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HYDROLOGICAL CONSTRAINTS ON TRICOLORED HERON AND SNOWY EGRET RESOURCE USE[1]

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Abstract. We investigated resource use by breeding Tricolored Herons (*Egretta tricolor*) and Snowy Egrets (*E. thula*) at a regional scale (1,312 km^2) during three years (1987–1989) with dissimilar water levels. We documented the direction and distance flown from the colony to feeding sites, habitat selection, daily movement patterns, feeding flock size, and diet at the Rodgers River Bay colony in Everglades National Park, Florida. The general pattern of flight direction was similar between the two species; both species flew northwest in 1987, a wet year, and northeast in 1988, a year with moderate surface water drying. During drought conditions in 1989, only Tricolored Herons nested successfully. Despite similarities in flight direction, habitat selection differed between the two species. Tricolored Herons were more consistent in habitat use among years, whereas Snowy Egret habitat selection was more variable. However, shifts in habitat selection in response to varying hydrologic conditions among years were greater than differences in habitat selection between the two species within a year. Prey selection was similar for the two species in 1987, indicating that they procured similar prey from different habitat types. Regardless of water conditions, Snowy Egrets were significantly more gregarious than Tricolored Herons, and feeding sites on consecutive days by radio-tagged Snowy Egrets were farther apart than those used by Tricolored Herons. Our results suggest that habitat selection occurs at a coarser scale than previously recognized and that studies conducted at single sites over short temporal scales may be ignoring important aspects of habitat selection.

Key words: Egretta thula, Egretta tricolor, *Everglades, habitat selection, hydrologic constraints, resource use, water level.*

INTRODUCTION

Studies of resource use are important in understanding an animal's behavior, adaptations to its environment, inter- and intraspecific interactions, and population dynamics. Although resource use can be investigated across a continuum of temporal and spatial scales, the scale at which the investigation is conducted will have dramatic effects on the observed patterns and conclusions about the underlying processes (Wiens 1981, Levin 1992, May 1993). For example, studies of an organisms' movements in response to changes in environmental parameters should be conducted over sufficiently long time scales to observe a range of environmental conditions, but shorter time scales may be adequate to examine physiological responses. Similarly, regarding spatial scale, studies of habitat selection should include an organism's entire home range, whereas more local scales may be appropriate for behavioral studies (May 1993).

Ciconiiformes are readily amenable to studies of habitat use, foraging behavior, and prey selection because they are large, conspicuous, and easily observable. Within the Ciconiiformes, Tricolored Herons (*Egretta tricolor*) and Snowy Egrets (*E. thula*) are of particular interest because they have been consistently characterized as one of the most ecologically similar species-pairs based on geographic range, body size, habitat use, and feeding behavior (Kushlan 1978, Recher and Recher 1980). Studies of resource partitioning between these two species have found differences in feeding behavior, prey selection, and habitat use; however, the segregating mechanisms have been inconsistent among studies (Willard 1977, Recher and Recher 1980). Because most of these studies have been conducted at local spatial scales (less than the area used by an entire colony) and short temporal scales (less than one year), they may have been

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inadequate to assess how Tricolored Herons and Snowy Egrets partition resources. In south Florida, rainfall, and therefore regional wetland water levels, often varies dramatically between years (Duever et al. 1994, Fennema et al. 1994). Because of this environmental variability and the ability of Tricolored Herons and Snowy Egrets to respond to it with a diversity of foraging behaviors (Kushlan 1977), quantification of resource use within a single breeding season also may result in a simplified view of resource partitioning.

We took advantage of large scale interannual fluctuations in hydrological conditions in south Florida from 1987–1989 to examine the effects of water level variation on breeding Tricolored Heron and Snowy Egret resource use across their entire foraging radius (1,312 km^2) surrounding the Rodgers River Bay colony in Everglades National Park (ENP), Florida. We present comparative data on distance and direction to foraging sites, habitat selection, daily movement patterns, prey use, feeding flock size, and colony-wide responses to changes in water level. We use these data to determine the relative strengths of environmental conditions and intrinsic differences between the species on resource use patterns. We argue that patterns of resource use exhibited at spatial scales less than the area used by the entire colony and temporal scales less than or equal to one breeding season may be misleading, especially if temporal variation in the environment is extreme.

METHODS

STUDY AREA

We studied breeding Tricolored Herons and Snowy Egrets during the 1987–1989 nesting seasons at the Rodgers River Bay colony (25°33.28′N, 81°04.28′W) in northwestern ENP. Since the late 1970s, this colony has contained the largest nesting populations of Tricolored Herons and Snowy Egrets in the freshwater portion of ENP (Ogden 1994). In both 1987 and 1988, approximately 2,000 pairs of wading birds nested at Rodgers River Bay colony, about 80% of which consisted of approximately equal numbers of Tricolored Herons and Snowy Egrets (Bancroft et al. 1990). Nesting numbers peaked in mid-May in 1987 and in mid-April in 1988. In 1989, Snowy Egrets and Tricolored Herons began nesting in late February, but abandoned their nests in mid-March (Bancroft et al. 1990). Approximately 200 pairs of Tricolored Herons began renesting in mid-April, and although nesting success was low, many remained through June.

HYDROLOGY

Daily water level data from the ornithology (OT) gauge, 11.5 km east of the Rodgers River Bay colony, provided an indication of water levels in the eastern half of the study area. When water levels are at or near ground level at this gauge, substantial shallow pools exist east of the colony; when water levels are high, inland marshes are flooded too deeply for efficient foraging. We analyzed water levels for January through mid-July, the period of peak nesting activity at the Rodgers River Bay colony (Bancroft et al. 1990). To simulate an "average" hydropattern to compare to the 3 years of our study, we used OT gauge data from 1980–1990 to calculate mean daily water levels. No water level data were available for the western coastal areas. The hydrology of the western half of the foraging area is complex. Much of the area is composed of perched wetlands primarily influenced by local rainfall; the remainder is a complex mosaic of ponds and small tidal creeks. Local rainfall, wind driven tides, and lunar tides in that order appear to be most influential on water depths.

FLIGHT DIRECTION

Because the relative proportion of habitats available to breeding wading birds varied relative to direction from the colony, flight-line counts provided a broad assessment of habitat use patterns (Erwin 1983). At the Rogers River Bay colony, birds flying east were generally selecting freshwater habitats and birds flying west were selecting marine or brackish habitats. We conducted counts approximately weekly when most nests contained eggs or nestlings. In 1987, we counted the number of Tricolored Herons and Snowy Egrets flying into and out of the colony in four 90% quadrants (northeast, southeast, southwest, and northwest) while we circled the colony for 15 min in a Cessna 172 aircraft at 143 km hr^{-1} and an altitude of 210 m. In 1987, we conducted eight censuses between 12 May and 25 June. In 1988, we counted all species flying into and out of the colony from a boat anchored approximately 150 m from the colony. Two observers working together censused two quadrants simultaneously for 15 min then moved to the opposite side of the colony and censused the remaining two quadrants. We conducted 13 censuses on consecutive days between 5 April and 30 June.

HABITAT AVAILABILITY

We distinguished five habitat types around the colony that correspond roughly to those of previous habitat classifications (Egler 1952, Duever et al. 1986). From fresh to salt water habitats these are:

Inland marsh. Sawgrass-dominated (*Cladium jamaicensis*) marsh in which hydrology is influenced by both upstream freshwater flow and local rainfall. This habitat contains tree islands and cypress (*Taxodium* spp.) domes and is divided by deeper sloughs.

Slough. Areas of deeper water (1–2 m) within the inland marshes provides the majority of freshwater reaching the estuaries. Compared to inland marsh, sloughs have a lower proportion of sawgrass and a higher proportion of submergent vegetation (e.g., *Eleocharis* sp., *Nymphaea* spp., and *Nuphar odorata*).

Mangrove—inland marsh interface. The narrow ecotonal area between the mangrove–coastal marsh and the inland marsh and slough habitats. Numerous mangrove "finger" projections extend into the inland marsh.

Mangrove—coastal marsh. A large and heterogeneous transitional area between the mangroves and the inland marshes and sloughs. These areas are dominated by emergent grasses, sedges and rushes (e.g., *Spartina* spp., *Juncus* spp., bulrush *Scirpus* spp., cattails *Typha* sp., and sawgrass) and water tolerant trees and shrubs (e.g., willow *Salix caroliniana,* buttonwood *Conocarpus erectus,* wax myrtle *Myrica cerifera,* and red mangrove *Rhizophora mangle*). This habitat also contains many small ponds.

Mangrove. Red and black mangrove (*Avicennia germinans*) forests that are essentially a continuous cover of woody vegetation. Some areas of higher elevation harbor less water-tolerant woody species.

We quantified the available habitat based on the mean foraging flight distances for breeding birds at the Rodgers River Bay colony. As 95% of all foraging locations were within 22 km of the colony (mean flight distance ± 2 SD), we used a 22-km radius circle (1,521 km^2) around the colony to define the foraging area available to breeding Tricolored Herons and Snowy Egrets. The portion of the circle that enclosed the Gulf of Mexico (209 km^2) was excluded from analyses. We used 13 U.S. Geological Survey 7.5 min orthophotomaps to digitize the boundaries of each of the five habitat types around Rodgers River Bay colony into a computer-compatible format. We surveyed the area in a Cessna 172 aircraft to verify habitat demarcations.

We calculated the area of each habitat type within the 22-km radius circle (availability) using Atlas Draw software (Strategic Locations Planning, Inc., San Jose, California). Because mangrove–inland marsh interface was an ecotonal habitat, we calculated its area by delineating a 0.5-km wide "corridor" around the digitized line separating inland marsh or slough and mangrove–coastal marsh habitats. Of the area contained in the mangrove–inland marsh interface corridor, 50% was subtracted from the area of mangrove–coastal marsh and 23% and 27% were subtracted from the area of slough and inland marsh habitat types, respectively. These values were proportional to the linear distance each habitat extended along the line bisecting the mangrove–inland marsh interface corridor. The above calculations yielded habitats in the following proportions (total area = 1,312 km^2): inland marsh, 0.290; slough, 0.068; mangrove–inland marsh interface, 0.076; mangrove–coastal marsh, 0.375; mangrove, 0.190.

HABITAT SELECTION AND FLOCK SIZE

To quantify habitat selection, we used following flights and radiotelemetry to compare habitat use patterns versus habitat availability. During following flights, we circled the colony in a Cessna 172 aircraft and waited until a bird of a preselected species flew from the colony. We followed the bird, remaining 60–180 m above it, until it landed and began feeding or it landed in a flock of other feeding birds. We returned to the colony and circled once before selecting another bird. Following flights were conducted in both the morning and afternoon during the period when most nests contained young (based on ground-based nest checks).

We also fitted nesting adult Snowy Egrets (n = 13) and Tricolored Herons (n = 10) with radiotransmitters. We caught birds using a walk-in trap placed above the nest platform (Jewell and Bancroft 1991) and attached solar/capacitor-assisted transmitters to them using a backpack-type harness (Dwyer 1972). Telemetered birds were then located from a Cessna 172 equipped with "side-looking" H-antennae. We could pinpoint radio-tagged birds by listening to either one antenna alone or both simultaneously using a switch-box. Because nesting wading birds generally return to the colony site at least once per day (Hafner et al. 1993), we assumed observations separated by 24-hr intervals were independent (Swihart and Slade 1985) and therefore recorded a maximum of one feeding location per day per radio-tagged bird. We used data only for radio-tagged birds with active nests. If their nest failed or the young fledged, we excluded subsequent locations from the analyses.

We marked each landing site or telemetry location on a 7.5 min orthophotomap, and recorded number and species composition of birds at the site. Foraging locations were later converted to Universal Transverse Mercator grid coordinates for calculation of flight distances and categorization of habitat type. Following flights and radio-tagged birds provided similar estimates of distance to feeding sites for Tricolored Herons in 1987 and 1988 and Snowy Egrets in 1987 (all $t < 1.6$, all $P > 0.12$), but in 1988, radio-tagged Snowy Egrets fed farther from the colony than the mean following flight distance ($t_{154} = 3.69$, $P < 0.001$). Therefore, we present both values for Snowy Egrets in 1988.

FOOD HABITS

To quantify differences in diet between the two species, we collected regurgitated boluses from nestling Tricolored Herons and Snowy Egrets during routine nest checks in 1987. Boluses were preserved in 10% formalin, and stored in isopropyl alcohol. The contents of each sample were identified to species and weighed (wet) to the nearest 0.01 g.

STATISTICAL ANALYSES

We used SPSS/PC+ (Norusis 1988) for all statistics except *G*-tests (Sokal and Rohlf 1995) and confidence intervals around observed proportions. Selection or avoidance of a habitat type or flight direction was considered significantly different from expected if the expected proportion fell outside the 95% confidence interval around the observed proportion (Neu et al. 1974). Kurtosis in flight-line counts ($t = 2.68$, $P < 0.01$) was reduced ($t = 1.67$, $P > 0.05$) through an arcsine transformation, and skewness in flight distances ($t = 8.15$, $P < 0.001$) was reduced ($t = 0.80$, $P > 0.20$) through a square root transformation (Snedecor and Cochran 1980).

RESULTS

HYDROLOGY

Long-term average water levels decreased from January though May and increased from June through July (Fig. 1). During our study, the 1987 hydrograph showed the highest overall water levels, the most extreme reversals in the spring drying pattern, and the highest minimum water level (10 cm). The 1988 hydrograph was most similar to the 11-year mean. In 1989, water levels were nearly always below ground level and exhibited erratic fluctuations. Drought conditions existed throughout south Florida during this period. For the five-month period, November–April, rainfall at 40-mile bend in ENP averaged 275 mm for a 32-year period through 1989. Rainfall was 408 mm, 307 mm, and 143 mm during November 1986–April 1987, November 1987–April 1988, and November 1988–April 1989, respectively.

FLIGHT DIRECTION

Because we used different methods in 1987 and 1988 to evaluate flight direction, we compared the distribution of landing sites (northeast, southeast, southwest, or northwest of the colony) of radio-tagged birds and following flights with flight-line count distributions for weeks which we had both types of data. We found no significant differences (all *G*s < 7.82, $P > 0.05$) among distributions in 5 of 7 weeks and 7 of 9 weeks for Tricolored Herons in 1987 and 1988, respectively, and in 5 of 7 and 7 of 12 weeks for Snowy Egrets in 1987 and 1988, respectively. We concluded that counting from the air and by boat both produced results generally consistent with following flights and telemetry and therefore differences in flight direction between years were not an artifact of sampling method.

We counted 4,043 Tricolored Herons and 4,762 Snowy Egrets during flight-line counts on 8 days (12 May–25 June) in 1987 and 13 days (5 April–30 June) in 1988. During 1989, the colony was small and flight-line counts were not conducted. During the high water conditions of 1987, 44% of the Tricolored Herons and 62% of the Snowy Egrets flew to the northwest (Table 1). In 1988, when water levels were lower, 49%

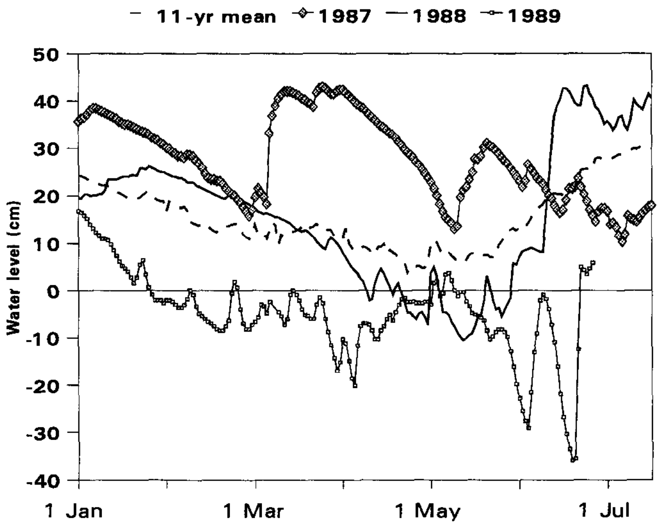

FIGURE 1. Water level (cm) at the OT gauge (located 11.5 km east of the Rodgers River Bay colony) from 1 January to 15 July 1987, 1988, 1989, and the 11-year mean hydrograph (1980–1990). The solid horizontal line at 0 represents ground level.

of the Tricolored Herons and 45% of the Snowy Egrets flew to the northeast. Although there were differences between Tricolored Herons and Snowy Egrets in direction flown to feeding sites in 1987 (G_3 = 93.2, $P < 0.005$) and 1988 (G_3 = 62.8, $P < 0.005$), the shifts between years were more pronounced (G_3 = 513.1, $P < 0.005$ for Snowy Egrets; G_3 = 149.9, $P < 0.005$ for Tricolored Herons).

The proportion of both Tricolored Herons and Snowy Egrets flying in the two westerly directions was positively correlated with water level at the OT gauge and the proportion flying northeast was negatively correlated with water level (Table 2). Thus, as water level declined at the OT gauge (in inland marsh and slough habitats), more birds flew east.

Tricolored Herons appeared less sensitive to water level fluctuations than Snowy Egrets. This is well illustrated in 1988 on the 25 April, 2 May, and 10 May counts, when water level at the OT gauge increased from −5.49 cm to 4.88 cm, then decreased to −8.84 cm. During all three counts, Tricolored Herons selected the northeast direction (all $P < 0.05$). In contrast, Snowy Egrets selected the northeast direction during low water levels on 25 April, shifted to the northwest when water levels increased, then returned to the northeast on 10 May as water levels again declined (all $P < 0.05$).

MOVEMENT PATTERNS

Mean (± SD) distance flown to feeding sites by Tricolored Herons varied among years from 12.8 ± 5.9 km in 1987 (n = 39, including 31 locations of 4 radio-tagged birds) to 8.6 ± 4.3 km

TABLE 1. Percentage of Tricolored Herons and Snowy Egrets flying in four directions from the Rodgers River Bay colony, Everglades National Park, Florida.

Species	Year	Total no. birds	Direction[c] % NE	% SE	% SW	% NW	G
Tricolored Heron	1987[a]	578	24	14−	18−	44+	113.3**
Snowy Egret	1987[a]	602	6−	12−	21	62+	418.6**
Tricolored Heron	1988[b]	3,465	49+	14−	9−	28+	657.7**
Snowy Egret	1988[b]	4,160	45+	13−	6−	36+	952.0**

[a] n = 8 days.
[b] n = 13 days.
[c] "+" indicates selection for that direction, "−" indicates selection against (Bonferroni Z-statistic, $P < 0.05$).
** $P < 0.01$.

in 1988 ($n = 91$, including 57 locations of 6 radio-tagged birds) to 5.4 ± 3.9 km in 1989 ($n = 135$, including 1 location of 1 radio-tagged bird) (ANOVA, $F_{2,262} = 50.07$, $P < 0.001$, all means significantly different from each other, Student-Neuman-Keuls test, all $P < 0.05$). Distances flown by Snowy Egrets to feeding sites were similar in 1987 (12.9 ± 4.8 km, $n = 68$, including 37 locations of 5 radio-tagged birds) and 1988 (13.1 ± 6.3 km, $n = 156$, including 91 locations of 11 radio-tagged birds; $t_{222} = 0.08$, $P > 0.9$). In 1988, radio-tagged Snowy Egrets fed farther from the colony (14.6 ± 6.9 km) than the mean following flight distance (10.9 ± 4.6 km). In 1987, flight distances were similar between the two species ($t_{105} = 0.24$, $P > 0.8$), but in 1988 Tricolored Herons flew shorter distances to feeding sites than did either radio-tagged Snowy Egrets or Snowy Egret following flights (both $t > 3.25$, both $P < 0.001$). The maximum distances to feeding sites we recorded were 27.0 km for a Tricolored Heron following flight in 1989 and 31.5 km for a radio-tagged Snowy Egret in 1988.

We investigated day-to-day distances moved by the two species by using distances moved by radio-tagged birds for which we had one or more pairs of feeding site locations on consecutive days. Tricolored Herons selected feeding sites that were closer together on consecutive days (2.8 km, $n = 7$ birds, 27 observations) than did Snowy Egrets (8.5 km, $n = 10$ birds, 43 observations, $t_{15} = 3.10$, $P = 0.007$).

HABITAT SELECTION AND FLOCK SIZE

To determine whether assessment of habitat selection was affected by methodology, we compared the distribution of following flights and radio-tagged birds among habitat types. The distribution of Tricolored Herons among habitats varied by methodology in 1987 ($G_3 = 8.17$, $P < 0.05$) and in 1988 ($G_4 = 14.4$, $P < 0.05$). However, with the exception of mangrove habitat in 1988, which was avoided by radio-tagged birds ($P < 0.05$) and for which following flight birds showed no selection, we found no differences in habitat selection/avoidance patterns between the two methodologies. The distribution of Snowy Egrets among habitats did not vary by methodology (both $G < 4.00$, both $P > 0.05$). Therefore we pooled the data across methodologies (within years) for analysis of habitat selection. Because of small sample sizes, we pooled slough and inland marsh habitats for analysis of habitat selection in 1987.

TABLE 2. Correlation coefficients (r) and probability levels (P) between arc sine percent of birds observed in each flight-line direction and water level at the OT gauge in 1987 and 1988 (all $n = 21$).

	Snowy Egrets		Tricolored Herons	
Direction	r	P	r	P
Northeast	−0.71	<0.001	−0.62	<0.01
Southeast	−0.33	ns	0.00	ns
Southwest	0.52	<0.05	0.54	=0.01
Northwest	0.61	<0.01	0.60	<0.01

In 1987, Tricolored Herons avoided inland marsh and slough habitats ($P < 0.05$, Fig. 2A). They fed primarily in mangrove–coastal marsh and mangrove habitats west of the inner bays (Fig. 3A), but showed no selection for any habitat type (all $P > 0.05$). In 1987, Snowy Egrets selected mangrove habitats (> 70% of all feeding sites) and avoided inland marsh and slough habitats (all $P < 0.05$, Figs. 2A and 3A).

In 1988, Tricolored Herons selected mangrove–coastal marsh (> 50% of all feeding sites) and mangrove–inland marsh interface (> 20%) habitats and avoided mangrove and inland marsh habitats (all $P < 0.05$, Figs. 2B and 3B). Snowy Egrets also selected mangrove–inland marsh interface, but in contrast to Tricolored Herons used slough habitats more than expected (both $P < 0.05$). Tricolored Heron use of mangrove–coastal marsh habitat was 50% greater than Snowy Egrets. In 1989, Tricolored Herons fed close to the colony (Fig. 4), almost exclusively (87%) in mangrove–coastal marsh habitat ($P < 0.05$) and avoided mangrove and inland marsh habitats (both $P < 0.05$).

Habitat selection by the two species differed in 1987 ($G_3 = 28.6$, $P < 0.005$) and 1988 ($G_5 = 41.9$, $P < 0.005$). Between 1987 and 1988, both species showed shifts in habitat selection, with Tricolored Herons being more consistent between years ($G_3 = 12.3$, $P < 0.01$) than Snowy Egrets ($G_3 = 89.0$, $P < 0.005$).

Feeding flock size differed between the two species ($G_3 = 304.4$, $P < 0.001$, Fig. 5). Three quarters of all Tricolored Herons fed solitarily and only 3% were associated with mixed species flocks of 50 birds or more. In contrast, only 10% of Snowy Egrets fed as single birds and 55% of the feeding aggregations with which they were associated contained more than 49 birds. The

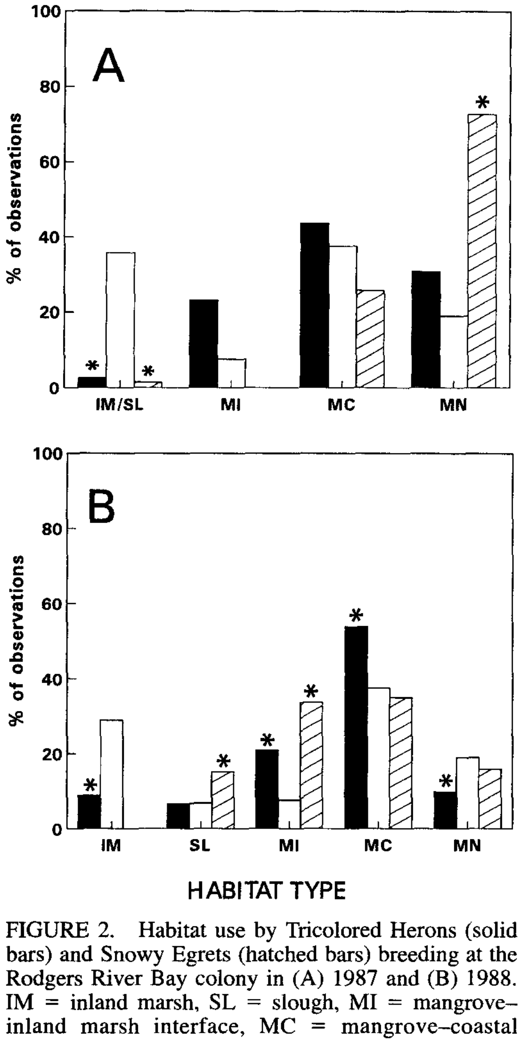

FIGURE 2. Habitat use by Tricolored Herons (solid bars) and Snowy Egrets (hatched bars) breeding at the Rodgers River Bay colony in (A) 1987 and (B) 1988. IM = inland marsh, SL = slough, MI = mangrove–inland marsh interface, MC = mangrove–coastal marsh, CM = coastal marsh, and MN = mangrove. An asterisk indicates a particular habitat type was used significantly greater or less than expected relative to the proportion of available habitat (Bonferroni Z-statistic, $P < 0.05$) (Neu et al. 1974).

differences between species appeared unrelated to environmental conditions. In both years, differences were greater between the species (both $G_3 > 32.8$, $P < 0.005$) than differences within species between years ($G_3 = 26.0$, $P < 0.005$ for Snowy Egrets; $G_3 = 2.4$, $P > 0.5$ for Tricolored Herons).

FOOD HABITS

In 1987, we collected 27 (total mass = 247.8 g) and 31 (total mass = 392.2 g) boluses from nestling Tricolored Herons and Snowy Egrets, respectively. Because of the diversity of prey types (> 30 species), we pooled all prey items that contributed < 10 g to the total prey mass into an "other" category. Consequently, the analysis included 7 prey types. For both Tricolored Herons and Snowy Egrets, *Poecilia latipinna* and *Fundulus confluentus* were the two most important species based on prey mass (Table 3). We found no differences between Snowy Egret's and Tricolored Heron's consumption of the 7 prey types using prey mass, prey number, or percent of bolus mass as dependent variables (repeated measures ANOVA, all $F_{1,56} < 2.45$, all $P > 0.12$). Thus, although habitat selection differed in 1987, Tricolored Herons and Snowy Egrets consumed similar prey.

DISCUSSION

SPATIAL SCALE AND RESOURCE PARTITIONING

All previous studies of the foraging ecology of Tricolored Herons and Snowy Egrets have determined at least one process by which the two species partition resources; however, conclusions regarding the methods of partitioning have varied according to the spatial scale of the investigation. Our use of a regional scale (the entire foraging area of an active colony) documented patterns of habitat selection not obvious in previous studies of wading bird ecology. During all three years of the study, we found significant differences in habitat selection between Tricolored Herons and Snowy Egrets. Although the specific habitat types selected by Tricolored Herons and Snowy Egrets will vary across studies, our results indicate that habitat selection must be quantified across the entire foraging range of the colony and over more than one breeding season to accurately address resource partitioning.

Obviously, no single spatial or temporal scale will be appropriate for assessing all ecological interactions; however, the scale at which the investigation is conducted must be addressed in the interpretation of the results (Meentemeyer 1989, Levin 1992). If species use several habitats across a heterogeneous landscape, studies confined to a single habitat or single breeding season may produce unrepeatable patterns or misleading impressions of their ecology (Wiens 1989). For example, Snowy Egrets tended to use inland or freshwater sites more than Tricolored Herons in

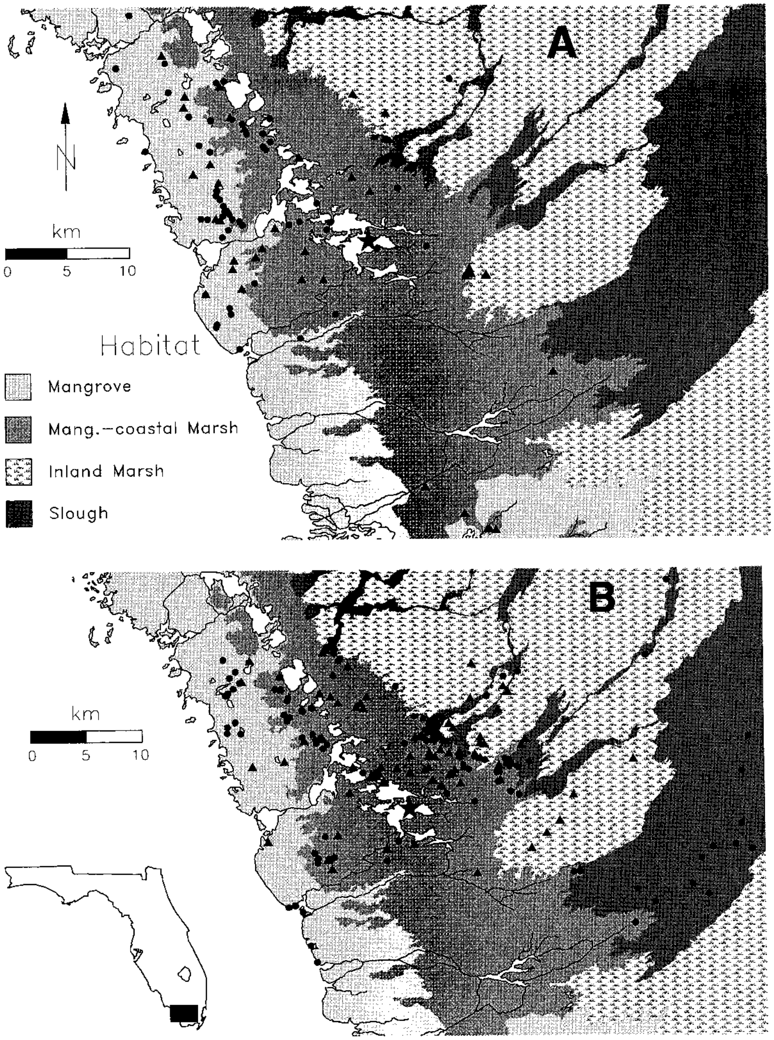

FIGURE 3. Foraging locations of Tricolored Herons (triangles) and Snowy Egrets (circles) breeding at the Rodgers River Bay colony (star) in (A) 1987 (n = 39 and 68, respectively) and (B) 1988 (n = 91 and 156, respectively).

coastal North Carolina (Custer and Osborn 1978a) and in Yucatán, Mexico (Ramo and Busto 1993). However in coastal New Jersey, no consistent segregation among freshwater and brackish habitats was found (Willard 1977). In brackish and marine environments of ENP, Snowy Egrets fed in more open habitats than Tricolored Herons (Recher and Recher 1980), whereas in Tampa Bay, Florida, Tricolored Herons used more open water habitats and Snowy Egrets fed more in tidal pools (Kent 1986). In freshwater habitats in north Florida, Tricolored Herons used the edges of deeper water habitats and Snowy Egrets fed primarily in open shallow habitats (Jenni 1969). These results emphasize the plasticity in habitat use shown by these two species. However, in most of these cases, resource partitioning may not have been accurately determined because either habitat use was quantified in an area less than that used by the entire colony and/or habitat use was not measured relative to available habitat. Although some questions may be better addressed at a local scale, our results suggest that fine scale habitat selection may not address resource partition-

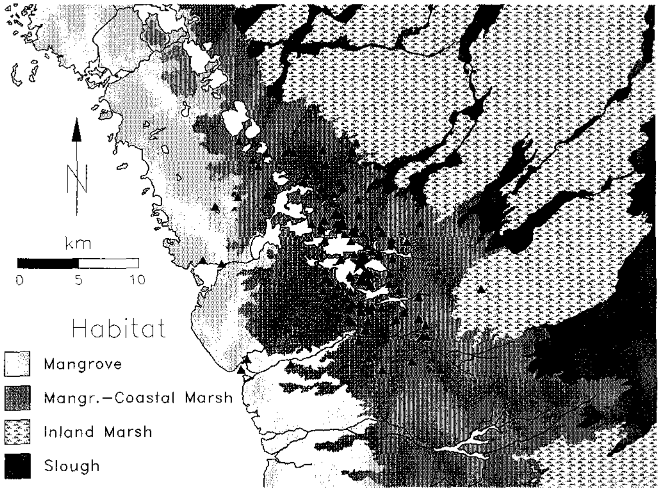

FIGURE 4. Foraging locations of Tricolored Herons (triangles, n = 135) breeding at the Rodgers River Bay colony (star) in 1989.

ing in Tricolored Herons and Snowy Egrets because coarser scale segregation has already occurred.

Similarly, use of foraging behaviors or prey selection may be inadequate axes to examine resource partitioning in Tricolored Herons and Snowy Egrets. Ciconiiformes have evolved a diverse array of foraging behaviors that enable them to take advantage of a variety of environmental conditions. Kushlan (1977) reported 38 different feeding behaviors used by Ciconiiformes of which 17 were used by Tricolored Herons and 20 by Snowy Egrets. The diversity of foraging behaviors suggests extreme opportunism (Meyerriecks 1962, Kushlan 1976, 1978), and implies that examination of resource partitioning through foraging behavior may be site-specific. For example, in northern Florida, Snowy Egrets were more active feeders than Tricolored Herons (Jenni 1969), whereas in Tampa Bay (Rodgers 1983, Kent 1986) and Florida Bay (Meyerriecks 1962), Tricolored Herons used more active foraging methods. In New Jersey, Snowy Egrets displayed a larger variety of behaviors than Tricolored Herons (Willard 1977), but in Tampa Bay, Tricolored Herons used slightly more diverse foraging behaviors (Rodgers 1983). Furthermore, differences in prey selection also are variable among studies. Kent (1986) found pronounced differences in prey selection between Snowy Egrets and Tricolored Herons, whereas others have found only moderate (Jenni 1969, Willard 1977) to slight differences (Ogden 1977, Kushlan 1978, Recher and Recher 1980). In our study, despite differences in habitat selection between the two species in 1987, prey use was similar. Our results indicate that in the Everglades, foraging behavior and prey selection may not be the most important mechanisms of resource partitioning in Tricolored Herons and Snowy Egrets because segregation through habitat selection has already occurred.

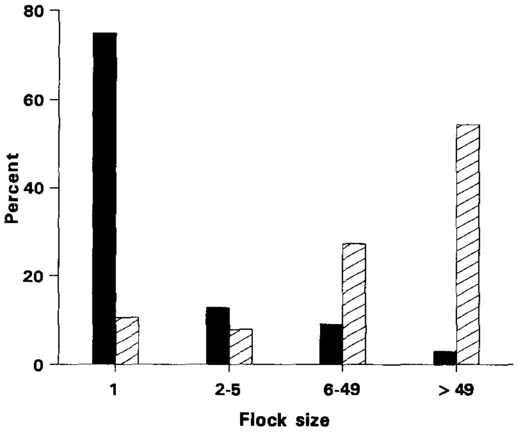

FIGURE 5. Percent of breeding Tricolored Herons (solid bars, n = 265) and Snowy Egrets (hatched bars, n = 214) found in four size categories of foraging flocks (1987–1989). Birds were either marked with radiotransmitters or followed from the Rodgers River Bay colony to the feeding site.

TABLE 3. Mean (± SE) number and percent of bolus mass for seven prey items in the boluses of nestling Snowy Egrets (SNEG, $n = 31$) and Tricolored Herons (TRHE, $n = 27$) at the Rodgers River Bay colony, 1987.

	Number		% bolus mass	
Prey item	SNEG	TRHE	SNEG	TRHE
Poecilia latipinna	7.4 ± 1.3	4.7 ± 1.1	49.7 ± 6.9	36.7 ± 7.2
Fundulus confluentus	1.4 ± 0.5	1.2 ± 0.3	11.8 ± 4.1	17.5 ± 4.5
Gambusia affinis	5.9 ± 1.5	5.9 ± 1.8	9.0 ± 1.9	13.3 ± 3.4
Anchoa spp.	3.6 ± 1.7	0.6 ± 0.4	13.3 ± 6.1	4.6 ± 3.2
Cyprinodon variegatus	0.5 ± 0.4	1.4 ± 0.6	0.7 ± 0.7	13.4 ± 5.1
Jordanella floridae	1.4 ± 0.4	1.0 ± 0.3	6.8 ± 3.4	6.9 ± 2.2
Other	3.7 ± 1.0	3.2 ± 0.8	8.6 ± 3.2	7.6 ± 2.7
Total bolus mass (g)			392.2	248.8

HYDROLOGIC CONSTRAINTS ON HABITAT SELECTION

Although habitat selection varied between the two species, our results suggest that annual variation in water levels had a greater effect on habitat selection than intrinsic differences between the species. Changes in water levels between years were correlated with significant shifts in direction flown to feeding sites, and consequently habitat selection. In 1987, when water levels were high in the freshwater marshes east of the colony, both species flew west to mangrove and mangrove–coastal marsh habitats. In 1988, when water levels were intermediate in depth, both species flew to habitats east of the colony. The shifts in flight direction and habitat selection between years were dramatic and more different than the differences between species in any given year.

The large spatial and temporal scales used in this study illustrate that even within a single geographic area, habitat selection is temporally variable and complex. However, our data support the hypothesis that variations in water level may not be as important in habitat selection for Tricolored Herons. Tricolored Herons did not show as extreme a shift to western mangrove habitats in 1987 when water levels were high, nor did they show selection for slough habitats when water levels declined in 1988. Also, the proportion of Snowy Egrets flying to the northeast, northwest, and southeast were more highly correlated with water level than they were for Tricolored Herons. Additionally, in this study when drought conditions existed in the foraging habitat around the colony in 1989, Tricolored Herons attempted to nest throughout the spring. However, Snowy Egrets abandoned their first nesting attempt and did not return to the colony site.

Differences between the species' responses to changing hydrologic patterns are most likely related to differential dependence on group foraging (Jenni 1969, Kushlan 1978, Smith 1995). Snowy Egrets have greater success feeding in large flocks than solitarily (Master et al. 1993) and are core species in the formation of large mixed-species feeding aggregations (Kushlan 1977, Caldwell 1981). These large feeding aggregations may require higher densities of food for initial formation. Foraging aggregations are ephemeral, changing as prey is depleted or becomes less available. This may explain why Snowy Egrets exhibited greater daily movements between feeding sites on consecutive days. Because they often feed in flocks of > 50 individuals, prey populations will deplete rapidly causing movements of individuals to other sites to find new food resources (Master 1989).

Although we occasionally observed Tricolored Herons feeding in large aggregations with other species of white wading birds, this was the exception. By feeding solitarily, Tricolored Herons may be better able to forage successfully at decreased prey densities (at least over short temporal scales) and thus may not be as closely tied to changes in water levels. Caldwell (1981) suggested that Snowy Egrets were dominant over Tricolored Herons in mixed-species flocks, which may make these flocks less attractive to Tricolored Herons. Additionally, landscape attributes of mangrove–coastal marsh habitat, which was selected by Tricolored Herons in 1988 and 1989, may not be suitable for large flocks of wading birds. Many of the ponds in this habitat type are small (< 30 m diameter) and may not support large foraging aggregations. Thus, as food resources become patchier during drought conditions, Tricolored Herons may be able to nest in conditions that Snowy Egrets may not be able to tolerate.

CONSERVATION RECOMMENDATIONS

The availability of food in the Everglades may be the single most important variable influencing nesting success (Frederick and Spalding 1994). The quality, quantity, and availability of food are determined by antecedent and current hydrological conditions (Loftus et al. 1990, Loftus and Eklund 1994). The greater shifts in habitat use and abandonment of this area during drought conditions by Snowy Egrets suggest that they may have stricter foraging requirements than Tricolored Herons. This was further supported in 1990 (another year of drought conditions) when moribund Snowy Egret nestlings were found at the Rodgers River Bay colony at the same time similar age, well-fed Tricolored Herons nestlings were present (Frederick et al. 1992). Apparently Tricolored Herons were finding sufficient food to successfully raise young, whereas Snowy Egrets were not. These differences in foraging requirements may explain why Snowy Egret populations appear to have been reduced more than populations of Tricolored Herons by Everglades degradation (Ogden 1994, 1996). Clearly, Everglades restoration will be important for the continuation of these two species as breeders in this ecosystem.

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