INFLUENCE OF ENVIRONMENT AND RESOURCE AVAILABILITY ON ACTIVITY PATTERNS OF *CAROLLIA CASTANEA* (PHYLLOSTOMIDAE) IN PANAMA

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Behavioral patterns of animals correlate with biotic (i.e., resources and conspecifics) and abiotic (i.e., weather and lunar cycle) factors. We studied the influence of ambient light, rain, sex, and resource availability on the activity pattern of the neotropical chestnut short-tailed bat (*Carollia castanea*; Phyllostomidae) in a tropical lowland forest in Panama. Time of emergence was tightly correlated with local sunset, in contrast to the time of return, which occurred sporadically over a span of hours. Activity by individuals peaked at the beginning of the night, coinciding with maximum availability of ripe fruits from understory pepper plants (Piperaceae), their main food source. Bats continued to forage during light and moderate rain and only stopped at heavy rain. Nightly activity level was similar in nonreproductive female and male *C. castanea* but the temporal distribution of activity differed. Females were more active in the 1st half of night, whereas activity of males was more evenly distributed throughout the night. In contrast to fruit-eating bats in the canopy, *C. castanea* did not exhibit a significant reduction in flight activity (lunar phobia) during bright nights around the full moon. We conclude that ecological conditions (availability of food and predation risk) and physiological constraints (small body size associated with high metabolic rate) are the most important factors that account for the observed activity patterns.

Key words: activity patterns, bat, lunar phobia, moonlight, Phyllostomidae

Activity is an integral part of animal behavior. Animals actively search for mates, defend resources, avoid predators, and forage. Being more active can be advantageous, because an animal encounters more food, grows faster, and thus can become a better competitor (Werner 1992). The level and pattern of foraging activity is often linked to endogenous rhythms that vary on a daily, seasonal, or lunar (synodic) basis (Erkert 1982). Furthermore, foraging activity is influenced by resource availability, climatic conditions, predation risk, and the animal's physical condition and reproductive status. These factors are believed to be major selective forces on decision-making by foraging animals (Lima and Dill 1990).

Simultaneous monitoring of resource availability, predation risk, and energetic rewards from foraging is crucial to better understand the cost–benefit trade-off made by foraging animals: An animal receives benefits from foraging in the form of energy to survive and reproduce; however, this is at the cost of being preyed upon and the loss of energy while foraging. For example, rodents assess the value of a resource patch by integrating potential cost of predation and richness of a patch in terms of its energetic reward (Kotler and Blaustein 1995) and adapt their time spent in that patch accordingly. They stay longer in microhabitats where food resources are high (Harris 1984; Kotler 1984; Price and Waser 1985) and spend less time when the threat of predators increases (Kotler 1984; Price et al. 1984; Vásquez 1996).

Field studies have shown that activity by insectivorous bats is sensitive to environmental conditions. For instance, time of emergence is thought to be influenced by light level and predation risk (e.g., Jones and Rydell 1994; Rydell and Speakman 1995). Furthermore, insectivorous bats cease foraging when declining resources result in poor foraging success or when high flight costs prevent the attainment of a positive energy balance (Anthony et al. 1981; Lang et al. 2006; Maier 1992; Meyer et al. 2004).

In this context, comparative studies of fruit-eating bats are of particular interest. In contrast to insectivorous bats, they feed on a diet rich in carbohydrates but relatively poor in nitrogen, lipids, and minerals (Thomas 1984; Wendeln et al. 2000). Therefore, frugivorous bats eat large amounts of fruits (Studier

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and Wilson 1991) but build up only small fat reserves (McNab 1976; Studier and Wilson 1991) and thus cannot tolerate long periods of food restriction.

Despite being energetically more restricted than insectivorous bats there is evidence that activity levels by some fruit-eating bats also are influenced by environmental conditions. Large neotropical fruit bats, such as *Artibeus jamaicensis*, *A. lituratus*, and *Vampyrodes caraccioli* (Morrison 1978), which mostly forage in and around the canopy for fruits that are produced synchronously in large quantities over a short period, react toward moonlight levels by reducing flight activity during bright nights around the full moon (lunar phobia). This has been interpreted mainly as avoidance behavior toward visually orienting predators such as owls and hawks (see also Handley et al. 1991) that are attracted by the large numbers of bats around mass-fruiting trees.

In our study we addressed the question how small fruit-eating bats that forage in the understory for fruits that are produced only in small quantities react to short-term changes in environmental variables. We hypothesized that they should react differently in their activity pattern compared to large fruit-eating bats foraging in the canopy, in particular with regard to moonlight. Because the probability of a predator encountering a bat foraging for small fruit crops in rather dense understory is low, predator pressure and thus the costs of being eaten should be lower than on bats foraging for large fruit crops in the canopy (Howe 1979). We radiotracked small (12-g) chestnut short-tailed bats (*Carollia castanea*; Phyllostomidae) in a neotropical lowland forest in Panama and assessed the influence of ambient light (sunset, sunrise, and amount of moonlight, which correlates with the moon phase), rain, sex, and resource availability on the time *C. castanea* spends in flight. *C. castanea* forages in the forest understory mainly for fruits of the pioneer plant *Piper* (Piperaceae—Fleming 1988; Thies and Kalko 2004).

MATERIALS AND METHODS

Study site and climate.—The study was conducted between March 1994 and August 1997 at the Barro Colorado Island field station of the Smithsonian Tropical Research Institute in Panama (9°09′N, 79°51′W). The island (15.6 km²) is covered with tropical moist, semideciduous forest. Rainfall is seasonal with a dry period between mid-December and April and a wet period between May and mid-December during which most (90%) of the annual precipitation (2,650 mm) falls (Paton 1996; Windsor et al. 1990). The annual average temperature is 27°C, with a diurnal variation of 9°C.

Study animals and radiotracking.—We followed guidelines of the American Society of Mammalogists for animal care and use as described by the Animal Care and Use Committee (1998). We caught bats in the forest with 12- or 6-m mist nets set along a trail. Individual *C. castanea* were tagged with 0.95- to 1.12-g 2-stage radiotransmitters (model BD-2A, Holohil Systems Ltd., Carp, Ontario, Canada) glued to the back with surgical adhesive (SkinBond, Smith and Nephew United, Inc., Largo, Florida) and released at the capture site. Only nonreproductive, adult bats that weighed >12 g (12.6 g ± 1.2 *SD*, *n* = 17) were tagged with the exception of one female late in lactation that was also tagged. The transmitter and glue represented 6–8% of the bats' body masses. This slightly exceeds the recommended 5% rule

(Aldridge and Brigham 1988; Neubaum et al. 2005) but is below the 10% limit above which transmitter mass may negatively affect the animal's flight behavior (Brander and Cochran 1969; Heithaus and Fleming 1978).

The transmitters fell off or were scratched off after 4–25 days (11.8 days ± 5.1 *SD*, *n* = 17 bats). Of the 17 tagged bats, we analyzed 13 individuals (7 males and 6 females) with 111 tracking nights for a total of 735.5 h starting from sunset, with 656.6 h of contact (89.4%). Individual bats were tracked for 7–13 nights (8.5 nights ± 1.7 *SD*, *n* = 13 bats).

Radiotracking started from the time the bats left the day-roost in the evening until they returned in the morning. For our purposes we defined foraging activity as the time the bats spent in flight. This may underestimate true foraging activity because nonflying bats may be handling food while hanging. However, some flight activity likely serves for purposes other than foraging. In the following, we will use the word "activity" as synonym for foraging activity. Moreover, only flights that took ≥1 min were considered as (foraging) activity. Data on activity were collected during the entire night (where possible), whereas triangulation data to determine home range were collected either the 1st half of the night (1800–2400 h) or the 2nd half (2400–0600 h). For definition of home range and analysis method see Weinbeer et al. (2006). If contact with the bat was lost for more than 20% (12 min) of any given hour, the hour was omitted from our analysis. We also excluded data from the night of capture because of the disturbance to the bat.

We calculated activity level per hour as the sum of minutes spent in flight during this hour. For each hour of the night we averaged flight time over all tracking nights. We then calculated the sum of mean flight time per hour over a 12-h period to obtain the overall mean activity level for each bat. We calculated home-range size with the minimum convex polygon method (Mohr 1947), not including the location of the day-roost.

Sunset, sunrise, moon cycle, and rain.—We recorded weather and light conditions in the forest following the scheme of Handley et al. (1991). Cloud cover was defined as clear (sky cloudless), few (sky one-fourth cloud covered), partly cloudy (sky one-fourth to one-half cloud covered), mostly cloudy (sky three-fourths cloud covered), and overcast (no clear sky visible). We viewed the sky above the laboratory building clearing because most of the tagged animals foraged in the forest nearby. Rainfall was classified as heavy (ground covered with water; noise of rain drowned out all other sounds), moderate (average intensity; noisy, but did not mask all other sounds), light (quiet; individual leaf drips could be distinguished and rain usually did not reach forest floor directly), and drip (only drips from leaves; frequently after actual rain had stopped). We also recorded the amount of rainfall measured at the Barro Colorado Island weather station.

Times of local moonrise and moonset were obtained from the Panama Canal Commission. We divided the moon phase into new moon, 1st quarter, full moon, and 3rd quarter. To account for possible cloud cover in addition to actual moon phase, we classified the light condition in the forest as dark (too dark to see hands), moderately dark (objects can be distinguished at close range), moderately light (possible to see for a considerable distance), and light (light enough to read).

To assess activity patterns by *C. castanea* with respect to different moon phases, we analyzed the data for the 1st half (1800–2400 h) and the 2nd half of the night (2400–0600 h) separately. For 3 days before and after 1st quarter moon (7 nights), we categorized the 1st half of night as light and the 2nd half as dark. For 3 days before and after 3rd-quarter moon (7 nights), we classified the 1st half of night as dark
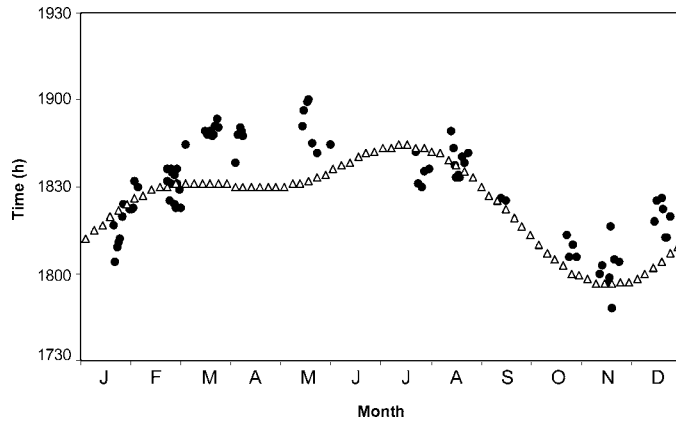
FIG. 1.—Time of emergence (closed circles) of *Carollia castanea* on Barro Colorado Island in relation to time of local sunset (open triangles) over 4 years (1994–1997).
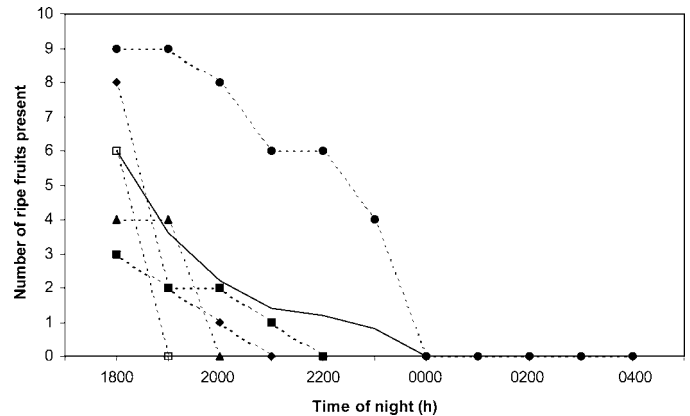

FIG. 2.—Fruit removal by *Carollia castanea* from 23 *Piper* plants (15 *P. aequale*, 7 *P. grande*, and 1 *P. marginatum*) on 5 nonconsecutive nights (dashed lines). Solid line indicates the mean over all 5 nights.

and the 2nd half as light. Seven nights around full moon were light almost all night long, and 7 nights around new moon were dark almost all night long. We omitted activity and home-range data from the 7 nights around full moon when the sky was overcast because this led to moderate to very dark conditions in the forest. However, we did include data from nights with overcast sky where either the whole night or the 1st or 2nd half of the night was classified as dark due to moon phase, because this did not influence light conditions in the forest.

Resource availability.—To assess food availability, we observed for 5 nights (1 each in November and December 1994; 3 in November 1995) the ripening and removal of fruits from 23 pepper plants of 3 species (15 *Piper aequale*, 7 *P. grande*, and 1 *P. marginatum*) growing in areas known to be used for foraging by *C. castanea*. We marked all ripe fruits (distinguished by their soft tissue and fruity smell) in the afternoon and returned to the plants every hour from 1800 to 2400 h, and every 2 h from 0100 to 0500 h to count the remaining fruit and to assess whether any fruits ripened during the night. Other measures of resource availability including crop size per hectare, removal rates, and fruit choice by *C. castanea* are described elsewhere (see Thies and Kalko 2004).

Statistical analysis.—To determine the influence of moonlight and cloud cover on the emergence time, we applied a 2-way analysis of variance (ANOVA). For the relation between emergence and return time as well as sunset and sunrise, we used Pearson's correlation.

Because activity data of a single bat on consecutive nights cannot be regarded as independent, we used for all tests the averaged activity level of each individual bat. This way, we obtained 1 measurement per category (1st or 2nd half of night, light level) per bat. ANOVAs were then calculated without replication (Sokal and Rohlf 1995). To test the influence of individuals, sex, and time of night (1st or 2nd half) on overall activity level, a 3-way ANOVA (without replication) was used. We applied a 2-sample *t*-test to test for differences between males and females in activity level between 1st and 2nd half of the night. A 3-way ANOVA (without replication) was used to test the influence of moonlight, individual, and time of night on overall activity level. To determine the influence of moonlight on home-range size we applied a nested ANOVA for females and males separately, with light level as a group variable, and individuals with light level as a subgroup (nested) variable. We chose $P < 0.05$ as level of significance for all tests. Analysis was performed with the computer program SYSTAT (SPSS Inc. 1997). Results are presented as mean $\pm$ SD.

RESULTS

Time of emergence and return.—All radiotagged *C. castanea* roosted under overhanging banks or in earth holes. Local sunset was positively correlated with time of emergence (Pearson's correlation, $F = 113.486$, $d.f. = 1$, 81, $R = 0.76$, $P < 0.0001$; Fig. 1). On average, individuals began leaving day-roosts shortly (6.3 ± 10.5 min; $n = 83$ nights) after local sunset. The earliest departure was 17 min before sunset and the latest 28 min after sunset. Time of emergence was not influenced by moonlight (2-way ANOVA, $F < 1$, $d.f.= 3, 77$, $P = 0.66$) or cloud cover (ANOVA, $F < 1$, $d.f. = 2, 77$, $P = 0.88$). We did not find a significant correlation between end of activity and local sunrise (Pearson's correlation, $F = 3.36$, $d.f. = 1, 39$, $P = 0.074$). Bats frequently returned to the day-roost long before sunrise ($n = 41$ nights), with the earliest return at 0125 h. The latest return occurred at 0558 h.

Resource availability.—The number of ripe fruits of *Piper* declined rapidly in the 1st half of night, with most fruits removed between 1800 and 2000 h (Fig. 2). After midnight, no ripe fruits were left on the study plants. No fruits ripened during the night. Thus, the night's total inventory of ripe fruits was established before the bats started to forage and was not replenished during the night.

Activity patterns.—*Carollia castanea* flew directly to a feeding area after it had left its day-roost. Mean flight time was highest in the 3 h after emergence (Fig. 3), when the bats flew up to 30 min per hour. Flight time averaged 72.3 ± 18.4 min ($n = 13$ bats) before midnight, and 104.2 ± 39.1 min ($n = 9$ bats) for the whole night. Individuals spent significantly more time in flight during the 1st half of the night (3-way ANOVA, $F = 35.89$, $d.f. = 1, 8$, $P < 0.001$). After the peak at the beginning of night, mean flight time per hour dropped for all individuals, without a pronounced 2nd peak between midnight and sunrise (Fig. 3). The duration of mean flight time throughout the night varied significantly from bat to bat (3-way ANOVA, $F = 3.55$, $d.f. = 11, 8$, $P = 0.041$). However, no significant difference was found in mean flight time by females
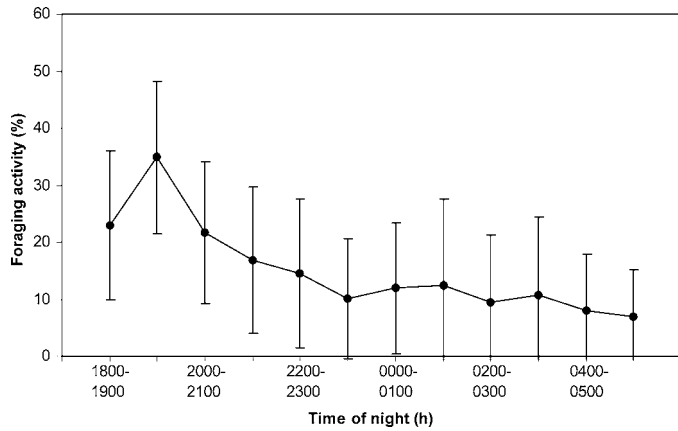
Fig. 3.—Activity pattern of 13 *Carollia castanea* ($\bar{X} \pm SD$ percentage time spent active per hour).

TABLE 1.—Activity levels of 13 individual *Carollia castanea* given as cumulative time spent in flight during the 1st half of the night (1800–2400 h) as well as throughout the night (1800–0600 h) and duration of single flights and hanging phases. n = numbers of single flights and hanging phases analyzed; M = male; F = female.

	Activity (min)		Flight (min)		Hanging (min)	
Sex	1800–2400 h	1800–0600 h	$\bar{X} \pm SD$	n	$\bar{X} \pm SD$	n
M	43.2	80.2	3.0 ± 2.4	89	17.2 ± 19.4	96
F	47.9		3.3 ± 2.4	100	15.1 ± 16.4	119
F	52.3	61.8	2.8 ± 2.4	91	22.3 ± 49.7	117
M	79.5		4.1 ± 3.3	98	11.5 ± 12.4	105
M	89.2		4.4 ± 2.3	55	9.2 ± 11.5	62
M	88.3		4.7 ± 2.8	50	5.7 ± 6.1	49
M	53.4	70.6	3.9 ± 2.8	73	19.8 ± 33.6	89
F	72.5	84.4	3.8 ± 4.7	149	13.6 ± 39.1	176
F	75.9	86.8	4.4 ± 3.4	102	12.0 ± 36.5	134
M	65.9	102.4	3.5 ± 2.3	195	17.1 ± 27.6	215
M	99.9	182.4	4.6 ± 3.2	292	11.5 ± 14.3	311
F	91.5	141.1	4.7 ± 3.9	141	14.4 ± 33.4	143
F	80.9	127.7	3.5 ± 2.4	297	12.5 ± 20.9	295
All	72.3 ± 18.4	104.2 ± 39.1	3.9 ± 3.1	1,732	14.3 ± 26.8	911

compared to males (3-way ANOVA, $F = 1.61$, $d.f. = 1, 8$, $P = 0.24$). Mean flight time of females averaged 100.3 ± 32.9 min ($n = 5$ individuals) compared to 108.7 ± 50.3 min ($n = 4$ individuals) for males. Although females and males were equally active over the whole night, they differed significantly in level of activity between the 1st and 2nd half of the night (2-sample *t*-test, $t = 2.97$, $d.f. = 7$, $P = 0.021$). Females spent more time flying in the 1st half of night and were less active during the 2nd half, whereas flight activity by males was distributed more evenly throughout the night. Furthermore, all females returned several times to the roost for longer resting periods, most of them exceeding 30 min, whereas with the exception of 1 individual, males did not return to the roost between foraging episodes.

Activity by *C. castanea* was characterized by short flights (mostly 1–3 min), interrupted by intervals of hanging from a branch, either feeding or resting (Table 1). The longest continuous flight lasted 38 min and the longest resting phase approximately 6 h (Table 1).

Activity patterns during dark versus moonlit nights.—We analyzed data from 11 individuals (5 males and 6 females) to compare activity pattern during moonlit and dark nights. Variation in moonlight did not have a significant effect (3-way ANOVA, $F < 1$, $d.f. = 1, 13$, $P > 0.05$) on average activity levels. The observed variance in mean flight time was best explained by differences among individuals (3-way ANOVA, $F = 6.64$, $d.f. = 10, 13$, $P = 0.001$) and by differences in activity between the 1st and 2nd half of a night (3-way ANOVA, $F = 38.01$, $d.f. = 1, 13$, $P < 0.001$).

To test whether use of space in *C. castanea* is influenced by moonlight, we compared the sizes of home ranges (excluding the day-roost) between moonlit and dark nights. As with flight activity, we did not find a significant difference in size of the nightly area covered, either by females (nested ANOVA, group variable: $F = 5.03$, $d.f. = 1, 25$, $P = 0.06$; nested variable: $F = 1.32$, $d.f. = 7, 25$, $P = 0.28$) or males (group variable: $F = 0.77$, $d.f. = 1, 18$, $P = 0.43$; nested variable: $F = 16.79$, $d.f. = 4, 8$, $P < 0.001$).

Activity pattern during rain.—It rained on 5 of 41 tracking nights in the dry season and 19 of 70 tracking nights in the wet season. Average duration of rainfall was 48 ± 53.5 min ($n = 5$) for dripping rain, 10.5 ± 5.3 min ($n = 13$) for light rain, 26.6 ± 27.2 min ($n = 18$) for moderate rain, and 27.1 ± 21.4 min ($n = 16$) for heavy rain.

Carollia castanea did not interrupt or alter activity in light or moderate rain, but bats stopped flying in heavy rain and sought shelter under leaves. Typically, foraging resumed before the rain had completely stopped. Because heavy rains normally did not last long, the short interruptions in foraging typically did not lead to major changes in activity. The 1 exception was once when, during the main foraging time of *C. castanea* between 1800 and 2000 h, more than 60 min of heavy rain fell, followed by 30 min of moderate rain. A tagged female spent this time in a protected place. This resulted in a lower-than-average cumulative flight time for the first 3 h for this individual (Fig. 4). Although the rest of the night was dry, the bat did not compensate for the lost foraging time. Between 2100 and 0400 h, she exhibited a similar level of activity as on previous nights. Between 0400 and 0500 h, a very brief 2nd activity peak occurred that was not present during the other 9 nights we tracked her.

DISCUSSION

Time of emergence and return.—Our results indicate a highly significant link between time of emergence by *C. castanea* and local sunset. This relationship is well established for other temperate and tropical bats (e.g., Audet 1990; Catto et al. 1995, 1996; Entwistle et al. 1996; Oxford et al. 1996). In comparison with many aerial insectivorous bats that begin foraging before sunset (Jones and Rydell 1994), *C. castanea* emerged later from its day-roost. It is likely that a trade-off between resource availability and predation risk influences emergence time in bats. For instance, many aerial insectivorous bats hunt for mass-emerging insects, such as dipterans, whose activity peaks before dusk. However, the bats' activity peak does not fully
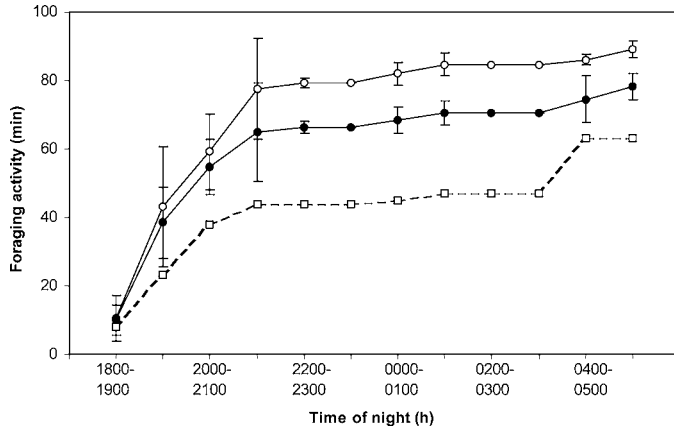
Fig. 4.—Cumulative flight time ($\bar{X} \pm SD$) of a female *Carollia castanea* during all tracking nights (solid circles), on only dry nights (open circles), and during 1 rainy night with 60 min of heavy rain between 1800 and 2000 h (open squares).

coincide with the peak of insect activity, but occurs at somewhat lower light levels when insect activity is already declining (Jones and Rydell 1994; Rydell et al. 1996). This delayed emergence has been interpreted in the context of predator avoidance behavior. Because frugivorous *C. castanea* does not depend on mass-emerging insects as its main food, it can "afford" to emerge later, probably minimizing the risk of predation at dusk.

Activity pattern.—The nightly activity pattern of *C. castanea* measured as (mean) time spent in flight per hour consisted of a single peak shortly after sunset. This unimodal activity rhythm is typical of many phyllostomid bats (e.g., Charles-Dominique 1991; Fleming and Heithaus 1986; Weinbeer et al. 2006; Williams and Williams 1970). In our study, peak activity of *C. castanea* coincided with maximum availability of its main food, ripe *Piper* fruits. The quantity of ripe *Piper* fruits for a given night is set at the beginning of the evening. In contrast to plants such as figs (*Ficus*) that produce huge fruit crops over a short period of time (Korine et al. 2000), *Piper* plants bear only few ripe fruits per night over a prolonged period of time (Fleming 1981, 1988; Thies and Kalko 2004). Thus, there is no need for *C. castanea* to maintain high activity levels because most of the fruits are harvested in the first 3 h after sunset.

Influence of moonlight on activity.—Examination of our radiotracking data does not reveal any significant changes in the time spent in flight in response to variation in light levels. This supports the results of a mistnetting study of phyllostomid bats in dry forest understory (Guanacaste) and wet forest (Puntarenas) in Costa Rica (LaVal 1970). However, our data contrast sharply with many studies that report drastic behavioral changes by phyllostomids in response to moonlight. Several phyllostomid bats reduce their activity almost completely around the time of the full moon (e.g., Crespo et al. 1972; Erkert 1974; Häussler and Erkert 1978; Lang et al. 2006; Morrison 1980).

Most animals with strong lunar phobia search for food in open spaces and are thus exposed to predators with excellent

nocturnal vision such as owls (Handley et al 1991). Hence, lunar phobia (i.e., the reduction of activity levels) is frequently seen as an avoidance behavior towards the presence of predators (Kotler 1984; Rydell and Speakman 1995). Consequently, the absence of activity changes in bats during moonlit nights is interpreted mainly as the absence of predators (Gannon and Willig 1997; Negraeff and Brigham 1995; Rodríguez-Durán and Vázquez 2001).

In frugivorous bats, it is likely that foraging strategy, activity pattern, and consequently, risk of predation are not only influenced by presence or absence of predators but also by the probability of being encountered by a predator, which in turn depends on the size of the fruit crop and display of fruits. Howe (1979) hypothesized that animals searching for fruits produced by plants with small fruit crops and continuously ripening fruits should face less predation pressure than frugivores feeding on synchronously fruiting plants such as figs. Large crops attract and concentrate many frugivores, which in turn attract predators. This assumption is supported by a study of mainly bat-dispersed figs. Removal rates were significantly lower around the time of the full moon than during the rest of the month (Korine et al. 2000). In contrast, plants such as the understory shrub *Piper*, the main food of *C. castanea*, produce few ripe fruits per night. Individual plants are therefore visited only a few times per night by only 1 or few frugivores, and thus the probability of a predator waiting for a bat at a food plant is low (Howe 1979). Hence, predator pressure on frugivorous bats feeding mostly on plants with small fruit crops should be lower than on bats eating mostly big-bang crops. So for *C. castanea*, the costs of being eaten by a predator seem to be low compared to the benefits gained in the form of energy by foraging, allowing the bats to forage even in moonlit nights.

The question is whether we can assess predation risk for *C. castanea* based on its foraging behavior. Predation is regarded as a strong selective force for the evolution of behavioral adaptations that reduce the risk of predation (Lima and Dill 1990). Evidence for predation risk could reveal the time spent at a food source. Frugivores that feed on fruits widely scattered over a large area, and that thus should suffer from less predation risk, should spend more time at a fruiting tree or bush (Werner and Anholt 1993). However, this is not true for *C. castanea*. Foraging behavior of *C. castanea* is characterized by very short flights (1–3 min) where the bat approaches a *Piper* bush, picks up a fruit in flight, and carries it immediately to a temporary "dining roost," a tree or bush at least 50 m away (Thies et al. 1998). The short flights and the distant feeding roosts imply some level of predation risk at the fruiting plants. We never observed *C. castanea* being attacked by a predator, but, in general, predation events are rare and difficult to observe. Also, antipredator behavior may be so effective that predators are seldom successful (Lima and Dill 1990).

In addition to the low probability of being encountered by a predator, other factors such as body size, diet, and energy demand also may influence the activity pattern of *C. castanea*. Because of its small size and frugivorous diet, *C. castanea* is presumably under constant energy stress. Werner and Anholt

(1993) predicted that under the threat of predation, individuals with large energy reserves should be less active because more can be lost (i.e., life) by foraging in a risky way than can be gained by additional energy intake. In contrast, individuals with low energy reserves can only gain by being more active, even if the risk of predation is high. Therefore, we argue that *C. castanea* faces a trade-off between the risk of being killed by a predator and the risk of not ingesting enough energy to survive until the next night. We therefore assume, because of its small body size and frugivorous diet, that *C. castanea* may not be able to "afford" the reduced levels of foraging activity on moonlit nights exhibited by larger species. The strategy of short foraging flights may allow *C. castanea* to minimize both the risk of predation and the energy costs of foraging.

Sex-specific differences in activity patterns.—A range of studies have investigated differences in activity patterns between males and females in various bat families (e.g., Audet 1990; Entwistle et al. 1996; Kunz et al. 1998; Wilkinson and Barclay 1997). The few frugivorous phyllostomid bats that have been studied to date all possess a polygynous mating system (Charles-Dominique 1991; Dechmann et al. 2005; Fleming and Heithaus 1986; Kunz et al. 1998; Morrison and Morrison 1981; Wilkinson 1985). During reproduction, small harem groups form where the female bats spend more time foraging in a larger area than the reproductively active (harem) males, which spend most of the time close to the roost (Charles-Dominique 1991; Kunz et al. 1998; Morrison and Morrison 1981). However, nonreproductive males spend as much time foraging as do females (Charles-Dominique 1991; Kunz et al. 1998). Our results are in accordance with these observations. We did not find differences in total time spent in flight between nonreproductive males and females of *C. castanea*. However, females and males differed in distribution of flight time and use of the day-roost during the night. Females tended to be more active during the 1st half of night and often returned several times to the day-roost for long resting periods. In contrast, activity by males was distributed more evenly throughout the night, with most of the night spent outside the day-roost. The short, intense feeding episodes by females early in the night, when resource levels were high, combined with prolonged stays in the day-roost, a place where risk of predation is presumably low, can be interpreted as a behavioral adaptation to maximize energy uptake while minimizing risk of predation. The activity pattern in adult, nonreproductive males also may be influenced by factors other than feeding and predator avoidance. We assume that the nonreproductive males that are not involved in harem defense may dedicate some of their activity to searching for mates, roost sites, or new feeding areas.

Influence of rain on activity.—Generally, heavy rain delays emergence time in insectivorous bats (Entwistle et al. 1996; Kronwitter 1988; Schmidt 1985; Usman et al. 1990) or leads to reduced activity (Audet et al. 1990; Catto et al. 1996). In our study, rain did not impact normal activity with the one exception and that only with heavy rain.

It has been suggested that rain interferes with echolocation or negatively affects thermoregulation (Fenton et al. 1977).

Because *C. castanea* finds its food mainly by olfaction (Thies et al. 1998), it is likely that thermoregulation is the important factor. Ambient temperature falls during heavy rain. Phyllostomid bats in general maintain high core temperatures even at low ambient temperatures (Audet and Thomas 1997; Cruz-Neto and Abe 1997), causing them to spend more energy in flight. For example, *Carollia perspicillata* doubled its metabolic rate at low ambient temperature (21°C), compared to thermoneutrality (Audet and Thomas 1997). Therefore, it makes sense to stop foraging during rain to avoid having to maintain high body temperature for flight when ambient temperature drops. However, because frugivorous phyllostomids are under energy stress, particularly at the beginning of the night, and because they also face rapid depletion of their food, costs of energy loss through maintenance of high body temperature during rain may in most cases be balanced by energy gain through feeding.

To summarize, the reasons why the small fruit-eating bat *C. castanea* does not change its foraging activity in moonlit nights compared to other, larger fruit-eating bats seem to be 2-fold. On one hand the low probability of being encountered by a predator due to the availability and abundance of its food source may make it less necessary to reduce foraging activity; on the other hand, however, the foraging behavior of *C. castanea* seems to indicate at least some level of predation risk so that maintaining foraging activity in moonlit nights also can be interpreted as the need to forage even under predation risk to maintain a positive energy balance. For future studies on the activity pattern of *C. castanea* and other fruit-eating bats it will be necessary to determine the predation risk perceived by the bat and to quantify the costs and benefits of being active.

RESUMEN

Estudiamos la influencia de la luz ambiental, lluvia, sexo, y disponibilidad de recursos en el patrón de actividad del murciélago neotropical castaño de cola corta, *Carollia castanea* (Phyllostomidae) en una selva tropical de tierras bajas en Panamá. La hora de salida de los murciélagos estuvo cercanamente correlacionada con la hora local de la puesta de sol, en contraste con la hora de regreso al refugio que ocurrió esporádicamente durante varias horas. La actividad de los individuos presenta un pico en el comienzo de la noche, que coincide con el momento de mayor disponibilidad de frutos maduros de las plantas de sotobosque de la familia Piperaceae. Los murciélagos continúan forrajeando durante periodos de luz y lluvia moderada, y sólo se detienen cuando hay lluvia muy fuerte. El nivel de actividad nocturna fue similar en hembras y machos no reproductivas pero la distribución temporal de la actividad es diferente entre uno y otro. *C. castanea* no presenta una reducción significativa en la actividad de vuelo durante noches muy brillantes por la luna llena. Concluimos que las condiciones ecológicas (disponibilidad de alimento y riesgo de depredación) y las limitantes fisiológicas (tamaño corporal pequeño asociado a una alta tasa metabólica) son los factores más importantes para explicar los patrones de actividad observados en este trabajo.

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