DISPERSAL AND HABITAT USE BY POST-FLEDGING JUVENILE SNOWY EGRETS AND BLACK-CROWNED NIGHT-HERONS

R. MICHAEL ERWIN, JOHN G. HAIG, J. DANIEL B. STOTTS, AND JEFF S. HATFIELD

ABSTRACT.—We studied the post-fledging dispersal movements and habitat use of juvenile Snowy Egrets (*Egretta thula*) (SNEG) and Black-crowned Night-Herons (*Nycticorax nycticorax*) (BCNH) in coastal Virginia using a dye (picric acid) and radiotelemetry. Results from monitoring radiomarked birds revealed significant differences both years between species, with SNEGs dispersing more widely than BCNHs. BCNH juveniles usually remained south of Delaware, but SNEGs often moved into Delaware and southern New Jersey. The maximum dispersal distance found for a SNEG was ca 340 km north of the natal colony. Temporal patterns of movement followed logistic relationships, with rapid initial movements, but relatively few movements after about 2–3 weeks for most birds. Cumulative distances moved by juvenile SNEGs during August-September differed from 1992 to 1993. No such year difference was found for BCNHs. Compared to SNEGs, BCNHs used manmade impoundments relatively more often than natural wetlands; however no quantitative assessment of habitat preferences could be made. *Received 25 May 1995, accepted 9 Dec. 1995*.

Little is known about survival, movements, or habitat use during the post-breeding period for most North American migratory birds (Finch and Stangel 1993). Even for large, conspicuous species such as colonial waterbirds, few quantitative dispersal data have been published. Numerous anecdotal reports indicate that many terns, gulls, and wading birds move northward along the coasts and large interior rivers of the United States after the nesting season. In some regions, the movement pattern is constrained by geography, with waterbirds often following major drainages (Gill and Mewaldt 1979) regardless of the cardinal direction or following a peninsula or island archipelago (e.g., in Florida, Powell and Bjork 1990, Strong and Bancroft 1994 on Great White Herons, Ardea herodias occidentalis). Studies of individual species revealed some extensive northward dispersal after breeding; e.g., Black-crowned Night-Herons (Nycticorax nycticorax) in the eastern United States (Bartsch 1952, Byrd 1978), Little Blue Herons (Egretta caerulea) in Mississippi (Coffey 1943) and elsewhere in the southeast (Townsend 1931), Great White Herons in Florida (Powell and Bjork 1990), and Cattle Egrets (Bubulcus ibis) in Africa (Siegfried 1970).

Studies of dispersal can yield information that has both basic and ap-

¹ National Biological Service, Patuxent Environmental Science Center, Laurel, Maryland 20708.

² Present address: 59 Ramona, San Francisco California 94103.

plied value. Better estimates of movement rates, habitat use, and mortality for most migrant species would assist in developing population viability analyses that are currently in demand for threatened or endangered species. Further, determining levels of site fidelity and identifying habitat types used during dispersal could have immediate management implications.

In this study, we followed movements during dispersal of juvenile Snowy Egrets (hereafter SNEGs) and Black-crowned Night-Herons (hereafter BCNHs) to address the following questions: (1) How do young birds move during the post-fledging period? Are there differences between species and years? (2) How much site fidelity do birds show during repeated observations? (3) What types of habitats do the species use during this period, and are there species differences?

STUDY AREA AND METHODS

We studied nesting ecology of two mixed-species colonies near the town of Chincoteague, Accomack County, Virginia (Fig. 1). The colonies are located in *Iva frutescens* shrubs along the margins of a saltmarsh island complex. The Causeway Colony, the largest in Virginia (Erwin et al., in press), had 230–640 SNEGs and 32–37 BCNHs in 1992–1993 in addition to large numbers of five other species. The Willis Colony had 300–390 SNEGs and 47–90 BCNHs in the two years and also included other wader species.

The habitat surrounding the colonies consisted of natural *Spartina* saltmarshes, creeks, and pannes, as well freshwater ponds and large impounded brackish marshes at the Chincoteague National Wildlife Refuge to the east.

Radio telemetry.—When nestlings were approximately two weeks old, we fixed 10 g radio transmitters to aluminum U.S. Fish & Wildlife Service bands and attached the package above the tarsometatarsal joint (see Erwin et al., in press). Radios were equipped with a mortality sensor that resulted in a 50% increase in pulse rate when the radio remained stationary for 12 h. The transmitters had a range of about 1–2 km on the ground and 5–18 km from aircraft depending on altitude and habitats. The battery life was rated at three months. We attached the radiotransmitters only to the largest chicks (presumably the A chick) in the brood to insure that we would have a reasonable sample size for monitoring post-fledging movements. We used radios only at the Causeway colony. A total of 10 and 19 radiomarked BCNHs fledged in 1992 and 1993, respectively (of totals of 10 and 20 initially marked); for SNEGs, the comparable figures were 19 and 20 (of totals of 20 initially marked both years).

In late July, when most young were fully feathered and capable of short flights (age 40–50 d), we conducted radio checks of the colonies 2–5 times weekly to estimate fledging age and to determine when to begin broader surveillance for dispersing individuals. During the initial period (1–2 weeks) after fledging, we concentrated our searches by vehicle and boat in the Chincoteague vicinity, especially on the Chincoteague National Wildlife Refuge about 6 km to the east. We began airplane surveys after all the birds had fledged. We made four flights between 12 August and 24 September in 1992 and six flights between 27 July and 2 October in 1993. We followed a regular search pattern that included the coastal areas of the DelMarVa peninsula and Delaware Bay. The basic route followed the Chesapeake shore of the peninsula from Cambridge, Maryland south to Cape Charles, Virginia, continued north along the Atlantic shore of the peninsula into Delaware Bay up to the Chesapeake

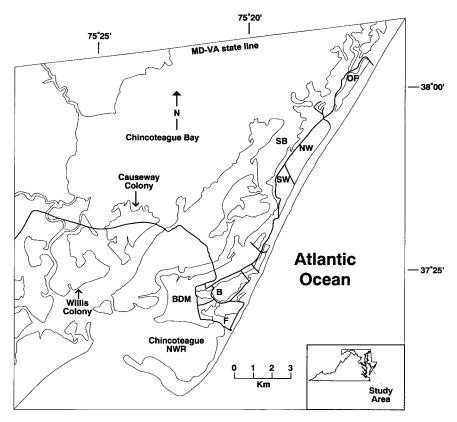


Fig. 1. Study area in coastal Virginia showing the south end of Assateague Island National Seashore, including Chincoteague National Wildlife Refuge, and two colony sites.

and Delaware (C and D) Canal, and finished along the New Jersey shoreline from Salem to Cape May. We made additional searches 1–2 times each year up the Delaware River to an area 10 km N of Philadelphia, and along the Atlantic shoreline of New Jersey from Cape May north to Manasquan. We made two flights in each year on the Chesapeake Bay side of the peninsula north of Cambridge to the C and D canal. On 1 October 1993, we made one search along the western shore of Chesapeake Bay from the lower Patuxent River south to the mouth of the James River in Virginia. Our search route and the limited range of the transmitters could have introduced some bias because we did not survey (except once) the western shore of Chesapeake Bay, nor did we effectively survey the interior of the peninsula. Funding and time precluded more exhaustive surveys. Nonetheless, species comparisons are still meaningful.

During aerial surveys, we usually maintained an altitude of 500–1000 m, scanning for birds with strut-mounted Yagi antennae. Upon detecting a signal, we circled to determine a location for the individual and identified a landmark (e.g., a named creek or impoundment) whenever possible. We recorded locations on maps, and later converted them to UTM coordinates. Because the precision of location was probably ±0.5 km, we used the center of

a large impoundment for the UTM coordinate when appropriate. All wetland locations were identified as either natural or manmade (ponds or impounded marshes).

Colormarking.—Just before most young SNEGs in the colonies fledged, we conducted a "roundup" with 7–12 participants. We held captured birds in wooden duck crates, dyed them with picric acid on the wings and back, and banded each prior to release. We marked 123 SNEGs in 1992 and 182 in 1993. After marking the birds, we continued to monitor the colonies for at least two weeks to record survival of radiomarked young and to look for any moribund or dead dyed birds. We dyed egrets in both the Causeway and Willis colonies.

To stimulate the reporting of colormarked egrets by the public and colleagues in other natural resource agencies, we sent information packages to national wildlife refuges, parks, state wildlife management areas, and state wildlife administrations from New Jersey to North Carolina. We also sent releases to a number of newspapers and magazines in the DelMarVa region. We solicited the following information: date, time, name of wetland used by the bird, wetland type, nearest town/village, band colors (if applicable), and size of associated group. Upon receiving a report, we converted map locations to UTM coordinates and, whenever possible, recorded the type of wetland used (impoundment, pond, creek).

Statistical tests.—We used the Multi-Response Permutation Procedure (MRPP) to test for large-scale differences in spatial distributions between species and years (Biondini et al. 1988). The MRPP compares the distribution of one group of points to another group using a permutation procedure (Manly 1991) and tests whether the two distributions are identical. We used this test only on the radio locations determined for birds that had left the Chincoteague vicinity. Locations reported for colormarked birds were biased because of the overrepresentation of sightings at public-access wetlands (e.g., refuges). These sightings were valuable, however, because they revealed locations that were not included in our aerial survey route.

To further investigate movements of the two species, we computed the number of relocations, total number of different wetlands used, and the cumulative distance (km) moved during the entire tracking period for each individual. Because of some locational imprecision when conducting aerial searches, we did not record a "new location" from a radiomarked bird unless it had moved ca 1–2 km from its previous location.

Because sampling intensity and duration differed between years (four aerial surveys over 6 weeks in 1992, six surveys over nine weeks in 1993), we selected a subset of radiomarked birds for standardized periods. To permit a reasonable time period for dispersal, we used data for only those individuals (N = 33 out of 48) resighted at least two times and followed at least 30 days from the time they left the colony site. After examining the raw data plots for each bird, we applied the logistic model for describing cumulative distances. The majority of individuals for which we had more than five observations revealed a sigmoidal (logistic) pattern in distances moved. We fit a separate 3-parameter logistic curve (Draper and Smith 1981) to each individual (using PROC NLIN procedure in SAS). From each of these logistic curves, we estimated the cumulative distances travelled by Day 5, 15, 30, 45, and 60. Next, to test for species and year effects, we conducted two-way ANOVAs on the cumulative distance variables for Days 5, 15, 30, 45, and 60 with Tukey tests to discern pairwise differences.

We wanted to determine gross habitat preferences for each species by comparing use of natural wetlands and manmade impoundments or ponds. However, because of our limited (coastal edge) search route and the difficulty in obtaining wetland area on the local (county) scales, we were unable to assess habitat preferences. Instead, we compared the number of individuals of each species found in the two types of habitats, and also the total number of the two wetland types used (regardless of how many individuals used them).

Table 1
SUMMARY OF NUMBERS OF JUVENILE SNOWY EGRETS (SNEG) AND BLACK-CROWNED NIGHT-
HERONS (BCNH) RADIOMARKED IN 1992 AND 1993 AT CHINCOTEAGUE, VIRGINIA

Species	Year	No. marked that fledged	No. censored ^a	Local relocation ^{b.c}
SNEG	1992	19	2	10
	1993	20	6	6
	Total uncensored		31	
BCNH	1992	10	0	9
	1993	20	1	15
	Total uncensored		29	

a Not relocated.

RESULTS

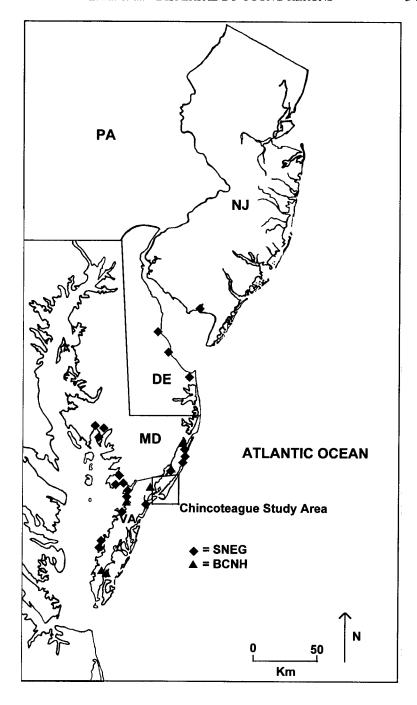
Dispersal.—From an earlier analysis, we found that juveniles fledged and left the colony when they were between 53 and 58 days old (Erwin et al., in press). Of the 29 and 39 radiomarked juveniles in 1992 and 1993, respectively, 19 and 21 individuals were recorded at least once in the wetlands within about 10 km of the nesting colony. Birds usually returned to the vicinity of the colony site at least once, or moved to the Chincoteague National Wildlife Refuge, about 6-10 km east of the colonies (Table 1). We found more juvenile BCNHs at least once in the local area (24/29 or 83%) than juvenile SNEGs (16/31 or 52%; $\chi^2 = 6.54$, P = 0.011). The remainder (as well as later dispersers from the Chincoteague vicinity) dispersed primarily to the north, but also west and south (Figs. 2, 3, and 4). We never located a few of the fledglings (=censored observations, Table 1); in 1992, we never located two SNEGs after fledging, whereas in 1993, we failed to locate one BCNH and six SNEGs. In 1992, SNEGs moved north into Delaware and New Jersey, whereas BCNHs were confined to Maryland and Virginia. Delaware Bay seemed to act as a partial barrier, with few birds crossing the bay into New Jersey. We received 99 reports of colormarked individual SNEGs, the majority from the Chincoteague National Wildlife Refuge. These sightings added a few new locations in 1992, with the northernmost bird reported from

^b Relocated at least once in the Chincoteague-S. Assateague Island block (Chincoteague National Wildlife Refuge) after fledging from colony.

^cChi-square test for local vs nonlocal relocation by species (using uncensored totals): $\chi^2 = 6.54$, P = 0.011.

⁻

Fig. 2. Locations of radiomarked Snowy Egrets and Black-crowned Night-Herons in 1992 during August-September.



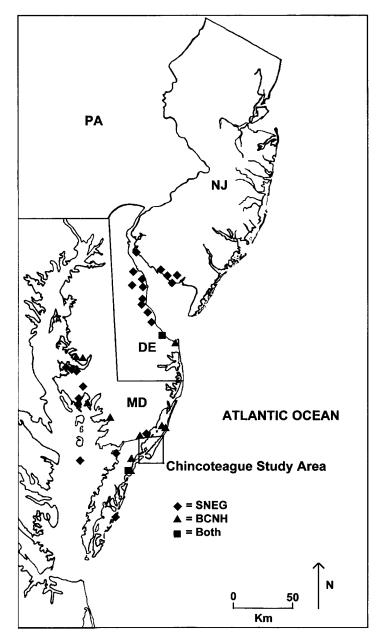


Fig. 3. Locations of radiomarked Snowy Egrets and Black-crowned Night-Herons in 1993 during late July-early October. All locations outside the Chincoteague block (nesting colony locale) are shown.

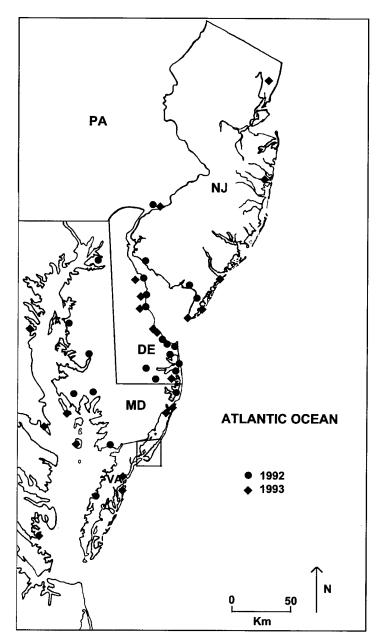


Fig. 4. Locations of dye-marked Snowy Egrets in 1992 and 1993. If two different symbols abut each other, the same location is indicated.

TABLE 2
SUMMARY OF MULTI-RESPONSE PERMUTATION PROCEDURE^a COMPARING SPATIAL PATTERNS OF DISPERSING SNOWY EGRETS (SNEG) AND BLACK-CROWNED NIGHT-HERONS (BCNH), 1992

AND 1993

Comparison	P Value	
Radiomarked:		
SNEG 92 vs 93	< 0.001	
BCNH 92 vs 93	0.02	
SNEG vs BCNH (1992)	0.01	
SNEG vs BCNH (1993)	< 0.001	
Dye-marked:		
SNEG 92 vs 93	0.18 ns	
Dye vs radiomarked (SNEG):		
1992	0.002	
1993	0.09 ns	

^a See Biondini et al. 1988.

the Tinicum National Wildlife Refuge south of Philadelphia about 210 km from the nesting colony (Fig. 3).

In 1993, both species generally dispersed slightly greater distances (cf Figs. 2, 3, and 4) and, the number of "lost" (censored) birds also increased. The radiomarked BCNHs moved north into Delaware, and more SNEGs were found farther north in New Jersey (Figs. 2 and 3). In 1992, no dyed SNEGs were reported west of the Chesapeake Bay, but three were seen in 1993 (Fig. 4). A total of 141 colormarked SNEGs were reported in 1993, mostly from the Chincoteague area. Also, we received a report of a dyed SNEG from far northern New Jersey in Lyndhurst, near the extensive tidal Hudson River wetlands known as the Meadowlands (Fig. 4). This location is 342 km north of the nesting colonies. In contrast, the longest distances recorded for radiomarked BCNHs were only 85 km in 1992 and 102 km in 1993.

Spatial pattern.—MRPP test results revealed significant differences (*P* < 0.05) for comparisons between years within species and between species within years for the radiomarked birds (Table 2). Dye-marked SNEGs showed no yearly difference, but their distribution was significantly different from radiomarked SNEGs in 1992 (Table 2). Although the MRPP test reveals that both species and yearly "geographic centroids" differed, the test does not indicate how the patterns differed.

Temporal pattern of dispersal.—We found a high degree of variability among individual SNEGs and BCNHs during both years of the study. A

TABLE 3
SUMMARY OF DISPERSAL MOVEMENT OF JUVENILE SNOWY EGRETS (SNEG) AND BLACK-CROWNED NIGHT-HERONS (BCNH) DURING LATE SUMMER, 1992 AND 1993

Group	Year	Na	Day ^b	Mean cum. distance ^c (±SD)	Mean total relocations ^d	Mean no. different locations ^e
SNEG	1992	11	5	37.2 (30.2)		
			15	50.6 (35.6)		
			30	52.5 (39.4)		
			45	52.5 (39.4)		
			60	52.5 (39.4)		
		Total			4.3	3.9
SNEG	1993	8	5	97.0 (66.7)		
			15	121.3 (61.5)		
			30	121.3 (61.5)		
			45	121.3 (61.5)		
			60	124.9 (53.9)		
		Total			6.1	4.4
BCNH	1992	6	5	17.5 (14.2)		
			15	18.4 (13.3)		
			30	21.3 (11.4)		
			45	28.1 (14.4)		
			60	44.2 (37.3)		
		Total			16.2	5.0
BCNH	1993	8	5	40.6 (47.2)		
			15	44.1 (45.1)		
			30	44.3 (44.9)		
			45	44.8 (44.4)		
			60	44.8 (44.4)		
		Total			4.3	3.0

^a Only birds followed for >30 days, with two or more locations, were included in the analysis.

few individual herons and egrets made return trips to the Chincoteague vicinity after short dispersals, while most moved increasing distances from the colony vicinity. The general pattern was for an initial move to local wetlands near the colony site and at the Chincoteague NWR. From here, a rapid movement occurred during the next 1–2 weeks, with less movement afterward (Table 3, Fig. 5). In both years, individuals of both species moved relatively little after about 30 days, with many individuals

^b To adjust for sampling intensity differences between years, values for specific numbers of days since colony departure (i.e., 5, 15, 30, 45, and 60) were predicted from the logistic curve for each bird.

^c Means of cumulative distances moved by individuals from the colony site (origin), based on predictions from individual logistic curves.

^d Mean number of relocations per individual during ground and air surveys in 1992 and 1993.

^e Mean number of different wetland locations per individual during surveys. Because of locational uncertainty from aerial surveys, a "move" to a new location required an estimated 1-2 km actual relocation.

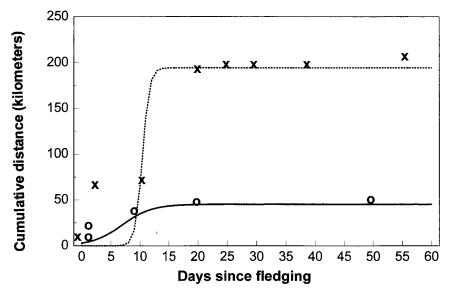


Fig. 5. Examples of cumulative distances moved over time by individual Snowy Egrets since fledging (1992 solid line, 1993 dotted line). Predicted logistic curves were generated using a three-parameter logistic equation. Symbols represent actual location distances for two individuals.

remaining in the same wetland complex (see last column in Table 3). Extreme cases in 1992 included a BCNH that spent 73 days in an impoundment at Chincoteague NWR from August 3 to October 14 (24 total relocations) and a SNEG that spent 24 days in a marsh also at Chincoteague NWR (9 relocations). In 1993, a BCNH spent 57 days (July 21 to September 15) at the same location as the previous year (13 relocations) and a SNEG spent 53 days from August 10 to October 1 at Fortesque Wildlife Management Area on the Delaware Bay shore of New Jersey.

We found several significant differences in the cumulative distances moved by dispersing birds (Table 4). For SNEGs, individuals averaged more than twice the cumulative distance in 1993 than in 1992, whereas BCNHs showed no year effect. Also, in 1993, we found a significant species effect (Tables 3 and 4).

Habitat use.—More birds of both species used natural wetlands than manmade ones (Table 5); however, habitat availability could not be assessed for the study area (see Methods). BCNHs were associated with manmade wetlands relatively more often than SNEGs in both years (Table 5). Because manmade impoundments only comprise a small fraction (15% in Delaware) of the total area of coastal estuarine emergent wetland in

TABLE 4

DIFFERENCES IN CUMULATIVE DISPERSAL DISTANCE BETWEEN SNOWY EGRETS (SNEG) AND BLACK-CROWNED NIGHT-HERONS (BCNH) IN 1992 AND 1993*

Comparison	Day	Difference between means (km)	Significance level (P < 0.05)
SNEG, 1992–1993	5	59.8	*
•	15	70.7	*
	30	68.9	*
	45	68.9	*
	60	72.4	*
BCNH, 1992-1993	5	23.1	ns
	15	25.7	ns
	30	23.1	ns
	45	16.7	ns
	60	0.6	ns
1992, SNEG-BCNH	5	19.7	ns
	15	32.2	ns
	30	31.2	ns
	45	24.4	ns
	60	8.3	ns
1993, SNEG-BCNH	5	56.4	ns
	15	77.2	*
	30	77.0	*
	45	76.6	*
	60	80.1	*

^a Two-way ANOVAs performed on cumulative distances at each predicted day, with Tukey multiple comparison test results. The corresponding one-way reparameterized ANOVAs with Tukey tests were used for interaction terms.

TABLE 5
HABITAT USE OF YOUNG RADIOMARKED BCNHs AND SNEGS IN THE DELMARVA REGION DURING THE DISPERSAL PERIOD (AUGUST—SEPTEMBER, 1992 AND 1993)

		Number using habitat:a	
Species	Natural	Impounded	Total
BCNH			
1992	14 (11)	11 (9)	25 (20)
1993	18 (15)	7 (10)	25 (25)
SNEG			
1992	30 (22)	4 (7)	34 (29)
1993	27 (12)	4 (6)	31 (18)

^a First number listed is the number of locations in that habitat type with one or more individuals; in parentheses is the number of individual birds using these habitats. An individual may be counted more than once if it was found in more than one wetland.

our region, our results suggest that BCNHs may show some preference for manmade over natural wetlands.

DISCUSSION

Dispersal pattern.—The MRPP test results suggest that juvenile SNEGs and BCNHs disperse in somewhat different ways, with SNEGs more free ranging (see Figs. 4–5). The greater tendency for BCNHs to remain in the local region of their natal colony is reflected by the high frequency with which we located individual BCNHs within the Chincoteague region in both years (Table 1).

Reports of the dye-marked SNEGs indicated that our radiomarking data were probably underestimating the overall movements of birds. At least one dye-marked SNEG was found 342 km north of the natal colony (about 130 km farther than the farthest radiomarked individual and well beyond the 240 km northward extent of our aerial surveys). Reports of dye-marked SNEGs also were reported from the southwestern shore of the Chesapeake Bay in 1993, an area beyond our normal aerial search route. Perhaps the censored birds rapidly left our DelMarVa search area. However, radiotelemetry studies are often plagued by a failure to distinguish radio failures from movements beyond the survey area.

The results from our dyed egrets and those from studies in southern New Jersey (W. Crans, Rutgers Univ., unpubl. data), from which SNEGs moved into southern New England after dispersal, suggest that SNEG dispersal is greater northward than our telemetry results suggests.

Both species showed a rapid initial movement away from the natal colony area, but made relatively restricted movements thereafter, resulting in a logistic relationship for cumulative distance traveled. Such a pattern may result from local depletion of prey resources during the long nesting period in the colonies. Others have noted a similar movement pattern. Powell and Bjork (1990) found that most radiomarked juvenile Great White Herons in Florida Bay rapidly moved north from the Bay to central Florida in summer. Strong and Bancroft (1994) described a rapid (>20 km the first 10 days) northward dispersal of young White-crowned Pigeons (*Columba leucocephala*) from the Florida Keys. Immature Spanish Imperial Eagles (*Aquila adalberti*) also make long solo flights soon after leaving the natal area (Gonzalez et al. 1989).

Variable water conditions may have contributed to yearly differences in dispersal by juvenile SNEGs. In 1993, the eastern shore region of Virginia suffered from a severe drought (B. Truitt, pers. comm.). Unlike the wetter conditions in 1992, by late July and early August 1993 during the wading bird dispersal period, most of the impoundments at the Chincoteague NWR were dry. This may explain why the cumulative distances

of radiomarked SNEGs averaged more than twice as far in 1993. Snowy Egrets seem to search widely for other wading birds and often concentrate in "drawdowns" in impoundments and tidal pools (Kushlan 1978, Erwin 1983). We received a report of seven dyed SNEGs in one salthay impoundment in New Jersey in August 1993 (W. Crans, unpubl. data). BCNHs, in contrast, are more generalized in feeding habitat use (Davis 1993). Because they may use freshwater ponds and creeks as well as tidal areas, they probably do not have to move as far to find adequate food.

Habitat use.—Habitat selection during the post-breeding dispersal phase for juveniles could not be fully evaluated since we lacked quantitative estimates of wetland types for our limited survey region. The general pattern seemed to show a tendency for BCNHs to use impounded areas, including both farm ponds and large wildlife impoundments, to a greater relative extent than did SNEGs.

Data on movements of juvenile Great White Herons in central-south Florida (Powell and Bjork 1990) suggested a seasonal component to habitat selection. Early and late in the season, birds seemed to settle into human-modified habitats towards the central part of the state, whereas during the middle period, they traveled shorter distances and settled into natural marshes in the southern Everglades. Gill and Mewaldt (1979) described the dispersal patterns of SNEGs and BCNHs leaving a south San Francisco Bay heronry. Both species followed nonrandom patterns, with BCNHs following the Bay edge and tributaries, while SNEGs mostly moved <50 km to the "nearest appropriate habitats." The farthest distance travelled by a SNEG in their study was 209 km from the natal colony. Neither of these studies addressed the issue of habitat use versus availability.

For young inexperienced juveniles, a critical ecological factor may be locating a concentrated source of prey, whether it be a small sewage treatment lagoon, a large impoundment, or a natural drying freshwater slough (Kushlan 1978, Powell and Bjork 1990). Site tenacity seemed to be high for many radiomarked individuals, with an average of only 3–5 different locations per species-year group (Table 3). Variation in the amount of time specific sites were used was enormous, ranging from one to 73 days at Chincoteague NWR.

ACKNOWLEDGMENTS

We thank John Schroer and his staff at Chincoteague National Wildlife Refuge, for the field logistical support, and the many volunteers (including Jason and Lindsay Erwin and David Jachowski) who assisted. W. Link helped with statistical advice, K. Fontaine assisted in preparing the manuscript, and M. Banker and K. Boone provided graphics help. C. Blem, T. Custer, C. Henny, J. Smith, and B. Watts provided useful comments on earlier drafts of the manuscript.

LITERATURE CITED

- BARTSCH, P. 1952. A note on the first bird banding in America. Bird-Banding 33:59-60.
- BIONDINI, M. E., P. W. MIELKE, JR., AND K. J. BERRY. 1988. Data-dependent permutation techniques for the analysis of ecological data. Vegetatio 75:161–168.
- BYRD, M. A. 1978. Dispersal and movements of six North American ciconiiforms. Pp. 161–185 in Wading birds (A. Sprunt, IV, J. C. Ogden, and S. Winckler, eds.) National Audubon Society Rept. No. 7, New York, New York.
- COFFEY, B. B., JR. 1943. Post-juvenal migration of herons. Bird-Banding 14:34-39.
- DAVIS, W. E. 1993. Black-crowned Night-Heron. Pp. 1–20 in The birds of North America, No. 74 (A. Poole and F. Gill, eds.) The Academy of Natural Sciences, Philadelphia and The American Ornithologists Union, Washington, D.C.
- Draper, N. R. and H. Smith. 1981. Applied regression analysis. 2nd edition. J. Wiley and Sons, Inc., New York, New York.
- ERWIN, R. M. 1983. Feeding habitats of nesting wading birds: spatial use and social influences. Auk 100: 960-970.
- ——, J. G. HAIG, D. B. STOTTS, AND J. S. HATFIELD. 1996. Growth, nest success, and survival of Black-crowned Night-Heron (*Nycticorax nycticorax*) and Snowy Egret (*Egretta thula*) chicks in coastal Virginia. Auk (in press).
- FINCH, D. M. AND P. W. STANGEL. 1993. Status and management of neotropical migratory birds. Gen. Tech. Rep. RM-229, Rocky Mountain Exper. Sta., U.S. Forest Service, Ft. Collins, Colorado.
- GILL, R., JR. AND L. R. MEWALDT. 1979. Dispersal and migratory patterns of San Francisco Bay produced herons, egrets, and terns. North Amer. Bird Bander 4:4–13.
- Gonzalez, L. M., B. Heredia, J. L. Gonzalez, and J. C. Alonso. 1989. Juvenile dispersal of Spanish Imperial Eagles. J. Field Ornithol. 60:369–379.
- KUSHLAN, J. A. 1978. Feeding ecology of wading birds. Pp. 249–298 in Wading birds (A. Sprunt, IV, J. C. Ogden, and S. Winckler, eds.) National Audubon Society Rept. No. 7, New York, New York.
- Manly, B. F. T. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, New York, New York.
- POWELL, G. V. N. AND R. BJORK. 1990. Studies of wading birds in Florida Bay: a biological assessment of the ecosystem. National Audubon Society report to the E. Ordway Dunn Foundation, National Audubon Soc., Tavernier, Florida.
- SIEGFRIED, W. R. 1970. Mortality and dispersal of ringed Cattle Egrets. Ostrich 41:122–135.
- STRONG, A. AND G. T. BANCROFT. 1994. Postfledging dispersal of White-crowned Pigeons: implications for conservation of deciduous seasonal forests in the Florida Keys. Conserv. Biol. 8:770-779.
- TOWNSEND, C. W. 1931. The post-breeding northern migration of North American herons. Proc. Intern. Ornithol. Congr. 7:366–369.