

FORAGING SOCIABILITY OF NESTING WADING BIRDS (CICONIIFORMES) AT LAKE OKEECHOBEE, FLORIDA

JEFF P. SMITH¹

ABSTRACT.—From 1989–1992 at Lake Okeechobee, Florida, I followed 356 adult Great Egrets (*Casmerodius albus*), 236 Snowy Egrets (*Egretta thula*), 82 Tricolored Herons (*E. tricolor*), and 286 White Ibises (*Eudocimus albus*) from several nesting colonies to foraging sites during chick-rearing periods. White Ibises departed in groups more often than the other species (64% of the birds followed), tended to travel in larger groups, rarely landed in areas devoid of other birds, and tended to join larger, more concentrated feeding flocks than other species. A majority of all species joined other birds at foraging sites. However, Great Egrets and Tricolored Herons often landed in areas devoid of other birds (29% and 43% of the birds, respectively) and more often landed near rather than in the immediate vicinity of other birds. A tendency toward group departures has been interpreted as support for the “information-exchange” hypothesis about the benefits of colonial nesting relative to food-finding. However, many of the birds in this study that departed in groups dispersed before landing, which is contrary to the expectations of the hypothesis. Many individuals did, however, choose foraging sites already occupied by other birds, which is indicative of reliance on “local enhancement” for identifying productive foraging grounds. Differences in degree of sociability among the species may, however, primarily reflect differences in foraging strategy. White Ibises are more social probably because foraging in groups enhances the effectiveness of the grope-foraging technique they employ, whereas Tricolored Herons and Great Egrets often employ foraging techniques more suited to solitary effort and are not as likely to benefit from foraging in aggregations. The evidence also suggested that Snowy Egrets, in particular, act as attractors for other species that rely on local enhancement to identify profitable foraging opportunities. This association may result from a combination of factors; i.e., white plumage serves as an attractor, but flocks of Snowy Egrets may also be particularly indicative of high-quality habitat and/or concentrations of universally attractive prey species. Received 29 Aug. 1994, accepted 1 Feb. 1995.

Researchers often have debated the issue of whether or not species benefit from colonial nesting because individual birds can exploit conspecifics or similar species for information about profitable foraging locations (Ward and Zahavi 1973, Krebs 1974, Ogden 1978, Custer and Osborn 1978, Pratt 1980, Erwin 1983, Waltz 1983). Ward and Zahavi (1973) initiated the concept of information-sharing at colonies; i.e., birds departing without prior knowledge of profitable foraging grounds may reduce their search time and gain advantage by following other birds to foraging grounds. Observation of birds traveling in groups from colonies was considered corroborating evidence. However, Erwin (1983) noted that

¹ Dept. of Wildlife Ecology and Conservation, Univ. of Florida, Gainesville, Florida 32611. (Present address: Forest and Rangeland Ecosystem Science Center, National Biological Service, 3200 S.W. Jefferson Way, Corvallis, Oregon 97331.)

individual birds might simply follow busy flight lines to “popular” foraging grounds and, therefore, not actually have to travel with other birds to gain advantage from colonial nesting. An extension of these ideas is the concept of local-enhancement (Krebs 1974, Kushlan 1977, Caldwell 1981, Erwin 1983, Master 1992). This theory holds that among species constrained by the demands of central-place foraging (sensu Orians and Pearson 1979) and the unpredictability of patchily distributed prey, colonial nesting increases foraging efficiency because individual birds can follow active flight lines or search commonly exploited areas and locate currently profitable patches of foraging habitat by cueing on the presence of other birds. A pronounced tendency to join other birds at feeding sites is taken as evidence of such a phenomenon.

Another issue related to the concept of local enhancement concerns whether or not certain species act as attractors in group-feeding situations. Several researchers have noted that highly visible white species such as Snowy Egrets (*Egretta thula*) and White Ibises (*Eudocimus albus*) often appear to attract other species (Armstrong 1970; Willard 1977; Kushlan 1977, 1978a, 1979; Caldwell 1981; Master 1992). However, Caldwell demonstrated using models that Snowy Egrets served as attractors for Tricolored Herons (*Egretta tricolor*), but Great Egrets (*Casmerodius albus*)—also white—did not. Thus, other aspects of the species’ ecology may be involved, such as relative tendencies toward aggregation and/or differences in species’ prey and foraging-habitat preferences.

In conjunction with a comprehensive study of the nesting and foraging ecology of wading birds at Lake Okeechobee, Florida (Smith and Collopy 1995, Smith et al. 1995), I monitored the foraging habits of nesting adults of four species during chick-rearing periods through aerial following-flights (also see Smith 1995). The demand for efficient foraging by adults peaks during the chick-rearing phase (e.g., Kahl 1964, Kushlan 1981). Therefore, evidence of reliance on mechanisms that facilitate efficient habitat selection should be particularly pronounced at such times. The four study species were Great Egrets, Snowy Egrets, Tricolored Herons, and White Ibises, all species that commonly nest in large mixed-species colonies at the lake (Smith and Collopy 1995, David 1994a). Herein, I examine species’ propensities for traveling in groups and for joining other birds at feeding sites. I present data on the size and composition of the feeding assemblages each species joined, including a comparison of species’ tendencies to join conspecifics versus other species. I also discuss how differences in degree of sociability may reflect differences in each species’ foraging behavior.

STUDY AREA AND METHODS

Study area.—Lake Okeechobee is the third largest freshwater lake in the United States (1732 km² surface area) and is classified as subtropical and eutrophic (Aumen 1995). It drains a watershed of nearly 12,000 km², primarily through the Kissimmee River from the northwest, and is situated upstream of the remnant Everglades and Florida Bay (Fig. 1). Management of the lake and its resources garners considerable attention. Aumen (1995) provides a detailed account of the natural and management history of the lake. Smith and Collopy (1995) discuss the history of wading bird nesting at the lake during the study, and David (1994a) discusses nesting population trends during the 12 years prior to this study. Zaffke (1984), David (1994b), and Smith et al. (1995) review the population dynamics of foraging wading birds at the lake, and Smith (1995) discusses other aspects of the foraging habits of nesting adults.

A large, earthen dike nearly surrounds the lake and forms a sharp boundary between relatively natural emergent-marsh (400 km² coverage) and open-water habitats inside the dike and a diverse array of natural and artificial wetland habitats outside the dike. All the data considered herein are of birds from colonies located within the diked boundaries of the lake (Fig. 1), but many of the foraging flights led to habitats outside the diked area (Smith 1995). The emergent marsh habitats on the lake used most regularly by foraging wading birds include moderate-stature, wet-prairie assemblages featuring *Eleocharis*, *Rhynchospora*, *Panicum*, *Nymphaea*, *Polygonum*, and sparse *Typha* (Zaffke 1984, Smith et al. 1995). Prey sampling in such habitats generally revealed moderate densities of prey, but often a high diversity of both invertebrate and vertebrate prey species (Bull et al. 1992; McIvor and Smith 1992; Chick and McIvor, in press; Smith, unpubl. data). At low lake stages, exposed beds of submerged vegetation such as *Hydrilla*, *Vallisneria*, and *Potamogeton*—often mixed with the emergent *Nelumbo lutea*—harbored very high densities of forage fishes and grass shrimp (*Palaemonetes paludosus*) and attracted large numbers of foraging birds (Smith et al. 1995). The primary nest substrate is willow (*Salix caroliniana*). Habitats outside the dike that are regularly used by foraging birds include the floodplains of Fisheating Creek, Nicodemus Slough, and the Kissimmee River; isolated “pocket” and slough wetlands interspersed with cattle pastures to the north and west; agricultural field ditches to the southwest; and residential ditch, pond, and canal habitats in several areas (Fig. 1; Zaffke 1984; David 1994b; Smith, in press, unpubl. data). Very little is known about prey populations in these habitats.

Field methods.—Each year from 1989–1992, I followed individual and small groups of unmarked adult birds from nesting colonies to foraging grounds in a Cessna 172 fixed-wing aircraft. Each season, I began following birds once eggs started to hatch and continued flights until most nestlings had fledged. I concentrated on large, mixed-species colonies in which I conducted concurrent nesting success studies (Smith and Collopy 1995), but I also periodically followed birds from other colonies. I followed birds every week and each week I tried to follow some individuals of each of the four study species from each of the focal colonies. Up to five other ciconiiform species nested in the colonies (Smith and Collopy 1995), but I did not collect following-flight data for them. I conducted surveys throughout the day, as long as activity levels were sufficient to ensure a consistent source of birds to follow.

I began each following-flight by circling above the chosen colony at an altitude greater than 150 m, and generally followed the first bird or closely associated, conspecific group of birds to depart. I then monitored the progress of the bird(s) by flying in slow, wide circles around and above it at horizontal and vertical distances sufficient to avoid disturbing its flight (always distances >150 m, usually much greater for white species). I followed each

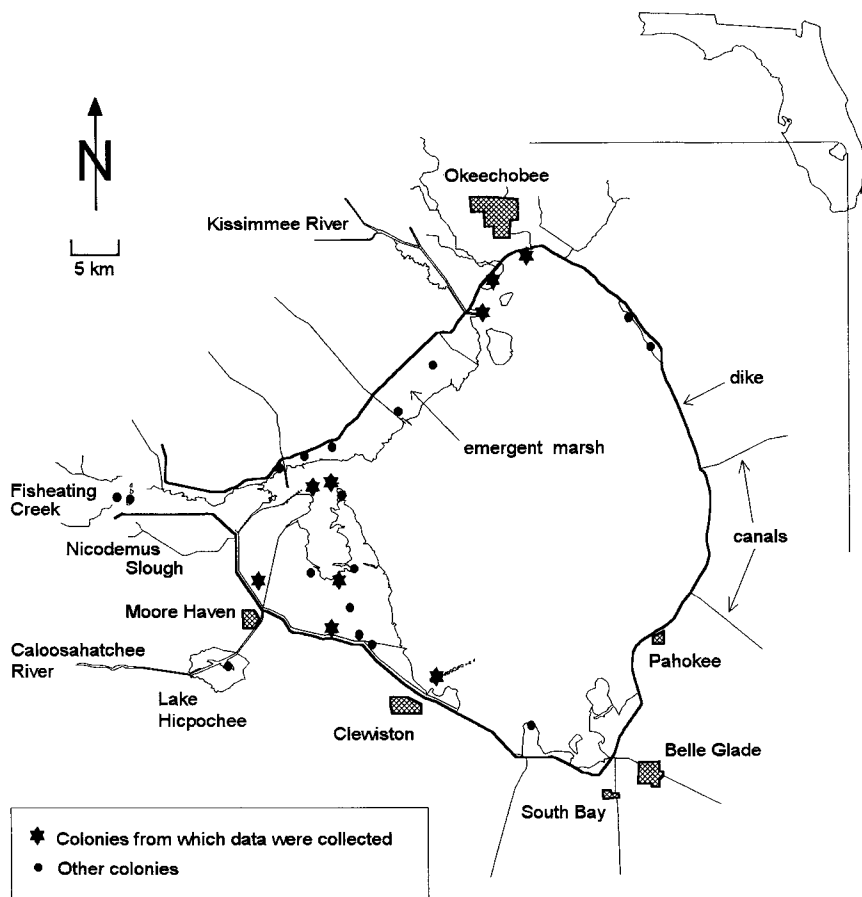


FIG. 1. A geographic overview of the Lake Okeechobee area showing the locations of nesting colonies used by the four study species.

bird until it landed in an area where foraging was possible and remained long enough that I could record an endpoint coordinate, a stop time, a description of the chosen habitat, and the flock joined, and I could take a photograph of the area. Recording these data usually took 2–3 min; if the bird began moving again before I finished, I continued the flight. The only time I deviated from this protocol was when I had followed a group of birds that did not all land in the same location. In this case, I attempted to document the first landing spot for all birds, but was unable to record the final details for each until the last bird had landed and I could return to previous landing spots to record additional data. Sometimes I was forced to abandon individuals that ultimately followed widely divergent paths. In these cases, I continued to follow the larger of the split groups or arbitrarily chose one of a split pair to finish following.

Analytical methods.—A primary assumption behind most parametric statistical tests is that the observations to be analyzed are independent of one another; i.e., the value of or random error associated with a given observation is not related to other such values in any systematic way (e.g., see Sokal and Rohlf 1981:401–402). The foraging habitat choices of birds that traveled in groups may have depended on the results of social interaction. If so, the individual-bird observations in each set would be interdependent, and one should analyze each group of observations as a single record. However, it is also possible that groups formed simply because several birds happened to depart for a known foraging location at the same time (*sensu* Bayer 1982). Thus, eliminating all apparently redundant group observations may unnecessarily sacrifice valid data. Accordingly, I ran the analyses discussed below twice, once with all individual-bird observations included and once with each set of group observations considered as a single observation. In all such cases, I found that although there were subtle differences in significance levels, there were no marked differences in the conclusions suggested. Therefore, the analyses I present below all represent datasets with each bird considered an independent unit.

I conducted a likelihood ratio Chi-square (χ^2) test of independence (Sokal and Rohlf 1981: 735–738; performed in SAS, SAS Institute, Inc. 1988) and χ^2 multiple comparisons (Fleiss 1981:140–141) to elucidate whether species differed in their tendency to travel in groups from colonies to foraging sites. I used a standard least-squares analysis of variance (ANOVA) with Bonferroni *t*-test multiple comparisons to determine whether species differed with regard to the size of the groups in which they traveled (performed in SYSTAT, Wilkinson 1990). I log-transformed ($\ln[x]$) the group-size data to normalize residuals.

I conducted a likelihood ratio χ^2 test of independence to determine whether species differed in their tendencies to land alone, near others, or in the immediate vicinity of other birds at foraging sites. A bird that landed alone landed in a habitat patch devoid of other birds; i.e., the presence of other birds could not have affected the birds' choice of the particular foraging spot (no birds in similar habitat within distances on the order of hundreds of meters). A bird that landed near others landed in a habitat patch where one or more other birds were already foraging but did not join a concentrated flock or land in the immediate vicinity of another bird. Estimating distances from the air is difficult, so the definition of what qualified as near was imprecise. Essentially, I classified a bird as having landed in the immediate vicinity of others if its foraging movements were likely to intersect those of other birds (inter-bird distances on the order of <10 m, usually 1–3 m). In contrast, I classified a bird as having landed only near others if the presence of other birds foraging nearby in the same habitat may have influenced the bird's selection, but it was unlikely the bird would cross paths with the other birds (inter-bird distances on the order of tens of meters).

I conducted a separate likelihood ratio χ^2 test of independence with χ^2 multiple comparisons to determine whether species differed in their tendency to join conspecifics at foraging sites. I limited the data to followed birds that landed near or in the immediate vicinity of others. I also conducted an ANOVA with Bonferroni *t*-test multiple comparisons to determine whether species differed with regard to the size of the feeding flocks each joined. Again, I limited the data to birds that landed near or in the immediate vicinity of others. I calculated flock sizes as the total of all birds considered near or in the immediate vicinity of the followed bird. I log-transformed ($\ln[x]$) the flock size data to normalize residuals.

RESULTS

Great Egrets were least likely among the species studied to travel to foraging sites in groups; only 9% of the birds followed departed the colonies with one or more traveling companions (Table 1). Tricolored

TABLE 1
CHI-SQUARE TESTS EXAMINING SPECIES' TENDENCIES TO TRAVEL IN GROUPS TO FORAGING LOCATIONS

Species	Total birds departed	Total birds followed to landing	Total birds departed in groups ^a	Mean group size ^b	Maximum group size	% Groups dispersed before landing	% Groups partially dispersed before landing
Great Egret	357	356	32 (9)	2.2 ± 0.79 (14)	4	29	0
Snowy Egret	242	237	64 (26)	2.3 ± 1.08 (27)	4	41	0
Tricolored Heron	84	81	16 (19)	2.5 ± 1.18 (6)	5	83	0
White Ibis	324	286	208 (64)	3.0 ± 1.05 (62)	11	31	19

^a Likelihood ratio $\chi^2 = 259.6$, $df = 3$, $P < 0.001$; χ^2 multiple comparisons with experiment-wise $\alpha = 0.05$ —White Ibises significantly more likely than others to depart in groups; Great Egrets significantly more likely to depart alone. Values in parentheses indicate percent of total.

^b ANOVA: $F = 3.75$, $df = 3, 105$, $P = 0.013$; Bonferroni t -test multiple comparisons with experiment-wise $\alpha = 0.05$ —White Ibis groups significantly larger than Snowy Egret groups (difference between White Ibises and Great Egrets significant if experiment-wise $\alpha = 0.10$). Birds that traveled alone were excluded from this analysis. The means and standard errors given represent back-transformed least squares estimates. The lower numbers in parentheses indicate group sample sizes.

Hérons and Snowy Egrets were significantly more likely than Great Egrets to depart in groups (19% and 26% of all birds, respectively), but only among White Ibises did a majority leave in groups (64% of all birds; Table 1). Moreover, when White Ibises traveled in groups, they tended to travel in larger groups than other species. The only significant difference with the experiment-wise $\alpha = 0.05$ was the comparison of White Ibises and Snowy Egrets (Table 1). However, Great Egret groups averaged smaller than Snowy Egret groups, but due to a smaller sample size, the difference relative to White Ibises was significant only if the experiment-wise α was relaxed to 0.10. Snowy Egrets and Tricolored Herons were significantly more likely than Great Egrets to depart in groups; however, more of the Snowy Egret and especially Tricolored Heron groups dispersed before landing (Table 1). As a result, only 2% of the Tricolored Herons landed with a traveling companion, compared to 7% of the Great Egrets and 15% of the Snowy Egrets. Half of the White Ibis groups also dispersed to some degree before landing, but still 41% of the individual ibises landed with one or more of their original traveling companions.

A majority of individuals of all species landed either with or near other foraging birds (Table 2). White Ibises were the most likely to land in the immediate vicinity of other birds, and rarely landed in areas devoid of

TABLE 2

CHI-SQUARE TESTS EXAMINING SPECIES' TENDENCIES TO JOIN OTHER BIRDS AT FORAGING SITES, AND AN ANOVA EXAMINING SPECIES' DIFFERENCES WITH REGARDS TO THE SIZE OF THE FEEDING FLOCKS EACH TENDED TO JOIN

Species	Total birds followed ^a	Landed alone ^a	Landed near others ^a	Landed with flock ^a	% Joining birds that landed near or with conspecifics ^b	Mean size of feeding flock joined ^c
Great Egret	356	102/66* (29)	59/51 (16)	195/239* (55)	87	11.7 ± 2.46 (1–650)
Snowy Egret	237	22/44* (9)	38/34 (16)	177/159 (75)	96	15.7 ± 1.13 (1–955)
Tricolored Heron	82	35/15* (43)	16/12 (20)	30/54* (37)	54	5.2 ± 1.29 (1–100)
White Ibis	286	19/53* (7)	25/41* (9)	242/192* (84)	97	30.9 ± 1.11 (1–735)

^a Likelihood ratio χ^2 test of species-specific proportions: $\chi^2 = 124.6$, $df = 6$, $P < 0.001$, indicating that species differed in their tendency to join other birds at foraging sites. Values for each species and category: observed/expected counts (asterisks indicate significant [$P \leq 0.05$] difference between observed and expected frequencies), with percentage of observed counts below in parentheses.

^b Likelihood ratio χ^2 test of species-specific proportions: $\chi^2 = 74.0$, $df = 3$, $P < 0.001$; χ^2 multiple comparisons with experiment-wise $\alpha = 0.05$ —Great Egrets and especially Tricolored Herons significantly less likely than other species to join conspecifics.

^c ANOVA: $F = 63.9$, $df = 3$, 777 , $P < 0.001$; Bonferroni t -test multiple comparisons with experiment-wise $\alpha = 0.05$ —White Ibises joined significantly larger flocks than all other species, and Snowy Egrets and Great Egrets joined significantly larger flocks than Tricolored Herons. Values for each species: back-transformed least squares means and standard errors, with the range of observed flock sizes given below in parentheses.

other birds. Moreover, ibises that joined groups joined significantly larger groups than other species (Table 2). Snowy Egrets also usually joined or at least landed near other birds. Great Egrets were less likely to land in the immediate vicinity of other birds but still usually landed at least near other birds rather than alone. Tricolored Herons were more likely to land alone than in the immediate vicinity of other birds but usually chose habitats already occupied by one or more birds. Great Egrets and Snowy Egrets joined significantly smaller groups than did White Ibises but significantly larger groups than Tricolored Herons (Table 2).

Tricolored Herons that joined other birds at foraging sites were significantly less likely than other species to join conspecifics or flocks that included conspecifics (Table 2), having done so only slightly more than half the time (54%). Great Egrets were also significantly less likely than Snowy Egrets and White Ibises to join conspecifics, but 87% of the joining birds did so. In addition, 37–43% of the Snowy Egrets, White Ibises, and Great Egrets that landed with other birds either joined or landed near only conspecific individuals, whereas the proportion dropped to only 17% for Tricolored Herons. Great Egrets and Tricolored Herons that joined

mixed-species flocks joined flocks that included Snowy Egrets (73 and 63% of the birds, respectively) more often than flocks that included White Ibises (54 and 29%). Snowy Egrets and White Ibises usually joined flocks that included conspecifics, but White Ibises joined flocks that included Snowy Egrets (67% of the birds that joined mixed flocks) more often than Snowy Egrets joined flocks that included White Ibises (50%).

DISCUSSION

My findings concerning each species' propensity to travel in groups were generally consistent with those of previous studies. Custer and Osborn (1978) found that White Ibises in North Carolina traveled with conspecifics on 17% of the monitored flights, whereas only 3–5% of the Snowy Egret, Tricolored Heron, and Great Egret flights involved more than one individual. Ogden (1978) noted that 29% of the Snowy Egrets and 15% of the Tricolored Herons that departed from a colony in the Everglades did so in groups. Maccarone and Parsons (1988) monitored foraging flights from two colonies off Staten Island, New York, and found that 7% of the Snowy Egret flights and 3% of the Great Egret flights involved groups of two or three birds. Erwin (1983) found that only 2–4% of the Snowy Egrets, Tricolored Herons, and Great Egrets departed in groups (2–3 birds) from the colony he studied in North Carolina. Even fewer Snowy Egrets and Tricolored Herons departed in groups from the colony he studied in Virginia (Erwin 1984). Frederick and Collopy (1988) indicated that most of the Great Egrets, Snowy Egrets, and White Ibises they followed from colonies in the Everglades were solitary travelers but that the ibises occasionally departed in groups. Thus, the data consistently indicate that White Ibises are the most likely to travel in groups and that Snowy Egrets are slightly more likely to do so than Great Egrets and Tricolored Herons.

The stronger tendency for ibises to travel in groups might suggest greater reliance on information exchange at the colony to ensure profitable foraging opportunities. Alternatively, Bayer's (1982) hypothesis may apply; i.e., group departures are a statistical artifact of grouped arrivals. Any tendency to travel in groups may simply be indicative of temporally consistent use of established flight lines to common foraging grounds (Erwin 1983). In general, the preponderance of solitary travelers observed during this and the other studies cited above suggests that information exchange at colonies is not a particularly important determinant of wading bird foraging success (J. C. Ogden, pers. comm.). Moreover, the nature of a species' foraging strategy may be a primary determinant of social tendencies. For instance, because ibises typically forage using a tactile, grope-foraging technique, they increase the efficiency of their foraging

primarily through habitat selection, rather than by actively searching for concentrations of prey (Kushlan 1979). Flocking and group feeding help insure that foraging time is spent in relatively profitable patches of habitat and reduces the time spent searching for such patches (Ward and Zahavi 1973, Krebs 1974, Kushlan 1979). In addition, the "beater" effect of foraging around other birds (Kushlan 1979) may increase the chance of random encounters with moving prey and, therefore, may be of particular benefit to tactile-feeding species like ibises. Traveling in groups from colonies may simply be one mechanism for insuring that foraging partners are available for interaction and may also facilitate location of productive habitat via local enhancement (Evans 1982, Erwin 1983). Other data provide additional support for this hypothesis. Among the species studied, White Ibises were the most likely to join other foraging birds at foraging sites, usually landed in the immediate vicinity of other birds as opposed to only nearby, and tended to join larger flocks than other species.

Traveling in groups may not have been common, but the majority of individuals of all species did choose to land with or near other wading birds at foraging sites. This fact suggests that all species frequently relied on local enhancement to identify at least quality foraging regions, if not specific prey-rich habitat patches (Krebs 1974, Kushlan 1977, Caldwell 1981, Erwin 1983, Master 1992). Again, however, differences in foraging strategies may also have influenced species' tendencies toward aggregation. For instance, Tricolored Herons were the least inclined to join concentrated feeding flocks and usually landed near smaller groups than other species. These results are consistent with previous studies that showed Tricolored Herons usually remain on the periphery of mixed-species aggregations (Willard 1977, Kushlan 1978b, Master 1992), are more often found in smaller groups (Kushlan 1976a, Erwin 1983) or less often in association with feeding flocks than other species (Willard 1977), and do not necessarily increase their foraging efficiency by associating with aggregations (Master et al. 1993, but see Caldwell 1981). Tricolored Herons often feed solitarily using either active disturb-and-chase or stealth techniques, depending on the habitat (Meyerricks 1962; Jenni 1969; Willard 1977; Murdoch 1978; Rodgers 1983; Kent 1986; Smith, unpubl. data). The efficiency of both techniques is probably less effective near dense aggregations (Kushlan 1978b). Thus, the species' strategy is best-suited to non-aggregation foraging, but choosing sites near other foraging birds—i.e., at least in similar habitat—might increase the probability of finding rich prey resources.

Tricolored Herons routinely achieve high levels of reproductive success compared to other ciconiiforms (e.g., Frederick and Collopy 1988, Bancroft et al. 1990, Smith and Collopy 1995). This fact suggests that their

solitary foraging strategy is productive, which in turn suggests that accruing benefits from local enhancement and information exchange at nesting colonies is not a crucial prerequisite for successful nesting in the region. However, it was noteworthy that Tricolored Herons were the only species for which I discovered significant negative associations between mean flight distances and colony-specific estimates of nest success and productivity (Smith 1995).

Master et al. (1993) found that, although Great Egrets expended less energy when foraging in association with mixed-species flocks, they did not increase foraging efficiency (but see Caldwell 1981). In contrast, Wiggins (1991) found that Great Egrets feeding in monospecific groups were less likely to expend energy chasing other birds and achieved higher capture rates and efficiency. The biomass intake rate of solitary birds was equivalent because they usually took larger fish, but solitary birds were more likely to expend considerable energy defending their feeding territory. He concluded that Great Egrets in Texas probably aggregate only when small fishes are sufficiently concentrated that a high rate of capture yields a similar or greater level of energy gain than fewer captures of larger fish. Erwin (1983) found that Great Egrets were not common in large groups, further indicating that the species often prefers to feed in smaller groups or solitarily. Such situations are probably more amenable to use of the species' usual foraging mode, a slow-stalking approach (Willard 1977, Kushlan 1978b, Hom 1983, Rodgers 1983, McIvor and Smith 1992).

My observations suggested that Great Egrets were most likely to congregate in large, dense groups (up to several hundred individuals) when foraging in relatively open, moderate-depth water in between or on the fringes of beds of submerged vegetation (unpubl. data). At these times, the most frequently captured prey were moderate-sized sunfish and bass (Centrarchidae), schooling fishes such as shad (*Dorosoma* sp.), and golden shiners (*Notemigonus crysoleucas*). Great Blue Herons (*Ardea herodias*) and Wood Storks (*Mycteria americana*) were common members of these aggregations. My observations of many such flocks (see McIvor and Smith 1992) suggested that the dense concentration of birds elicited chaotic movements among the fishes that rendered them more susceptible to capture. The occurrence of such large groups was probably dependent on the fact that the fish had become concentrated by a severe drought (Smith et al. 1995). Otherwise, although I frequently observed Great Egrets feeding with mixed-species flocks in a variety of situations, I more commonly observed scattered individuals in wet-prairie habitats dominated by *Eleocharis* or *Panicum* (Smith et al. 1995). In addition, nesting Great Egrets were unusual because, especially during drought periods,

they took advantage of a unique, relatively asocial foraging opportunity—panhandling fish scraps at residential cleaning stations (Smith 1995).

Snowy Egrets were less prone to travel in groups, but like White Ibises, they usually joined other birds at foraging sites. Snowy Egrets have frequently been cited as the primary attractor and a core species in mixed-species aggregations (Willard 1977, Caldwell 1981, Erwin 1983, Master 1992). Jenni (1969) also noted that Snowy Egrets tended to be more social than Tricolored Herons. Master et al. (1993) suggested that Snowy Egrets may be obligate aggregation foragers, because gains in foraging efficiency derived from aggregation foraging (Caldwell 1981, Master et al. 1993) may be essential to meet the species' more stringent daily energy requirements (Kent 1986). Itzkowitz (1984) regularly observed transient, solitarily foraging Snowy Egrets at Stone Harbor, New Jersey, but his observations usually occurred after early-morning aggregations had dispersed (Master 1992 and pers. comm.). I also regularly observed solitary Snowy Egrets foraging at Lake Okeechobee. A common example involved the use of energetically expensive, aerial foraging methods to exploit surface concentrations of small fishes in deep-water *Hydrilla* habitats (McIvor and Smith 1992, Smith et al. 1995), which suggests that energy constraints may not have been a critical issue for the adult birds (also see Edelson and Collopy 1990). Snowy Egrets also are well known for their use of foot-stirring as a disturbance technique, a strategy most suited to solitary foraging (Meyerriecks 1962, Willard 1977, Hom 1983, Rodgers 1983, Master et al. 1992). These observations confirm that Snowy Egrets employ a diverse array of aggregation and solitary foraging strategies (also see Kushlan 1978b), but, nonetheless, at Lake Okeechobee, I observed far more birds in aggregations than alone (Table 2, but also confirmed by systematic, lakewide surveys [Smith et al. 1995] of foraging birds; Smith, unpubl. data).

Tricolored Herons that chose foraging sites with other birds present were more likely to choose areas occupied by white-plumaged species than those occupied by only conspecifics and were more likely to associate with Snowy Egrets than with White Ibises or Great Egrets. This is consistent with Caldwell's (1981) finding that the species was preferentially attracted to monospecific flocks of model Snowy Egrets as opposed to Great Egret or mixed-species flocks. However, Great Egrets in this study joined only other Great Egrets 37% of the time, which differs from Caldwell's (1981) findings that the species was preferentially attracted to monospecific flocks of model Snowy Egrets but never to monospecific flocks of Great Egrets. Nonetheless, during my study, Great Egrets that did join non-conspecific individuals joined Snowy Egrets more often than

other species. In addition, White Ibises joined flocks that included Snowy Egrets more often than flocks that included White Ibises.

I did not gather information about the relative availability of flocks of different composition over the entire study area, so I cannot be sure that the indicated trends reflect preferences. However, White Ibises were generally the most abundant species observed in the region, followed by Great Egrets, and then Snowy Egrets (Smith et al. 1995). Thus, the results seem to lend support for the hypothesis that Snowy Egrets, in particular, act as an attractor for other species. White plumage undoubtedly plays a role in this association (Armstrong 1970, Kushlan 1977). Kushlan (1978a) showed that White Ibises sometimes act as an attractor for other species in the Everglades. However, there must be additional factors at work, since Snowy Egrets are commonly singled-out as an attractor species. Caldwell (1981) suggested that Snowy Egrets are prime indicators of high-quality foraging habitat because their high visual acuity facilitates prey location and their high position in the interspecific dominance hierarchy enables them to usurp prime feeding sites from other similar-sized species. Another possibility is that flocks of Snowy Egrets may be indicative of certain types or concentrations of universally attractive prey. Great Egrets often focus on larger fishes and feed in water too deep for the smaller species, but they also regularly exploit smaller fishes, especially when feeding in association with mixed-species flocks (Willard 1977; Custer and Osborn 1978; Hom 1983; Bancroft et al. 1990; Smith, unpubl. data). White Ibises typically select less-active and cryptic crayfish (*Procambarus* sp.) and other benthic invertebrates—many of which are less-digestible and nutritionally inferior to fish—but often switch to fish when they are highly concentrated (Kushlan and Kushlan 1975; Kushlan 1976b, 1979). In contrast, Snowy Egrets usually aggregate to feed on concentrations of small, schooling fishes (e.g., mosquitofish, *Gambusia holbrooki*, or sailfin mollies, *Poecilia latipinna*, in freshwater marshes of southern Florida) or relatively visible and moderate-sized crustaceans such as grass shrimp (Jenni 1969; Kent 1986; Bancroft et al. 1990; McIvor and Smith 1992; Smith, unpubl. data). Thus, flocks of Snowy Egrets may guarantee the presence of prey species that most wading bird species (including Tricolored Herons) will exploit when available, whereas aggregations of other species may not provide such a guarantee for non-conspecific individuals.

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LITERATURE CITED

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