Sharks, marine fish, and lagoon morphology: Factors affecting the foraging behavior of the greater bulldog bat

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Abstract: Noctilio leporinus, the greater bulldog bat, is a piscivorous bat species that forages over open bodies of fresh and salt water in the lowland tropics of Central and South America. Previous studies have found a distinct peak of fishing activity at high tide, possibly due to an influx of sharks and other marine predatory fish that may drive small fish toward the shallow water where fish are more accessible to bats. We hypothesized that bat foraging activity is driven by the combined effects of predatory fish activity and lagoon bed morphology in the lagoon of the Rio Sirena, Corcovado National Park, Costa Rica. Specifically, we predicted that small fish would be more available to bats at high tide when more predatory fish have entered the lagoon and when the region of shallow water is greater due to lagoon morphology. Additionally, we predicted that this increased prey availability would result in an increase in bat fishing activity in shallow water. On two successive nights during high and low tide, we sampled bat fishing attempts classified by distance from waterline, small fish abundance, and large fish jumps. Contrary to expectation, we found greater large fish activity, as indicated by the frequency of large fish jumps, at low tide than at high tide. As predicted, however, we found significantly greater small fish abundance in shallow waters at high tide than at low tide. We recorded a significantly greater number of bat fishing attempts at high tide than at low tide, with more fishing attempts within 0-1 m from the shore than 1-2 m and 2+ m from the shore at both tides. Our results suggest that lagoon morphology, through its effects on prey availability, may be the primary factor influencing *N. leporinus* foraging behavior.

Key Words: bat foraging, fish abundance, fishing bat, Noctilio leporinus, *piscivory*

Introduction

Noctilio leporinus, the greater bulldog bat, is a piscivorous bat that forages over open bodies of fresh and salt water in the lowland tropics of Central and South America. Its diet is composed almost entirely of fish, though it may also take insects from the water surface. As it flies over the water, it uses echolocation to detect ripples caused by small fish. If a fish is detected, *N. leporinus* dips its large hind feet in the water and drags them for 10 to 20 cm, attempting to gaff the fish with its scimitar-like hind claws (Brandon 1983).

Two previous studies, Yale et al. (1998) and Veysey et al. (2000), examined the effects of time of day and tide on *N. leporinus* foraging behavior in the Rio Sirena Lagoon, Corcovado National Park, Costa Rica. Both studies found distinct peaks of bat foraging at dawn, possibly because the bats were preparing for the upcoming day's fast (Veysey et al. 2000). Both studies also found distinct bat activity peaks at high tides occurring during the night, and suggested that an influx of sharks and other predatory marine fish at high tide may push the small fish on which *N. leporinus* forages into the shallow margins of the lagoon, where they are more easily caught by *N. leporinus*. We suggest an additional and complementary hypothesis in which the morphology of the lagoon's bed has a strong effect on small fish availability. The effect of lagoon bed morphology combined with the presence or absence of sharks and other predatory marine fish may be the driving force behind *N. leporinus* foraging behavior.

We predicted greater large fish activity at high tide than at low tide, as we expected large marine fish to be more abundant in the lagoon at high tide than at low tide. At high tide, the margins of the lagoon within our study area were primarily broad shallows, while the comparably shallow water along the lagoon margins at low tide were less expansive due to the steep slope of the lagoon bed (Figs. 1 and 2). We predicted that at high tide, small fish would seek the broad shallows to hide from predatory marine fish, whereas at

low tide, when marine predators may be absent, they may not need this predator avoidance strategy. If predators are present, such a strategy may not be effective because shallow water at low tide is limited (Fig. 2). Considering these factors, we predicted greater small fish abundance in shallow water near the waterline at high tide.

At high tide, prey may be more available to *N. leporinus* due to the predicted increase in fishable area and fish abundance. Small fish in shallow water may be easier to locate and catch, as they are closer to the surface. Therefore, we also predicted an increase in *N. leporinus* fishing attempts at high tide, with the greater proportion of fishing attempts occurring within 1 m of the waterline where water was shallowest.

Methods

We chose a study site in the Rio Sirena lagoon (see Fig. 1), Corcovado National Park, Costa Rica, with intermediate turbulence and higher bat activity, as previously determined by Veysey et al. (2000). We collected data on two successive nights during high and low tide (3-4 February: high tide at 22:18, tide height = 244 cm, low tide at 4:39, tide height = 40 cm; 4-5 February: high tide at 23:24, tide height = 250 cm, low tide at 5:45, tide height = 30 cm). To minimize the confounding effects of waves and tide, we began collecting data one hour past peak high tide and one hour before low tide.

As an index of large fish activity, we counted the number of audible large fish jumps during 12 6-min intervals at high and low tide. We measured small fish abundance at high and low tide using a flashlight to count all fish visible within 1.5 m semicircles, haphazardly located along the waterline, for 24 2-min intervals. During the daylight hours we measured lagoon margin slope at high and low tide. During 12 6-min intervals we counted the number of bat fishing attempts (bat contact with the water) and classified each attempt by distance from the shore (0-1 m, 1-2 m or 2+ m).

For analysis, we log-transformed the total number of bat fishing attempts and the small fish abundances to normalize their distributions. We assessed the effect of tide on small fish abundance, large fish jumps, and bat fishing attempts using one-way ANOVAs. Tukey-Kramer HSD pairwise comparisons were used to compare fishing attempt distances within tides.

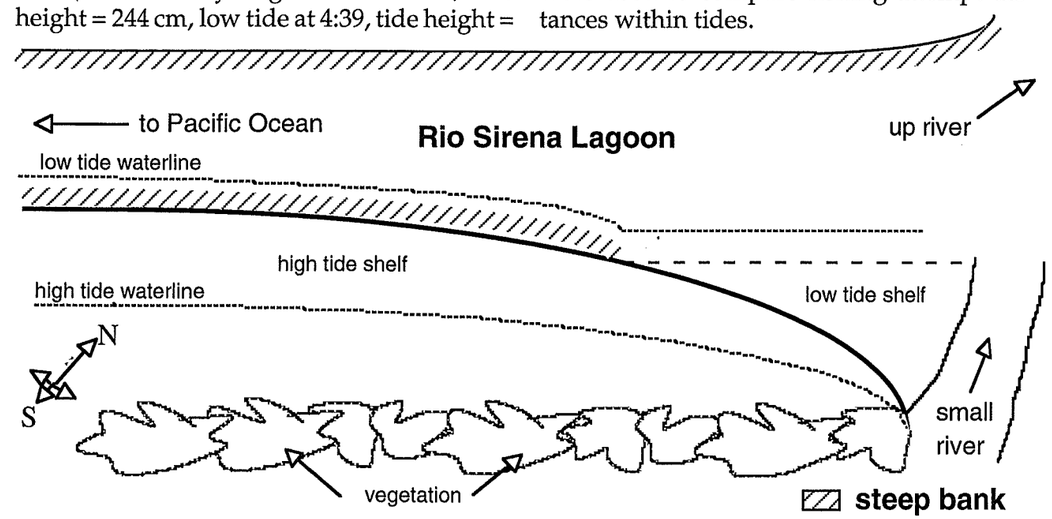

Fig. 1. Map of the study site on Rio Sirena Lagoon in Corcovado National Park, Costa Rica. Activity of bats and fish was recorded along the southern shore of the lagoon. Map not to scale.

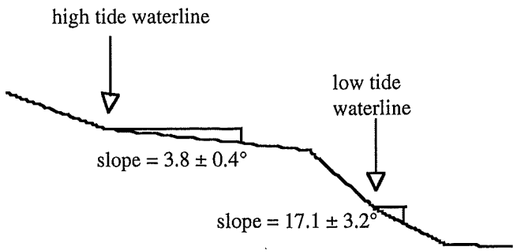

Fig. 2. Cross section of Rio Sirena Lagoon bed within our study area. Slope was significantly greater at low tide (n = 10). Triangles denote areas used extensively by *N. leporinus* for fishing activity.

Results

There was significantly greater large fish activity at low tide than at high tide (ANOVA, F = 32.72, df = 1, 21, P < 0.0001; Fig. 3). We found significantly greater small fish abundance at high tide than at low tide (ANOVA, F = 14.73, df = 1,23, P = 0.0009; Fig. 4). The slope of the low tide lagoon bed margin was significantly steeper than that of the high tide lagoon bed margin (Welch's ANOVA, F = 17.5, df = 1, P = 0.002; Fig. 2). We observed a significantly greater number of bat fishing attempts per 6-min interval at high tide (29.4 ± 6.0) than at low tide (6.1 ± 1.9) (ANOVA, F = 24, df = 1,22, P < 0.0001; Fig. 5). At both high tide and low tide there was a greater number of bat fishing attempts within 1 m of shore than in 1-2 m and 2+ m from the shore (high tide, ANOVA, F = 36.11, df = 2, 33, P < 0.0001, Tukey-Kramer HSD, P < 0.05; low tide, ANOVA, F = 16.06, df = 2, 33, P < 0.0001, Tukey-Kramer HSD, P < 0.05; Fig. 5). Additionally, there was a trend toward greater number of bat fishing attempts in the 1-2 m range at high tide versus low tide (Fig. 5).

Discussion

Assuming that the number of large fish jumps is a good indicator of the presence of predatory fish, our results do not support the hypothesis that sharks and marine fish enter the lagoon at high tide. We found more fish jumps at low tide than at high tide, contrary

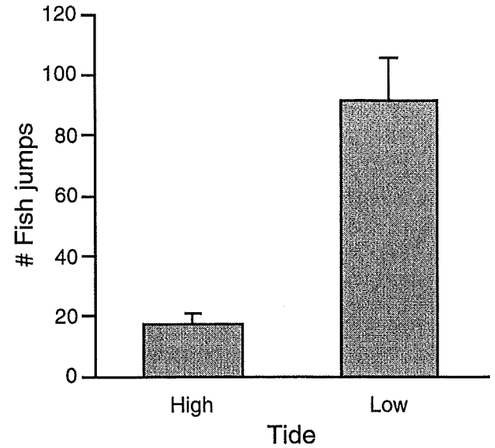

Fig. 3. Mean number (± 1 SE) of large fish jumps at night at high and low tide at Rio Sirena Lagoon during 6-min sampling intervals (n = 12) for each tide.

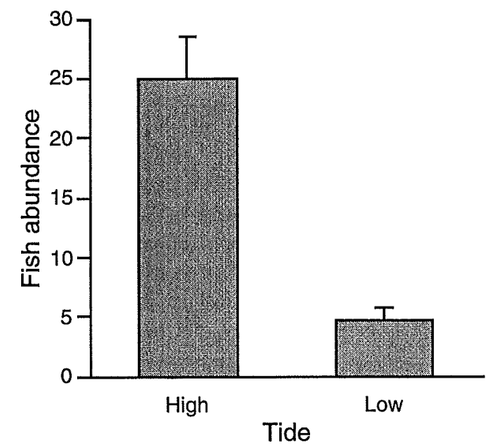

Fig. 4. Mean number (± 1 SE) of small fish counted at night at high and low tide at Rio Sirena Lagoon during 2-min samples (n = 24) in a 1.5 m radius semicircle from the waterline for each tide.

to our prediction. Sharks were observed at high tide several times while collecting pilot data, but only once during our sampling. It may be that predatory fish are only present in the lagoon sporadically, or that the number of large predatory fish (marine or freshwater) in the lagoon is constant, and that the decrease in lagoon volume at low tide concentrates all fish into a smaller area. With both predator and prey fish in closer proximity to one another, predatory (and consequently jumping) activity may be increased. Development of a more sophisticated assessment of predatory fish activity may be needed to fully understand this effect.

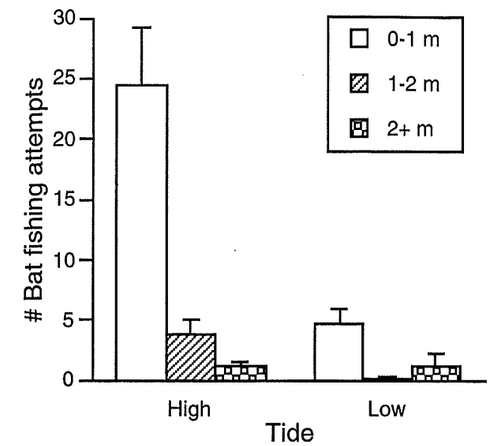

Fig. 5. Mean number (± 1 SE) of bat fishing attempts in three distance intervals from the waterline at high and low tide in Rio Sirena Lagoon (n = 12) during 6 min sampling periods for each tide.

We found more small fish in the shallow water at high tide (Fig. 4) despite low levels of large fish activity (fish jumps). These results suggest that small fish distribution across tides may not be as directly related to shark and marine fish activity as previously proposed. Small fish distribution may instead be more strongly affected by lagoon bed morphology. If predator abundance is constant across tides, we suggest that, in general, small fish seek refuge in the broad shallow areas when they are available, which occurs at high tide (Figs. 1, 2). This may explain the increased small fish abundance at high tide (Fig. 4).

At low tide the lagoon bed is steep and shallow water is limited, which may lead small fish to use a different predator avoidance strategy. For example, we observed that during the day small fish were present at high and low tides but tended to stay in schools. They were seen most frequently in the waters 1+ m from the waterline (pers. observation). It may be that at night low tide, when shallow water is largely unavailable, small fish aggregate into schools in deeper water to avoid predation.

The greater number of bat fishing attempts at high tide is consistent with results found by Yale et al. (1998) and Veysey et al. (2000). We suggest that the observed increases in shallow water area, small fish abundance, and bat fishing activity at high tide are related. Although bats showed a significant preference for fishing within 0-1 m of the waterline at high and low tide (Fig. 3), we also recorded more fishing attempts in the 1-2 m range at high tide than at low tide. This is likely related to the low slope and corresponding increased area of shallow water (and thus hunting area) extending beyond 1 m from shore at high tide. At low tide bat fishing attempts were largely restricted to the 0-1 m range as predicted, although bats did make some attempts in both the 1-2 m and 2+ m ranges.

We conclude that lagoon bed morphology directly affects small fish availability at high and low tide, and therefore that bed morphology affects ease of location and capture of small fish by bats. Based on these relationships, we infer that lagoon bed morphology is an important driving force affecting *N. leporinus* foraging success.

We noted an increase in bat foraging in the hour following high tide versus the hour preceding (pers. observation). This corroborates the results of Veysey et al. (2000), and may be due to the effect of water turbulence and lagoon bed substrate. Yale et al. (1998) found no effect of turbulence on bat foraging attempts, while Veysey et al. (2000) found highest bat fishing activity at intermediate turbulence (in a zone overlapping with our study site). Veysey et al. (2000) found low bat fishing activity at low turbulence. These results may be attributed to variation in lagoon bed substrate (i.e., rocks vs. sand) in their low turbulence zone (pers. observation). In our observations, bats preferentially fed in the calmer waters following high tide when the outgoing tide moderates the effect of incom-

ing waves. At the highest tide waterline, the lagoon bed at the margins has a more cobbled substrate (pers. observation) which may cause surface turbulence that interferes with echolocation of small fish by bats.

Our study was limited to comparisons between low and high tides. To more fully assess the effect of lagoon bed morphology and fish abundance on *N. leporinus* foraging behavior, a continuous temporal study across tides should be considered. For instance, as the waterline drops below the high tide flat, bat foraging activity should substantially decrease due to the sudden change in lagoon bed slope. Additionally, confounding factors such as moonlight intensity, changing lagoon bed characteristics over time, and the effect of waves and turbulence also are likely to influence *N. leporinus* foraging behavior, and warrant further attention.

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