Evidence for Exploitative Competition: Comparative Foraging Behavior and Roosting Ecology of Short-Tailed Fruit Bats (Phyllostomidae)

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ABSTRACT

Chesnut short-tailed bats, Carollia castanea, and Seba's short-tailed bats, C. perspicillata (Phyllostomidae), were radio-tracked (N = 1593 positions) in lowland rain forest at Tiputini Biodiversity Station, Orellana Province, Ecuador. For 11 C. castanea, mean home range was 6.8 ± 2.2 ha, mean core-use area was 1.7 ± 0.8 ha, and mean long axis across home range was 438 ± 106 m. For three C. perspicillata, mean home range was 5.5 ± 1.7 ha, mean core-use area was 1.3 ± 0.6 ha, and mean long axis was 493 ± 172 m. Groups of less than five C. castanea occupied day-roosts in earthen cavities that undercut banks the Tiputini River. Carollia perspicillata used tree hollows and buildings as day-roosts. Interspecific and intraspecific overlap among short-tailed bats occurred in core-use areas associated with clumps of fruiting Piper hispidum (peppers) and Cecropia sciadophylla. Piper hispidum seeds were present in 80 percent of the fecal samples from C. castanea and 56 percent of samples from C. perspicillata. Carollia perspicillata handled pepper fruits significantly faster than C. castanea; however, C. castanea commenced foraging before C. perspicillata emerged from day-roosts. Evidence for exploitative competition between C. castanea and C. perspicillata is suggested by our observations that 95 percent of ripe P. hispidum fruits available at sunset disappear before sunrise (N = 74 marked fruits). Piper hispidum plants produced zero to 12 ripe infructescences per plant each night during peak production. Few ripe infructescences of P. hispidum were available during the dry season; however, ripe infructescences of C. sciadophylla, remained abundant.


Key words: bats; Carollia castanea; Carollia perspicillata; core-use area; day-roost; Ecuador; home range; Piper hispidum; radio-telemetry; rain forest.

THE SEVEN LIVING SPECIES OF SHORT-TAILED BATS recognized in the genus Carollia (Pacheco et al. 2003) all have a strong dietary dependence on fruits of pepper plants in the genus Piper (Piperaceae). Many of the approximately 2000 species of peppers (Gentry 1990) have their seeds dispersed principally by caroline bats (Bonaccorso 1979, Fleming 1981, Thies & Kalko 2004). Short-tailed bats are among the most numerous bats sampled by mist nets at ground level in Central and South America (Bonaccorso 1979, Fleming 1988, Bernard & Fenton 2002), and through seed dispersal these bats strongly influence plant regeneration in forest light gaps (Fleming 1988).

The feeding behavior, social ecology, and movements of Seba's short-tailed bat Carollia perspicillata, a habitat generalist throughout lowland Neotropical forests, have been intensively studied in tropical dry forests (Heithaus & Fleming 1978, Herbst 1986, Williams 1986, Bonaccorso & Gush 1987, Fleming 1988). Tropical dry forests produce few species of zoochorous fruits during the dry season compared to the wet season (Frankie et al. 1974, Herbst 1986). In highly seasonal Santa Rosa National Park, Costa Rica, wet season commuting flights between the day-roost and foraging areas by C. perspicillata averaged 850 m (Fleming 1988) but increased to a mean of 1320 m per night in the dry season. In moist tropical forest of Panama, adult male C. perspicillata, but not females, expanded their home ranges tenfold in the dry season (Thies 1998). Bernard and Fenton (2003) recorded linear movements ≤ 2500 m by C. perspicillata in heavily fragmented forests of Brazil; however, this species and C. breviceps infrequently moved between forest fragments.

The chestnut short-tailed bat Carollia castanea is restricted to mesic lowland forests from Honduras to Bolivia (Koopman 1982), a much smaller geographic range than that of C. perspicillata. Carollia castanea is an extreme feeding specialist with stronger reliance on peppers and especially on species of peppers found in interior forest understory (Bonaccorso 1979, Thies & Kalko 2004). Carollia castanea does not enlarge home range during the dry season on Barro Colorado Island (Thies 1998).

Our present study compares the movements, foraging behavior, and roost selection of C. castanea and C. perspicillata in wet tropical rain forest at the Tiputini Biodiversity Station (TBS), Ecuador. We hypothesized that C. castanea and C. perspicillata differ in spatial and temporal use of the rain forest for roosting and feeding requirements; however, we also expected there to be significant dietary overlap between them. Furthermore, we hypothesized that exploitative competition over the limited numbers of available pepper fruits, a preferred food for both species of Carollia, would be intense at TBS. Using radiotelemetry, we documented patterns of spatial and temporal use including home range, core-use area, commuting distances between day-roosts and foraging patches, fidelity to day roosts, and flight emergence times. We designed feeding
experiments in flight cages to measure handling rates for consumption of fruits. Finally, we examined the habitat and abundance of *Piper hispidum* (Piperaceae), the only common pepper species at the TBS, and determined the standing crop and rates of harvesting of these fruits.

**METHODS**

**STUDY AREA.**—Our study was undertaken late in the wet season and the transition to dry season from 26 October 2002 through 8 January 2003 and during the dry season from 6 March to 10 April 2004 at the TBS. This field station lies at 0°32’ S and 76°26’ W within Yasuni National Park, Orellana Province, Ecuador, and forms a 650 ha research reserve at 300 m elevation. TBS consists primarily of *terra firme* forest with lesser areas of seasonally inundated *varzea* forest underlain by young soils eroded from the Andes Mountains. Annual rainfall is 2500–3000 mm. Although no month typically receives less than 100 mm of rain, March and April tend to receive the least rainfall in the year. The Tiputini River forms the western boundary of TBS and has a channel approximately 40 m wide and 5–10 m deep.

**RADIOTELEMETRY.**—*Carollia castanea* and *C. perspicillata* were captured in 50 denier, 2.5 cm mesh, black mist nets set at ground level. Although, a third species, *C. brevicauda*, occurs at TBS, it was rare at our netting sites but elsewhere is a common cloud forest bat (Dinerstein 1985, Jarrín-V 2001). Captured bats were placed in individual soft cloth bags, and within minutes of capture were transported to the station laboratory. For each bat, body mass, sex, age class, reproductive condition, and length of forearm length were recorded. A radiotransmitter within 1 h of capture and then released at the site for the second time in this study), and *C. castanea* “H” (lactating). Radiotransmitters usually were shed from bats within 7–17 days.

Output from the radiotransmitters was monitored with TRX 2000S tracking receivers (Wildlife Materials, Carbondale, IL, USA) and 3-element Yagi antennas. Tracking stations were established at mapped reference locations usually within 20–100 m of activity centers for each bat. Receivers were moved as necessary to improve reception or to record multiple bearings for triangulation on a stationary bat. Bearings to the nearest degree were taken with KB-14/360 RB compasses (Suunto, Helsinki, Finland) and recorded with time and signal strength. If a bat was flying or at a roost only briefly, position sighted along a single bearing and distance was estimated from signal strength and gain (Law & Lean 1999, Winkelmann et al. 2000, Bernard & Fenton 2003). Relationship of signal strength to distance was experimentally calibrated in the study area at standardized gain settings. Comparisons of triangulation and single-bearing determinations of position were equivalent in accuracy (usually ± 5 m at distances ≤ 180 m). Positions from a single-bearing were used only when the receiver was estimated to be ≤ 180 m from the transmitter and when topographical features that distort radio wave reception, such as deep creek ravines or steeply sloped hills, were avoided. If contact was broken with a moving bat, it usually was re-established within 20 min by walking along the bearing of last contact.

For an individual bat within a given night, a telemetry position was recorded for each observed night roost. During prolonged flights, positions were recorded for an individual bat at intervals ≥ 3 min during which time a bat hypothetically could fly across its entire home range. Ideally, an observation team attempted to record approximately 20 positions for each radiotagged bat per night while rotating through a sequence of all bats within receiver range. Most telemetry positions were recorded between 1830 and 2230 hr; however, some observations were made on each bat between 0300 and 0600 hr.

A map of our 76 ha study area (Fig. 1) was created from 82 reference points along 2.2 km of interconnecting trails. Positions determined for each bat were analyzed with Antelope home range software (http://www.nbb.cornell.edu/neurobio/jbsv@downloads/programs.html—J. Bradbury and S. Vehrencamp, pers. comm.). We used Anderson Fourier analysis (Wilkinson & Bradbury 1988) to calculate minimum area probabilities (MAP = 0.95) and minimum convex polygons (MCP) for home range as well as core-use area (MAP = 0.50). Means for sexes, species, and seasons were compared statistically (*P* < 0.05) using two sample *t*-tests and *F*-tests for equality of variance (SatistiXL version 1.4 software).

**STANDING CROP AND FRUIT REMOVAL.**—Standing crop (number of ripe and unripe infructescences, hereafter called fruit) per individual pepper plant was determined by direct counts on 33 plants marked with numbered paper tags. Ripe fruits were counted and marked with colored thread placed near the fruit 1 h before sunset. Fruits that were removed or remained intact were assessed at dawn. Fruit ripeness was judged by color (becoming dark green with ripeness) and/or texture (soft and easily bruised by touch).
EXPERIMENTAL OBSERVATIONS OF CAPTIVE FEEDING BEHAVIOR.—Captive bats were held singly in 1.5 × 1.5 × 1.8 m flight cages constructed of mesh shade cloth. Ripe fruits were collected from pepper plants in late afternoon. In each experiment, ten pepper fruits were suspended from the ceiling of the cage on wire hooks. An observer sat quietly in the flight cage viewing feeding behavior in the light of a dim penlight and whispered observations to a person with a stopwatch and datasheet recording outside the cage. Handling time was defined as the time interval between grasping a fruit through complete consumption. Fruits were replaced immediately after each consumption, thus the number available remained constant. Feeding observations usually began 1 h after sunset on the night following capture, giving bats time to habituate to the flight cage and food presentation.

RESULTS

Carollia perspicillata and C. castanea are similar in appearance, coloration, and morphology; however, C. castanea is significantly smaller in body mass, length of forearm, and wing loading (two sample t-tests with equal variances, \( P < 0.001 \); Table 1). In neither species did we find sexual dimorphism in these characters. Nine fecal samples of free-ranging C. perspicillata were collected with seeds from \( P. hispidum (N = 5) \), \( C. sciadophylla (N = 3) \), \( Ficus \) sp. (\( N = 1 \)); thus \( P. hispidum \) represented 36 percent of the diet by frequency of occurrence. Ten fecal samples from free-ranging C. castanea included seeds of \( P. hispidum (N = 8) \), \( C. sciadophylla (N = 1) \), and \( Miconia \) sp. (\( N = 1 \)); thus peppers represented 80 percent of the fruits in the diet. We observed no instances of multiple types of seeds in a single fecal sample as reported by Thies and Kalko (2004).

ACTIVITY AND MOVEMENTS OF CAROLLIA CASTANEA.—We recorded 1349 radiotelemetry positions from 11 C. castanea (Table 2), each bat was monitored between 2–17 nights. Bat C was tracked during two separate periods on 19 nights that spanned 72 days. Home range, core-use area, and the length of the long axis across home range were independent of the number of telemetry positions when sample size exceeded \( N = 60 \), thus we excluded bats D (\( N = 24 \)) and I (\( N = 26 \)) from Table 2 and from calculations of means. Mean home range (MAP = 0.95) for C. castanea was 6.7 ± 2.2 ha (\( N = 11 \) bats; Table 2), and no significant differences by sex or by season were noted (t-test: two sample, equal variances). Mean minimum convex polygon home range was 11.9 ± 3.7 ha. Mean core-use area was 1.7 ± 0.8 ha (\( N = 11 \) bats). Core-use areas (MAP = 0.50) ranged from 0.7 to 3.3 ha (Table 1) and represented 17–33 percent of the home range of any individual. During the wet season, core-use areas of all individuals contained at least one clump of fruiting \( P. hispidum \) (Fig. 1.); however, in the dry season some core-use areas included \( C. sciadophylla \) but not \( P. hispidum \). The mean long axis across home range was 438 ± 106 m (\( N = 11 \) bats).

Adult female C, first captured on 29 October 2002, was radiotracked for nine days, then netted and tagged again on 30 December 2002, and radiotracked ten additional days. During the first tracking period, ripe pepper fruit production peaked and the respective home range and core-use area of Bat C were 3.1 and 0.7 ha. During

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**TABLE 1.** Mean ± SD of body mass, length of forearm, and wing loading for C. castanea and C. perspicillata at TBS (sample size in parentheses).

<table>
<thead>
<tr>
<th>Species</th>
<th>Body mass (g)</th>
<th>Forearm length (mm)</th>
<th>Wing-loading (g/cm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. castanea</td>
<td>11.8 ± 0.4 (13)</td>
<td>35.4 ± 1.0 (13)</td>
<td>0.23 ± 0.03 (7)</td>
</tr>
<tr>
<td>C. perspicillata</td>
<td>17.2 ± 0.6 (7)</td>
<td>40.7 ± 1.7 (7)</td>
<td>0.29 ± 0.04 (7)</td>
</tr>
</tbody>
</table>
TABLE 2. Minimum-area probabilities (MAP) and minimum convex polygons (MCP) for home range (MAP = 0.95), core-use area (MAP = 0.05), and long axis of home range for *C. castanea* and *C. perspicillata*. Sample size (N) = number of telemetry data points.

<table>
<thead>
<tr>
<th>Bat, Sex*</th>
<th>N</th>
<th>MAP 0.95 (ha)</th>
<th>MCP (ha)</th>
<th>Axis (m)</th>
<th>Map 0.5 (ha)</th>
<th>Tracking nights</th>
<th>Season</th>
<th>Commuteb (m)</th>
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<tr>
<td>Carollia castanea</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>A, F</td>
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<td>18.9</td>
<td>575</td>
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<td>Wet</td>
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<td>8.2</td>
<td>405</td>
<td>2.1</td>
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<tr>
<td>C, F</td>
<td>124</td>
<td>3.1</td>
<td>8</td>
<td>352</td>
<td>0.6</td>
<td>7</td>
<td>Wet</td>
<td>175</td>
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<tr>
<td>C, F</td>
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<td>5.1</td>
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<td>416</td>
<td>1.2</td>
<td>10</td>
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<td>190</td>
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<tr>
<td>C (total)</td>
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<td>5.3</td>
<td>13</td>
<td>452</td>
<td>1</td>
<td>17</td>
<td>Wet</td>
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<td>13.7</td>
<td>560</td>
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<td>8</td>
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<td>9</td>
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<td>H, F</td>
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<td>9.6</td>
<td>370</td>
<td>1.6</td>
<td>13</td>
<td>Dry</td>
<td>60</td>
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<tr>
<td>J, M</td>
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<td>8.2</td>
<td>427</td>
<td>0.9</td>
<td>12</td>
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<tr>
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<td>8.3</td>
<td>330</td>
<td>0.9</td>
<td>8</td>
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<td>90</td>
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<tr>
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<td>11.3</td>
<td>335</td>
<td>1.9</td>
<td>12</td>
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<td>16.8</td>
<td>619</td>
<td>1.7</td>
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<td>Dry</td>
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<td>11.9</td>
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<td>3.7</td>
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<td></td>
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<tr>
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<td>735</td>
<td>1</td>
<td>10</td>
<td>Wet</td>
<td>600</td>
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<tr>
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<tr>
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<tr>
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<tr>
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<td>5.9</td>
<td>172</td>
<td>0.6</td>
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</tbody>
</table>

*First letter refers to individual identity, second letter refers to sex: M = male, F = female.

bDistance from the day-roost to the closest foraging patch

The second tracking period, the number of pepper fruits ripening each night greatly decreased qualitatively (assessment by FJB). Much of the original home range and core-use area of October were still occupied by Bat C in January, but the home range and core-use area expanded to 5.1 and 1.2 ha, respectively (Fig. 2A). The long axis across the home range of Bat C increased from 352 m in October–November to 416 m in December–January.

*Carollia castanea* roosts exclusively in earthen cavities among roots of trees growing along the banks of rivers or lakes (Thies 1998, and this study). Eleven individuals radio-tagged at TBS were followed to day-roosts, all of which were in cavities having 1–2 m horizontal entrances along undercut, steep banks of the Tiputini River or its tributary creeks. Each individual tracked to its day-roost ≥ 10 days occupied an alternate roost at least once. On several occasions, rising waters of the Tiputini River forced relocations to cavities higher on the riverbank.

The mean emergence time from the day roost of *C. castanea* was 9.9 ± 7.8 min after sunset (N = 26 observations on 11 bats; Fig. 3). Mean emergence time relative to sunset did not differ between wet and dry seasons. Several brief flights intermixed with roosting in foliage typically occurred immediately after emergence. During the wet season, *C. castanea* invariably began their foraging in peppers with ripe fruits. During the late dry season (March–April 2004) when few pepper fruits were available, some individuals moved directly upon emergence to feed in *C. sciadophylla*. On 24 March 2004, Bat M abruptly moved its entire foraging activity from a concentration of peppers near the Tiputini River to an area 250 m northward along Guacamayo Trail (Fig. 2B) where it apparently foraged on *C. sciadophylla*.

**ACTIVITY AND MOVEMENTS OF CAROLLIA PERSPICILLATA.**—We radio-tagged seven *C. perspicillata*, but only three individuals provided adequate data for analysis of spatial use (home range was independent of the number of telemetry positions when sample size exceeded N ≥ 40; Table 2). Mean home range (MAP = 0.95) for three *C. perspicillata* was 5.5 ± 1.7 ha. Mean minimum convex polygon home range was 11.1 ± 5.9 ha. Mean core-use area (MAP = 0.50) was 1.3 ± 0.6 ha and ranged from 0.8 to 2.2 ha (Table 2) which was 22 to 28 percent of the home range of any individual. Core-use areas of all individuals contained at least one clump of
fructing peppers and represent areas of intense foraging. The mean long axis across home range was 493 ± 172 m.

Day-roosts of *C. perspicillata* at TBS include tree hollows (*N* = 2) and buildings (*N* = 1). Unfortunately, we could not visually assess the numbers of individuals of *C. perspicillata* emerging from any day-roost because this species emerges well after dark. Although, colony size within day-roosts at TBS remains unknown, this species often forms social units of 10–20 individuals in hollow tree roosts at other sites (F. J. Bonaccorso, pers. obs.) and where caves are occupied group size may exceed 100 individuals (Fleming 1988).

The mean emergence time of radio-tagged *C. perspicillata* is 23.8 ± 11.4 min after sunset (*N* = ten observations on four individuals; Fig 3). Upon emergence, *C. perspicillata* flew directly to patches of *P. hispidum* or *C. sciadophylla*. Bat Y made nightly commutes of 600 m from its day-roost in a tree-hollow to its primary foraging area; whereas, bats U and W made commutes of < 100 m to initial foraging patches each night.

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**FIGURE 2.** (A) Expansion of the home range by *C. castanea* “C” and (B) seasonal shift in core-use areas used for foraging by *C. castanea* “M.”

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**FIGURE 3.** Mean emergence time from day-roost in minutes after sunset (solid triangles and left axis) and mean handling times in seconds to consume one *Piper hispidum* fruit (open squares and right axis). Vertical bars indicate one tail of the 95 percent confidence intervals. Numbers in parentheses represent sample size for observations of a particular behavior for a given bat species.

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**EXPERIMENTAL OBSERVATIONS OF FOOD HANDLING AND RATES OF FEEDING.**—Mean handling times for pepper fruits were 86.0 ± 35.1 s (*N* = 15) for *C. castanea* and 62.6 ± 19.1 s (*N* = 36) for *C. perspicillata* (Fig. 3). Masses of fruits ranged from 0.7 to 1.4 g. Captive *C. perspicillata* handled individual peppers significantly faster than *C. castanea* (*t*-test, two-sample with unequal variance, *P* < 0.026; Table 2). Both bat species removed individual fruits, flew to a feeding roost, and fed with their heads downward while holding the fruit to the mouth with their thumbs. After consuming a fruit, bats typically licked their face and wings clean of food fragments then searched for another fruit. Feeding continued until a bat filled its digestive tract, thus ending a bout of feeding that typically was followed by about 20 min of quiescent roosting. Similar feeding behavior has been observed in free-ranging *C. perspicillata* (Fleming 1988) and by both species in experimental flight cages (Bonaccorso & Gush 1987; F. J. Bonaccorso pers. obs.).

**DISTRIBUTION AND ABUNDANCE OF PEPPER FRUITS.**—Three 50 × 3 m transects (450 m²) in secondary forest contained 61 pepper plants representing three species of which 58 individuals were *P. hispidum*. Two transects extended along forest edge bordering man-made clearings and included 55 pepper plants. The third transect, completely under closed canopy forest of about 15 yr age, contained 14 *P. hispidum*. *Piper hispidum* in light gaps and forest edge attain shrub stature of ≤ 5 m in height. Three 50 × 6 m transects (900 m²) under closed canopy primary forest contained only five *P. hispidum* all of which were small in stature and bearing almost no fruits.

**FRUIT CROPS AND REMOVAL RATES OF RIPE PEPPER FRUITS IN A NATURAL ECOSYSTEM.**—Pepper fruits (infructescences) consist of hundreds of individual drupes on a cylindrical spadix. The spadices of
**P. hispidum** stand erect above the horizontal branches thus facilitating removal during flight by carolline bats. To remove a fruit, a bat typically hovers briefly to grasp a ripe fruit with its jaws and with a slight twisting force causes the release of the fruit at an abscission point. Frugivorous bats removed 70 out of 74 (94.6%) marked fruits from *P. hispidum* plants on the night they ripened. The four remaining fruits were present throughout the next day, but were removed during the second night after ripening.

At TBS, *P. hispidum* produced a few ripe fruits per plant virtually each day at least from late October to mid-January. On 15 November 2002, the standing crops for 34 *P. hispidum* on transect one ranged from 1 to 350 fruits per plant and totaled 3174 fruits (mean = 79.3 ± 114.9). The standing crops of five *P. hispidum* on 7 January 2003 ranged from 7 to 60. Sequential ripening of a few fruits per night from a standing crop is typical in the genus *Piper* (Fleming 1981, 1985). Zero to 12 fruits per plant ripened each day in late afternoon. Compared to non-ripened fruits, ripe *P. hispidum* fruits are noticeably a darker green and if squeezed gently, ripe fruits easily bruise. Ripening is accompanied by increased water content and by marked weakening of the abscission boundary between the branch and the fruit. Ripe fruits were removed by forces < 50 g, whereas unripened fruits required forces > 300 g as measured by a Pesola® spring balance clipped to a fruit.

**DISCUSSION**

*C. castanea* and *C. perspicillata* depleted ripe pepper fruits to zero or nearly zero before each sunrise at TBS. In similar observations on Barro Colorado Island, Panama, *C. castanea* and *C. perspicillata* harvested all marked ripe peppers before midnight (Thies & Kalko 2006). Our telemetry results demonstrate strong spatiotemporal overlap among multiple individuals of both species of bats at clumps of *Piper hispidum* and *Cecropia sciadophylla* when ripe fruits were available (Fig. 1). These two plant species at TBS represent the most numerous items in fecal samples of both bats. Pepper fruits are rich in nitrogen and lipids and thus are regarded as high-quality dietary items for fruit bats (Herbst 1986). Ripe fruits of *C. sciadophylla*, the less preferred food item by frequency of occurrence at TBS, remained abundant at sunrise and attracted many diurnal birds and primates to feed (J. R. Winkelman & F. J. Bonaccorso, pers. obs.). These results led us to conclude that exploitative competition is intense among carolline bats for highly nutritious but limited pepper fruits.

The foraging tactics of *C. castanea* are distinct from those of *C. perspicillata* (Table 3). *C. castanea* relies on early emergence and short, direct commuting flights from day roosts in order to arrive at pepper patches before the larger bodied *C. perspicillata*. *C. perspicillata* is at disadvantage because its mean emergence time is 14 min later than that of *C. castanea* (Fig. 3; two-tailed t-test, *P* < 0.001). Additionally, the mean distance for commuting from day roost to a foraging patch is greater for *C. perspicillata* (267 vs. 87 m; Table 2). Some individual *C. castanea* may complete one foraging bout and enter a prolonged roosting period in response to a digestive bottleneck (full gut capacity) before *C. perspicillata* even begins to feed. The early emergence of *C. castanea*, however, may carry a higher risk of predation by crepuscular raptors, particularly from bat falcons (*Falco rufuginus*) observed by us perching at dusk along the Tiputini River. By comparison, *C. perspicillata* has an advantage in having a larger body size, rapid fruit handling, and a large gut storage capacity, all of which counter its late emergence and long commuting flights.

Core-use areas associated with foraging by *C. castanea*, although stable over days or weeks, are dynamic over longer periods as fruit abundance and host-plant species change. Examples of changing use of space can be seen by the expansion of home range by bat C (Fig. 2A), and the complete shift in core-use areas by bat M (Fig. 2B). In Papua New Guinea, Bonaccorso et al. (2002) attributed similar fluidity in home ranges and core-use areas of the rain forest occupying pteropodid fruit bat, *Dobsonia minor*, to spatiotemporal shifts in fruit production. In dry tropical forest, the spatiotemporal patchiness of food resources is more extreme. During the dry season in Santa Rosa National Park, Costa Rica, *C. perspicillata* commutes up to 3700 m from day roosts to foraging areas (Heithaus & Fleming 1978, Fleming 1988), whereas maximum commutes of 600 m were recorded at TBS. Thus, in wet rain forests, where fruit resources are abundant, diverse, and relatively stable, short-tailed bats maintain small annual home ranges and short commuting flights from the day roost. Whereas, during periods of food scarcity in seasonal environments (Heithaus & Fleming 1978) or at any time in highly fragmented forests (Bernard & Fenton 2003), carolline bats range over relatively large distances and/or greatly expand their home ranges as influenced by fruit dispersion and availability.

Mean size of home range, core-use area, or long axis across the home range for *C. perspicillata* and *C. castanea* at TBS were not significantly different (Table 2). *C. perspicillata* and *C. castanea* at TBS occupy mean MAP home ranges of 5.5 and 6.8 ha, respectively and are similar to values for small pteropodid bats that consume peppers in Papua New Guinea (Winkelmann et al. 2000, Bonaccorso et al. 2002). Small frugivorous bats (Phylllostomidae & Pteropodidae) typically maintain small annual home ranges of < 15 ha in moist to wet tropical forests. Moreover, most foraging activity is confined to even smaller core-use areas where concentrations of preferred food plants ripen fruits over prolonged periods as do many species of the Piperaceae, Solanaceae, and Moraceae (Fleming 1985, Gentry 1990).

Different methodologies used to calculate home ranges by vertebrate biologists make comparisons between studies difficult. Minimum Convex Polygons (MCP) in our study approximately doubled home range size calculated by Minimum Area Polygons (MAP) (Table 2). Lawson and Rodgers (1997) discuss difficulties in comparing home range size among methodologies and caution that “MCP is often considered a relatively more comparable home-range estimate. . . despite being less suitable biologically as a descriptive statistic.” We concur that MAP methods are biologically more meaningful in describing home range and fine-grained patterns of habitat use by bats. Home range measurements for *Carollia* conducted by Thies (1998) and Bernard and Fenton (2003) used MCP; thus we present values using both MAP and MCP (Table 2). Each species of *Carollia* at TBS had MCP home ranges similar to those
TABLE 3. Foraging tactics of Carollia castanea and C. perspicillata and outcomes of foraging on preferred but limited pepper fruits at TBS.

<table>
<thead>
<tr>
<th>Carollia castanea</th>
<th>Carollia perspicillata</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Small body size, small gut capacity</td>
<td>• Large body size, large gut capacity</td>
</tr>
<tr>
<td>• Early emergence and short commute with first access to pepper patch</td>
<td>• Late emergence and long commute with late access to pepper patch</td>
</tr>
<tr>
<td>• Predation risk from crepuscular raptors</td>
<td>• Avoid predation risk from crepuscular raptors</td>
</tr>
<tr>
<td>• Slow fruit handling rate</td>
<td>• Fast fruit handling rate</td>
</tr>
<tr>
<td>• Brief foraging bouts leading to digestive bottleneck</td>
<td>• Long foraging bouts before digestive bottleneck</td>
</tr>
<tr>
<td>• Pepper depletion leads in return to day roost or foraging on less preferred food species</td>
<td>• Pepper depletion usually leads to foraging on less preferred food species</td>
</tr>
</tbody>
</table>

in undisturbed moist forest in Panama during the wet season (Thies 1998) but much smaller than Carollia from heavily fragmented forests in Brazil (Bernard & Fenton 2003). In the latter case, MCP calculations included grassland that bats transited to reach disjunct forest patches.

There is no overlap in roost occupancy by C. castanea and C. perspicillata. Carollia castanea exclusively uses earthen riverbank cavities both at TBS and on Barro Colorado Island (Thies 1998), and appears to be limited in distribution by riparian and lacustrine habitat presence. Carollia perspicillata uses hollow tree cavities and buildings as day roosts at TEP, and elsewhere additionally uses caves and culverts (Williams 1986, Fleming 1988). Tree cavities in tropical forests are relatively common and are independent of riverine habitats.

Although C. castanea and C. perspicillata overlap temporally and spatially as they forage in wet Neotropical forests and compete for some of the same fruits, Bonaccorso (1979) determined that C. perspicillata feeds on more plant species including some fruits too large for C. castanea to handle. Not only is Carollia perspicillata nearly 50 percent larger in body mass but it is capable of ingesting six pepper fruits during the time required by C. castanea to handle four peppers based on our cage observations. However, if rate of ingestion is adjusted according to metabolic rate and body mass scaling (McNab 1969), there is no difference in the time required to satisfy energetic requirements per individual by the two species. Benefits of having a larger body size are that C. perspicillata has the ability to feed at a faster rate and to select larger food items than C. castanea can handle, however, a counterbalancing consequence is that it must also find more food to support a larger body. Norwithstanding, small size has an advantage for Carollia castanea. For example, on Barro Colorado Island where there are 12 common species of peppers in the genus Piper, C. castanea specializes on peppers restricted to forest understory whereas C. perspicillata favors peppers found in large gaps (Thies & Kalko 2004). The smaller size and lesser wing loading of C. castanea enhance its ability to fly within forest clutter to exploit forest understory peppers not heavily utilized by larger congeners. Taken from another perspective, on an absolute-mass basis, an individual of the smaller bodied C. castanea requires less of the limited but nutritious pepper fruits to support itself, and survives as an extreme pepper specialist; whereas the larger bodied C. perspicillata is somewhat more of a feeding generalist. Despite exploitative competition for a limited supply of a preferred food species, each bat species coexists through subtly different foraging tactics.

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LITERATURE CITED


