DETERMINANTS OF GREAT BLUE HERON COLONY DISTRIBUTION IN COASTAL MAINE

JAMES P. GIBBS,[1,3] SUSAN WOODWARD,[2] MALCOLM L. HUNTER,[1] AND
ALAN E. HUTCHINSON[2]
[1]*Wildlife Department, College of Forest Resources, University of Maine, Orono, Maine 04469 USA, and*
[2]*Maine Department of Inland Fisheries and Wildlife, Bangor, Maine 04401 USA*

ABSTRACT.—The distribution of nesting Great Blue Herons (*Ardea herodias*) in coastal Maine was studied by examining the relationship between colony size and availability of food supplies near colonies, the selection of nesting habitat, and the spacing of colonies. Nineteen colonies (size range 4–252 nests) were located, all on marine islands. The number of nests in a colony was correlated positively ($r = 0.82$) with the area of tidal and inland wetlands within a 20-km radius of a colony. Nest and colony characteristics were highly variable, and suitable nesting habitat did not seem to limit colony size or distribution. The degree of forestation, presence of hardwoods, and distance of an island from towns and other islands with colonies were apparently important factors in selection of nesting islands. Colonies were uniformly distributed along the coast at intervals of about 16 km. We present a model for the observed dispersion of heron nests based on the conclusion that food competition between members of the same colony probably limits the size of colonies, whereas food competition between members of adjacent colonies may determine colony distribution. *Received 7 February 1986, accepted 16 June 1986.*

THE value of nesting in colonies has been examined by a number of workers (Lack 1968, Ward and Zahavi 1973, Hoogland and Sherman 1976, Krebs 1978, Burger 1981, Gotmark and Andersson 1984), but less is understood of what determines where a group of birds will form a colony or how large that group will be. Determinants of colony location tend to complement factors that contribute to colonial nesting behavior. Two examples are increased protection from predators through the selection of inaccessible nesting grounds (e.g. Cullen 1957, Burger and Lesser 1978, Nelson 1978) and enhanced utilization of resources by nesting close to food resources (Ward and Zahavi 1973; Kushlan 1976a, 1978).

Determinants of the number of individuals in a colony are less well understood. Among other factors, competition for sites may limit colony size, i.e. the number of individuals breeding in a colony, in some groups, e.g. some sulids (Nelson 1966), while food availability may limit colony size in ardeids (Werschkul et al. 1977, McCrimmon 1978, Beaver et al. 1980), phalacrocoracids, alcids, sulids, and larids (Furness and Birkhead 1984). Measuring a relationship between food availability and colony size is difficult because food resources used by colonial birds are typically patchy and temporary and are spread over vast areas around colonies.

Our purpose was to examine possible determinants of the distribution of nesting Great Blue Herons (*Ardea herodias*) in the coastal region of Maine. Nesting Great Blue Herons are large and conspicuous, and thus colony locations and sizes can be readily determined over a large area. Great Blue Herons also feed primarily in local, relatively permanent, wetland habitats. Relationships between colony size and an index of food resource availability, i.e. wetland availability, can be determined easily. We describe the pattern of nest dispersion for Great Blue Herons in the region. We then examine the relationship between the number of herons breeding in a colony and availability of foraging habitat; the selection of nesting habitat by herons by comparing the characteristics of nesting areas with those of similar, but unused, areas; and the spacing of colonies.

METHODS

Study area.—The study was confined to the coastal region of Maine, from Casco Bay to Machias Bay, a straight-line distance of about 300 km (Fig. 1). The

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[3] Present address: Division of Biological Sciences, 105 Tucker Hall, University of Missouri-Columbia, Columbia, Missouri 65211 USA.

coastline is extremely irregular, forming innumerable small bays and peninsulas, beyond which lie about 2,000 islands. Upland vegetation is dominated by spruce-fir forest (Davis 1966). Great Blue Herons nest in the region in large numbers [about 25% of the Atlantic coast population (calculated from Custer and Osborn 1977) and a majority of the Maine breeding population (Tyler 1977)], in small to medium-size (<250 nests), single-species colonies. Heron colonies are formed exclusively on forested marine islands from which herons travel to mainland areas to feed. Potential nesting sites for Great Blue Herons are found on about 450 isolated, forested islands that are present throughout the coastal region. Estuarine and saltmarsh feeding habitat for Great Blue Herons is also found throughout the region in varying concentrations.

Inventory of colonies.—An aerial survey was conducted by personnel of the Maine Department of Fisheries and Wildlife from a fixed-wing aircraft in mid-April 1983 to locate active colonies in the region. All herons nesting on the same island or within 0.25 km of each other were considered to represent a single colony. The number of nests in a colony was determined by ground counts of all active nests. In 15 of 19 colonies these counts were made during the breeding season from 2 to 21 June 1983. After the breeding season, from 1 August to 21 October 1983, 10 of these colonies were recensused, and the 4 remaining colonies were censused for the first time. For colony estimates, we used the postseason counts for these 4 colonies because there were no seasonal differences between the replicate counts ($P < 0.05$, $n = 10$, Wilcoxon paired-sample test).

Comparison of colony size with availability of feeding habitat.—We measured the area of wetlands within a 20-km radius of each colony and compared these with the number of nests in each colony. A 20-km radius was used because it approximates the longest distance Great Blue Herons travel from a colony to forage (Parris and Grau 1979, Piefer 1979, Thompson 1979). Existing wetland maps (McCall 1972) were used to locate all wetlands that lay partly or entirely within 20 km of each colony. In 1967 the Maine legislature passed the Wetlands Act that prohibits disturbance of wetlands; thus, it is unlikely that wetland areas have been altered significantly since McCall's (1972) survey. Areas of wetlands were summed for each colony for three wetland types: mudflat exposed at low tide; tidal wetlands; and inland, freshwater wetlands. Because only the shallower edges of ponds and lakes are accessible to wading birds, we adjusted the areas of these wetlands to include just a 5-m-wide littoral zone of each. Data were analyzed using stepwise linear regression with a forward selection procedure (SAS Inst. 1982).

We also examined the relationship between the number of nests in a colony and the number of nests in other colonies within the 20-km foraging range of that colony to test if potential food competitors may have limited colony size (Furness and Birkhead 1984).

Selection by herons of nest sites within forest stands.—In 14 accessible colonies, nest-tree, unused-tree, and forest-stand parameters were measured. A complete inventory of trees lying within the peripheral nest trees was made in most colonies, but in two large colonies trees were sampled using 12-m-radius plots randomly placed within the colonies. We determined species, diameter at breast height (DBH), and height for all trees greater than 10 cm DBH and 4 m in height. Relative tree condition was also estimated on the basis of upper crown foliage as: *dead,* i.e. lacking living foliage; *intermediate,* i.e. some live foliage present, or near complete foliage with some unfoliated branches present; or *complete,* i.e. complete foliage present. Measurements also were made of nest characteristics: nest height (m), nest distance from tree bole (m), and compass orientation with respect to tree bole. The number, dimensions, and genus of twigs and sticks of 5 fallen nests found in the Burying Island colony were determined. Colony area, delimited by the peripheral nest trees, was measured.

Single-factor ANOVA was used to detect differences in nest and nest-tree parameters among colonies. Within colonies, differences in height and DBH between nest trees and unused trees were examined using a two-tailed t-test. We used Chi-square analysis to examine whether the distribution of nest trees and unused trees was the same across the three condition classes.

Selection by herons of colony sites within islands.—Locations of all colony sites within islands were examined with respect to elevation, aspect, slope, and orientation relative to the center of a nesting island. Forest habitat used for nesting also was compared with the remaining unused habitat on nesting islands. Two characteristics were examined: forest type and canopy closure. Data on forest characteristics were collected by cover typing colony sites and nesting islands using recent aerial photographs (USDA, ASCS-16-79, 1980–1981) and on-site visits. Data were assembled into separate 2 × 2 contingency tables for Chi-square analysis.

Selection by herons of nesting islands.—Island selection for breeding habitat was examined by comparing the physiographic and vegetative features of two types of islands: those used for nesting by herons in 1983 (occupied, $n = 19$) and those not occupied by herons but presumably suitable for nesting (null). To obtain a null group we identified a population of islands that were located in the same range as occupied islands (along the Maine coast between Casco Bay and Machias Bay, within 15 km of the mainland and in a marine or estuarine environment) and supported a forest stand (contiguous group of >10 trees of heights >4 m). We excluded islands if they were inhabited by more than 100 people, or were joined to the mainland by a road. From this population 50

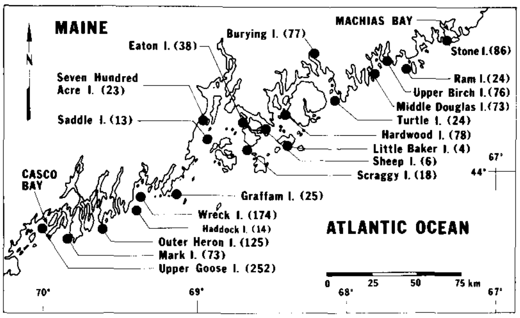

Fig. 1. Abundance and distribution of Great Blue Herons breeding in coastal Maine in 1983. All colonies were found in marine islands and are named by their respective island names. Nests per colony are given following colony name.

islands were selected randomly to comprise the null group, i.e. about 11% of the population of unused, but suitable, heron nesting islands, as we defined them.

We measured the following variables for each occupied and null island: (1) the area (ha) of the island above mean high tide; (2) the extent of forest (>4 m) covering the island, as a percentage; (3) the presence or absence of a stand of hardwood trees on the island; (4) the shortest straight-line distance (km) from the island to the mainland, (5) the average distance (km) from the island to the nearest two heron colonies on other islands; (6) the shortest straight-line distance (km) from the island to a town with at least 1,000 inhabitants in 1980 (U.S. Dept. of Commerce 1981); and (7) the area of estuarine wetlands within 20 km of the island. Only estuarine wetlands were measured because preliminary analysis indicated that these wetlands were more important in determining heron numbers in colonies than mudflat and inland wetlands.

We used single-factor ANOVA to compare variables measured on occupied and null nesting islands (except for the presence of hardwoods, which was compared using Chi-square analysis) to test the null hypothesis that islands used by herons were not different from other unused islands of similar habitat. The comparison also tested whether herons selected islands according to the habitat and geographical features that we measured.

Distribution of colonies.—Because preliminary analysis indicated that the distance of an island to adjacent heron colonies was important in distinguishing occupied from null islands, we further examined whether one colony affected the location of another by testing the null hypothesis that occupied islands were randomly spaced along the coast. We did this by comparing the distribution of the 19 occupied islands with 150 distributions of 19 islands randomly selected from the pool of potential null islands that were available to nesting herons throughout the region. Paired comparisons were made between the occupied distribution of nesting islands and each of the 150 null distributions to test whether both the variance and magnitude of the average distance (km) from an island to the nearest two islands in groups were equal. Variance ratio tests and two-tailed t-tests were used for comparing distributions.

RESULTS

Inventory of colonies.—Nineteen colonies with 1,203 nests were located along the Maine coast in 1983 (Fig. 1). Sixteen were active in 1982, 2 were previously unknown, and 1 was either previously unknown or its location had been misidentified (Maine Dept. of Inland Fisheries and Wildlife unpubl. data). Colony size ranged from 4 to 252 nests (mean ± SD = 63.3 ± 63.93). Since the last complete survey of heron colonies was undertaken in 1977 (Korschgen 1979), the breeding population appears to have remained stable after a long period of increase following the early 1900's. Disturbance by fishermen and milliners had greatly reduced the number of Great Blue Herons breeding in the region by the turn of the century (Palmer 1949).

Comparison of colony size with the availability of feeding habitat.—There was a significant positive correlation between colony size and the area of tidal and inland wetlands within 20 km of the colonies ($r = 0.82$, df = 3,18, $P < 0.001$). In the forward step-wise linear regression, area of tidal wetlands was entered into the regression model first and explained a majority of the variance in colony size ($r^2 = 0.62$, Fig. 2). The addition of inland freshwater wetlands explained 5% more variance in colony size ($r^2 = 0.67$). Mud-flat area was never entered into the model and did not seem to be an important determinant of colony size. Colony size was not correlated with the number of nests in other colonies within the foraging range of 20 km ($r = -0.13$, $P > 0.05$).

Selection by herons of nest sites within forest stands.—We measured 2,342 trees in 14 colonies: 679 nest trees supporting 786 nests, and 1,663 unused trees. Variability between sites was large in all respects (see Appendix); analysis of variance detected differences ($P < 0.001$) among colony sites for every variable measured. No distinct requisites for nest-site or colony-site habitat could be identified with regard to tree species, tree diameter, tree height, stand basal area, or stand density. Colony stands ranged from stands of substantial hardwoods ($\bar{x}$ DBH = 41 cm, $\bar{x}$ height = 18 m) to stands of stunted spruce trees ($\bar{x}$ DBH = 20 cm, $\bar{x}$ height = 10 m), although stands of spruce and fir, which dominate the region, were used most frequently.

Despite the variability, a number of correlates of nesting-tree use were identified within given colonies. In 9 of 13 colonies, herons occupied trees whose mean height was greater ($P < 0.05$) than the mean height of unused trees in the colony stand. In the remaining colonies no differences were found. In the 9 colonies where heights differed, nest trees were also of greater mean DBH ($P < 0.05$) than unused trees. Within a stand herons consistently occupied approximately 25% of the available nest trees. Distributions of nest trees and unused trees across the three condition classes were different ($P < 0.001$). Nest trees were less likely to have complete foliage (42%) than unused trees (57%).

Mean nest density for 11 colonies was 149.1 (±53.35 SD) nests/ha. Nesting trees usually contained only one nest (87%), and aggregations of more than two nests in one tree were uncommon (<2% of the nesting trees). Most nests were also located in the tops of nest trees. Mean nest height as a percentage of mean nest-tree height was 90%, and nest height correlated well with nest-tree height ($r = 0.85$, $P < 0.001$). Nests were oriented in all directions, but in colonies at more exposed locations nests showed a noticeable shift toward the east, i.e. on the lee side of the prevailing winds, and nearer to the tree bole, than nests in less exposed locations.

Nests examined ranged in depth (underside of bowl to rim) between 0.25 and 0.5 m and in width between 0.75 and 1.25 m. Twigs with which nests were constructed ranged in number between 150 and 300, in diameter between 2 and 20 mm, and in length between 0.1 and 1.5 m. Twigs used were primarily from alder, aspen, fir, and spruce trees. Nests were composed of 55% hardwood twigs, 42% softwood twigs, and 3% herbaceous plant stems and unidentified twigs.

Selection by herons of colony sites within islands.—Heron colonies usually occupied a small portion of a given nesting island (<10%) and were located high on the interior of nesting islands where they were invisible from the shore (17 of 19 colonies, J. Gibbs pers. obs.). No preference for sites with respect to slope, aspect, or orientation relative to the center of a nesting island was apparent. Analysis of forest habitat used for nesting vs. unused habitat on islands indicated that colonies were disproportionately found in forest with hardwoods ($P < 0.05$) and forest with a noncontiguous canopy ($P < 0.05$).

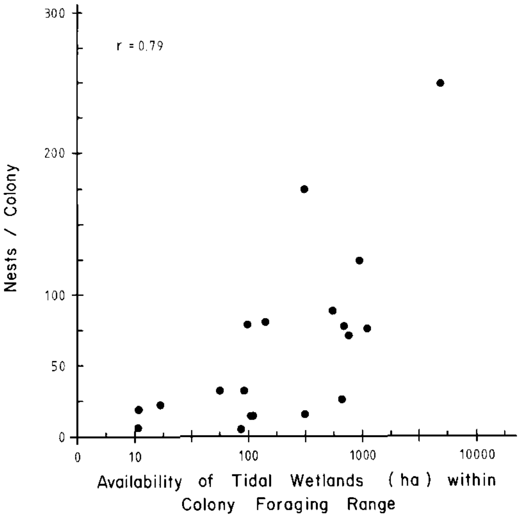

Fig. 2. Relationship between the number of nests in a colony of Great Blue Herons and the availability of tidal wetlands (ha present) within the foraging range (20 km) of a colony.

Selection by herons of nesting islands.—Herons nest on a small proportion (<5%) of seemingly suitable nesting islands in coastal Maine. Several differences between the islands used for nesting (occupied) and those that were not used (null) were found (Table 1). Occupied islands were best distinguished from null islands by being farther from other occupied islands and towns. The occurrence of stands of hardwood trees and the degree of island forestation were also important factors. It is possible that the presence of hardwoods was not independent of distance from towns. Notably, occupied islands with hardwood stands ($n = 12$) were farther from towns and mainland than occupied islands without hardwood stands ($n = 7$) (Kruskal-Wallis test, $P < 0.05$). They were not different with regard to other variables measured. However, the presence of hardwood stands on null islands was not associated with the distance of null islands from towns (≤5 km vs. >5 km, χ^2, $P > 0.05$). Furthermore, hardwood

TABLE 1. Heron nesting island characteristics. Values are means ± SD.

	Occupied	Null	P[a]
Area (ha)	20.3 ± 22.94	16.6 ± 24.27	NS
Degree of forestation (%)	84.4 ± 18.68	61.2 ± 35.41	**
Presence of hardwoods	63%	14%	***
Distance to nearest mainland (km)	3.0 ± 2.73	1.9 ± 2.21	NS[b]
Average distance to nearest 2 heron colonies (km)	16.1 ± 4.76	10.4 ± 3.75	***
Distance to nearest town (km)	8.0 ± 2.66	5.9 ± 3.12	**
Area of estuarine wetlands within 20 km (ha)	580.5 ± 1,057.04	755.4 ± 1,480.71	NS

[a] Result of one-way ANOVA, except for presence of hardwoods, which was tested using Chi-square analysis; *** = $P < 0.001$, ** = $P < 0.01$, NS = not significant.

[b] $0.05 < P < 0.1$.

stands were available within 2 km of all occupied islands that did not support hardwoods. It is notable that proximity to wetlands was not an important factor. Null islands actually had more wetland area within 20 km of them, and only 5% of the occupied islands vs. 16% of the null islands were located in estuaries.

Distribution of colonies.—In the comparison of occupied with null island distributions, distances between null islands were significantly more variable ($P < 0.05$) or significantly smaller ($P < 0.05$), or both, in 123 of 150 comparisons (82%). There was no difference for the remaining 27 comparisons. The mean interisland distance of the 150 null distributions pooled together was 11.7 km (±8.03 SD, CV = 69%) vs. 16.1 km (±4.76 SD, CV = 30%) for the occupied distribution (Fig. 3). When compared using a log-likelihood ratio goodness-of-fit test, the two distributions depicted in Fig. 3 differed significantly ($P < 0.01$).

DISCUSSION

Great Blue Herons nested in a great variety of vegetative and physiographic settings. They tended to use nest sites in the tops of taller trees in a given forest stand, perhaps because of ground predators, greater visibility, and flight access (Vermeer 1969, Gray et al. 1980). Herons seemed to affect their nest sites. The lack of canopy of nest trees relative to unused trees, and the reduction of forest canopy cover in colony areas compared with unused areas on nesting islands, probably were due to the detrimental effect of heron excrement on nesting vegetation (Kernes and Howe 1967, Weise 1978).

Humans present a threat to Great Blue Herons and other ardeids (Bjorklund 1975, Werschkul et al. 1976, English 1978, Burger 1981), and apparently human presence has affected selection of nesting islands because herons used islands that were farther from towns (Table 1). For Herring Gulls (*Larus argentatus*) nesting in coastal Maine, hatching success is inversely related to human disturbance (Hunt 1972). By nesting in these locations, perhaps out of the range of most small boats and picnickers (Hunt 1972), herons may reduce the frequency or intensity of human disturbance.

Reducing disturbance may have a cost, however, if it requires flying farther to feed. Compared with null islands, occupied islands were located farther offshore and less frequently in estuaries, and thus had less wetland area nearby on average than did null islands. This indirectly suggests that nesting farther from sources of human disturbance may be more important in breeding-site selection than proximity to feeding areas.

The presence of hardwoods on an island apparently also affected the selection of nesting islands, although it is not clear why. Hardwood trees do not seem to be important substrates for nesting because, while hardwood and mixed stands were present on 12 occupied islands, herons built nests predominantly in hardwoods on only 3 of these islands. Apparently, it is proximity of hardwoods that affects site use by herons. It is plausible that herons nest near hardwoods to obtain nest materials more easily. Because the nests examined contained at least 150 twigs each, over half of which were from hardwood trees, and because herons bring only one or two twigs at a time to the nest (J. Gibbs pers. obs.), presumably a large number of flights must be made to obtain twigs to construct or rebuild nests each season. A substantial reduction in nest-building effort may accrue to herons that nest near hardwood stands. Mainland areas support an abundance of hardwood stands and are accessible to herons that nest nearby. Herons that nest farther from mainland areas may not be able to utilize mainland hardwood stands because of the increased flight distance involved, and may instead rely on island hardwood stands. This may explain why occupied islands farther from the mainland supported hardwood stands while islands nearer did not.

Despite these findings, we doubt that the availability of suitable habitat for nesting is an important influence on the location of heron colonies in the region. Colonies usually occupied only a small proportion (<10%) of the forest on a nesting island, and only a small proportion (<5%) of seemingly suitable nesting islands was occupied. This underutilization of available habitat and the observed variability in the characteristics of sites used for nesting support the conclusion that suitable nesting sites were not limited. While hardwoods clearly affected site use, the presence of hardwoods is not limiting site use because colonies on at least three islands without hardwoods have thrived for more than 10 successive nesting seasons (Tyler 1977).

The distance of an island from islands already occupied by herons has an important influence in the location of colonies. Increased distance from islands already occupied by herons was one of the most important characteristics distinguishing occupied from null islands (Table 1), and the spacing of colonies was more uniform and at greater distances than expected from a random distribution of sites (Fig. 3). Fasola and Barbieri (1978) found that mixed-species heron colonies in Italy were spaced irregularly such that each colony had the same quantity of feeding grounds within its foraging range. In coastal Maine, colony spacing does not reflect the distribution of feeding grounds in this way; an even spacing along the coast is maintained despite great variation in the availability of feeding grounds along the coast.

This uniform spacing of colonies is maintained despite great variations in colony size (4–252 nests). Colony size apparently was not limited by nesting habitat availability at breeding sites because usually only a small portion (<10%) of suitable nesting areas on islands was occupied. Colony size also does not seem to be restricted by the number of food competitors nesting in nearby colonies (see Furness and Birkhead 1984) because there was no significant negative relationship between the number of nests in a colony and the number of nests in other colonies within the foraging range of a colony. The uneven distribution of wetland habitat, however, may make this test for such effects invalid (Furness and Birkhead 1984). Colony size seems to be determined mostly by local food availability because there was a positive linear relationship between colony size and the area of tidal and inland wetlands within 20 km of each colony. Burger (1981) found a similar relationship between the size of multispecies heronries and an estimate of foraging habitat along the New Jersey coast, and Werschkul et al. (1977) found that Great Blue Heron colony size was positively related to the size of estuaries near colonies in coastal Oregon.

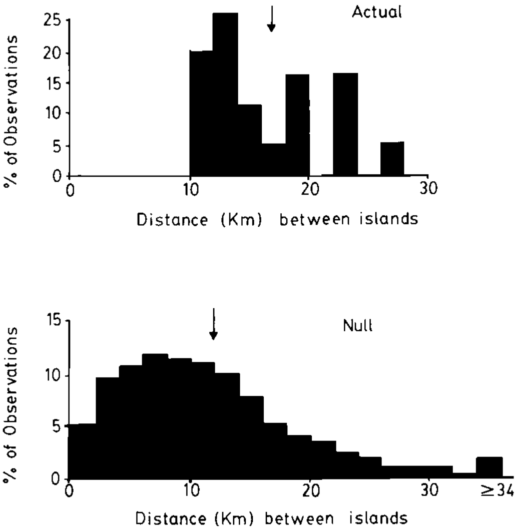

Fig. 3. Comparison of island spacing in occupied vs. null nesting island distributions. The "actual" histogram represents distances between the 19 islands occupied by herons in 1983; the "null" histogram represents distances between 2,850 unoccupied islands pooled from 150 distributions of 19 islands each. Arrows indicate group means.

This relationship between wetland abundance and colony size can perhaps be best explained in terms of the distances that herons fly from colonies to forage. Because herons must feed within a certain range of the colony, colonial nesting might force them to compete with

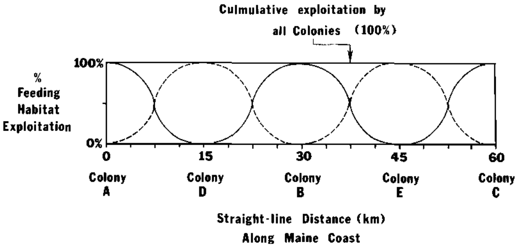

Fig. 4. An idealized distribution of Great Blue Heron colonies in coastal Maine. Curves represent the percentage of feeding habitat exploitation by each colony. Colonies are spaced at distances equivalent to the upper ranges of heron foraging flights, and feeding habitat exploitation by herons nesting in a given colony decreases with distance from the colony. However, cumulative exploitation of feeding areas by colonies remains at 100% throughout the region. Colonies A, B, and C (solid line) represent established colonies initially; colonies D and E (dotted line) represent newer colonies that filled the gaps between established colonies (see text).

other colony members for food resources around the colony (Burger 1981) if food was limiting within available patches. This range equals the distance at which it is energetically feasible for herons to fly between foraging areas and the colony (Orians 1971), ca. 1-5 trips per day (Pratt 1970, Pierce 1982). It is reasonable to assume that this distance would be roughly equal for all individuals, and, given an unlimited supply of nest sites, nest material, and mates, the quantity of food or availability of feeding territories within this range would determine the abundance of birds nesting in a colony. Other workers (Lack 1954, Burton 1956, Vermeer 1970, Fasola and Barbieri 1978, Burger 1981) have speculated that ardeid colony size is related to the availability and quality of feeding habitat near colonies.

We have developed a verbal model or scenario that explains how the present distribution of colonies may have originated because of the pattern of resource exploitation by colonies. We make three assumptions concerning coloniality in herons:

(1) Herons nest in colonies as large as permitted by resource limitations (i.e. foraging habitat availability). This may be because reproductive success increases with colony size (Thomas 1986) because of lowered predation rates (Patterson 1965, Robertson 1973) or increased foraging success through information transfer (Krebs 1974), or other reasons. Such enhancement has not been documented in some bird species (Hoogland and Sherman 1976).

(2) Herons are not limited by nesting site availability (this paper). Thus, they may nest in locations where competition at nearby foraging areas is minimal. They should particularly avoid competing with conspecifics from other colonies because the costs of competition are not offset by the benefits of nesting with these birds.

(3) There is a negative correlation between the distance from a wetland to the colony and the frequency with which the wetland is visited by foraging herons (Custer and Osborn 1978, Thompson 1979), and, beyond a certain range, there are no visits.

Given these assumptions, we can speculate how the observed distribution of heronries came into existence since 1900 when protection laws were enacted that allowed this population of herons, which had been greatly reduced by human disturbance (Palmer 1949), to reoccupy the coast. Herons that dispersed from an existing colony to form a new colony would have benefited most by locating the new colony far beyond the foraging range of the existing colony, thereby gaining exclusive access to unexploited feeding areas. Once the region was occupied fully by colonies with nonoverlapping foraging ranges, new colonies would have been established at the outer reaches of the foraging ranges of existing colonies, i.e. roughly halfway between colonies, because feeding habitat exploitation by existing colonies would have been lowest in these areas. Once these "gaps" were filled and the population reached carrying capacity, this pattern of colony distribution would have remained stable because there were no new locations to establish a colony where the benefits of reduced competition would exceed the costs of nesting in a smaller colony. This pattern of colony location is presented graphically in Fig. 4.

If colonies were founded in this manner we predict three manifestations: (1) distribution of colonies at an interval that is some function of heron foraging distances, (2) a correlation between colony size and the availability of feeding habitat within a similar interval, and (3) full exploitation of available feeding habitat. Our results support the first and second predictions, although additional data on lengths of foraging flights would strengthen our conclusions. Obtaining information on competition between colonies and exploitation of available habitats would require watching large numbers of marked herons on the foraging areas.

Whether this model can account for patterns of nest dispersion in other populations of colonial birds probably depends on the availability and distribution of potential nest sites and food resources for other populations. Where nesting sites are scarce (Nelson 1966), food resources are found in widely separated areas (Kushlan 1976a), or food resources are very abundant and cannot be defended (e.g. Kushlan 1976b, 1978, 1981), birds will probably form colonies near these resources. Where nesting sites and food resources are available throughout a region and birds are territorial while foraging (e.g. Krebs 1974, Custer and Osborn 1978), a uniform distribution of colonies, with sizes that vary with local food resource availability, may occur as predicted by this model.

This study has three practical implications for habitat management for Great Blue Herons in coastal Maine. First, given that wading bird abundance is correlated with coastal wetland abundance locally (Werschkul et al. 1977, Burger 1981, this paper) and by state (Custer and Osborn 1977), any large-scale decrease in wetlands area probably will cause a decline in the number of breeding herons. Second, increased levels of disturbance also may cause a decline in breeding populations given that alternative nesting areas are not available to herons in the region that are more distant from sources of human disturbance than areas currently in use. Third, potential nest sites should be conserved to replace those that will decline because of occupancy (see Kernes and Howe 1967, this paper); these should be selected primarily for their proximity to existing colonies to retain the original geographic setting of a colony relative to other colonies.

ACKNOWLEDGMENTS

We thank Philip Conkling, James Connors, David and Lisle Gibbs, Amy-lyn Gumprecht, Karen Gustafson, Joan Howard, Thane Joyal, Sandra Lovett, Kathy Owens, and Thomas Smith for their assistance. Cassie and Harold Gibbs and Albert Doan were supportive of these efforts. Thomas Custer, Bill Drury, Tony Gaston, Lisle Gibbs, Bill Glanz, John Krebs, James Kushlan, Jerry Longcore, Gordon Orians, and Ray Owen kindly offered their advice during the preparation of this manuscript.

This study was financed through the Maine Chapter of The Nature Conservancy's Small Grants Program, 1982. Indispensible support also was provided by the Maine Department of Inland Fisheries and Wildlife's Marine Wildlife Study. The Maine Department of Marine Resources facilitated visits to offshore islands. The College of Forest Resources of the University of Maine generously loaned forest mensuration equipment and the use of a word processor, and the University of Maine Honors Program provided funds for the preparation of the manuscript. This paper is Maine Agricultural Experiment Station Publication No. 1129.

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APPENDIX. Nesting vegetation characteristics. Means ± SD are given. Colonies are ordered from south to north.

	Nest-tree characteristics			Stand characteristics		
Colony name	Predominant genus	n	DBH (cm)	Height (m)	Basal area (sq m/ha)	Density (no. trees >10 cm DBH/ha)
Upper Goose Is.	*Fagus/Acer/ Betula*	86	40.9 ± 13.8	18.4 ± 2.4	—	—
Mark Is.	*Abies*	68	21.3 ± 6.1	11.3 ± 3.1	10.5	356.1
Outer Heron Is.	*Picea*	117	29.4 ± 5.7	15.0 ± 2.1	29.6	720.4
Saddle Is.	*Abies*	11	25.2 ± 4.4	13.2 ± 2.1	—	—
Seven Hundred Acre Is.	*Picea*	33	36.7 ± 8.0	18.2 ± 1.1	35.7	602.5
Eaton Is.	*Picea*	29	36.1 ± 11.0	19.9 ± 2.7	31.6	832.3
Scraggy Is.	*Picea*	23	24.4 ± 5.5	14.1 ± 2.4	—	—
Little Baker Is.	*Picea*	4	31.4 ± 11.2	13.4 ± 1.5	37.5	695.8
Hardwood Is.	*Picea*	53	32.6 ± 9.6	20.3 ± 1.5	—	—
Burying Is.	*Picea*	67	32.3 ± 6.4	18.1 ± 2.8	27.1	555.6
Turtle Is.	*Picea*	31	37.5 ± 8.0	21.4 ± 1.8	50.1	689.9
Middle Douglas Is.	*Betula*	70	19.4 ± 5.3	11.8 ± 3.4	18.4	764.4
Upper Birch Is.	*Picea*	63	25.6 ± 5.7	14.5 ± 2.7	26.8	602.8
Ram Is.	*Abies*	24	23.4 ± 8.5	14.5 ± 3.0	—	—