

FORAGING BEHAVIORS IN FISH-EATING BATS (*NOCTILIO LEPORINUS*)

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Abstract: Predator-prey interactions are largely affected by prey availability, which can be influenced by many abiotic and biotic factors. We studied the fish-eating bats, *Noctilio leporinus*, in Corcovado National Park, Costa Rica. Using model selection, we assessed the relative importance of four factors (tide, time, location, and number of fish jumps) on bat foraging and abundance. The best predictors of bat abundance were location, time of night, and the interaction of these two factors. These also were the best predictors of bat fishing frequency, although few fishing attempts were observed. Contrary to conclusions from previous studies in the same lagoon, tide and fish activity were not significant predictors of bat abundance or foraging. Circling behavior, which was most common near the roost, may facilitate defense of roost or assembly of small groups that aid in foraging. Bats upstream often flew in a straight line past our observers possibly searching for more optimal foraging locations. These bats probably forage at a range greater than our sample area.

Key words: bat foraging behavior, coastal systems, greater bulldog bat, predator-prey interactions, Río Sirena

INTRODUCTION

Prey density may be the most important factor influencing foraging behavior among carnivorous animals. Prey density may also affect feeding success, particularly when prey are difficult to find or hunt, or when abundant refugia from predation are available.

In aquatic systems, both marine and aerial piscivores prey on fish, and fish density determines the success of these predators. Suitable prey fish below some threshold depth may be out of reach to all but the most effective diving terrestrial piscivores. In coastal systems, tidal fluctuations may interact with

bottom topography to determine the abundance and distribution of habitats that subject fish to aerial predation. In addition, tide likely influences marine predatory fish density, which could drive prey from deep water refugia into shallower water where they are vulnerable to aerial attack. Thus, the presence and activity of aquatic predators may benefit terrestrial piscivores by increasing prey accessibility. Alternatively, the prey fish distribution and position in the water column may be unrelated to predation or tide.

Fish-eating bats (*Noctilio leporinus*) have been reportedly observed every year since at least

1994 in a large lagoon at the mouth of the Río Sirena in Corcovado National Park. Since 1998, the bats have been the subject of four other Dartmouth FSP projects (Yale et al. 1998, Veysey et al. 2000, Leslie et al. 2001, Valderrama and Madigan 2005). Previous work suggested that bats may focus their hunting effort on times and places where large aquatic predators including bull sharks (*Carcharhinus leucas*) and crocodiles (*Crocodylus acutus*) are feeding most actively, driving smaller fish to shallower water (Leslie et al. 2001, Veysey et al. 2000). Bat foraging may also vary with tide, which simultaneously alters the total volume of water in the lagoon, the proportion of shallow water, and perhaps the density of marine predatory fish. Yale et al. (1998), Veysey et al. (2000) and Leslie et al. (2001) all found that bat fishing attempts peaked at high tide, most likely due to an increase in small fish density.

We found a colony of *N. leporinus* living in a large, common mangrove tree (*Mora oleifera* : Fabaceae) ~200 m northeast of the mouth of the Río Sirena (within 5 m of the present boat landing). We observed bats foraging in the lagoon at night. Preliminary daytime observations suggested that fish activity varied systematically by tide and/or time of day and roughly correlated with hunting activity by herons and shorebirds.

If bat foraging depends on prey density, then factors that determine prey availability should also influence foraging behavior. In Río Sirena lagoon, tide, time of night, location of observation, and fish activity (as measured by fish jump frequency) are likely to influence prey availability and subsequently bat abundance and fishing behavior. Specifically, we predicted that bats would forage more at high tide downstream of their nest, where a broad shelf with shallow water may act as a refuge for prey fish from aquatic predators but make them highly susceptible to bat attack.

METHODS

Starting at dusk on 8 and 9 February 2008, we sampled a *N. leporinus* colony at the Río Sirena Lagoon ca. 1.5 km northwest of Estación Biología Sirena, Corcovado National Park, Costa Rica. We observed bats at 3 locations along the river: at the roost, 50 m downstream from the roost, and 50 m upstream from the roost. Beginning at 1800, 2200, and 0430, which roughly corresponded to the peaks of high, low and then a second high tide [Feb 8-9 high: 15:59, low: 22:02, high: 04:14; Feb 9-10 high: 16:37, low: 22:42, high: 04:52], we conducted 5 10-min observations (separated by 2 minutes) of all visible individuals. We used a flashlight to illuminate bats, following individuals for as long as

possible, and recording their fishing attempts (contact with the water), locations (0-2, 2-4, or 4+ m from either bank), and flight patterns (circular or straight). We also recorded the maximum number of bats observed during that time period, and counted the number of audible fish jumps (large or small fish), as Leslie et al. did to quantify large fish activity in 2001.

We created a depth map of the lagoon and upstream region to

evaluate a potential correlation between lagoon depth variation and fish and bat activity. We used 80 GPS and depth measurements at ca. 5 m intervals at or near high tide on 8 February. We also remeasured a point in the center of the river at low tide to calculate local tidal flux.

RESULTS

TABLE 1. Comparison of alternative models predicting bat abundance in Río Sirena Lagoon, Costa Rica. Each row represents one theoretical driver of bat abundance and behavior. The three righthand columns indicate the best linear statistical model (minimum AIC with all parameters being statistically significant at $P < 0.05$) that includes this theoretical driver; ΔAIC values are reported relative to the best model overall.

Variable	Biological Reason	Best Model	r^2	ΔAIC
Location (L)	Proximity to nest may affect number of flying bats	$Y=f(T, L, T*L)$	0.902	0
Time (T)	More bats fly at certain times of night	$Y=f(T, L, T*L)$	0.902	0
Tide (TD)	Bat activity may vary with water depth	$Y=f(TD, L)$	0.709	9.3
Fish Jumps (F)	Fish jumping indicates marine predator activity which may influence bat activity	$Y=f(L, F, T*L)$	0.913	-0.42

On each of two nights, we observed 44 bats emerge from their roost on the Río Sirena Lagoon beginning at dusk (~18:15) and returning at dawn (~05:30). Generally, bat density and behavior differed as a function of time of observation (dawn, dusk or night) and by location of observation.

Circular flight patterns were significantly more common near the bat roost. We observed more than 3 times as many bats flying in circular pattern in this location than at the upstream or downstream sampling points ($F = 37.4$, $df = 2,7$, $P = 0.0002$; Fig. 1c). None of the other main effects or interactions were significant predictors of flight pattern. Bats flying in a circular path sometimes fished, often landed briefly near the nest entrance, and occasionally entered the nest. Many of the straight-flying bats at the sites away from the roost flew well out of sight, frequently in an upstream direction.

Although few fishing attacks were observed overall, the proportion of bats fishing reached a maximum of 23% ($\pm 1 \text{ SE} = 18.3 - 83.2\%$) at dawn at the downstream site (Fig 1e). The model predicting proportion of bats fishing included location, time, and a time*location interaction ($F = 7.29$, $df = 8,8$, $P = 0.0055$). However, only the location*time interaction was a significant predictor of bat fishing proportion ($F = 12.82$, $df = 4,8$, $P =$

0.0015; Fig. 1e). Downstream, a greater proportion of bats foraged at dawn ($P=0.0004$), while at the roost, fishing behavior didn't vary much over time ($P = 0.49$), with the greatest proportion of bats fishing at dusk. Upstream, no bats foraged at dawn, and more foraged at dusk than at night (Fig 1e).

When time and location were held constant, the two nights of observation were very similar with respect to bat abundance counts and the proportion of circular flight. Note that the paired observations tend to fall on the line of equality in Fig. 1b and 1d. In contrast, the regression line for bat feeding proportion had a slope that was significantly different from 1 ($F = 18.3$, $df = 1,5$, $P = 0.008$; Fig. 1f). This regression was strongly driven by one observation period dawn on the first night at the downstream site), in which 6 of 18 bats fished (a proportion of 0.33). Also shown in Fig. 1f is the regression line excluding this high fishing proportion, which falls very close to the line of equality. Because all three variables were similar on different nights, we elected to use date of observation as a replicate measure for all analyses.

Location, time, and the interaction between location and time were the best predictors of bat abundance according to AIC model selection (ANOVA, $F = 10.4$; $df = 8,9$; $P = 0.001$; Table 1). The model

containing fish jumps was essentially equivalent ($\Delta AIC < 2$) so we preferred the simpler model. Location (roost, upstream, or downstream) was a significant predictor of bat abundance ($F = 28.8$; $df = 2,9$; $P = 0.0001$), as was observation time (dusk, night, or dawn) ($F = 7.4$; $df = 2,9$; $P = 0.014$). The interaction of location and time was a non-significant predictor of bat abundance ($F = 2.7$; $df = 4,9$; $P = 0.10$).

DISCUSSION

Our results differed from previous studies, which found evidence of strong interactions between bat foraging behavior and tidal cycles, time of night, (Yale et al. 1998, Veysey et al. 2000), prey location, and lagoon morphology (Leslie et al. 2001). We found no evidence that bat foraging behavior was related to tide, water depth, and fish activity at the surface of the lagoon. Likewise, we did not detect indirect interactions between aquatic predators and bats influencing prey location and availability. Surprisingly, we also observed few fishing attempts, which suggests that changing environmental pressures may have caused a shift in *N. leporinus* foraging behavior. *N. leporinus* can be insectivorous (LaVal and Rodríguez-H. 2002), and a shift of main prey type from fish to insects may explain the reduced interaction of bat foraging behavior

with abiotic factors correlated to fish availability.

We expected to see more bats downstream during high tide where a broad shelf with shallow water would drive fish seeking refuge from marine predators close to the surface, but more bats were observed upstream. Because bats echolocate prey better in calm water (Siemers 2001), it is possible that bats avoid areas with strong current or wave action close to the ocean. Additionally, if elevated frequency of fish jumps correlates with higher marine predator density, it is possible that predatory fish, sharks, and crocodiles may compete with *N. leporinus* for similar prey rather than facilitate bat fishing success.

Although a previous study (Valderrama and Madigan 2005) observed more circular flights at high tide when more bats foraged, we found that location, not tide or foraging behavior, influences flight pattern. Circular flight patterns of *N. leporinus* which were most common immediately around the roost may increase ability to protect the roost. Circling bats may also coordinate foraging through direct communication with scouts that return to the roosts after finding successful hunting grounds. *N. leporinus* are reported to forage in small groups that benefit from sharing information on prey location (Brooke 1994), so circling may facilitate the assembly of these

groups before leaving the roost area. In contrast, the straight flight patterns observed upstream and downstream may be more beneficial for locating and catching prey. Although we observed few fishing attempts, bats frequently moved beyond the range of our observers, particularly upstream. *N. leporinus* are strong fliers (Hayward and Davis 1964), and may prefer sites far upstream or in nearby rivers. This suggests that the foraging area is considerably greater than the 200-300 m visually assessed in this study. Further studies on *N. leporinus* foraging would benefit from broader sampling conducted over larger river sections.

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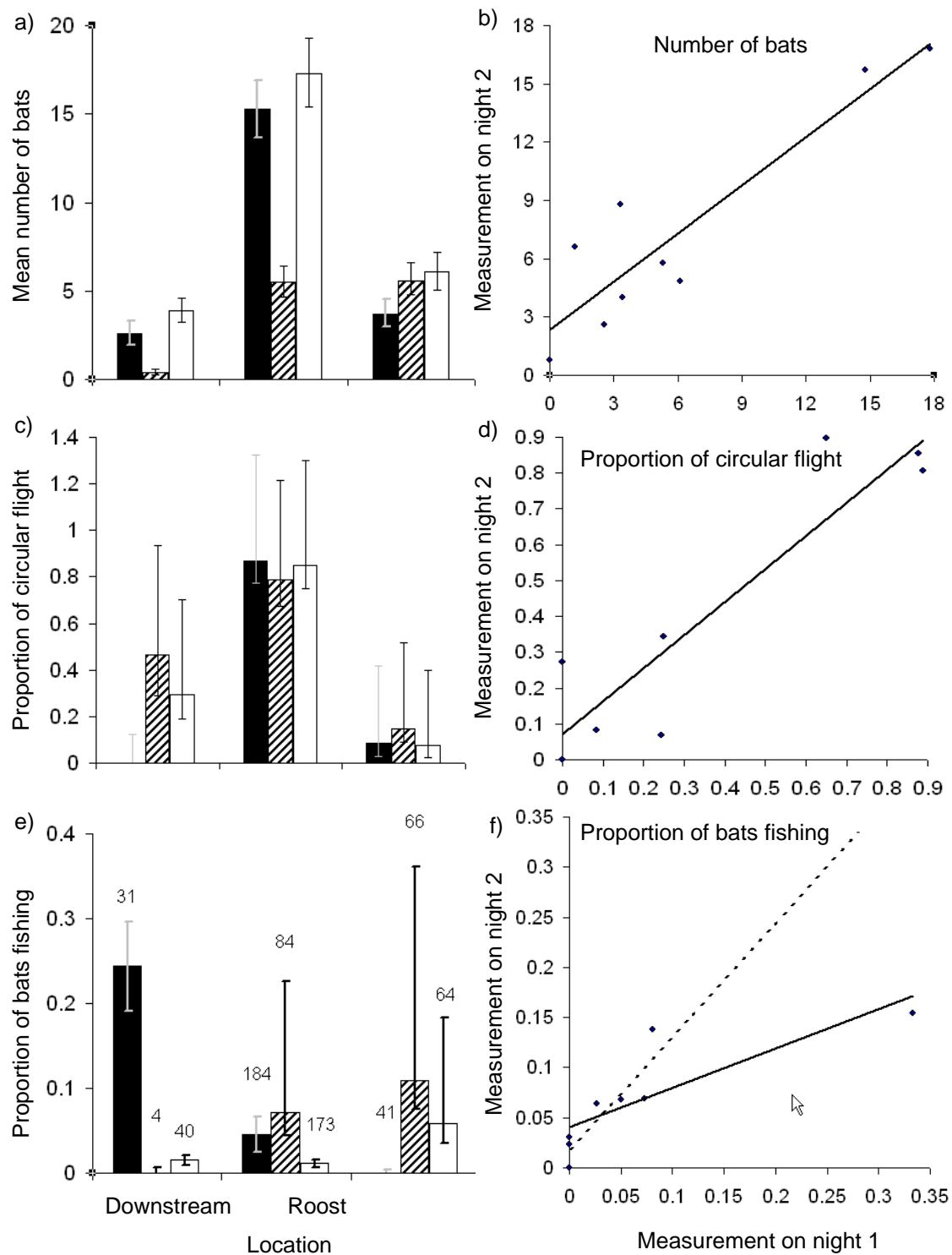


Figure 1. Left side: Mean (± 1 SE) bat number, proportion of circular flight, and the proportion of bats fishing by location and time of day; dawn, dusk, and night = black bars, hatched bars, and white bars, respectively (back-transformed to original units). Numbers over the bars in (e) refer to the total bat count at each time and location. Right side: Comparisons of nights (paired for site and time).



Figure 2. Roost of *N. leporinus* in *Mora oleifera* (Fabaceae) along the Río Sirena, Corcovado, Costa Rica. White arrow indicates the entrance hole (oval opening 10 x 15 cm diameter). Note the guano at the base of the tree, just below the high tide line.



Figure 3. Close up of *N. leporinus* flying next to roost – 12 Feb 2008. Photo by Alex Spinoso.

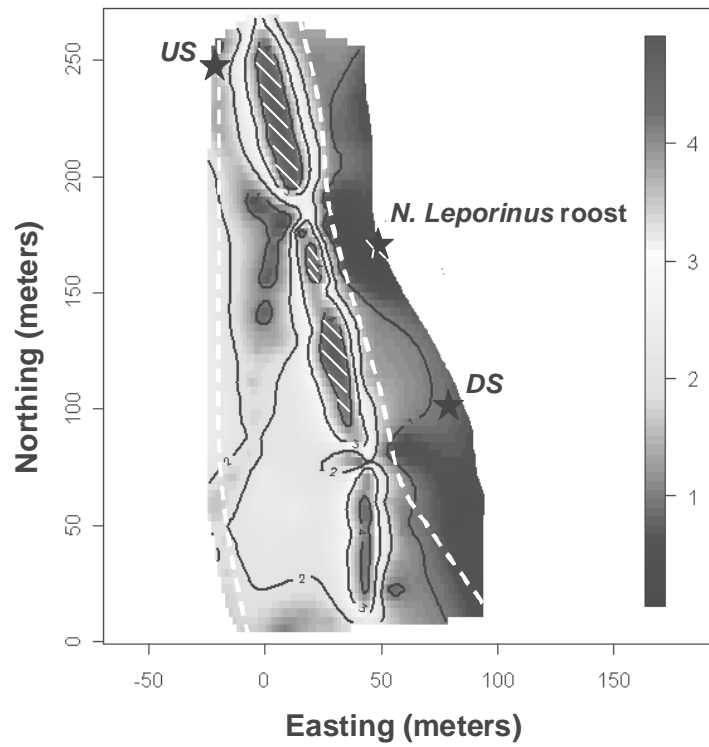


Figure 4. Contour map of depth in the Río Sirena lagoon. Stars show observations sites (Roost location near boat launch at N 8.48128 W 83.59694). Hatched area corresponds to the main canal; white dotted line corresponds to the approximate low tide line.