SPATIAL RELATIONSHIPS BETWEEN NESTING COLONIES AND FORAGING AREAS OF GREAT BLUE HERONS

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ABSTRACT.—I examined spatial relationships between nesting colonies of Great Blue Herons (Ardea herodias) and their aquatic foraging areas by synthesizing data from a survey of nesting colonies, a study of foraging Great Blue Herons, and a wetland inventory. I assessed whether Great Blue Herons gained energetically by nesting colonially at sites central to foraging areas versus solitarily and dispersed evenly over foraging areas.

Nesting colonies (n = 29) were closer to local concentrations of foraging habitat and to points of minimum aggregate travel to all regional foraging areas than expected by chance. The number of nests per colony correlated positively with the availability of foraging habitat (in hectares) within commuting distance of a colony and negatively with foraging costs (km flown per ha wetland visited). Through computer simulations I found that an equally sized, hypothetical population of solitarily nesting herons dispersed evenly over foraging areas would experience higher foraging costs than colonially nesting herons. The spatial arrangement of wetlands upon the landscape of inland Maine limits the availability of sites with efficient access to heron foraging areas, and favors clumped nesting patterns. Received 2 October 1990, accepted 23 February 1991.

COLONIAL birds often forage far from nesting or roosting sites (e.g. Hamilton et al. 1967), and species that depend on spatiotemporally clumped foods in theory benefit energetically by nesting in colonies central to the food distribution (Horn 1968, Wittenburger and Hunt 1985). My purpose was to evaluate two assumptions of Horn's (1968) geometrical model: (1) that colonies of a large, colonially nesting wading bird were located centrally to the food distribution, and (2) that energy expenditures were less for colony members than for an equally sized, hypothetical population distributed evenly over the same food distribution (Wittenburger and Hunt 1985). In Maine, Great Blue Herons (Ardea herodias) feed primarily in local and relatively permanent aquatic habitats (Palmer 1949) where food availability varies spatially and temporally (Krebs 1974). Thus, the distribution and abundance of nesting herons can be compared with that of various types of wetlands ranked according to their foraging profitability to herons. I compared the spatial configuration of aquatic foraging areas near (1) occupied colony sites and seemingly suitable—but unoccupied—sites, (2) nests of colonial breeders and nests of a hypothetical, equally sized population of dispersed, solitarily nesting herons, and (3) nesting colonies of varying size.

METHODS

Colony and null sites.—I studied 29 nesting colonies (i.e. aggregations of >1 nesting pair) in inland Maine (Maine State Planning Office and Maine Dep. Inland Fish. Wildl., Augusta, Maine, unpubl. data). The sample included colonies active in 1980–1986 that were >15 km from marine or estuarine habitats, and >5 km from other colonies. Maximum estimates of nesting populations (nests per colony) during 1980–1986 were used. A sample (n = 30) of seemingly suitable, but unoccupied, sites (null sites) was chosen for comparison with colony sites. I located null sites at randomly generated longitudinal and latitudinal coordinates in Maine (stratified by county to reflect the geographical distribution of colonies studied) that in 1980 lay within a forested area (>1 ha of trees, >10 m high with contiguous canopy), >5 km from colony sites or other null sites, >15 km from marine and estuarine areas, and <1 km from a stream, river, lake, or other wetlands (because heron colonies are typically near water; Short and Cooper 1985).

Compilation of foraging habitat data.—I compiled information on aquatic habitats (wetlands) within a 15-km radius of each colony and null site (hereafter referred to as the foraging range or foraging area). A 15-km distance approximates the farthest Great Blue Herons regularly travel between colonies and foraging areas (Parris and Grau 1979, Thompson 1979, Dowd and Flake 1985). Data on type, area, and location of wetlands whose geographical center lay within the foraging range of each colony were obtained

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from the Maine Wetlands Inventory (Maine Dep. In-
land Fish. Wild., Augusta, Maine; see McCall 1972),
which describes approximately 20,000 wetlands lo-
dated during a state-wide inventory in 1963-1973 of
wetlands >10 acres (ca. 4 ha). Because Maine’s Wet-
lands Act of 1967 prohibited disturbance of wetlands
>10 acres, wetland areas probably have not been al-
tered significantly since this survey. Although many
wetlands <10 acres were excluded from the Maine
Wetlands Inventory, about 80% of the gross wetland
area in Maine is composed of wetlands >10 acres, and
Great Blue Herons prefer to forage at wetlands >10
acres (Gibbs et al. in press).

I grouped aquatic habitats in the Maine Wetlands
Inventory (McCall 1972) as four general types: (1)
swamps (shrub swamps [Type 6], wooded swamps [Type
7], and seasonally flooded basins or flats [Type 1] with
>50% coverage by woody vegetation); (2) bogs (Type
8); (3) marshes and meadows (inland fresh meadows
[Type 2], inland shallow fresh marshes [Type 3], in-
land deep fresh marshes [Type 4], and seasonally
flooded basins or flats [Type 1] with ≤50% coverage
by woody vegetation); and (4) lake and river shorelines.

Portions of lakes with areas of woody or emergent
vegetation were tallied as swamp or marsh and mead-
ow, respectively. The Maine Wetlands Inventory pro-
vided areal information for lakes (inland open fresh
water [Type 5]) but not for rivers. Only the shallower
edges of lakes and rivers are accessible to wading
birds, however, so I measured the lengths of lacus-
trine and riverine shorelines from maps (DeLorme
Publ. Co. 1989) with a digital planimeter. From these
length measurements, I calculated area of shoreline
habitat based on an average 5-m-wide littoral zone.

Different types of wetlands are of different foraging
value to herons, so it was necessary to assign wetlands
of each type a weight proportional to the type’s fre-
quency of use by foraging Great Blue Herons. A study
of 87 freshwater wetlands in eastern and central Maine
(Gibbs et al. in press), which included >3,500 h of
observation of bird activity, provided a basis for de-
riving weighting factors. Based on numbers of Great
Blue Herons sighted per hour per unit wetland area
(areas of lacustrine wetlands were adjusted to include
just a 5-m-wide littoral zone), I calculated weights
equal to frequency of use of each wetland type as a
proportion of the most intensively used wetland type.
The factors were as follows: lake and river shorelines
(1.0), marshes and meadows (0.25), bogs (0.16), and
wooded and shrub swamps (0.12). The area (ha) of
each wetland was multiplied by its respective weight
to estimate foraging habitat availability at that wet-
land.

Spatial analyses.—I compared availability of forag-
ing habitat near colony and null sites by summing
the areas of wetlands occurring within 5, 10, and 15
km of each site. I also compared average foraging costs
between null and colony sites, which equaled the sum
of flight distances (km) to all wetlands in the foraging
area divided by foraging habitat availability (ha) (i.e.
average distance flown to access 1 ha of foraging hab-
itat).

I determined the point in each foraging area at
which travel to all wetlands would be minimized, and
I hypothesized that if heron colonies were located
centrally to foraging areas, colony sites would be, on
average, closer to this point than would null sites.
For every point on a grid with cells 0.1 km² overlying
each foraging range, I calculated the length of a sin-
gle, linear flight to each wetland and multiplied that
by the weighted area of the wetland to which the
flight was made. I considered points of minimum
aggregate travel to occur where the sum of weighted
flight distances was minimized.

I compared foraging habitat availability and flight
costs for Great Blue Herons nesting in colonies with
those for an equally sized, hypothetical population
of herons nesting solitarily and dispersed evenly over
the same foraging areas. Hypothetical solitary nests
were located within 7.5 km of each colony, and cal-
culations of foraging habitat availability and flight
costs were restricted to a 7.5-km-wide foraging range
of each colonial and solitary nesting pair to accommo-
date all birds within the 15-km-radius area for which
wetland data were available. Although Great Blue
Herons fly farther than 15 km to feed, most foraging
flights probably are shorter (Custer and Osborn 1978,
Dowd and Flake 1985), and use of a 7.5-km foraging
range for this analysis would therefore still produce
useful comparative data. An iterative procedure was
used to obtain a hyperdispersion of solitary nests.
Within each foraging area, a single nest was initially
located at random. A sample (n = 500) of additional
nest locations was subsequently generated at random,
from which the nest that maximized the nearest
neighbor distance (Clark and Evans 1954) among pre-
viously located nests was retained. This procedure
was repeated until a number of solitary nests in the
foraging area that equaled the number of nests in the
associated colony was obtained. Although it is doubt-
ful that all locations of hypothetical solitary nests
were in suitable nesting habitat, inland Maine’s land-
scape is heavily forested (ca. 90%; Powell and Dickson
1984) and undeveloped, particularly in the remote
regions where Great Blue Herons nest. Herons are
remarkably plastic in their choice of nesting sub-
strates (Beaver et al. 1980), and most locations of hy-
pothetical nests were therefore probably situated in
or quite near suitable habitat.

RESULTS

Local availability of wetlands influenced
where Great Blue Herons formed nesting col-

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TABLE 1. Availability of foraging habitats and average foraging costs within different ranges of Great Blue Heron nesting colonies and null sites in inland Maine, 1980-1986 (mean ± 1 SD).

<table>
<thead>
<tr>
<th>Distance (km)</th>
<th>Colony sites (n = 29)</th>
<th>Null sites (n = 30)</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>River and lake shorelines (ha/100 km²)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>≤5</td>
<td>28.0 ± 16.6</td>
<td>14.5 ± 10.6</td>
<td>0.001</td>
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<tr>
<td>≤10</td>
<td>23.4 ± 9.5</td>
<td>14.0 ± 7.5</td>
<td>0.001</td>
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<tr>
<td>≤15</td>
<td>19.5 ± 6.0</td>
<td>12.6 ± 5.1</td>
<td>0.001</td>
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<tr>
<td>Bogs (ha/100 km²)</td>
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<tr>
<td>≤5</td>
<td>92.2 ± 179.3</td>
<td>23.2 ± 40.2</td>
<td>0.045</td>
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<tr>
<td>≤10</td>
<td>60.0 ± 68.7</td>
<td>28.4 ± 44.0</td>
<td>0.039</td>
</tr>
<tr>
<td>≤15</td>
<td>54.9 ± 62.5</td>
<td>25.4 ± 30.1</td>
<td>0.023</td>
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<tr>
<td>Meadows and marshes (ha/100 km²)</td>
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<tr>
<td>≤5</td>
<td>75.9 ± 154.6</td>
<td>72.3 ± 137.6</td>
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</tr>
<tr>
<td>≤10</td>
<td>61.3 ± 68.8</td>
<td>58.4 ± 44.0</td>
<td>0.92</td>
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<tr>
<td>≤15</td>
<td>63.0 ± 93.3</td>
<td>72.0 ± 91.3</td>
<td>0.71</td>
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<td>Shrub and wooded swamps (ha/100 km²)</td>
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<td></td>
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<tr>
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<td>172.0 ± 194.5</td>
<td>153.7 ± 170.1</td>
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<tr>
<td>≤10</td>
<td>149.0 ± 125.4</td>
<td>121.5 ± 102.5</td>
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<tr>
<td>≤15</td>
<td>141.1 ± 105.6</td>
<td>126.2 ± 83.2</td>
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<td>Total (ha/100 km², weighted by wetland type)</td>
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<tr>
<td>≤5</td>
<td>82.2 ± 61.0</td>
<td>54.9 ± 44.6</td>
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<tr>
<td>≤10</td>
<td>66.2 ± 30.3</td>
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<tr>
<td>≤15</td>
<td>60.9 ± 31.9</td>
<td>49.8 ± 25.9</td>
<td>0.15</td>
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<td>Foraging costs (km flown/ha wetland accessed)</td>
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<tr>
<td>≤5</td>
<td>1.5 ± 0.9</td>
<td>3.2 ± 5.6</td>
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<tr>
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<td>3.0 ± 2.7</td>
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<tr>
<td>≤15</td>
<td>2.8 ± 1.1</td>
<td>3.2 ± 1.2</td>
<td>0.45</td>
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</tbody>
</table>

P-value according to Mann-Whitney U-test.

See Methods for weighting procedure.

Great Blue Herons nested colonially in inland Maine at sites central to the distribution of foraging areas, and colonially nesting herons experienced lower foraging costs, on average, than would be expected had they nested solitarily and dispersed evenly over foraging areas. An energetic advantage accrued to colonial nesters because aquatic foraging areas were distributed unevenly upon the landscape of inland Maine. Wetlands occurred in complexes along stream and river courses and lakeshores, and wetland complexes were scattered across the landscape and isolated by large expanses of forested upland. Colonies typically formed near a wetland complex and centrally to other wetland complexes in a region. Solitary nests and null sites, however, typically were located neither near nor centrally to wetland complexes in the foraging area, and therefore had, on average, less foraging habitat nearby.

DISCUSSION

Great Blue Herons nested colonially in inland Maine at sites central to the distribution of foraging areas, and colonially nesting herons experienced lower foraging costs, on average, than would be expected had they nested solitarily and dispersed evenly over foraging areas. An energetic advantage accrued to colonial nesters because aquatic foraging areas were distributed unevenly upon the landscape of inland Maine. Wetlands occurred in complexes along stream and river courses and lakeshores, and wetland complexes were scattered across the landscape and isolated by large expanses of forested upland. Colonies typically formed near a wetland complex and centrally to other wetland complexes in a region. Solitary nests and null sites, however, typically were located neither near nor centrally to wetland complexes in the foraging area, and therefore had, on average, less foraging habitat nearby.

Energetic aspects of traveling between nests and foraging areas may induce herons to nest in the same general area, but are unlikely to lead to formation of the tightly packed nesting colonies observed. Herons likely nest closely...
Fig. 1. Mean availability of foraging habitats (ha wetland per km$^2$ of landscape) within 15 km of 29 Great Blue Heron nesting colonies and 30 null sites in inland Maine, 1980-1986.
Great Blue Herons form colonies in forest stands of widely varying height, stocking, and species composition (e.g. Gibbs et al. 1987), and such plasticity in habitat use may occur in response to the variability of vegetation at locations that provide efficient access to foraging areas.

To facilitate this analysis, I made a number of simplifications about patterns of habitat ex-

Fig. 2. Displacement of Great Blue Heron nesting colonies and null sites from points of minimum aggregate travel (filled dots) to all aquatic habitats within 15 km of colonies.

Fig. 3. Size of nesting populations of Great Blue Herons at colonies in inland Maine and abundance of foraging habitats within 15 km of colonies (A), availability of foraging habitat per nesting pair (B), and average costs of accessing foraging areas (C).
exploitation by Great Blue Herons. I assumed that herons ranged over the entire foraging area and made separate foraging flights to each wetland. During the critical period of colony formation, individual herons typically scatter throughout the colony foraging range to feed (Van Vessem et al. 1984, Simpson et al. 1987, Marion 1989), but thereafter activities of individuals may be restricted to a few, defended areas (Van Vessem et al. 1984, Marion 1989). Also, herons may well visit more than one wetland on each foraging trip, and frequency of wetland visitation probably declines with distance of a wetland from the colony (Custer et al. 1978). These simplifications of habitat-use patterns might be warranted because all colony members likely use the entire foraging area surrounding a colony during the nesting season (Van Vessem et al. 1984, Down and Flake 1985), and my analysis was concerned with foraging energetics of average individuals. A more sophisticated analysis would consider how foraging energetics interact with life history traits of individual herons to affect their choice of a nesting colony (Brown et al. 1990). Additionally, I assumed that sighting frequency of herons at various types of wetlands reflected foraging habitat quality (see Van Horne 1983). Size of a nearby colony (Fig. 3B) and distance of a wetland from a colony (Custer et al. 1978) may influence the sighting frequency of herons at a wetland. Increased competition for foraging areas could represent a potential cost of colonial nesting not assessed in my study. Densities of hypothetical solitary nesters were, by definition, equal to those of colonial nesters in this study, however, so numbers of conspecifics with overlapping foraging ranges were similar for colonial and solitary nesters.

Numbers of Great Blue Herons nesting at colonies in inland Maine were proportional to the availability of local foraging habitats (see also Werschkul et al. 1976, Burger 1981, Gibbs et al. 1987). Recruitment of nesting herons into colonies could follow a pattern of "ideal-free" distribution (Fretwell and Lucas 1970), whereby herons settle among available colonies in densities such that cost-to-benefit ratios of nesting are similar in all colonies (Brown et al. 1990). Four surveys of reproductive success in nesting colonies of Ardea spp. have found no relationship between colony size and reproductive success (Werschkul et al. 1976, Quinney 1983, Van Vessem and Draulans 1986, Marion 1989). Trade-offs among nesting in colonies of various sizes that are related to foraging might include increased availability of foraging habitats (Fig. 3A) and lower foraging costs near larger colonies (Fig. 3C), but more wetland available per nesting pair of herons in smaller colonies (Fig. 3B) and shorter foraging flights from small colonies because of fewer competitors (Marion 1989).

Acknowledgments

N. Edelson’s surveys of inland Maine’s heron colonies provided a basis for my study. The Hirundo Wildlife Trust, with the assistance of R. Owen, provided financial support for this study. J. Connolly retrieved the data from the Maine Wetlands Inventory (Federal Aid Project W-62-R), and J. Longcore kindly shared information on heron foraging habitats. L. Goss, M. Hunter, and an anonymous reviewer provided helpful comments on the manuscript. This publication is No. 1543 of the Maine Agricultural Experiment Station.

Literature Cited


