Foraging Behavior of the American White Pelican (Pelecanus erythrorhyncos) in Western Nevada

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Abstract.—The foraging behavior of American White Pelicans (Pelecanus erythrorhyncos Linn.) breeding at Pyramid Lake in western Nevada was examined between 1984 and 1986. Pelicans seen feeding at Pyramid Lake during February and early March pirated fish from Double Crested Cormorants (Phalacrocorax auritus). When feeding with conspecifics, pelicans usually engaged in some form of “cooperative herding,” either driving fish into shallow water or surrounding them in more open areas. Members of groups of two to six birds caught significantly more fish than single birds or those in larger groups. Strike frequency initially increased with group size, reaching an upper asymptote at a flock size of four. Tests with decoys revealed that pelicans were attracted to areas by the presence of other pelicans. Received 23 January 1990, accepted 5 July 1991.

Key words.—cooperation, foraging, herding, pelicans, piracy.

Churchill County, Nevada. Observations were made using 7x35 mm binoculars and a Celestron 1000 mm spotting scope on 19 days between June and August 1984, 55 days from February through August 1985, and on five days in August 1986. Group size, strikes per individual per minute, and captures of fish per individual per minute were recorded. Two censuses of prey types were made in 1984 and five in 1985 using a seine net. In 1985 regurgitates were collected from 50 near-fledglings on the breeding colony on Anaho Island.

In order to test the response of pelicans to groups of varying sizes, pelican decoys were constructed using commercial White-fronted Goose (Anser albi-frons) floater decoys as a base. The bill of each decoy was carved from blocks of styrofoam, angled to simulate a foraging pelican. Each decoy was initially painted to resemble a pelican in breeding plumage. In the latter portion of the season (June to August) the decoys’ white crowns were painted black to simulate birds in the post-nuptial molt (Knopf 1975).

Twenty-two experimental tests of anchored decoys were conducted during the 1985 season to determine whether pelicans were attracted to areas by the apparent presence of other pelicans. Each test lasted a maximum of 45 minutes. Decoys were deployed in groups of one to seven, and distributed in crescent or random patterns. To determine whether pelicans were drawn to an area by the apparent presence of conspecifics, rather than to habitat characteristics, or to the presence of waterbirds, equal numbers of unmodified goose decoys were deployed in similar patterns for an equivalent time period before or after each experiment. Positive responses to a decoy group were recorded if a pelican approached on the surface to within 2 m of a decoy (Close Approach in Table 2) or executed a tight wheeling flight low over the decoys in an apparent prelude to landing (Flyover in Table 2). Similar criteria are described by Barnard and Thompson (1985).

The responses of fish to a herding situation were tested in a series of three simulations using one, two, and three decoys connected above the waterline by 30 cm of monofilament line. Each set of decoys was drawn through the water by assistants standing ap-

Both the American White Pelican (Pelecanus erythrorhyncos) and the Great White Pelican (P. onocrotalus) have been cited as examples of cooperative feeders (Goldsmith 1840, Rand 1954, Wrangham 1982, Alcock 1984, Welty 1986), but claims of cooperative behavior rest on anecdotal accounts of fish herding (Goss 1888, Mills 1925, Cottom et al. 1942, Low et al. 1950). Several authors (Behle 1958, Hall 1925, Woodbury 1966, Knopf and Kennedy 1980, O’Malley and Evans 1984, Smith et al. 1984 for P. erythrorhyncos and Din and Eltringham 1974a, 1974b for P. onocrotalus) have made reference to pelican foraging behavior, but no study has been directed specifically at actual feeding behavior.

White Pelicans rarely dive for fish (Bent 1924, Hall 1924, Gunter 1958). Measurements of bill and neck lengths of five adult pelicans collected in Nevada suggest that they are restricted to foraging on prey in the upper 1.25 m of the water column. Clearly, any activity that would concentrate fish in shallow water or restrict their movement within a given area would be to the pelicans’ advantage. I here discuss pelican foraging behavior with special attention to the effects of flock size on possible cooperative activity.

STUDY AREA AND METHODS

White Pelican feeding was studied at Pyramid Lake, Washoe County, Nevada; the Stillwater National Wildlife Refuge; and Carson/Humboldt Sinks, Churchill County, Nevada. Observations were made using 7x35 mm binoculars and a Celestron 1000 mm spotting scope on 19 days between June and August 1984, 55 days from February through August 1985, and on five days in August 1986. Group size, strikes per individual per minute, and captures of fish per individual per minute were recorded. Two censuses of prey types were made in 1984 and five in 1985 using a seine net. In 1985 regurgitates were collected from 50 near-fledglings on the breeding colony on Anaho Island.

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proximately 5 m on either side of a slough in the Stillwater Refuge.

Statistical analysis was performed using the SYSTAT (Systat Inc. 1986) and SAS (SAS Inc. 1986) statistical packages. Levels of significance for statistical tests were obtained from Rohlf and Sokal (1981).

RESULTS

Foraging Locations and Habitat

Preferred foraging habitat during daylight hours away from Pyramid Lake consisted of open water 0.3 to 2.5 m deep. Pelicans were also seen probing at the base of drowned vegetation in flooded areas of the Stillwater Refuge. Foraging sites at Pyramid Lake were concentrated around the mouth of the Truckee River and within 500 m of the southwest and southeast shores of the lake and along the eastern shore of Anaho Island. No foraging groups were seen in the northern half of the lake.

Prey Species and Food Requirements

Large numbers of Asiatic Carp (Cyprinus carpio) were netted in sloughs throughout the Stillwater Refuge and along the delta of the Truckee River. Observations at Anaho Island (Anderson 1987) indicated that chicks close to fledging are fed once per day. Analyses of the regurgitates of near-fledged young pelicans on Anaho Island in August 1985 revealed that these birds had been fed a mean of 9.9 fish (4.3 S.D., range 1-17, N = 50). Mean mass of individual fish was 138 g (84.3 g ± 1 S.D., range 51.4-663.1 g, N = 364). Mean total mass of fish per regurgitate was 1199.9 g (414.6 g ± 1 S.D.). There was a significant negative correlation between fish size and total fish fed to young birds (Pearson r = −0.25, P < 0.01, N = 357). Eighty-five percent of the fish by number and 98.3% by weight consisted of Carp and Lahontan Tui Chub (Gila bicolor).

Foraging Behavior

Piracy

Flocks ranging in size from 50 to 300 pelicans were observed at the mouth of the Truckee River in 11 observation sessions during February, March, and April of 1985 between 0500 and 0930 hrs. All of these birds were in the company of Double-Crested Cormorants (P. auritus). The pelicans were distributed throughout the cormorant flocks, and exhibited none of the cohesion of movement and probing behavior seen at other sites in the Lahontan Basin. In a total of 37 hours of observation, conducted on April 13-15, 22-24, and 26 1985, 52 instances of piracy by pelicans on cormorants were recorded. In 26 of these cases one of the attacking pelicans gave the characteristic "head toss" associated with swallowing at the conclusion of the attack, and on two occasions the fish was dropped and lost to all birds. At no time during this period were pelicans seen to attempt to catch fish independently in Pyramid Lake.

Group Foraging

The general pattern of foraging was as follows. Flocks of pelicans feeding in open water or in areas with a sharp drop-off near shore moved in double or treble file, occasionally probing with their bills. The rear or occasionally mid-column segment of the flock swept around to one side, and gradually moved around and ahead of the leaders. The leaders fanned out in a line or arc, still oriented in the original direction of movement, at which point the breakaway section turned to face them. As the groups moved together, both segments commenced probing and striking. In some cases the groups disintegrated after a brief interval of striking, in others the whole group reformed and repeated the sequence.

In June and July of 1984 and 1985 I observed mixed pelican and cormorant flocks driving schools of chub in towards the shelving lake shorelines, beginning their drive in water over 7 m deep. As the birds approached the shoreline the disturbance caused by the bunched fish was clearly visible. Drives lasted up to 10 minutes, after which the birds dispersed along the lakeshore.

Groups of pelicans feeding in the Stillwater Marshes and along the Humboldt River foraged almost exclusively in water less than 2 m deep. Members of the flocks formed a line or arc facing the shore and moved in toward the bank. As the birds reached the shallows it was often possible to see the disturbance caused by fish swimming ahead of the flock. On two occasions
carp were driven out of the water onto the bank where they were seized by members of the driving flock.

**Group Size and Foraging Success**

Herding groups generally consisted of less than 10 birds (Fig. 1) but on occasion flocks of up to 150 birds at Stillwater and over 300 birds at Pyramid Lake were observed in coordinated fishing activity. Ninety-seven percent of all feeding flocks seen (N = 322) consisted of 20 or fewer birds. The tendency of large groups (> 50 birds) to rapidly sub-divide and reform into local clusters precluded an accurate estimate of effective group size, especially when the flock was feeding among partially submerged vegetation in the Stillwater Marshes. Analysis of capture rates was limited therefore to groups of 10 or fewer.

Analysis of foraging success as a function of group size (Table 1) revealed a significant difference in individual capture success (F = 4.89, P < 0.0001). Single birds did significantly worse than members of groups of sizes 2-6 (Fisher’s LSD test, P < 0.05).

In flocks of up to 10 birds initiation of striking by any member of the flock was followed in less than four seconds by striking by the rest of the flock. Strikes per bird per minute increased initially with flock size (Fig. 2), reaching an asymptote at a flock size of four. Strikes ranged from a relatively slow probing thrust, with the bill held closed to a rapid stabbing motion. Strike efficiency (captures per bird per strike) declined with increasing group size (Fig. 3). In flocks larger than 10 individuals coordination of striking within the entire flock decreased noticeably.

**Herding Simulations**

Schools of carp responded to the approach of moving decoys by bunching up and moving away. It proved possible with the “flock” of three decoys to steer the

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**Table 1. Pelican foraging success. Individual birds in groups of two through six had significantly higher mean capture rates than birds foraging alone (Fisher’s Least Significant Difference test). Mean captures for flocks of three were also significantly larger than mean captures in flocks of two.**

<table>
<thead>
<tr>
<th>Flock Size N</th>
<th>Mean Captures/Bird/Min</th>
<th>S.E.</th>
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</thead>
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<tr>
<td>1 115</td>
<td>0.035</td>
<td>0.017</td>
</tr>
<tr>
<td>2 61</td>
<td>0.065$^1$</td>
<td>0.025</td>
</tr>
<tr>
<td>3 39</td>
<td>0.128$^1$</td>
<td>0.034</td>
</tr>
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<td>4 58</td>
<td>0.078$^1$</td>
<td>0.018</td>
</tr>
<tr>
<td>5 31</td>
<td>0.097$^1$</td>
<td>0.023</td>
</tr>
<tr>
<td>6 16</td>
<td>0.056$^2$</td>
<td>0.018</td>
</tr>
<tr>
<td>7 14</td>
<td>0.063</td>
<td>0.023</td>
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<tr>
<td>8 14</td>
<td>0.063</td>
<td>0.023</td>
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<tr>
<td>9 11</td>
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</tr>
<tr>
<td>10 14</td>
<td>0.040</td>
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</tr>
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</table>

$^1$P < 0.05
Foraging Behavior of White Pelicans

Following a successful capture, additional pelicans joined the group in five cases, birds left the group in three cases, and flock size remained the same in seven cases. A chi-square test assuming equal probability of arrivals, departures, and constancy in flock size, showed these results to be indistinguishable from random (chi-square = 1.6, P > 0.1).

Night Fishing

In 10 night observation sessions in 1985 I observed that after dark groups of 20 to 150 pelicans would move up the creeks and sloughs within the Stillwater Refuge, apparently driving fish ahead of them until they reached a weir or road culvert. On moonlit nights the disturbance caused by the fish was visible, and the noise of trapped fish beating against the culvert was audible at a distance. Additional pelicans would line the banks on each side of the slough, periodically leaping in front of the advancing flock, and taking fish concentrated by the "beaters." Once the swimming flock reached a culvert or some other constriction in the slough, birds at the rear of the "beating" flock flew to the front of the group and landed immediately below the slough or constriction. The birds at the front of the flock and those lining the banks lunged forward, striking at fish struggling to get past the constriction or break back downstream.

Although it was impossible to obtain accurate counts of prey capture for entire flocks during night feeding bouts, 11 captures were recorded in 10 minutes by the

Table 2. Pelican Responses to decoys. A "close approach" indicates that a pelican landed near the decoys and/or approached to within 2 m. "No Response" indicates that pelicans did not approach or fly low over the decoys. "Goose" refers to unmodified White Fronted Goose decoys.

<table>
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<th>Response</th>
<th>Decoy Type</th>
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<th>2</th>
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<th>5</th>
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<td>1</td>
<td>1</td>
<td>0</td>
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<td>4</td>
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<td>3</td>
<td>3</td>
<td>2</td>
<td>1</td>
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</tr>
</tbody>
</table>
leading seven birds of a flock of 150 feeding at the mouth of a culvert in the Stillwater Refuge between 0200 hrs and 0430 hrs. Groups of up to 200 birds returned to the same culvert for five nights in succession. Smaller groups of three to 15 pelicans were seen feeding in sloughs during daylight hours.

**Discussion**

Group foraging is clearly an important component of White Pelican feeding behavior. While numbers of birds were seen feeding alone, the majority were seen in groups (Fig. 1). The increased individual success of group members compared to birds foraging alone (Table 1) provides a clear incentive for group formation. The tests with decoys indicated that the presence of other pelicans was a strong attractant. Observed success on the part of an individual or group did not appear to increase the attraction of a given site. The decoys obviously catch no fish, yet pelicans landed in their immediate vicinity, and often remained near them until approached by an observer.

The patterns of movements by individuals within groups was clearly consistent with the notion that the pelicans were driving or “beating” for prey. While it is possible that at least some of the increase in foraging was due to a “confusion effect” (Gottmark et al. 1986), the effectiveness of beating was shown both by direct observation of pelican flocks and fish responses to moving decoys.

Water throughout the pelicans’ feeding range was quite turbid. Guillet and Crowe (1983) state that turbid water is potentially beneficial to foraging pelicans since it reduces visual cues to the prey and forces greater reliance on their lateral line systems to detect predators. They also suggest that fish in turbid water are more likely to panic and do not display coordinated escape responses. In combined flocks of pelicans and cormorants diving by the cormorants would affect fish movement, but groups of pelicans were seen foraging in deep water without cormorants.

The increase in strike frequency and simultaneous decline in strike efficiency seen in Figs. 2 and 3 may be regarded as consequences of a form of local enhancement. Once a group has formed, near simultaneity in striking is a logical outcome of group feeding where position within the flock does not give an individual advantage. A bird striking too soon runs the risk of scaring off prey that may be only partially aware of the pelicans’ location. A bird striking too late in a large group may eliminate itself from competition for prey items. In cases where fish are being driven into shallow water, the longer the flock delays striking, the easier it will be to catch the fish. Once one bird begins to strike however the other flock members do likewise.

If the pelicans are taking their cue to strike from each other rather than from some degree of concentration or behavior on the part of the prey, then the proportion of “early strikers,” birds willing to strike in response to co-specifics rather than in response to cues from catchable fish, would increase as group size increased. As a result of this increase in premature striking, strike efficiency will decrease with group size. Single birds that strike only in response to prey availability will capture the most fish per strike. Birds foraging in groups may strike to pre-empt other group members or in response to a perceived intent to pre-empt on the part of another group member, and hence will catch fewer fish per strike.

Vigg (1978) has shown that chub are restricted to deep water during the Winter and Spring, and hence are out of reach of the pelicans. A pelican able to pirate fish from cormorants at Pyramid Lake saves itself the energy cost of the 120 km commute to the Humboldt Sinks or Stillwater Marshes. In spite of this, the kleptoparasitism seen between pelicans and cormorants seems to play a relatively minor role in overall foraging by birds at the Anaho colony, although reports from other colonies (O’Malley and Evans 1983, Hart 1989) indicate that it may be a widespread phenomenon. Relatively few pelicans engaged in kleptoparasitic behavior, and cormorants freely approached pelican decoys deployed at Pyramid Lake. The cormorants seemed to restrict their foraging range to Pyramid Lake, and were rarely seen in the Stillwater Refuge and Humboldt Sinks.
The negative correlation between size of fish and total fish fed to young suggests that some birds may be reducing the required captures per day by taking a few large rather than many small fish. Assuming that the number of fish collected from regurgitate was an indication of daily food requirements, the relatively low rates of successful prey capture seen in birds foraging during the daytime seem insufficient in themselves to support both the adult bird itself and a near-fledgedling on the colony. The apparent higher rate of capture observed at night suggests that nocturnal fishing was of importance both in individual survival and reproductive success.

Group foraging by pelicans appears to satisfy the requirements of true cooperative behavior, which I define as a series of events in which a group of individuals actively perform some pattern of behavior that results in a mutual reduction of some cost and/or a mutual increase in some benefit. In discussing possible cooperative behavior it is important to separate the phenomena of social facilitation (Thorpe 1956) in which individuals adapt their behavior to imitate successful foragers, and local enhancement (Hinde 1959) in which individuals obtain positional information on scattered prey patches by interacting with other foragers. Social facilitation may be the primary force behind some aspects of pelican foraging behavior, including the synchrony in striking observed in groups.

The results of the decoy experiments show that local enhancement certainly occurs in pelican foraging in that pelicans are drawn to specific sites by the presence of other foraging pelicans. I suggest however that this behavior is relatively simple, may well be passive on the part of individuals already at the feeding site, and can hardly be regarded as "cooperative" in the sense outlined above.

In contrast to traditional forms of local enhancement, the active herding behavior discussed here in White Pelicans and found in some other birds (Bartholomew 1942, Emlen and Ambrose 1970, Leck 1971) is relatively complex and requires active participation by group members. That the result of this process leads to the ultimate mutual benefit of all group members in no way implies any intent of mutual assistance; each bird is acting for its own immediate good. The "sharing" of benefits may be treated from a Darwinian perspective as an interesting higher order interaction. The unitary nature of fish caught by pelicans differentiates their cooperative foraging behavior from the group hunting seen in Harris Hawks (Parabuteo unicinctus) by Bednarz (1988), in which large prey items were divided among members of family groups. Further examination of this phenomenon may provide useful insights into the development of complex social relationships among individuals.

ACKNOWLEDGMENTS

Versions of this manuscript benefited immensely from comments by P. August, B. Drury, R. Evans, R. Morris, G. Burness, and an anonymous reviewer. Funding was made possible by a Grant-in-Aid from Sigma Xi and the Frank M. Chapman Fund of the American Museum of Natural History.

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