

Foraging Flights and Habitat Use of Nesting Wading Birds (Ciconiiformes) at Lake Okeechobee, Florida

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Abstract.—I monitored the foraging flights of four species of nesting adult wading birds at Lake Okeechobee, Florida, from 1989-1992 during chick-rearing periods. Median flight distances were: Great Egret (*Casmerodius albus*, N = 356) 3.7 km, range 0.1 - 33.3; Snowy Egret (*Egretta thula*, N = 236) 2.8 km, range 0.1 - 29.8; Tricolored Heron (*E. tricolor*, N = 82) 2.4 km, 0.1 - 22.3; and White Ibis (*Eudocimus albus*, N = 286) 2.7 km, range 0.1-33.3. Flights at the lake averaged moderate to short in comparison to those monitored in other areas of the southeastern United States. I found little evidence that increasing foraging flight distances influenced levels of nesting success and nestling production. Tricolored Herons were the possible exception; linear regressions of annual median flight distances versus colony-specific estimates of nest success and productivity revealed significant negative relationships. The association arose primarily because flights during two seasons averaged longer and success lower at one colony. Instead of foraging nearby in agricultural field ditches along with Snowy Egrets and Great Egrets, Tricolored Herons at this colony frequently traveled relatively long distances to forage in natural habitats within the diked boundaries of the lake. The dike that surrounds the lake produces an abrupt transition between natural habitats on the lake and diverse natural and artificial habitats off the lake. Tricolored Herons that nested on the lake generally foraged within the diked boundaries of the lake, but the dike's presence may help ensure that the other species nesting on the lake have access to diverse foraging opportunities under a wide range of hydrologic conditions. For all species, patterns of habitat use shifted significantly in response to fluctuations of the lake stage. There was evidence that high lake stages and rising water increased the flight distances of Snowy Egrets and perhaps Great Egrets, and that interruptions in otherwise steady surface-water trends (rising or falling levels) increased the flight distances of White Ibises. However, the variety of accessible habitats was such that nesting birds usually could adjust their patterns of habitat use in response to changing hydrologic conditions without having to extend their foraging distances to a degree sufficient to reduce levels of nesting success and productivity. Instead, variation in the quality of habitats accessible under different hydrologic conditions probably did contribute to observed variation in nest productivity. Received 25 August 1994, accepted 16 May 1995.

Key Words.—*Casmerodius albus*, *Egretta thula*, *Egretta tricolor*, *Eudocimus albus*, foraging flights, foraging habitat, Great Egret, nesting ecology, Snowy Egret, Tricolored Heron, White Ibis.

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For most species of birds, the energetic and logistic demands of nesting peak when chicks hatch and adults must supply food to their rapidly growing young (e.g., Kahl 1964, Kushlan 1981). The strain may be particularly great for species with nidicolous young, because the adults must operate as "central-place foragers" (sensu Orians and Pearson 1979) and make repeated trips to and from the nest each day. If food is plentiful near the nest, then the added energetic burden may not be great, but it will increase as the distance to profitable foraging grounds increases. If the distance is too great, nest

productivity may decline due to decreased prey delivery rates or adult birds might choose to abandon their nesting effort because the energetic costs or logistic demands of long-distance travel exceed the benefits of high quality foraging habitats (Wittenberger and Hunt 1985, Bryan and Coulter 1987).

Studies of ciconiiform wading birds in the Florida Everglades have indicated a positive association between colony abandonments and foraging flights exceeding 25-30 km in length (Frederick and Collopy 1988; Bancroft *et al.* 1990, 1994). Frederick and Spalding (1994) suggested, based on ener-

getic calculations, that the abandonments probably occurred because increasing flight distances reduced the rate and total amount of prey delivery to nestlings, not because the adults were physically taxed. Regardless, any study of the causes of reproductive failure among wading birds should consider how variation in travel distances and the accessibility of quality foraging habitats affects the species studied (Bancroft *et al.* 1994, Frederick and Spalding 1994, Ogden 1994). In this manuscript, I compare foraging-flight and nest-productivity data for four species of wading birds from Lake Okeechobee, Florida, to test the research hypothesis that increasing foraging-flight distances are correlated with decreasing nesting success and nestling production.

I also analyze variation in foraging-flight distances and patterns of habitat use of nesting adult wading birds in relation to hydrologic trends. Managing water levels in Lake Okeechobee is a primary concern for resource managers, because the lake serves as a principal flood-control and water-storage facility in the region (Aumen 1995). Wading birds are highly visible members of south Florida wetland communities and are considered bioindicators of change in hydrological and ecological conditions in wetland ecosystems (Custer and Osborn 1977; Curry-Lindahl 1978; Hafner and Britton 1983; Bildstein *et al.* 1990; Kushlan 1986, 1993; Ogden 1994). Consequently, they often garner considerable attention among resource managers in the region. Hydrologic trends influence the distribution of vegetation (Richardson and Harris 1995), the productivity of wading bird prey populations (Loftus and Eklund 1994), the concentration of prey organisms (Kushlan 1976a), and whether or not an area is accessible to foraging wading birds. Therefore, hydrology is a primary determinant of wading bird foraging efficiency and consequent nesting success (Bancroft *et al.* 1994, Frederick and Spalding 1994, Ogden 1994, Smith 1994, Smith and Collopy 1995).

My study spanned both high-water periods and a two-year drought, thereby providing an ideal opportunity to study wading

bird responses to both high and low-water extremes. Previous analyses revealed that high lake stages eliminate foraging habitat on the lake for wading birds, often resulting in relatively greater use of habitats outside the diked confines of the lake, whereas low and declining lake stages attract large, diverse foraging populations (Zaffke 1984, David 1994, Smith *et al.* 1995). In contrast, moderately high stages increase the availability of nesting habitat (typically flooded stands of willow, *Salix caroliniana*) compared to low stages (Smith and Collopy 1995). Additional questions of interest addressed in this manuscript include: 1) Do high lake stages and rising water, or conversely excessive drying, result in longer foraging flights or shifts in habitat use that are correlated with decreases in wading bird nest productivity?; 2) Are habitats outside the diked confines of the lake an important foraging resource for birds nesting on the lake?

STUDY AREA AND METHODS

Study Area

Lake Okeechobee is the third largest freshwater lake in the United States (1,732 km² surface area; Herdendorf 1982). It lies upstream of the remnant Everglades (26°33' N, 80°45' W) and drains a 12,000 km² watershed, primarily through the Kissimmee River from the northwest (Fig. 1). Aumen (1995) provides a detailed account of the natural and management history of the lake. The large earthen dike that encircles the lake (Fig. 1) creates an abrupt transition from extensive emergent-marsh (average 400 km² total surface area), submerged-vegetation, and open-water habitats inside the dike ("on-lake") to a wide variety of natural and artificial wetland habitats outside the dike ("off-lake"). Smith *et al.* (1995) and Richardson and Harris (1995) discuss the dynamics of on-lake vegetation communities. Off-lake habitats include: the perennial Kissimmee River and Fisheating Creek riparian floodplains; diverse pocket (i.e., isolated, shallow, often ephemeral wetlands) and slough wetlands interspersed with cattle pastures to the north and west; myriad agricultural field ditches and canals to the south and east; and residential canals and retention ponds in several areas.

Field Methods

I documented foraging-flight characteristics and habitat choices for four species of commonly nesting wading birds during chick-rearing periods (March-July; range varied by species, colony, and year) from 1989 to 1992. The species included Great Egret (*Casmerodius albus*), Snowy Egret (*Egretta thula*), Tricolored Heron (*E. tricolor*), and White Ibis (*Eudocimus albus*). I followed individual and small groups of unmarked adult birds from

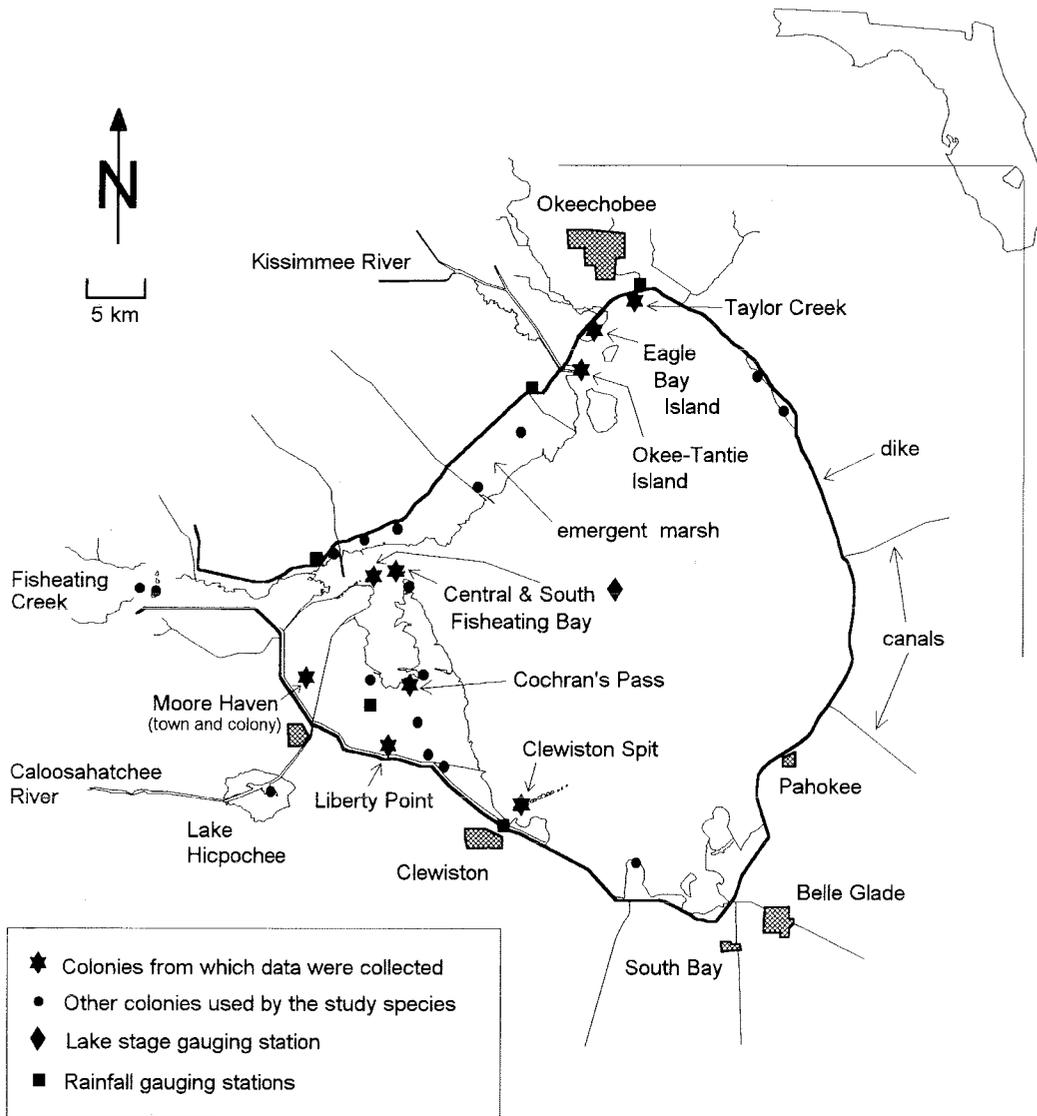


Figure 1. Lake Okeechobee area showing the locations of nesting colonies used by the four study species and the locations of lake stage and rainfall gauging stations.

nesting colonies to foraging grounds in a Cessna 172 fixed-wing aircraft at vertical and horizontal distances exceeding 150 m. I concentrated on large, mixed-species colonies located within the diked confines of the lake in which I conducted concurrent nesting success studies (Smith and Collopy 1995), but I also periodically followed birds from other colonies (Fig. 1). I followed each bird until it landed in an area where foraging was possible and it remained long enough for me to record a LORAN C coordinate (accurate to 0.18 km), a stop time, a description of the chosen habitat and flock joined, and a photograph of the area. Recording these data usually took 2-3 minutes. If the bird began moving again during this time range, I continued the flight (rate of occurrence: Great Egret: 41 or 11.5% of flights, 1.3 ± 0.63 stops per flight for flights including ≥ 1 stop;

Snowy Egret: 17 or 7.2% of flights, 1.1 ± 0.33 stops per flight; Tricolored Heron: 2 or 2.5% of flights, 3.0 ± 2.83 stops per flight; White Ibis: 0 flights). I recorded the total flight time, including any temporary stops, in seconds and calculated the straight-line travel distance in kilometers based on LORAN coordinates for the colony and the landing point. I discuss additional details of the survey methods in Smith (1995).

Analytical Methods

A lack of independence among observations for individual birds that traveled to foraging sites in groups might invalidate statistical tests that treat each bird as an independent observation. It also is possible, however, that some groups formed simply because several birds

happened to depart for a known foraging location at the same time. In this case, eliminating all apparently redundant group observations may unnecessarily sacrifice valid data (see Smith, 1995 for a more detailed discussion). Where appropriate, I ran the statistical analyses discussed below twice to determine the effect on results, 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 there were subtle differences in significance levels, but no marked differences in the conclusions suggested. Therefore, I present only results derived from datasets that included individual-bird observations as independent units.

Where appropriate, I conducted the following analyses for each species: 1) linear regressions of median foraging-flight distances versus colony-specific, annual estimates of nesting success and nestling production derived from concurrent studies of marked nests (nesting success = proportion of hatched nests that produced at least one threshold-age nestling; nestling production = mean number of threshold-age nestlings produced per hatched nest; threshold age = 14 days for White Ibis, 21 days for other species; see Smith and Collopy 1995 for details); 2) linear regressions of lakewide mean foraging flight distances versus proportions of marked nests that failed, with the statistics calculated for consecutive 15-day periods extending over each season; 3) various ANOVA's (distances log transformed [$\ln(x)$] to normalize residuals) to determine if flight distances varied depending on whether the endpoint was on- or off-lake; 4) non-statistical comparisons of colony-specific proportions of on-lake flights; 5) likelihood-ratio chi-square (χ^2) tests of independence comparing study-wide proportions of on- and off-lake flights versus intervals of lake stage; 6) linear regressions of colony-specific, annual proportions of on-lake flights versus estimates of nesting success and nestling production; 7) multiple regression analyses to elucidate relationships between

foraging-flight distances and three hydrologic variables; and 8) likelihood-ratio χ^2 tests of independence to elucidate relationships between study-wide patterns of habitat use and intervals of lake stage. All regression and ANOVA analyses were calculated in SYSTAT; all χ^2 analyses were calculated in SAS. In all cases, significance was assigned if $P \leq 0.05$.

For the multiple regression analyses, the hydrologic variables included the number of days of rising water (DRISE, intermittent and continuous) and total rainfall (RAIN, cm) during the 30-days prior to each flight, and the lake stage on the day of the flight (STAGE, m NGVD—National Geodetic Vertical Datum of 1929, nearly equivalent to distance above mean sea level—for convenience I will hereafter drop the NGVD qualifier; see Fig. 2 for a study-period hydrograph). I acquired daily lake stage and rainfall records from the South Florida Water Management District, West Palm Beach. The STAGE readings were collected at a central, open-water gauging station (Fig. 1) and I assumed these data represented basin-average conditions (see Smith *et al.* 1995 for a discussion of potential limitations). Daily rainfall was measured at several, primarily perimeter gauging stations (Fig. 1); I matched data sources to colonies based on proximity (mean distance 4.3 km, maximum 7.3 km) and calculated RAIN as a simple 30-day sum. I calculated DRISE from the stage data. For this analysis, I pooled flight data (distances log-transformed) from all years and colonies to maximize sample sizes and the environmental variability reflected in the analyses. I began by calculating saturated models that included all possible interactions, but ultimately eliminated interaction variables not significant at the $P \leq 0.05$ level (using the backward selection method in SYSTAT).

In the χ^2 tests comparing patterns of habitat use versus intervals of lake stage, I aggregated the foraging-flight observations according to final end-point habitat types and the current lake stage. To insure reasonable sample sizes, the habitat categories to which I assigned

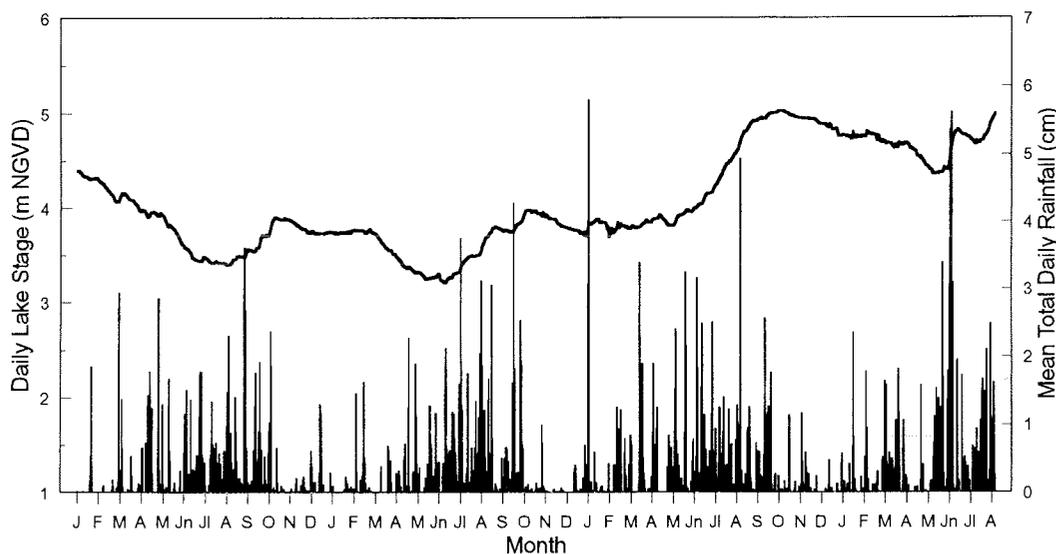


Figure 2. Daily lake stage (line) and basin-average total daily rainfall (bars) at Lake Okeechobee from January 1989 through August 1992.

observations represented only broad-scale vegetation/habitat types. The number of lake stage and habitat categories, and the cutoff points for the stage intervals varied some by species. Slight adjustments helped produce distributions of data valid for χ^2 analyses (i.e., <20% of cells with expected value <5; SAS Institute, Inc. 1988).

I distinguished three classes of off-lake habitat: 1) AG = agricultural field ditches, canals, and occasionally flooded fields, located just north of Moore Haven and around the south end of the lake (Fig. 1); 2) PS = cattle pasture ditches, ponds, and occasionally flooded pastures interspersed with remnant pocket wetlands and natural hardwood-hammock and pine-woodland slough wetlands, located west and north of the lake; and 3) PANH = residential fish-cleaning stations and associated canals where Great Egrets panhandled fish scraps from fishers, and bait shops where Great Egrets stole bait minnows, located around the towns of Okeechobee and Clewiston (Fig. 1). The on-lake habitat categories included: 1) MS-OF = mixed submerged vegetation—primarily *Hydrilla*, *Vallisneria*, and *Potamogeton*—and outer littoral-zone fringe habitats that included emergent stands of *Scirpus*, cattail (*Typha* sp.), lotus (*Nelumbo lutea*), and maidencane (*Panicum hemitomon*), and frequently floating mats of water hyacinth (*Eichhornia crassipes*) and duckweed (*Lemna* sp.); 2) MS-A = the same as MS-OF but usually deeper habitats that Snowy Egrets and Great Egrets accessed by aerial foraging; 3) HM-LOT = mixed *Hydrilla* mat and lotus habitats, a subcategory of MS-OF that Snowy Egrets and Tricolored Herons were particularly attracted to; 4) HM-HYC = mixed *Hydrilla* and hyacinth mats, another subcategory of MS-OF distinguished in the Tricolored Heron analysis; 5) MP = mixed emergent wet-prairie usually dominated by mixes of *Eleocharis*, *Rhynchospora*, *Panicum*, *Nymphaea*, and cattail; 6) MTR = mid-littoral-zone transitional bog and slough habitats featuring *Pontedaria* and diverse emergent/submergent mixes; and 7) UTR = shallow, upper-littoral-zone transitional habitats featuring grass/sedge mixes, *Polygonum*, and flooded terrestrial species.

The dike around the lake prevents lake stage fluctuations from directly influencing the hydrology of habitats outside the dike. However, lake stage readings provide a general index to surface-water conditions in the region, in that fluctuations in the lake stage are due primarily to variation in regional rainfall (Aumen 1995). Therefore, for purposes of the above analyses, I assumed that the lake stage variables reflected average hydrologic conditions both on and off the lake. The rainfall data were collected at primarily perimeter gauging stations and therefore applied equally well to habitats on and off the lake.

RESULTS

I followed 356 Great Egrets from seven colony sites, 236 Snowy Egrets from six colony sites, 85 Tricolored Herons from five colony sites (82 to landing), and 286 White Ibises from three colony sites over the four-year study period (Fig. 1 for colony names and locations, and Fig. 3 for flight distributions). I provide study-wide median flight times and distances for reference in Table 1.

Flight Distances and Reproductive Success

Regressions of colony-specific median flight distances versus levels of nest productivity revealed significant combined-year trends consistent with the research hypothesis (i.e., inverse relationships) only for Tricolored Herons (Great Egret: success, $r^2 = 0.03$, $F_{1,8} = 0.24$, n.s.; production, $r^2 = 0.05$, $F_{1,8} = 0.42$, n.s.; Snowy Egret: success, $r^2 = 0.02$, $F_{1,6} = 0.11$, n.s.; production, $r^2 = 0.05$, $F_{1,6} = 0.33$, n.s.; Tricolored Heron: success, $r^2 = 0.83$, $F_{1,4} = 19.88$, $P = 0.011$; production, $r^2 = 0.79$, $F_{1,4} = 14.66$, $P = 0.019$; White Ibis: success, $r^2 = 0.01$, $F_{1,4} = 0.01$, n.s.; production, $r^2 = 0.01$, $F_{1,4} = 0.02$, n.s.; Fig. 4). For all species, the regressions of flight distances versus 15-day proportions of marked-nest failures failed to support the hypothesis that longer foraging flight distances result in reduced nesting success (Great Egret: $r^2 = 0.02$, $F_{1,21} = 0.41$; Snowy Egret: $r^2 = 0.01$, $F_{1,18} = 0.15$; Tricolored Heron: $r^2 = 0.02$, $F_{1,10} = 0.30$; White Ibis: $r^2 = 0.01$, $F_{1,14} = 0.08$; all n.s.; Fig. 5).

On- Versus Off-lake Flights

Fifty-five percent (197/356) of the Great Egret flights, 82% (193/236) of the Snowy Egret flights, and 68% (194/286) of the White Ibis flights ended on the lake. For Great Egrets, the proportion of on-lake flights was particularly high (range 77-93%) at the interior-marsh Moore Haven and Liberty Point colonies, and at the interior-island Central Fisheating Bay colony (Table 2). In contrast, on-lake flights were less common at the relatively peripheral Eagle Bay Island, Okee-Tantie Island, and Clewiston Spit island colonies (range 27-50%). Snowy Egrets usually chose on-lake feeding sites far more than off-lake sites; two exceptions were at Clewiston Spit in 1991 (15% on-lake) and Moore Haven in 1992 (17%) when the pattern was reversed (82-100% on-lake otherwise; Table 2). For White Ibises in 1989 and 1992, the proportion of on-lake flights was higher at the interior-marsh Moore Haven (92% in 1989, 69% in 1992) and Cochran's Pass (83% in 1989) colonies, and lower at the peripheral-island colony at Eagle Bay (61% in 1989 and 9% in 1992; Table 2). Oth-

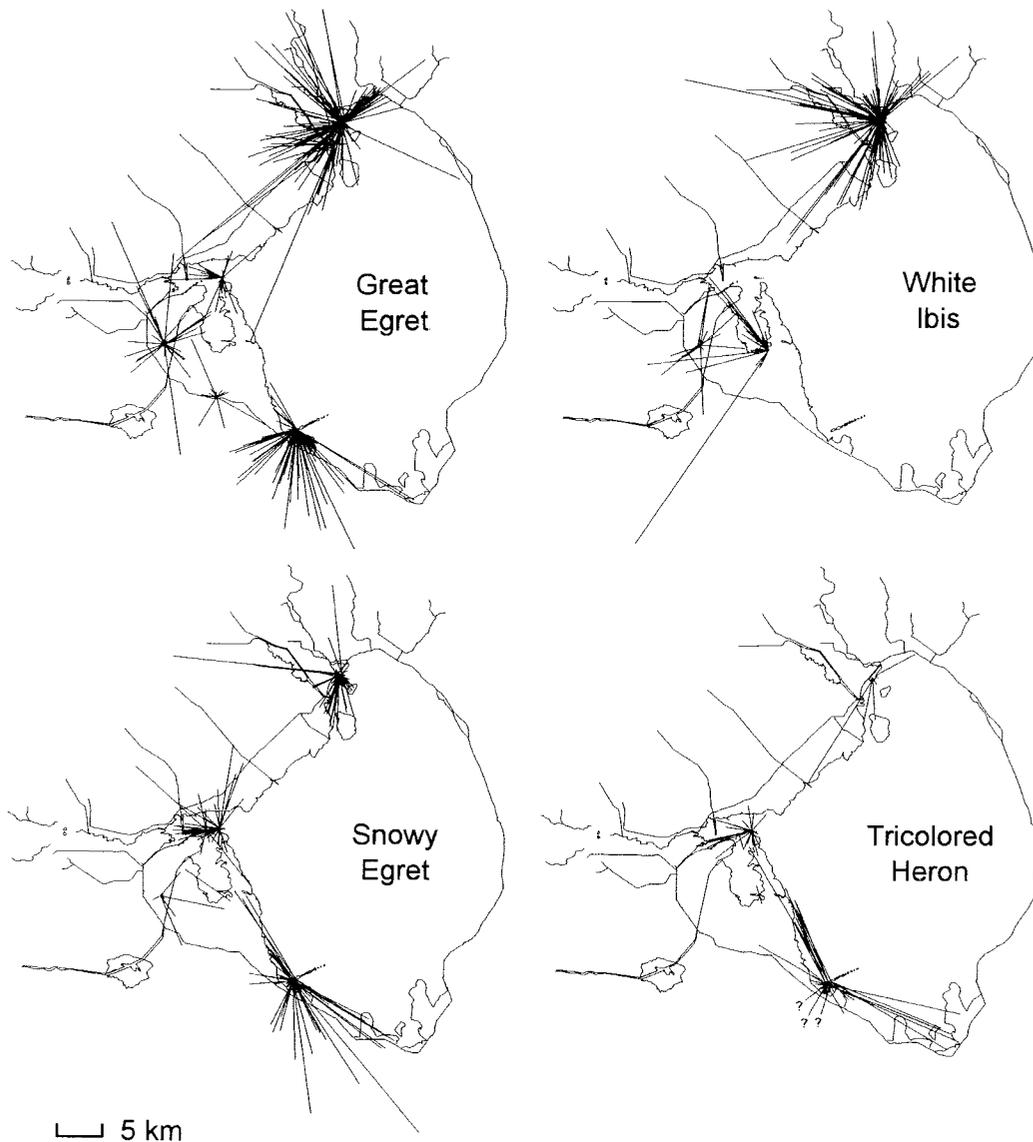


Figure 3. Distributions of foraging flights for each species, all years combined.

erwise, for White Ibises at Eagle Bay Island, the proportion of on-lake flights was highest in 1990 (73%) when the lake stage was lowest, and lowest in 1992 when the lake stage was highest (9%).

I successfully followed only one Tricolored Heron to an off-lake destination, a small grassy ditch near an agricultural field. I was unable to finish tracking three other individuals (because of visibility problems re-

Table 1. Study-wide median foraging-flight times and distances by species.

Species	N	Flight Time (min)	Range	Flight Distance (km)	Range
Great Egret	356	6.4	0.2-49.0	3.7	0.1-33.3
Snowy Egret	237	4.7	0.1-62.4	2.8	0.1-29.8
Tricolored Heron	82	4.0	0.3-50.0	2.4	0.1-22.3
White Ibis	286	3.8	0.2-52.1	2.7	0.1-33.3

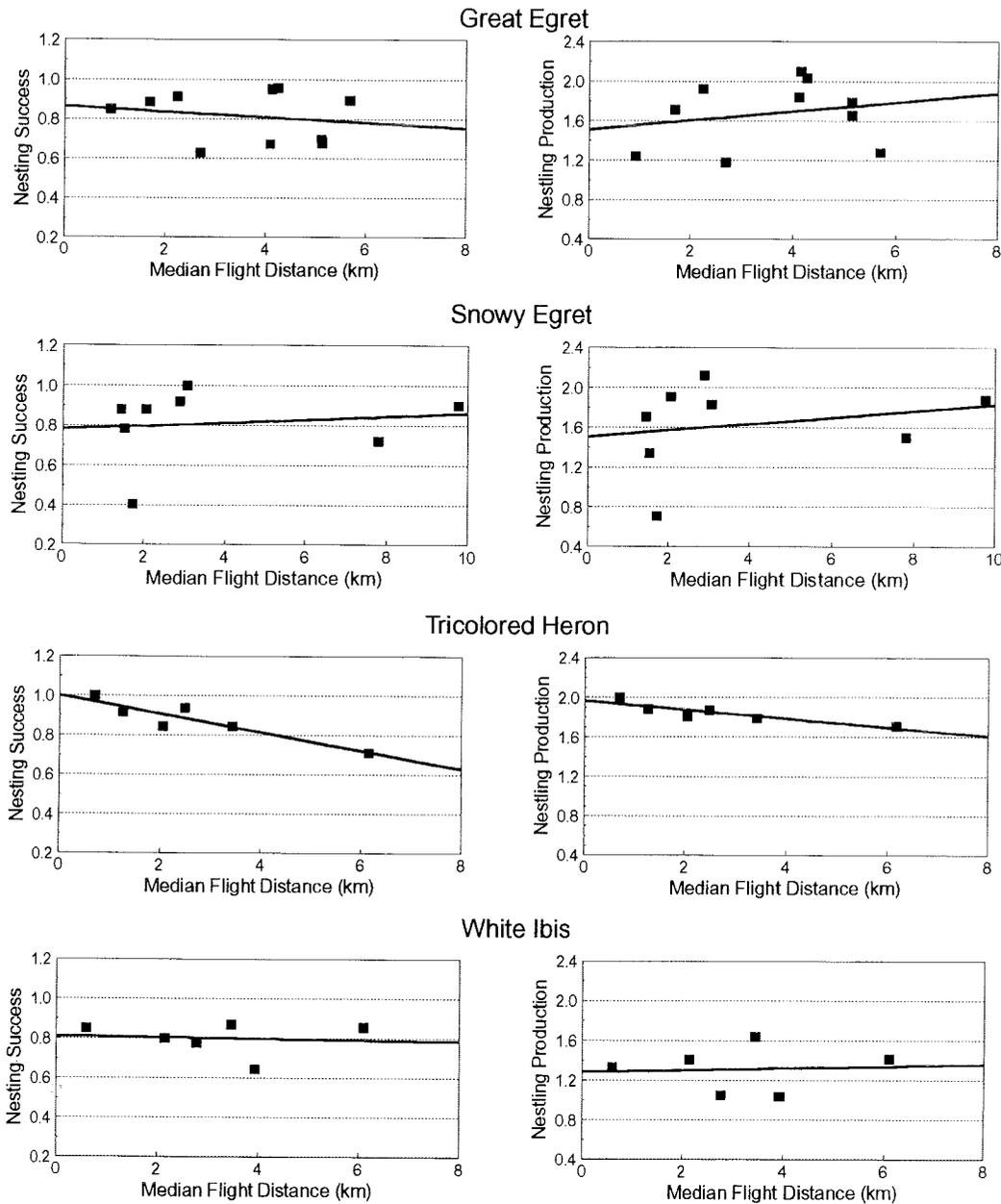


Figure 4. Plots by species of colony-specific estimates of nesting success (percent of hatched nests that succeeded in producing one or more threshold-age young [14-days old for White Ibis; 21-days old for other species]) and nestling production (number of threshold-age young produced per hatched nest) versus median foraging-flight distances.

lated to the species' dark coloration) that landed somewhere in the agricultural fields southwest of the lake (Fig. 3). All four off-lake flights occurred at the Clewiston Spit colony (1 each in 1989 and 1991, 2 in 1990). Tricolored Herons seemed less likely than other species to travel off the lake to forage.

For Great Egrets, the proportion of on-lake flights was highest at moderate lake stages and lowest at low lake stages; the χ^2 analysis confirmed a significant association (likelihood-ratio $\chi^2_2 = 6.91$, $P = 0.032$), with the shift toward more off-lake flights at low lake stages most responsible for the signifi-

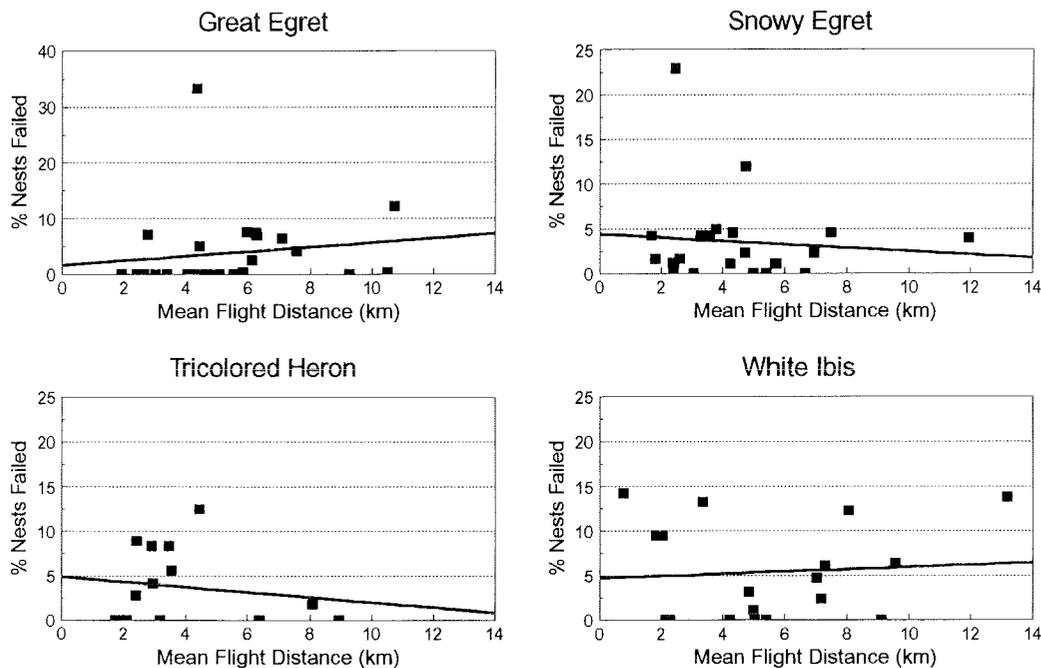


Figure 5. Plots by species of lakewide percentages of marked nests that failed during consecutive 15-day periods each season versus mean foraging-flight distances for the same periods.

cant finding (Fig. 6). For Snowy Egrets, the proportion of on-lake flights decreased progressively as the lake stage increased, with the shift toward more off-lake flights becoming strongly significant at high stages (likelihood-ratio $\chi^2_2 = 31.08$, $P = 0.001$; Fig. 6). For White Ibises, the proportion of on-lake flights was highest at moderately high lake stages and decreased at both lower and higher stages, with the shift toward more off-lake flights at high stages strongly significant (likelihood-ratio $\chi^2_3 = 20.39$, $P = 0.001$; Fig. 6).

Unbalanced distributions of samples across colonies and years (Table 2) precluded three-factor factorial ANOVA's of flight distance versus year, colony, and on/off-lake main effects. Three-factor additive ANOVA's were also not appropriate, because many of the possible two-factor factorial ANOVA's revealed significant year or colony by on/off-factor interactions (Table 3). Nonetheless, with few exceptions, colony-specific median flight distances were longer for off-lake flights than for on-lake flights (Table 2). Moreover, although several significant interactions indicated that the magnitude of dif-

ferences varied depending on the year and colony, all of the possible within-years and within-colonies two-factor ANOVA's except one (Snowy Egrets at Eagle Bay Island) indicated significant on/off main effects (Table 3), with off-lake flights averaging longer than on-lake flights.

Examination of year- and colony-specific median on/off-lake flight distances revealed some interesting variations from a general pattern (Table 2). Great Egret and White Ibis on-lake flights averaged longer than usual in 1989 at Eagle Bay Island, when many birds sought foraging grounds in receding marsh pools southwest of the colony (Figs. 1 and 3; and see Smith *et al.* 1995). Great Egret and White Ibis off-lake flights averaged shorter than usual at Eagle Bay Island in 1992, when birds were attracted to pasture and pocket wetlands located just outside the dike to the southwest (wetlands recently regenerated by high rainfall). Great Egret and Snowy Egret on-lake flights averaged longer than usual at Clewiston Spit in 1992 when a high lake stage (Fig. 2) forced birds to travel further north and south (or off-lake) to find suitable habitat. White Ibis off-lake flights

Table 2. Median on- and off-lake foraging-flight distances (km) by species, nesting colony, and year.

Species	Colony	Year			
		1989	1990	1991	1992
Great Egret	Taylor Creek			—/1.5 ^a (0/5) ^b	
	Eagle Bay Island	4.8/3.6 (6/16)	1.3/6.7 (21/28)	1.1/6.2 (25/31)	1.5/4.9 (7/6)
	Okee-Tantie Island			0.3/9.0 (7/10)	
	Central Fisheating Bay			2.2/4.4 (28/2)	
	Moore Haven	1.7/5.3 (43/7)			1.8/16.0 (10/3)
	Liberty Point	1.6/4.8 (15/2)			
	Clewiston Spit		2.7/7.7 (12/18)	2.1/7.8 (19/27)	8.1/6.8 (4/4)
Snowy Egret	Eagle Bay Island	3.5/1.5 (15/2)	2.6/12.4 (34/4)	1.6/2.6 (14/2)	0.1/— (1/0)
	Central Fisheating Bay			2.7/6.5 (36/8)	
	South Fisheating Bay		0.6/9.4 (17/2)		
	Moore Haven	1.7/— (12/0)			0.3/7.8 (1/5)
	Cochran's Pass	7.8/— (1/0)			
	Clewiston Spit	4.3/— (4/0)	2.1/6.3 (53/3)	2.1/9.8 (3/18)	12.0/— (2/0)
Tricolored Heron	Eagle Bay Island	0.7/— (1/0)	6.2/— (7/0)		
	Central Fisheating Bay			2.5/— (25/0)	
	South Fisheating Bay		1.3/— (5/0)		
	Cochran's Pass	2.7/— (1/0)			
	Clewiston Spit	4.8/— (9/0)	2.1/4.5 (31/1)	3.4/— (2/0)	
White Ibis	Eagle Bay Island	6.1/7.8 (19/12)	1.7/7.3 (107/40)	1.2/9.2 (20/19)	0.1/2.4 (1/10)
	Moore Haven	3.5/6.7 (11/1)			0.6/4.1 (11/5)
	Cochran's Pass	2.7/17.3 (25/5)			

^aOn/off-lake median flight distances.

^bOn/off-lake flight sample sizes.

from the interior-marsh Cochran's Pass colony in 1989 averaged unusually long.

White Ibis nestling production decreased significantly as the proportion of off-lake flights increased ($r^2 = 0.72$, $F_{1,4} = 10.43$, $P = 0.032$; Fig. 7). A positive association was sug-

gested for nesting success also, but the trend was statistically insignificant ($r^2 = 0.20$, $F_{1,4} = 0.10$, n.s.; Fig. 7). The same was true for Great Egret nesting success ($r^2 = 0.13$, $F_{1,8} = 1.19$, n.s.; Fig. 7). No other positive or significant associations were shown (Great Egret:

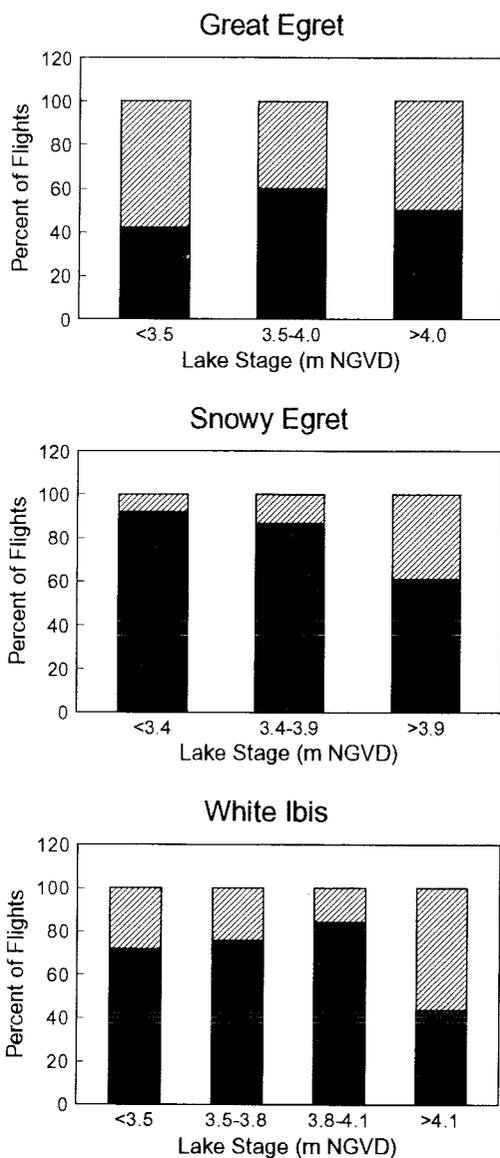


Figure 6. Study-wide proportions of flights ending on-lake (solid bars) and off-lake (hatched bars) in relation to intervals of lake stage for Great Egrets, Snowy Egrets, and White Ibises.

production, $r^2 = 0.03$, $F_{1,8} = 0.27$; Snowy Egret: success, $r^2 < 0.01$, $F_{1,6} < 0.01$; production, $r^2 = 0.01$, $F_{1,6} = 0.08$; all n.s.; Fig. 7).

Flight Distances and Hydrology

For Great Egrets, multiple regression analysis failed to reveal significant associations between flight distances and hydrologic variables ($R^2 = 0.01$, $F_{3,352} = 1.56$, $P = 0.199$;

main-effects-only model), but correlations of flight distance with DRISE (positive) and RAIN (negative) approached significance ($t_{354} = 1.74$, $P = 0.082$ and $t_{354} = -1.64$, $P = 0.102$, respectively). Thus, although the effects were weak, both rising water and a lack of rainfall during the drought might have forced a few Great Egrets to travel longer distances to find suitable foraging habitats. A negative correlation with RAIN would be consistent with evidence of an increase in the proportion of off-lake flights at low lake stages. An examination of STAGE and RAIN records around the days when the longest flights occurred provided additional evidence that reversals in established surface-water recessions probably caused at least a few birds to travel greater distances to forage. The lack of statistically significant regression results suggested that such cases were, however, the exception rather than the rule.

For Snowy Egrets, multiple regression analysis ($R^2 = 0.04$, $F_{3,232} = 3.11$, $P = 0.027$; main-effects-only model—no significant interactions) revealed that flight distances averaged longer at high lake stages (STAGE, $t_{234} = 2.61$, $P = 0.010$) and during periods of high rainfall (RAIN, $t_{234} = 2.13$, $P = 0.034$). The low R^2 for the model indicated, however, that hydrologic variation was not a strong determinant of foraging-flight distances.

For Tricolored Herons, multiple regression analysis failed to reveal significant associations of flight distances and hydrologic variables ($R^2 = 0.005$, $F_{3,77} = 0.13$, $P = 0.940$; main-effects-only model).

For White Ibises, multiple regression analysis ($R^2 = 0.08$, $F_{4,281} = 6.27$, $P < 0.001$) revealed that flight distances averaged longer at higher lake stages ($t_{284} = 2.55$, $P = 0.011$) and during reversals in established drying trends, but declined in response to a persistent and steady rising-water trend. The latter details were indicated by significant positive correlations of flight distance with DRISE ($t_{284} = 3.32$, $P = 0.001$) and RAIN ($t_{284} = 3.07$, $P = 0.002$), and a significant negative correlation with the DRISE \times RAIN interaction term ($t_{284} = -3.87$, $P < 0.001$). In other words, an increase in either main-effect variable (in each

Table 3. Two-factor ANOVA results for comparisons of on- and off-lake flight distances at specific colonies and within years for Great Egrets, Snowy Egrets, and White Ibises (compare with Table 2).

	Great Egret	Snowy Egret	White Ibis
Within colonies across years ^a			
Eagle Bay Island ^b	YR: $F_{3,132} = 0.60, P = 0.616$ OO: $F_{1,132} = 16.60, P = 0.001$ INT: $F_{3,132} = 3.94, P = 0.010$ $R^2 = 0.31$	YR: $F_{2,65} = 4.89, P = 0.011$ OO: $F_{1,65} = 2.34, P = 0.131$ INT: $F_{2,65} = 2.76, P = 0.071$ $R^2 = 0.20$	YR: $F_{3,220} = 8.08, P < 0.001$ OO: $F_{1,220} = 28.28, P < 0.001$ INT: $F_{3,220} = 4.07, P = 0.008$ $R^2 = 0.28$
Moore Haven	YR: $F_{1,59} = 0.36, P = 0.552$ OO: $F_{1,59} = 25.15, P < 0.001$ INT: $F_{1,59} = 2.10, P = 0.152$ $R^2 = 0.31$		
Clewiston Spit ^c	YR: $F_{2,78} = 3.05, P = 0.053$ OO: $F_{1,78} = 10.07, P = 0.002$ INT: $F_{2,78} = 3.17, P = 0.047$ $R^2 = 0.36$	YR: $F_{1,63} = 0.13, P = 0.715$ OO: $F_{1,63} = 11.06, P = 0.001$ INT: $F_{1,63} = 0.67, P = 0.417$ $R^2 = 0.34$	
Within years across colonies ^d			
1989	COL: $F_{2,83} = 0.93, P = 0.398$ OO: $F_{1,83} = 5.08, P = 0.027$ INT: $F_{2,83} = 4.05, P = 0.021$ $R^2 = 0.27$		COL: $F_{2,67} = 1.50, P = 0.232$ OO: $F_{1,67} = 8.65, P < 0.005$ INT: $F_{2,67} = 2.91, P = 0.061$ $R^2 = 0.27$
1990	COL: $F_{1,75} = 0.74, P = 0.392$ OO: $F_{1,75} = 60.83, P < 0.001$ INT: $F_{1,75} < 0.01, P = 0.988$ $R^2 = 0.47$	COL: $F_{2,107} = 1.28, P = 0.283$ OO: $F_{1,107} = 18.69, P < 0.001$ INT: $F_{2,107} = 1.10, P = 0.337$ $R^2 = 0.25$	
1991 ^e	COL: $F_{3,141} = 1.22, P = 0.305$ OO: $F_{1,141} = 32.14, P < 0.001$ INT: $F_{3,141} = 2.09, P = 0.104$ $R^2 = 0.33$	COL: $F_{2,74} = 2.67, P = 0.076$ OO: $F_{1,74} = 16.53, P < 0.001$ INT: $F_{2,74} = 1.50, P = 0.229$ $R^2 = 0.49$	
1992	COL: $F_{2,28} = 2.44, P = 0.105$ OO: $F_{1,28} = 8.11, P = 0.008$ INT: $F_{2,28} = 5.30, P = 0.011$ $R^2 = 0.51$		COL: $F_{1,23} = 23.41, P < 0.001$ OO: $F_{1,23} = 104.18, P < 0.001$ INT: $F_{1,23} = 5.27, P = 0.031$ $R^2 = 0.85$

^aYR = year main effect; OO = on/off-lake main effect; INT = interaction.

^bExcluding 1992 data for Snowy Egrets.

^cIncluding only 1990 and 1991 data for Snowy Egrets.

^dCOL = colony main effect; OO = on/off-lake main effect; INT = interaction.

^eExcluding Taylor Creek data for Great Egrets.

case indicating rising water) led to longer flights if the change followed an extended period of low rainfall and receding water (i.e., both variables previously low, contribution of interaction term relatively unimportant), but led to shorter flights if the change insured the persistence of an established rising water trend (i.e., both variables already high, contribution of interaction term dominant). The low R^2 again indicated that the hydrologic variables explained a significant

but small portion of the variance in the data. Examination of specific STAGE and RAIN measurements around dates when the longest flights occurred further confirmed that inconsistent rising trends and especially abrupt reversals to rising water were likely causes of occasional long flights.

Patterns of Habitat Use

In opposition to the null hypothesis of no association between lake stage and habitat

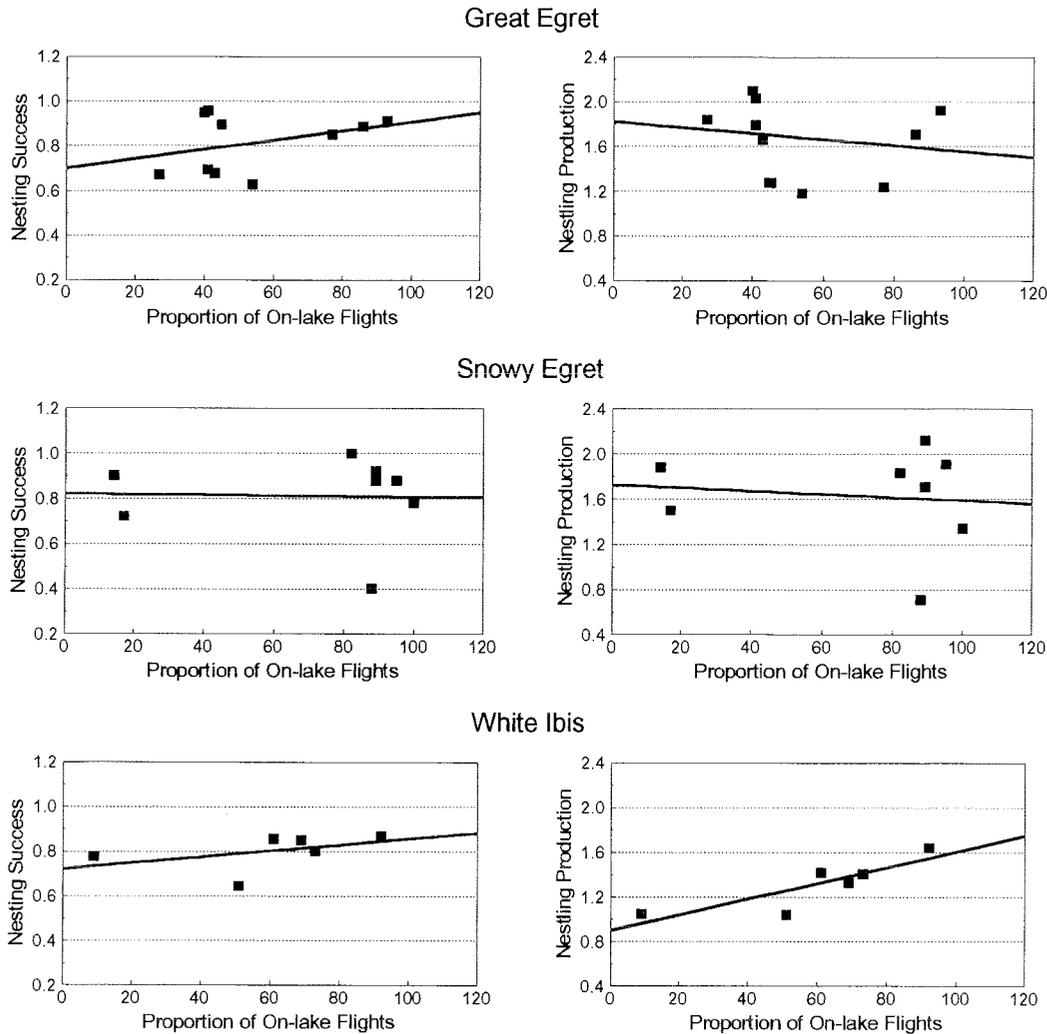


Figure 7. Colony-specific proportions of on-lake flights versus estimates of nesting success (percent of hatched nests that succeeded in producing one or more threshold-age young [14-days old for White Ibis; 21-days old for other species]) and nestling production (number of threshold-age young produced per hatched nest) for Great Egrets, Snowy Egrets, and White Ibises.

use, Great Egrets significantly altered their pattern of habitat use in response to changing lake stages (Table 4). At low lake stages, when Great Egret use of off-lake habitats increased (Fig. 6), agricultural field habitats (AG) and panhandling (PANH) increased in relative importance; individual cell χ^2 values indicated that this shift constituted a significant change in behavior (Table 4). Great Egrets also used mixed-submerged and outer-fringe habitats (MS-OF) on the lake significantly more than expected at low lake stages (although aerial foraging [MS-A, N = 10;

lumped with MS-OF to boost cell sample sizes] was used only at moderately high stages of 3.8-4.1 m). In contrast, Great Egrets used mixed-prairie and mid-littoral zone transitional habitats (MP-MTR—lumped together to boost cell sample sizes) significantly less than expected at low lake stages, largely because these habitats were nearly dry. At moderate stages, however, Great Egrets used MP-MTR habitats more than any other habitat type and the shift represented a significant change in behavior. At high lake stages, the pattern of habitat use shifted significantly to-

Table 4. Chi-square analysis for Great Egrets examining study-wide patterns of habitat use in relation to lake stage (overall likelihood-ratio $\chi^2_{10} = 64.22$, $P < 0.001$; asterisks indicate cells responsible for significant pattern of variation).

Lake Stage (m NGVD)	Habitat Categories ^a						Observed Total
	AG	PS	PANH	UTR	MP-MTR	MS-OF	
≤3.5	*12/6 ^b (21) ^c	8/13 (14)	*13/7 (23)	1/4 (2)	*3/18 (5)	*20/9 (35)	57
3.5-4.0	24/25 (10)	50/52 (21)	19/27 (8)	14/16 (6)	*93/75 (40)	33/38 (14)	233
>4.0	3/7 (5)	21/15 (32)	9/8 (14)	*9/4 (14)	19/21 (29)	5/11 (8)	66

^aOff-lake: AG - agricultural field ditches and peripheral canals; PS - pasture and slough wetlands; PANH - pan-handling stations. On-lake: MS-OF - mixed-submerged vegetation and open outer-fringe habitats; MP-MTR - mixed emergent prairie and complex middle littoral zone transitional habitats; UTR - upper littoral zone transitional habitats.

^bObserved/expected number of flights.

^cRow percentage corresponding to observed count.

ward upper-transitional habitats (UTR). Off-lake pasture and slough wetlands (PS) were used proportionately more at high lake stages also, but this shift in pattern was not quite significant at the $P = 0.05$ level (Table 4).

Snowy Egrets significantly altered their pattern of habitat use in response to changing lake stages (Table 5). Snowy Egrets used off-lake AG habitats (primarily agricultural field ditches and canals) much more than expected at high lake stages and much less than expected at low lake stages. The same pattern was shown for off-lake PS habitats, but the shift in use was not statistically signif-

icant. The only habitat type that Snowy Egrets used significantly more than expected at low stages was MS-OF, and the relative volume of use suggested (but did not confirm because I did account for habitat availability) a strong preference for these habitats. Snowy Egrets continued to rely on submerged vegetation habitats at higher lake stages, but shifted to using aerial foraging techniques (MS-A) and HM-LOT habitats. The latter habitat class included thick beds of *Hydrilla*, floating mats of water hyacinth, and large surface leaves of lotus that provided support in water too deep for wading (Smith *et al.* 1995). In

Table 5. Chi-square analysis for Snowy Egrets examining study-wide patterns of habitat use in relation to lake stage (overall likelihood $\chi^2_{12} = 112.37$, $P < 0.001$; asterisks indicate cells responsible for significant pattern of variation).

Lake Stage (m NGVD)	Habitat Categories ^a							Observed Total
	AG	PS	MS-OF	HM-LOT	MS-A	MP	UTR	
≤3.4	*2/11 ^b (2) ^c	7/9 (6)	*69/39 (62)	20/22 (18)	*7/15 (6)	5/11 (4)	2/4 (2)	112
3.4-3.9	2/5 (4)	5/5 (9)	11/18 (21)	8/11 (15)	*14/7 (26)	*10/5 (19)	3/2 (6)	53
>3.9	*20/7 (28)	8/6 (11)	*2/25 (3)	19/14 (26)	10/9 (14)	9/7 (13)	4/3 (6)	72

^aOff-lake: AG - agricultural field ditches and peripheral canals; PS - pasture and slough wetlands. On-lake: MS-OF - mixed submerged vegetation and open outer-fringe habitats; HM-LOT - *Hydrilla* mat and lotus habitats; MS-A - mixed submerged habitats exploited by aerial foraging; MP - mixed emergent prairie; UTR - upper littoral zone transitional habitats.

^bObserved/expected number of flights.

^cRow percentage corresponding to observed count.

contrast, other MS-OF habitats, accessible only by wading, were largely unavailable to foraging birds at high stages, hence the significant decline in use. Like Great Egrets, Snowy Egrets used MP habitats significantly more often than expected only at moderate lake stages and UTR habitats proportionately more at high lake stages (although the latter trends were not pronounced).

Small sample sizes for Tricolored Herons precluded χ^2 analysis with habitat and stage categories partitioned at the level of detail possible for other species. An analysis with two lake-stage and five habitat categories suggested significant changes in habitat use as a function of lake stage (Table 6); however, these results must be interpreted with caution because the χ^2 statistics may be unreliable due to small sample sizes. Tricolored Herons used primarily MS-OF habitats at low lake stages. Use of these habitats declined at higher stages, but Tricolored Herons continued to use thick surface mats of *Hydrilla* mixed with floating hyacinth (HM-HYC) for support in habitats too deep for wading. Moreover, regardless of the lake stage, Tricolored Herons consistently chose to forage in deep-water *Hydrilla* flats where the large surface leaves of intermixed lotus plants provided the necessary support (H-LOT). The only other apparently significant finding was that Tricolored Herons, like other species, increasingly turned to UTR habitats at high lake stages.

White Ibises significantly altered their pattern of habitat use in response to changing lake stages (Table 7). The single off-lake habitat category (OFF) included a diverse mix of pasture, cattle feedlot, and shallow ditch and slough habitats; trends in use were consistent for all subcategories, so I combined them for the final presentation. Overall, the trends indicated were similar to those shown for Great and Snowy Egrets: OFF and UTR habitats used proportionately more at high stages; MP habitats used proportionately more at moderate stages; and primarily MS-OF habitats used at low stages.

DISCUSSION

Mean flight distances recorded during this study were frequently shorter than those from studies conducted in the Everglades and other regions of the United States (Table 8). The longest Great Egret, Tricolored Heron, and White Ibis flights were similar to those documented in other studies, but the longest Snowy Egret flight was less than half as long as the longest flight documented by Bancroft *et al.* (1990, 1994).

Bancroft *et al.* (1990, 1994) and Frederick and Collopy (1988) found that nest failure increased among several species of wading birds in the Everglades when foraging-flight distances extended to 25-30 km and beyond. These authors believed that large-scale reversals to rising water were to blame for the increasing travel distances and

Table 6. Chi-square analysis for Tricolored Herons examining study-wide patterns of habitat use in relation to lake stage (overall likelihood ratio $\chi^2_4 = 71.91$, $P < 0.001$; asteriss indicate cells responsible for significant pattern of variation).

Lake Stage (m NGVD)	Habitat Categories ^a					Observed Total
	MS-OF	HM-HYC	HM-LOT	MP	UTR	
≤3.7	*38/25 ^b (70) ^c	*0/9 (0)	6/7 (11)	6/4 (11)	4/9 (7)	54
>3.7	*0/13 (0)	*13/4 (48)	5/4 (19)	0/2 (0)	*9/4 (33)	27

^aAll habitats on-lake: MS-OF - mixed submerged vegetation and open outer-fringe habitats; HM-HYC - *Hydrilla* and water hyacinth mat habitats; HM-LOT - *Hydrilla* and lotus habitats; MP - mixed emergent prairie; UTR - upper littoral zone transitional habitats.

^bObserved/expected number of flights.

^cRow percentage corresponding to observed count.

Table 7. Chi-square analysis for White Ibises examining study-wide patterns of habitat use in relation to lake stage (overall likelihood ratio $\chi^2_9 = 171.10$, $P < 0.001$; asterisks indicate cells responsible for significant pattern of variation).

Lake Stage (m NGVD)	Habitat Categories ^a				Observed Total
	OFF	MS-OFF	MP	UTR	
≤3.5	49/56 ^b (28) ^c	*103/65 (60)	*11/32 (6)	*10/20 (6)	173
3.5-3.8	8/11 (24)	*5/12 (15)	*20/6 (61)	*0/4 (0)	33
3.8-4.1	4/8 (16)	*0/9 (0)	*11/5 (44)	*10/3 (40)	25
>4.1	*31/18 (56)	*0/21 (0)	11/10 (20)	*13/6 (24)	55

^aOff-lake: OFF - all off-lake habitats combined, mostly flooded pasture, pasture ponds and ditches, and pocket and slough wetlands, plus some agricultural field ditches and cattle feedlots. On-lake: MS-OFF - mixed submerged vegetation and open outer-fringe habitats; MP - mixed emergent prairie; UTR - upper littoral zone transitional habitats.

^bObserved/expected number of flights.

^cRow percentage corresponding to observed count.

colony failures. My data suggested that high lake stages and reversals in established drying trends due to high rainfall probably forced some individuals of all species to travel increasing distances, but significant associations were shown only for Snowy Egrets and White Ibises. Flight distances generally increased when birds traveled off the lake to feed; however, few birds traveled as far as 25-30 km. Moreover, I uncovered little evidence that variation in foraging-flight distances was a significant determinant of nesting success and productivity at the lake. Significant negative associations between flight distances and estimates of nesting success and productivity were shown only for Tricolored Herons, but the data for this species were limited in scope and some results were insignificant.

The lake region provides a high diversity of foraging opportunities within a relatively limited area for birds nesting on the lake. The close proximity of such an array of choices may generally preclude the need for extensive travel to find foraging opportunities. Instead, nesting birds faced with changing hydrologic trends and habitat conditions may shift to different regions of the lake or to shallower off-lake habitats without having to significantly extend their travel distances.

It also is possible that for most species the relationship between foraging flight energetics and nesting success is not a continuous function. Instead, increased flight distances may lead to nest failure only after reaching a critical threshold. A relatively abrupt transition may occur where the distance to foraging sites becomes so great that the adult birds are no longer able to compensate for extended prey-delivery intervals by carrying back larger prey loads. If this is the case, one may not be able to detect an association between flight distances and nest failure rate in the absence of a threshold situation. Still another possibility is that annual comparisons of colony-average flight distances and nesting success may obscure more pronounced variation at the intra-seasonal level or at the level of individual nesting pairs. I attempted to address the former possibility by comparing flight distances versus nest failure rates over 15-day periods within seasons, but for an ideal analysis the temporal distribution of data would need to be more complete. Studying the flights and success of individual pairs would be the best way to answer the question, but such a study would require a difficult, expensive, and intensive radio-telemetry monitoring effort.

Table 8. Mean and maximum foraging-flight distances (km) for nesting adult wading birds during various studies.

Species	Source	Location	Years	N	Mean Distance	Maximum Distance
Great Egret	Custer and Osborn 1978	Newport River Estuary, NC	1976	144	3.6	≅27
	Thompson 1979	Upper Mississippi River	1978	18	8.6	35.2
	Frederick and Collopy 1988	Everglades, FL	1986-87	149	4.8	≅22
	Bancroft <i>et al.</i> 1990	Everglades, FL	1987-89	132	6.5	31.6
	Frederick 1993	Everglades, FL	1992	3	3.9	≅5
	This study	Lake Okeechobee, FL	1989-92	356	5.2 ^a	33.3
Snowy Egret	Custer and Osborn 1978	Newport River Estuary, NC	1976	37	3.7	≅19
	Frederick and Collopy 1988	Everglades, FL	1986-87	16	9.6	≅18
	Bancroft <i>et al.</i> 1990	Everglades, FL	1987-89	284	14.1	65.7
	This study	Lake Okeechobee, FL	1989-92	237	4.3 ^a	29.8
Tricolored Heron	Custer and Osborn 1978	Newport River Estuary, NC	1976	81	2.6	≅13
	Bancroft <i>et al.</i> 1990	Everglades, FL	1987-89	309	7.6	26.7
	This study	Lake Okeechobee, FL	1989-92	81	5.1 ^a	22.3
White Ibis	Bateman 1970	Alabama	1969	3 ^b	10.3	22.9
	Kushlan 1976	Everglades, FL	1972-75	—	—	≅44
	Custer and Osborn 1978	Newport River Estuary, NC	1976	138	1.6	6.7
	Bildstein <i>et al.</i> 1990	Coastal South Carolina	1979-86	—	—	≅40
	Frederick and Collopy 1988	Everglades, FL	1986-87	191	8.4	≅25
	Bancroft <i>et al.</i> 1990	Everglades, FL	1987, 89	33	11.5	>17.9
	Frederick 1993	Everglades, FL	1992	102	12.6	≅36
	This study	Lake Okeechobee, FL	1989-92	286	4.9 ^a	33.3

^aSimple arithmetic means provided for consistency with data from other studies.^bThree birds followed repeatedly by radio telemetry.

Variation in flight distances alone may not have affected prey delivery rates or the size of prey loads to a degree sufficient to influence productivity levels at the lake; however, changing hydrologic conditions led to shifts in habitat use among nesting birds, and attendant variation in habitat quality may have contributed to observed annual and colony-specific variation in nest productivity. For instance, all species achieved high levels of nesting success and nestling production during the drought seasons of 1989 and especially 1990 (Smith 1994, Smith and Collopy 1995). Habitat selection analyses for the larger non-breeding population (Smith *et al.* 1995) and the habitat use studies summarized herein for nesting populations revealed that mixed-submerged habitats—dominated primarily by *Hydrilla* and *Vallisneria*—were a strong attractor for foraging birds of all species when the lake stage was low. Prey sampling showed that these habitats harbored unusually high densities of small fish and shrimp (McIvor and Smith 1992, Chick and McIvor 1994), and observations of foraging birds indicated that foraging success and profitability were generally high in such habitats (McIvor and Smith 1992, Smith, unpub. data).

White Ibises foraged in mixed-submerged and outer fringe habitats less frequently than other species, but like the others shifted to such habitats at the height of the drought when upper-elevation habitats were largely dry and prey organisms were heavily concentrated in the submerged-vegetation zone (Smith *et al.* 1995). This was probably the only time that White Ibises switched from a diet dominated by invertebrates to one dominated by fish (Smith, unpub. data; cf. Kushlan 1976b, 1979). The high concentration of energy-rich fishes was the likely reason for the generally elevated levels of nesting success and productivity. The regression of proportions of on-lake flights versus estimates of nest productivity seemed to confirm that White Ibises fared better when on-lake foraging conditions were favorable.

Great Egrets foraged in various habitats on the lake in 1990, but a majority of those

followed (58%) traveled off the lake to dispersed foraging sites in agricultural field ditches near Clewiston and in various habitats adjacent to Eagle Bay Island (Fig. 3). The lack of nesting in 1990 at interior-marsh sites such as Moore Haven and Liberty Point, where on-lake foraging was typical (Table 1, Fig. 3), was a result of drought conditions (Smith and Collopy 1995). The agricultural field ditches and canals, in particular, may have constituted an unnaturally persistent source of flooded habitat during the drought when many natural habitats had dried. The nearly significant negative correlation between rainfall and the proportion of off-lake flights is consistent with this interpretation. Furthermore, it was in 1990 at the height of the drought that Great Egrets turned most heavily to panhandling fish scraps in residential areas (24% of the birds followed in 1990 versus 5-9% in other years; 41% of the total number of birds followed off-lake in 1990). No other species employed the panhandling strategy, and to a degree it obviated the need to find remnant, flooded habitats. Nestling regurgitant samples confirmed that many chicks were fed carcasses of filleted sunfish (Centrarchidae) taken from the fish-cleaning stations. This food type, along with minnows stolen from bait shop tanks, constituted a minimum of 10-12% of the aggregate mass of prey represented in 151 nestling regurgitant samples collected in 1990 (McIvor and Smith 1992). Most lakewide measures of Great Egret nesting success and nestling production were highest for the study in 1990 (Smith and Collopy 1995), suggesting that having to rely more on panhandling and other off-lake habitats for foraging was generally not a disadvantage for the species (but see below).

In 1991, some Great Egrets switched to nesting at the Central Fisheating Bay site located in the midst of very productive submerged vegetation foraging grounds. The site was unavailable prior to 1990 and the onset of drought conditions. Snowy Egrets and Tricolored Herons initiated nesting at the site in 1990, but the newly emerged vegetation may not have been sufficient to support the larger Great Egret nests until 1991. Great

Egrets nesting at this colony generally foraged nearby (Fig. 3); regularly employed energetically expensive aerial foraging techniques; fed their young an unusually diverse mixture of larger fish; and achieved a high level of nesting success and productivity (Smith, unpub. data).

Snowy Egrets turned to off-lake habitats more at higher lake stages in 1991 and 1992 when much of the littoral zone on the lake was too deep for wading, water levels were unsteady or rising, and previously heavily used floating mats of vegetation in Fisheating Bay began to resubmerge or disperse. My data indicated that variation in flight distances and proportions of on- and off-lake flights were not determinants of Snowy Egret nest productivity. A possible exception to this generality was at the interior Moore Haven colony in 1992, where a moderately long median flight instance (7.8 km) and a low proportion of on-lake flights (17%) coincided with moderate estimates of nesting success (72%) and nestling production (1.55). These data were consistent with trends in colony turnover and success, which suggested that high lake stages and fluctuating water levels adversely affected Snowy Egrets in 1992 (Smith and Collopy 1995). The interior-marsh colonies were the most likely to pose problems during high water, because the distance to accessible higher-elevation foraging habitat was relatively great.

Annual, lakewide estimates of Tricolored Heron nesting success did not vary significantly over the course of the study (Smith and Collopy 1995), but colony-specific estimates varied much more (evident in Fig. 4). Murdich (1978) found that Tricolored Herons were more generalized in their use of habitats than Snowy Egrets and Great Egrets, but at Lake Okeechobee birds nesting at Clewiston Spit regularly traveled longer distances to find suitable foraging sites than birds from other colonies (Fig. 3). This fact suggested that, although the Clewiston spoil islands may have provided suitable nesting habitat, the availability of favorable foraging habitat was more restricted than at other colony sites. Unlike Snowy Egrets and Great Egrets, Tricolored Herons were apparently

not drawn to the adjacent agricultural fields, but instead chose to travel longer distances to reach mixed-submerged, lotus, and outer-fringe habitats at the edge of Fisheating Bay and toward the south end of the lake (Fig. 3). The combination of more long-distance flights and lower colony-wide nesting success and productivity at Clewiston was the principal reason why the plots of flight distance versus colony success and productivity revealed significant negative trends.

The myriad agricultural ditches southwest of the lake attracted many Great Egrets and Snowy Egrets that nested at Clewiston Spit, Great Egrets primarily during the drought and Snowy Egrets primarily at high lake stages. However, the Great Egret nestlings born at Clewiston Spit in 1990 suffered significantly more than nestlings born at Eagle Bay Island from infections of the nematode parasite *Eustrongylides ignotus* (Spalding *et al.* 1994). Although no evidence exists to link infections at Lake Okeechobee to particular habitats, the oligochaetes that serve as intermediate hosts for the parasite appear to prosper in artificially disturbed and nutrient-enriched environments (Spalding *et al.* 1993, Frederick and Spalding 1994). Examinations of hundreds of small fishes collected on the lake in several habitat types revealed no infected fish (M. S. Spalding pers. comm.), which are the second intermediate hosts for the parasite. Both cattle pasture ponds and agricultural field ditches readily fit the description of preferred habitat for the oligochaetes, but the higher incidence of infection at Clewiston Spit suggested that the agricultural field ditches may be a greater source of parasites. Thus, agricultural field ditches may have provided Great Egrets with alternate foraging habitat during the drought, but the birds may have incurred unexpected costs. This is one area where additional research is greatly needed.

The multiple regression results examining variation in flight distances versus hydrologic trends, although never strongly significant, were consistent with the results of logistic regression analyses designed to elucidate the environmental determinants of nest failure for six species on the lake

(Smith 1994). Of particular import are the findings for White Ibises, which suggest that abrupt reversals in established drying trends led to increased flight distances, but additional rainfall and an increase in the number of days of rising water led to shorter flights if water levels were already rising. In other words, the steadiness of the surface water trends rather than the direction of change was the determining factor. The logistic regression results for White Ibises (and some other species) indicate that the probability of nest failure declined during periods of either protracted and steady drying or slow and steady rising water. Thus, although there was little evidence that increasing flight distances alone led to reduced nesting success and productivity, longer flight distances may have amplified the negative impact of unfavorable surface-water trends on White Ibis foraging efficiency.

The patterns of habitat use on the lake shown for nesting adults were similar to those demonstrated for the general foraging population (Smith *et al.* 1995). Exposed beds of submerged vegetation and outer-fringe habitats were widely used at low lake stages. Mixed-prairie habitats, particularly those featuring mixes of *Eleocharis*, *Panicum*, and *Nymphaea*, were widely used at moderate lake stages. Upper-elevation transitional mixes featuring grasses and sedges or *Polygonum* were widely used at higher stages. The foraging-flight data also indicated, however, that among all species except perhaps Tricolored Herons there were always some nesting individuals that chose to forage off the lake. Among Great Egrets and White Ibises, the proportion was always fairly high (28-60% and 24-55%, respectively), but Snowy Egrets regularly traveled off the lake only at higher lake stages. The increase in off-lake flights for Snowy Egrets and White Ibises at higher lake stages was consistent with the observation that relatively low numbers of birds foraged on the lake during the 1991 and 1992 nesting seasons (Smith *et al.* 1995), and with previous observations of increasing abundance along Fisheating Creek and in other off-lake areas when the lake stage is high (Zaffke 1984, David 1994, Smith unpub. da-

ta). Thus, off-lake habitats such as the pocket and slough wetlands interspersed with pasture land and the original Kissimmee River and Fisheating Creek floodplains, should be regarded as important resources for wading birds that nest on or near the lake (cf. Kushlan 1986). Such habitats will be of particular importance whenever management action or natural events lead to high lake stages. The availability of diverse off-lake habitats may insure that birds nesting on the lake have access to a variety of nearby foraging habitats under a wide range of hydrologic conditions, and thereby eliminate the potential restriction on successful nesting that long foraging-flights might otherwise represent.

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