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Area-dependent Changes in Bird Densities in Iowa Marshes

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Species richness and density of Iowa marsh birds were positively correlated with marsh area, but area accounted for 69% of the variation in species richness and only 19% of the variation in density. Although densities of five of nine species examined correlated with marsh area, total density was not significantly correlated with area when the effects of species richness were eliminated. Area was the most frequent significant variable in regression equations for species richness, total density, and the densities of nine individual species on six variables. Unlike species-area relationships, density-area relationships are relatively weak, and knowledge of other ecological factors would provide more useful information for the design of nature preserves. The increases in total density and densities of four individual species with area provide only limited support for the MacArthur-Wilson island biogeography hypothesis, but data on reproductive success will be needed to provide an unequivocal test.

INDEX DESCRIPTORS: Iowa marsh birds, density-area relationship.

The relationship between the area of a habitat patch and the number of bird species occurring in the patch has been much studied, especially after publication of the island biogeography hypothesis (Mac-Arthur and Wilson, 1963, 1967). The species-area relationship for birds using habitat "islands" has been examined in prairie remnants (Samson, 1980), shelterbelts (Martin, 1980), cemeteries (Lussenhop, 1977), parks (Gavareski, 1976), marshes (Tyser, 1983; Brown and Dinsmore, 1986, 1988), and especially forests (Galli et al., 1976; Anderson and Robbins, 1981; Burgess and Sharpe, 1981; Harris 1984; Robbins et al., 1989). Although many conservationists contend that area should be an important factor in nature-preserve design (Diamond, 1975; Samson, 1980; Anderson and Robbins, 1981; Harris, 1984; Tilghman, 1987), most studies of area effect use presence/ absence data. Haila (1988) argues that in order to show an area effect, one must detect decreasing density in smaller sites.

Forest area has been shown to affect bird densities (Ambuel and Temple, 1983; Blake and Karr, 1987; Tilghman, 1987). If such a relationship is found in marshes, this information could be used to design marsh preserves to ensure the maintenance of minimum viable populations. A density-area relationship also would provide additional support for the island biogeography hypothesis. We previously reported on the relationship between marsh area and bird species richness (Brown and Dinsmore, 1986, 1988). Here, we examine the relationship between marsh area and bird densities and the effects of some habitat variables on this relationship. Our objectives were to (1) determine if marsh birds exhibited a density-area relationship that might be useful for natural resource managers; and (2) compare the species-area and density-area relationships to determine if both support the dynamic equilibrium hypothesis.

METHODS

We selected 30 marshes of similar physical characteristics in 11 counties in northwestern and north-central Iowa. The marshes ranged from 0.2 to 182.0 ha and fulfilled four criteria: (1) each site was a Type III (seasonal marsh) or Type IV (semipermanent marsh) wetland (Stewart and Kantrud, 1971); (2) each site had 40-60% of its area in open water, corresponding to the hemimarsh stage, which is highest in bird species richness and density (Weller and Spatcher, 1965; Weller and Fredrickson, 1974); (3) 15 sites were isolated (\leq 25 ha of other marshes within a 5-km radius), and 15 were within wetland complexes (\geq 55 ha of other marshes within a 5-km radius); and (4) the sites were evenly distributed over five size classes (\leq 1 ha, 1-4.9 ha, 5-10.9 ha, 11-20 ha, and \geq 20 ha).

Field work was conducted during May and June of 1983 and 1984. Each marsh was visited three times annually between sunrise and 1000. Species densities for each marsh were compiled by noting all birds seen or heard within fixed-radius (18 m) circular plots (area = 0.1 ha) during 6-min observation periods (Edwards et al., 1981). Plots were randomly placed 18 m from open-water areas so that the band of vegetation at the open-water and vegetation interface was sampled. During the last 2 min of each observation period, tape recordings of secretive birds (bitterns in 1983 and rails in both years) were played in an attempt to detect their presence (Marion et al., 1981). All birds and nests we saw while moving between plots were included in the species richness measurement. The number of plots/ site ranged from 2 to 7 (n = 95, 1983) and 2 to 6 (n = 91, 1984). Areal coverage varied from nearly 100% at small sites to less than 1% at large sites.

A species was considered to be breeding at a site if an active nest was found, flightless young were seen, or adults were observed during two of the three visits. Two exceptions were made each year. Blackcrowned night-herons (*Nycticorax nycticorax*) and Forster's terns (*Sterna forsteri*) occurred during all three visits each year at one site, but they were actually breeding in nearby marshes.

Marsh areas were measured from aerial photographs by using a digital planimeter. Each May, average water depth was determined by placing 1-4 transects across each site and measuring depth at 10-m intervals. The proportion of marsh in open water was estimated visually. The total area of all other marshes within a 5-km radius of each study site was used as an inverse measure of isolation. The distance of each marsh from Des Moines, Iowa was used as an inverse measure of its proximity to the prairie pothole region of the northcentral U.S. and south-central Canada (range). Iowa marshes are on the periphery of the prairie pothole region, and Des Moines approximately marks the southern end of the pothole region in Iowa. The farther north a marsh is from Des Moines, the closer it is to the main breeding range for many of the species present. Johnson and Grier (1988) found that some duck species they examined preferred the central portion of their range and occupy it before using more peripheral areas.

The average number of individuals of each species detected per plot at each marsh was used as a measure of apparent density (average number of detections per visit/number of plots in marsh). Our results are not true density estimates, but indices of bird abundance in each marsh. Total bird density is the sum of all individual species densities. Simple and partial correlations and stepwise regression (Zar, 1974) were used to examine the effects of marsh area, range, water depth, isolation, and percent open water on the number of breeding species present (species richness) and total bird density. Density-area and density-habitat relationships were examined for nine species which

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accounted for 97% of all bird detections (d): blue-winged teal (Anas discors) d = 73, virginia rail (Rallus limicola) d = 135, sora (Porzana carolina) d = 70, American coot (Fulica americana) d = 162, marsh wren (Cistothorus palustris) d = 229, swamp sparrow (Melospiza georgiana) d = 103, red-winged blackbird (Agelaius phoeniceus) d = 645, yellow-headed blackbird (Xanthocephalus xanthocephalus) d = 1792, and common grackle (Quiscalus quiscula) d = 56.

RESULTS AND DISCUSSION

The only habitat variables examined (water depth and percent open water) were significantly related to marsh bird density in only four cases (Table 1). Previous studies have found significant habitat effects (e.g., Weller and Spatcher, 1965; Weller and Fredrickson, 1974), but the marshes we sampled were originally selected to minimize habitat variation. Marsh isolation influenced American coot, swamp sparrow, red-winged blackbird, and common grackle densities. Range was the second most common significant regression variable. Species richness, total density, and blue-winged teal and American coot densities were higher in marshes closer to the center of the prairie pothole country whereas red-winged blackbird and common grackle densities were lower.

Marsh area accounted for 69% of the variation in the number of breeding bird species in our study area. Although there was a significant relationship between area and total density, area accounted for only 19% of the variation in total density and density regression equations were generally dominated by other variables (Table 1). The species-area relationship was strong (r>0.8) in both years, and the inclusion of additional regression variables did not greatly increase (14%) the amount of variation explained. The density-area relationship

Table 1. Regression equations for species richness, total density, and densities of nine bird species (birds/0.1-ha plot) on marsh habitat variables. All variables listed are significant (P < .05) and appear in the order of their importance. n = 30 in 1983, 30 in 1984.

	YEAR	EQUATION	R ²	Р
Species richness	1983	3.69 + 3.66 (Log Area) + 0.02 (Range)	0.78	0.0001
	1984	4.57 + 3.76 (Log Area) + 0.02 (Range)	0.80	0.0001
	Both	4.13 + 3.71 (Log Area) + 0.02 (Range)	0.79	0.0001
Total density	1983	-0.86 + 0.02 (Range) + 0.04 (% Open Water)		
		+ 0.03 (Water Depth)	0.58	0.0001
	1984	5.49 + 1.38 (Log Area)	0.27	0.0031
	Both	0.004 + 0.01 (Range) + 1.4 (Year) + 0.75 (Log Area) + 0.02 (% Open Water)	0 47	0.0001
	1097	+ 0.75 (Log Alea) + 0.02 (% Open water)	0.47	0.0001
blue-winged teal	1985	No significant relationship 0.65 ± 0.001 (Rappe)	- 0.15	- 0.0317
	Both	-0.00 + 0.001 (Range) = 0.1 (Log Area)	0.1)	0.0517
	Dotti	+ 0.004 (Water Depth)	0.26	0.0006
Virginia rail	1983	No significant relationship	-	-
	1984	0.16 + 0.11 (Log Area)	0.14	0.0424
	Both	No significant relationship	-	
Sora	1983	No significant relationship	-	-
	1984	0.31 - 0.004 (Water Depth)	0.18	0.0350
	Both	0.29 - 0.005 (Water Depth) + 0.08 (Log Area)	0.16	0.0081
American coot	1983	0.13 + 0.17 (Log Area)	0.19	0.0151
	1984	-0.03 + 0.002 (Range) - 0.004 (Isolation)	0.37	0.0026
	Both	-0.03 + 0.002 (Range) - 0.004 (Isolation)	,	
		+ 0.11 (Log Area)	0.36	0.0001
Marsh wren	1983	No significant relationship	-	-
	1984	0.14 + 0.25 (Log Area)	0.37	0.0003
	Both	0.25 + 0.17 (Log Area)	0.12	0.0059
Swamp sparrow	1983	0.07 + 0.0004 (Isolation)	0.37	0.0003
	1984	0.13 + 0.0002 (Isolation)	0.17	0.0241
	Both	0.10 + 0.0003 (Isolation)	0.27	0.0001
Red-winged blackbird	1983	2.55 + 0.002 (Isolation) - 0.021 (% Open Water)	_ /_	
	100/	- 0.005 (Range)	0.49	0.0005
	1984	1.88 - 0.55 (Log Area)	0.26	0.0042
	Both	1.92 - 0.015 (% Open Water) + 0.001 (Isolation) + 0.5 (Year) = 0.004 (Range) = 0.26 (Log Area)	0.38	0.0001
Yellow-headed blackbird	1097	No significant relationship	0.90	0.0001
	1905	$2 40 \pm 1.39$ (Log Area)	0.29	0.0023
	Both	0.63 + 1.04 (Log Area) + 1.02 (Year)	0.26	0.0029
Common grackle	1983	No significant relationship		
	1984	0.06 + 0.0004 (Isolation)	0.40	0.0002
	Both	0.18 + 0.0003 (Isolation) - 0.0008 (Range)	0.25	0.0003

was relatively weak in both years (r < 0.6) and the inclusion of additional regression variables provided a greater increase (147%) in the amount of variation explained. The density-area relationship was not significant when the effect of species richness was eliminated. Deciduous forest birds in northeastern United States exhibit a similar pattern: area accounts for 79% of the variation in species richness and 25% of the variation in density (Tilghman, 1987). Other studies have found no relationship between area and bird densities (Nilsson and Nilsson, 1978; Martin, 1980) or that other habitat variables were more important than area (Ambuel and Temple, 1983; Blake and Karr, 1987). Unlike species-area relationships, density-area relationships seem to provide little useful information for the design of nature preserves for marsh birds.

In most cases, the variables included in the regressions changed between years. Area was the most frequent significant regression variable, but accounted for the greatest amount of variation in only two species: marsh wren and yellow-headed blackbird (when both years were combined). Density-area patterns exhibited by marsh birds provide only limited support for the dynamic equilibrium hypothesis, but while density may be preferable to presence/absence data for measuring area and habitat effects, there are limitations (Haila, 1988; Pulliam, 1988; Van Horne, 1983). Ultimately, reproductive success and not density should be measured (Haila, 1988).

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