

## REPRODUCTIVE SUCCESS, GROWTH AND SURVIVAL OF BLACK-CROWNED NIGHT-HERON (*NYCTICORAX NYCTICORAX*) AND SNOWY EGRET (*EGRETTA THULA*) CHICKS IN COASTAL VIRGINIA

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**ABSTRACT.**—We studied reproductive success, growth, and survival of Black-crowned Night-Heron (*Nycticorax nycticorax*) and Snowy Egret (*Egretta thula*) chicks in two mixed-species heronries on marsh islands in Chincoteague Bay, Accomack County, Virginia in 1992 and 1993. We attached radio transmitters with mortality sensors to the oldest chicks (A-chicks) in 11 to 22 nests of both species to monitor survival during the mid- to late nestling period and into the postnesting dispersal period. For both species, we found significant differences between 1992 and 1993 in growth rates and survival. Mass growth rates of chicks were higher in 1993 than in 1992 for both species. Culmen-length growth rates varied significantly due to year-colony effects for night-herons, but only for hatching order for egrets. Differences in survival rates due to hatching order were found for the egrets in both years, but were found only in 1992 for night-herons. As with mass growth rates, survival of chicks was higher in 1993 than 1992. Survival of radio-marked A-chicks did not differ between species or years for the period from hatching to fledging or from fledging through the end of the study (ca. two months postfledging). Survival ranged from 0.80 to 1.00 from the time radio transmitters were attached (ca. two weeks of age) until dispersal age (53–55 days for egrets; 55–60 days for night-herons). After birds left the colony, survival rates were lower during the next 40 to 55 days, ranging from 0.25 to 0.60. These results suggest that, at least for Snowy Egrets, A-chicks may be buffered from annual variations in food conditions, but that growth and survival of other brood members may provide a barometer of local conditions. Despite problems of variability in measurement, some of these parameters show promise as bioindicators of estuarine conditions. We recommend that a cost-efficient wading-bird monitoring program would include: (1) estimating numbers of nesting birds of selected species (e.g. Snowy Egrets) at particular estuaries, and (2) monitoring “initial brood sizes” and survival of young to at least two weeks of age in a sample of nests for each focal species. However, additional biomonitoring (e.g. marsh forage fish, contaminant loads) is necessary to evaluate how well top trophic-level organisms such as fish-eating birds respond to changes in estuarine production or quality. Received 12 December 1994, accepted 18 March 1995.

RELIABLE BIOLOGICAL INDICATORS are being sought by a number of federal and state agencies to monitor estuarine ecosystem health and integrity (Gray 1980, Diamond and Filion 1987, Fox and Weseloh 1987, Peakall and Shugart 1993). Colonially nesting wading birds (Ciconiiformes) have been identified as one potential bioindicator group by a number of researchers (Custer and Osborn 1977, Kushlan 1993, Parsons 1994, Custer in press, Erwin and Custer in press), although others (Morrison 1986, Temple and Wiens 1989) have expressed reservations about the usefulness of birds as environmental indicators.

As part of an evaluation of wading birds as

indicators, we investigated the reproductive success, growth and survival of young Black-crowned Night-Herons (*Nycticorax nycticorax*) and Snowy Egrets (*Egretta thula*) at two salt-marsh colonies in coastal Virginia in 1992 and 1993. Nesting studies have been done on these species in other areas (e.g. Frederick and Collopy 1989a, b, Custer and Peterson 1991, Frederick et al. 1992, Parsons 1994), thus providing a basis for year and geographic comparison. These other studies, however, were not designed to evaluate how survival relates to growth and success, since investigators did not follow birds through the entire nesting period (but see Frederick et al. 1993), nor did they attempt to

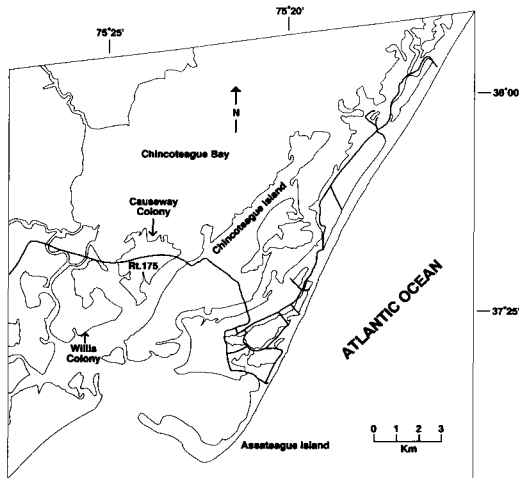


Fig. 1. Location of nesting colonies in Chincoteague Bay, Accomack County, Virginia.

determine survival rates beyond the fledging period. This is a major gap in the demography of almost all migrant bird species, although some recent data exist for a few other waterbirds, including Roseate Spoonbills (*Ajaia ajaja*; Bjork and Powell 1994) and Great White Herons (*Ardea herodias occidentalis*; Powell and Bjork 1990) in Florida.

Our objectives focused on the following major questions: (1) How closely coupled are reproductive success, growth rates, and survival of young for the two species of wading birds? How sensitive are they to annual changes? (2) Which species and nesting parameters might be useful and cost effective in a biomonitoring program?

#### STUDY AREA AND METHODS

We conducted our studies at two large mixed-species heronries (800 to 2,000 nests) on marsh islands near Chincoteague, Accomack County, Virginia (37°56'N, 75°25'W) in 1992 and 1993 (Fig. 1). In 1992, we restricted our study to the northern colony (Causeway site), but in 1993 expanded the study to include the southern (Willis site) colony. Since ardeid nests are most susceptible to disturbance in the nest-building to egg-laying stage (Tremblay and Ellison 1979), we limited our visits to one early in the period (mid-May) and then one or two per week from late incubation (>23 May) onward. During late incubation, we marked 20 to 45 egret and night-heron nests with plastic vinyl flagging in marsh elder (*Iva frutescens*) shrubs, and checked nests once or twice weekly. Chicks were marked on the tarsus with pieces of colored pipe

cleaner and on body down with small amounts of brightly colored fingernail polish for individual identification. Aluminum leg bands and radio transmitters were attached (see section on late-nesting-period survival) when the birds' tarsi were of sufficient size (8 to 14 days) to retain an adult-sized band. We assigned hatching orders to chicks based on observed hatching dates or, for unknown dates, we used relative size (length of the bird's culmen; Custer and Peterson 1991). A-chicks were the first hatched, B-chicks the second hatched, and so on, through E-chicks. Chicks were followed only if they were seen alive at least once.

*Nest success.*—To sample nests in close to a random manner, we selected study nests from 6 to 10 areas of the colonies each year. We then compared the average clutch size and average "initial brood size" (i.e. number hatched) for each species by year. We used Fisher's exact test (Lehmann 1975) with Monte-Carlo *P*-value estimate statistics (Cytel 1991) to test for differences between years.

The traditional Mayfield method for estimating nest success (Mayfield 1975, Hensler and Nichols 1981) was not appropriate to use in our study. Instead, nest success was calculated in two ways. First, we compared the number of birds per nest that survived 14 days (i.e. the age up to which we were certain of finding all young on a visit); second, we compared the number of successful (i.e.  $\geq 1$  chick survived 14 days) versus unsuccessful nests using Fisher's exact tests. Since brood size had a significant effect on the number of chicks surviving to 14 days (see Results), we analyzed the difference in the number of chicks surviving to 14 days for nests in which at least one chick hatched for each brood size. "Initial brood size" was defined as the total number of chicks known to have hatched in a nest. All chicks were included, regardless of whether their hatching dates were known precisely. When we found chicks whose hatching (or pipping) was not observed, we estimated the age/hatching date by comparing culmen length to Custer and Peterson's (1991) equation and by comparing the chick's initial size to those of its siblings. Sample sizes for most brood sizes were unequal for the two years. Only for brood sizes of three for both species in both years were there sufficient samples to make meaningful comparisons; however, we analyzed all brood sizes, using Fisher's exact test with Monte-Carlo *P*-value estimates (Cytel 1991). Thus, comparisons with small numbers of nests may not be very powerful. If it is assumed that a random sample of brood sizes in both years was obtained, we can combine all brood sizes and evaluate whether the average number of chicks produced per nest is the same in both years for both species.

*Growth rates.*—On each visit, we measured chick mass (to nearest 0.1 g) using an Ohaus electronic balance that was calibrated daily. We also measured culmen length (to nearest 0.1 mm) from the edge of the

feathers to the tip of the culmen. Birds whose exact hatching dates were unknown were excluded from the analyses. In addition, to insure a linear relationship, we followed Custer and Peterson's (1991) methodology of only including measurements from birds between ages 5 and 18 days when calculating age-mass relationships, and between ages 3 and 18 days for calculating age-culmen relationships. To avoid autocorrelation, we calculated individual chick growth slopes for the relationships between mass and age, and between culmen length and age. Any bird with two or more measurements in the age period of interest was included in the study regardless of whether the bird survived or died; hence, some negative growths were recorded (i.e. mass losses). Means were then generated for individual results. For each species separately, we conducted two-way ANOVA and Tukey tests (Sokal and Rohlf 1981) to assess year-colony and hatching-order effects, with interaction terms. When we compared growth rates for both parameters for both species between colonies in 1993, no significant model effects were obtained (in ANOVA, all  $P > 0.05$ ); therefore, any differences found were judged to be year effects.

*Survival.*—Because young wading birds become mobile and harder to capture after about two weeks of age, we conducted survival analyses in three parts: (1) during the period when all chicks were very young (<20 days old) and easy to find during nest checks; (2) from hatching through fledging for radio-marked A-chicks only; and (3) for radio-marked young after they dispersed (i.e. postfledging) from colony. For the first two parts, only birds with hatching dates known to within one day were included.

For the early-nesting period, chicks that were found dead, were missing from their nest at a young age (<5 days old), or were missing after having been noted to be weak and losing mass were assumed to have died at the midpoint between the two visits, unless a more accurate determination of date of death was made in the field. Birds that appeared healthy but disappeared at the next visit became "censored" (see the Lifetest Procedure in SAS for a discussion of censored data; SAS Institute 1987) for the survival analysis on the day they were last known to be alive. The average age of censoring for birds that were not radioed was approximately 16 days. The Lifetest program calculates Kaplan-Meier probabilities of survival through time, incorporating the censored data, and also tests for homogeneity among strata. In this case, strata refer to either year and colony ("year-colony"), or hatching order. We used the log rank statistic (Lawless 1982) to test for differences among strata. First, the number of chicks in a brood was used as a covariable to evaluate the effect on survival of chicks of each species-hatching order combination. Since our  $P$ -values exceeded 0.05, we combined all brood sizes. We tested for differences in survival caused by hatching order for each year-colony stratum, keeping spe-

cies separate. Then, differences caused by year-colony were tested for each hatching-order combination. First, the two 1993 colonies were compared separately, and then the 1992 colony was added.

To estimate survival of a sample of birds during the late-nesting period until dispersal, we attached small (10-g) oval radios with mortality sensors to A-chicks between the ages of 7 and 21 days ( $\bar{x} = 2$  weeks). Radio transmitters were attached to blank aluminum leg bands applied above the tarsometatarsus bone. We attached the radio to the band using both epoxy and monofilament fishing line. In only one case was the radio thought to have contributed to the death of the bird, so that bird was not included in the study. In 1992, 20 radio transmitters were used on Snow Egrets, 10 on night-heron chicks. In 1993, 20 were used on each species. When mortality occurred, we were able to reuse transmitters from several chicks. We visited the colonies one to three times per week during late nesting to monitor bird activity with portable receivers and hand-held Yagi antennas. When a mortality signal was heard (50% higher pulse rate), we usually located the bird within a day. A bird was considered to have fledged on the midpoint date between the last day recorded in the colony and first day it was missed. The age of death was similarly calculated; if the bird had not died, it became censored at the age at which it fledged. Daily survival rates for the two species in the two years were calculated as Kaplan-Meier statistics (Lawless 1982) and, again, the log rank statistic was used to test for differences among strata.

We were able to make accurate calculations of age of dispersal for most of the radio-marked birds in our study. In addition, we used ANOVA to determine whether, each year, the two species had the same age of dispersal, and if birds of the same species dispersed at the same age in both years.

We analyzed postdispersal survival using capture-recapture models (Pollock et al. 1990). After almost all the birds had fledged, we followed them using motor vehicles and fixed-wing aircraft at intervals of 3 to 12 days from 12 August through 24 September in 1992 and from 27 July through 2 October in 1993. We flew a regular search pattern on every search that covered most of the coastal areas from: Cape May, New Jersey to Salem, New Jersey; the Atlantic coast from the Chesapeake and Delaware Canal, Delaware to Cape Charles, Virginia; and the eastern shore of the Chesapeake Bay from Cape Charles to Kent Island, Maryland. Additional searches were made several times while crossing the Delmarva peninsula, by flying up the Delaware River 15 km north of Philadelphia and along the mid- and southern New Jersey shore north to Manasquan. One search was made along the western shore of the Chesapeake Bay in August 1993. The radios had a range of 5 to 18 km from the aircraft and about 1 to 2 km on the ground. When we heard a mortality signal, we attempted to locate the

TABLE 1. Clutch-size<sup>a</sup> and brood-size<sup>b</sup> analyses between years (1992 and 1993) for Black-crowned Night-Heron and Snowy Egret chicks.

Year	No. nests	No. nests with clutch (or brood size)				
		1	2	3	4	5
<b>Black-crowned Night-Heron clutch size (<math>FF = 2.70^{ns}</math>, 3 df)</b>						
1992	15	0	1	11	3	0
1993	44	0	1	25	15	3
<b>Snowy Egret clutch size (<math>FI = 25.22^{**}</math>, 2 df)</b>						
1992	22	0	5	13	4	0
1993	48	0	0	11	37	0
<b>Black-crowned Night-Heron initial brood size (<math>FI = 9.31^*</math>, 4 df)</b>						
1992	15	3	3	8	1	0
1993	44	0	6	25	11	2
<b>Snowy Egret initial brood size (<math>FI = 21.11^{**}</math>, 3 df)</b>						
1992	22	2	9	8	3	0
1993	48	0	4	13	31	0

<sup>ns</sup>,  $P > 0.05$ ; <sup>\*</sup>,  $P < 0.05$ ; <sup>\*\*</sup>,  $P < 0.01$ .

<sup>a</sup> Clutch-size calculations based on greatest number of eggs seen in nest that hatched at least one egg.

<sup>b</sup> Initial brood size was initial number of chicks seen alive in nests that hatched at least one egg.

<sup>c</sup> Fisher's exact test (Lehmann 1975) and Monte Carlo  $P$ -value estimates (Cytel 1991).

bird within a day or two, and determine probable cause of death.

We computed survival rates using program JOLLY, which suggested a number of models to fit our data while incorporating an open-population model (i.e. allowing both deaths and emigration; Pollock et al. 1990). The data were not sufficient to run goodness-of-fit tests to compare model efficiency, so we used a simple model (Model D) that yielded a single constant survival rate over the entire period, rather than day- or week-specific rates (as in the nestling survival data). Time-period-specific models did not fit the data significantly better. In addition, we used program CONTRAST (Hines and Sauer 1989), which incorporates associated variance and covariance estimates to conduct Z-tests on survival rate data to compare the survival rates between species and years.

*Nest success, growth, and survival relationships.*—We examined whether any growth statistics or indices were associated with survival or nest-success measures. The LIFETEST procedure in SAS produces log rank statistics and marginal test statistics for the survival and covariate parameters (SAS Institute 1987). We used the slopes of individual growth as a covariate of survival rate. For each species, we examined all combinations of brood order and year-colony for the effect of growth as a covariate.

To test whether the difference in mass of siblings is a reliable indicator of general feeding conditions

TABLE 2. Summary of differences between years in "final brood sizes"<sup>a</sup> for Black-crowned Night-Heron and Snowy Egret nests<sup>b</sup> in 1992 and 1993.

Parameter and year	No. nests	No. nests by final-brood-size categories				
		0	1	2	3	4
<b>Black-crowned Night-Heron</b>						
Brood size <sup>c</sup> 1 (no test)						
1992	3	2	1			
1993	0	—	—			
Brood size 2 ( $FI = 3.08^{ns}$ , 2 df)						
1992	3	1	0	2		
1993	6	0	3	3		
Brood size 3 ( $FI = 2.39^{ns}$ , 2 df)						
1992	8	2	0	1	5	
1993	25	2	0	2	21	
Brood size 4 ( $FI = 4.582^{ns}$ , 3 df)						
1992	1	0	0	1	0	0
1993	11	1	0	1	5	4
Brood size 5 (no test)						
1992	0					
1993	2	0	0	0	0	1
<b>Snowy Egret</b>						
Brood size 1 (no test)						
1992	2	1	1			
1993	0					
Brood size 2 ( $FI = 1.295^{ns}$ , 2 df)						
1992	9	2	1	6		
1993	4	0	1	3		
Brood size 3 ( $FI = 14.59^{**}$ , 3 df)						
1992	8	1	5	0	2	
1993	13	0	0	8	5	
Brood size 4 ( $FI = 5.09^{ns}$ , 3 df)						
1992	3	0	0	2	1	0
1993	31	1	0	8	20	2

<sup>a</sup> Final brood size defined as no. birds surviving  $\geq 14$  days.

<sup>b</sup> Nests required  $\geq 1$  hatching to qualify.

<sup>c</sup> Refers to initial brood size (at hatching).

in the colony at the time, we compared differences in A- versus C-chicks with survival data. Because differences would be expected to accentuate with time, we used the differences in mass of chicks on the last day both were weighed. We combined these values for all nests in all year-colonies, and then tested with linear regression for a relationship between these differences and the number of birds surviving per nest to 14 days of age. We conducted a permutation test (Manly 1991) using 1,000 permutations to calculate the  $P$ -value associated with the regression slope and, thus, avoided the assumption of normally distributed residuals.

*Colony census.*—We were interested in examining the relationship between the reproductive measures described above and the numbers of nesting birds in the study colonies and the region. We made counts of the number of birds at both heronries in late May both years by walking the perimeter of the colonies

TABLE 3. Results of tests comparing mass and culmen-length growth rates ( $\bar{x} \pm$  SD, with  $n$  in parentheses) for Black-crowned Night-Heron and Snowy Egret chicks in 1992 and 1993.

Year	Colony	Chick	Mass (g) growth per day <sup>a</sup>	Tukey test <sup>b</sup>	Culmen-length (mm) growth per day <sup>c</sup>
<b>Black-crowned Night-Heron</b>					
1992	Causeway	A	31.28 $\pm$ 10.54 (8)	A a	1.87 $\pm$ 0.32 (8)
1992	Causeway	B	35.94 $\pm$ 9.70 (7)	A a	1.90 $\pm$ 0.24 (7)
1992	Causeway	C	7.41 $\pm$ 10.18 (4)	B a	1.59 $\pm$ 0.57 (4)
1993	Causeway	A	39.33 $\pm$ 5.31 (11)	A a	2.23 $\pm$ 0.18 (10)
1993	Causeway	B	34.88 $\pm$ 7.35 (9)	A a	2.21 $\pm$ 0.21 (9)
1993	Causeway	C	33.85 $\pm$ 11.99 (9)	A b	2.17 $\pm$ 0.36 (9)
1993	Causeway	D	26.83 $\pm$ 3.94 (2)	A a	1.76 $\pm$ 0.30 (2)
1993	Causeway	E	4.10 (1)	A	1.58 (1)
1993	Willis	A	39.18 $\pm$ 12.17 (15)	A a	2.27 $\pm$ 0.26 (15)
1993	Willis	B	43.88 $\pm$ 9.22 (16)	A a	2.24 $\pm$ 0.39 (16)
1993	Willis	C	31.33 $\pm$ 14.30 (15)	A b	2.04 $\pm$ 0.26 (13)
1993	Willis	D	41.34 $\pm$ 30.35 (3)	A a	2.22 $\pm$ 0.53 (4)
<b>Snowy Egret</b>					
1992	Causeway	A	15.53 $\pm$ 4.51 (15)	A a	1.99 $\pm$ 0.66 (17)
1992	Causeway	B	10.43 $\pm$ 7.21 (12)	AB a	2.14 $\pm$ 0.57 (13)
1992	Causeway	C	0.28 $\pm$ 2.07 (5)	B a	1.48 $\pm$ 0.92 (6)
1992	Causeway	D	-1.83 (1)	AB a	2.07 (1)
1993	Causeway	A	14.23 $\pm$ 3.91 (11)	A a	1.80 $\pm$ 0.16 (11)
1993	Causeway	B	15.32 $\pm$ 3.17 (13)	A a	1.94 $\pm$ 0.19 (13)
1993	Causeway	C	9.44 $\pm$ 12.80 (7)	A ab	1.52 $\pm$ 0.40 (8)
1993	Causeway	D	17.03 $\pm$ 12.76 (3)	A a	1.28 $\pm$ 0.41 (5)
1993	Willis	A	17.65 $\pm$ 12.76 (15)	A a	1.84 $\pm$ 0.36 (17)
1993	Willis	B	16.99 $\pm$ 5.23 (16)	A a	1.87 $\pm$ 0.28 (17)
1993	Willis	C	14.38 $\pm$ 7.80 (14)	AB b	1.67 $\pm$ 0.39 (19)
1993	Willis	D	5.01 $\pm$ 11.46 (7)	B a	1.55 $\pm$ 0.43 (9)

<sup>a</sup> Main effects for night-herons: year-colony,  $F = 8.71^{***}$ , 2 df; hatching order,  $F = 2.47^*$ , 4 df; interaction,  $F = 2.32^*$ , 5 df. Main effects for egrets: year-colony,  $F = 6.68^{**}$ , 2 df; hatching order,  $F = 8.72^{***}$ , 3 df; interaction,  $F = 3.36^{**}$ , 6 df; <sup>a</sup>,  $P > 0.05$ ; <sup>\*</sup>, very close to  $P = 0.05$ ; <sup>\*\*</sup>,  $P < 0.05$ ; <sup>\*\*\*</sup>,  $P < 0.001$ .

<sup>b</sup> Results of Tukey multiple-comparison procedure (overall  $\alpha = 0.05$ ), where uppercase letters compare growth rates among chicks of different hatching orders within same year and colony, while lowercase letters compare years and colonies of chicks of same hatching order. Growth-rate means that share a given letter of same case are not significantly different (Tukey comparison).

<sup>c</sup> Main effects for night-herons: year-colony,  $F = 9.85^{***}$ , 2 df; hatching order,  $F = 1.77^m$ , 4 df; interaction,  $F = 0.87^m$ , 5 df. Main effects for egrets: year-colony,  $F = 1.82^m$ , 2 df; hatching order,  $F = 5.43^{**}$ , 3 df; interaction,  $F = 0.84^m$ , 6 df. Statistical symbols as in footnote a.

with three to six observers and periodically flushing all adults. The colony was divided into sections generally 50 to 100 m long (5 to 40 m wide) using local landmarks. Each person would count the number of individuals of one or two species that would flush from the colony. In addition, population estimates of other colonies from the mid-Atlantic region were solicited from the Virginia Coast Reserve (The Nature Conservancy) and biologists from the states of Maryland and Virginia.

## RESULTS

*Nest success.*—A comparison of clutch sizes for the two species using Fisher's exact tests indicates a year effect for egrets (in 1993, clutches were larger) but not for night-herons (Table 1). Comparing mean initial brood sizes for each species between the two years, we found that

both species had larger initial broods in 1993 than in 1992 (Table 1).

When comparing chick production per nest (based on successfully hatched nests), we found for both species in both years that the initial brood size had a significant effect on the number of chicks that survived 14 days (for night-herons in 1992 [ $FI = 13.08$ ,  $P = 0.043$ ] and 1993 [ $FI = 41.68$ ,  $P < 0.001$ ]; for egrets in 1992 [ $FI = 15.94$ ,  $P = 0.008$ ] and 1993 [ $FI = 15.50$ ,  $P = 0.017$ ]). We performed separate analyses by species and brood size, but small sample sizes limited our interpretations (Table 2). Egrets with brood size 3 produced significantly more chicks per brood to 14 days in 1993 than in 1992; night-herons with brood size 3 showed no significant year effect (Table 2).

When we compared successful with unsuccessful nests, we again found yearly differences.

TABLE 4. Effect of hatching order (by year-colony) on survival rates of Black-crowned Night-Heron and Snowy Egret chicks through 20 days.

Colony	Year	<i>n</i>	$\bar{s}^a$	$X^2$
<b>Black-crowned Night-Heron</b>				
Causeway	1992	25	0.706	8.21*
Causeway	1993	40	0.947	1.63 <sup>ns</sup>
Willis	1993	60	0.765	5.77 <sup>ns</sup>
<b>Snowy Egret</b>				
Causeway	1992	47	0.484	13.89**
Causeway	1993	52	0.691	18.97**
Willis	1993	81	0.618	19.39**

<sup>ns</sup>,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ .

<sup>a</sup> Mean survival (daily) in broods of four (3 df) calculated from Kaplan-Meier estimates during period from hatching to mid-nestling (15 to 20 days) period. Only initial broods of four were used.

For night-herons in 1992, we recorded 5 unsuccessful and 10 successful nests, while in 1993 there were only 3 unsuccessful nests and 41 successful nests in two colonies ( $FI = 5.93$ ,  $P = 0.02$ ). For egrets, we recorded 4 unsuccessful and 18 successful nests in 1992, and only 1 unsuccessful and 47 successful nests in 1993 ( $FI = 3.53$ ,  $P = 0.07$ ).

*Growth.*—We first evaluated whether brood size had an effect on the growth rate of chicks of either species for all year-colony combinations. No results were significant (all  $P > 0.05$ ), so data were combined from all brood sizes for the rest of the analyses.

Mass differences were more variable and more divergent among brood members than were culmen differences for both species (Table 3). For mass growth in night-herons, a two-way ANOVA indicated that both the main effects of year-colony and hatching order were significant (hatching order was at critical limit,  $P = 0.0501$ ), and that for the year-hatch order interaction also was significant (Table 3). For culmen length, only the year-colony effect was significant (Table 3).

For egrets, mass growth rates were significantly different due to the main effects of year-colony and hatching order, and their interactions (Table 3). Mass gain of C- and D-chicks in 1992 was much reduced, compared to A- and B-chicks (Table 3). For culmen, the main effect of year-colony was not significant, but hatching order was (Table 3).

The year-colony effect was already apparent in egret C-chicks that grew significantly faster at Willis in 1993 than at Causeway in 1992 (Table 3); for D-chicks, the differences are even

TABLE 5. Effects of year-colony on survival rates in Black-crowned Night-Heron and Snowy Egret chicks through 20 days for given hatching orders.

Hatching order	<i>n</i>	$\bar{s}^a$	$X^2$
<b>Black-crowned Night-Heron</b>			
1	42	0.902	2.17 <sup>ns</sup>
2	38	0.892	0.05 <sup>ns</sup>
3	36	0.725	5.34 <sup>ns</sup>
4	8	0.000	7.76*
<b>Snowy Egret</b>			
1	51	0.823	2.45 <sup>ns</sup>
2	51	0.750	8.03*
3	48	0.415	10.40**
4	26	0.168	3.96 <sup>ns</sup>

<sup>ns</sup>,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ .

<sup>a</sup> Mean survival (daily) for each hatching order calculated for the three year-colonies. Means based on Kaplan-Meier estimates during period from hatching to mid-nestling (15 to 20 days).

more obvious, even though sample sizes are not adequate for testing. The single egret chick from 1992 that survived long enough to permit weighing had a negative growth rate. In contrast, in 1993, D-chicks grew an average of 5 and 17 g/day at the Willis and Causeway sites, respectively.

*Survival.*—For the early-nesting period, we first examined the data on chick survival to 20 days for a species difference. For each brood member order (A-D), we found no differences in survival between species for any combination of year and colony (all  $P > 0.05$ ). However, the order in which chicks hatched had a significant effect on survival in all three cases for egrets, but only at the Causeway colony in 1992 for night-herons (Table 4). When year effects are considered for each brood order, differences were noted for both species but most strongly for egrets (Table 5, Fig. 2). A-chicks of both species were the only ones consistent in showing no year effect in survival to 20 days (Table 5). Figure 3 illustrates the differences among years and colony sites for each of the brood orders separately. In general, D-chicks suffered such low survival that statistical power was low.

During the late-nesting period, radio-marked A-chicks of both species had very high survival rates from the time of marking (ca. two weeks old) until fledging age in both years (Fig. 4). Within both years, there were no significant differences ( $P > 0.05$ ) in survival rates between species.

In examining dispersal age, we were ham-

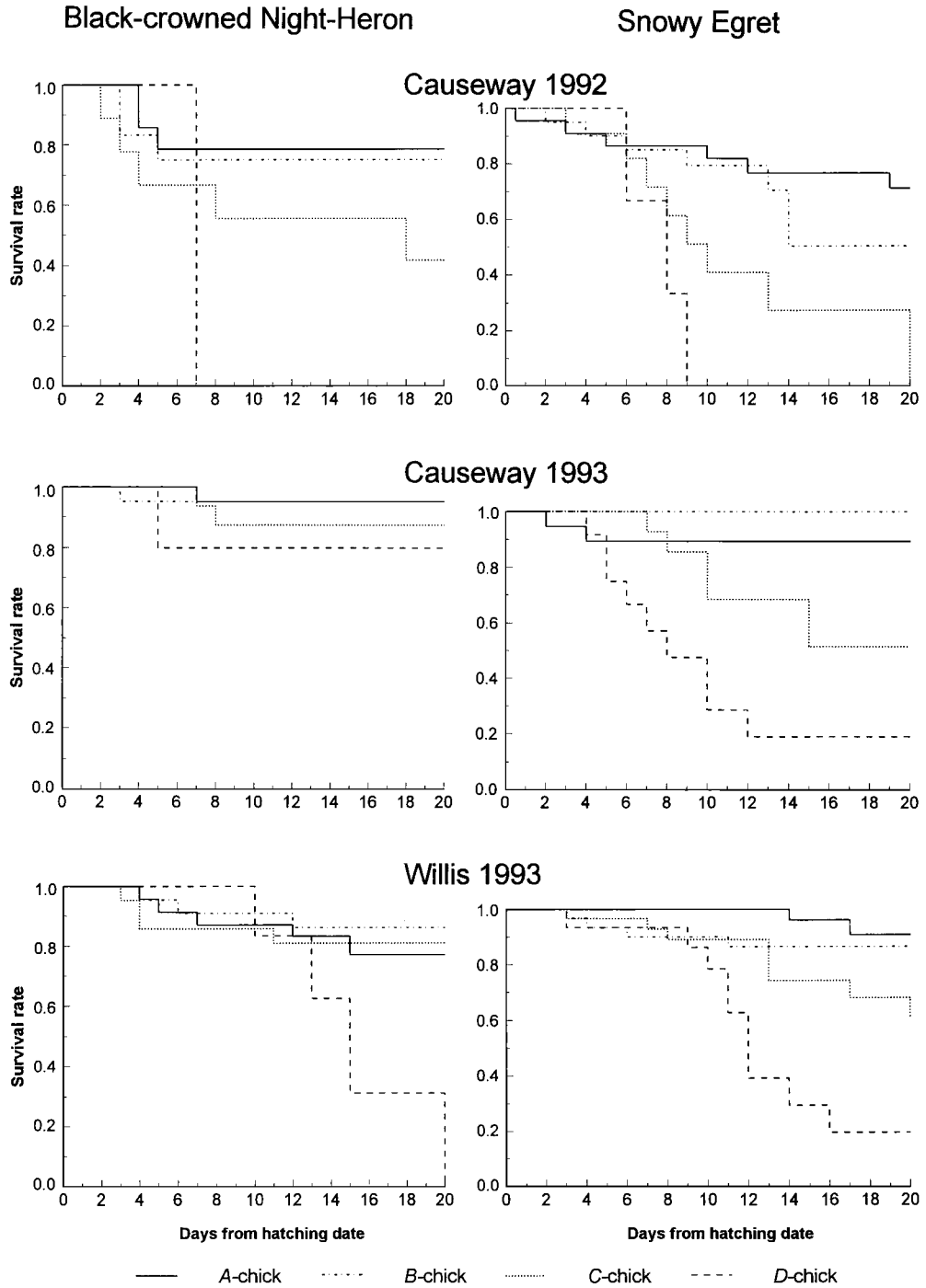


Fig. 2. Survival function estimates for Black-crowned Night-Heron and Snowy Egret chicks during early growth period (to 20 days) at each colony site.

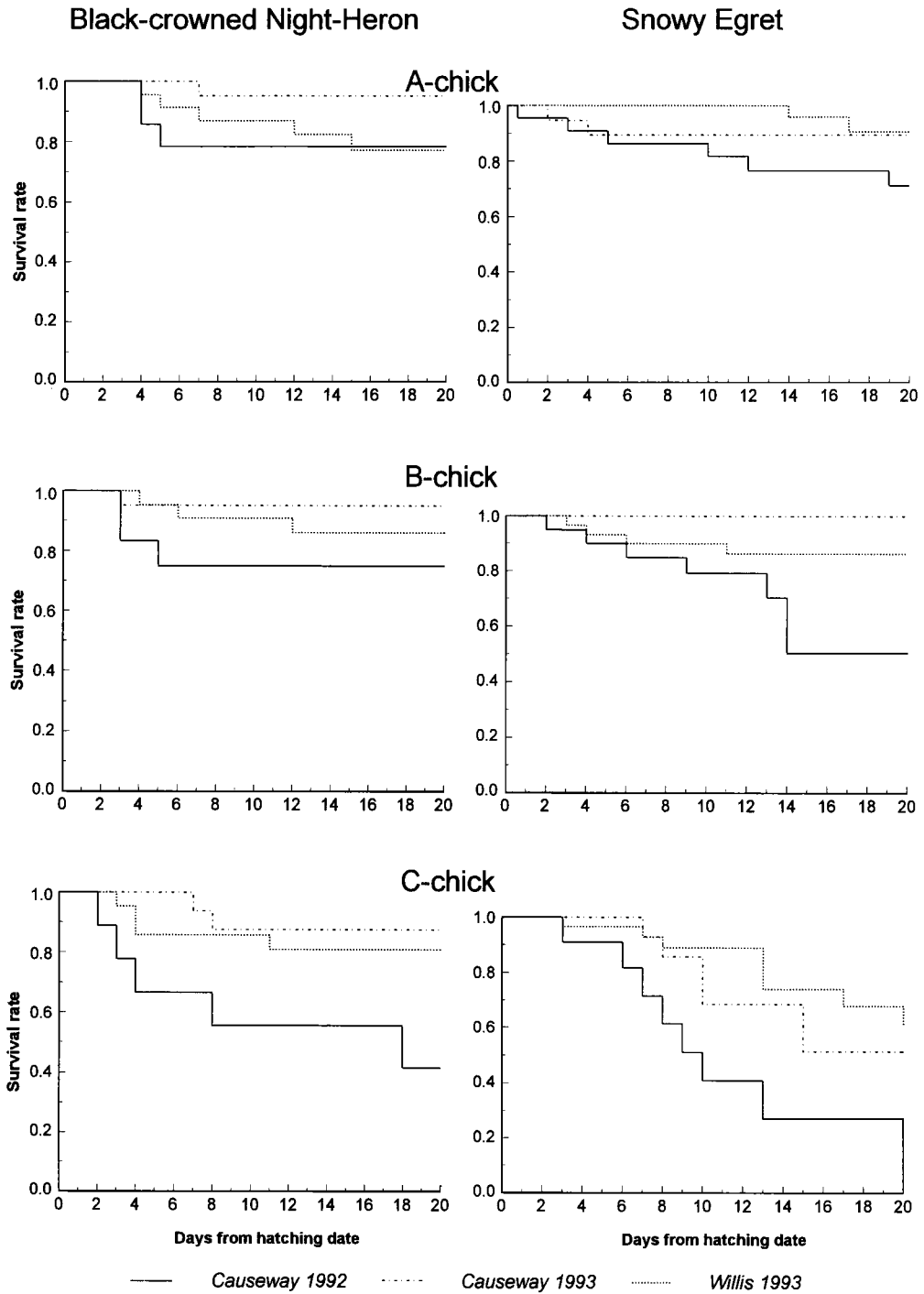


Fig. 3. Survival-function estimates (to 20 days) for each brood member of nestling Black-crowned Night-Herons and Snowy Egrets at each study colony. Because of limited sample size, *D*- and *E*-chicks were not included.



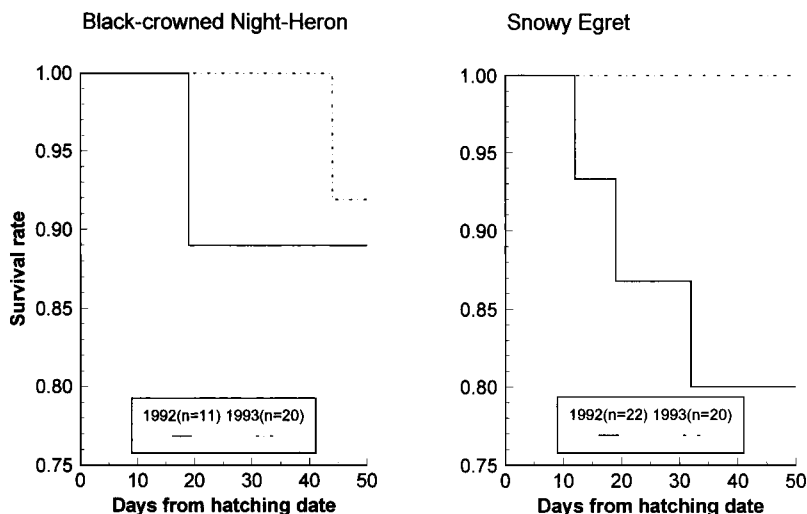


Fig. 4. Survival-function estimates of radio-marked Black-crowned Night-Heron and Snowy Egret A-chicks from hatching until dispersal from colony in 1992 and 1993.

pered because of chick mortality and lack of precise information concerning hatching dates; for these reasons, we did not include all radio-marked birds in the analysis. With a reduced sample, no year effects for either species were found (night-herons,  $F = 3.68$ ,  $P > 0.05$ ; egrets,  $F = 2.70$ ,  $P > 0.10$ ), but we did detect a significant species difference in 1993 ( $F = 4.19$ ,  $P = 0.05$ ; Table 6).

After dispersal, survival was estimated using capture-recapture models. We found survival of A-chicks to be lower during the postdispersal phase than during the late-nestling phase (Fig. 5 and Table 7). Approximately six weeks after dispersal began, survival rates ranged only from 0.35 to 0.65 for the two species in both years (Fig. 5), compared to rates of 0.80 to 1.00 during the nestling period (Fig. 4). The probable causes of mortality included predation (9), collision with powerline wires (1), and unknown (2). On most occasions, we recovered the radio only; typically, only a few feathers were present. Most of these radio recoveries (with no carcass) were located in wooded areas under a large tree where a Great Horned Owl (*Bubo virginianus*) perched. Without direct evidence or observations, however, we cannot confirm whether owls, other predators, or scavengers carried the corpses to their recovery location. Recovery locations ranged from a powerline site near Salem, New Jersey, east to a salt-marsh near Cape Henlopen, Delaware, and a wooded cemetery near Saxis,

Virginia, on the upper Eastern Shore of Virginia.

*Growth, success, and survival.*—We conducted separate analyses for influences of growth (mass) rate on survival (to 20 days) for each combination of hatching order, species, and year-colony; none of these were significant (log rank  $X^2$ , all  $P > 0.1$ ). However, sample sizes were limited for some of the hatching orders. When we combined all hatching orders, survival in egrets showed a significant association with growth rates at two of three year-colony combinations (Causeway 1992,  $X^2 = 16.34$ ,  $P < 0.001$ ; Willis 93,  $X^2 = 12.16$ ,  $P = 0.002$ ). When all year-colony and brood orders were combined, we

TABLE 6. Average age ( $\pm$  SD) of dispersal for Black-crowned Night-Heron and Snowy Egret chicks in Virginia in 1992 and 1993.<sup>a</sup>

Year	<i>n</i> <sup>b</sup>	Age (days)
<b>Black-crowned Night-Heron</b>		
1992	7 (11)	60.3 $\pm$ 7.1
1993	14 (20)	55.8 $\pm$ 3.1
<b>Snowy Egret</b>		
1992	12 (22)	56.3 $\pm$ 5.6
1993	13 (20)	53.0 $\pm$ 3.7

<sup>a</sup> ANOVA between species for 1992 ( $F = 1.66$ , 1 df,  $P = 0.215$ ) and 1993 ( $F = 4.19$ , 1 df,  $P = 0.051$ ).

<sup>b</sup> Sample size of radio-marked birds. Number in parentheses indicates total number of birds radio-marked (including reused radios); birds were removed from sample if hatching date was uncertain, or in a few cases of mortality.

TABLE 7. Weekly estimated survival rates\* ( $\hat{s}$ ) of immature Black-crowned Night-Herons and Snowy Egrets dispersing from Chincoteague colonies, 1992 and 1993.

Year	$\hat{s} \pm \text{SE}$ (95% confidence interval)
<b>Black-crowned Night-Heron</b>	
1992	0.846 $\pm$ 0.068 (0.712–0.979)
1993	0.845 $\pm$ 0.040 (0.766–0.924)
<b>Snowy Egret</b>	
1992	0.919 $\pm$ 0.038 (0.846–0.993)
1993	0.833 $\pm$ 0.042 (0.750–0.916)

\* Using computer program JOLLY (Pollock et al. 1990).

found a highly significant association ( $X^2 = 27.43, P = 0.001$ ). This was not the case for night-herons ( $P > 0.10$ ).

For both species, we examined whether the proportional mass of a "subordinate" chick (C) compared to A-chicks influenced the number of chicks per nest surviving to 14 days. For egrets, we found an effect ( $r^2 = 0.15, P = 0.006$ ); however, for night-herons, no effect was evident ( $r^2 < 0.001, P = 0.80$ ).

*Colony censuses.*—Black-crowned Night-Herons, Snowy Egrets, and other wading-bird species nested in greater numbers in both study colonies and in the region in 1993 than in 1992 (Table 8). The other species included Great Egrets (*Casmerodius albus*), Cattle Egrets (*Bubulcus ibis*), Little Blue Herons (*Egretta caerulea*), Tricolored Herons (*E. tricolor*), and Glossy Ibises (*Plegadis falcinellus*). However, the pattern within colonies in the region was inconsistent, with some colonies decreasing in 1993 (Table 8). This indicates probable immigration into the Chincoteague colonies in 1993 from other coastal colonies nearby. The total numbers of all wading birds in these mixed-species colonies increased from 1992 to 1993 in the region.

## DISCUSSION

Growth rates in mass and culmen length found at our colonies are the highest reported in North America for Black-crowned Night-Herons. Mass increases of greater than 39 g/day for A-chicks exceed those reported from Cape Cod, Massachusetts ( $\bar{x} = 33.5$  g/day, range 26.2–37.6 among brood members; Parsons and Burger 1981), Texas (38.4 g/day for A-chicks; Custer and Peterson 1991), or Alberta, Canada (31.3

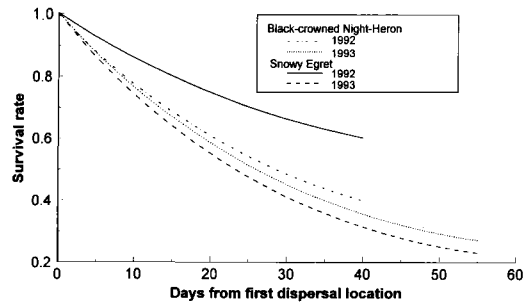


Fig. 5. Survival rates of dispersed Black-crowned Night-Heron and Snowy Egret chicks from a Virginia colony in 1992 and 1993 as determined by aerial radiotelemetry. Note that X-axis is days from first dispersal location in both years. The first location flight in 1992 was 16 days later than first flight in 1993.

g/day reported, averaged for brood members; Wolford and Boag 1971). In 1993, at the Virginia colonies, we found culmen-length growth of A-chicks of 2.23 to 2.27 mm/day at the two sites, not significantly higher than the 2.1 mm/day mean reported for A-chicks in Texas (Custer and Peterson 1991), but markedly higher than the 1.97 mm/day reported from Alberta in 1964 (Wolford and Boag 1971).

For Snowy Egrets, comparisons are more limited. Growth rates in mass of 17.7 g/day for A-chicks in 1993 in Virginia at the Willis colony exceeded the reported 14.1 g/day for A-chicks in Texas (Custer and Peterson 1991). Culmen-length growth rates were similar between the two studies with ranges from 1.80 to 1.99 mm/day in Virginia in the two years, compared to 2.0 mm/day in Texas (Custer and Peterson 1991).

We were surprised to find lower survival rates (range 0.25 to 0.60) during the 40- to 60-day postfledging period than during the late-nesting (ca. 14- to 40-day) period (range 0.80 to 1.0) for both species. In the Great White Heron, Powell and Bjork (1990) found that, of 42 immature herons that dispersed to southern Florida from the Keys, only 10% survived the first six months. In contrast, in American Crows (*Corvus brachyrhynchos*), Caffrey (1992) reported that young only had a 70% survival to fledging, but from fledging to two months postfledging had an 89% survival rate. Because crows are resident species, they may not be faced with the hazards encountered by naive first-year migrant birds moving over great distances into unknown areas shortly after fledging.

TABLE 8. Differences in numbers of nesting wading birds at major Maryland-Virginia heronries, 1992 and 1993.

Colony	Black-crowned Night-Heron		Snowy Egret		All species <sup>b</sup>	
	1992	1993	1992	1993	1992	1993
Willis Marsh, Virginia <sup>a</sup>	47	90	308	391	742	1,182
Causeway, Virginia <sup>a</sup>	32	37	233	636	872	2,032
Chimney Pole, Virginia	—	—	76	102	226	294
Cobb Island, Virginia	36	61	180	28	672	251
Wreck Island, Virginia	41	80	232	150	788	584
Fisherman Island, Virginia	260	235	64	44	480	484
Coards Marsh, Virginia	12	14	30	80	82	166
Heron Island, Maryland <sup>c</sup>	—	—	208	329	874	1,759
South Point, Maryland <sup>c</sup>	—	—	72	70	713	1,035
$\bar{x}$ (including study sites)	62	74	140	183	546	779
$\bar{x}$ (excluding study sites)	71	78	108	100	480	572

<sup>a</sup> Includes Great Egrets, Cattle Egrets, Little Blue Herons, Tricolored Herons, and Glossy Ibises.

<sup>b</sup> Study sites at Willis Marsh and Causeway.

<sup>c</sup> Based on flight-count data, with conversions to nest estimates (D. Brinker pers. comm.).

From the perspective of using wading birds as potential bioindicators in estuarine wetlands, our data suggest that Snowy Egrets are a better "indicator species" candidate than are Black-crowned Night-Herons. When comparing growth rates, reproductive success, chick survival, and total nesting populations, Snowy Egrets revealed stronger relationships than did Black-crowned Night-Herons. Survival was significantly associated with mass growth rates for egrets but not night-herons. For both species, A-chicks seemed relatively immune to yearly variations, while B-, C-, and D-chick growth and survival seemed sensitive to between-year changes. Our data suggest that food conditions in the estuary may have been inferior in 1992 compared to 1993. Unfortunately, no fisheries data were being collected in the region to evaluate independently estuarine productivity. Such data are vital to validate the utility of "bioindicators."

Black-crowned Night-Herons may not be good "bioindicators" because of their generalized feeding in both freshwater and estuarine environments, both in Massachusetts (Kornhisser and McColpin 1994) and Virginia. Young birds, small mammals, frogs, and fish comprised the diet of young Black-crowned Night-Herons during the nesting season at our study site (Erwin and Custer in press). For estuarine indicator species, both Snowy Egrets and Tricolored Herons (Frederick et al. 1992, Ramo and Busto 1993) are probably good candidates because of their

stronger affinities to brackish and salt-marsh habitats for feeding.

#### ACKNOWLEDGMENTS

We thank the staff of the Chincoteague National Wildlife Refuge for their logistical support during the project. We also thank Dr. and Ms. Robert Baker for their field assistance and help with photography. Numerous staff members from Patuxent Wildlife Research Center also assisted us on occasion. Tom Custer and Kathy Parsons provided suggestions and ideas during the development of the project. We appreciate the useful comments of T. Bancroft, T. Custer, P. Frederick, G. M. Haramis, R. Hines, G. Schnell, and an anonymous reviewer on earlier drafts of the manuscript.

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