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DETERMINANTS OF SPECIES-AREA RELATIONSHIPS FOR MARSH-NESTING BIRDS

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Abstract. To clarify the underlying causes of the species-area relationship in marsh-nesting birds, I studied eight freshwater tidal marshes of the Connecticut River that differed in area, degree of isolation, mudflat cover, water cover, tidal regime, and extent of individual plant communities. I measured these habitat variables on aerial infrared photos, and surveyed bird populations by mapping the distribution of all birds in marshes under 5 ha in area and establishing 50-m radius plots in marshes over 5 ha. From surveys, I determined species richness, population densities, and total populations. Analysis revealed a positive relationship between species richness and area, but no correlation between area and habitat heterogeneity. Other habitat variables were poor predictors of species richness. The lack of a relationship between habitat and species richness appeared to be a consequence of most vegetation types present not being sufficiently distinct for birds to differentially associate with them. I also found no relationship between bird population density and area, suggesting that habitat quality in marshes did not improve with increasing size, and species evenness declined with increasing richness because greater richness was associated with the presence of more rare species. Larger marshes had more rare species, species with larger populations, and species with a minimum threshold area for occurrence. Thus, my results are consistent with theoretical predictions that larger populations are less prone to local extinction and, as individuals are added to a community, more rare species are present.

The positive relationship between species richness and habitat area has been called one of the few laws of community ecology (Schoener 1976). Such relationships have been reported for marsh bird communities (Burger et al. 1982, Brown and Dinsmore 1986, Craig and Beal 1992, Colwell and Taft 2000, Shriver et al. 2004, Guadagnin and Maltchik 2007), but the factors contributing to them remain unclear.

Area might influence species richness because larger marshes: 1) preferentially accumulate species, such as those requiring larger home ranges, because sites below a threshold size are unsuitable or not recognized as suitable (Klopfer and Ganzhorn 1985, Ahlering et al. 2006, Betts et al. 2007), or because the probability of being colonized by rarer species is higher (Craig and Beal 1992, Hubbell 2001), 2) contain more species because the larger and denser (Benoit and Askins 2002) populations are less prone

to local extinction (assuming stochastic population fluctuations drive extinctions; Rosenzweig 1995), and 3) accumulate species because habitat quality increases with increasing area (Wilcove 1985, Gibbs and Faaborg 1990, Burke and Nol 1998). Although population density is not related solely to habitat quality, ideal free distribution theory predicts that density relates directly to area when populations have not saturated sub-optimal habitats (Fretwell 1972).

Potential habitat effects on richness include increasing heterogeneity that permits more marsh species to be present because they require either specific or multiple habitats (Weller 1999, Lor and Malecki 2006, Guadagnin and Maltchik 2007). One habitat feature, water level, is frequently cited as a determinant of the presence of certain species (Weller 1999, DesGranges et al. 2006).

In addition to the effects that area and habitat (i.e., local phenomena) may have on species richness, habitat isolation (i.e., landscape-level phenomena) may further influence richness, with degree of isola-

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tion inversely related to richness (MacArthur and Wilson 1967). In support of this contention, Fairbairn and Dinsmore (2001) found that the presence of additional habitat within 3 km was positively related to richness in Great Plains marshes. However, other investigators have reported no apparent relationship between proximity and species richness in marsh habitats (Shriver et al. 2004, Rehm and Bal-dassarre 2007).

Most investigators examining species-area relationships have not been able to separate the effects of habitat area from those of habitat characteristics because these variables are often correlated (Wiens 1989). Despite this tendency, Craig and Beal (1992) separated area and habitat in a study of breeding birds in an estuary and found that measures of habitat were independent of area, with species richness positively related to area and negatively related to habitat heterogeneity and extent of water cover. However, these authors considered the entire salt-to-freshwater continuum of the estuary and, as a result, a variety of habitats were examined, including saline cordgrass, brackish cattail-reed, and freshwater bulrush-sedge marshes.

To better understand the underlying causes of the species-area relationship, I focused on a single habitat, the freshwater tidal marshes of the Connecticut River that had similar plant communities and did not exhibit a gradient in water salinity. In this habitat, I examined bird species richness and populations in marshes that differed in area, degree of isolation, mudflat cover, water cover, tidal regime, and extent of individual plant communities.

METHODS

Study areas. The Connecticut River estuary is a virtually intact system that has been in its present state for about 3000 years (Hill and Shearin 1970). I studied eight sites that included the largest and smallest marshes in this system. These sites comprised 72% of the total area of freshwater tidal marshes on the river, and included all vegetation and habitat types present in these marshes. The sites included five larger marshes (Cromwell Meadows, Pecauset Meadows, Whalebone Creek, Pratt/Post Cove, and Chapman's Pond) and three smaller marshes (< 5 ha; Pecauset II, Cromwell II, and Cromwell III). Daily tidal flooding, similar plant communities, and surrounding floodplain forest characterized the sites. The sites differed in degree of isolation from other marshes, mudflat cover, amount of open water, mean tidal range, and extent of cover by individual plant communities (Table 1).

Habitat evaluations. Classification of plant associations was based on Metzler and Damman's (1985) analysis of vegetative associations of the Connecticut

River floodplain and on the classification of tidal wetlands employed by the Connecticut Department of Environmental Protection (R. Rozsa, pers. comm.). I simplified these classifications to focus on cover present at my study sites. Associations that predominated in areas of tidal flooding (0.3 – 0.8 m) were characterized by 1) river bulrush (*Scirpus fluviatilis*), 2) calamus (*Acorus calamus*), 3) water horsetail (*Equisetum fluviatile*), 4) cattail (*Typha angustifolia*), 5) tussock sedge (*Carex stricta*), and 6) reed (*Phragmites communis*). Associations in sites flooded by tides less than 0.3 m were dominated by 7) sensitive fern (*Onoclea sensibilis*), 8) *Osmunda* spp., and 9) reed canary grass (*Phalaris arundinacea*), whereas those flooded by tides more than 0.8 m were dominated by 10) pickerelweed (*Pontederia cordata*), 11) tuckahoe (*Peltandra virginica*), and 12) water smartweed (*Polygonum* spp.).

Using direct observation and photos, I prepared field maps of each site, delineating the early June extent of the 12 plant associations. I transferred data with ESRI Arcview 3.3 and Image Analysis software to digitally enhanced computer images derived from aerial infrared photographs (scale = 1:2500). For each site, I then determined cover by vegetation associations, the extent of open water and mudflats at low tide and total habitat area (vegetated area, mudflat, and water cover). I assumed that the nearby Connecticut River had an equal effect on all sites, so did not include it in measures of water cover. I also evaluated marsh isolation (Fairbairn and Dinsmore 2001) by digitally measuring the amount of additional marsh habitat present within 2 km of the center of each marsh, and derived measures of mean tidal range at each site from nearby Connecticut River sampling stations (NOAA 2007).

I used Simpson's Index, an index that does not assume any underlying abundance distribution (Rosenzweig 1995), to compute indices of heterogeneity for the sites:

$$SI = \Sigma [(n^2 - n) / (N^2 - N)],$$

where n is the cover by a particular habitat, and N is the total cover by all habitats (Simpson 1949). For habitat calculations, I included vegetation, mudflat, and water cover.

Bird surveys. I gathered population data during the height of the breeding season (8 May–21 June; Craig 1990, 2004). I visited each site three times each year, with surveys beginning 30 min before sunrise (about 04:45 during May and June) and ending by 11:00. For the first 30 min, I searched for inconspicuous species that might vocalize before or at first light. By about 05:15, when light levels permitted visual observations, I began collecting data on

all species. I recorded the time of first encounter of each species to construct species accumulation curves, and recorded only marsh specialist species that breed in interior marsh vegetation.

At sites <5 ha, I recorded the location and movements of all birds encountered on maps. Cumulative observations of movements provided information on territorial and home range distributions that helped verify that I counted all individuals present. During counts, I used a recorder (Optimus CTR-117, Radio Shack, Fort Worth, Texas) to play back calls (Walton and Lawson 1994) of secretive species from a sufficient number of locations (about 5) to ensure that birds anywhere in the marsh could detect them. The sequence of playback was Virginia Rail (*Rallus limicola*), King Rail (*R. elegans*), Sora (*Porzana carolina*), Black Rail (*Laterallus jamaicensis*), Least Bittern (*Ixobrychus exilis*) and American Bittern (*Botaurus lentiginosus*), with 30 sec of calls followed by 30 sec of silence between successive calls.

For sites larger than 5 ha where every individual could not be counted, I established transects through marsh interiors paralleling the boundaries of the generally elongated marshes, with 50 m radius circular plots placed at 150 m intervals (Conway and Gibbs 2005). I surveyed the maximum number of points possible for the size and configuration of each site. To assess whether the plots approximated a random sample of habitats present, I visually evaluated the percent cover by vegetation types in all plots during early June 2000, and compared these cover estimates with those from my habitat evaluations from aerial infrared imagery. I found no difference between the results of my visual evaluation and estimates based on aerial infrared imagery ($\chi^2_8 = 8.5, P = 0.4$).

Within plots, I noted all species encountered during a 5-min passive listening/observation period, and also noted species beyond 50 m and between sampling stations for use in determining species richness and densities of species not detected by plot surveys. Following the listening/observation period, I played back calls of the species noted above. I plotted the locations of survey points on field maps so that points could be located on subsequent visits.

Using two survey methods could complicate comparisons because of differences in sampling intensity and non-homogeneity of variances, but different methods were needed to effectively sample marshes that differed considerably in size. I sampled all sites until species accumulation curves reached an asymptote and, as recommended by Rosenzweig (1995), I also evaluated the significance of differences in sampling intensity with $-\ln$ Simpson's Index (Simpson 1949).

Population/ community analyses. I determined species richness for the eight sites using cumulative lists of species encountered during the three visits

each year. Species evenness, how evenly populations are spread among species (Hurlbert 1971), was determined using the coefficient of variation. This measure describes proportionate variation that increases as evenness among species declines and decreases as it becomes similar. When I performed exploratory analyses with other evenness indices (Smith and Wilson 1996), the coefficient of variation performed nearly identically.

I computed densities of species at small sites from counts for the entire site. At larger sites, I computed site-specific densities of passerines and less conspicuous species from survey plots. I determined densities of larger, wide-ranging and easily detected species (e.g., swans) from counts for an entire site. To smooth differences in site-related variance and to provide the most representative estimates of density, I computed the average adult breeding density of each species as determined by my three visits/site/year. From density computations, I estimated total populations at each site by multiplying density/ha by the area of the site.

For Marsh Wrens (*Cistothorus palustris*), Swamp Sparrows (*Melospiza georgiana*), and Red-winged Blackbirds (*Agelaius phoeniceus*), most individuals detected were males. Females were secretive and less frequently observed, so density evaluations for these species refer specifically to densities of territorial adult males. Densities of species where males or females were equally likely to be encountered were interpreted as total densities/ marsh. Because of these differences, I analyzed the densities of these two groups separately.

Statistical analyses. I performed nonlinear regression analyses to seek the relationship between species richness and area and habitat heterogeneity and area. In calculating regressions, I used a global model that fitted data to equation parameters shared for both years of observation (Mostulsky and Christopoulos 2004).

I performed exploratory stepwise multiple regressions for each years' data to provide insights into the comparative relationship of independent variables to species richness. Models included terms for habitat area, habitat heterogeneity, percent water cover, percent mudflat cover, tidal range and isolation. I then analyzed the relationship between species richness and habitat variables using a repeated measures general linear model.

Normality and homogeneity of variance assumptions of multivariate analysis were often best met by log-transforming data before conducting tests, and doing so also made relationships among independent and dependent variables linear. Where variances were unequal, I weighted the dependent variable. I evaluated collinearity among variables by examining data plots, correlation matrices of variables,

TABLE 1. Characteristics of marshes studied, including area of different plant associations, low tide mudflats, low tide open water, mean tidal range, amount of additional marsh habitat within 2 km, and computations of habitat heterogeneity.

Habitat (ha)	Study Site							
	Pecausett	Pecausett II	Cromwell II	Cromwell III	Whalebone	Chapman	Pratt	
Total area	26.74	1.50	130.97	3.27	1.48	29.59	44.87	41.53
Water	8.66	0.01	18.79	0.01	0.03	5.54	23.06	5.92
Mudflat	0.80	0.01	4.52	0.15	0.07	12.73	0.67	10.20
<i>Osmunda</i>	0.09	0.00	0.05	0.00	0.00	0.00	0.86	0.01
<i>Onoclea</i>	1.28	0.11	1.80	0.04	0.05	0.00	0.00	0.03
<i>Carex</i>	0.74	0.09	0.00	0.00	0.12	0.54	6.10	10.26
<i>Peltandra</i>	0.80	0.00	3.78	0.29	0.00	0.09	1.34	1.45
<i>Typha</i>	0.24	0.00	1.08	0.00	0.00	0.89	5.56	7.99
<i>Phragmites</i>	0.07	0.00	0.05	0.00	0.00	0.01	1.26	0.82
<i>Pontederia</i>	0.00	0.00	5.27	0.00	0.00	12.68	0.00	9.48
<i>Polygonum</i>	0.00	0.00	0.28	0.00	0.28	0.00	0.00	0.00
<i>Acorus</i>	1.43	0.45	1.27	0.29	0.97	4.19	3.67	4.91
<i>Equisetum</i>	4.00	0.18	1.31	1.21	0.00	0.00	0.00	0.00
<i>Scirpus</i>	9.15	0.66	48.92	1.22	0.04	5.67	3.02	0.71
<i>Phalaris</i>	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00
Marsh proximity (ha)	14.19	39.43	9.11	108.97	55.21	63.35	5.94	5.49
Mean tidal range	0.70	0.70	0.67	0.67	0.67	0.82	0.85	0.87
Habitat SI	0.25	0.31	0.45	0.29	0.48	0.28	0.31	0.19

and collinearity diagnostics (SPSS 2006). In assessing test results, I considered the significance of parameter estimates, confidence intervals, r^2 (coefficient of determination), n^2 (partial eta-squared—an estimate of effect size) and the corrected Akaike’s Information Criterion (AIC_c)—a comparative measure of model fit to data.

RESULTS

Marsh communities were dominated by Red-winged Blackbirds, Swamp Sparrows and Marsh Wrens, with these three species accounting for 89% of all individuals present. Mallards (*Anas platyrhynchos*) and Virginia Rails (*Rallus limicola*) were also present at most sites. Other species encountered, particularly rarer species, were present primarily at larger sites.

Habitat. Nonlinear regression yielded a non-significant habitat heterogeneity-area relationship ($r^2_{1,6} = 0.4, P = 0.12$), with a quadratic model fitting data better than a linear model (AIC_c probability of best fit = 0.99). The largest site, Cromwell Meadows, was dominated by *Scirpus* communities, but had the most habitat types, apparently due to a greater range of microelevations (hence, high tide water depths)

than at other sites. Other sites exhibited greater evenness of cover among vegetation types, although Whalebone Creek had high cover by floating-leaved communities, and *Scirpus* and *Equisetum* communities dominated Pecausett Meadows. The smallest sites had fewer plant communities (Table 1).

Populations. Relationships between population density and area varied among species, but were apparent for the most common species (Fig. 1). Patterns included: 1) increasing density with increasing area for Marsh Wrens and Canada Geese (*Branta canadensis*), 2) decreasing density with increasing area for Mallards, and 3) no relationship for Mute Swans (*Cygnus olor*), Virginia Rails, Swamp Sparrows, and Red-winged Blackbirds. For Canada Geese, Mallards, Marsh Wrens, Swamp Sparrows, and Red-winged Blackbirds, population sizes increased with area (Fig. 2), whereas populations of Mute Swans and Virginia Rails were not influenced by area.

The combined densities of all territorial male passerines (GLM: $n^2_{1,6} = 0.09, P = 0.47$) and other species ($n^2_{1,6} = 0.19, P = 0.28$) were not related to area (Fig. 1). In contrast, total populations of males (GLM males: $n^2_{1,6} = 0.75, P = 0.01$) and other species ($n^2_{1,6} = 0.78, P = 0.004$) increased with area

(Fig. 2).

Species richness and area. I found no relationship between $-\ln$ Simpson's Index of bird species diversity and area (GLM: $n^2_{1,6} = 0.12, P = 0.4$). Further, all species accumulation curves reached asymptotes, indicating nearly complete sampling of species (Fig. 3).

Species richness was greatest at the two largest sites (Cromwell Meadows and Pratt/Post Coves). A power function provided the best fit to the species-area relationship in this system ($r^2_{1,14} = 0.85, P < 0.001$; AIC_c probability of best fit > 0.99). When I investigated the components of this relationship, exploratory examination with stepwise multiple regression selected a model with habitat area as the only variable included (GLM: $n^2_{1,6} = 0.87, P = 0.001$; Fig. 4). As a further exploratory procedure, I also repeated the stepwise regression with area excluded and, in this case, a model including only percent water cover was selected (GLM: percent water $n^2_{1,5} = 0.59; P = 0.027$). However, of the two models, species-area had the highest probability of being correct (AIC_c probability > 0.99). In all instances, isolation, percent mudflat cover, tidal range, and habitat heterogeneity were poor predictors of species richness.

Bird species evenness decreased with increasing habitat area (GLM: $n^2_{1,6} = 0.54; P = 0.04$). Pecauset Meadows was an outlier from this trend, with consistently lower evenness than would be predicted from the response of other sites. Similarly, species evenness showed a modest negative relationship with species richness that varied between years (1999: $r^2_{1,6} = 0.72, P = 0.01$; 2000: $r^2_{1,6} = 0.47, P = 0.06$).

DISCUSSION

My results suggest that the species-area relationship in freshwater tidal marshes of the Connecticut River is largely due to the effect of area, with larger sites having rarer species, species with larger populations, and species that apparently occur only in marshes of some minimum size. This relationship was not a consequence of sampling artifacts (Rosenzweig 1995) and species found were, based on multiple years of observations (Craig 1990, 2004), almost entirely those previously known to occur at these sites. The findings are consistent with theoretical predictions that, as individuals are added to a community, more rare species are present (Hubbell 2001), and larger populations are less prone to local extinction (Rosenzweig 1995).

Species in larger marshes with home ranges generally over 20 ha (pers. obs.) were the American Bittern, Mute Swan, Mallard, Blue-winged Teal (*Anas discors*), and Canada Goose, and these species were observed less frequently in the smallest marshes. American Bitterns and Blue-winged Teal were also among the least frequently encountered species and, along with Least Bitterns, Soras, and Spotted Sandpipers, were present only in larger marshes, even though apparently suitable habitat (Craig 1990, 2004) was present in all marshes. In previous years (Craig 1990, 2004, Craig and Beal 1992), other rare species (e.g., Black Rail) have also been observed only at the largest sites, and rarer species were most likely to be present in larger marshes. Moreover, the more com-

TABLE 2. Mean 1999-2000 population densities/ha of marsh birds in freshwater marshes of the Connecticut River.

Marsh	American Bittern	Least Bittern	Mallard	Mute Swan	Canada Goose	Blue-winged Teal	Virginia Rail	Sora	Spotted Sandpiper	Marsh Wren	Swamp Sparrow	Red-winged Blackbird
Pecauset	0.01	0.00	0.08	0.07	0.05	0.00	0.03	0.00	0.00	0.06	0.28	2.38
Pecauset II	0.00	0.00	0.11	0.34	0.00	0.00	0.45	0.00	0.00	0.00	0.89	3.58
Cromwell	0.00	0.05	0.07	0.01	0.10	0.00	0.15	0.01	0.03	0.59	1.66	1.59
Cromwell II	0.00	0.00	0.38	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.88	2.19
Cromwell III	0.00	0.00	1.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.95
Whalebone	0.00	0.01	0.08	0.03	0.10	0.00	0.13	0.00	0.04	1.04	0.13	1.38
Chapman	0.00	0.00	0.04	0.09	0.05	0.00	0.25	0.00	0.00	0.48	0.40	1.47
Pratt & Post	0.01	0.00	0.13	0.08	0.18	0.01	0.10	0.00	0.00	0.92	0.74	1.84

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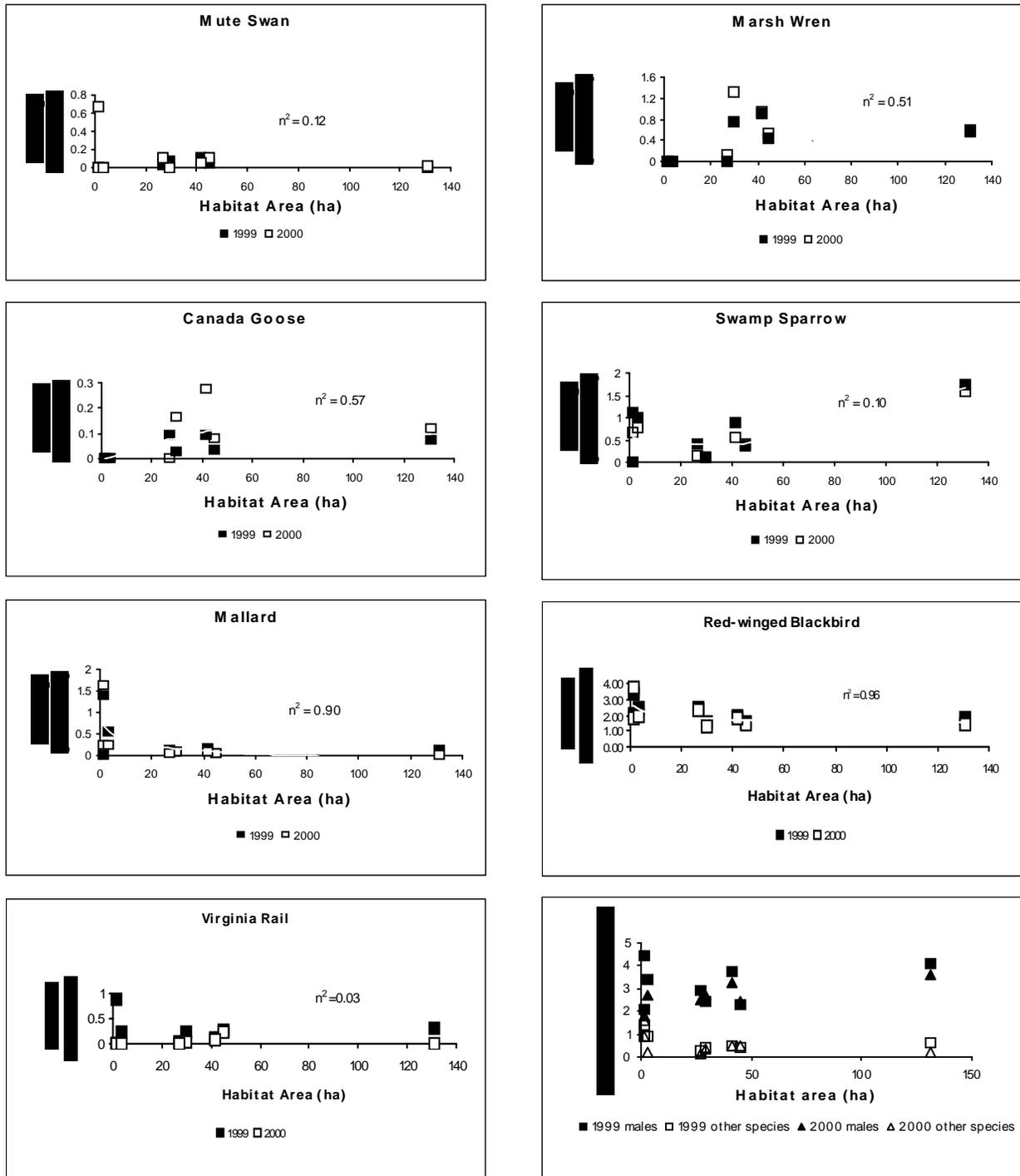


FIG. 1. The relationship between population density and habitat area was variable among marsh bird species and within the marsh bird community.

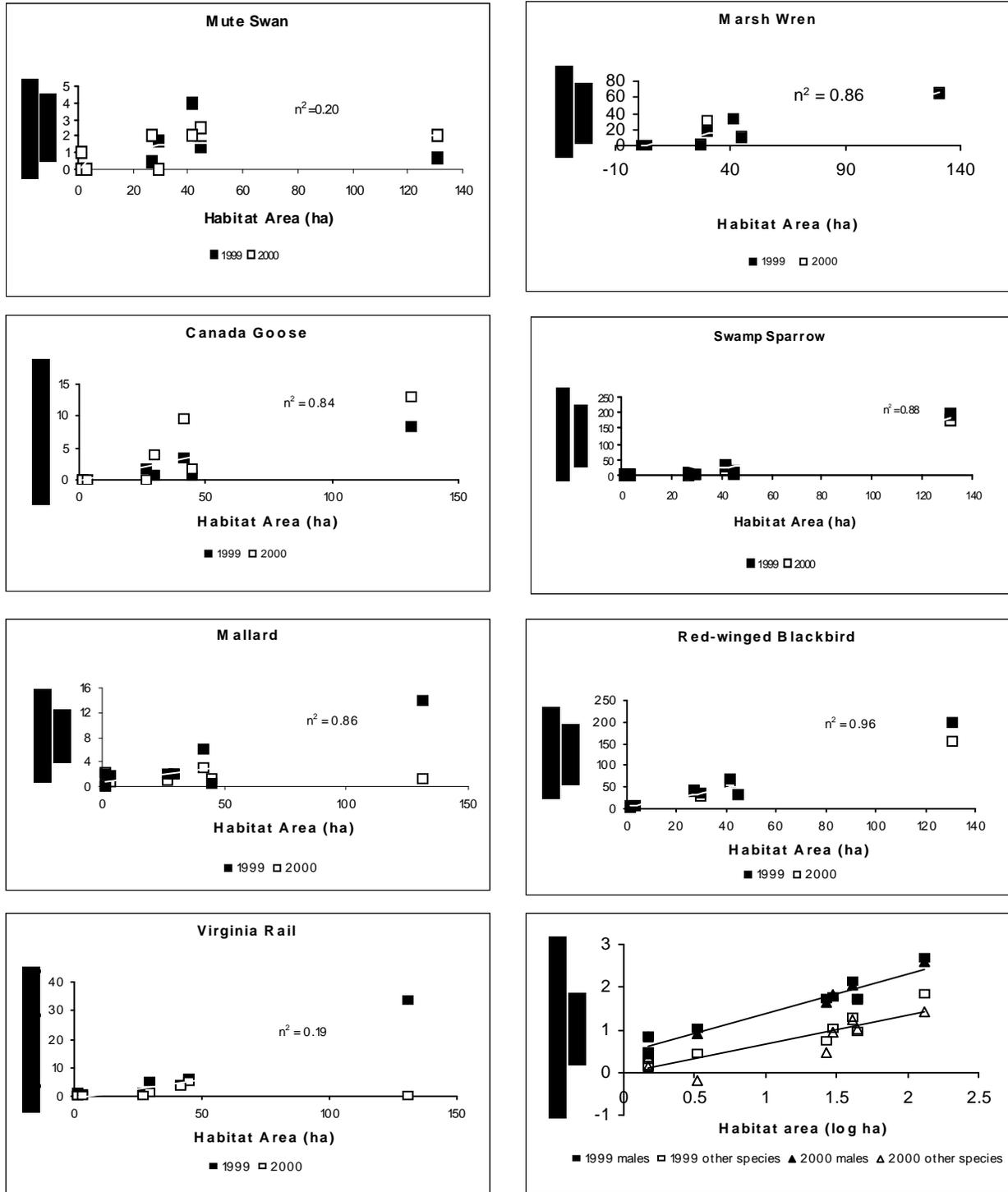


FIG. 2. Total populations increased with habitat area for most species and for the marsh bird community.

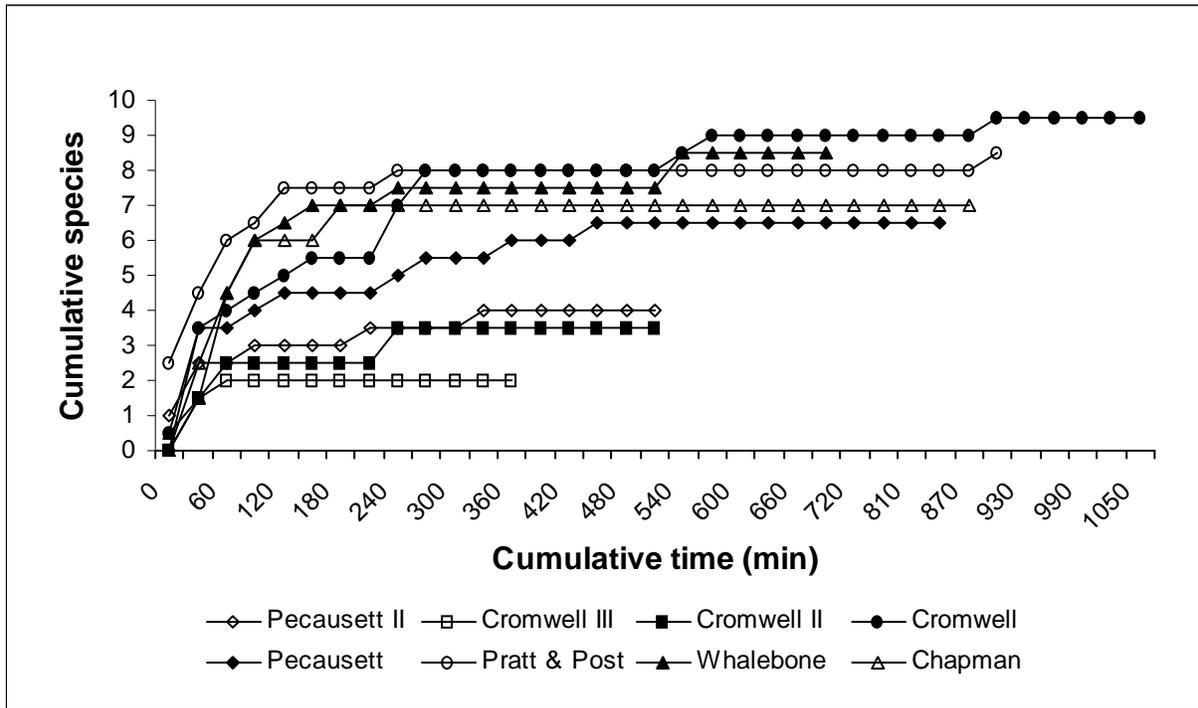


FIG. 3. Species accumulation curves show horizontal asymptotes, indicating complete sampling.

mon, smaller species with smaller home ranges, Virginia Rails, Marsh Wrens, and Swamp Sparrows, were absent from some or all of the three smallest sites even though suitable habitat was present.

The relationships for area and species occurrence observed in my study appear to be general ones in avian communities. Brown and Dinsmore (1986) found that 68% of bird species either declined in abundance or were absent in freshwater marshes under 5 ha (i.e., a minimum threshold area was reached). Betts et al. (2007) further demonstrated that area threshold models best accounted for patterns of presence for 60% of forest passerines studied. At least 40% of grassland bird species in habitats ranging in size from 4–271 ha have also exhibited positive presence-area relationships, although geographic location and landscape context also influenced occurrence (Johnson and Igl 2001).

I found no relationship between species richness and marsh isolation. Similarly, Shriver et al. (2004) reported no relationship between richness and the presence of additional habitat within 1 km for salt marsh birds in Long Island Sound. In a synthesis of 118 studies examining effects of isolation on birds, other vertebrates, and invertebrates, Watling and Donnelly (2006) found that area, and not isolation, had the greatest effect on richness, particularly

among birds. Isolation was significantly related to richness in only a third of the studies, and most of these examined true islands rather than habitat patches. Hence, my observation that habitat isolation plays little or no role in influencing marsh bird richness is consistent with the results of a broad range of studies. However, because some studies of marsh birds have revealed an isolation-species richness relationship (e.g., Fairbairn and Dinsmore 2001), additional landscape factors, such as degree of human habitation (Shriver et al. 2004), may also help determine whether a relationship is present.

I found no relationship between population density and area, a potential indicator of increasing habitat quality at larger sites, in my study. Such results are consistent with MacArthur and Wilson’s (1967) implicit assumption from island biogeographic theory (Diamond and May 1976) that population density is independent of area, and that density is a poor indicator of habitat quality (Wiens 1989, Vickery et al. 1992, Seigel et al. 2005). My results may indicate that the criterion for a positive relationship to exist, i.e., populations being densest in the best habitats (Fretwell 1972), is not met because habitat quality among the similar marshes of this system improves little with increasing area.

The decrease in evenness I found with increasing richness contrasts with He and Legendre's (2002) prediction that greater evenness should promote greater richness by reducing the frequency of random local extinction. However, Seigel et al. (2005) also found that evenness declined with increasing bird species richness in restored tidal marshes. The decreased evenness is a consequence of more rare species being present in marshes with greater richness.

Although species richness in my study was positively related to area in the absence of a habitat-area correlation, other investigators (Wiens 1989, Rosenzweig's 1995) have suggested that species-area relationships exists principally because of a positive habitat-area relationship. Even without such a relationship, I found that area was the variable that most influenced species richness. The absence of any relationship in my study appeared to be because most vegetation types were not sufficiently distinct for birds to differentially associate with them. Observations of habitat use (Craig 1990, 2004) have indeed suggested that different vegetation types were generally not associated with particular bird species, even though some types were related to differing amounts of tidal flooding (Metzler and Damman 1985). This absence of species-habitat associations likely also explains why my results contrast with those of other

studies of marsh habitats (Weller 1999, Paxton and Watts 2002, Guadagnin and Maltchik 2007).

In addition to the factors I examined, long-term regional population phenomena clearly influence the occurrence of species. For example, Mute Swans and Canada Geese have expanded from brackish to freshwater parts of the river since 1974 (Craig 1990, 2004). Hence, for these species, factors other than area and habitat conditions also influence their present distribution. Other, more common species (Virginia Rails and Mallards) have distributions in any particular year that are controlled in part by density-independent factors such as the extent and duration of spring flooding (Craig 1990, 2004, this study). For these species, local distributions in any year can, therefore, be predicted only in part by habitat and area.

My results support the hypothesis that area is important for maintaining species richness. Protecting larger marshes may, therefore, be necessary for maintaining bird diversity. Larger areas appear to attract rarer species, those most susceptible to loss from fragmenting systems (Davies et al. 2000), sustaining larger, less extinction-prone populations, and enhancing the presence of species with a minimum threshold area for occurrence. However, preserving larger areas alone may be insufficient for ensuring

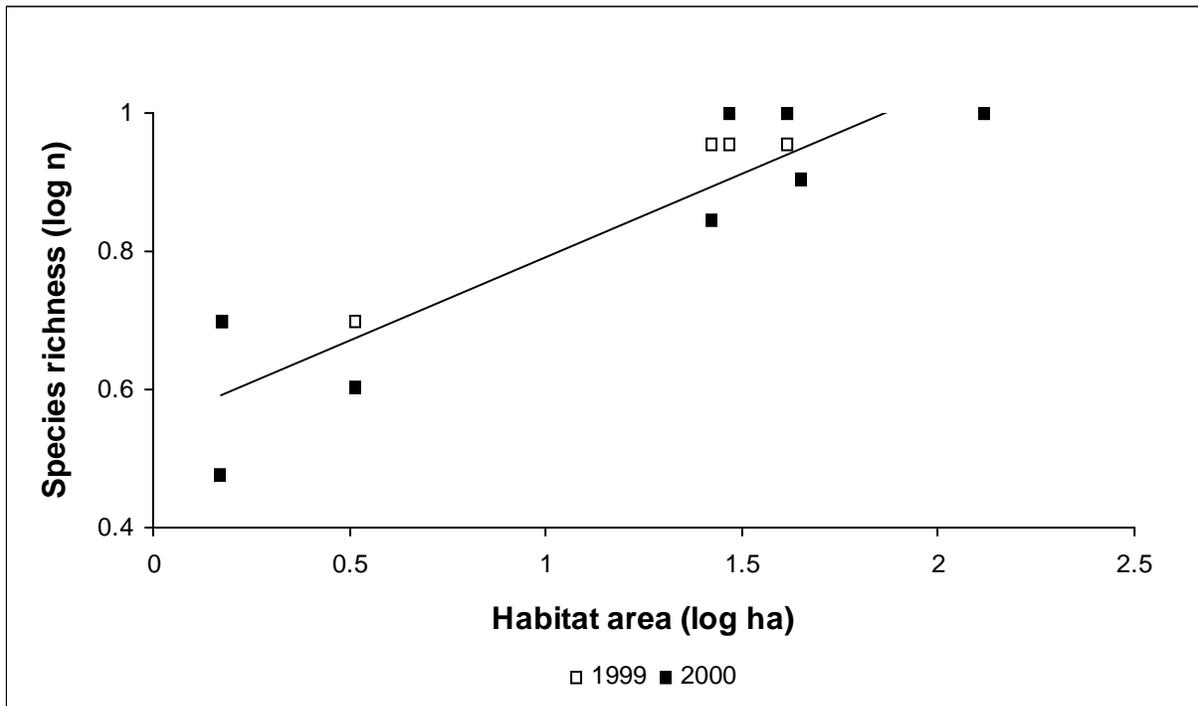


FIG. 4. Species richness showed a strong increase with habitat area.

the persistence of diversity because habitat factors, proximity to additional habitat, regional population phenomena and density independent events also influence species richness at the local scale.

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