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The Effect of Lunar Illumination on Movement and Activity of the Red Fig-eating Bat (*Stenoderma rufum*)¹

Key words: Chiroptera; ecology; lunar phobia; Luquillo Experimental Forest; Phyllostomidae; Puerto Rico; radio telemetry.

MOONLIGHT is an environmental variable which depresses nocturnal activity in animals including insects (Williams & Singh 1951), rodents (Clarke 1983, Kotler 1984), and birds (Nelson 1989, Brigham & Barclay 1992). Moonlight also has been reported to reduce activity in bats by causing them to emerge later, or to restrict their flight and feeding to shadows (Reith 1982, Jones & Rydell 1994). Among the New World phyllostomids, *Artibeus jamaicensis* (Morrison 1975) and *Desmodus rotundus* (Crespo *et al.* 1972) significantly reduce activity during periods of high lunar illumination. This behavior, termed lunar phobia (Morrison 1978), suggests that flying in moonlight may significantly increase risk of predation by visually oriented predators. Predation pressure is a probable cause of this behavior because neither resource abundance and distribution, nor social activity in bats, is correlated with lunar illumination (Morrison 1978). Reduction in activity during periods of high lunar illumination is assumed to hold true for many other bat species (Erkert 1988).

Using radio telemetry, we examined the effects of lunar illumination on the movement patterns of the red fig-eating bat, *Stenoderma rufum*, on Puerto Rico (Greater Antilles). In general, we evaluated differences in a variety of movement and activity parameters, the extent to which these parameters are

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TABLE 1. Results of a series of ANOVAs (F value, followed by significance in parentheses) measuring the effects of age-sex groups (adult males, adult females, or juveniles) and moon phase (light or dark) on each of the movement parameters measured for *S. rufum*. All distances are in kilometers, with standard errors given in parentheses.

Source	df	Total distance/h	Maximum distance	Minimum distance	Mean distance/move	Moves/h	% Time/roost
Moon (A)	1	0.00 (0.95)	0.10 (0.76)	2.50 (0.15)	0.55 (0.48)	0.55 (0.48)	0.06 (0.81)
Age-sex (B)	2	0.34 (0.72)	0.13 (0.88)	0.18 (0.84)	0.51 (0.62)	0.10 (0.90)	0.03 (0.97)
A × B	2	0.16 (0.85)	0.40 (0.69)	0.05 (0.95)	0.02 (0.98)	0.17 (0.84)	1.01 (0.40)
Error	10						

affected by sex and age of bats, and whether reduced foraging activity occurs during periods of high lunar illumination. Because Puerto Rico lacks most of the visually oriented bat predators commonly found in mainland tropical settings, our prediction was that foraging activity and movement would not vary due to the amount of lunar illumination present.

Our study site was located in the Luquillo Experimental Forest (LEF), also known as the Caribbean National Forest (18°10' N, 65°30' W), in the northeast corner of Puerto Rico within the Luquillo Mountains. The tabonuco forest, the tropical rain forest life zone within the LEF, is found on mountain slopes below 650 meters. Rainfall is substantial, over 2000 mm annually.

This tropical forest has been a focus for forestry and ecological research throughout this century (Brown *et al.* 1983, Mosquera & Feheley 1984). However, relatively little is currently known about the ecology and behavior of resident mammals. The present composition of the mammalian community in the LEF appears to be a product of biogeographic, abiotic, and human-mediated events (Willig & Gannon 1996). Bats compose the major portion of the Puerto Rican mammal fauna in terms of species richness and density (Willig & Bauman 1984, Willig & Gannon 1996), and are the only indigenous mammals. All other mammal species were introduced in Post-Columbian times. Of the 14 extant bat species, nine occur within the LEF.

The red fig-eating bat (*Stenoderma rufum*) is a Caribbean endemic, known only from the islands of Puerto Rico, St. John, and St. Thomas (Genoways & Baker 1972, Willig & Gannon 1996). As a result, it is a little studied species and is rare in scientific collections. Only *S. rufum* from Puerto Rico has been collected in appreciable numbers (Gannon *et al.* 1992). It is frugivorous, feeding on a variety of fruit including *Cecropia schreberiana*, *Manilkara bidentata*, and *Prestoea montana*, and has been indicated as an important seed disperser within the LEF (Gannon & Willig 1994). It comprises at least 25 percent or more of the bats in the tabonuco forest life zone (Willig & Bauman 1984, Gannon & Willig 1994). Almost all data available on this species are derived from work on individuals from this population; nonetheless, relatively little is known concerning its autecology.

Bats were captured during the summer (June, July, and August) of 1989, using mist nets at sites established within the tabonuco forest near El Verde Field Station (Terrestrial Ecology Division, University of Puerto Rico). Age, sex, and reproductive condition were recorded for each captured bat. Age was determined for each individual as evidenced by epiphyseal-diaphyseal fusion of long bones in the wing (Anthony 1988). Radio transmitters (model BD-2, Holohil Systems, Ltd., Ontario, Canada) were attached to the dorsal pelage of selected *S. rufum* using surgical cement ("Skin Bond", Pfizer Hospital Products Group, Inc., Largo, Florida), as described by Wilkinson and Bradbury (1988). Each transmitter weighed 1.2 g. This is under the maximum mass (approximately 5% of body mass) recommended to

TABLE 2. Movement parameters (means in meters, followed by standard error in parentheses) of *S. rufum* during the light (full) and dark (new) phases of the moon. Total = light and dark phases combined.

Group	N	Total distance/h	Maximum distance	Minimum distance	Mean distance/move	Moves/h	% Time/roost
Light phase	8	232.5 (41.6)	146.5 (13.9)	19.3 (8.6)	63.9 (9.0)	3.6 (0.3)	72.0 (8.0)
Dark phase	8	223.2 (30.2)	152.0 (17.3)	15.2 (1.4)	54.5 (6.0)	4.0 (0.3)	74.2 (4.2)
Total	16	227.8 (24.9)	149.2 (10.7)	21.3 (3.5)	59.2 (5.3)	3.8 (0.2)	73.1 (4.4)

minimize flight and behavioral disturbance (Aldridge & Brigham 1988). All adults were reproductively inactive when tagged (females were neither pregnant, as determined by abdominal palpation, nor lactating; testes were not descended in males). This minimized confounding effects such as increased energy demands for pregnant or lactating females.

Twenty-four hours or more after release, bats were tracked by two observers, each using a hand-held telemetry receiver and antenna (model TRX-1000S, Wildlife Materials, Inc., Carbondale, Illinois). Location of individual bats was determined by triangulation of signals simultaneously obtained by two field receivers. Logistics were simplified because of a series of well-maintained trails throughout the forest. Two-way radios allowed field observers to make simultaneous measurements that could be verified immediately in the field. Telemetry accuracy using this protocol in the LEF was extremely good, as evidenced by field tests (Gannon 1991, Lindsey & Arendt 1991).

We collected intensive focal data on location and movement of individuals. Each radiotagged bat was tracked continuously on two consecutive nights. The first night of tracking was begun at 2000 hr, approximately 1.5 h after dusk. The second night of tracking began at 0000 hr and continued until 0400 h (about 2 h before dawn). Bat location and activity were recorded every 5 minutes to generate a log of nightly activity over 8 hours, a period that spanned most of a night. For each bat, distance traveled per hour, maximum distance traveled per move, minimum distance traveled per move, mean distance traveled per move, number of moves per hour, and percent of time spent flying (versus feeding in night roosts) were determined from the log of nightly activity. These data were examined for association with phases of lunar illumination. Nine individuals (2 adult males, 4 adult females, and 3 juveniles) were observed during a dark lunar phase (3 days on either side of a new moon when lunar illumination was at its lowest), and nine individuals (2 adult males, 4 adult females, and 3 juveniles) were tracked during a light lunar phase (3 days on either side of a full moon, when lunar illumination was at its peak). Two-way Analysis of Variance (ANOVA) was used to ascertain the effect of lunar phase and age-sex on each movement parameter (Sokal & Rohlf 1981). Juveniles, regardless of sex, were combined into one group to enhance power of statistical tests.

Locating and following individual bats over each of the two night sample periods was relatively easy to accomplish by two individuals on foot. Each of the 16 bats we followed exhibited fidelity to a single feeding area of about 2 km², and roosted nearby in the forest canopy during the day. Subsequent longer periods of radio tracking of the same individuals (Gannon & Willig 1994) demonstrated that fidelity to the same feeding and roosting area continued for at least several weeks. Actual tracking time over the two nights varied slightly for some individual bats due to weather conditions. On three occasions (2 dark phases and 1 light phase) we were forced to curtail radiotracking due to heavy rains. Tracking time for all 16 bats averaged 6.05 h (range 2.33 to 8.00 h).

For each of the six parameters of activity or movement which we tested, no significant differences occurred due to age-sex, lunar phase, or their interaction (Table 1). Actual sample differences between each group were slight (Table 2). All tracked individuals remained active throughout the night, returning to a day roost shortly before dawn. As we predicted, *S. rufum* did not alter any activity or movement parameters in response to the amount of lunar illumination present.

These observations lend support to the idea that lunar phobia is a behavior related to predator avoidance. Lunar phobia and other behaviors resulting in predation avoidance can incur high costs by increasing energy or time required to obtain critical resources. Unlike most mainland settings, the tabonuco forest harbors few chiropteran predators. Marsupials are absent; snake species richness and density are low. The Puerto Rican boa (*Epicrates inornatus*), the only potential snake predator of bats in the forest, is listed as endangered because of its rarity. Only two owls are present on Puerto Rico. The short-eared owl (*Asio flammeus*) is uncommon and found mostly in open country. The Puerto Rican screech owl (*Otus nudipes*) occurs in wooded areas including the LEF. It is a small owl (23–25 cm) that feeds mostly on invertebrates (Snyder *et al.* 1987, Wetmore 1916). On occasion, it has been known to take small vertebrates (lizards and birds) up to the size of 12 g. None of the frugivorous bat species on Puerto Rico are small enough to be feasible prey for the screech owl (*Stenoderma rufum* is the smallest frugivore, averaging 25 g, more than twice the maximum known prey size). Thus, there is no evidence that the screech owl is a predator of these bats.

Presumably, this endemic bat has evolved in Puerto Rico, in the absence of visually-oriented nocturnal predators. The absence of predators should shift the balance between the costs and benefits associated

with foraging on bright nights, thereby selecting against lunar phobia by *Stenoderma*, as well as in other island populations of frugivorous bats which lack such predators.

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Postfire Resprouting of *Hypericum irazuense* in the Costa Rican Páramos: Cerro Asunción Revisited¹

Key words: Costa Rica; fire; *Hypericum irazuense*; páramo; regeneration; *Vaccinium consanguineum*; vegetation.

THE SHRUBBY PÁRAMO VEGETATION on the highest peaks of the Cordillera de Talamanca in southern Costa Rica is dominated by the bamboo *Chusquea subressellata* and by evergreen shrubs in the Ericaceae, Hypericaceae, and Compositae families (Weber 1959, Cleef & Chaverri 1992). The Costa Rican páramos have burned periodically in this century, and at intervals throughout the Holocene as evidenced by charcoal fragments in sediment cores from glacial lakes (Horn 1993).

Janzen (1973) was the first to describe postfire vegetation dynamics of páramo shrubs and bamboo, based on observations made three years after a fire on the south slope of Cerro Asunción along the Inter-American highway. Janzen focused on height recovery by the bamboo and two commonly associated evergreen shrubs: *Vaccinium consanguineum*, and *Hypericum irazuense* (his *H. caracasenum*). Janzen did not specifically address fire survival, but his qualitative observations and photographs make clear that both shrubs resprouted vigorously, with apparently little mortality.

However, subsequent studies of shrub dynamics on other burn sites within the Buenavista páramo and in the Chirripó páramo some 30 km to the east (Williamson *et al.* 1986, Horn 1989), have revealed significant disparity in the fire response of these two shrub species. *Vaccinium consanguineum* has shown consistently high (90–98%) rates of resprouting at all other sites examined, but *Hypericum irazuense* has shown very low (4–14%) rates of resprouting.

The very different response of *Hypericum irazuense* following the 1969 Asunción fire has generated discussion. Williamson *et al.* (1986), comparing the Asunción fire to a 1973 fire on nearby Cerro Zacatales, hypothesized a link between fire history and resprout success, with more frequently burned sites showing lower resprout success because of the depletion of energy (root) reserves. This relationship holds when comparing only these two fires, as the Asunción site was apparently fire free for a longer interval prior to the 1969 fire than was the Zacatales site prior to the 1973 fire (Asunción, ~30 yr, based on ring counts on shrub stems by Janzen, 1973; Zacatales, ~10–12 yr based on ring counts by Williamson *et al.* 1986 and Horn 1989). However, the relationship did not appear to hold following a fire that occurred on Cerro Sábila, another peak in the Buenavista páramo, at about the same time as the Asunción and Zacatales fires (Horn 1989). Before the Sábila fire, the site had been fire-free for about as long as the Asunción site (≥ 29 yr, based on ring counts), but following the fire only 14% of burned *Hypericum irazuense* shrubs resprouted.

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