* bat abundance in that habitat? c) what is the seasonal pattern of fruit use by *Artibeus* bats? and d) do bats disperse seeds from one forest habitat to another?

METHODS

Study Site

The study was conducted at the Cocha Cashu Biological Station (11°54'S, 71°22'W, elev. 350 m) in Manu National Park, Department of Madre de Dios, Peru. Mean annual temperatures at the study site range from 23-24°C. Annual precipitation is about 2000 mm. Rainfall is concentrated from November to May with a total of 100 mm during the dry season. More complete descriptions of the area and its ecology can be found in Terborgh (1983, 1990).

The Manu River is a meander river. In the vicinity of Cocha Cashu, during the rainy season, meander loops can erode as much as 25 m of riverbank from the shore, while depositing silt to form an equivalent amount of new land on the opposite shore. Primary succession on the newly created ground results in a series of relatively distinct vegetation zones. Each zone has a different physiognomy and is dominated by a different species (Gentry and Terborgh 1990).

Successional zones in the vicinity of the station, from younger to older, are dominated by *Tessaria integrifolia* (Compositae), *Gynerium sagitatum* (Gramineae), *Cecropia membranacea* (Moraceae), and *Ficus-Cedrela* (Moraceae and Meliaceae), respectively (Foster 1990). Mature forest in the area is dominated by *Otoba parviflora* with *Dipteryx alata* as the most prominent emergent *(A. Gentry*, pers. comm.) and is reported as a pre-climax forest (Gentry and Terborgh 1990). Janson and Emmons (1990) call this area a *Dipteryx-Quararibea* association. I studied canopy frugivorous bats in successional forests in the *Gynerium* and *Cecropia* zones and in mature forest (Fig. 1).

Fruit Phenology

The phenologies of fruit species that are important for canopy bats in the two habitats (M. Romo, unpubl. data) are listed in Table 1. I used these phenological data plus non-quantitative personal observations to describe spatial and temporal availability of fruit species for canopy bats in the forest zones studied. Availability of these major fruit resources was used to define several, important fruiting periods.

Bat Capture

I mist-netted bats in mature and successional forests during the late rainy season (14 Mar.-11 Apr. 1989) and dry season (29 Sep.-9 Nov. 1989; 21 Jun.-15 Oct. 1991). Total sampling efforts in mature and successional forest were nearly equivalent with 1740 and 1548 mist-net hrs, respectively (1 mist-net-hour = one net open for 1 hr). I opened from six to 10 mist nets each night for 5 to 6 hrs beginning

Table 1. Fruiting season, relative tree density, and relative fruit abundance of species whose fruits are eaten by canopy bats at Cocha Cashu Biological Station, Perú.

Species (Family)	Fruiting season	Ref.[a]	Tree Density[b]	Ref.[a]	Fruit Abundance[b]	Ref.[a]
Successional Forest						
Cecropia membranacea (Moraceae)	Jan-May	2	+++	6	+++	4,5,6
Ficus insipida (Moraceae)	Feb-Mar	1,2	+++	3,5	++	3
Clarisia biflora (Moraceae)	Oct-Nov	3,6	+++	5	++?	
Mature forest						
Spondias mombin (Anacardiaceae)	Jan-Feb	1	++?[c]		+++	6
Calophyllum brasiliense (Guttiferae)	Feb-Mar	1	?		?	
Clarisia biflora (Moraceae)	Oct	3,6	++[d]	7	?	
Dipteryx alata (Leguminosae)	May-Aug	2,6	+++[e]	7	++?	
Ficus insipida (Moraceae)	Feb-Mar	1	+	8	+++	1,3
F. trigonata (Moraceae)	Mar-Apr	6	+	3	?	
F. paraensis (Moraceae)	Mar-Jul, Oct	3,6	+	3,6	+++	1,3
F. schultesii (Moraceae)	Jun-Oct	3,6	+[f]	3,6	+++	1,3,6
F. ypsilophlebia (Moraceae)	Mar,Oct-Dec	3,6	+	3,6	+++	1,6
F. sp. 1 (Moraceae)	Jun-Aug	6	+?		+++?	
F. sp. 4 (Moraceae)	Jun	6	+?		+++	1
F. sp. 5 (Moraceae)	Jul-Aug	6	+?		+++	1
F. sp. A (Moraceae)	Jun	6	+?		+++	1
Less important species						
Iriartea deltoidea (Palmae)	Apr-Nov	1,6	+++		+++	
Socratea exorrhiza (Palmae)	Mar-Nov	6	+		+++	
Salacia sp. (Hippocrataceae)	?		?		?	
Marcgravia macrocarpa (Marcgraviaceae)	Oct-Dec	3,6	?		?	
Senna ruiziana (Leguminosae)	Mar-Apr	6				
Inga sp. (Legumonisae)						

[a]=References: 1=Terborgh 1983; 2=Janson and Emmons 1990; 3=C. H. Janson pers. comm; 4=Mitchell 1990 or C. L. Mitchell pers. comm.; 5=Losos 1993; 6=pers. obs; 7=J. Terborgh unpubl. data.

[b]=Tree density and fruit abundance: +=rare, approximately <1 individual/ha; ++=moderate, 1-2 individuals/ha; +++= abundant, 2-3 individuals/ha; ?= unknown. Fruit abundance: ++ = fruits not easily found underneath the tree., +++= fruits abundant underneath the tree.

[c]=3 indiv/ha in plots at Cocha Cashu

[d]=1 indiv/ha; (J. Terborgh unpubl. data);

[e]=3 indiv/ha; (J. Terborgh unpubl. data);

[f]=around 1 to 5 indv/km^2. (J. Terborgh unpubl. data);

at sunset; peak hours for capture of canopy frugivorous bats (Ascorra *et al.*, in press; Bonaccorso 1979). For the most part, nets were not opened during full moon periods because of decreased bat activity ("lunar phobia", Morrison 1978*a*, 1978*b*). Nets were checked every 15 to 30 min; all bats captured were held in cloth bags, usually for 2 to 3 hrs.

Distance between nets ranged from 30 to 100 m. Mist-nets were placed at ground level (to 3.5 m height) and across trails when possible (Palmeirim and Etheridge 1985). Canopy frugivorous bats (as well as understory frugivorous bats), with the exception of *Chiroderma villosum* and *C. trinitatum*, fly mainly at this height, according to capture data from Pakitza, a station located near Cocha Cashu, where 96 and 85% of individual frugivorous bats (canopy and understory) were captured below 10 and below 4 m, respectively (Ascorra *et al.,* in press). Also, for canopy frugivorous bats (Stenoderminae) alone, 94% and 78% of individuals were captured below 10 and 4 m, respectively.

Diet Composition of *Artibeus* Bats

Bat diet composition was determined through seed identification in fecal samples and beneath feeding roosts (deposits). Fecal samples were obtained during bat manipulation in nets or later taken from the cloth holding bags. Passage of seeds through the gut is rapid (15-60 min; Fleming and Heithaus 1981). Collected seeds were identified by comparison with seeds from fruiting trees or in reference collections at the station, or by specialists. Fecal

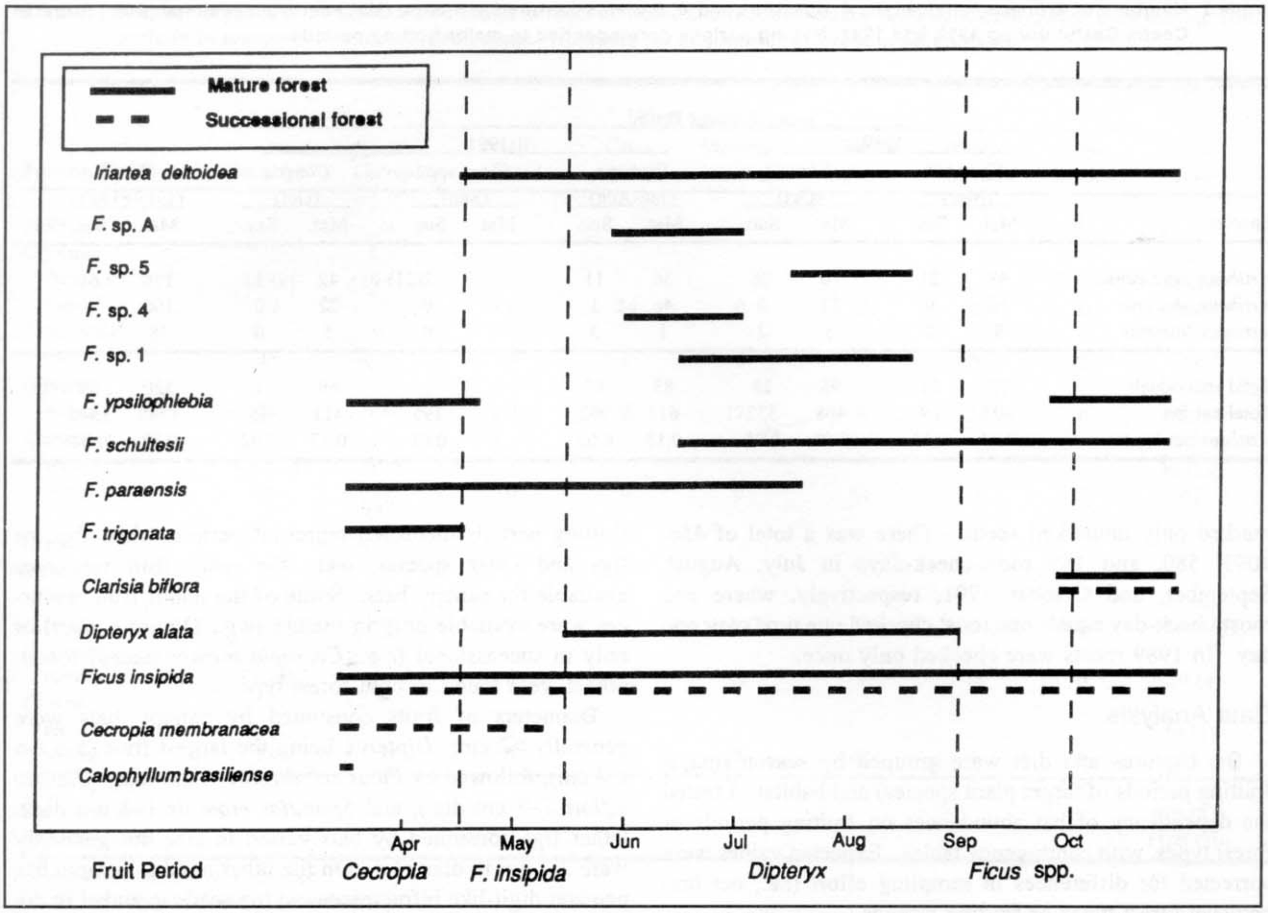

Figure 2. Duration of fruiting periods of major plant species consumed by *Artibeus* spp. in mature and successional forest at Cocha Cashu (March-November only). Names of fruiting periods (separated by vertical lines) given below X-axis. Unidentified *Ficus* species = F. sp. A, 5, 4, and 1.

samples are useful for recording consumption of small-seeded fruits.

On the other hand, detection of large-seeded species in fecal samples is variable requiring the presence of a very characteristic pulp. Therefore, large-seeded species were not considered. For each fecal sample, presence of seeds was used as one record of that fruit in the diet, regardless of the number of seeds contained within that fecal sample.

The proportions of fecal samples containing each small-seeded fruit species were averaged with the proportions (from the total of small-seeded species only) of feeding-roost deposits containing each small-seeded fruit species to provide indices to the use of each small-seeded fruit species. Use of large-seeded species was based on proportional occurrence (number of seeds of each fruit species/total number of seeds of both small- and large-seeded fruit species) in feeding roost deposits only.

I searched for roosts in approximately 20 ha of mature forest during 82 days in 1989 (9, 8, 43, 22 days during "*Cecropia*", "*Ficus insipida*", "*Dipteryx*" and "*Clarisia*" fruiting periods, respectively; see results for description of fruiting periods) and 85 days in 1991 (58, 15 and 12 days during "*Dipteryx*", "*Ficus* spp." and "*Clarisia*" periods). I searched 3.5 ha of successional forest where the presence of roosts was notoriously lower, for 50 days in 1991 (32, 11 and 7 days during "*Dipteryx*", "*Ficus* spp." and "*Clarisia*" periods, respectively).

Feeding roost deposits with fresh seeds were marked with flagging. The numbers and species of seeds below feeding roosts were recorded. Fecal samples containing fig seeds and found underneath feeding roosts were considered to represent one fruit unless fruit peduncles were found with the feces. In that case, each peduncle was counted as a separate fruit. To prevent double counting of seeds at a feeding roost, I marked all large seeds with indelible ink (nigrosin). On subsequent visits, I counted, recorded, and

Table 2. Numbers of *Artibeus jamaicensis*, *A. obscurus* and *A. lituratus* captured in mature (Mat.) and successional (Suc.) forest at Cocha Cashu during 1989 and 1991. Netting periods corresponded to major fruiting periods.

	Fruiting Period											
	1989				1991							
	Cecropia (Mar)		*Clarisia* (Oct)		*Dipteryx* (Jun-Aug)		*Ficus* spp. (Sep)		*Clarisia* (Oct)		Total (1989+1991)	
Species	Mat.	Suc.	Mat.	Suc.	Mat.	Suc.	Mat.	Suc.	Mat.	Suc.	Mat.	Suc.
Artibeus jamaicensis	48	21	70	26	36	11	-	2	42	1	196	61
Artibeus obscurus	16	0	22	0	46	1	-	0	22	0	106	1
Artibeus lituratus	9	2	3	2	1	3	-	0	5	0	18	7
Total individuals	73	23	95	28	83	15	-	2	69	1	320	69
Total net hrs	303	69	408	337	617	902	-	195	412	45	1740	1548
Artibeus/net-hr	0.24	0.33	0.23	0.08	0.13	0.02	-	0.01	0.17	0.02	0.18	0.04

marked only unmarked seeds. There was a total of 456, 1093, 580, and 189 roost-check-days in July, August, September, and October 1991, respectively, where one roost-check-day equals one roost checked one time over one day. In 1989 roosts were checked only once.

Data Analysis

Bat captures and diet were grouped by season (major fruiting periods of target plant species) and habitat. I tested the dependency of bat abundances on fruiting periods or forest types, with contingency tables. Expected values were corrected for differences in sampling effort (*i.e.*, net hrs) between forest types or fruiting periods.

Considering that small- and large-seeded species can be recovered from feeding roost deposits, but not from fecal samples, I examined the potential bias of sampling methodologies used to characterize diets. I compared distributions of fruit records (in each fruiting period) between roost data alone and roost data combined with fecal data, via contingency tables.

RESULTS

Fruit Phenology and Fruit Characteristics

Fruit species used by canopy bats showed marked seasonal differences in fruiting phenology (Table 1). I defined the following important fruiting periods: "*Cecropia*" (March-April), "*Ficus insipida*" (May), "*Dipteryx*" (June-August), "*Ficus*" spp. (September), and "*Clarisia*" periods (October) (Fig. 2). Each period was characterized by different species and abundances of food resources. Fruits of some fig species were available year-round, providing a continuous fruit resource for bats. Nevertheless, figs were more abundant during the rainy season, because *Ficus insipida*, a common tree in late-successional forest, fruits mainly during this time. The particular fruiting periods identified represent periods when figs, or figs and other species, were the main fruit resources available for canopy bats. Some of the major fruit resources were available only in mature (*e.g.*, *Dipteryx alata*) or only in successional (*e.g.*, *Cecropia membranacea*) forest; others were found in both forest types.

Diameters of fruits consumed by canopy bats were generally >2 cm; *Dipteryx* being the largest fruit (5-6 cm x 4 cm), followed by *Ficus schultesii* (~4 cm dia.), *Clarisia biflora* (~3 cm dia.), and *Spondias mombin* (~3 cm dia.). Other figs consumed by bats varied in size but generally were 2-3 cm in diameter. On the other hand, *Cecropia* has pendant digit-like infructescenses; the seeds included in the soft pulp.

Canopy Bat Abundance in Mature and Successional Forest

A total of 389 *Artibeus jamaicensis*, *A. obscurus*, and *A. lituratus* was captured during this study. *Artibeus* bats generally were a more common component of the total bats captured in any fruiting period in mature forest (39-65%) than in successional forest (18-44%), excluding October when only one *Artibeus* from a total of two bats was captured (Table 2). *Artibeus jamaicensis* and *A. obscurus* comprised from 80 to 92% of the canopy frugivore bats I captured in mature forest at different fruiting periods. In successional forest, *A. jamaicensis* alone comprised from 63 to 84% of the canopy frugivorous bats captured. *Artibeus obscurus* rarely occurred in successional forest; only 1 of 107 individuals captured (as compared to 61 of 257 *A. jamaicensis*) was captured there (Table 2). *Artibeus liturartus* was, in general, rare. It comprised only 1 to 11% and 0 to 16% of the canopy frugivore fauna captured in any fruiting period in mature and successional forests, respectively. Therefore, much of the following discussion about canopy bats in mature forest concerns only *A. jamaicensis*

Table 3 . Number of records of fruit species found in fecal samples and feeding roosts used by *Artibeus* spp. bats during fruiting periods in mature and successional forest. Numbers for successional forest in parenthesis.

	Fruit Species Found								
Fruiting Period	*Ficus* spp.	*Cecropia*	small-seeded	*Calophyllum*	*Dipteryx micrantha*	*Clarisia biflora*	*Iriartea, Socratea*	large-seeded	Total
1989									
Cecropia									
feces[a]	22 (2)	10 (12)	2						34 (14)
roosts[b]	30	1	0	24	0	2	7	0	64
F. insipida									
roosts	35	0	0	1	0	0	5	7	48
Dipteryx									
roosts	29	0	0	0	172	0	22	0	223
Clarisia									
feces	28 (11)	1 (1)	1						30 (12)
roosts	7	0	0	0	0	51	3	1	62
1991									
Dipteryx									
feces	25 (6)	0	2						27 (6)
roosts	56 (8)	0	0	0	450 (7)	0	5	0	511 (15)
Ficus spp.									
roosts	27 (4)	0	0	0	19	107	16	0	169 (4)
Clarisia									
feces	19 (1)	0	0						19 (1)
roosts	13	0	0	0	2	67	1	0	83
Total in feces									110 (33)
Total in roosts									1160 (19)

[a] only small-seeded species considered

[b] small- and large-seeded species considered

and *A. obscurus*.

Based on sampling effort, *Artibeus* bats were captured in equal proportions in successional and mature forest only when fruits consumed by bats were readily available in successional forest (*i.e.*, "*Cecropia*" 89) (X^2=1.8, df=1, P<0.50). During other fruiting periods, significantly more frugivorous bats were captured in mature forest than in successional forest ("*Clarisia*" 89: X^2=25.1, df=1, P<0.001, "*Dipteryx*" 91: X^2=82.94, df=1, P<0.001, "*Clarisia*" 91: Fisher Exact Test, P<0.01).

In mature forest, similar numbers of bats were captured in different fruiting periods in 1989 (X^2=0.04, df=1, P<0.90; *i.e.*, "*Cecropia*" and "*Clarisia*" fruiting periods) and 1991 (X^2=1.8, df=1, P<0.50; *i.e.*, "*Dipteryx*" and "*Clarisia*" fruiting periods). In contrast, in successional forest the distribution of bats captured between seasons in 1989 was significantly different (X^2=28.55, df=1, P<0.001; when a "*Cecropia*" fruiting period was included), but not in 1991 (when a "*Cecropia*" fruiting period was not included, Fisher Exact Test, P>0.25). One should keep in mind that different fruiting periods were being compared in 1989 ("*Cecropia*" and "*Clarisia*" fruiting periods) and 1991 ("*Dipteryx*", "*Ficus*", and "*Clarisia*" fruiting periods).

Fruit Use by Canopy Bats

Fecal samples containing small seeds were obtained from 143 (36.7%) captured *Artibeus* bats (Table 3). Of these, 110 and 33 fecal samples were obtained from bats netted in mature and in successional forest, respectively. The percentages of fecal samples containing small seeds varied between fruiting periods, with the highest percentage being recorded during the *Cecropia* 89 fruiting period (46% and 61% in mature and successional forest, respectively) and the lowest during *Clarisia* 91 (27.5%) and *Dipteryx* 91 (32.7%) fruiting periods in mature forest. Fig seeds were the most common item found in bat feces, except during the *Cecropia* 89 period in successional forest, when *Cecropia* seeds predominated.

A total of 1179 records of eaten fruits were recovered from feeding roost-checks of 455 different roosts during 1989 and 1991 (Table 3). Few feeding roosts were found in successional forest during 1991 (14 roosts) despite 50

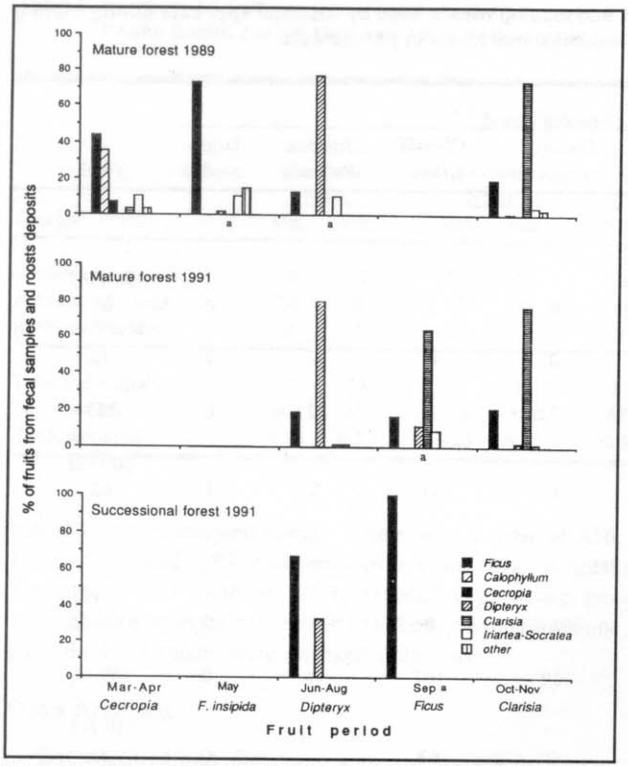

Figure 3. Percentages of fruit species (fecal samples and feeding roost data combined) consumed by *Artibeus* spp. bats by fruiting period in mature and successional forest. The letter "a"=fruiting periods where fecal data not available, thus, only roost data are represented.

days of searching between June and October.

Large-seeded species predominated among seeds deposited underneath feeding roosts. Species-specific feeding roosts of canopy frugivorous bats could not be distinguished. Deposits beneath most (91%) roosts in 1991, however, at some point contained big (4-7 cm) *Dipteryx* seeds, which can be handled only by the large canopy frugivores, I studied. Deposits under other feeding roosts contained *Clarisa biflora*, large-fruited *Ficus* spp., *Iriatea*, or *Socratea*; species consumed also by large canopy frugivorous bats. I found only three feeding roosts containing small (2-3 cm long) *Dipteryx* seeds, and presumably from small canopy frugivorous bats.

A comparison between: a) feeding roost data alone with b) the combination of feeding roost data and fecal data, of the distributions of major fruit items (both small- and large-seeded species) in mature forest, by major fruiting periods showed no evidence for sampling bias ("*Cecropia*" 89: X^2=5.2, df=5, P<0.50; "*Clarisia*" 89: X^2=2.53, df=2, P<0.50; "*Dipteryx*" 91: X^2=5.64, df=3, P<0.50; "*Clarisia*" 91: X^2=4.03, df=3, P<0.50).

Figs, a resource available year-round, dominated the diet during the first half of the year, whereas *Dipteryx* and *Clarisia* were more important during the latter half (Fig. 3). Comparison of fig records (from roost and fecal data combined) among fruiting periods in 1989 revealed significant differences in fig use (relative to other fruit resources) through time (X^2=64.4, df=3, P<0.001; Fig. 3). When fruiting periods in the first and second parts of the year were compared separately, significant differences in fig use were found for periods in the first part ("*Cecropia*" and "*F. insipida*" 89: X^2=4.26, df=1, P<0.05) but not for fruiting periods in the second part ("*Dipteryx*" and "*Clarisia*" 89: X^2=1.33, df=1, P<0.50). Similarly, no significant difference was found in proportional use of figs among "*Dipteryx*", "*Ficus* spp." and "*Clarisia*" fruiting periods in 1991 (X^2=0.75, df=2, P<0.90).

Seed Movement Between Forest Types

The movement of seeds by canopy bats from habitats where adult plants occur to "new" habitats lacking adults was common during the "*Cecropia*" period when bats were regularly encountered in both mature and successional forests. During this period, *Cecropia* seeds were regularly disseminated into mature forest; 10 of 34 fecal samples (29%) collected from bats captured in mature forest contained *Cecropia* seeds. In addition, some *Ficus* seeds from mature forest were disseminated into successional forest (2 of 14 fecal samples). Seeds recovered from feces looked similar to those recovered from *Cecropia membranacea* trees in successional forest, although seeds from other *Cecropia* species from mature forest are not known.

During other fruiting periods, dissemination of seeds by bats appeared to be concentrated in mature forest (as were the bat captures), although some large seeds of *Dipteryx*, a mature forest tree, were recovered under roosts in successional forest (Fig. 3).

DISCUSSION

The most common species of canopy bat in Manu, as in almost any part of lowland neotropics, is *A. jamaicensis* (Bonaccorso and Humphrey 1984, Fenton *et al.* 1992, Fleming 1986, Fleming *et al.* 1972, Handley *et al.* 1991, Wilson 1989). However, I found that *Artibeus* bats were regularly captured in successional habitats only when *Cecropia* fruits were available there. This seasonal and limited use of successional habitats is indicated by low numbers of both captures and roosts found outside the "*Cecropia*" fruiting period. Canopy frugivorous bats frequented mature forest during other fruiting periods where they were found to feed regularly on *Ficus*, *Dipteryx*, and *Clarisia* fruits. These data demonstrate that bats, like other frugivorous vertebrate taxa, move locally to track fruit resources (Levey 1988, Loiselle and Blake 1991, Terborgh 1983). The responses of different bat species to fruit occurrence, however, appeared to differ. For example *A. obscurus*, was never found in successional forest (even when *Cecropia* was fruiting), whereas numbers of *A. jamaicensis* increased in this habitat during the same period.

It is important to remember that these results reflect responses to particular combinations of plant species and densities occurring in Cocha Cashu during the study period. Also, the study was made at seasonal periods, not continuously year-round, so the conclusions are the interpretations of patterns during this period. Yearly differences in fruit abundance and phenology undoubtedly occur and are expected to result in different patterns of bat activity, fruit consumption, and seed dispersal among years. For example, in 1989, Losos (1993) found significant bat activity in successional forest (indicated by the number of seeds dispersed by bats found in seed traps) during the "*Dipteryx*" fruiting period, a pattern not observed in 1991.

Yearly differences in bat activity and consequently seed dispersal may reflect differences in the abundance of fruits with high caloric value among years. For example the crop of *Dipteryx alata* was unusually large in 1991 compared with previous years (J. Terborgh, pers. comm.). This increased availability of nutritious fruits (*i.e.*, *Dipteryx* fruit pulp contains: 96±16 cal/100 g of wet weight, unpubl.data) may have accounted for the concentration of canopy bats in mature forest and their absence from successional forest in 1991. In 1989, however, when *Dipteryx* fruits were less abundant, *Artibeus* appeared to concentrate on *Ficus* (*F. insipida* especially) and consequently, used successional forest more often for nearby feeding roosts.

Dissemination of seeds into new habitats may be crucial for regeneration of some plant species (*e.g.*, pioneer plants, *cf.* Howe and Smallwood 1982, or *Dipteryx*, see Foster 1990). In several tropical forests, bats have been recognized as important agents for moving seeds across habitat types and/or long distances (*e.g.*, Charles-Dominique 1986, Fleming and Heithaus 1981, Gorchov *et al.* 1993, Nepstad *et al.* 1990, Vazquéz-Yañez *et al.* 1975). *Cecropia* trees are rare in mature forest at Cocha Cashu. Consequently, it is highly likely that the *Cecropia* seeds found in the feces in mature forest came from the dense stand of individuals fruiting in the successional forest. In this study, bats dispersed seeds across habitats, carrying *Cecropia* seeds to mature forest and forest seeds (*Dipteryx* and *Ficus*) to successional forest (see Table 3).

Finally, it is important to note that the sampling methods used to characterize bat diet (*e.g.*, seeds collected from roost deposits or from fecal samples) may critically influence how we interpret and understand patterns of food preference. In particular, importance of large-seeded species in canopy bat diet is greatly underestimated when using fecal data alone. In contrast, feeding roost-deposit data record both large- and small-seeded fruit species, but likely underestimate small-seeded species, as these seeds may be defecated in flight, or under the next tree visited. However, my results suggest that roost records alone should be adequate to characterize the diets of canopy bats at least in habitats were they feed upon small- and large-seeded fruits, as in mature forest at Cocha Cashu. Although the small seeds of *Cecropia*, from the successional forest, were underepresented in roost deposits in mature forest, the difference in the distribution of major fruit items between roost data alone and roost and fecal data combined was not significant. Nevertheless, data from roost deposits may not adequately characterize the fruit diet of bats if the bats consume a great proportion of their diet from resources occurring in a different forest from the one in which their feeding roosts are located. Therefore, use of both fecal and roost data is necessary for understanding seasonal patterns of food consumption.

ACKNOWLEDGMENTS

I wish to thank Bette Loiselle for her support during all stages of manuscript preparation. I am grateful to World Wildlife Fund for financial support. I thank John Terborgh for his financial and logistic support through my field seasons at Cocha Cashu. I also thank Victoria Sork, Al Gentry, and Robin Foster for their suggestions. Charles Janson kindly provided me with unpublished data. My special thanks to Liz Losos, a great field companion, and to Alexi Herrera and Ricardo Sánchez for untiring help during days and nights in the field. Enrique Ortiz, Willy Silva, César Flores, Percy Nuñez, and many other volunteers also assisted with field work. Finally, I thank the Dirección General Forestal y de Fauna of Perú for permission to carry out research in Manu National Park.

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Associate Editor: Mercedes Foster
Received: January 25, 1995
Accepted: May 13, 1996