DISTRIBUTION, SPECIES ABUNDANCE, AND NESTING-SITE USE OF ATLANTIC COAST COLONIES OF HERONS AND THEIR ALLIES

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ABSTRACT.—In 1975 and 1976, eight teams of investigators located 262 colonies of nesting herons and their allies along the Atlantic coast from Florida to Maine. Fourteen species were found in Florida, numbers decreasing to seven in Maine. Colonies censused in the extreme south and north of the study area were lower in number of species and number of adults than those in the intermediate area. More than 90% of the colony sites surveyed in 1975 were active in 1976. The total number of nesting adults per colony, number of species per colony, and number of nesting adults of each species per colony in 1976 were significantly correlated with their respective values for 1975. Abandoned and new colonies appeared to be satellites of nearby reused colonies; they had fewer individuals and species than reused colonies and were closer to reused colonies than reused colonies were to each other. *Received 30 July 1979, accepted 7 March 1980.*

GREY Herons (*Ardea cinerea*) in Scotland, England, and Wales traditionally use the same colony sites (Burton 1956, Garden 1958). Colony sites of Black-crowned Night Herons (*Nycticorax nycticorax*) in Massachusetts (Erwin 1978) and those of herons and their allies (here collectively termed herons) along the Atlantic coast (Custer and Osborn 1977) are also used year after year. In this study, we attempted to assess the use of Atlantic coast heron colonies over a 2-yr period. This study was part of an attempt to examine colonially nesting herons as biological indicators of environmental quality (Ohlendorf in press). Other aspects of this program have included a survey of chemical residues in eggs of herons (Ohlendorf et al. 1978), an inventory of heron colonies along the Atlantic coast (Custer and Osborn 1977, Osborn and Custer 1978), and studies of heron nest-site selection (Beaver et al. in press), feeding-site selection (Custer and Osborn 1978a), and use of feeding habitat around a nesting colony (Custer and Osborn 1978b).

METHODS

During the summers of 1975 and 1976, Atlantic coast heron colonies from Florida to Maine were surveyed and censused. Detailed descriptions of the survey and census techniques are given by Custer and Osborn (1977) and Osborn and Custer (1978). Briefly, eight teams of cooperators located colonies from historical information, air and ground searches, and contacts with local residents. The cooperators usually visited the colonies two or more times during each breeding season. They gathered information on the number of nesting adults, number of nests, and stage of nesting.

In this report we used the maximum estimate of breeding adults for each species in each colony. Population estimates were usually calculated as twice the number of active nests. If nest counts were unavailable, we assumed that adult counts during nest-building and egg-laying stages reflected the numbers breeding in the colony. From incubation onward, we assumed that only one adult was in the colony, and adult counts during this period were doubled.

Nesting areas within 1 km of one another were considered as one colony, as this was the inter-colony distance used by cooperators to combine nesting groups of herons. (If we had used a distance greater

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 The Auk 97: 591–600. July 1980

TABLE 1. Number of Atlantic coast heron colonies surveyed and censused (in parentheses) by region in 1975 and 1976.

Region	Comparative data				
	Reoccupied	Abandoned	New	Other[a]	Total
1	15 (15)	2 (2)	0	25 (25)	42 (42)
2	35 (32)	9 (9)	2 (2)	9 (9)	55 (52)
3	82 (69)	5 (5)	4 (4)	14 (13)	105 (91)
4	27 (18)	0	1 (1)	14 (0)	42 (19)
5	11 (10)	0	0	7 (7)	18 (17)
Total	170 (144)	16 (16)	7 (7)	63 (54)	262 (221)

[a] Other includes colonies not surveyed in one of the 2 yr.

than 1 km, more colonies would have fallen into the reoccurring category. If the distance were less than 1 km, more colonies would have been considered new or abandoned.)

We included only colonies with four or more pairs in either year, because this was the arbitrary threshold established in 1975 (Custer and Osborn 1977). This eliminated 29 nesting sites in 1976 that were mainly located in the Florida Keys (Osborn and Custer 1978), which were surveyed only in 1976. Furthermore, 43 inland colonies that we reported in our Atlas (Osborn and Custer 1978) were excluded from the analysis. These inland colonies were mainly Great Blue Heron (*Ardea herodias*) colonies that occurred inland along major river drainages.

Colonies were omitted from the comparative analysis when either the area was not surveyed in both years, such as a large portion of the Florida Keys, or comparable census information was lacking in one of the 2 yr, such as on Long Island, New York. We assume that the comparative data on 193 colonies, of which 167 were censused, is a representative sample of nest site use by herons along the Atlantic coast (Table 1).

For regional comparison, we used the ecosystem classification of Bailey (1976). This classification scheme divided the Atlantic coast into five regions based on the environmental features of temperature, rainfall, vegetation, and soil. The first region included Fisherman Island, Florida (26°41′N, 80°3′W) and all colonies to the south. The second region was north of Fisherman Island to, but not including, Saint Phillips Island, South Carolina (32°17′N, 80°55′W). The third region included Saint Phillips Island North to Barnegat Inlet, New Jersey (39°46′N, 74°7′W). The fourth region was north of Barnegat Inlet to Appledore Island, Maine (42°59′N, 70°37′W). The fifth region was the entire coast of Maine north of Appledore Island.

TABLE 2. Estimated number of breeding herons in 1975 and 1976 and percent change from 1975 numbers. Data are calculated from colonies active in both years (n = 144), new colonies in 1976 (n = 7), and colonies active in 1975 and inactive in 1976 (n = 16).

Species	Estimated number of breeding herons (number of colonies with species present)		Change from 1975 (%)
	1975	1976	
Great Blue Heron	7,314 (63)	8,016 (63)	+10
Green Heron	468 (27)	276 (19)	−41
Little Blue Heron	7,424 (69)	7,126 (60)	−4
Cattle Egret	37,240 (54)	41,628 (52)	+12
Reddish Egret	18 (2)	10 (2)	−44
Great Egret	15,104 (96)	13,162 (85)	−13
Snowy Egret	33,848 (97)	23,008 (87)	−32
Louisiana Heron	29,114 (78)	25,248 (73)	−13
Black-crowned Night Heron	12,944 (76)	9,740 (77)	−25
Yellow-crowned Night Heron	506 (19)	540 (16)	+7
Wood Stork	2,490 (4)	3,570 (4)	+43
Glossy Ibis	12,312 (47)	7,226 (43)	−41
White Ibis	64,180 (20)	38,278 (24)	−40
Roseate Spoonbill	674 (7)	1,442 (5)	+114
Total	223,636 (160)	179,270 (151)	−20

TABLE 3. Distribution of herons in Atlantic coast nesting colonies in 1975 (X) and 1976 (Y).

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Species	FL	GA	SC	NC	VA	MD	DE	NJ	NY	CT	RI	MA	ME
Great Blue Heron	XY	XY	XY	XY	XY	XY	XY	Y					XY
Cattle Egret	XY	XY	XY	XY	XY	XY	XY	XY	Y	Y		XY	Y
Great Egret	XY	XY	XY	XY	XY	XY	XY	XY	XY	Y	XY	XY	Y
Snowy Egret	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
Lousiana Heron	XY	XY	XY	XY	XY	XY	XY	XY	XY			Y	Y
Black-crowned Night Heron	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
Glossy Ibis	XY	XY	XY	XY	XY	XY	XY	XY	XY	Y	X	XY	XY
Little Blue Heron	XY	XY	XY	XY	XY	XY	XY	XY	XY		XY	XY	
Green Heron	XY	XY	XY	XY	XY	XY		XY		Y			
Yellow-crowned Night Heron	XY		XY	XY	XY	XY	XY	XY					
White Ibis	XY	XY	XY	XY									
Reddish Egret	XY												
Wood Stork	XY												
Roseate Spoonbill	XY												
Total number of species	14	10	11	11	10	10	9	10	7	6	5	7	7

Population estimates were transformed to $\log_{10}$ to obtain homogeneous variance among samples for later comparison of means. In text and tables, however, the antilogs of population means (geometric means) are used to present them in their original units.

RESULTS

The 1975 and 1976 surveys included 262 heron colonies (Table 1). For those colonies for which we have comparative census information, an estimated breeding population of over 220,000 adults nested in the 160 colonies in 1975, while about 180,000 adults nested in the 151 colonies in 1976 (Table 2). In 1975 and 1976, White Ibises (*Eudocimus albus*) and Cattle Egrets (*Bubulcus ibis*), the two most abundant species, each exceeded 35,000 breeding adults. Snowy Egrets (*Egretta thula*) and Louisiana Herons (*Hydranassa tricolor*) exceeded 20,000 breeding adults, and Great Egrets (*Casmerodius albus*) and Black-crowned Night Herons each exceeded 9,000. The remaining eight species [Great Blue Heron, Green Heron (*Butorides striatus*), Little Blue Heron (*Florida caerulea*), Reddish Egret (*Dichromanassa rufescens*), Yellow-crowned Night Heron (*Nyctanassa violacea*), Wood Stork (*Mycteria americana*), Glossy Ibis (*Plegadis falcinellus*), and Roseate Spoonbill (*Ajaia ajaja*)] had less than 9,000 breeding adults in at least 1 yr.

TABLE 4. Mean (geometric) number of breeding individuals and median number of species per colony in 1976.

Region	Mean number of herons/colony[a]	N	Median number of species/colony[b]
1	68 A[c]	39	2 A
2	424 C	46	5 B
3	234 BC	86	4 B
4	123 AB	25	2 AB
5	73 A	17	1 A

[a] Significant differences detected by ANOVA ($P < 0.05$).
[b] Significant differences detected pairwise median test (overall $\alpha = 0.05$).
[c] Results of a Student-Neuman Keuls multiple range test. A significant difference ($P < 0.05$) is indicated by means that share no common letter.

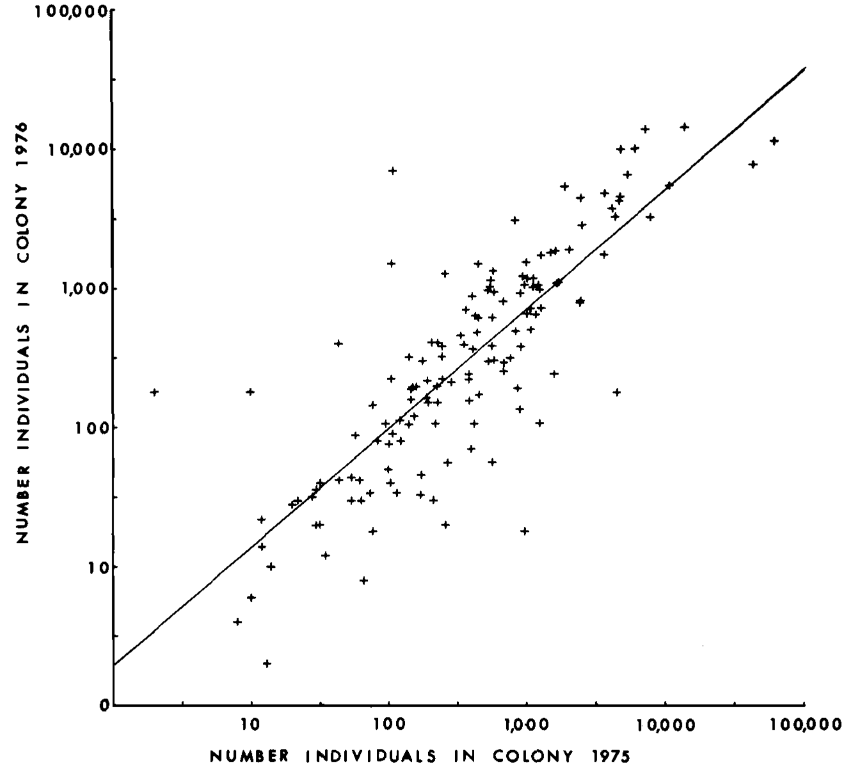

Fig. 1. Number of herons nesting in a colony in 1976 as a function of the number nesting in 1975; $n = 144$, $r^2 = 0.662$, $P < 0.01$.

In both years, Great Egrets and Snowy Egrets were present in more than 85 colonies; Louisiana Herons and Black-crowned Night Herons were present in over 70 colonies; and Little Blue Herons, Great Blue Herons, Cattle Egrets, and Glossy Ibises were present in 40 or more colonies (Table 2). The remaining six species nested each year in less than 40 colonies. The total population of herons appeared to decline 20% between 1975 and 1976, and nearly all of this decline can be accounted for by changes in the White Ibis and Snowy Egret populations. In addition, individual species populations fluctuated markedly between years. Eight of 14 species changed 25% or more between years.

The number of breeding heron species decreased northward from 14 in Florida to seven in Maine (Table 3). The number of breeding adults per colony was lowest in the extreme southern and northern regions of the Atlantic coast (Table 4). The mean (geometric) number of herons per colony in regions 1 and 5 was significantly smaller than in region 2 or 3. In addition, region 4 had significantly fewer adults per colony than region 2. The number of species per colony in 1976 was also significantly lower in the extreme regions than in regions 2 and 3 (Table 4).

Most colonies were active in both years. Of 186 colonies active in 1975, 170 (91%) were active and 16 (9%) were abandoned in 1976 (Table 1). Of 177 colonies active in 1976, 7 (4%) were newly established. Most of the new and abandoned colonies were found in regions 2 and 3, but then these regions contained 137 of the 193 (71%) colonies of known status in both years.

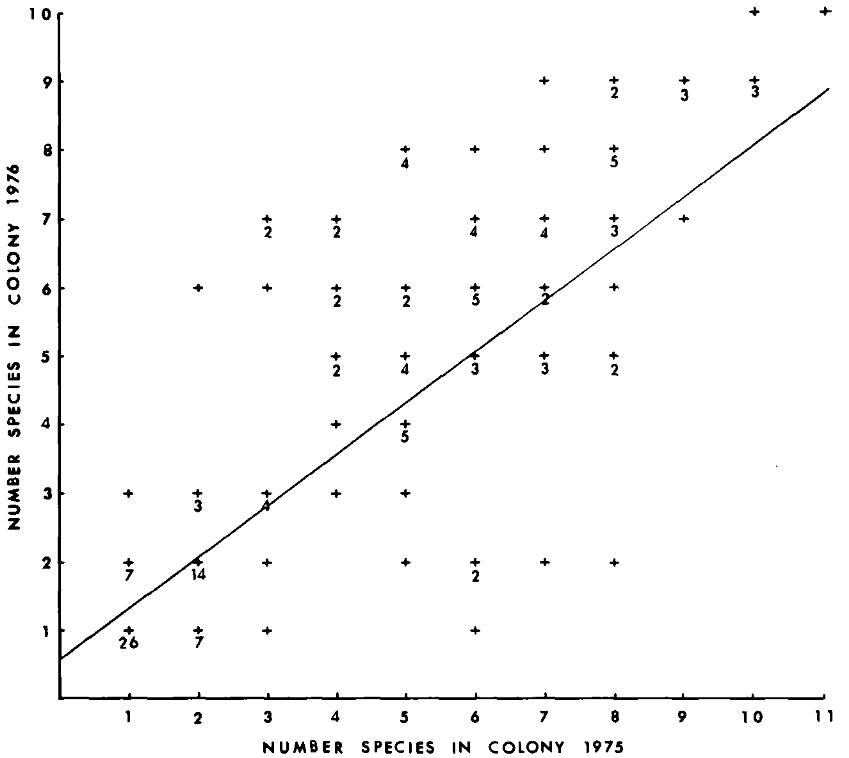

Fig. 2. Number of heron species nesting in a colony in 1976 as a function of the number of species nesting in 1975; Number below + signs indicates number of colonies observed at that pair of values; $n = 144$, $r^2 = 0.711$, $P < 0.01$.

The composition of colonies active in both years was similar. The number of nesting herons per colony in 1976 was significantly correlated with the number in 1975 (Fig. 1). For the Great Blue Heron, Little Blue Heron, Cattle Egret, Great Egret, Snowy Egret, Louisiana Heron, Black-crowned Night Heron, and Glossy Ibis, which were all present in 30 or more colonies, the number of breeding herons per colony in 1976 was significantly correlated between years ($P < 0.01$). In addition, the number of species nesting in each colony was significantly correlated between years (Fig. 2).

The mean (geometric) distance between reused colonies was not significantly different (ANOVA, Student-Neuman Keuls multiple range test, overall $\alpha = 0.05$) in region 1 (5.7 km, $n = 15$), 2 (6.1 km, $n = 35$), or 3 (8.6 km, $n = 82$). Colonies in regions 1 and 2, however, were significantly closer to each other than were those in region 5 (13.3 km, $n = 27$). Region 4 was not included in the test because of the of large number of colonies of uncertain status in 1975.

Because regions 2 and 3 contained most of the new and abandoned colonies (Table 1), were not significantly different in number of herons per colony or number of species per colony (Table 4), and were not significantly different in distance between reused colonies, we combined them in a comparison of new and abandoned colonies. Abandoned and new colonies in 1975 had significantly fewer nesting individuals and fewer species per colony than did colonies active in both years (Table 5). In addition,

TABLE 5. Mean (geometric) number of nesting herons and median number of heron species per colony for reused, abandoned, and new colonies in regions 2 and 3 combined.

Colony status	Mean number of herons/colony		Number of colonies	Median number of species/colony	
	1975	1976		1975	1976
Active 1975 and 1976	453[a]	381[a]	101	5[b]	5[b]
Abandoned 1976	72	—	14	3	—
New 1976	—	34	6	—	1

[a] Significant differences detected, t-test ($P < 0.05$).
[b] Significant differences detected, pairwise median test (overall $P < 0.05$).

abandoned colonies and new colonies were significantly closer to reused colonies than reused colonies were to each other (Table 6).

DISCUSSION

This study strengthens earlier observations that herons use nesting sites traditionally. More than 90% of the colonies that were active in 1975 were also active in 1976. Twenty-one of 25 (84%) colonies surveyed in Georgia, North Carolina, and portions of the Chesapeake Bay before 1975 were active in 1975 (Custer and Osborn 1977). In Scotland, 31 of 72 (43%) Grey Heron colonies censused in 1928–29 were still active in 1954 (calculated from Garden 1958). In the same period 127 of 273 (47%) Gray Heron colonies in England and Wales were still active (calculated from Burton 1956). Even though some colonies were abandoned, the total number increased during this period from 110 to 177 colonies in Scotland and from 280 to 301 colonies in England and Wales. In contrast, Black-crowned Night Herons in Massachusetts shifted nesting locations frequently from the early 1950's to 1977 (Erwin 1978); during this period 5 colonies were reused, 4 were abandoned, and 7 were newly established (Erwin unpubl. data).

In addition to the reuse of colony sites, several other colony characteristics were predictable. The total number of nesting adults per colony, the total number of species per colony, and the number of nesting adults of each species per colony in 1976 were all positively correlated with their respective values in 1975.

Although colony sites were generally reused, herons often shifted nesting locations within the confines of the colony (see Osborn and Custer 1978). If our definition of a colony had encompassed disjunct groups of herons less than 1 km from one another, more colonies would have been considered new and abandoned. In fact, we suspect that most new and abandoned colonies were satellites of nearby colonies;

TABLE 6. Mean (geometric) distance from reused, new, or abandoned colonies to nearest stable colony for regions 2 and 3. Number of colonies is in parentheses.

Colony status	Distance to nearest stable colony (km)	
	1975	1976
Active 1975 and 1976	7.74 (117)[a]	7.74 (117)[a]
New	—	3.8 (6)
Abandoned	4.24 (14)	—

[a] Significant differences detected by t-test ($P < 0.05$).

they had fewer species than reused colonies and were closer to reused colonies than reused colonies were to each other.

Several factors appear to influence the yearly location and composition of colonies. A major factor is the nesting habitat itself. Herons can destroy their nesting habitat through overfertilization by defecation (Jenni 1969, McDonald 1971, Wiese 1978; see Kushlan 1978 for a review). Such a natural phenomenon could initiate a shift to a nearby alternate site, which in turn would increase in abundance and species composition as the parent colony continued to decline. After a decline or abandonment, this process could be reversed as vegetation recovered.

Colony shifts may occur because of changes in feeding habitat (see Kushlan 1978). Some species wander before breeding and establish colonies near available food resources. If inland feeding habitat is temporarily unavailable because of fluctuating water levels, more birds may attempt to nest in coastal sites. If inland habitats are exceptionally good, more birds may shift to inland sites. These inland/coastal shifts are probably most prevalent in the southern portion of the Atlantic coast, where extensive inland wetlands occur. These shifts should increase the year-to-year variability, both at the colony-site level and coastal regional level.

Colony abandonment has been attributed to human disturbance and habitat alteration (Allen 1938, Majic and Mikuska 1970, Erwin 1978). The severity of the disturbance should have a major influence in determining whether or not herons will eventually reuse the site. Predation may also influence the use of colonies. Jenni (1969) suggested that in Florida ground predators may be a major factor in the location of heron colonies. Finally, the sequence of arrival of the herons at the colony may influence the use of nesting sites at the subcolony or colony level. For example, early arrival at one site may influence the final number of herons nesting in that subcolony or colony.

Our earlier results (Custer and Osborn 1977) indicated that colonies in the far north Atlantic coast had fewer species and individuals per colony than those farther south. In addition to this trend, the 1976 data indicated fewer individuals and fewer species per colony in the southern portion of the Atlantic coast. This new trend occurred because of the addition of the Florida Keys to the 1976 survey. Recher (1971) also found lower heron species diversity in the Florida Keys and the north Atlantic coast than in southern Florida. Recher and Recher (in press) concluded that regional patterns of heron species diversity are best explained by patterns of prey availability and prey diversity.

Three sources of error were shown for estimating breeding populations of Grey Herons in England (Reynolds 1974). These descrepancies also apply to our study. First, estimates vary among individual observers. Because the same observer may repeatedly make the same errors, variability of the overall estimate is reduced by using the same person. Erwin (in press) reported major census differences among observers and suggested that corrections be made for individual observer bias. We did not attempt to assess or correct investigator estimates, however; except for South Carolina and north of Delaware, all investigators were the same in both years (Osborn and Custer 1978).

A second bias is the time of year when counts are made (Reynolds 1974), as colonies may be active over several months (Kushland and White 1977, Ogden 1978) and the peak of nesting within a colony may vary among species (McCrimmon 1978, Ogden 1978). Multiple censuses are therefore required so that the maximum number breeding of each species is not underestimated. Even with multiple censuses, however, understimates will occur, because more individuals will breed during the season than are estimated at any one moment in time (Beaver et al. in press). This underestimate will be greatest in the far south, where the nesting season may last almost all year (Kushlan and White 1977). A major research need for interpreting future surveys is to determine on a regional scale the proportion of the total population of each species nesting in colonies at any one time.

A third bias in estimating total population is the presence of undetected heronries (Reynolds 1974). Disappearing colonies can be counted; new ones, however, often are not discovered and may contribute to an underestimate of the population size. New colonies probably are of minor importance to the species totals, because, as we found here, new colonies generally are small and contain few species.

We can not assess the significance of increases or decreases in population numbers between 1975 and 1976. The survey errors mentioned above, coupled with the possibility of population shifts between coastal and inland areas, make any conclusion about changes in numbers very tenuous. It therefore seems likely that even more accurate population estimates would still detect large yearly fluctuations and that trends from colony censuses could be detected only by large sampling programs over many years. Declines for a particular species over several years could serve as an indicator for more intense investigation.

We estimated that the heron population decreased 20% between 1975 and 1976. The Grey Heron population in England and Wales varied from −39% to +28% from year to year between 1928 and 1970 (calculated from Stafford 1971). The largest declines followed severe winters and may have resulted from mortality or from birds being physiologically unable to breed (Nicholson 1935, Alexander 1945, Stafford 1971). Significant declines in Cattle Egret populations of the United States have also followed severe winters (Bock and Lepthien 1976).

Summer weather may likewise have an impact on heron populations. In 1976, prolonged periods of wet and cool weather resulted in extensive nestling mortality along the North Carolina coast (J. Parnell pers. comm.). Breeding population estimates after such an event can be affected in two ways. First, immediate reduction in breeding numbers might occur as nests are deserted. Second, reduction in the population several years hence might occur because of lowered recruitment into the breeding population.

Heron numbers are also influenced by the availability and productivity of feeding habitat. The abundance of feeding habitat has been suggested to affect the number of nesting Grey Herons (Burton 1956). The abundance of wetlands and number of herons were found to be significantly correlated for Atlantic coastal states (Custer and Osborn 1977). Reduction in quality and stability of habitat has been linked to declines in numbers of herons nesting in the interior wetlands of the Everglades National Park (Robertson and Kushlan 1974). Additionally, lower prey availability may account for the lower number of White Ibises nesting in the Florida Keys than in nearby inland sites (Kushland and Robertson 1977).

We feel that our data strengthen the utility of using herons as biological indicators (see Ohlendorf et al. in press for review). We undertook the 1976 survey of Atlantic coast heron colonies as part of a biological indicator program to assess colony stability. If we were to sample herons at colony sites repeatedly, we wanted to know the probability that a given site and a given species would be present year after year. Although we were able to address the question of stability only for a 2-yr period, our results strongly support earlier investigations (Burton 1956, Garden 1958, Custer and Osborn 1977), which indicated that heron colony sites are used repeatedly. Our results also indicate that species composition and abundance within colonies are predictable year after year.

Acknowledgments

We are grateful for the assistance of L. J. Blus, P. D. Creighton, and W. H. Drury in 1975; B. Berg, R. Bollengier, Jr., R. M. Erwin, R. Farror, R. Ferren, B. French, J. J. Hatch, R. Kane, C. E. Korschgen, J. C. Ogden, and A. Sprunt, IV in 1976; and M. A. Byrd, H. W. Kale, II, J. A. Kushlan, S. Nesbitt, R. R. Odom, J. F. Parnell, W. B. Robertson, Jr., R. F. Soots, Jr., and D. A. White in both years. Their contributions are the basis for this study.

We thank B. M. Braun, P. J. Burgess, J. E. Clarke, P. R. Hochman, and C. Mansfield for technical assistance; G. L. Hensler and T. J. Fergin for statistical assistance; R. M. Erwin for supplying unpublished information; and D. L. Beaver, B. A. Cain, G. H. Hensler, D. A. McCrimmon, Jr., J. C. Ogden, H. M. Ohlendorf, J. F. Parnell, and D. H. White for reviewing the manuscript.

This work was supported by the Office of Biological Services, U.S. Fish and Wildlife Service.

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