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EFFECTS OF FOOD DENSITY ON THE BEHAVIOR AND DISTRIBUTION OF NONBREEDING AMERICAN FLAMINGOS IN YUCATAN, MEXICO[1]

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Abstract. We sampled potential food items of American Flamingos (*Phoenicopterus ruber ruber*) in the Celestún Estuary, Yucatán, Mexico, from October 1992 to January 1993, to explore the influence of food density and distribution on flamingo behavior in relation to the ideal free distribution model. Food items were found in the substrate and vegetation and were dominated by four groups: gastropods (40%), muskgrass bulbils (26%), crustaceans (11%), and chironomids (10%). Overall, food was patchily distributed and food abundance decreased over time. Flocks initially concentrated in areas where food was most abundant, but appeared to deplete food resources in these areas after which they dispersed throughout the Celestún Estuary. Time spent feeding also was lower in the first two time blocks ($\bar{x}$ = 26%) when food was most abundant, and then increased and remained constant (56%) in the remaining five time blocks. Mean flock size was 457, and did not differ among locations through time, except in the last time block when flocks tended to be larger ($\bar{x}$ = 821). We concluded that the distribution of flamingo flocks was consistent with the ideal free model based on food density and distribution, but that major perturbations (storms) can dramatically affect flamingo distribution. However, relative payoff for individuals within flocks has yet to be determined.

Key words: American Flamingo; foraging; ideal free; nonbreeding; Mexico; Phoenicopterus ruber ruber; *Yucatán.*

INTRODUCTION

Flamingos (Phoenicopteridae) breed colonially and regularly aggregate in large feeding flocks during the nonbreeding season (Allen 1956). Breeding colonies of 30,000 Greater Flamingos (*Phoenicopterus ruber roseus*) have been recorded in France (Ogilvie and Ogilvie 1986), and feeding flocks of 915,000 Lesser Flamingos (*Phoeniconaias minor*) have been observed in Kenya (Vareschi 1978). Many costs and benefits are associated with gregariousness, but inter- and intraspecific comparisons suggest that predator avoidance and food distribution are the two main environmental influences on flock formation in the nonbreeding season (see review in Pulliam and Millikan 1982). Among flamingos, however, few studies have measured food density and distribution while assessing foraging behavior of nonbreeding birds.

Schmitz and Baldassarre (1992b) studied American Flamingos in Yucatán, Mexico, and related feeding behavior to variation in flock size following a major habitat perturbation (Hurricane Gilbert), but they did not measure food density or distribution. Bildstein et al. (1991) also studied foraging behavior of nonbreeding American Flamingos (*Phoenicopterus ruber ruber*) in Venezuela, but food sampling was unsuccessful.

We were interested in exploring how food density and distribution affects distribution and behavior of nonbreeding American Flamingos. A basic model that incorporates these aspects of habitat selection is the ideal free model (Fretwell and Lucas 1970), which assumes (1) that individuals are ideal in their perception of food patch profitability (i.e., they select the habitat best suited for survival and reproduction), and (2) that individuals are free to enter any habitat. The model also assumes that resources are distributed in patches and that individuals are equal in their competitive abilities. As a result, the proportion of individuals in each patch matches the proportion of resources in that patch (Kacelnik et al. 1992), whereby average payoff for individuals should be equal across patches regardless of food density. A related prediction based on this model is that if the amount of food available in

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one site is higher than others, individuals should move into this site, but as more individuals occupy the patch it becomes less profitable as a result of depletion. Also, as the number of individuals in a patch increases, so does interference, whereby an individual's payoff is reduced as a result of competition (Milinski and Parker 1991). The ideal free model predicts that at equilibrium, all predators distribute themselves whereby the interaction of food abundance and interference balance, and each individual receives the same payoff (Sutherland 1983).

In Mexico, the population of American Flamingos on the Yucatán Peninsula constitutes the northernmost mainland flock in the Americas. This population breeds in the Río Lagartos and Uaymitún area from April to September, but scatters along the northern coast of the Yucatán Peninsula during the nonbreeding season when up to 75% can occur in the Celestún Estuary (Espino-Barros and Baldassarre 1989). The objective of our study was to explore the influence of food density and distribution on the distribution and behavior of nonbreeding American Flamingos in Yucatán, Mexico, and relate these data to predictions of the ideal free model.

STUDY AREA

We conducted the study on the Celestún Estuary, on the northwest coast of the Yucatán Peninsula, Mexico (Fig. 1). The Celestún Estuary is a narrow coastal lagoon parallel to the Gulf of Mexico and connected to the gulf at the southwestern end. It is approximately 22.5 km long and averages 2.2 km wide and 0.5 m deep (subject to tidal variation and freshwater input). A bridge linking the barrier beach town of Celestún to the mainland bisects the estuary.

Bottom sediments are soft, consisting of clay, limestone, sand, and organic matter (Batllori 1990). The 2,800 ha of open water are bordered by red mangrove (*Rhizophora mangle*), white mangrove (*Laguncularia racemosa*), and black mangrove (*Avicennia germinans*). Widgeongrass (*Ruppia maritima*), muskgrass (*Chara* sp.), shoalgrass (*Halodule wrightii*), and turtlegrass (*Thalassia testudinum*) dominate the open-water vegetation. A 59,130-ha area including the estuary was declared a national faunal refuge in 1979. Our study site was the open-water area north of the bridge (about 1,300 ha) because this area is traditionally most used by flamingos during the nonbreeding season (Espino-Barros and Baldassarre 1989).

METHODS

FOOD SAMPLING AND ESTUARY CHARACTERIZATION

The few food habits records of American Flamingos show that their diet includes organic ooze, widgeongrass seeds, muskgrass oogonia and bulbils, annelids, mollusks, crustaceans, and insect larvae (Gallet 1950, Allen 1956, Rooth 1965, and Schmitz et al. 1990). Our sampling design targeted these plant structures and macroinvertebrates.

We established 22 permanent transects at 500-m intervals north of the bridge and perpendicular to the length of the Celestún Estuary. We then selected two random points along each transect, one east and one west of the transect marker. Potential food items in the rooted vegetation then were sampled by filling a 250-ml beaker with vegetation collected with a 15 × 15-cm^2 Eckman dredge. Potential food items in the substrate were sampled by removing a section of substrate with an Eckman dredge; to ensure sampling a constant volume, an 11-cm diam × 7-cm deep core was removed and strained through a 1-mm mesh sieve. We sampled the water column by moving a 30-cm diameter dip net back and forth 1 m (2 m total) just below the surface of the water. Sampling was conducted from a boat to minimize disturbance of the site.

All samples were preserved in 70% ethanol and taken to the laboratory for identification and counting. Numbers of potential food items from vegetation, substrate, and water column samples were combined because flamingos feed within all three strata (Allen 1956, Rooth 1965, Schmitz and Baldassarre 1992b).

We conducted seven sampling rounds, the first on 12 and 13 October 1992 during which all transects were sampled. Subsequent sampling rounds occurred at 8–12 day intervals starting on 15 November 1992 and ending on 5 January 1993, during which a subset of 2–5 transects was sampled. The subset was chosen randomly for the second round. We alternated sampling of odd or even number transects thereafter.

We prepared a vegetation map of the Celestún Estuary by conducting a qualitative vegetation survey on 30 September 1992. We also noted vegetation type at all sample sites, which revealed that underwater vegetation was distrib-

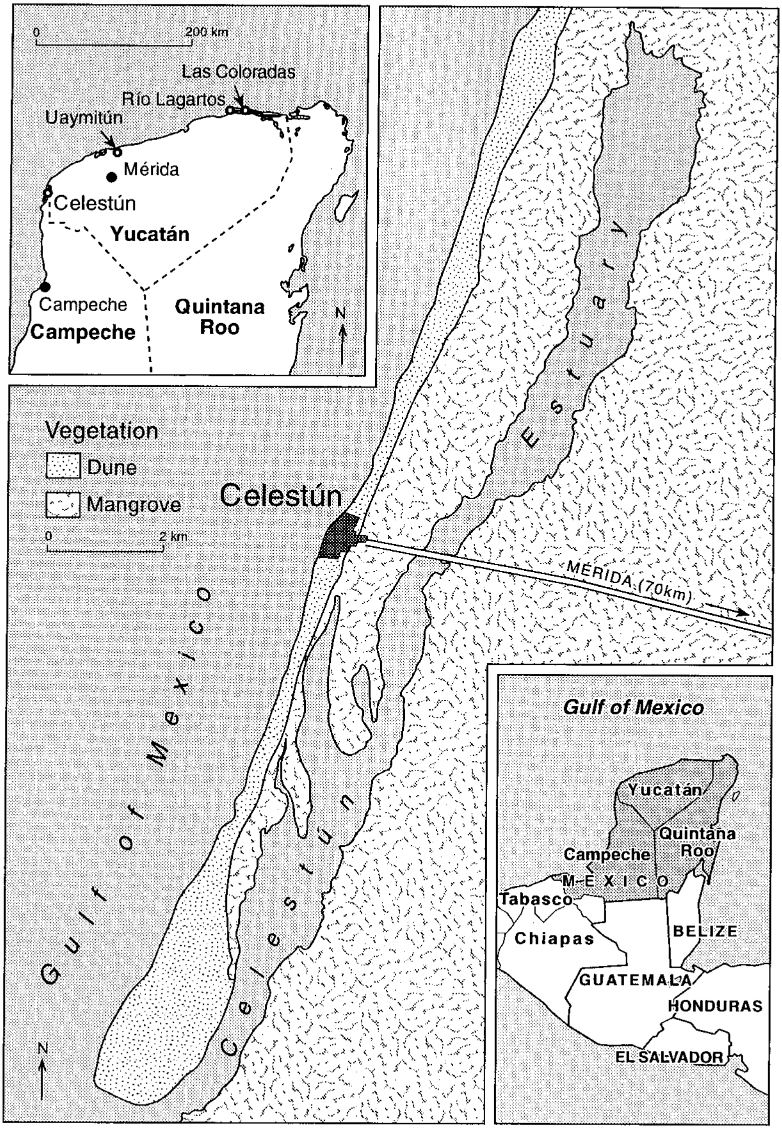

FIGURE 1. Study area map of the Celestún Estuary on the Yucatán Peninsula, Mexico.

uted in a north-south gradient. Generally, widgeongrass dominated the lower one-third of the Celestún Estuary near the bridge, muskgrass dominated the northern one-third, and a transition zone of mixed widgeongrass-muskgrass occurred from approximately 3.0–5.5 km north of the bridge. Thus, we divided the estuary into three vegetation zones (1, 2, 3) south to north. We further divided these zones into an east (E) and west (W) section because vegetation biomass in the west was greater than in the east, hence there was a total of six sample locations (1E, 1W, 2E, 2W, 3E, 3W).

We used a portable refractometer to measure salinity at the center of each transect. We took measurements two and seven days after a 1 October 1992 storm, and once during November and December 1992. We monitored water level by taking measurements every 1–2 days from a permanent marker at the bridge that was 10 m in from the edge of the estuary.

Salinity was compared among zones and

TABLE 1. Salinity (ppt) in the northern half of the Celestun Estuary, 1992.[a]

Zone	3 October		9 October		16 November		16 December		n
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
1	35Aa	0.2	15Ab	0.4	6Ac	0.1	7Ad	0.5	7
2	36Aa	1.2	17Bb	0.4	6Ac	0.4	7Ac	0.4	6
3	33Ba	0.7	16ABb	0.7	6Ac	0.3	8Bd	0.2	9

[a] Means denoted with the same capital letter are not different ($P > 0.05$) among zones. Means denoted with the same small letter are not different ($P > 0.05$) among dates.

months using analysis of variance (ANOVA). Data from potential food items were grouped by location and compared among sampling rounds using ANOVA. Analysis of potential food items was performed on the total number of food items, then on plant structures (widgeongrass seeds, muskgrass oogonia and bulbils combined), gastropods (only Lymnaeidae), crustaceans (all groups combined), and chironomids because these were the most abundant groups. Post-hoc comparisons among means were done using the Fisher's protected least significant differences test.

BEHAVIOR

We conducted behavioral observations from 06:00–17:00, from 10 October 1992 through 31 January 1993. Observations were done from a boat or from one of three blinds using a 15–60 × spotting scope or 8 × 40 binoculars. To characterize the behavior of the entire flock, we used scan sampling techniques (Altmann 1974), where the behavior of 10 birds in the flock was recorded every three minutes during a 15-min time period. We selected the birds by visually dividing the flock into 10 equal sections, then pointing the scope or binoculars to each section and recording the behavior of the bird in the center of the field of view. We recorded the following behaviors: feeding (subdivided into walk-feed or stamp-feed, Allen 1956), resting, preening, walking, flying, alert, aggression, and courtship (Rooth 1965, Kahl 1975).

We also noted flock size and location in the Celestún Estuary using the transect markers as reference points. We defined a flock as a continuous group of individuals that were within at least 30 m of each other. We recorded flock density as of 3 December and classified it qualitatively as packed (three or more individuals within one body length), medium (one individual within one body length, three within stretched neck length), and loose (at most, one individual within neck length); density numbers were assigned 1, 2, and 3, respectively. On days when behavior was sampled, we were usually able to watch all flocks present on the Celestún Estuary. Total numbers of flamingos in the estuary were determined three times in October, then once monthly from November 1992 through February 1993.

Data were averaged by location and grouped into seven time blocks of 10–13 days each (centered on the food sampling dates); time block 1 = 17–31 Oct, time block 2 = 11–21 Nov, time block 3 = 22 Nov–1 Dec, time block 4 = 2–11 Dec, time block 5 = 12–21 Dec, time block 6 = 22 Dec–1 Jan, and time block 7 = 2–11 Jan. We used ANOVA to compare all behavioral data among time blocks. Post-hoc comparisons among means were done using the Fisher's protected least significant differences test. We compared means of time spent feeding and in aggressive encounters among flock size categories of 100, 250, 500, 750, 1,000, and 1,500. Data were assigned to a category by approximating actual flock size to the nearest category value.

RESULTS

ESTUARY CHARACTERIZATION

After the storm on 1 October 1992, water levels at the edge of the Celestún Estuary nearly tripled from an average of 55 cm to 140 cm; prestorm water level was not reestablished until early November. Salinity averaged 35 ppt one day after the storm, declined to 16 ppt six days later, and stabilized at 6–7 ppt thereafter (Table 1). Overall, salinity differed among sampling dates ($P < 0.01$) within each zone except between November and December in zone 2 ($P = 0.04$). Salinity differed among zones on three of the four sampling dates ($P = 0.02$–0.05).

FOOD SAMPLING

We found 15 invertebrate taxa, most of which were identified to the order or family level (Table

TABLE 2. Classification and percentage (number in parentheses) of invertebrate taxa found in the potential food samples of the Celestun Estuary, October 1992–January 1993.

Phylum	Subphylum	Superclass	Class	Order	Family
Platyhelminthes			Turbellaria (<1)		
Nematoda			Adenophorea (<1)		
Mollusca			Gastropoda	Mesogastrpoda	Lymnaeidae (35.9)
					Vitrinellidae (1.5)
				Mytiloida	Mytilidae (2.5)
			Bivalvia	Veneroida	Veneridae (<1)
					Solecurtidae (<1)
Annelida			Polychaeta (3.0)	Sabellida	Spirorbidae
				Phylodocida	
			Oligochaeta	Haplotaxida (<1)	
Arthropoda	Crustacea (10.7)		Malacostraca	Mysida (<1)	
				Amphipoda (1.9)	
				Isopoda (2.3)	
				Tanaidacea (6.5)	
		Insecta		Diptera	Chironomidae (10.2)

2). Only one water column sample contained potential food items (three crustaceans), thus most food items were distributed in the vegetation and substrate. Of the animal sources, gastropods were the most abundant (40% of all potential food), followed by crustaceans (11%), and chironomids (10%); the remaining 12 taxa comprised 3%. Of the three plant items, muskgrass bulbils were the most abundant (26% of all potential food), followed by widgeongrass seeds (6%) and muskgrass oogonia (4%).

All potential food items were found in all time blocks (Oct–Jan), with the exception of chironomids, which were not found in time block 1. Means of the four main categories of potential food items (total number, plant items, gastropods, chironomids) were not different ($P = 0.13$–0.99) within locations among time blocks. Pooled means from the six locations exhibited a decreasing trend in total number of food items over time (Fig. 2).

There were, however, a few statistical differences among locations within time blocks 1–3 (Fig. 3). In time block 1, locations E1 and E2 were not different ($P = 0.25$) and had the highest mean total number of food items ($P = 0.001$–0.02) and gastropods ($P = 0.01$–0.04) compared to the remaining locations. Crustaceans, which did not differ between E1 and W1 ($P = 0.06$), were higher there than at other locations ($P = 0.001$–0.03). In time block 2, locations E2 and W2 did not differ ($P = 0.5$) and had the highest mean total number of food items, mainly due to differences in plant items ($P = 0.001$–0.04). Chironomids differed among locations within time blocks 3, 5, and 6, being most abundant in E2 ($P = 0.003$–0.03) during time block 3, and E3 and W3 ($P = 0.005$–0.02) in time block 5. Crustaceans tended to be scarce or absent in E3 and W3. All other comparisons were not significant ($P > 0.05$).

Flock attributes and behavior. Total number of flamingos in the Celestún Estuary increased from none on 1 October 1992 to 5,700 on 23 February 1993 (Fig. 4). The number of feeding flocks also increased, from none to eight on 21 January 1993 (Table 3). Overall, flock size ranged from 14 on 17 October 1992 to 2,500 on 23 January 1993 (mean = 457, SE = 28, $n = 192$). Flock sizes did not differ ($P > 0.05$) among locations within time blocks, except in time block 7 ($P < 0.01$), when flocks >1,000 occurred in 39% of the observations (mean = 821, SE = 155, $n = 18$). Flock density did not vary over time, ranging from loose to packed in all locations, except in time block 7 ($P = 0.02$) when flocks tended to be looser in E2 and W2, and packed in E3 and W1.

All feeding flocks initially concentrated in E2 during time blocks 1 and 2 (October–early November), but expanded to occupy five of the six locations by time block 7 (February). Among all flocks observed, 72% were on the east side of the estuary, and birds never were observed in location W3.

Flamingos were observed feeding in the substrate and vegetation using the stamp-feed method 75% of the time and walk-feed method 25% of the time. They were not observed filter feeding within the water column. Time spent feeding in

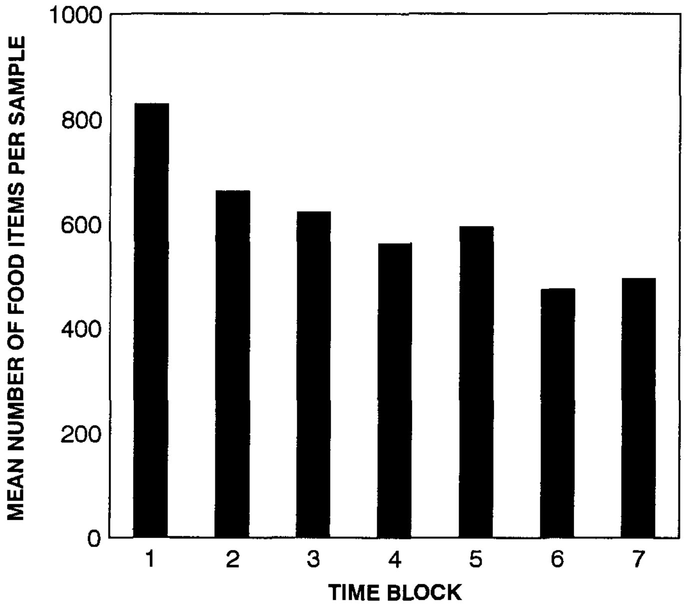

FIGURE 2. The mean number of total potential food items per time block, pooled across all sample locations.

time blocks 1 and 2 (2–65%) was, on average, 50% lower than in subsequent time blocks (10–98%), but percent feeding among locations within time blocks did not differ ($P = 0.2$–0.8). Time in aggressive encounters ($\bar{x} = 4\%$, range = 0–12%) did not differ among locations within time blocks or among time blocks ($P = 0.06$–0.6), except in time block 6, when aggression was higher in W2 and E3.

We used behavioral data from time blocks 3–7, when food distribution was least variable, in order to determine whether time spent feeding and in aggressive encounters changed as flock size increased. Neither mean time spent feeding (45–58%; overall $\bar{x} = 56\%$) or in aggressive encounters (3–5%) was different among flock size categories ($P = 0.39$ and 0.36, respectively).

DISCUSSION

INFLUENCE OF FOOD ON FLAMINGO BEHAVIOR AND DISTRIBUTION

Flamingo flocks in the Celestún Estuary appeared to be distributed as predicted by the ideal free model because (1) groups of birds initially settled in patches where food density was highest (i.e., E2), and (2) as food declined in these patches, flocks distributed themselves over other patches. These latter patches had similar food density and average time spent feeding by flocks in each patch also was constant (i.e., 56%).

All flamingos initially established in E2 during time block 1, continued to feed there during time block 2, although potential food items were then most abundant in nearby locations E1 and W2 contradictory to the ideal free model. Flamingos may have initially located in E2 because of prior experience, sampling, or cuing in the presence of other flamingos (see review in Stephens and Krebs 1986). They possibly remained in E2 during time block 2 because there were only an average of 700 birds present, thus they may have satisfied food requirements. By time block 3, however, flamingos had moved to E1, and from blocks 4–7 had expanded to occupy all locations in the Celestún Estuary (except W3). Flamingos likely moved into these locations because by time block 4 they had reduced the food resources in E2 and E1 to similar levels of other locations (Fig. 3). Hence, payoff among locations was probably equal, as reflected by the constant feeding time; equal payoff is a prediction of the ideal free model.

By time block 3, the number of flocks also had increased, but average flock size and feeding time remained constant, with the exception of the large flocks forming in time block 7. These large flocks coincided with an increase in courtship and in-

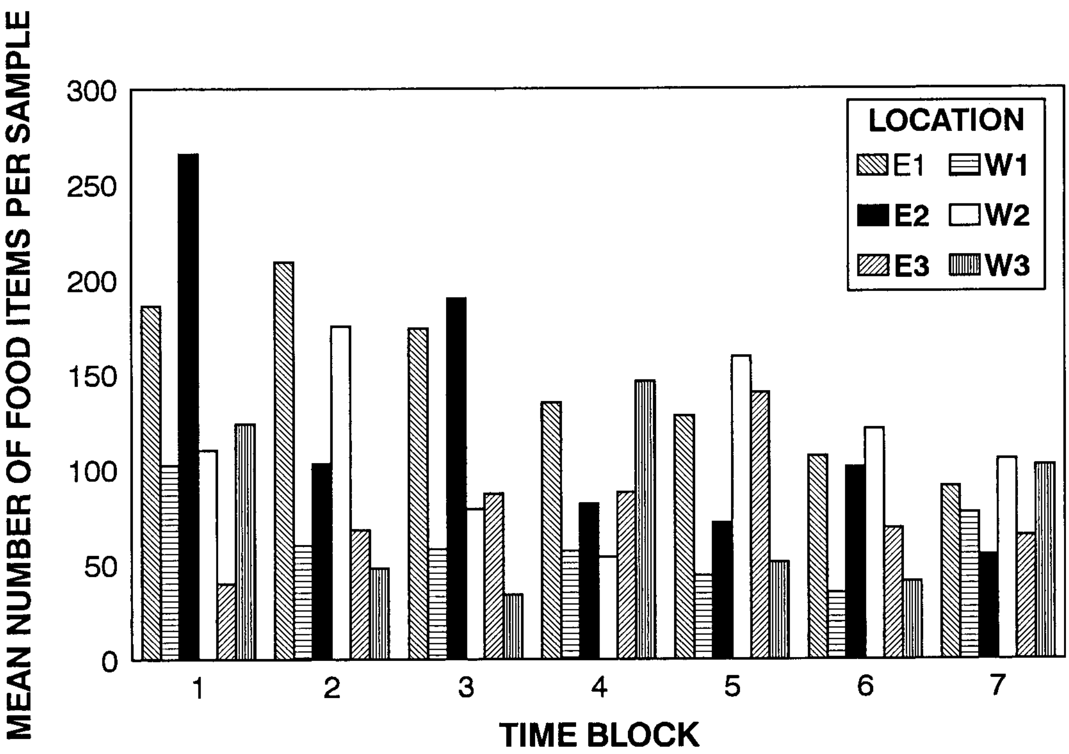

FIGURE 3. The mean number of total potential food items within each time block and location combination.

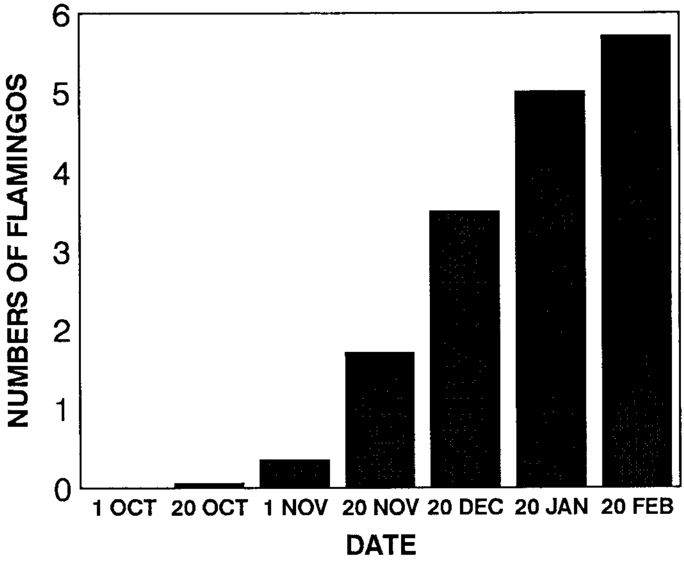

FIGURE 4. Number of American Flamingos censused in the Celestún Estuary from October 1992 through February 1993.

TABLE 3. Means ($\bar{x}$), sample sizes (n), and standard errors (SE) by location of flamingo flock attributes and percent time spent feeding and in aggressive encounters in Celestún.

Block	Location																	
	E1			W1			E2			W2			E3			W3		
	$\bar{x}$	n	SE	$\bar{x}$	n	SE	$\bar{x}$	n	SE	$\bar{x}$	n	SE	$\bar{x}$	n	SE	$\bar{x}$	n	SE
1 Number of flocks	0.0	10	0.0	0.0	10	0.0	1.4	10	0.2	0.0	10	0.0	0.0	10	0.0	0.0	10	0.0
Flock size	—	—	—	—	—	—	229	14	44.2	—	—	—	—	—	—	—	—	—
Density	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Feeding	—	—	—	—	—	—	21	14	5.7	—	—	—	—	—	—	—	—	—
Aggression	—	—	—	—	—	—	2	14	0.6	—	—	—	—	—	—	—	—	—
2 Number of flocks	0.0	6	0.0	0.0	6	0.0	1.7	6	0.5	0.0	6	0.0	0.0	6	0.0	0.0	6	0.0
Flock size	—	—	—	—	—	—	429	14	74.7	—	—	—	—	—	—	—	—	—
Density	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Feeding	—	—	—	—	—	—	32	14	7.2	—	—	—	—	—	—	—	—	—
Aggression	—	—	—	—	—	—	3	14	1.3	—	—	—	—	—	—	—	—	—
3 Number of flocks	3.0	5	0.4	0.6	5	0.4	0.8	5	0.5	0.0	0	0.0	0.0	0	0.0	0.0	0	8.0
Flock size	485	12	82.6	633	3	283.3	97	3	23.3	—	—	—	—	—	—	—	—	—
Density	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Feeding	67	12	4.5	58	3	15.2	49	3	28.3	—	—	—	—	—	—	—	—	—
Aggression	5	12	1.0	8	3	1.4	1	3	1.1	—	—	—	—	—	—	—	—	—
4 Number of flocks	1.0	6	0.4	0.2	6	0.2	3.5	6	0.2	0.8	6	0.4	0.0	0	0.0	0.0	0	0.0
Flock size	212	2	112.6	450	1	0.0	479	19	83.9	299	7	48.8	—	—	—	—	—	—
Density	3.0	2	0.0	2.0	1	0.0	2.4	12	0.2	2.8	5	0.2	—	—	—	—	—	—
Feeding	55	2	1.6	33	1	0.0	48	20	7.3	65	7	9.0	—	—	—	—	—	—
Aggression	2	2	0.8	2	2	0.0	3	20	0.9	5	7	1.0	—	—	—	—	—	—
5 Number of flocks	1.5	6	0.5	0.2	6	0.2	3.2	6	0.4	2.3	6	0.4	0.0	0	0.0	0.0	0	0.0
Flock size	750	7	77.1	265	1	0.0	466	16	90.5	470	12	117.7	—	—	—	—	—	—
Density	2.3	7	2.0	1.0	1	0.0	2.1	12	0.2	2.5	11	0.2	—	—	—	—	—	—
Feeding	62	8	9.0	0	1	0.0	52	16	7.4	58	12	4.9	—	—	—	—	—	—
Aggression	5	8	1.6	0	1	0.8	3	16	0.7	6	12	1.2	—	—	—	—	—	—
6 Number of flocks	1.9	8	0.4	0.9	8	0.2	3.1	8	0.2	1.6	8	0.3	1.0	8	0.2	0.0	0	0.0
Flock size	476	5	117.6	254	4	69.6	430	25	72.6	286	9	76.1	453	3	74.1	—	—	—
Density	2.8	5	0.2	2.5	4	0.3	2.5	23	0.1	2.3	9	0.2	2.0	3	0.0	—	—	—
Feeding	60	5	0.8	49	4	0.8	48	4	0.8	53	9	0.7	58	3	2.0	—	—	—
Aggression	3	5	0.6	5	4	2.9	1	25	0.5	6	9	1.8	6	3	2.9	—	—	—
7 Number of flocks	0.0	4	0.0	0.2	4	0.2	2.5	4	0.3	1.7	4	0.5	1.5	4	0.5	0.0	0	0.0
Flock size	500	2	0.0	643	7	134.2	1012	4	253.6	243	3	56.7	2250	2	250.0	—	—	—
Density	2.0	3	0.6	1.3	7	0.2	2.5	4	0.3	2.3	3	0.3	1.0	2	0.0	—	—	—
Feeding	46	3	21.1	60	7	13.3	68	4	12.0	82	3	0.0	46	2	0.8	—	—	—
Aggression	12	3	5.7	2	7	0.6	4	4	2.5	2	3	0.1	—	—	—	—	—	—

creased disturbance by boats (Arengo and Baldassarre 1995), thus factors other than feeding may have been influencing flock size. Nevertheless, equal payoff per individual is suggested because the average time spent feeding for flocks remained constant among flock sizes. Average time spent in aggressive encounters, used as a measure of interference among individuals within a flock, also remained constant.

Coefficients of variation among sample means (82–248%) reflect high variability within locations. Such variation suggests a patchy distribution, which is the type of circumstance in which flocking will occur because flocks provide information about the location of food and patch quality (Clark and Mangel 1984). Nonetheless, certain patches (E2, E1, W2) were richer in the first two time blocks. Flamingos only fed in E2 during these blocks, but feeding time was significantly lower than other time periods (26% versus 56%). Bildstein et al. (1993) found that the number of feeding bouts was greater in free-ranging birds than in captive individuals maintained on superabundant, ad libitum diets. Schmitz and Baldassarre (1992b) found that flamingos fed 89% of the time following Hurricane Gilbert, when food availability was thought to be lower. Thus, the percent time spent feeding by American Flamingos may be inversely related to food abundance.

INDIVIDUAL BEHAVIOR

Although we did not record behavior of individuals within flocks, Schmitz and Baldassarre (1992a) found asymmetries in fighting abilities of American Flamingos and Bildstein et al. (1991) found differences in feeding rates between adults and juveniles. This is important because an assumption of the ideal free model is violated by individual differences, which could result in unequal payoffs. The despotic behavior of some individuals can result in their monopolizing resources through dominance, which may be the case in flamingos (Schmitz and Baldassarre 1992a). Thus, although flocks may distribute in an ideal free manner, individuals within a flock may be distributed as predicted by the ideal despotic model (Fretwell and Lucas 1970). Overall, we believe that the distribution of flamingo flocks in the Celestún Estuary is consistent with the ideal free model based on food density and distribution, but the relative payoff for individuals within flocks awaits determination.

ENVIRONMENTAL INFLUENCES

Although our data on food density and distribution on the behavior of feeding flamingos seemingly support the ideal free model, major disturbances clearly overpowered same in the Celestún Estuary. For example, flamingos cannot feed by treading the bottom (the primary method we observed) when water depth exceeds 60 cm (Allen 1956). Some flamingos during our study were present in the Celestún Estuary before the 1 October storm, but none were seen until two weeks after, when water depths returned to 60 cm.

Following the storm, we suspect that the increased salinity caused muskgrass biomass to decline to zero. However, new growth of muskgrass occurred by 15 November, dense beds were observed by 25 December, and by February 1993 growth had surpassed levels prior to the storm. We did not observe flamingos feeding in location W3 where beds of muskgrass were densest, and flamingos generally were observed feeding more frequently in the eastern side of the Celestún Estuary where vegetation biomass was lower. Gallet (1950) also suggested that dense vegetation excluded feeding flamingos.

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LITERATURE CITED

ALLEN, R. P. 1956. The flamingos: their life history and survival. Research Report No. 5 of the National Audubon Society, New York, NY.

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behavior 49:227–267.

ARENGO, F., AND G. A. BALDASSARE. In press. American Flamingos and ecotourism on the Yucatán Peninsula, Mexico. Rec. Int. Wildl. Manage. Conf., San José, Costa Rica. The Wildlife Society, Bethesda, MD.

BATLLORI, E. 1990. Caracterización Ecológica del Refugio Faunístico "Ría de Celestún" al Noroeste de la Península de Yucatán. Internal Report, CINVESTAV-IPN, Mérida, Yucatán, Mexico.

BILDSTEIN, K. L., C. B. GOLDEN, AND B. J. MCGRAITH. 1993. Feeding behavior, aggression, and the conservation biology of flamingos: integrating studies of captive and free-ranging birds. Amer. Zool. 33: 117–125.

BILDSTEIN, K. L., P. C. FREDERICK, AND M. G. SPAULDING. 1991. Feeding patterns and aggressive behavior in juvenile and adult American flamingos. Condor 93:916–925.

CLARK, C. W. AND M. MANGEL. 1984. Foraging and flocking strategies: information in an uncertain environment. Amer. Nat. 123:626–641.

ESPINO-BARROS, R., AND G. A. BALDASSARRE. 1989. Numbers, migration chronology, and activity patterns of nonbreeding Caribbean Flamingos in Yucatan, Mexico. Condor 91:592–597.

FRETWELL, S. D., AND H. L. LUCAS, JR. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19:16–36.

GALLET, E. 1950. The flamingos of the Camargue. Blackwell, Oxford, England.

KACELNIK, A., J. R. KREBS, AND C. BERNSTEIN. 1992. The ideal free distribution and predator-prey populations. Trends Ecol. Evol. 7:50–55.

KAHL, M. P. 1975. Ritualized displays, p. 142–149. *In* J. Kear and H. Duplaix-Hall [eds.], Flamingos. T. and A. D. Poyser, Berkhamsted, Hertfordshire, England.

MILINSKI, M., AND G. A. PARKER. 1991. Competition for resources, p. 137–168. *In* J. R. Krebs and N. B. Davies [eds.], Behavioral ecology. 3rd ed. Blackwell, Oxford, England.

OGILVIE M., AND C. OGILVIE. 1986. Flamingos. Alan Sutton, Gloucester, England.

PULLIAM, H. R. AND G. C. MILLIKAN. 1982. Social organization in the nonreproductive season, p. 169–197. *In* D. S. Farner and J. R. King [eds.], Avian biology. Academic Press, New York, NY.

ROOTH, J. 1965. The flamingos on Bonaire (Netherlands Antilles): habitat, diet, and reproduction of *Phoenicopterus ruber ruber.* Utigaven "Natuurwetersch Stud. Suriname in de Ned. Antilles," No. 41.

SCHMITZ, R. A., A. ALONSO AGUIRRE, R. S. COOK, AND G. A. BALDASSARRE. 1990. Lead poisoning of Caribbean Flamingos in Yucatan, Mexico. Wildl. Soc. Bull. 18:399–404.

SCHMITZ, R. A., AND G. A. BALDASSARRE. 1992a. Contest asymmetry and multiple bird conflicts during foraging among nonbreeding American Flamingos in Yucatan, Mexico. Condor 94:254–259.

SCHMITZ, R. A., AND G. A. BALDASSARRE. 1992b. Correlates of flock size and behavior of foraging flamingos following Hurricane Gilbert in Yucatan, Mexico. Condor 94:260–264.

STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton Univ. Press, Princeton, NJ.

SUTHERLAND, W. J. 1983. Aggregation and the 'ideal free' distribution. J. Anim. Ecol. 52:821–828.

VARESCHI, E. 1978. The ecology of Lake Nakuru (Kenya). I. Abundance and feeding of the Lesser Flamingo. Oecologia 32:11–35.