

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. Inland Fish. Wildl., Augusta, Maine; see McCall 1972), which describes approximately 20,000 wetlands located during a state-wide inventory in 1963–1973 of wetlands >10 acres (ca. 4 ha). Because Maine's Wetlands Act of 1967 prohibited disturbance of wetlands >10 acres, wetland areas probably have not been altered 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], inland deep fresh marshes [Type 4], and seasonally flooded basins or flats [Type 1] with \leq 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 meadow, respectively. The Maine Wetlands Inventory provided 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 lacustrine 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. Shoreline data were compiled within 3 concentric 5-km-wide bands, each divided into 8 equally sized sectors (24 sectors total) that surrounded colony and null sites.

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 frequency 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 deriving 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 wetland.

Spatial analyses.—I compared availability of foraging 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 habitat).

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 single, 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 calculations 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 accommodate 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 previously 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 doubtful that all locations of hypothetical solitary nests were in suitable nesting habitat, inland Maine's landscape 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 substrates (Beaver et al. 1980), and most locations of hypothetical nests were therefore probably situated in or quite near suitable habitat.

RESULTS

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

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 \pm 1 SD).

Distance	Colony sites (<i>n</i> = 29)	Null sites (<i>n</i> = 30)	<i>P</i> ^a
River and lake shorelines (ha/100 km²)			
≤5 km	28.0 \pm 18.6	14.5 \pm 10.6	0.001
≤10 km	23.4 \pm 9.5	14.0 \pm 7.5	0.001
≤15 km	19.5 \pm 6.0	12.6 \pm 5.1	0.001
Bogs (ha/100 km²)			
≤5 km	92.2 \pm 179.3	23.2 \pm 40.2	0.045
≤10 km	60.0 \pm 68.7	28.4 \pm 44.0	0.039
≤15 km	54.9 \pm 62.5	25.4 \pm 30.1	0.023
Meadows and marshes (ha/100 km²)			
≤5 km	75.9 \pm 154.6	72.3 \pm 137.6	0.92
≤10 km	61.3 \pm 68.8	58.4 \pm 44.0	0.92
≤15 km	63.0 \pm 93.3	72.0 \pm 91.3	0.71
Shrub and wooded swamps (ha/100 km²)			
≤5 km	172.0 \pm 194.5	153.7 \pm 170.1	0.70
≤10 km	149.0 \pm 125.4	121.5 \pm 102.5	0.35
≤15 km	141.1 \pm 105.6	126.2 \pm 83.2	0.54
Total (ha/100 km², weighted by wetland type^b)			
≤5 km	82.2 \pm 61.0	54.9 \pm 44.6	0.04
≤10 km	66.2 \pm 30.3	48.9 \pm 24.2	0.02
≤15 km	60.9 \pm 31.9	49.8 \pm 25.9	0.15
Foraging costs (km flown/ha wetland accessed)			
≤5 km	1.5 \pm 0.9	3.2 \pm 5.6	0.04
≤10 km	2.1 \pm 0.9	3.0 \pm 2.7	0.06
≤15 km	2.8 \pm 1.1	3.2 \pm 1.2	0.45

^a *P*-value according to Mann-Whitney *U*-test.

^b See Methods for weighting procedure.

onies. Total wetland area (weighted by wetland type) was greater and average foraging costs lower at colonies than at null sites at ranges of 5 km (i.e. *locally*) and 10 km but not at 15 km (i.e. *regionally*) (Table 1, Fig. 1). The area of river and lake shorelines and of bogs was greater within the foraging ranges of colonies than within those of null sites, but the area of wooded and shrub swamps and of marshes and meadows was similar (Table 1). Dispersion of wetlands also influenced where Great Blue Herons formed nesting colonies; colonies were located closer to the point of minimum aggregate travel to all possible foraging areas ($t = 2.03$, $P = 0.047$) than were null sites ($3.6 \text{ km} \pm 2.6 \text{ [SD]}$ vs. $5.1 \text{ km} \pm 3.2$; Fig. 2).

Numbers of Great Blue Herons nesting in colonies varied widely (2–80 nests). Two correlates of colony size were identified. Larger colonies had more available foraging habitat within $\leq 15 \text{ km}$ ($r = 0.64$, $P < 0.01$; Fig. 3A). More foraging

habitat was available per nesting pair, however, in smaller than larger colonies (Fig. 3B). Larger colonies also had lower average costs of accessing wetlands within 15 km of colonies than did smaller colonies (km flown/ha wetland accessed, $r = 0.57$, $P < 0.01$; Fig. 3C). Wetland availability and foraging costs together explained about half the variance in colony size (Adj. $r^2 = 0.47$), and partial correlation analysis indicated that they contributed independently ($P < 0.05$).

Computer simulations of dispersed nesting patterns revealed that, within a 7.5-km-wide foraging radius originating from nests of each colonial and solitary pair of herons, foraging habitat availability would be, on average, 23% higher (mean $[\pm \text{SD}]$ difference = $33.8 \text{ ha} \pm 88.9$, paired *t*-test, $t = 8.33$, $P < 0.001$) for colonial birds (mean = 183.5 ha) than if they had nested solitarily (mean = 149.7 ha). Similarly, average foraging costs would be 10% lower (mean difference = 0.14 km flown per hectare wetland accessed ± 0.65 , paired *t*-test, $t = 4.87$, $P < 0.001$) for birds nesting colonially (mean = 1.30 km/ha) than if they had nested solitarily (mean = 1.44 km/ha).

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

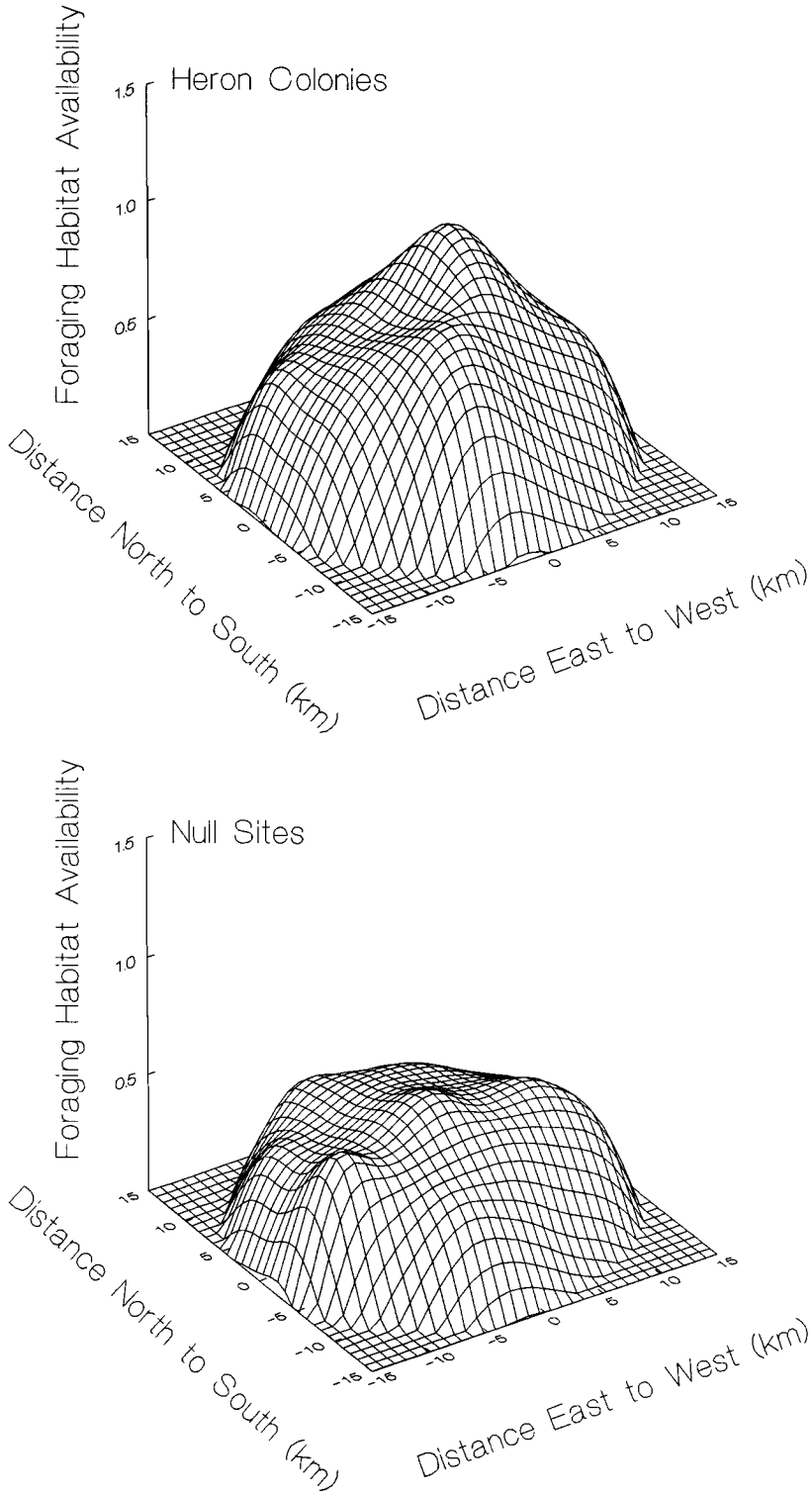


Fig. 1. Mean availability of foraging habitats (ha wetland per km² of landscape) within 15 km of 29 Great Blue Heron nesting colonies and 30 null sites in inland Maine, 1980–1986.

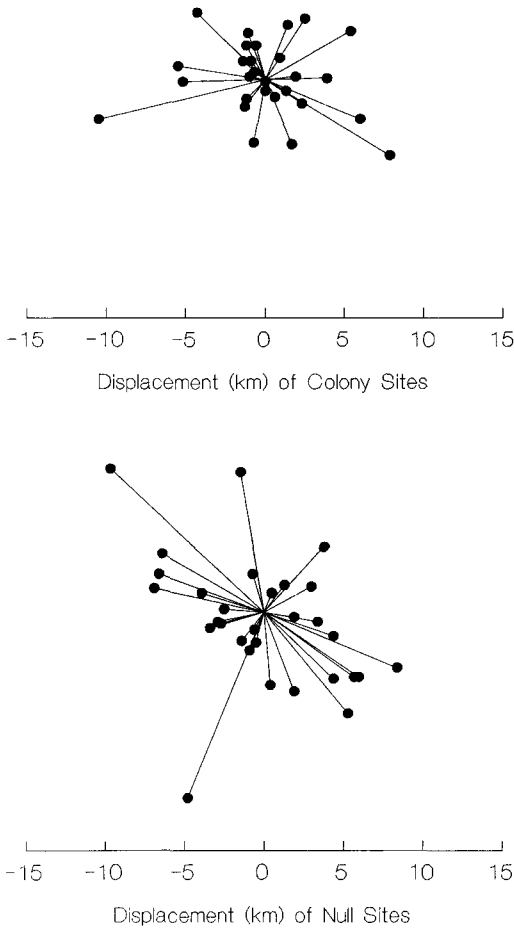


Fig. 2. Displacement of Great Blue Heron nesting colonies and null sites from points of minimum aggregate travel (filled dots) to all aquatic habitats within foraging areas.

together to facilitate food finding (Krebs 1974), social stimulation (Simpson et al. 1987, Draulans 1988), and predator avoidance (Simpson et al. 1987). The main implication of my study is that the spatial arrangement of wetlands upon the landscape of inland Maine limits the availability of energetically profitable locations for Great Blue Herons to form nesting colonies. 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-

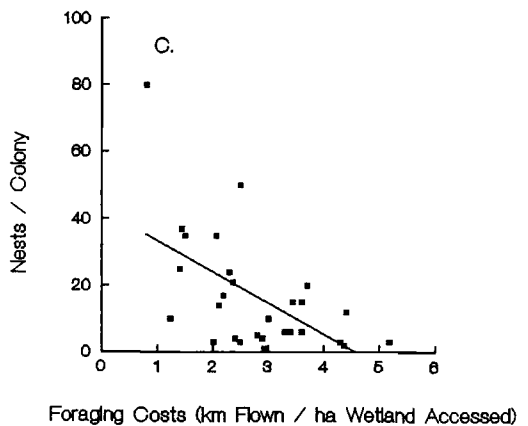
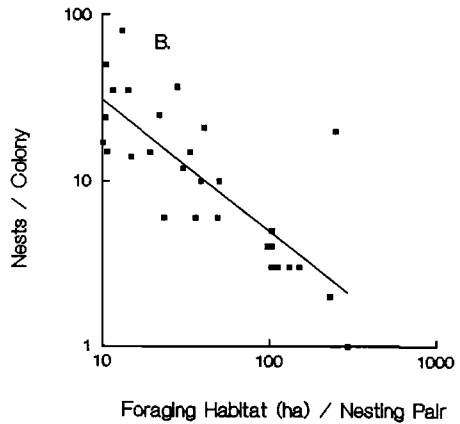
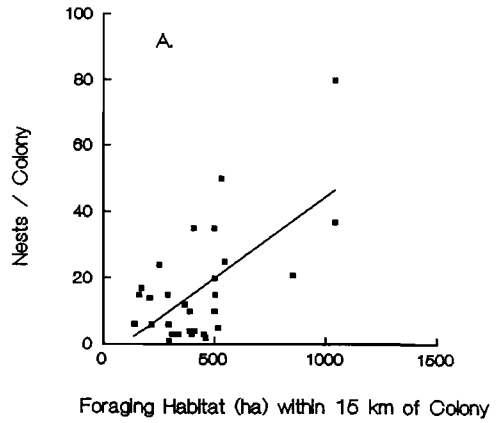


Fig. 3. Size of nesting populations of Great Blue Herons at colonies in inland Maine and abundance of foraging habitats within 15 km of colonies (A), availability of foraging habitat per nesting pair (B), and average costs of accessing foraging areas (C).

ploitation 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).

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