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CORRELATES OF FLOCK SIZE AND BEHAVIOR OF FORAGING AMERICAN FLAMINGOS FOLLOWING HURRICANE GILBERT IN YUCATAN, MEXICO[1]

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Abstract. Activity budgets of individual American Flamingos (*Phoenicopterus ruber ruber*) wintering on the north coast of the Yucatan Peninsula, Mexico, were measured from mid-January through mid-March 1989 for feeding aggregations ranging in size from 1–8,000 individuals to determine potential social influences on foraging. For groups of $<3,500$, aggregation size was related positively ($r = 0.90$) to feeding head down, whereas feeding head up and alert behaviors were related negatively ($r = -0.85$ and $r = -0.85$, respectively). Overall, feeding time was higher and aggression was much lower than observed in foraging flocks of American Flamingos in Venezuela. We relate these differences to changes in food abundance and availability following Hurricane Gilbert.

Key words: *Foraging; flock size; American Flamingo; hurricane.*

INTRODUCTION

Among birds, foraging in aggregations has been hypothesized to result ultimately from a gain in individual fitness due to either decreased predation on individual flock members (Goss-Custard 1970, Hamilton 1971, Orians 1971, Caraco 1979) or an increase in foraging efficiency (Murton et al. 1971, Krebs et al. 1972). Indeed, both anti-predator and foraging benefits of flocking can occur concurrently (Powell 1974, Caraco 1979).

American Flamingos (*Phoenicopterus ruber ruber*) regularly aggregate in large feeding flocks during the nonbreeding season (Allen 1956, Rooth 1965). However, excepting general information on time budgets of nonbreeding American Flamingos (Espino-Barros and Baldassarre 1989), there are few detailed data describing foraging behavior (but see Bildstein et al. 1991). There are no data relating feeding behavior to variation in aggregation size. Further, in September 1988, Hurricane Gilbert struck the Yucatan Peninsula and caused major changes in salinity and vegetation within American Flamingo foraging areas. Thus, the hurricane provided an opportunity to quantify foraging behavior of flamingos following a major environmental disturbance. Such data are of comparative value relative to feeding behavior of American Flamingos elsewhere or for future comparisons in Yucatan when habitats return to pre-hurricane conditions.

Our primary objective was to describe individual feeding rates in American Flamingo aggregations of different sizes following a major perturbation within their foraging habitat, and secondly to relate these data to possible benefits of group foraging.

STUDY AREA

The Celestun Estuary on the north coast of the Yucatan Peninsula is the principal site for the Yucatan population of the American Flamingo during the nonbreeding period. Espino-Barros and Baldassarre (1989) provide a map of our study area and describe the estuary. However, the extensive beds of widgeongrass (*Ruppia maritima*) and muskgrass (*Chara* spp.) they reported were entirely absent during this study, which immediately followed the occurrence of Hurricane Gilbert in September 1988. The loss of vegetation probably was due to changes in salinity and water clarity associated with a 3-m storm tide that occurred during the hurricane. Espino-Barros and Baldassarre (1989) reported that water salinity varied in the Celestun Estuary from 8–24 ppt prior to the storm, compared to the 18–34 ppt that we recorded in February 1989. As of September 1991, the submergent vegetation had recovered to about 25% of pre-hurricane cov-

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erage (pers. comm., R. Singelton, Ducks Unlimited de Mexico, A.C.).

METHODS

Flamingos were observed from January through March 1989 from observational blinds in the northern third of the Celestun Estuary, which received the majority of foraging use by flamingos during our study. All observations were made during daylight with a 15 × 60× spotting scope. The total number of flamingos using the estuary was determined by a monthly census conducted by boat. Wind was categorized for each observation as calm, slight breeze, moderate, and gusting. Cloud cover was estimated as 0–25%, 25–50%, 50–75%, and 75–100%.

Individuals were observed using the focal-animal sampling technique (Altmann 1974). Focal animals were selected by choosing a bird in the center of view of the spotting scope and then counting left or right of this individual a random number (1–10) of birds. Sampling began on the edge and proceeded to the center of an aggregation by moving the field of view of the spotting scope to a different location of the aggregation with each observation.

Activity budget data were collected on each focal animal during 3-min sampling periods, with behaviors recorded at 15-sec intervals. Activities recorded were feeding, walking, resting (Allen 1956), preening and comfort, alert, courtship (Kahl 1975), and aggression (Rooth 1965). Flamingos were only observed using the "stamping-marking time" (Rooth 1965) method of feeding whereby the head is held alternately above and below the surface of the water while the feet tread in the substrate, presumably to expose food items. Frequent cocking of the head, when above the surface, indicated that an individual was observant of conspecifics while still treading the substrate. We therefore separated feeding behavior into distinct parts of: (1) feeding head up, which occurred when an individual lifted its head above the surface of the water and maintained a curved neck but still treaded the substrate, and (2) feeding head down, which occurred when the bird was treading the substrate but the head was under water and the bird was actively feeding (Jenkin 1957, Rooth 1965). Alert behavior often was synchronized with other flock members, and was characterized by the absence of treading of the bottom and a straightened neck with the head held well above the body (Kahl 1975).

Data were only recorded on animals observed feeding at the beginning of the sampling period. Since resting and preening were often observed in feeding aggregations shortly before the end of a feeding bout, data were collected only when at least 75% of the birds in the aggregation were actively foraging. We could not determine the amount of actual food intake, and therefore defined flamingo feeding rate as the amount of time spent filtering for potential food items. We assumed that the amount of food that was filtered per unit time remained constant.

Feeding aggregations themselves were very large, and often exceeded 1 km in width. We defined an aggregation as any continuous group of individuals where neighbors were able to interact behaviorally without flying, although individuals on opposite sides of the aggregation obviously could not interact directly. Feeding aggregations were always separated by a distance of greater than 1 km.

Distance from the focal animal to the nearest bird (bird lengths), distance from the focal animal to the edge of the aggregation (m) and density of birds around the focal animal were visually estimated for each observation period. Bird length was the estimated length from the forward edge of the body to the tip of the tail. Distance from the edge of the aggregation was the distance from the focal animal to a polygon formed by the outermost members of an aggregation. The local density was determined by counting all of the birds within five bird lengths from the focal animal.

The Mann-Whitney test (Conover 1980) was used for two-sample comparisons. Relationships between activity budget data and aggregation size were determined by linear regression analysis using aggregation size grouped in increments of 500 as the independent variable and the means of activity budget data for each grouping of aggregation size as the dependent variable. All percentage data were arcsine transformed to approximate a normal distribution (Zar 1984).

RESULTS

There were 19,300 flamingos using the Celestun Estuary on 29 January, 9,500 on 24 February, and 5,100 on 31 March. The mean aggregation size during the first 4 weeks ($n = 503$; $\bar{x} = 1,711$) was higher ($P = 0.001$) than during the second 4 weeks ($n = 429$; $\bar{x} = 1,160$). From these birds,

TABLE 1. Correlates of percent time (mean ± SE) spent in various activities for two ranges of aggregation size for American Flamingos wintering in Yucatan, Mexico (1–3,500, $n = 7$; 3,501–8,000, $n = 4$).

Aggregation size	Behavior							
	Feeding head down	Resting	Walking	Preening/comfort	Courtship	Feeding head up	Vigilance	Aggression
1 to 3,500	59.8 ± 0.6	0.1 ± 0.6	3.2 ± 0.3	3.2 ± 0.3	0.1 ± 0.1	29.3 ± 0.5	2.1 ± 0.2	2.3 ± 0.2
r	0.90	−0.20	−0.54	−0.73	0.20	−0.85	−0.85	−0.01
P	0.01	0.66	0.11	0.10	0.66	0.01	0.01	0.79
3,501 to 8,000	59.6 ± 3.2	2.3 ± 2.3	2.6 ± 0.9	2.3 ± 1.9	0.0 ± 0.0	27.1 ± 2.3	1.1 ± 0.5	4.9 ± 1.4
r	0.10	−0.59	−0.71	0.92	—	0.20	0.41	−0.92
P	0.88	0.41	0.29	0.08	—	0.79	0.58	0.08

we obtained 931 observations on their foraging behavior from 21 January to 16 March 1989.

The mean amount of time spent in each behavioral category was: feeding head down (60%), feeding head up (29%), walking (3%), preening (3%), aggression (2%), alert (2%), resting (0.1%), and courtship (<0.1%). There was no linear relationship ($P = 0.14$ to 0.94; $r = -0.36$ to 0.47) between aggregation size (1–8,000) and mean time spent in any of the 8 behavioral categories. However, aggregation sizes of 1 to 3,500 flamingos were recorded for 95% ($n = 887$) of all observations, and when activity was compared within this range of aggregation sizes, there was a linear relationship ($P < 0.01$) between the average amount of time spent feeding with head down ($r = 0.90$), feeding with head up ($r = -0.85$) and alert behaviors ($r = -0.85$; Table 1). The numbers of individuals in aggregations of 1 to 3,500 flamingos also was related to density ($r = 0.80$; $P = 0.03$), and distance to the aggregation edge ($r = 0.79$; $P = 0.03$).

Aggregation sizes that exceeded 3,500 flamingos occurred infrequently (5% of the total number of observations) and focal birds showed wide variation in time budgets. There also were no significant linear relationships ($r = -0.68$ to 0.59; $P = 0.15$ to 0.53) among this range of aggregation sizes and focal animal measurements (distance to nearest bird, distance to aggregation edge, and density). Further, none of the 8 behavioral categories was significantly correlated ($P = 0.08$ to 0.88) to group size above 3,500 although preening ($r = 0.92$; $P = 0.08$) and aggression ($r = -0.92$; $P = 0.08$) approached significance (Table 1). However, sample sizes for these correlations were small.

Aggregations larger than 3,500 occurred at times of greater cloud cover ($\chi^2 = 318.3$; 75–100%; $P < 0.001$), and greater wind velocities ($\chi^2 = 23.8$; gusting; $P < 0.001$). Espino-Barros and Baldassarre (1989) did not detect any differences in the amount of time spent feeding in relation to variations in wind between the four daily time periods in which they sampled. However, it is probable that very large aggregations periodically formed when weather fronts passed over the area. The greatest difference between the mean amount of time spent in each behavioral category for aggregation sizes of 1–3,500 and 3,501–8,000 was in aggression ($P = 0.07$), with little difference in feeding head up ($P = 0.95$), resting ($P = 0.33$), walking ($P = 0.53$), preening ($P = 0.57$), courtship ($P = 0.82$), feeding head down ($P = 0.35$), and alert ($P = 0.28$).

DISCUSSION

A major impact of Hurricane Gilbert appears to have been a sharply elevated feeding rate, which probably was influenced by a change in food abundance and availability. We did not measure food density, but recall that the only feeding method we observed was "stamping-marking time," although American Flamingos commonly "walk-feed" (Allen 1956, Rooth 1965, Bildstein et al. 1991). We believe that stamp-feeding was the predominant mode of foraging during our study because Hurricane Gilbert destroyed the submergent vegetation and associated populations of gastropods; the latter probably were the main food of the flamingos (Espino-Barros and Baldassarre 1989). Flamingos fed on the seeds of widgeongrass and the tubercles of muskgrass that remained in the bottom sediments, but these items probably represented secondary foods (Schmitz et al. 1990). The stamping method may therefore have been the most efficient way to secure these food items from the mud, but concurrently required an increased overall foraging effort. For example, feeding flocks of American Flamingos in Venezuela primarily walk-fed (29–52%) versus stomp-fed (9–15%). Overall, American Flamingos in Yucatan fed 87–89% of the time versus 44–64% in Venezuela, a 25–43% increase.

Our interpretations of group size and behavioral interactions are cautious because of the hurricane. Nonetheless, Clark and Mangel (1984) proposed that formation of aggregations is of greatest value when food resources are unevenly distributed, and when the aggregation itself yields information about food location and abundance. However, Caraco (1980) asserted that aggression would increase with aggregation size due to an increased probability of encounters, and thus represented a cost of increasing group size. As aggregation size increased, we did note an increase in the density of foraging flamingos within five bird lengths of the focal animal, but we did not find a correlation between aggression and aggregation size ($r = 0.01$; $P = 0.79$; 1–3,500 individuals). The mean rate (2.3%) of aggression for aggregation sizes less than 3,500 individuals was lower ($P = 0.07$) than the mean rate (4.9%) of aggression for aggregation sizes greater than 3,500 individuals, but our incidence of aggression was very low when compared to feeding American Flamingos in Venezuela (19–44%; Bildstein et al. 1991). Perhaps our rates were lower because the already high feeding time (89%) precluded benefits from increasing aggression in an area where food was in short supply to begin with. In other words, under conditions of reduced food abundance, flamingos may gain more by feeding than elevating levels of aggression toward conspecifics.

Feeding rate did increase with group size, but placing the head below water obviously precludes monitoring activity and conditions above the surface. Nevertheless, distance to the nearest neighbor did not vary with group size or density of birds, indicating that flamingos were aware of the location of adjacent foragers (Allen 1956) and maintained a stable individual distance (Conder 1949). Individuals in larger aggregations may allocate the minimal time necessary to monitor conspecifics and maximize time feeding because of the benefit of higher food density, albeit food density was probably lower than pre-hurricane levels. Thus, feeding head down would occur when the benefit of food intake exceeded the benefit derived from informational updating on conspecific location and behavior or vigilance for potential predators. That feeding head down increased with aggregation size implies that attention to conspecifics was reduced because benefits of eating food increased, which could be especially beneficial if food was restricted by the hurricane.

The major food resource probably was not being renewed because there was no plant growth in the estuary. Hence, one would expect a behavioral response to diminishing food supplies. However, comparison of the mean percent time spent in all 8 behavioral categories did not differ ($P = 0.09$ to 0.70) between the first and second four weeks. Distance between the focal animal and the nearest neighbor also did not differ ($P = 0.53$) between the time periods. However, the density of birds within five bird lengths of the focal animal did decrease ($P < 0.001$) from 2.3 in the first four weeks to 1.5 in the next four weeks, and the total number of flamingos feeding on the entire estuary decreased ($P < 0.001$) between each census. Therefore, to respond to gradually diminishing food resources, individual flamingos may have maintained a consistent rate of food intake in feeding aggregations by leaving the estuary, and reducing local density. Indeed, during normal years most of the nonbreeding population of American Flamingos in Mexico is concentrated in the Celestun Estuary, but following Hurricane Gilbert they were distributed along the entire north coast of the Yucatan Peninsula.

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