EFFECTS OF TIDE ON THE PATTERNS OF FISHING ACTIVITY IN *NOCTILIO LEPORINUS*

DANIEL J. MADIGAN AND CHAD M. VALDERRAMA

Abstract: The greater bulldog bat, *Noctilio leporinus*, forages for fish mostly at high tide, and displays two types of fishing behavior depending upon the presence or absence of jumping fish. Using infrared binoculars, we observed bat hunting behavior to assess differences in fishing patterns between high and low tides. We followed individual bats and recorded hunting patterns, time fishing, and number of fishing attempts. Bats showed target-orientated circular-flight hunting behavior during high tide and linear-flight hunting behavior during low tide, probably as a response to fish abundance. This suggests that bats alter their hunting modes with resource availability, probably to maximize foraging efficiency.

Key Words: bulldog fishing bat, foraging efficiency

INTRODUCTION

Noctilio leporinus, the greater bulldog bat, is a nocturnal fishing bat that relies on echolocation to find its prey. After it locates a fish, it dips into the water attempting to spear fish with its claws or scoop fish into the pouch between its legs (Brandon 1983). The bat is only successful in catching fish once every 50-200 passes through a hunting area (Schnitzler et al. 1994). The bat has two main hunting modes. When there are fish jumping, the bat performs circular high flight searches, dipping when it detects a fish. When fish jumping is absent, the bat flies low, sweeping in a linear, trawl-like fashion through areas where it has fished successfully in the past (Schnitzler et al. 1994).

We studied bat hunting activity at the Rio Sirena Lagoon at Corcovado National Park, Costa Rica, in which the greater bulldog bat fishes predominantly at high tide (Yale et al. 1998, Veysey et al. 2000). There are higher fish abundances at high tide in the lagoon (Leslie et al. 2001). We hypothesized that the hunting patterns of the greater bulldog bat would change with tide, and that the bats would prefer high flying circular patterns at high tide when there are more fish and low flying linear patterns at low tide when there are fewer fish.

METHODS

Our study was conducted in the Rio Sirena Lagoon in Corcovado National Park. We observed *N. leporinus* fishing behavior for 4 h on two nights on 2-3 February 2005. These two sessions occurred during a high tide and a low tide on each night, beginning at 2100 and 0400 the first night and at 1730 and 2330 the second night. Using infrared night vision binoculars, we followed individual bats, recording time spent fishing (run time), fishing pattern (circular or linear), and number of dips into the water (attempted fish captures), until the individual was no longer

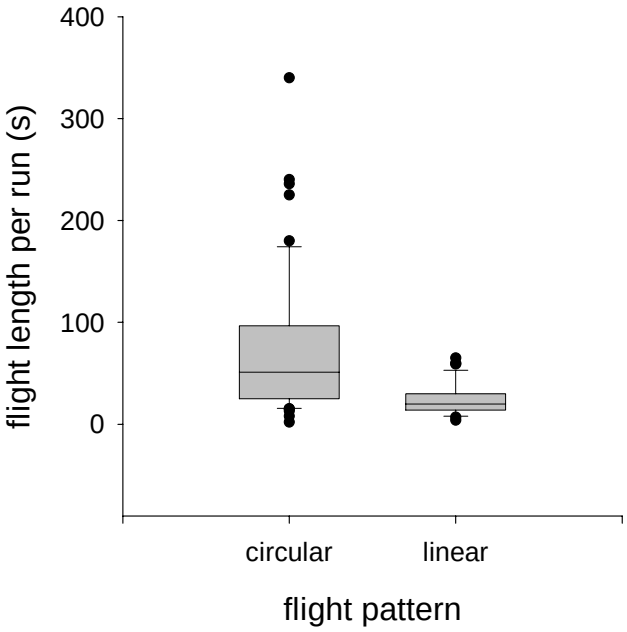

Figure 1. Flight length per run (s) of bulldog bats with respect to flight pattern. Circular flight patterns were significantly longer than linear flight patterns (n = 89, P < 0.001). Mean flight length and quartiles ± SE are shown for each flight pattern. Dots indicate observations >2 SE from the mean.

visible. Number of dips and flight time were used to estimate fishing efficiency for each observed bat. Bat patterns over the water were assessed as linear or circular. In circular mode, the bat cycled over a given region of the lagoon at least twice; in linear mode, the bat swept low over the lagoon once, sometimes dragging its feet in the water, and flew out of sight. Water velocity was assessed every 30 min by recording the travel time of a floating stick over 10 m, and relative tide was assessed by observing water level.

A contingency analysis was performed to assess differences in hunting patterns between different tides. Differences in bat fishing patterns with respect to run length, number of dips, and dips/run were analyzed with multiple ANOVAs. We analyzed these data using JMP 5.0.1 and verified assumptions of parametric tests before conducting analyses of variance.

RESULTS

Bat fishing patterns differed between tides, with more circular patterns at high tide and greater occurrences of linear, low flying patterns at low tide (X^2 = 47.08, df = 81, P < 0.0001, Table 1). Circular fishing runs lasted significantly longer (73.9 ± 10.1) than linear fishing runs (22.1 ± 2.6; F = 15.92, df =1, 85, P < 0.001, Fig. 1) and resulted in more dips/run (7.5 ± 1.2) than did linear pattern fishing (3.1 ± 0.5; F = 7.61, df =1, 87, P < 0.01, Fig. 2). However, the number of dips/minute did not differ between circular (7.9 ±1.1) and linear (8.7 ± 1.1) fish-

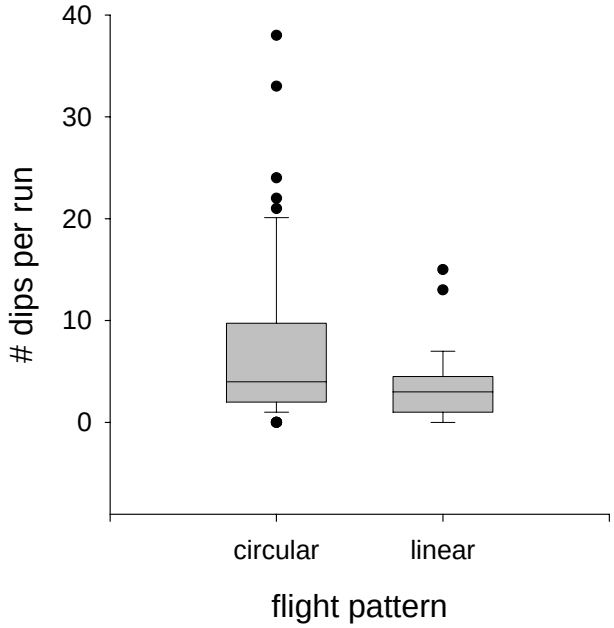

Figure 2. Number of dips per run of bulldog bats with respect to flight pattern. Circular flights had a greater number of dips per run than linear flights (n = 89, P < 0.001). Mean dips/run and quartiles ± SE are shown for each flight pattern. Dots indicate observations >2 SE from the mean.

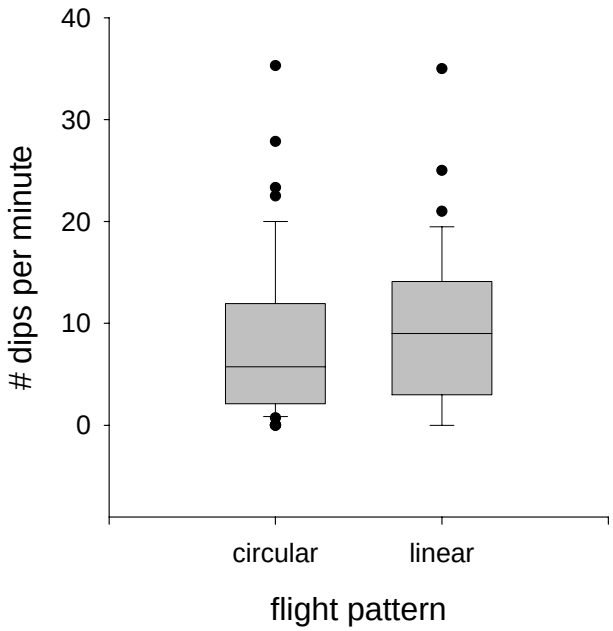

Figure 3. The number of bulldog bat dips per minute during one run with respect to flight pattern. The number of dips per minute during a circular run is not significantly different from the number of dips per minute during a linear run (n = 89, P = 0.96). Mean dips/minute and quartiles ± SE are shown for each flight pattern. Dots indicate observations >2 SE from the mean.

ing patterns (F = 0.64, df =1, 85, P = 0.43, Fig. 3).

DISCUSSION

As expected, the bats used high flying circular fishing patterns during high tide, when fish were more available. During low tide, when fish are scarce (Leslie et al. 2001), bats used low flying linear fishing patterns, probably where they have previously been successful in obtaining fish.

Greater run length in circular fishing patterns may indicate that runs in this hunting mode are generally longer, or that the fishing bat performs longer runs during high tide. Greater dips/run in the circular fishing mode suggest that bats make more attempts at catching fish during circular runs than in linear runs. However, bats were much easier to follow for longer periods of time during circular flight, and both of these relationships may have been results of this sampling bias.

We were unable to determine the success of bat fishing attempts, as after catching a fish the bats either transferred the fish to their mouths while in flight or flew off to roost and eat (Brandon 1983). Dips/min was the only indicator we had of fishing efficiency. Based on this measure, our results suggest that though the two fishing methods differ in flight patterns and fish-targeting, neither is more efficient with respect to dips per unit time.

This study showed a significant difference in fishing patterns of the greater bulldog bat at high and low tide. The use of infrared binoculars allowed us to follow individuals, allowing the opportunity to observe runs by individual bats, an important first step in assessing the foraging efficiency of this bat. The two fishing types probably differ in energy expenditure per unit time and fish-capturing efficiency. Further studies could quantify these unknown variables to better understand the tradeoffs between circular and linear fishing in greater bulldog bats.

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Table 1. Contingency analysis for observations of circular (n = 52) and linear (n = 37) fishing patterns during high and low tides. Column percentages represent the proportion of observations for the column patterns during the row tide; row percentages represent the relative proportions of circular and linear patterns observed during that tide.

Count	Circular	Linear	Total
High tide	20	1	21
High tide (incoming)	10	5	15
High tide (outgoing)	13	1	14
Low tide (incoming)	9	21	30
Low tide (outgoing)	0	9	9
Total	52	37	89