NOCTURNAL FORAGING IN THE AMERICAN WHITE PELICAN

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Abstract. Nocturnal foraging was examined in American White Pelicans (Pelecanus erythrorhynchos) at the Dauphin River, about 50 km from a breeding colony on Lake Winnipeg, Manitoba, Canada. From two to three times as many pelicans foraged at night as in the daytime, with foraging flocks being larger at night. In contrast, more pelicans were present at adjacent loafing sites during the day. Capture rates were highest for flocks of up to 100 foragers in the daytime, but showed no relationship to flock size at night. Rates of bill dipping and mean duration of dips were significantly greater at night, but capture rates were significantly lower. Lower capture rates at night were to some extent offset by the capture of more large fish, probably because they were more accessible at that time. Most of the day-night differences in capture efficiency appeared to be due to lower visual sensitivity of pelicans at night.

Key words: Nocturnal foraging; American White Pelicans; Pelecanus erythrorhynchos; foraging.

INTRODUCTION

The American White Pelican (Pelecanus erythrorhynchos) is a large, opportunistic fish-eating bird that uses a wide range of foraging habitats, including rivers, marshes, and lakes. They commonly breed on relatively inaccessible islands and reefs located far from their foraging grounds. Regular foraging trips range up to 100 km or more (Behle 1958; Johnson and Sloan 1978; Knopf and Kennedy 1980, 1981; Trottier et al. 1980; O'Malley and Evans 1984). On a typical foraging trip, flocks depart from and return to the colony during daylight hours, with peaks of travel near midday, when birds make use of thermal updrafts that form as land heats in the sun (O'Malley and Evans 1982). Individuals remain at the foraging grounds for up to two or three days during the incubation period, decreasing to one day as energetic demands of young increase after hatching (Knopf 1979, O'Malley and Evans 1982).

Although white pelicans normally lay two eggs, they rarely fledge more than one young (Knopf 1979, Cash and Evans 1986). Hall (1925) and Anderson (1987) estimated that post-hatching pelicans require an average of 1.1 to 1.2 kg x day⁻¹ of fish prior to fledging. Growth rates of young are strongly influenced by food intake (Evans and McMahon 1987, see also Schreiber 1976), and even when only a single young is raised its frantic begging ("convulsions," Cash and Evans 1987) suggests that food limitation during the chick rearing period is chronic.

Given apparently high food demands coupled with travel constraints on diurnal foraging in pelicans, we examined the possibility that pelicans may significantly increase their daily food gathering capacity by foraging extensively at night. Nocturnal foraging when food requirements cannot readily be met during daylight hours is known to occur in other species (e.g., McNeil and Robert 1988). Observations of pelicans foraging at night have been reported (Low et al. 1950, Schaller 1964, O'Malley and Evans 1984, Anderson 1987), but quantitative measures of foraging activity and success at night are lacking. Examination of this potentially important aspect of the American White Pelican foraging system was the objective of this study. To gain insight into the importance of nocturnal relative to diurnal foraging, data were gathered and compared for both time periods.

American White Pelicans normally feed by moving on the water surface and dipping their bill down into the water column. When prey is captured, the forager raises its head well above the water surface to swallow. To assess relative foraging effort directed towards foraging at night, we determined the number of foraging and loafing pelicans at a riverine foraging site, and assessed relative rates of bill dipping, prey capture, and prey size. Because pelicans could be under visual constraints at night not unlike those faced by humans (Sillman 1973), we also examined the extent to which pelicans were able to form and
maintain flocks while foraging at night. American White Pelicans foraging during the day are known to favor shallow water (Low et al. 1950, Knopf and Kennedy 1980), often close to shore where they can concentrate prey for greater ease of capture (Behle 1958). We examined forager location and water depth to determine if a similar preference for shallow near-shore foraging also occurs at night.

STUDY AREA AND METHODS

We studied a heavily used riverine foraging site, Dauphin River in south-central Manitoba, Canada (51°58'N, 98°07'W). The study site was approximately 50 km from a breeding colony on Lake Winnipeg (Koonz and Rakowski 1985). The river varied from 50 to 210 m wide (x = 115 m), thus making it possible to observe pelicans at all times of day or night from an adjacent bank.

Most pelican foraging occurred along a segment of river extending from the mouth upstream for 6 km to the base of a series of rapids, with lesser activity along and above the rapids up to 17 km from the river mouth. Maximum water depth varied from 4 to 5 m above and below the rapids and was less than 0.5 m along the rapids. Sandbars used for loafing were present over a region extending from 2.5 to 5.5 km upstream from the mouth. To avoid visual problems with vegetation at night, nocturnal observations were conducted only from 0-4 and 13-17 km from the river mouth. Daytime observations extended over the entire study area, but only data from 0-4 and 13-17 km were used when required to make valid day-night comparisons.

Observations were conducted daily in late spring from 31 May to 10 June 1985, from 11 to 28 May 1986, and in late summer from 23 August to 5 September 1985. These dates included late incubation to early brood rearing, and late to post-brood rearing periods, respectively. Either a 16-36 \times 50 spotting scope or 10 \times 50 binoculars were used for observations made during the day. Nocturnal observations were conducted with a Javelin model #325 infrared scope. Effective range of the night scope on fog- and rain-free nights was approximately 300 m, well beyond the distance to the opposite bank. Observations of nocturnal foraging were taken between evening and morning civil twilight as illustrated in Figure 1.

Flock size (estimated to within about 10% for those over 50) and location of foraging and loafing pelicans were recorded during a total of 80 vehicle-based surveys at preselected times of day and night. A flock was operationally defined as any group containing pelicans that were within approximately 5 m of each other (O'Malley and Evans 1982), and for purposes of analyses also included solitary birds. Foraging flocks were recognized by the presence of bill dipping. Pelicans were assumed to be loafing if standing on a solid substrate, including exposed sandbars or in shallow water adjacent to shore, and were not dipping. Distance to shore (nearest 10 m) was noted for foragers at the time surveys were taken. Foraging-site water depths were obtained with a meter stick or calibrated rope attached to a metal weight.

Rates of bill dipping, prey capture, and estimates of prey size were obtained from focal bird samples in 1985, supplemented with focal group (flock) samples in 1986. Focal individuals were selected by randomly directing the spotting or night scope towards a previously unsampled foraging flock or lone individual. Samples lasted either until the designated forager departed from an area visible to the observer, or until a maximum of 5 min elapsed. Verbal records of forager location and distance to shore, along with relevant foraging data were recorded into a cassette recorder for subsequent analyses. During dipping episodes, the times that the bill struck the water and was subsequently raised were noted. The time between these two events is referred to as "dipping time." If a pelican's head was raised in a swallowing motion, "capture" was recorded on tape. The period extending from the moment that the bill was raised from the water until the prey was fully swallowed is referred to as "swallowing time."

Randomly selected focal groups were observed in 1986 for a maximum of 2 min each during the day, and until approximately 50% of foragers had left the flock or the flock passed beyond visual range at night. Subsamples within the field of vision of the spotting or night scope provided data on mean dip rates \times bird\(^{-1}\). There was usually sufficient time between bill dips within subsamples to scan the flock to assess the number and size of captured prey.

Each captured fish was classed into one of five size classes: Very Small: less than \(\frac{1}{4}\) the length of a pelican's bill, Small: \(\frac{1}{4}\) to \(\frac{1}{2}\) bill length, Medium: \(\frac{1}{2}\) to \(\frac{3}{4}\) bill length, Large: \(\frac{3}{4}\) to one bill
FIGURE 1. Relationship between time of day and mean ± SE rates of bill dipping and prey capture in (A) late spring 1985, (B) late summer 1985, and (C) late spring 1986. Horizontal half-filled bars indicate civil twilight. No sampling was done between 6:30 and 10:30 hr. Note that bill dip and capture rate scales on the ordinates differ by a factor of ten.

length, and Very Large: exceeding one bill length. Small and Very Small fish were often hidden in the gular pouch. In these cases, fish size was estimated by examining the amount and shape of pouch distention. Instances where fish size could not be determined reliably were excluded from subsequent size analysis. For statistical comparisons, normality was first assessed and either Bartlett's or Hartley's $F_{\text{max}}$ tests used to check for equality of variances (Neter and Wasserman 1974). Following significant differences detected by analysis of variance, multicomparisons were done using Duncan's or Scheffe's tests (Berenson et al. 1983). Whenever variance-stabilizing transformations were ineffective, nonparametric Kruskal-Wallis rank tests ($K$) were used, fol-
TABLE 1. Mean ± SD dipping time (D), and swallowing time (S), when prey were or were not captured.

<table>
<thead>
<tr>
<th>Success</th>
<th>Variable</th>
<th>Day</th>
<th>Night</th>
<th>K</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>BD</td>
<td>D₀</td>
<td>1.3 ± 0.7 (1,131)</td>
<td>1.6 ± 0.8 (4,814)</td>
<td>191.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>PC</td>
<td>D₀</td>
<td>2.0 ± 1.0 (140)</td>
<td>1.8 ± 1.7 (46)</td>
<td>5.3</td>
<td>&lt;0.025</td>
</tr>
<tr>
<td>PC</td>
<td>S₀</td>
<td>1.2 ± 0.9 (140)</td>
<td>1.9 ± 1.2 (46)</td>
<td>17.7</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

¹ BD = Bill dipping without prey capture (n unsuccessful prey capture attempts in parentheses). PC = Bill dipping with prey capture (n prey captures in parentheses).

followed by Mann-Whitney U tests for paired comparisons. For the latter tests, the alpha level was adjusted downwards in accordance with the number of comparisons made, i.e., 0.05/n comparisons.

RESULTS
PREY CAPTURE TECHNIQUES

Except for rare instances of kleptoparasitism (see below), prey capture at Dauphin River was exclusively associated with bill dipping. Dipping time (D₀), which was taken as the period between a pelican's bill striking and subsequently raising above the water, averaged from 1–2 sec. For unsuccessful prey capture attempts, D₀ was significantly longer at night than during the day (Table 1). Conversely, D₀ when prey was successfully captured was longer during the day than at night. Dipping time was significantly longer for successful than for unsuccessful prey capture attempts during the day (Kruskal-Wallis, K = 83.29, P < 0.001), but not at night (K = 0.18, P > 0.60).

The period between when prey was brought to the surface and subsequently swallowed, or swallowing time (S₀), was similar in duration to D₀ and was significantly longer at night than in the daytime (Table 1).

Kleptoparasitism, or food theft, has been reported previously in American White Pelicans (O'Malley and Evans 1983), but was rare at Dauphin River, occurring in only 8 of 469 (1.7%) flocks. Only two of these instances occurred at night. Attempts at food theft usually occurred only after an extended period (30.0 ± 34.2 min, n = 5) in which no prey were captured, and were directed only towards conspecifics that had captured fish larger than about 20 cm in length. Larger fish appeared to be harder to swallow rapidly, thereby exposing potential hosts to theft. Of those attempts where fish size and success of the kleptoparasite were both observed, three large fish (>35 cm in length) were successfully stolen while three smaller fish (<35 cm) were not. Pelicans that captured very large prey always swam or flew away from the flock and were usually pursued by others.

FORAGING EFFORT AND SUCCESS

From two to three times as many actively foraging pelicans were present at night as in the daytime during surveys in both late spring and late summer (Table 2). In contrast, loafers were more numerous during the day, significantly so in late spring (Table 2). Total number of pelicans, including both foragers and loafers, was marginally greater at night. Taken together, these results suggest foraging effort was higher at night than in the daytime.

Dip rates provided another measure of foraging effort. Although highly variable in rate of occurrence (Fig. 1), dip rates were greater at night.

TABLE 2. Mean ± SD number of diurnal and nocturnal foragers and loafers per survey at Dauphin River in 1985.

<table>
<thead>
<tr>
<th>Season</th>
<th>Variable</th>
<th>Day</th>
<th>Night</th>
<th>K</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Late spring</td>
<td>Foragers</td>
<td>51.7 ± 56.7</td>
<td>160.7 ± 78.2</td>
<td>11.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Loafers</td>
<td>136.1 ± 57.6</td>
<td>41.2 ± 40.0</td>
<td>11.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>187.8 ± 69.1</td>
<td>201.9 ± 72.7</td>
<td>0.7</td>
<td>&gt;0.400</td>
</tr>
<tr>
<td></td>
<td>n surveys</td>
<td>18</td>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late summer</td>
<td>Foragers</td>
<td>292.5 ± 252.7</td>
<td>622.1 ± 394.2</td>
<td>5.4</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>Loafers</td>
<td>1,092.5 ± 561.1</td>
<td>986.7 ± 574.8</td>
<td>0.2</td>
<td>&gt;0.60</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>1,385.0 ± 574.0</td>
<td>1,608.8 ± 717.5</td>
<td>2.0</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td></td>
<td>n surveys</td>
<td>16</td>
<td>9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 3. Percentage capture of different prey sizes during the day and night (n prey captured in parentheses).

<table>
<thead>
<tr>
<th>Prey size</th>
<th>Day</th>
<th>Night</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Very Small</td>
<td>67.1 (722)</td>
<td>17.7 (25)</td>
<td>61.4 (747)</td>
</tr>
<tr>
<td>Small</td>
<td>23.2 (250)</td>
<td>59.6 (84)</td>
<td>27.4 (334)</td>
</tr>
<tr>
<td>Medium</td>
<td>8.0 (86)</td>
<td>5.0 (7)</td>
<td>7.6 (93)</td>
</tr>
<tr>
<td>Large</td>
<td>1.5 (16)</td>
<td>8.5 (12)</td>
<td>2.3 (28)</td>
</tr>
<tr>
<td>Very Large</td>
<td>0.2 (2)</td>
<td>9.2 (13)</td>
<td>1.2 (15)</td>
</tr>
</tbody>
</table>

1 Prey captures at each size are expressed as a percentage of identified sample. See methods for definition of prey sizes.

during the late spring in both 1985 (t = 8.34, df = 265, P < 0.001) and 1986 (t = 4.37, df = 475, P < 0.001). Dip rates did not differ between day and night in late summer of 1985 (t = 1.73, df = 210, P > 0.05), largely because of one high rate at 11:00 hr (Fig. 1B).

Prey captures occurred during both day and night (Fig. 1), but rates were significantly lower at night (late spring 1985, t = 6.39, P < 0.001; late summer 1985, t = 2.24, P < 0.05; late spring 1986, t = 8.65, P < 0.001). There was a strong positive correlation (P < 0.01 for each comparison) between dip and capture rates, especially during the daytime (Fig. 1) (late spring 1985 day, r = 0.787, night, r = 0.453; late summer 1985 day, r = 0.759, night, r = 0.465; late spring 1986 day, r = 0.660, night, r = 0.452).

In addition to capture rates, size of prey captured provided an important measure of foraging success. During the day, frequency of capture decreased with prey size (Table 3). Results obtained at night were more strongly affected by a greater proportion of instances where prey size could not be determined (63.4% undetermined compared with 54.5% during the day). Although this increased uncertainty at night would presumably bias against noting small and very small fish, there still were more fish recorded for these size classes at night than for any larger size class. Large and Very Large fish, which were easily observed during both day and night, were captured more frequently at night and made up a significantly greater proportion of the identified diet at night than during the day, even when Small and Very Small categories were excluded from the analysis ($\chi^2 = 39.1, P < 0.001$).

FLOCK SIZE

Foraging flock sizes recorded during surveys usually ranged from one to about 200 pelicans, although one unusually large daytime group in late summer reached approximately 1,000 birds. In both late spring and summer, mean flock sizes of foraging birds were significantly larger at night than during the day (Table 4). This difference paralleled a similar day-night difference in forager numbers (Table 2), suggesting that larger flocks were simply a reflection of greater numbers of foragers along the river. Loafing flock size did not differ between day and night in late spring. During late summer, loafing flock size was significantly greater at night (Table 4), even though numbers of loafers were greater during the day (Table 2).

The relationship between flock size and capture rate was variable (Fig. 2). In late spring, daytime capture rates were highest for flocks containing 21–100 foragers in 1985 and 2–20 foragers in 1986. There was no detectable relationship between flock size and capture rate at night. With the possible exception of late summer (Fig. 2B), there was no tendency for large flocks (≥ 100) to be more successful at capturing prey.

WATER DEPTH AND DISTANCE FROM SHORE

Most foragers were located in shallow water (≤ 1.5 m), especially in late spring (Fig. 3). This correlation between water depth and forager abundance was statistically significant ($P < 0.005$) for each sample period (late spring 1985 day, $r = -0.637$, night, $r = -0.709$; late summer 1985 day, $r = -0.533$, night, $r = -0.650$; late spring 1986 day, $r = -0.714$). Because water depth decreased towards shore, similar correlations were

TABLE 4. Mean ± SD flock size of foragers and loafers at Dauphin River in 1985 (n flocks in parentheses).

<table>
<thead>
<tr>
<th>Season</th>
<th>Variable</th>
<th>Day</th>
<th>Night</th>
<th>K</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Late spring</td>
<td>Foragers</td>
<td>9.8 ± 25.5 (95)</td>
<td>28.9 ± 40.2 (50)</td>
<td>19.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Loafers</td>
<td>22.9 ± 32.8 (107)</td>
<td>23.2 ± 28.2 (16)</td>
<td>0.3</td>
<td>&gt;0.50</td>
</tr>
<tr>
<td>Late summer</td>
<td>Foragers</td>
<td>3.8 ± 35.9 (1,220)</td>
<td>9.7 ± 40.8 (578)</td>
<td>45.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Loafers</td>
<td>89.6 ± 119.5 (195)</td>
<td>206.5 ± 215.8 (43)</td>
<td>12.4</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Figure 2. Relationship between flock size and mean ± SE capture rate in (A) late spring 1985, (B) late summer 1985, and (C) late spring 1986.

Most prey were captured in water less than 1 m deep during the day (99.4% of captures) and at night (94.8%).

Discussion
This study indicates that American White Pelicans forage extensively at night, at least during the breeding season. Significantly, the only claim to the contrary (Audubon, in Palmer 1962) re-
FERRED SPECIFICALLY TO THE BEHAVIOR OF WHITE PELICANS ON WINTERING GROUNDS, WHEN ENERGY NEEDS WOULD PRESUMABLY BE REDUCED. HOWEVER, EVEN DURING THE BREEDING SEASON IT REMAINS TO BE DETERMINED WHETHER WHITE PELICANS FORAGE IN MARSHES AND ON OPEN LAKES AT NIGHT.

SEVERAL BROAD SIMILARITIES EMERGED BETWEEN NOCTURNAL AND DIURNAL FORAGING BEHAVIOR. AT BOTH TIMES, MOST FORAGING WAS DONE IN SHALLOW WATER CLOSE TO SHORE, DIP RATES WERE WELL IN EXCESS OF CAPTURE RATES, DURATION OF INDIVIDUAL DIPS WERE SIMILARLY BRIEF, AND OVERALL SIZE RANGE OF PREY CAPTURED WERE SIMILAR WITH SMALL PREY BEING BY FAR THE MOST COMMON. LARGE NUMBERS OF LOAFERS WERE PRESENT AT BOTH TIMES. DAY-NIGHT SIMILARITIES IN USE OF COORDINATED FORAGING WERE ALSO PRESENT AT DAUPHIN RIVER (McMAHON 1991). EVIDENTLY, OBSERVATIONS OF PELICAN FORAGING DURING DAYLIGHT HOURS CAN IN LARGE PART BE EXTRAPOLATED TO FORAGING AT NIGHT.

SUPERIMPOSED ON DAY-NIGHT SIMILARITIES IN FORAGING WERE SEVERAL SMALLER BUT POTENTIALLY IM-

FIGURE 3. Relationship between water depth and abundance of foragers on the river, plotted on a semi-log scale, during surveys conducted in (A) late spring 1985, (B) late summer 1985, and (C) late spring 1986. Nocturnal surveys were not conducted in late spring of 1986. Vertical lines show standard error.
portant differences. The larger number of foragers present at night than during the day seems unlikely to be due to differential capture success. Although nocturnal foragers obtained relatively more large fish, few large fish were caught at any time, and overall capture rates were significantly depressed at night relative to daytime levels. Fewer foragers in the daytime seems more likely to reflect constraints imposed by diurnal travel back to the breeding colony.

Some day-night differences may have been a reflection of relative prey availability. The most common species of fish found within or near Dauphin River include: Lake whitefish (*Coregonus artedii*), sucker (*Catostomus commersoni, C. catostomus*), yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), fathead minnow (*Pimephales promelas*), and johnny darter (*Etheostoma exile*) (Keleher 1952; Scott and Crossman 1973; Lysack 1980, 1981). Numerous small schools of perch, minnows and darters normally predominate in shallow water during the daytime (Carlander and Cleary 1949, Emery 1973, Hall and Werner 1977). This may explain the large numbers of small pelican flocks and the predominance of Small and Very Small fish in their diet during the daytime. At night, large nocturnal fish species including walleye, sucker, and whitefish typically move into shore and remain active in shallow water until dawn (Carlander and Cleary 1949, Lawler 1969, Emery 1973). This corresponds with the large pelican flocks that occurred at night, and agrees with our finding that large fish made up a significantly greater proportion of successful catches at night. Swallowing time was also greater at night, possibly because of the greater proportion of Large and Very Large fish captured at that time.

Other day-night differences included rate of bill dipping, which was highest during the night, and frequency of prey capture, which was lowest at night. Reduced visual sensitivity during the night may have contributed to both of these effects. Night vision capabilities of white pelicans have not to our knowledge been directly assessed, but it is known that at least one pelican species (*P. occidentalis*) has visual pigments similar to most other birds (Sillman 1973). Elevated rates of bill dipping at night are suggestive of non-visual "probing" for food. Diurnal foragers were frequently seen moving their heads as though scanning the water prior to dipping their bills in a manner suggestive of visual searching (Pulliam 1973, Barnard 1980). This behavior was associated with a relatively high capture efficiency during the daytime. Scanning behavior was rarely seen at night (3 instances, McMahon 1991), and capture efficiency was correspondingly depressed.

The presence of larger foraging flocks at night may also relate to visual ability. While foraging during the day, white pelicans make use of local enhancement, shifting positions to join currently successful foragers (O'Malley and Evans 1982, McMahon 1991). At night, darkness would almost certainly reduce the ability of foragers to monitor each others' success. Under these conditions, any benefits of group foraging would presumably best be achieved by remaining close together, in larger flocks.

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