Literature Cited

Aucoin, L. E., A. K. Frank, B. R. Arnold and M. N. Conte. 2000. Has Jesus left the building? Recovery of *Basiliscus basiliscus* from a population decline at Corcovado National Park. Pp. 102 – 107 *in* L. E. Aucoin, M. N. Conte and J. A. Macintosh, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Babineau, M. R. and C. E. T. Paine. 1999. Population declines and changes in demographic structure of basilisk lizards (*Basiliscus basiliscus*) along three tropical streams. Pp. 61 - 63 *in* M. R. Babineau and D. R. Hogan, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Berg, E. S., S. C. Braman, B. W. Wright and M. P. Ayres. 1998. We found Jesus Christ in Corcovado: stream size and population structure of *Basiliscus basiliscus*. Pp. 82 - 85 *in* E. S. Berg and R. F. Douzinas, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Braden, D. M., P. B. Erickson, M. R. Kang, G. A. Miller-Messner and A. J. Sepulveda. 2001. "I'm not dead yet": *Basiliscus basiliscus* population change, habitat characteristics, and putative migration in three riparian habitats. Pp. 69 - 74 *in* P. B. Erickson, C. L. Glastris, M. L. Grace and C. M. Leander, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Van Devender, R. W. 1983. *Basiliscus basiliscus* (Chisbala, Garrobo, Basilisk, Jesus Christ Lizard). Pp. 379 – 380 *in* D. H. Janzen, ed. Costa Rican Natural History. Chicago, IL: University of Chicago Press.

Temporal patterns in foraging activity of insectivorous bats on the Osa Peninsula, Costa Rica

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Abstract: Bat foraging activity may be influenced by fluctuations in prey abundance, predators, or endogenous feeding rhythms linked to diurnal fasting schedules. To evaluate the relative importance of these factors, we used an ultrasound detector to quantify foraging activity of insectivorous bats at Corcovado National Park, Costa Rica. Bat activity was highest at dusk and increased slightly again at dawn. Because insect abundances followed a similar pattern, fasting schedules and prey abundance had approximately equal predictive power for determining bat activity through the night. Moonlight did not affect bat activity, which suggests that bats are not affected by increased predation risk during times of high light, and runs counter to the hypothesis of lunar phobia, which is well regarded by many chiroptologists. Bat species composition changed through the night, suggesting that bat species partition food resources over time. This could affect the patterns observed in bat foraging activity through the night. Bats effectively exploit the increased insect abundance at dusk and dawn, but further research is necessary to determine if this is driven by endogenous rhythms, fluctuations in prey abundance, or both.

Key Words: Chiroptera, lunar phobia, Pettersson D240X ultrasound detector, predation, Sonobat

Introduction

Bats (Chiroptera) are the second most diverse order of mammals, comprising a quarter of all mammal species worldwide. Their extensive adaptive radiation reflects their ability to exploit a wide variety of resources. Bats have unique physiological adaptations to a nocturnal, airborne lifestyle that include highly regulated metabolic levels and echolocation for prey capture and nocturnal flight. Two factors that may be particularly important in determining patterns in bat foraging activity are temporal fluctuations in prey abundance and predator avoidance tactics (Morrison 1978). By feeding when more insects are present, bats could maximize their foraging efficiency. If increased visibility due to higher light levels increases the probability that bats will be preyed upon, they may tend to limit foraging to the darkest parts of the night. Erkert (1982) has suggested that peaks in activity often observed at dawn and dusk are due to diurnal feeding schedules. Bats may need to feed when they first emerge from their daytime fasting and then again before dawn to maintain their daytime metabolic needs.

In the past, it has been logistically difficult to study bat foraging behavior (but see recent studies at Corcovado National Park, of the piscivorous *Noctilio leporinus*; Yale et al. 1998, Veysey et al. 2000 and Leslie et al. 2001). Recent advances in ultrasound detection technology have made it possible to monitor species-specific feeding patterns of bats, especially insectivorous bats.

We evaluated the potential effects of foraging efficiency, feeding schedules and predation on the activity of insectivorous bats in Corcovado National Park. If bats maximize foraging efficiency, bat activity patterns should track prey abundance patterns throughout the night. If endogenous feeding schedules dictate bat foraging, bat activity should peak at dawn and dusk irrespective of insect density. Alternatively, bats might avoid predation risk from the great potoo (*Nyctibius grandis*) by decreasing foraging activity during these twilight hours when they are especially visible (Stiles and Skutch 1989). In this case, we would expect them to have

decreased activity during times of high moonlight (lunar phobia).

Methods

This study was conducted during the nights of 2 - 3 Feb 2002 (waning moon at 3/5 full) on the airstrip at La Estación Sirena, Corcovado National Park, Costa Rica. All sampling points were located 50 – 500 m west of the main building of the station. Bat activity was measured using a Pettersson D240X ultrasound detector in the heterodyne mode with frequency set to 45 kHz. As insectivorous bats forage, they emit a series of search phase calls that sound like a sequence of rapid rhythmic clicks on the detector. Each set of these calls was counted as a bat "pass". The set frequency of the detector is the center of a frequency range of incoming sound that is converted into an audible heterodyne signal. This system allowed us to measure the number of bat passes within a radius of approximately 10 m.

Insect abundance was measured using a Maglite® flashlight (3 D-cell batteries) by counting all insects passing through a vertical flashlight beam in 15 sec intervals. We estimated the beam to extend 15 m vertically and up to 0.5 m in diameter.

On the night of 2 Feb, we continuously sampled insect abundance and bat activity from 18:00 until 05:00 the next morning. We used the following continuous rotation: two 5 min counts of bat passes followed by five 15 sec measures of insect abundance at haphazardly selected points within a 10 m radius of the sampling site. After each rotation, we moved our sampling site approximately 50 m east or west along the airstrip. We also recorded cloud cover and presence or absence of moonlight at the end of each sampling interval.

On the night of 3 Feb, we collected additional bat activity and insect measurement samples at 19:15, 21:00, 00:15 and 04:15. We recorded bat foraging calls at 00:15 and 04:15. We then used SonoBat software [DNDesign, Jacksonville, FL] to compare call sonograms and classify sonotypes into putative species based on search phase calls. This allowed us to compare species composition at different points during the night.

Bat activity and insect abundance data for 2 and 3 Feb were analyzed as a single data set because there appeared to be low variation in temperature, cloud cover and moonlight between the two nights of sampling. We evaluated all possible linear regressions to determine which factors (insect abundance, twilight/no twilight, moonlight/no moonlight) best explain patterns in log bat activity. We defined twilight samples as those collected during elevated light levels at dawn and dusk. We used t-tests to compare insect abundance in twilight and non-twilight hours and insect activity during times of moonlight and no moonlight in the non-twilight hours. Insect abundance was log transformed, $\log_{10}(x+1)$ to improve normality.

Results

Insect activity and bat activity both peaked strongly at dusk and tended to be greater again at dawn (Fig. 1). One-parameter models with insect abundance or twilight explained nearly equal amounts of variation in bat activity ($r^2 = 0.18$, df = 37, P = 0.009 and $r^2 = 0.16$, df = 36, P = 0.013, respectively; Table 2). Moonlight had no relationship with bat activity ($r^2 = 0.07$, df = 30, P = 0.10) and no multi-parameter model explained additional variation in bat activity (Table 2). When data points from the twilight hours were excluded, insect abundance and bat activity were independent ($r^2 = 0.01$, df = 31, P = 0.62; Fig. 2).

Insect abundance was greater during twilight hours than non-twilight hours (t = 7.86, df = 36, P < 0.01) and tended to decrease during moonlit non-twilight hours (t = 1.94, df = 30, P = 0.06; Table 1).

We recorded search phase calls of four bat sonotypes (A - D) on 4 Feb. Five calls were recorded just after midnight (00:03 to 00:43), four of sonotype A and one of sonotype B.

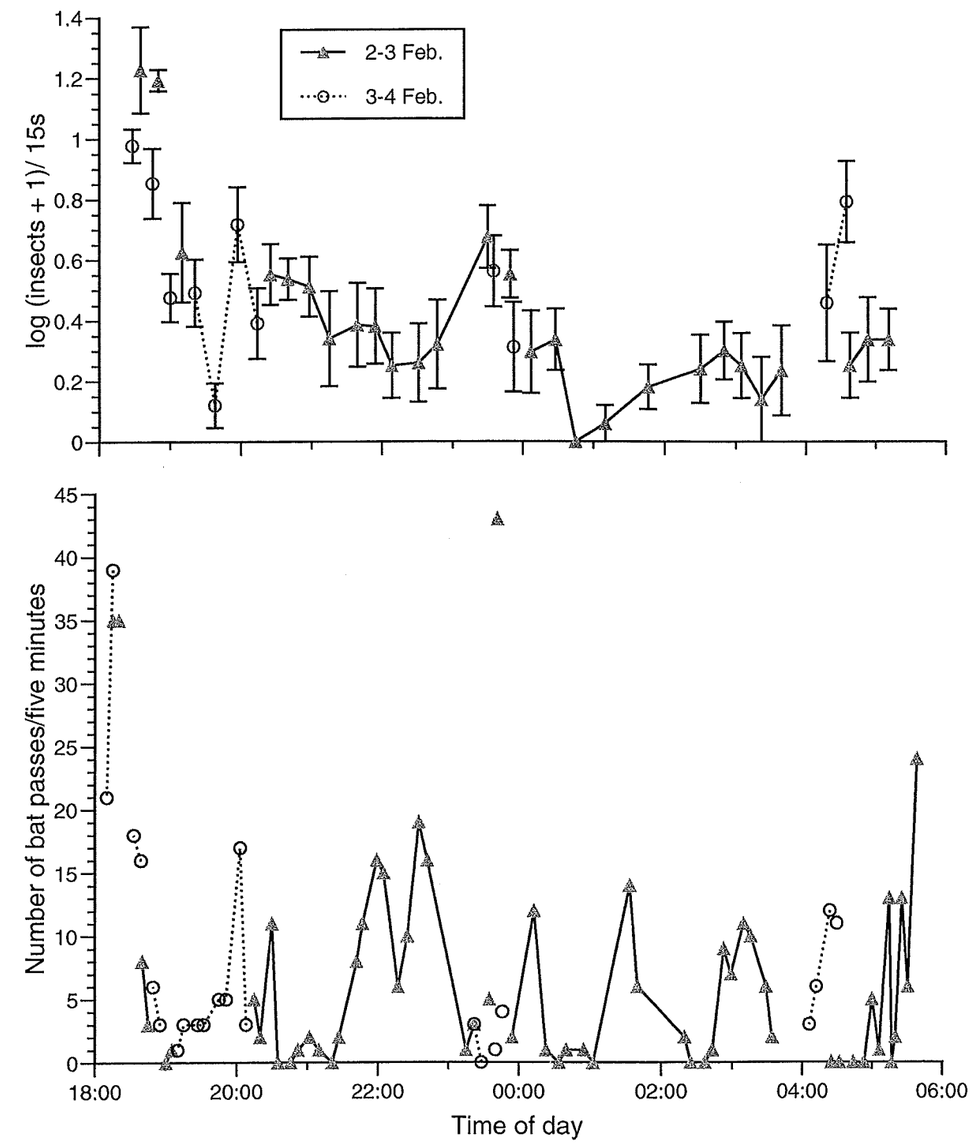

FIG. 1. Relative abundance of flying insects (upper) and foraging insectivorous bats (lower) during the nights of 2-3 and 3-4 February 2002 at Corcovado National Park, Costa Rica.

Before dawn (04:50 to 05:01), we recorded two calls of sonotype C and one of sonotype D.

Discussion

Our results best support the hypothesis of endogenous feeding rhythms (highest just before and after times of diurnal fasting). Bat activity was also statistically related to prey abundance, but this was confounded with fasting schedules because insect abundance was greatest at dusk. Because bat ac-

TABLE 1. Insect abundance and bat activity (mean ± SE) during twilight and non-twilight, and with and without moonlight. Means for moonlight and no moonlight are for times of no twilight only.

Light Conditions	Insect passes/15 s	n	Bat passes/5 min
Twilight	9.00 ± 1.60	6	13.50 ± 3.02
No twilight	2.00 ± 0.17	32	5.52 ± 0.88
Moonlight	1.11 ± 0.15	17	5.97 ± 1.53
No moonlight	4.65 ± 0.85	15	9.68 ± 2.14

tivity was not correlated with insect abundance when twilight hours were excluded, it seems that insect abundance is not the proximate driver of bat activity; this runs counter to the foraging efficiency hypothesis.

Past studies at Corcovado found that piscivorous bat foraging was greatest at times of high fish abundance and also at dusk and dawn (Yale et al. 1998, Veysey et al. 2000 and Leslie et al. 2001). It is possible that this composite pattern also holds for insectivores, and that we failed to detect it because of sampling error in our measurements of insect abundance and bat activity. Our sampling for bats was sensitive to chance occurrences of one individual repeatedly passing overhead; consequently, activity levels sometimes varied greatly from one minute to the next (note one instance where replicate counts were 5 vs. 44 at 23:55 on 2 Feb; Fig. 1, lower). Such large variation in bat activity levels made correlations with insect abundance difficult. Additionally, we were not sampling insect abundance simultaneously with bat activity, so perhaps we did not observe the insects immediately affecting bat activity. While insect abundance did decrease slightly with the presence of moonlight, we found no evidence that moonlight discourages bat foraging. This provides further evidence that bat activity is not very responsive to fluctuations in prey abundance.

TABLE 2. Comparison of goodness of fit (r^2) and significance of full model (P) for alternative linear regression models predicting patterns of bat activity with 1, 2 or 3independent variables.

Model	r^2	P
One parameter		
log insects alone	0.17	0.009
twilight alone	0.16	0.013
moon/no moon alone	0.07	0.101
Two parameter		
log insects & moon	0.18	0.037
log insects & twilight	0.21	0.244
moon & twilight	0.19	0.272
Three parameter		
log insects, moon, twilight	0.22	0.536

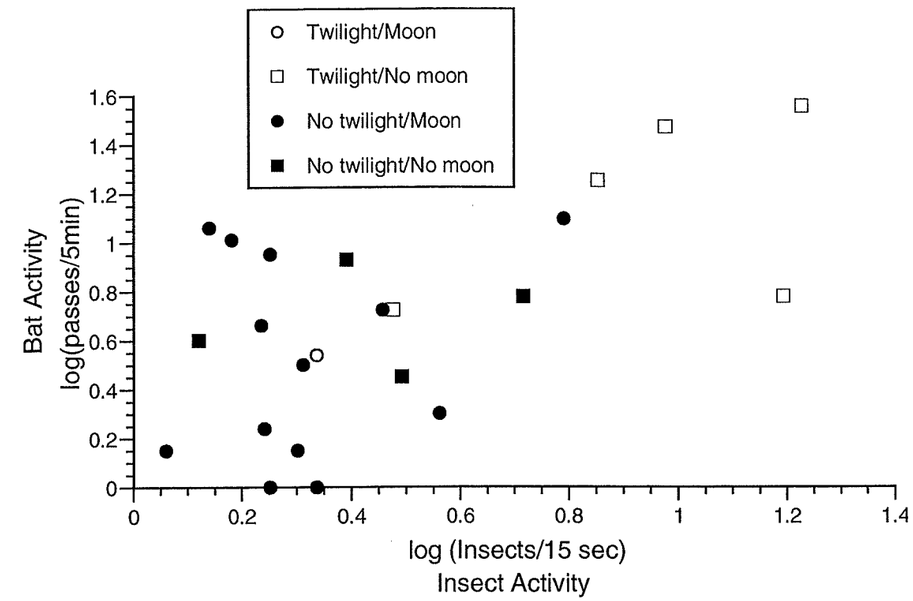

FIG. 2. Average bat activity and insect activity during 30 min time intervals on 2-3 February and 3-4 February, 2002.

Results refute the hypothesis that bat activity is reduced during times of relatively high light. Neither twilight nor moonlight were associated with reduced bat activity. This may indicate that insectivorous bats at Corcovado do not face meaningful predation risks and/or that predation risk does not vary predictably with ambient light. In any case, the lack of an effect of moonlight was surprising because lunar phobia is regarded as a general feature of bat biology by many chiroptologists (R. Laval, pers. comm.).

As part of this study, we screened for unique sonotypes (putative species) at 00:00 and 05:00. Krivak-Tetley et al. (in this volume) sampled calls at 18:00 and 21:00 on 30 - 31 January at the same site and found little overlap in species composition between these times. None of the calls we recorded at 00:00 and 05:00 were from the same species as calls collected in the early evening. These patterns are consistent with the hypothesis that bat species composition changes through the night due to temporal resource partitioning (Bonaccorso 1979), which implies that interspecific competition is reduced by adaptations of some species to alternative feeding patterns and/or specialization on prey types that vary in abundance over the night.

Bat foraging clearly peaks at dusk, but whether this is due to endogenous rhythms, high insect abundances at that time or a combination of the two remains unclear. Progress could be made by further studies that contain more and better estimates of variation in insect abundance and bat activity. Studies with other feeding guilds (e.g. frugivores), for whom insect patterns should be irrelevant, would also be informative.

Literature Cited

Bonaccorso, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. *Bull. Florida State Mus. (Biol. Sci.).* 24(4): 359 - 408.

Erkert, H. G. 1982. Ecological aspects of bat activity rhythms. Pp. 201 - 242 *in* T. Kunz ed. Ecology of bats. New York, NY: Plenum.

Leslie, P. S., J. A. Musnicki and R. M. Owens. 2001. Sharks, marine fish, and lagoon morphology: factors affecting the foraging behavior of the greater bulldog bat. Pp. 64 - 68 *in* P. B. Erickson, C. L. Glastris, M. L. Grace and C. M. Leander, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Morrison, D. W. 1978. Lunar phobia in a Neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Animal Behavior*. 26: 852 - 855.

Stiles, F. G. and A. F. Skutch. 1989. *A Guide to the Birds of Costa Rica*. Ithaca, NY: Cornell University Press.

Veysey, J. S., J. A. Macintosh, K. W. Manaras and C. B. Shannon. Same bat channel, same bat time? The effects of time and tide on foraging behavior of the piscivorous bulldog bat. Pp. 95 - 101 *in* L. E. Aucoin, M. N. Conte and J. A. Macintosh, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Yale, R. C., R. F. Douzinas and K. C. Deem. 1998. Tidal effects on fishing bat behavior in the Rio Sirena lagoon at Corcovado National Park. Pp. 78 - 81 *in* E. S. Berg and R. F. Douzinas, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.