Differential habitat use and reproductive patterns of frugivorous bats in tropical dry forest of northwestern Costa Rica

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Abstract: To determine if frugivorous bats in tropical dry forest differentially use a particular habitat and if this use is related to their reproductive patterns, I monitored populations from one site from January 1994 to January 1997 in Parque Nacional Palo Verde in northwestern Costa Rica. Abundance, reproductive condition, sex ratio, age-classes, and recapture data were compared across seasons and years. During 56 nights of sampling, 13 species of frugivores and 5 nectarivores were captured (N = 998). *Carollia perspicillata*, *Artibeus jamaicensis*, and *Sturnira lilium* were significantly more abundant in 1994 than in 1995 or 1996. *Carollia perspicillata* and *A. jamaicensis* were captured year-round, but there were peaks of abundance in the dry season and the middle of the rainy season. Sixteen percent of 244 adult female *C. perspicillata* and 20% of 87 *A. jamaicensis* were reproductive, principally in February through June. Forty-three percent of 28 adult female *S. lilium* were reproductive from February to June and in October and December. Fifty-four percent of 26 adult female *Centurio senex* were reproductive between December 1995 and February 1996. Few subadults were captured at this site. Sex ratios were significantly different across seasons for *C. perspicillata* and *A. jamaicensis*. Seventy-three *C. perspicillata* were recaptured and 25 (34%) of these were recaptured after more than 4 months. The results of this study indicate that the abundance of some tropical frugivorous bats varies between years and (or) over seasons at a particular site within tropical dry forest.

Résumé : Pour déterminer si les chauves-souris frugivores de la forêt tropicale sèche utilisent leur habitat particulier de diverses façons et si cette utilisation est reliée à leurs patterns de reproduction, j'ai suivi les populations de chauves-souris, de janvier 1994 à janvier 1997, à un site dans le parc national de Palo Verde, dans le nord-ouest du Costa Rica. L'abondance, la condition reproductrice, le rapport mâles : femelles, les classes d'âge et les données de recapture ont été comparés d'une saison à l'autre et d'une année à l'autre. Au cours de 56 nuits d'échantillonnage, 13 espèces de chauves-souris frugivores et 5 espèces de chauves-souris nectarivores ont été capturées (N = 998). En 1994, *Carollia perspicillata*, *Artibeus jamaicensis* et *Sturnira lilium* ont été significativement plus abondants qu'en 1995 ou 1996. *Carollia perspicillata* et *A. jamaicensis* ont été capturés pendant toute l'année, mais leur abondance était maximale au cours de la saison sèche et au milieu de la saison des pluies. Seize pour cent des 244 femelles adultes de *C. perspicillata* et 20 % des 87 femelles adultes d'*A. jamaicensis* étaient en état de se reproduire, surtout de février à la fin de juin. Quarante-trois pour cent des 28 femelles de *S. lilium* se sont reproduites entre février et juin et entre octobre et décembre. Cinquante-quatre pour cent des 26 femelles adultes de *Centurio senex* se sont reproduites de décembre 1995 à février 1996. Peu de subadultes ont été capturés à cet endroit. Les rapports mâles : femelles étaient significativement différents d'une saison à l'autre chez *C. perspicillata* et *A. jamaicensis*. Soixante-treize des *C. perspicillata* ont été recapturés, 25 (34 %) d'entre eux après plus de 4 mois. Les résultats de cette étude indiquent que l'abondance de certaines chauves-souris tropicales frugivores varie d'une année à l'autre et (ou) d'une saison à l'autre à un site donné dans la forêt tropicale sèche.

[Traduit par la Rédaction]

Introduction

The destruction of tropical dry forest in the Neotropics (Janzen 1988; Maass 1995; Quesada and Stoner 2002) and the resulting fragmentation of habitats threaten movement patterns of many terrestrial and arboreal vertebrates (Fenton et al. 1992; Greenberg 1996; Guindon 1996; Laurance et al. 1997; Stoner and Timm 2002). Furthermore, several studies have indicated that some species of bats are sensitive to habitat disturbance (Fenton et al. 1992; Law et al. 1999; Medellín et al. 2000; Schulze et al. 2000). Frugivorous and nectarivorous bats play an essential role in the maintenance and regeneration of Neotropical forests through seed dispersal and pollination (Heithaus et al. 1974, 1975; Howell 1979; Morrison 1978; Uhl et al. 1981; Hopkins 1984; Charles-Dominique 1986; Fleming 1988; Helverson 1993; Valiente-Banuet et al. 1996; Vieira and Carvalho-Okano 1996). It is important to identify differential habitat use that may indicate changing habits over seasons or through years if efforts to conserve both the fauna and flora within these areas are to succeed.

Direct evidence of differential habitat use can be obtained

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by tracking and recapture studies. Size constrains the use of radio-tracking on bats, since only a 0.5-g transmitter may be used on a 10-g bat (Aldridge and Brigham 1988). Mark–recapture studies involve a large investment in sampling because recapture rates for bats are generally low (Fleming 1988). Indirect evidence of differential habitat use may include seasonal changes in abundance or sex ratio (if only one sex is moving), or absence of individuals in reproductive condition or particular age-classes from the population during parts of the year (indicating that reproduction occurs in another area).

The principal objective of this study was to determine if frugivorous bats in tropical dry forest differentially use one site and if this use is related to their reproductive patterns. To address this question I determined the relative seasonal abundance, reproductive condition and age-classes, and seasonal changes in sex ratio of the most common species of frugivorous and nectarivorous bats captured at one study site within the dry forest. I predicted that bat abundance and reproductive activity would be greatest at the beginning of the dry season and in the middle of the rainy season, corresponding to previously described peak flowering and fruiting periods in the tropical dry forest of this region (Frankie et al. 1974; Fleming 1988). I expected to find equal sex ratios of adults within a species because previous studies had demonstrated that sex ratios of adults of several phyllostomid bats are approximately 1:1 (Silva Taboada 1979; Fleming 1988).

Materials and methods

The study was conducted in the tropical dry forest of Parque Nacional Palo Verde, Guanacaste Province, in northwestern Costa Rica. Palo Verde covers about 20 000 ha and encompasses a variety of habitats, including lowland deciduous forest, upland deciduous forest, riparian forest, seasonal wetland, mangrove habitat, desert habitats associated with limestone cliffs, pastures, and regenerating forests (Tosi 1969; Hartshorn 1983). Rains usually begin in mid-April and continue until mid-December, but the months of January through March are completely dry. Average annual rainfall is 1440 mm and the average temperature is 26°C (Maldonado et al. 1995). Based on rainfall (Maldonado et al. 1995) and fruit and flower availability (Frankie et al. 1974; Fleming 1988), four seasons were recognized during each year: (1) dry season (January–March): no rain, highest peak in fruiting and flowering; (2) early rainy season (April–June): beginning of rains, few species in fruit and flower; (3) mid rainy season (July–September): heavier rains, second peak in fruiting and flowering; and (4) late rainy season (October–December): last rains of the year, lowest availability of fruits and flowers.

Sampling was conducted using mist nets in the area near the Guayacán waterhole, ca. 3 km west of the Hacienda Park Ranger Station (10°20′N, 85°20′W). This natural waterhole is oval and varies in diameter from 4 m during the rainy season to 1 m during the driest months, but apparently has not gone completely dry for more than 25 years. The water runs out of the waterhole and down a cement canal 15 m long and empties into a cement watering trough. As it is one of the few remaining natural sources of fresh water within Parque Nacional Palo Verde, the waterhole attracts numerous mammals from the surrounding area and therefore was the best sampling location within the study area to maximize the number of individuals and species captured. Two large rivers, Río Tempisque and Río Bebedero, border Parque Nacional Palo Verde, but they contain brackish water. The Guayacán waterhole is one of the main sources of fresh water in Palo Verde, not only in the dry season but also in the rainy season, since rainwater is principally absorbed into the limestone soils.

Bats were captured in Japanese mist nets (50/2 denier, 38 mm mesh, 2.6 m wide; Avinet Inc., Dryden, N.Y.) from January 1994 through January 1997. During 1 or 2 nights each month, one 6-, one 9-, and one 12-m net were opened at dusk for approximately 4–6 h, which corresponds to peak foraging times of most phyllostomid bats (Davis and Dixon 1976; LaVal 1970; Fenton and Kunz 1977). The nets were placed in the same general area but never in exactly the same position each time, to avoid bats learning where the nets were (LaVal and Fitch 1977). The 9-m net was placed parallel to the length of the water hole and the other two nets were placed in the forest approximately 50 m on either side of the 9-m net. The time during which the mist nets remained open could not be standardized, as it depended upon the weather conditions (nets were shut during heavy rain). Sampling was carried out on an average of 4 nights per season during all years except the late wet season of 1996, when sampling was not done.

Each individual bat captured was identified to species using a key by Timm and LaVal (1998), and age-class, sex, and reproductive condition were determined. Starting in January of 1995 all adults were marked with permanent plastic numbered collars (modified from Gannon 1993). Age-class (adult or subadult) was distinguished by illuminating the dorsal surface of the extended wing and examining the epiphyseal–diaphyseal fusion of the fourth metacarpal–phalangeal joint on the ventral surface (Anthony 1988). Those with open joints were classified as subadults and those with fused joints as adults. Reproductive condition of females was determined by abdominal palpation and examination of teats (Racey 1988). The following categories were recognized: (*i*) palpably pregnant (this condition was probably only recognized when the gestation period was about half over); (*ii*) lactating; and (*iii*) non-reproductive.

Relative abundance of species was estimated for each night of sampling by multiplying the number of individuals per square metre of net by the number of hours. This relative index of comparison allowed nights with unequal sampling times to be compared over seasons and years. A Kruskal–Wallis test was used to evaluate differences in this index over years and across seasons for the most abundant frugivores and nectarivores (SPSS Inc. 1995). A heterogeneity *G* test was used to determine differences in sex ratio between seasons through years for the most common frugivores (Sokal and Rohlf 1995).

Results

I sampled for 56 nights, for a total of 274 h, 840 net-hours, and 3931 m^2 of net. Sampling effort was approximately equal over seasons through years (N = 16 nights in the dry season: 5 in 1994, 4 in 1995, 6 in 1996, and 1 in 1997; N = 12 nights in the early rainy season: 4 in 1994, 4 in 1995, and 4 in 1996; N = 12 nights in the mid rainy season: 3 in 1994, 4 in 1995, and 5 in 1996; and N = 16 nights in the late rainy season: 8 in 1994 and 8 in 1995). I captured a total of 1249 individuals representing 47 species and 7 families of bats. Of this total, 998 individuals were frugivores (13 species) and nectarivores (5 species). The remaining 251 individuals included aerial insectivores of the families Emballonuridae, Molossidae, Mormoopidae, Natalidae, and Vespertilionidae, gleaning insectivores of the family Phyllostomidae, and fish-eating bats of the family Noctilionidae (for a complete list see Stoner and Timm 2002).

Seven frugivores and one nectarivore accounted for 96.8% of all frugivores and nectarivores captured (Table 1). *Carollia perspicillata* was the most abundant species,

Table 1. The most common species of bats captured at the Guayacán waterhole in Parque Nacional Palo Verde, Costa Rica, during 56 survey nights between January 1994 and January 1997.

	No. of individuals	No. of nights captured	Months of capture[a]
Carollia perspicillata	472	47	1–12
Artibeus jamaicensis	174	40	1–12
Sturnira lilium	111	33	1–12
Artibeus lituratus	65	27	1–2, 6–12
Glossophaga soricina	43	17	1–12
Artibeus phaeotis	39	21	1–2, 6, 9–12
Centurio senex	38	11	1–2, 8, 12
Artibeus watsoni	25	14	1–2, 6, 9–12

[a]January = 1.

accounting for 47.3% of frugivores and nectarivores captured. The second most common frugivore was *Artibeus jamaicensis* (17.4%), followed by *Sturnira lilium* (11.1%), *Artibeus lituratus* (6.5%), *Artibeus phaeotis* (3.9%), *Centurio senex* (3.8%), and *Artibeus watsoni* (2.5%). *Glossophaga soricina* was the only nectarivorous species captured more than once and accounted for 4.3% of frugivores and nectarivores captured. Representative specimens of these species from this locality are deposited at the Museo Nacional de Costa Rica and the Universidad de Costa Rica, San José.

Carollia perspicillata, *A. jamaicensis*, and *S. lilium* were significantly more abundant (estimated as the number of bats per square metre of net multiplied by the number of hours) in 1994 than in 1995 or 1996 (H = 11.9, 7.33, and 11.1, respectively, df = 2, $P < 0.01$; Fig. 1). No significant differences were found between years for *A. lituratus* ($H = 5.34$, df = 2, $P > 0.05$) or *G. soricina* ($H = 5.34$, df = 2, $P > 0.05$). Although they were not compared statistically, owing to the small sample size, the abundance of *A. phaeotis* and *A. watsoni* over years was similar. In contrast, *C. senex* was captured primarily during one period during the 3 years of sampling at this site: 35 of the 38 individuals were captured in December 1995 and January and February 1996.

In spite of the significant variation in abundance over the 3 years of sampling, consistent seasonal differences in abundance were found for three of the most common frugivores across years (Fig. 2). *Carollia perspicillata* was captured year-round, but two peaks of abundance were apparent, one in the dry season and the other in the mid rainy season ($H = 19.43$, df = 3, $P < 0.001$). *Artibeus jamaicensis* showed a similar pattern of abundance, with significant peaks in the dry and mid rainy seasons ($H = 8.32$, df = 3, $P < 0.04$). *Artibeus lituratus* showed significant differences in seasonal abundance, with a peak in the dry season, but in contrast to the other species there was no peak in abundance in the mid rainy season ($H = 14.09$, df = 3, $P < 0.003$). *Sturnira lilium* showed no significant differences in seasonal abundance throughout the year ($H = 3.26$, df = 3, $P > 0.05$), nor did *G. soricina* ($H = 2.42$, df = 3, $P > 0.05$).

Patterns of capture of some of the other frugivorous species also suggest that their abundance varies seasonally at the site sampled (Table 1); however, these were not compared statistically because the sample size was small. During the 3 years of sampling, the majority of *A. phaeotis* and *A. watsoni* were captured in February and June and individuals of these species were never captured in March, April, May, July, or August. The fact that similar patterns were observed during 3 years of sampling suggests that these species are only present seasonally at this site. *Centurio senex* was captured primarily during the late rainy and dry seasons.

Carollia perspicillata showed the lowest percentage of reproductive adult females, with only 16% detectably pregnant or lactating during the 3 years of sampling at this site (N = 244). Pregnant and lactating females of this species were observed from February to June and one pregnant individual was observed in December (Fig. 3*a*). Twenty-one percent of 88 adult female *A. jamaicensis* were detectably pregnant or lactating, the majority being observed from February through June (Fig. 3*b*). Forty-three percent of 28 adult female *S. lilium* were reproductive from February to June and in October and December (Fig. 3*c*). The majority of reproductive female *A. lituratus* (N = 28), *A. phaeotis* (N = 26), *A. watsoni* (N = 9), and *G. soricina* (N = 17) were found in February and June. Fifty-four percent of 26 adult female *C. senex* were reproductive in December 1995 and January and February 1996.

Few subadults of any of the species were captured at this site. The highest percentage was observed for the nectarivore *G. soricina*, with 12% subadults of the 43 individuals captured, observed in March, April, and July. Of 472 *C. perspicillata* captured, only 2.8% were subadults and these were present in May and June. Similarly, for *A. jamaicensis* only 4.4% of 174 captures were subadults, also observed in May and June. Only one subadult was captured for each of *S. lilium*, *A. lituratus*, and *A. phaeotis* and none were recorded for *C. senex* or *A. watsoni*.

Although no significant difference in the total numbers of male and female *C. perspicillata* was found for the entire study ($G_{pooled} = 2.9$, df = 1, $P > 0.05$), there was significant heterogeneity in the sex ratio across seasons throughout each year ($G_{total} = 36.5$, df = 8, $P < 0.005$; $G_{heterogeneity} = 33.5$, df = 7, $P < 0.005$). There were significantly more females during the dry season in 1995, 1996, and 1997, while there were significantly more males at the beginning of the rainy season in 1995 and 1996; sampling was not carried out during the rainy season in 1997 (Fig. 4*a*). The overall sex ratio for *A. jamaicensis* was about 1:1 ($G_{pooled} = 0.54$, df = 1, $P > 0.05$), but this ratio also demonstrated significant heterogeneity across seasons throughout each year ($G_{total} = 28.23$, df = 8, $P < 0.005$; $G_{heterogeneity} = 27.69$, df = 7, $P < 0.005$). Similar to *C. perspicillata*, there were more females in the dry season in 1996 and 1997 and more males at the beginning of the rainy season in 1995; no *A. jamaicensis* were captured at the beginning of the wet season in 1996 (Fig. 4*b*). Sex ratios were not statistically compared for the other species, as sample sizes were to small over seasons through years.

One hundred and thirty-three (13.3%) of the 998 frugivores and nectarivores captured were recaptures of marked individuals. Recaptures of *A. jamaicensis* (3), *A. lituratus* (1), *A. phaeotis* (4), *A. watsoni* (1), *C. perspicillata* (99), *C. senex* (8), and *S. lilium* (17) were made. The number of recaptures per individual ranged from 1 to 5 (2.24 ± 0.55; mean ± SD). Time elapsed between initial marking and recapture ranged between 1 and 27 months (5.47 ± 2.14).

Carollia perspicillata, the most common bat numerically, was also the most common species recaptured. Seventy-

Fig. 1. Relative abundances of the five most common bat species (estimated as the number of bats per square metre of net multiplied by the number of hours) across years in Parque Nacional Palo Verde, Costa Rica. Values are shown as the mean ± SE; an asterisk indicates a significant difference using the Kruskal–Wallis test ($P < 0.01$).

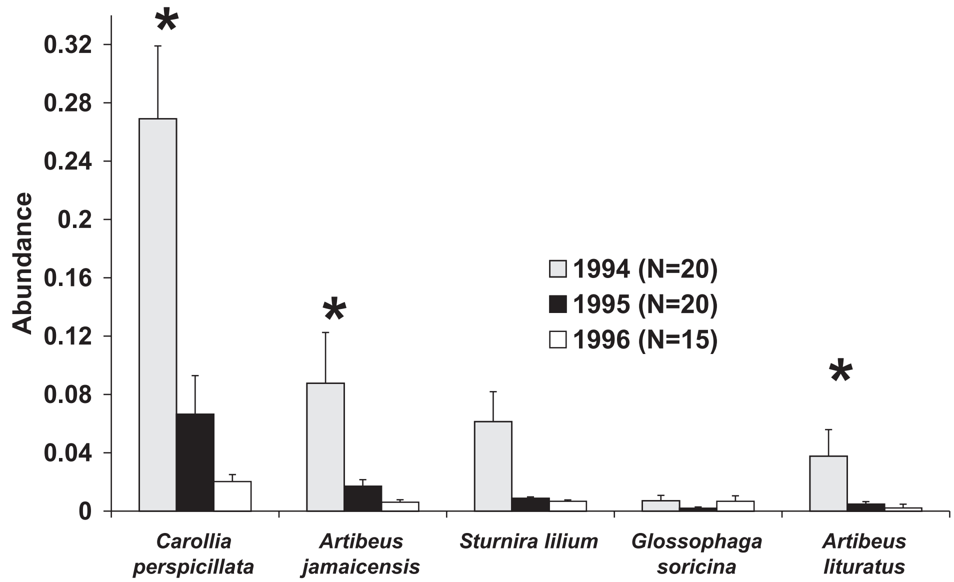
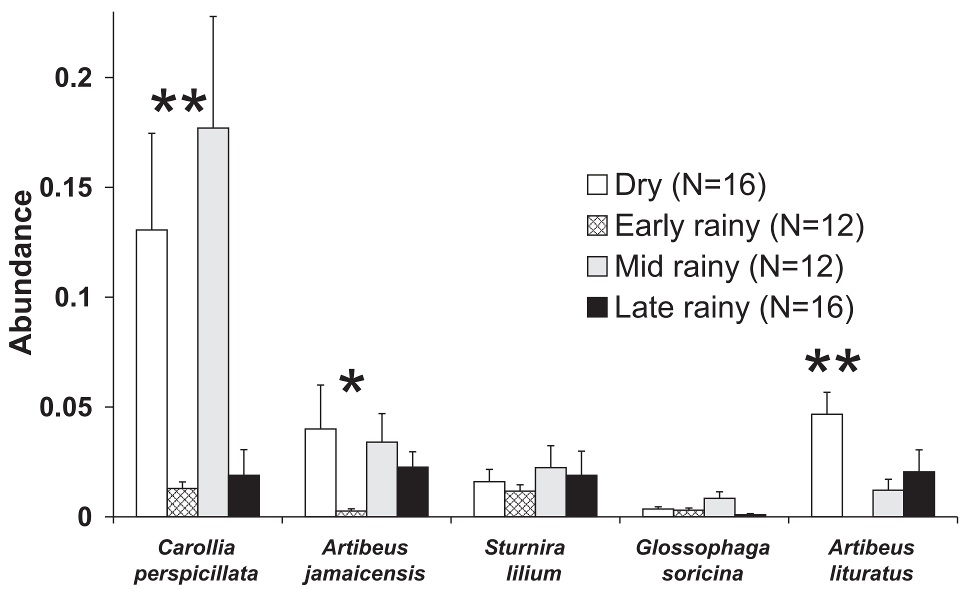


Fig. 2. Relative abundances of the five most common bat species (estimated as the number of bats per square metre of net multiplied by the number of hours) across seasons in Parque Nacional Palo Verde, Costa Rica. Values are shown as the mean ± SE; asterisks indicate significant differences using the Kruskal–Wallis test (*, $P < 0.05$; **, $P < 0.005$).



three individuals were recaptured and 25 (34%) of these were recaptured after more than 4 months (Table 2). Females were never recaptured more than once, while males were recaptured up to 3 times. Recaptures do not indicate the annual reproductive pattern of this species, as no females were found to be lactating or pregnant on more than one occasion.

Discussion

The results of this study indicate that the abundance of some tropical frugivorous bats varies between years (*A. jamaicensis*, *C. perspicillata*, *C. senex*, and *S. lilium*) and (or) over seasons (*A. jamaicensis*, *C. perspicillata*, and *A. lituratus*) at one site within tropical dry forest. As predicted, there was a greater abundance of *C. perspicillata* and *A. jamaicensis* at the beginning of the dry season and the middle of the rainy season, which corresponds to peak production of flowers and fruits of the dry forest in this region (Frankie et al. 1974). This study does not demonstrate whether these frugivores are simply changing their foraging area within the vicinity or are moving into another habitat within the region. In spite of the fact that sampling near water sources has been identified as a potential bias in abundance studies of bats (Findley 1993), it is unlikely that the higher abundance of *A. jamaicensis*, *A. lituratus*, and

Fig. 3. Reproductive condition of adult female *Carollia perspicillata* (*a*), *Artibeus jamaicensis* (*b*), and *Sturnira lilium* (*c*) captured by month in Parque Nacional Palo Verde, Costa Rica.

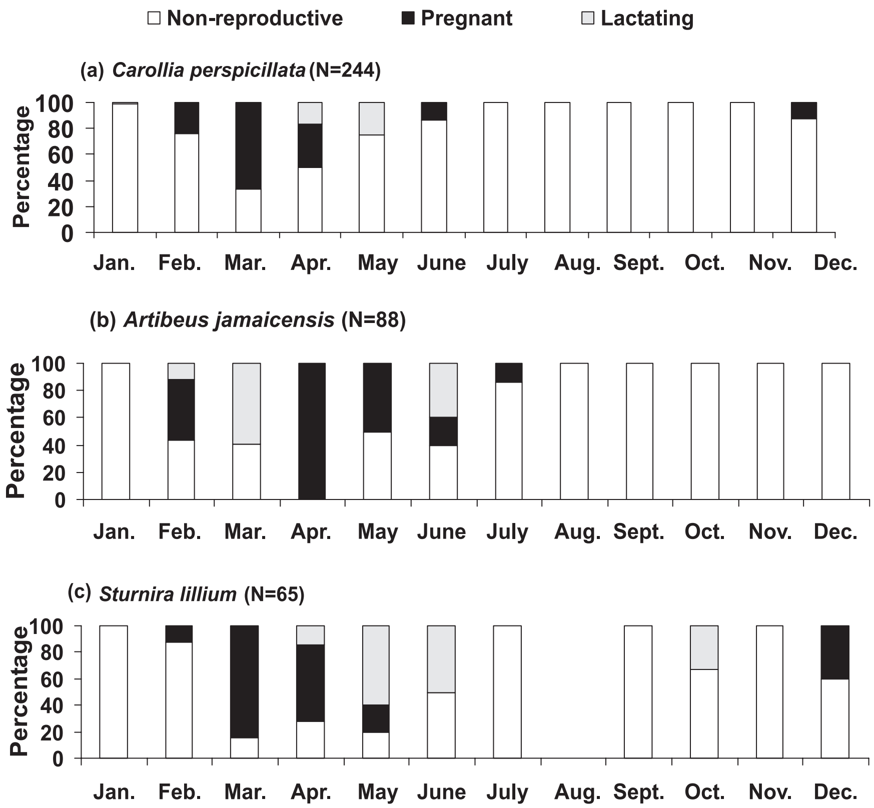


Fig. 4. Percentages of adult male and female *Carollia perspicillata* (N = 459) (*a*) and *Artibeus jamaicensis* (N = 170) (*b*) captured across seasons through years in Parque Nacional Palo Verde, Costa Rica. An asterisk indicates a significant difference in the partitioned G test of heterogeneity for that season (P < 0.05).

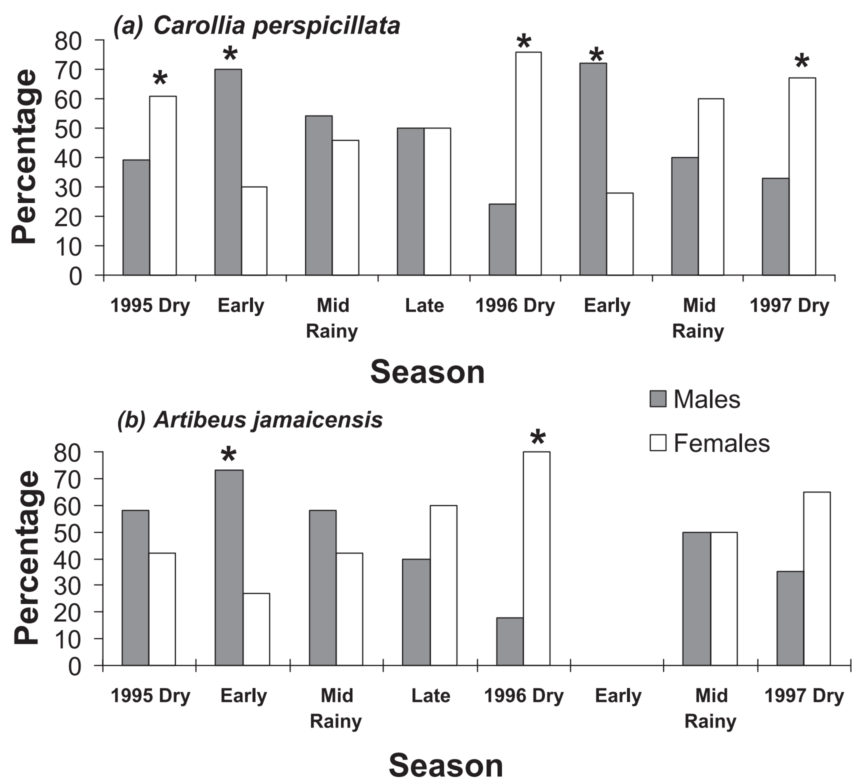


Table 2. Dates of recapture of adult *C. perspicillata* captured more than 4 months apart and reproductive status of females.

Individual ID No.	Sex	Initial capture date[a]	Recapture date[a]
25	Male	Dec. 1994	Feb. 1995, Mar. 1997
11	Male	Jan. 1995	July 1995, June 1996
32	Male	Jan. 1995	Feb. 1995, Jan. 1996
33	Female	Jan. 1995 (N)	Jan. 1996 (N)
42	Male	Jan. 1995	May 1996, June 1996
47	Male	Jan. 1995	Feb. 1995, Jan. 1996, Apr. 1996
119	Male	Jan. 1995	Feb. 1995, Apr. 1995, May 1995
132	Male	Jan. 1995	Feb. 1995, Apr. 1996
146	Male	Jan. 1995	Feb. 1995, Nov. 1995
109	Female	Feb. 1995 (N)	Jan. 1996 (N)
133	Female	Feb. 1995 (N)	Feb. 1996 (N)
146	Male	Jan. 1995	Feb. 1995, Nov. 1995
156	Female	Feb. 1995 (N)	Feb. 1996 (P)
233	Male	Feb. 1995	Jan. 1996
243	Female	Feb. 1995 (P)	Mar. 1996 (N)
262	Female	Feb. 1995 (P)	Mar. 1996 (N)
276	Male	Feb. 1995	Mar. 1997
298	Male	Feb. 1995	Apr. 1996
333	Male	Apr. 1995	Apr. 1996
399	Male	June 1995	Sept. 1995
434	Male	June 1995	Apr. 1996
461	Male	June 1995	Feb. 1996, Apr. 1996
654	Male	Nov. 1995	May 1996
599	Female	Jan. 1996 (N)	Mar. 1997 (P)
689	Female	Jan. 1996 (N)	Apr. 1996 (N)

[a]P, pregnant; L, lactating; N, non-reproductive.

C. perspicillata is strictly related to the waterhole, as these species were significantly more abundant during part of the rainy season as well as in the dry season (Fig. 2).

The low percentage of reproductive adult females, the age structure (few subadults), the difference in sex ratio over seasons, and the recapture data indicate that many individuals are present only seasonally in the area sampled. The pattern of reproduction and age-class structure of *C. perspicillata* and *A. jamaicensis* in the habitat sampled at Palo Verde were different from those reported for these species in other areas. Females of both of these frugivores demonstrated one extended season of reproduction (February–June) in Palo Verde, differing from the bimodal peaks that have been observed for these species in other studies (Fleming 1988; Handley et al. 1991). Reproductive females were not observed in the mid rainy season, contrary to the prediction. Furthermore, in contrast to the low number of subadults observed in May and June at the site sampled within Palo Verde, bimodal peaks in the number of subadults coinciding with the reproductive peaks have been documented for these species in other areas, with as much as 50% of captures representing subadults (Fleming 1988; Handley et al. 1991). The low number of subadults at this site indicates that the majority of pregnant females are giving birth in another area. It appears that the majority of females move from this site before pregnancy is detectable by external palpation, thus accounting for the low percentage of pregnant and lactating females (Figs. 3*a* and 3*b*) as well as the low number of subadults. As predicted, the overall adult sex ratio was 1:1 (Silva Taboada 1979; Fleming 1988); however, the significant heterogeneity of sex ratios over seasons for the two most common frugivores (Figs. 4*a* and 4*b*) suggests that more females are present at this site during the dry season and more males at the beginning of the rainy season. It appears that some of these females give birth in the area, while the majority move to another site at the beginning of the rainy season. Finally, the recapture data for *C. perspicillata* (Table 2) suggest that many females are not at this site year-round, as most recaptures in subsequent years were made during the same month or season as the original capture.

Other species such as *G. soricina* and *S. lilium* were present at the site sampled year-round, as indicated by the comparisons of abundance over seasons (Fig. 2), as well as the presence of reproductive females (Fig. 3*c*). Although the sample size is small, both of these species appear to have a reproductive pattern of bimodal polyestry at Palo Verde, which has been described for these species at other sites (Fleming et al. 1972). Similarly, bimodal polyestry appears to be the pattern for *A. phaeotis* and *A. lituratus* at this site.

During periods of lower resource availability, frugivorous and nectarivorous bats in tropical dry forests may be expected to change habitats within the dry forest to areas with greater resources for purposes of survival or reproduction (Fleming 1988). Although information on latitudinal seasonal movements of bats exists (Barbour and Davis 1969; Cockrum 1991; Fleming et al. 1993; Wilkinson and Fleming

1996; Ceballos et al. 1997), few studies have documented short-distance movements or differential habitat use (i.e., changing habitats within an area). In a study carried out in the tropical dry forest at Santa Rosa National Park, Guanacaste, Costa Rica, Fleming (1988) suggested that *C. perspicillata* might migrate from the area, based on seasonal changes in the sex ratio of captured bats and roost numbers. In the Monteverde region of Costa Rica's Tilaran highlands, Timm and LaVal (2000) reported that five species of frugivorous bats show strong seasonal variation in abundance, which suggests elevational migrations into and out of the area. Similarly, studies in the subtropical forest in the Manantlán Biosphere Reserve, Jalisco-Colima, Mexico (Iñiguez Davalos 1993), and in the tropical dry forest in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico (Stoner 2002), documented seasonal variation in abundance of frugivores and nectarivores, with peaks coinciding with the highest availability of resources.

Many factors likely affect the seasonal and annual changes in abundance, reproduction, age structure, and sex ratio observed in the current study; however, given the importance of frugivorous bats in tropical ecosystems, it is important to identify changes in local abundance which imply that they are moving into new habitats within the dry forest or possibly utilizing migratory corridors that take them to different areas. Two of the most common species in the habitat sampled, *C. perspicillata* and *A. jamaicensis*, are important components of tropical ecosystems (Fleming et al. 1972; Heithaus et al. 1975). Because of the wide distribution and abundance of *C. perspicillata* and its euryphagous tendencies, this species is believed to be an important pollinator and seed disperser for many tropical trees (Fleming 1988). *Artibeus jamaicensis*, the second most abundant bat at Palo Verde, has been described as an important disperser of seeds, especially for many large-fruited species such as some figs (Morrison 1978). Documentation of differential habitat use is the first step in identifying movement patterns of these bats. Future studies should attempt to determine whether these frugivores are simply changing their foraging area within the vicinity or are moving into another habitat within the region.

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