# TIDAL EFFECTS ON FISHING BAT BEHAVIOR IN THE RIO SIRENA LAGOON AT CORCOVADO NATIONAL PARK

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*Abstract.* A population of fishing bats (*Noctilio leporinus*) has been fishing within the Rio Sirena tidal lagoon for several years. We hypothesized that the foraging behavior and habitat requirements of fishing bats were linked to tidal cycles. Over three nights, we recorded the time and location of 977 bat flights and 536 fishing attempts while monitoring tidal flux, water turbulence and fish abundance. Peaks in bat foraging activity occurred in the hour before high tide on each night and shifted between nights with the shift in high tides. Bats foraged over both calm and turbulent water, showing that fishing bats do not necessarily require calm water for fishing. The predatory activity of large marine fish during high tide may facilitate bat foraging by causing small fish to aggregate near the shores of the lagoon (in shallow water where it is easier for bats to fish).

*Key Words: foraging, habitat requirements,* Noctilio leporinus

## INTRODUCTION

The greater bulldog bat (*Noctilio leporinus*) is found along the Pacific coast in Central and South America in lowland areas with access to open water (Emmons 1997). It is specialized for catching small fish, but sometimes supplements its diet with insects, aquatic invertebrates, and terrestrial invertebrates. Fishing bats rely on echolocation to detect ripples on the water's surface caused by small fish. When prey have been located, the bat flies low over the water's surface and drags its scimitar-shaped claws through the water in an attempt to gaff a fish (Brandon 1983).

Fishing bats are thought to forage over relatively still water (Brandon 1983). However, bats were fishing every night in the Rio Sirena lagoon even though it was sometimes quite turbulent from tidal fluxes. Bat activity appeared to vary with time of night and change location within the lagoon. Our objective was to characterize foraging habitat for fishing bats and identify the qualities that made Rio Sirena lagoon a site that can reliably sustain *N. leporinus* populations. (*N. leporinus* were also present in 1996 and presumably other years.) Because tidal flux affects fish density and distribution, as well as water turbulence, we hypothesized that the tide is a main factor influencing when and where fishing bats forage in the Rio Sirena lagoon. We predicted that bats would prefer to fish over calm water, because this should facilitate echolocation of prey, that bats would forage over shallow waters near shore where fish are easier to locate and capture, and that the density of small fish near shore would increase when large predatory marine fish invade the lagoon at high tides.

## METHODS

We observed bat activity in the Rio Sirena lagoon at Corcovado National Park, Costa Rica, during the nights of 4 - 6 February 1998. We divided the lagoon into 6 sections of equal shore area and identified two zones of turbulence within the lagoon, with the narrower sections of Zone 1 (sections 1-2, Appendix) having higher levels of turbulence than the wider sections of Zone 2 (sections 3-6, Appendix).

We recorded data in eight 0.5 h sample periods during nights 1 and 2 (one additional sample period on 4 February, night 0), observing each section for 5 min in each sample period. During each 5-minute observation bout, we recorded bat flights, bat fishing attempts, large fish activity, density of small fish near the shore and levels of water turbulence. After each sample, we also recorded at what distance from shore the majority of the fishing attempts occurred. We measured bat flights as the number of times bats flew across an imaginary plane, perpendicular to the shore, bisecting each section. Bat contact with the water surface in the section area was defined as a fishing attempt. We measured large fish activity as the number of times a larger fish audibly disturbed the surface of the water. Small fish density near shore was determined by counting the number of fish present in five 15 x 15 cm plots haphazardly located along the shoreline of each section within 1 m of the shore. We used an ordinal scale of 0 to 5 to estimate levels of water turbulence for each sample: 0 = still water and 5 = maximal turbulence.

For analyses, we averaged each group of 6 5-minute observations in the lagoon, and treated the average as one observation. Sections were grouped within zones, and times were grouped into 8 75-minute intervals. We compared bat flights, fishing attempts, large fish activity, small fish abundance, and turbulence with a three-way ANOVA that included night, time and zone. We used correlations to evaluate relationships among dependent variables, and we used a chi-square to test the null hypothesis that bat fishing activity was evenly distributed across the lagoon.

## RESULTS

We observed *Noctilio leporinus* foraging in the lagoon during every sample period throughout both nights of the study. Bats made 977 flights over the water's surface and 536 fishing attempts during 8.5 h of observation. The bat population consisted of at least eight individuals, the maximum number seen simultaneously.

Periods of bat flights and feeding shifted approximately one hour later each night (Figure 2; Table 1). There were two peaks in bat activity, one during the late evening, and the other in the early morning (Table 1; Figure 1). The shift in the first peak of activity coincided with the change in the time of high tide (20:48 on day 0, 21:55 on day 1, and 23:05 on day 2). In contrast to the first activity peak, the second activity peak occurred at about the same time each night (c.a. 04:00), just before dawn and after the tide had receded from the entrance of the lagoon. Low tide occurred below the level of the lagoon, and lagoon water reached its lowest levels approximately 2.5 h before actual low tide.

There were higher levels of water turbulence during high tide, especially in Zone 1 (Figure 1, Table 1); waters within Zone 2 remained calm throughout the night. Bats fished in the channel (Zone 1) while the tide was coming in and the water was most turbulent, and fished throughout the lagoon during low tide, when waters were calm. Small fish abundance near the shore and large fish activity within the lagoon were negatively correlated with water turbulence (Table 2). The density of small fish

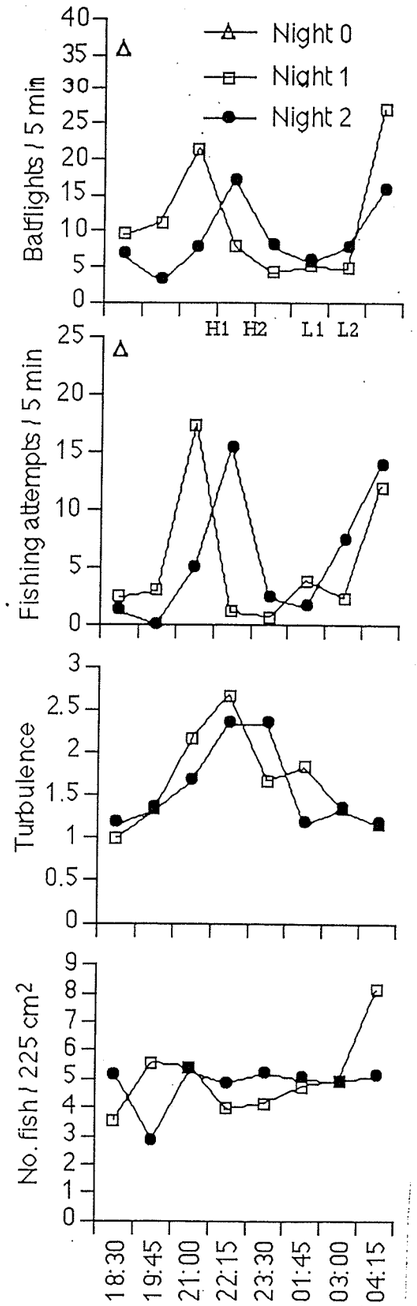


FIG. 2. Bat flights, bat fishing attempts, water turbulence and small fish density in the tidal lagoon north of the Sirena fields station, over three consecutive nights. Approximate times of the high and low tide are indicated by H1, H2, L1, L2.

near shore and the frequency of fishing attempts increased with large fish activity (Table 2). Bats showed a strong preference for fishing within 1 m of shore: in Zone 1, 95% of fishing attempts occurred within 1 m of shore ($X^2$ = 160.58, P < 0.005); in Zone 2, 83% of fishing attempts occurred with 1 m of shore ($X^2$ = 936.28, P < 0.005).

## DISCUSSION

Tidal flux affected bat foraging patterns in the Rio Sirena lagoon. The first peak in bat activity shifted with high tide, supporting the hypothesis that tide had an effect independent from time of night. The second peak in bat activity was just before dawn on both nights and did not clearly vary with tides. Because low tide occurs well below the level of the lagoon, the effect of low tide on the lagoon was much longer than the effect of high tide and may, therefore, have less of a synchronizing effect on bat activity. It could also be that bats need to feed before roosting and that pre-dawn feeding occurs irrespective of tidal cycles.

Bats were able to feed over both calm and turbulent waters, suggesting that they do not require calm water to echolocate underwater prey. They showed a strong preference for fishing near shore, perhaps because fish are easier to echolocate and capture in shallow waters. We hypothesize that the feeding activity of large fish in the lagoon cause small fish to aggregate and take refuge from predation in shallow waters near the shore. The increase in small fish density and bat fishing attempts with higher activity of large fish support this position. We would expect accessibility to fish in shallow waters to be a common characteristic of habitats occupied by fishing bats.

It is possible that the population of fishing bats in the Rio Sirena lagoon is considerably greater than eight (the maximum number that we observed). It seems that it would have been energetically taxing for only eight bats to be responsible for all the activity that we observed over two nights. *Noctilio albiventris* average only 120 minutes of foraging time per individual per night (Fenton et. al., 1993). If *N. leporinus* in the Rio Sirena lagoon fish for a similar amount of time, the total population size could easily be 30 - 50 individuals. Locating the roosting sites for these bats would allow studies of individual foraging schedules of bats.

Future studies could further our understanding of habitat requirements by observing multiple populations of fishing bats. No bats were observed fishing in the neighboring Rio Claro lagoon during peak activity periods on the same nights of our study (J. Mooney, pers. comm.). A comparison of the structure of these two areas would give further insight into the habitat requirements of *N. leporinus*.

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TABLE 1. Results from three-way ANOVAs testing for changes in night, time and zone within the Rio Sirena lagoon.

| | DF | F-statistics | | | | |
|---|---|---|---|---|---|---|
| | | Bat flights | Bat fishing attempts | Fish abundance | Water turbulence | Large fish activity |
| Night | 1 | 2.05 | 0.52 | 0.07 | 0.26 | 0.66 |
| Time | 7 | 7.48*** | 4.86*** | 0.76 | 7.32*** | 1.81 |
| Zone | 1 | 0.47 | 1.53 | 34.73*** | 234.32*** | 24.94*** |
| Night x Time | 7 | 2.80* | 4.33*** | 1.49 | 1.06 | 2.79* |
| Night x Zone | 1 | 0.05 | 0.71 | 0.61 | 0.01 | 0.06 |
| Time x Zone | 7 | 2.41* | 3.08** | 0.52 | 1.83 | 5.51*** |

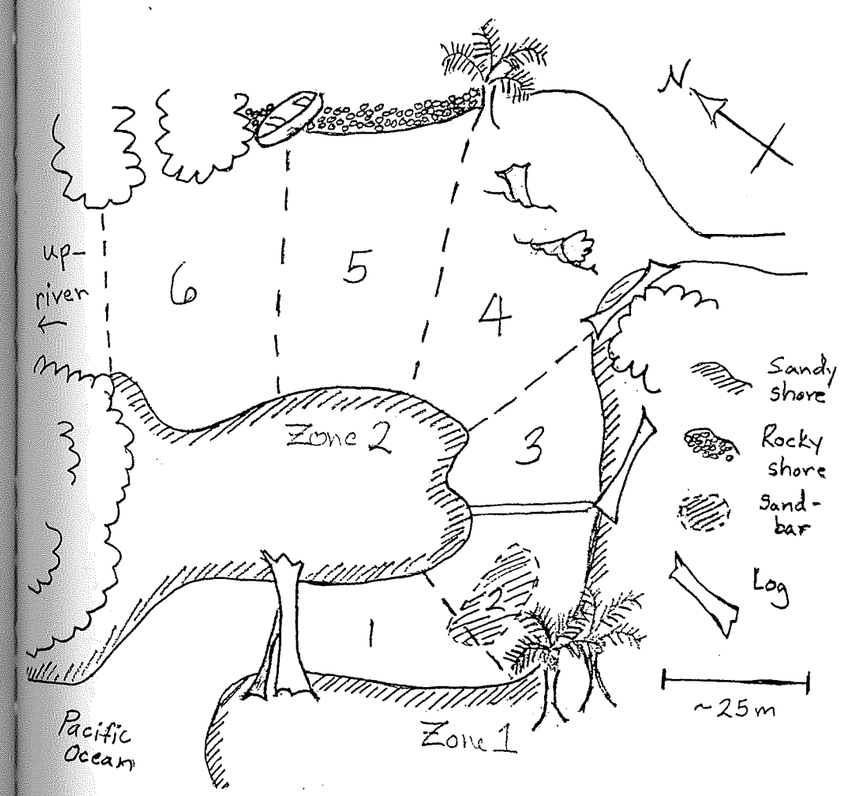
* P < 0.05; ** P < 0.01; *** P < 0.001.





TABLE 2. Correlation matrix among bat fishing activity and lagoon conditions.

| | Bat flights | Bat fishing attempts | Fish abundance | Large fish activity |
|---|---|---|---|---|
| Bat fishing attempts | 0.75*** | | | |
| Fish abundance | 0.09 | 0.13 | | |
| Large fish activity | 0.24* | 0.40*** | 0.29** | |
| Water turbulence | 0.14 | 0.04 | -0.39*** | -0.40*** |

* P < 0.05; ** P < 0.01; *** P < 0.001.

APPENDIX. A sketch of sample sections and zones in the Rio Sirena lagoon, including important landmarks.