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EFFECT OF GROUP SIZE AND LOCATION WITHIN THE GROUP ON THE FORAGING BEHAVIOR OF WHITE IBISES[1]

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Abstract. We studied adult White Ibises (*Eudocimus albus*) on a South Carolina salt marsh to determine the effects of social grouping on the birds' foraging behavior. White Ibises on our study site fed almost exclusively on fiddler crabs (*Uca* spp.). Four social categories were recognized: (1) central adults in flocks of ≥ 15 birds, (2) peripheral adults in flocks of ≥ 15 birds, (3) adults in small flocks of five or fewer birds, and (4) solitary adults (singletons). We used a paired sampling scheme to compare the behavior of central birds with the behavior of birds in the other three social groupings. Although peripheral adults did not differ significantly from central adults in number of steps, number of crabs captured, or number of capture attempts, they looked up more often and for longer periods of time than did central adults. Behavior of solitary ibises was similar to that of ibises in small flocks, but both foraged differently than central adults in large flocks. Birds in the center of large flocks took fewer steps, probed more frequently, and scanned the surroundings less often than birds in the other two social groupings; there were no differences in capture rates. Thus, White Ibises used two distinct types of foraging strategies depending on flock size and their position within the flock. Ibises in small flocks, singletons, and, to some extent, ibises on the edges of large flocks, stepped quickly to capture fiddler crabs before the crabs could retreat into burrows. Centrally-located ibises in large flocks were unable to use this foraging technique because the surrounding members of the flock created a disturbance that caused the fiddler crabs to remain in their burrows. These birds, therefore, probed into crab burrows and found their prey by tactile means. Our results support the predator-protection advantage of feeding within a flock independent of the feeding-efficiency hypotheses.

Key words: White Ibis; Eudocimus albus; *foraging; flock size; ciconiiformes; vigilance; salt marsh; behavior.*

INTRODUCTION

Optimal foraging theory predicts that animals should forage in such a way as to maximize the net rate of energy intake (for a review, see Krebs et al. 1983) because this will ultimately maximize reproductive output. Within this context, several hypotheses have been proposed to account for why birds feed in close proximity to one another. The two most widely accepted benefits of group foraging are: (1) increased probability of locating or exploiting suitable food resources (Ward and Zahavi 1973, Krebs 1974) and (2) decreased vulnerability to predators (Page and Whitacre 1975, Kenward 1978, Caraco 1979). Either by watching where other individuals are feeding or by gaining information on food patches at a gathering spot, such as a roost, a bird might increase the likelihood of foraging in an area containing sufficient food resources. Also, an individual might increase prey intake by copying the foraging techniques of successful flock members (Krebs et al. 1972), or simply by foraging at a faster rate (Abramson 1979, Jennings and Evans 1980). Members of flocks might experience increased protection from predators presumably because the increased number of eyes can detect an approaching predator earlier than a single pair of eyes (Pulliam 1973, Elgar and Catterall 1981) and because early detection increases the chance of escape. Thus, an individual can increase its foraging efficiency because of decreased vigilance. Obviously, these two hypothesized benefits of group foraging do not have to be mutually exclusive (cf. Abramson 1979). Studies simultaneously testing the two hypothesized advantages of flocking have produced conflicting re-

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sults (e.g., Smith 1977, Kenward 1978, Jennings and Evans 1980, Fleischer 1983). For example, some studies have shown that birds foraging in flocks decreased their time looking up while increasing their foraging rate (Powell 1974, Abramson 1979, Goldman 1980, Jennings and Evans 1980). In other investigations, however, the decrease in time spent vigilant by flock members did not affect the foraging success as compared to solitary individuals or birds in smaller groups (Smith 1977, Fleischer 1983). These discrepancies may reflect, at least in part, individual variation in foraging efficiency as a function of flock size and position within the flock as well as species and prey type differences.

On the other hand, increasing flock size may decrease foraging success because of food depletion (Goss-Custard 1969, Smith 1975, Horwood and Goss-Custard 1977), fighting over food (Goss-Custard 1977a, Fleischer 1983), alteration of search paths (Goss-Custard 1976), decreased prey availability because of disturbance by other flock members (Goss-Custard 1970, 1976), or the increased likelihood that as flock size increases, some birds will be displaced into less preferred areas (Zwarts 1976, Goss-Custard 1977b).

In addition to potential differences in foraging efficiency based on the size of the flock, position within the flock can affect an individual's rate of food intake. Birds on peripheries of flocks have been shown to spend more time scanning the surroundings as compared to other group members (e.g., Jennings and Evans 1980). Age (Bildstein 1983) and dominance status (Morse 1967, Russell 1978) also can influence where a bird forages within a group, thereby affecting its foraging behavior.

In this study we examine the costs and benefits of flock foraging by documenting differences in the foraging behavior of White Ibises (*Eudocimus albus*) foraging in flocks of various sizes and at different positions within the flocks. We then discuss our results in light of current flock foraging theory.

STUDY AREA AND METHODS

From June to August 1983 and 1984, we watched White Ibises foraging on the North Inlet marsh near Georgetown, South Carolina. Our 65-ha study site is dominated by *Spartina alterniflora,* and contains mud flats, oyster reefs, and tidal creeks (see Christy et al. 1981). Between 10,000 and 20,000 White Ibises breed on Pumpkinseed Island about 5 km from the marsh. Up to several hundred White Ibises typically feed on the marsh study area at any one time (Bildstein 1983). On the marsh, ibises usually feed in groups of from 2 to 75 individuals and almost exclusively on fiddler crabs (*Uca pugilator* and *U. pugnax,* Henderson 1981). Although other studies have described White Ibises as tactile, nonvisual foragers (Kushlan 1978, 1979), on North Inlet marsh, ibises used both tactile and visual methods for detecting prey.

We used spotting scopes to observe the foraging behavior of ibises from an 18.5-m tower located on the marsh edge. Data were collected throughout the day, but most records were taken between 08:00 and 14:00. Typically, ibises fed on the higher elevations of the marsh where *Spartina* was less than 30 cm high. These areas of the marsh were usually covered by standing water for only a few hours before and after high tide. We restricted our observations to periods when water had not inundated the high *Spartina* marsh because during these times fiddler crabs return to their burrows (pers. observ.).

To assess if foraging behavior and capture rates of adult (third year and older) ibises differed with respect to flock size or position within the flock, we made sequential, 4-min, paired observations of birds in four social situations. One observer paired (within 5 min) the observation of an individual in one social group (defined below) with an observation of an individual in a different social group. We used this paired sampling scheme to compare birds under similar conditions, thereby minimizing the effects of time of day, weather, season, and prey abundance and availability. Most ibises, regardless of social grouping, used the same areas of the marsh for foraging. We limited our observations to adults because, on North Inlet marsh, the foraging behavior of recently fledged juveniles and second-year birds (nonbreeders) differs from the foraging behavior of third-year and older birds (breeding adults) (Henderson 1981, Bildstein 1983). Young (<2 years) ibises sometimes foraged within adult flocks, but they rarely comprised $>10\%$ of the flock (see also Bildstein 1983). We recognized four social categories: (1) central adults in flocks of ≥ 15 birds, (2) peripheral adults in flocks of ≥ 15 birds, (3) adults in small flocks of five or fewer birds, and (4) solitary adults (singletons). Paired focal individuals were always >100 m

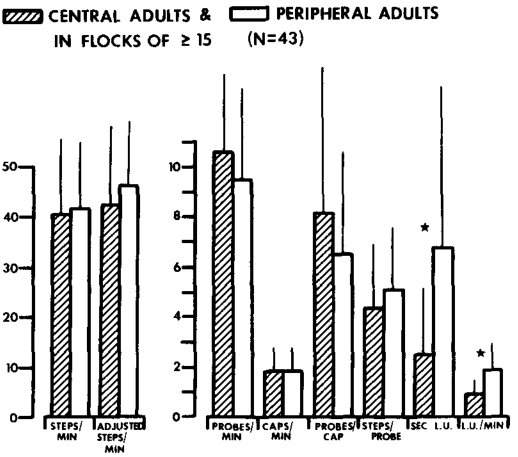

FIGURE 1. Comparison of foraging behavior of White Ibises in the center of large (≥15 birds) flocks and on the peripheries of large flocks. N represents the number of paired observations and asterisks indicate significant ($P \leq 0.05$) differences between the groups for that variable. Bars equal +1 SD.

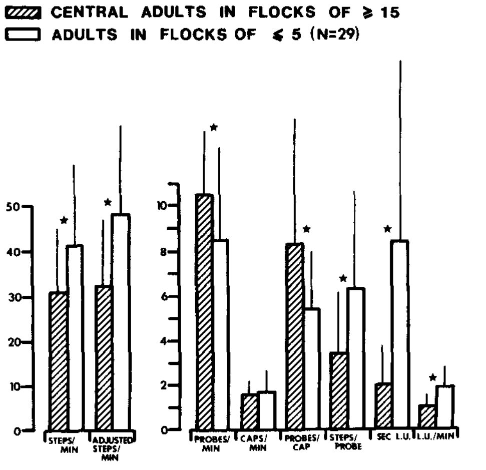

FIGURE 2. Comparison of the foraging behavior of White Ibises in the center of large (≥15 birds) flocks and ibises in small (≤5 birds) flocks. N represents the number of paired observations and asterisks indicate significant ($P \leq 0.05$) differences between groups for that variable. Bars equal +1 SD.

apart, except for central and peripheral individuals within the same flock. Ibises were considered central if they were part of the central 50% of the aggregation, and peripheral if they were not. Distinction between central and peripheral ibises was not possible for small flocks. All of the birds observed were readily visible as they foraged in short *Spartina*. Each bird was watched for 4 min, during which time we dictated into a cassette tape recorder the number of steps, the number of probes into crab burrows or probes at surface crabs, the number of *Uca* captured, and the number of times and the total amount of time the bird looked up and scanned the surroundings. From the tapes we derived eight foraging variables: number of steps/minute, number of probes/minute, number of crabs captured/minute, number of times the bird looked up/minute, number of seconds spent looking up/minute, probe to capture ratio, and step to probe ratio. We also computed the number of steps/minute during the time actually spent foraging (i.e., adjusted number of steps), which took into account (i.e., subtracted) the amount of time spent looking up. The time individuals spent scanning the surroundings was inversely proportional to the time spent foraging because the ibises that we watched did not noticeably engage in other behaviors (e.g., preening).

To compare estimates of energy expended during foraging bouts, we used the equations of Fedak et al. (1974) and Wiens and Dyer (1977) to calculate the energetic costs incurred by ibises in the different social categories. We estimated that ibises travelled at 1 km/hr while foraging, and that each step took 0.75 sec. These values were estimated by determining the distance travelled by some focal individuals over a given time interval and by recording the number of steps/second taken by ibises while actively foraging. To formulate a mean time budget for each group, we multiplied the average number of steps/minute by 0.75 sec to yield the number of seconds of each minute spent moving. For the remainder of the minute, the ibises were assumed to be expending energy equal to the existence metabolic rate (Kendeigh et al. 1977). Our estimates of travelling speed and time budgets should provide some indication of the relative energetic costs for individuals in different social groupings. This, in turn, may be useful in assessing costs and benefits of foraging in flocks. However, because these are rough estimates, caution should be used when interpreting the results of our energy expenditure analysis.

To determine if an individual foraged similarly irrespective of its position within a flock, we followed seven White Ibises which were initially either on the edge or in the center of one of the large flocks. We followed these birds for

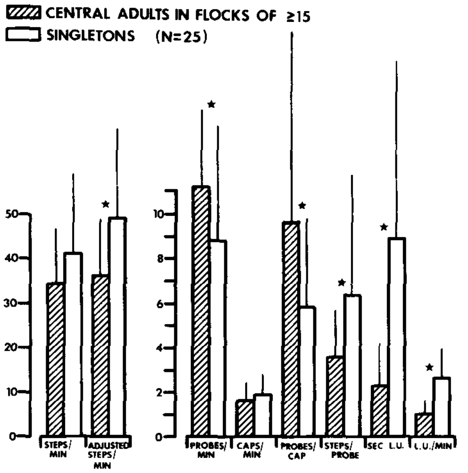

FIGURE 3. Comparison of foraging behavior of White Ibises in the center of large (≥15 birds) flocks and ibises foraging alone. N represents the number of paired observations and asterisks indicate significant ($P \leq 0.05$) differences between groups for that variable. Bars equal +1 SD.

up to 25 min and noted when a bird changed position within the flock. We compared the eight foraging variables between the two data sets (i.e., center vs. periphery) as paired samples.

Data were analyzed with Wilcoxon's matched-pairs signed-ranks test. All tests were two-tailed, and we considered a significant difference to exist if $P \leq 0.05$.

RESULTS

CENTRAL VS. PERIPHERAL ADULTS IN LARGE FLOCKS (N = 43)

The only significant differences in foraging behavior were that peripheral ibises looked up more often and for longer periods of time than did central birds. Although not statistically significant ($0.10 > P > 0.05$), central adults probed more often, had a higher probe to capture ratio, and took fewer steps between probes than did peripheral ibises. The number of steps, adjusted steps, and rate of prey capture were similar between the two groups (Fig. 1).

CENTRAL ADULTS IN LARGE FLOCKS VS. ADULTS IN SMALL FLOCKS (N = 29)

White Ibises in small flocks looked up more often and spent more time scanning the surroundings than did their counterparts in large groups. Birds in small flocks stepped more often and took more adjusted steps/minute than did central ibises in larger aggregations. Ibises in small flocks took more steps between capture attempts than did birds in large flocks. Ibises in large flocks probed significantly more frequently, and probed more often between captures compared to ibises in small flocks. Capture rates were similar between birds in large flocks and birds in small flocks (Fig. 2).

CENTRAL ADULTS IN LARGE FLOCKS VS. SINGLETONS (N = 25)

Singletons looked up more often and for longer periods of time than did central birds. Although number of steps was not statistically different, adjusted steps were significantly higher for singletons as compared to central adults in large flocks. Singletons also took more steps between probes, whereas central ibises probed more frequently and had a lower success rate per probe than did singletons. Capture rates were similar between the two groups (Fig. 3).

ENERGY EXPENDITURE OF IBISES IN DIFFERENT GROUPS

Even though adults in small flocks, singletons, and, to some extent, peripheral adults, stepped

TABLE 1. Comparisons of prey intake, time budgets, and energy expended by White Ibises foraging within different social situations on the North Inlet marsh, Georgetown, South Carolina.

Comparison	Number prey/min	% Difference in intake	% Time		Energy expended (kcal/min)		Energy expended % difference
			Walking	Stationary	Walking	Stationary	
Central[a]	1.8	0.0%	51%	49%	0.074	0.042	+0.9%
Peripheral	1.8		52%	48%	0.077	0.040	
Central	1.6	+6.2%	39%	61%	0.056	0.052	+7.4%
Small flock	1.7		51%	49%	0.075	0.041	
Central	1.6	+18.7%	43%	57%	0.062	0.048	+5.4%
Singleton	1.9		52%	48%	0.076	0.040	

[a] See text for descriptions of groups.

more often than ibises foraging in the centers of large flocks, they did not expend significantly greater amounts of energy (Table 1). The largest increase (7.4%) was between birds in small flocks and central birds in large flocks, and it amounted to only 0.48 kcal/hr, or 4.9 kcal (5 to 6 *Uca*, J. W. Johnston, pers. comm.) per foraging day (=10.25 hr; cf. Kushlan 1977a). This amounts to only 3.0% of the daily energy expenditure of 165 kcal/day for ibises breeding in a similar climate (Kushlan 1977a).

COMPARISON OF INDIVIDUALS CHANGING POSITIONS

Results from observations on the seven individuals that changed position in a flock are consistent with the paired observations of central vs. peripheral adults in large flocks. Both the number of steps and adjusted steps were approximately 40% higher at peripheral positions, while peripherally-located ibises had lower probing rates (central $\bar{x}$ = 11.3/min vs. peripheral $\bar{x}$ = 8.6/min) and probe to capture ratios (central $\bar{x}$ = 9.2 vs. peripheral $\bar{x}$ = 5.4) than central birds. Centrally-located ibises looked up less frequently (central $\bar{x}$ = 0.8/min vs. peripheral $\bar{x}$ = 1.5/min) and for less time (central $\bar{x}$ = 1.3 sec/min vs. peripheral $\bar{x}$ = 3.4 sec/min). They also took fewer steps between probes as compared to peripherally-located ibises (central $\bar{x}$ = 2.6 steps/probe vs. peripheral $\bar{x}$ = 5.3 steps/probe). Capture rates were similar between the two groups (central $\bar{x}$ = 1.5 *Uca*/min vs. peripheral $\bar{x}$ = 1.8 *Uca*/min). All the above comparisons, except capture rates, were statistically different ($P \leq 0.05$, Wilcoxon's matched-pairs signed-ranks test).

DISCUSSION

ADVANTAGES ASSOCIATED WITH FLOCKING

Birds that foraged in the center of large flocks spent less time vigilant and more time foraging than other ibises. An increased amount of time spent in search of food is presumed to provide an animal with a greater rate of energy intake (e.g., Murton 1971, Powell 1974, Caraco 1979); this was not the case in our study. None of the comparisons demonstrated an advantage, in terms of prey intake, to ibises foraging in the center of large flocks, despite the greater proportion of time central birds spent searching for fiddler crabs. As different types of locomotion (Tucker 1975) and activities (e.g., Schartz and Zimmerman 1971, Mugaas and King 1981) are associated with varying degrees of energy expenditure, the constant rate of *Uca* captured across groups in our study should be viewed with caution. Our results, however, suggest that there was little difference in energy expenditure associated with the different foraging techniques.

DISADVANTAGES ASSOCIATED WITH FLOCKING

That centrally-located ibises did not increase their capture rates despite devoting more time to foraging than did other ibises suggests that there are disadvantages associated with foraging among a large number of birds.

Prey depletion (Zwarts 1980) appeared to be insignificant as we did not record a decrease in individuals' capture rates over the 4-min observation period, nor over the time span that a flock was on the marsh (unpubl. data). These results may reflect the fact that ibis flocks moved over the marsh and, therefore, may not have spent enough time in a location to appreciably deplete the local fiddler crab numbers.

Another suggested disadvantage, fighting over food (Goss-Custard 1977a, Silliman et al. 1977), also probably was not associated with the larger ibis flocks on our study site. Only during a brief 2-week period during late July 1984 did we observe any interference or aggression between foraging conspecifics, and even then, encounters were very infrequent (<0.5/hr).

Alteration of search paths and the prediction that as flock size increases so does the probability that some birds will be forced to forage in less-preferred areas (Zwarts 1976, Goss-Custard 1977b) were not specifically examined in this study. Although we do not believe that these two potential disadvantages were important factors here, one would have to quantify search paths (e.g., Smith 1977) and know the dynamics of the resource patches used by ibises to properly address these hypotheses.

Depressed availability of surface crabs due to activity of birds appears to be the major disadvantage to White Ibises foraging in the center of large flocks. Goss-Custard (1970) showed that Common Redshanks (*Tringa totanus*) walking on the surface caused invertebrates to retreat into burrows. We believe that this was the proximate cause of the lower than expected capture rates of ibises located centrally within large flocks. We noticed crabs withdrawing to their burrows in response to our presence when we walked on the marsh. This response of fiddler crabs may have created the dichotomy in foraging behavior between the central birds in large flocks and the other three groups. White Ibises foraging in the center of large aggregations tended to be tactile foragers (i.e., they probed into fiddler crab burrows in search of prey). This contention is supported by their increased number of probes, the fewer steps between capture attempts, and the greater number of probes between captures. On the other hand, ibises foraging alone, ibises on the edges of large flocks, and ibises in small flocks tended to forage visually, i.e., by chasing crabs on the surface and capturing them before they retreated into burrows. Our data also support this notion, as individuals in the latter three groups took more steps (frequently ran) and probed less than their centrally located counterparts. Ibises on the peripheries of large flocks, ibises in small flocks, and ibises foraging alone were the first to reach undisturbed areas and, thus, were able to locate and capture crabs on the surface.

Our results do not support the hypotheses that by foraging within a flock an individual increases prey intake by copying the foraging behavior of successful flock members or that the increased protection gained by flock members allows them to procure more resources. Ibises feeding in the center of large flocks, however, do gain an advantage of increased predator protection without suffering lower feeding rates. Thus, our results support the predator-protection hypothesis (e.g., Pulliam 1973) independent of feeding-efficiency hypotheses.

Why then do ibises sometimes forage on the edge of large flocks, in small flocks, and by themselves? Some studies have suggested that social (Morse 1970, Russell 1978) or sexual (Peters and Grubb 1983) dominance plays a role in determining where an individual forages. The shorter bill of females (Kushlan 1977b) might preclude them from reaching the bottom of some fiddler crab burrows, thus making them less efficient foragers in a situation where they must locate crabs by tactile means (i.e., in the center of large flocks). Therefore, birds on the edges of large flocks, in small flocks, or foraging solitarily (those birds that hunt prey visually and capture prey from the surface), may have been females. Our results, however, suggest that this is not the case, as the seven focal ibises generally changed their foraging behavior when they changed positions within the large flocks. Although our preliminary results suggest that sexual and social factors do not affect where adult White Ibises forage within flocks, more data are needed to confirm these observations.

White Ibises foraging in the center of large flocks spent less time being vigilant compared to other ibises, but they gained no benefits in terms of prey intake. By altering their foraging behavior, individuals in each situation managed to catch prey at the same rate. Specifically, central ibises in large flocks spent more time foraging to offset the depressed availability of fiddler crabs on the surface. On the other hand, ibises in the other three situations were more vigilant, but were able to capture crabs on the surface. Thus, White Ibises' foraging behavior changed in response to the pattern of prey availability (behavior) (see also Kushlan 1978). In foraging flocks where members are not feeding on highly mobile prey, such as fiddler crabs, the costs of flock foraging may not be so great because the "prey" do not drastically alter their behavior in response to the high density of birds. Most studies that have documented increased food intake of flock members have dealt with birds feeding on grain, seeds, or relatively immobile invertebrates during the winter (e.g., Powell 1974, Abramson 1979, Caraco 1979, Goldman 1980, Jennings and Evans 1980). Alternatively, most studies which have not shown an increase in prey intake for flock members were conducted on birds that were foraging on mobile prey, such as active insects, fish, and crabs (e.g., Smith 1977, Fleischer 1983, this study). Thus, one proposed benefit of foraging in a flock, increased prey intake, may vary from species to species and according to the prey type and its availability. Certainly, a single explanation for the advantage of flock foraging cannot be extended across all taxa or even within a given species subjected to different environmental influences.

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