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RELATIONSHIP BETWEEN HABITAT AREA AND THE DISTRIBUTION OF TIDAL MARSH BIRDS

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ABSTRACT.—To assess the relationship between marsh area and relative abundance of tidal marsh bird species, we surveyed birds on 86 circular plots in 40 salt and brackish tidal marshes in Connecticut. We measured marsh area in two ways: the amount of contiguous marsh vegetation not interrupted by broad barriers (>500 m of open water or >50 m of upland habitat) and by narrow barriers (>30 m of open water or >10 m upland). We determined the relationship between marsh area and the relative abundance of particular species (mean number of individuals per survey plot) with linear or logistic regression. When the broad barrier definition was used, we found that all three species of short grass meadow specialists, Willets (*Catoptrophorus semipalmatus*), Seaside Sparrows (*Ammodramus maritimus*), and Saltmarsh Sharp-tailed Sparrows (*A. caudacutus*), were less abundant or absent in survey plots in smaller marshes. The Seaside Sparrow and Willet also showed a significant tendency to be less frequent in smaller marshes when the narrow barrier definition was used. In contrast, species that used a wider range of wetland types, as in the Virginia Rail (*Rallus limicola*), Marsh Wren (*Cistothorus palustris*), and Swamp Sparrow (*Melospiza georgiana*), were equally frequent on plots in marshes of different areas. Our results are consistent with the hypothesis that fragmentation of marsh systems with artificial habitat causes a decline in the density of short grass meadow specialists in the remaining patches of appropriate habitat.
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Connecticut lost about 30% of its tidal wetlands between the 1880s and the 1970s (Rozsa 1995), and most of the remaining marshes have been heavily modified by ditching, tidal restriction, and the spread of common reed (*Phragmites australis*). These habitat changes are associated with population declines in salt marsh birds (Brawley et al. 1998, Benoit and Askins 1999, Clarke et al. 1984, Craig 1990), but the role of habitat fragmentation in these declines remains an open question. Species that are sensitive to the negative effects of habitat fragmentation would decline not only in areas where habitat has been altered, but also in remaining small patches of apparently suitable habitat.

Habitat fragmentation is associated with changes in the composition of bird communities in a wide range of habitats, including deciduous forests in Japan and eastern North America (Roberts and Norment 1999, Askins 2000, Askins et al. 2000), shrubsteppe in Idaho (Knick and Rotenberry 1995), temperate rain forests in Chile (Willson et al. 1994), and tropical rain forests in Brazil (Laurance et al. 2002). Some species (usually habitat specialists) in each of these habitats are area sensitive, with a tendency to decline or disappear in small remnant patches of apparently suitable habitat. However, area sensitivity has not been demonstrated conclusively in North American marsh birds despite the fact that Brown and Dinsmore (1986) and Craig and Beal (1992) showed that there was a positive relationship between the number of species of birds and marsh area, and that some species were missing from smaller marshes. The results of both of these studies were inconclusive because more time was spent surveying birds in large marshes than in small marshes. Consequently, more species may have been detected in larger marshes because of the passive sampling effect (Connor and McCoy 1979, Horn et al. 2000). Because there was less surveying effort in smaller marshes, fewer individuals would be detected, increasing the chance that some species would be missed even if none of the species were area sensitive. Moreover, neither study showed that the density of particular species of marsh birds was lower in smaller marshes than in larger marshes. In both forests (Robbins et al. 1989, Askins et al. 1990) and grasslands (Vickery et al. 1994, Johnson and Igl 2001), area sensitive species tend to have lower densities in small patches of habitat than in large blocks of continuous habitat. This may be due to negative

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edge effects such as higher predation rates in smaller patches (Johnson and Temple 1990, Faaborg et al. 1995).

We especially focused on two species of sparrows that are salt marsh specialists, the Seaside Sparrow (*Ammodramus maritimus*) and Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*), because they are taxonomically and ecologically similar to area sensitive sparrows of dry grasslands. Moreover, in New England the two salt marsh sparrows are largely restricted to short grass meadows, salt and brackish tidal wetlands dominated by low grasses such as *Spartina patens*, *Distichlis spicata*, and *Juncus gerardi* (Greenlaw and Rising 1994, Post and Greenlaw 1994, Benoit and Askins 1999). In many respects, these habitats are structurally similar to upland grasslands. Studies in dry grasslands such as prairie preserves in Illinois (Herkert 1994a), blueberry barrens in Maine (Vickery et al. 1994), fields in western New York (Norment et al. 1999), and restored grasslands in the northern Great Plains (Johnson and Igl 2001) showed that Vesper Sparrows (*Pooecetes gramineus*), Savannah Sparrows (*Passerculus sandwichensis*), Grasshopper Sparrows (*Ammodramus savannarum*), Baird's Sparrows (*A. bairdii*), and Henslow's Sparrows (*A. henslowii*) were more likely to be detected on standard plots in large grasslands than in plots of the same size in small grasslands. Moreover, these species tend to be missing in survey plots located in the smallest grasslands. Consequently, an important concern in managing or restoring grasslands is to provide large enough areas of contiguous habitat to support populations of these sparrows. Similarly, if the salt marsh sparrows are area sensitive, then it will not be sufficient to consider the total amount of suitable habitat needed to support populations; it also will be important to maintain or create large blocks of uninterrupted short grass meadow.

Our goal was to determine whether specialized marsh birds are area sensitive. If they are, then we would expect them to display either of the following patterns: (1) a lower density in smaller marshes, or (2) a tendency to be absent from survey plots in marshes smaller than some minimum area. We completed surveys in a large number of tidal marshes to test these predictions.

METHODS

Survey plots.—During the summers of 1995 and 1996, we surveyed birds and vegetation on 86 standardized circular plots in 40 brackish and salt marshes along the coast and tidal rivers of Connecticut (see Benoit and Askins 1999 for locations and descriptions of these sites, including the number of survey plots per site). We surveyed 20 marshes during each of the two years. These encompassed nearly all salt and brackish marshes >10 ha in the state as well as some marshes <10 ha. The 50-m radius plots were located ≥200 m apart and ≥75 m from upland habitats. We recorded all birds detected during an observation period during each of two visits, one in June and the other (≥2 weeks later) in July. We commenced the study in early June because Seaside and Saltmarsh Sharp-tailed sparrows are still migrating during late May (Saunders 1959). We conducted observations between 05:00 and 10:00 EST, and we surveyed ≤4 plots per day. The observation period consisted of 10 min of passive observation followed by 7 min of broadcasting, in sequence, the taped calls of the following species: Least Bittern (*Ixobrychus exilis*), American Bittern (*Botaurus lentiginosus*), Virginia Rail (*Rallus limicola*), King Rail (*R. elegans*), Clapper Rail (*R. longirostris*), Sora (*Porzana carolina*), and Black Rail (*Laterallus jamaicensis*). Playback was not necessary for highly detectable birds such as sparrows, Willets (*Catoptrophorus semipalmatus*), and Marsh Wrens (*Cistothorus palustris*). We quantified the relative abundance of each species as the total number of individuals seen or heard during the initial 10 min plus any additional birds that responded to conspecific calls during the playback period. We counted only the adults of each species. Individuals of the same species had to be detected simultaneously to be recorded as different individuals. These survey methods were appropriate for sampling bird distribution across a regional landscape and were not intended to characterize particular marshes.

We chose survey plots by stratified random design. We mapped major vegetation types using aerial photographs supplemented with field checking. We initially classified vegetation into three categories (Table 1): (1) short grass meadow (areas dominated by low marsh grasses such as *Spartina patens*, *Juncus gerardi*, and *Distichlis spicata*), (2) cattail (areas dominated by *Typha* spp.), and (3) *Phragmites* (areas dominated by *Phragmites australis*). We used a table of random numbers to select coordinates of survey plots in each sufficiently extensive vegetation type on a grid superimposed on a map of each site. Each marsh had 1–5 survey plots, depending upon its size.

We used the line intercept method (Brower and Zar 1977) to estimate percent cover of different species of plants on each plot. Two 50-m perpendicular transects were laid out from the center of each plot. One of the transects was oriented toward the nearest tidal creek. We calculated percent cover from the total distance that the line intercepted the foliage of each plant species. Based on the dominant vegetation indicated by

TABLE 1. Mean percent cover for different plant species and water features for six vegetation categories in 40 tidal marshes on the coast of Connecticut, 1995–1996.

	Vegetation categories					
	Short grass meadow	*Phragmites*	Cattail	Brackish mixture	Short *S. alterniflora*	Other
No. of survey plots	36	14	7	14	6	9
Cover types						
Tall *S. alterniflora*	7 ± 10[a]	1 ± 4	0 ± 0	5 ± 12	9 ± 5	23 ± 32
Short *S. alterniflora*	10 ± 12	0 ± 0	0 ± 0	0 ± 0	58 ± 9	0 ± 0
Spartina patens	33 ± 19	4 ± 8	0 ± 0	15 ± 12	7 ± 11	0 ± 1
Juncus girardi	16 ± 20	1 ± 3	0 ± 1	11 ± 12	0 ± 0	3 ± 8
Distichlis spicata	10 ± 12	1 ± 3	0 ± 0	2 ± 6	0 ± 0	0 ± 0
Phragmites australis	1 ± 2	73 ± 13	15 ± 12	21 ± 15	0 ± 0	16 ± 22
Typha angustifolia	0 ± 0	3 ± 6	53 ± 15	7 ± 11	0 ± 0	13 ± 19
Forbs	4 ± 6	1 ± 2	4 ± 4	5 ± 6	0 ± 0	6 ± 9
Scirpus spp.	0 ± 0	1 ± 2	5 ± 12	15 ± 15	0 ± 0	5 ± 12
River	5 ± 10	2 ± 5	4 ± 7	6 ± 10	4 ± 10	0 ± 0
Mosquito ditch	1 ± 1	0 ± 1	0 ± 0	0 ± 1	2 ± 1	0 ± 1
Pool	1 ± 3	2 ± 4	2 ± 2	2 ± 4	0 ± 0	2 ± 4
Creek	3 ± 6	7 ± 11	6 ± 10	1 ± 2	14 ± 12	9 ± 15

[a] Mean (± SD) percent cover for all vegetation plots.

these percent cover values, we classified each survey plot into one of the following categories: short grass meadow, cattail, *Phragmites*, short *Spartina alterniflora*, or brackish mixture (areas of short grass intermixed with patches of tall plants such as *Phragmites*, *Typha*, or *Scirpus*; Benoit and Askins 1999; Table 1). The proportion of plots in each marsh with a particular vegetation type was used as a measure of proportion of the marsh covered by that vegetation. Because of the stratified random selection of plots, this measure emphasized any large scale heterogeneity in vegetation types within the marsh.

Marsh area and birds.—We used either linear or logistic regression to determine the relationship between marsh area and the abundance of species that nest primarily in marshes. We determined the total area of each marsh complex by using a geographical information system with hydrology maps downloaded from the Univ. of Connecticut Map Library web site, http://magic.lib.uconn.edu. For this analysis, we defined marsh area as any marshlands connected by tidal flow, where marsh patches were separated by broad barriers of <500 m of open water or <50 m of uplands. The marsh area of small tributaries was included only up to a distance of 500 m from the main river.

For regression analyses, we used data from survey plots only if the plot had the appropriate vegetation for the bird species in question, as determined by the results from multiple regression analysis (Benoit and Askins 1999), and from previously published findings on habitat requirements. We used data from short grass meadow plots for analysis of Willets, Seaside Sparrows, and Saltmarsh Sharp-tailed Sparrows, while data from *Phragmites*, cattail and brackish mixture plots were used for Marsh Wrens and Swamp Sparrows. We used data from cattail and brackish mixture plots for analysis of Virginia Rails. If more than one survey plot in the same marsh complex had appropriate vegetation, then we used the mean number of individuals for these survey plots as a measure of the density of a species in the marsh.

We used linear regression to assess the relationship between marsh area and density for the following species of marsh specialists: Willets, Marsh Wrens, and Saltmarsh Sharp-tailed Sparrows. Linear regression analysis was not appropriate for species with a large number of plots with zero values, so we used logistic regression. In some of the regressions for Willets and Seaside Sparrows it was not possible to use logistic regression because of a dichotomous pattern in which a species was absent at all sites smaller than a threshold area and present at all sites larger than that area. In these cases we used the logistic transformation to normalize abundance and then used linear regression analysis. When regression results were not significant, we assessed the power of the tests by calculating the power for the correlation coefficients for the same data, as recommended by Zar (1999).

We also used the following equation developed by Simberloff and Gotelli (1984) to determine the probability that the minimum habitat area occupied by a particular species is larger than one would expect based on chance:

$$P = \frac{\binom{(S - L_i + 1)}{N_i}}{\binom{S}{N_i}}$$

where P is the probability that a smaller marsh would not be occupied if the distribution were random, S is

TABLE 2. Relationship between the relative abundance (mean number of individuals per survey plot) and habitat area using the "broad barrier" criterion[a] for three species of salt marsh specialists and three generalist marsh species in tidal marshes on the coast of Connecticut that were surveyed in June and July, 1995–1996.

	Linear regression[b]			Logistic regression[b,c]		Minimum area (ha)[d]	Simberloff-Gotelli test
	F	df	*P*	Wald χ^2	*P*		*P*
Salt marsh specialists							
Willet	17.5[e]	1, 17	0.001			138	0.009
Saltmarsh Sharp-tailed Sparrow	5.7	1, 17	0.029			10	0.263
Seaside Sparrow				5.0	0.03	67	0.001
Marsh generalists							
Virginia Rail				1.03	0.31	80	0.357
Marsh Wren	2.1	1, 12	0.173			8	1.000
Swamp Sparrow				3.45	0.63	55	0.070

[a] Separate marshes were defined by barriers of >500 m of open water or >50 m of upland.
[b] We used the ln transformation to normalize the distribution of habitat area for all regression analyses.
[c] Distributions were analyzed with linear regression analyses except for species with a large number of plots with zero values, in which case we used logistic regression analyses.
[d] Area of smallest marsh at which a species was detected.
[e] It was not possible to calculate an equation with logistic regression for this species because of the dichotomous pattern, with Willets absent at all sites <138 ha and present at all sites ≥138 ha. We therefore used the logistic transformation to normalize Willet abundance (y): new y = ln((1.6 − (y + 0.01))/(y + 0.01)). We then completed a linear regression analysis.

the number of sites, N_i is the number of sites where species i occurs, and L_i is the size rank of the smallest site occupied by species i. As in the regression analyses, we used only those plots with suitable habitat for each species. Only one randomly chosen plot was used for each marsh so that the samples would be independent. This is a conservative test of area sensitivity because the key variable is the rank of the smallest site even in cases in which the smallest site is substantially smaller than the median or mean area of sites occupied by the species.

We defined the boundaries separating different marshes more conservatively, with narrower barriers, in a second set of regression and Simberloff-Gotelli analyses. In this case, boundaries of a marsh were delimited by the smallest barriers one can see in the field or on an aerial photograph: (1) any body of water >30 m wide at its narrowest point, (2) roads or railroad tracks, or (3) ≥10 m of adjacent uplands (as designated by the hydrology maps). In this way, we could determine whether narrow interruptions in marsh habitat were related to bird distributions.

To ensure that any relationship between bird abundance and marsh area were not due to a confounding variable, we also completed multiple regression analyses for all species that showed a significant relationship with marsh area. The dependent variable was the mean number of individuals per plot and the independent variables were marsh area (as defined by broad barriers), the proportion of the entire marsh that had appropriate vegetation for a particular species, and the mean percent cover of pools, creeks, and ditches in the marsh. Previous studies have shown that the percent cover of water features is an important predictor of the distribution of marsh birds (Craig and Beal 1992, Reinert and Mello 1995, Benoit and Askins 1999). Only those survey plots with suitable habitat for a particular species were included in the analysis, which helped to control for relationships with vegetation structure and composition.

RESULTS

Using linear regression, and the broader definition of marsh area (in which marshes must be separated by wide barriers to be considered separate), we found that the density of both Willets and Sharp-tailed Sparrows exhibited a positive relationship with marsh area (Table 2, Fig. 1). In contrast, Marsh Wrens were not area dependent (Table 2, Fig. 2). The statistical power for the correlation between ln marsh area and density of Marsh Wrens was 0.73, indicating that there was a 27% chance of a type II error.

We used logistic regression to analyze the distributions of Virginia Rails, Swamp Sparrows (*Melospiza georgiana*), and Seaside Sparrows because these species were absent from a large proportion of the plots and consequently did not have normal distributions. When we used the broad barrier definition of marsh area, there was a significant positive relationship between frequency of occurrence and marsh area for Seaside Sparrows, but not for Virginia Rails or Swamp Sparrows (Table 2, Figs. 1 and 2). The statistical power for the latter two species was 0.85 and 0.72, respectively.

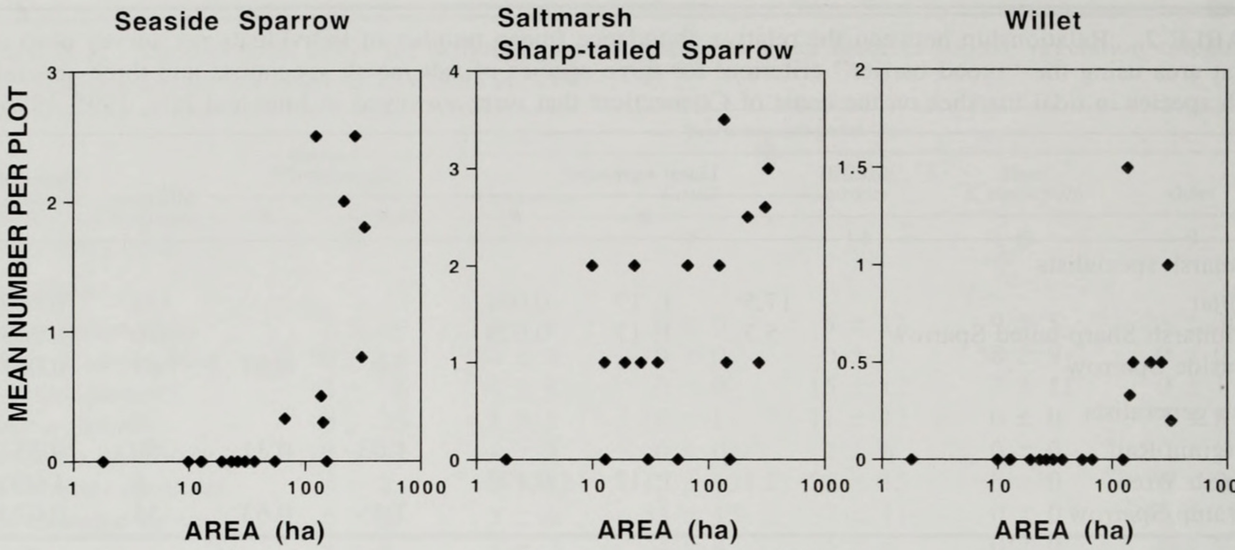

FIG. 1. The densities of salt marsh specialists were positively related to the size of the marsh. Data were collected from 50-m radius plots in short grass meadow habitat of tidal marshes along the Connecticut coast, 1995–1996. Marshes separated by >500 m of open water or >50 m of upland habitat ("broad barrier" criteria; see text) were considered distinct.

Using the narrow barrier definition of marsh area (in which small patches of marsh vegetation separated by narrow barriers were considered as separate marshes) in regression analyses, we found that only the Willet and Seaside Sparrow were significantly less frequent in smaller marshes than in larger marshes (Table 3). The statistical power for species that did not show significant relationships with marsh area was 0.56 for Saltmarsh Sharp-tailed Sparrow, 0.97 for Swamp Sparrow, 0.99 for Marsh Wren and 0.94 for Virginia Rail.

Using the Simberloff-Gotelli equation with data for the broad barrier definition of marsh area, we found that the smallest marsh where a species was detected was larger than expected by chance for Seaside Sparrows and Willets, but not for Saltmarsh Sharp-tailed Sparrows or the more generalist marsh species (Table 2). Using the narrow barrier definition of marsh area, only the Seaside Sparrow had

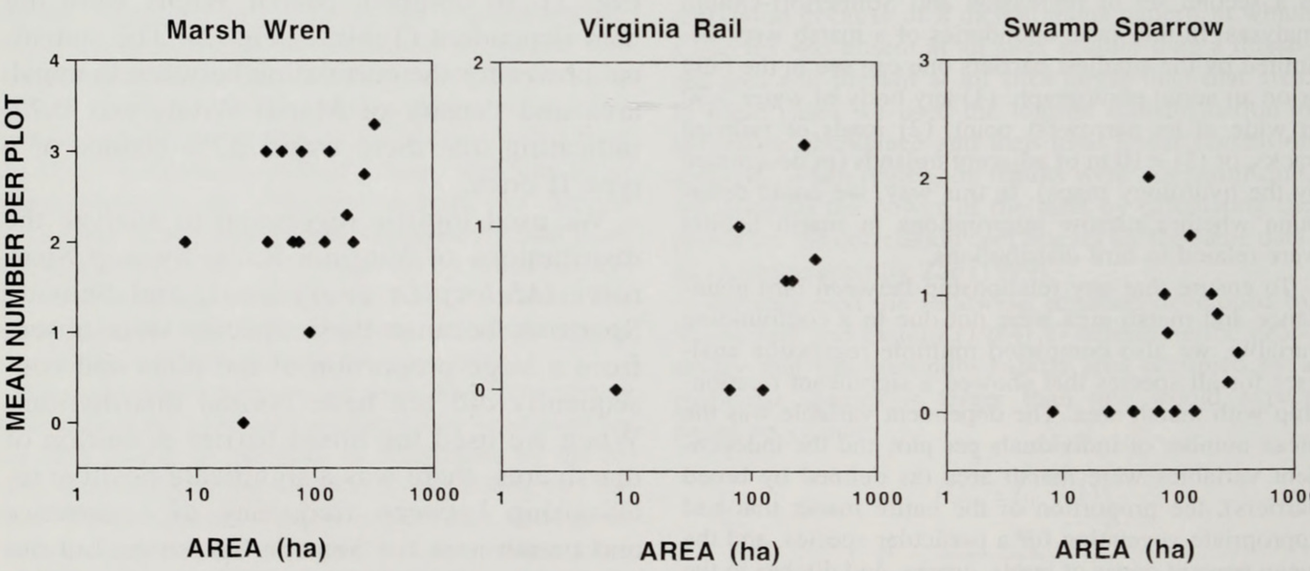

FIG. 2. The densities of generalist marsh species were not related to the size of the marsh. Data were collected from 50-m radius plots in tall grass meadow habitats of tidal marshes along the Connecticut coast, 1995–1996. Marshes separated by >500 m of open water or >50 m of upland habitat ("broad barrier" criteria; see text) were considered distinct.

TABLE 3. Relationship between the relative abundance (mean number of individuals per survey point) and habitat area using the "narrow barrier" criterion[a] for three species of salt marsh specialists and three generalist marsh species in tidal marshes on the coast of Connecticut that were surveyed in June and July, 1995–1996.

	Linear regression[b]			Logistic regression[b,c]		Minimum area (ha)[d]	Simberloff-Gotelli test
	F	df	*P*	Wald χ^2	*P*		*P*
Salt marsh specialists							
Willet				4.5	0.03	16	0.081
Saltmarsh Sharp-tailed Sparrow	3.6	1, 24	0.07			4	0.231
Seaside Sparrow				4.1	0.04	15	0.048
Marsh generalists							
Virginia Rail				0.01	0.91	10	0.429
Marsh Wren	0.1	1, 22	0.73			4	1.000
Swamp Sparrow				0.07	0.93	8	0.217

[a] Separate marshes were defined by barriers of >30 m of open water or >10 m of upland.
[b] We used the ln transformation to normalize the distribution of habitat area for all regression analyses.
[c] Distributions were analyzed with linear regression analyses except for species with a large number of plots with zero values, in which case we used logistic regression analyses.
[d] Area of smallest marsh at which a species was detected.

a minimum area significantly larger than expected by chance (Table 3).

Multiple regression analysis indicated that marsh area was the best predictor of the mean number of individuals per plot for each of three short grass meadow specialists (Willet, Saltmarsh Sharp-tailed Sparrow, and Seaside Sparrow; Table 4). The two other independent variables, percentage of the entire marsh covered with short grass meadow and percent cover of pools, ditches and creeks, were not significantly related to abundance for any of these species. The overall model for the Saltmarsh Sharp-tailed Sparrow was not significant (P = 0.083), but marsh area tended to explain more variation than the other two variables (Table 4).

DISCUSSION

Although area dependent relationships have been shown for many species of grassland birds (Herkert 1994a, Vickery et al. 1994, Johnson and Igl 2001), this study is the first to conclusively demonstrate such a relationship for salt marsh sparrows. Both species of sparrows that are associated with short grass meadows were more frequent in plots in larger marshes than in similar plots in smaller marshes, and marsh area was a better predictor of the density of these species than the per-

TABLE 4. Multiple regression analysis with mean number of individuals per survey plot as the dependent variable and marsh area, percent of marsh covered with short grass meadow, and percent cover of small water features (pools, creeks, and ditches) as independent variables. Data are from surveys of tidal marshes on the coast of Connecticut, 1995–1996.

	Model		Marsh area[a,b]			Percent short grass meadow[b,c]			Percent water[b,d]		
Species	*F*	*P*	*t*	*P*	Trend	*t*	*P*	Trend	*t*	*P*	Trend
Willet[e]	10.1	0.001	5.4	0.0002	+	0.1	0.92		1.4	0.19	
Saltmarsh Sharp-tailed Sparrow	2.8	0.083	2.4	0.0342	+	1.0	0.32		1.0	0.32	
Seaside Sparrow[f]	8.7	0.002	5.1	0.0003	+	0.1	0.92		0.0	0.97	

[a] Separate marshes were defined by the broad barrier criterion (separation by >500 m of open water or >50 m of upland).
[b] To normalize distributions, we used the ln transformation for marsh area and percent cover water, and the arcsine transformation for percent short grass meadow.
[c] Percent of marsh surface covered with short grass meadow.
[d] Percent of marsh surface covered with creeks, ditches, and pools.
[e] We used the logistic transformation to normalize Willet abundance (y): new y = ln((1.6 − (y + 0.01))/(y + 0.01)). We then completed a linear regression analysis.
[f] We used the logistic transformation to normalize Seaside Sparrow abundance (y): new y = ln((2.6 − (y + 0.01))/(y + 0.01)). We then completed a linear regression analysis.

centage of the site covered with short grass meadow or with pools and other water features. Although Saltmarsh Sharp-tailed Sparrows were detected in some of the smallest marshes, they exhibited a significant positive relationship with marsh area. The Seaside Sparrow, which had a lower overall abundance than the Sharp-tailed Sparrow (Benoit and Askins 1999), was restricted to the largest marshes. The mean size of Seaside Sparrow territories in ditched marshes was <1 ha (Marshall and Reinert 1990), which is not large enough to explain their absence in marshes smaller than 67 ha (Table 2). Saltmarsh Sharp-tailed Sparrows are not territorial and have small home ranges (1.2–5.7 ha for males and smaller for females; Woolfenden 1956, Greenlaw 1993, Greenlaw and Rising 1994) so, as in the Seaside Sparrow, this species is more frequent in larger marshes for some reason other than minimum area requirements for territories or home ranges. Perhaps larger marshes have lower rates of nest predation (Johnson and Temple 1990) or a better food supply (Burke and Nol 1998).

Willets are another short grass meadow species that appear to be area sensitive. Marsh area was a better predictor of their abundance than percent cover of short grass meadow or of water features, and they were absent in marshes <138 ha (Table 2). This species was more abundant during the 19th Century, but hunting and egg collecting probably contributed to its extirpation from Connecticut's marshes (Bevier 1994). After an absence of nearly 100 years from the state, it has recolonized a handful of salt marshes (Craig 1990). The current association of Willets with large marshes may indicate that the few individuals present have their choice of the best habitat, which probably are the largest marshes with abundant nesting and feeding sites. Although nesting attempts have been detected at smaller marshes (Bevier 1994), Willets often nest in high density clumps to enhance synchronous nesting and increase predator-mobbing effectiveness (Burger and Shisler 1978, Howe 1982), so it is likely that birds establishing new breeding territories will join the existing nesting populations on the large sites.

Even though the minimum habitat areas listed for Seaside Sparrows and Willets (Table 2) are significantly larger than expected by chance, these values should not be interpreted as the smallest habitat areas that can accommodate these species. They merely reflect the minimum areas for our sample of 40 marshes. The distribution of these species indicates that they tend to be absent from small marshes.

In contrast to the short grass meadow specialists, two species associated with cattail marsh and *Phragmites*, the Marsh Wren and Swamp Sparrow, did not show a significant relationship with marsh area. Statistical power was great enough in these analyses (>0.7 for the "broad barrier" data and >0.9 for the "narrow" barrier data) that we can be reasonably confident that a substantial relationship does not exist. Herkert (1994b) found that in Illinois prairies certain grassland birds were area sensitive while other species responded only to the structure of the vegetation. This also may be the case with tidal marsh birds. Marsh Wrens and Swamp Sparrows appear to respond to plant structure because they are found in many different types and sizes of wetlands as long as there is tall, sturdy vegetation for their nests (Kroodsma and Verner 1997, Mowbray 1997, Benoit and Askins 1999).

The Virginia Rail also nests in a wide variety of marsh types and it, too, may choose nest sites based primarily on the structure of the vegetation (Conway 1995). We recorded Virginia Rails only in relatively large marshes (Fig. 2), but the relationship between the occurrence of this species and marsh area was not significant. This may have been due to our small sample size, but the power of this test was relatively high (0.72). In a survey of water birds in numerous wetlands in Maine, Gibbs et al. (1991) reported a moderately higher frequency of Virginia Rails in larger marshes than in smaller marshes, but this may merely reflect greater sampling effort in larger marshes. Even though Brown and Dinsmore (1986) sampled more plots in large marshes than in small marshes, they found that Virginia Rails were equally frequent in marshes of different areas. If Virginia Rail frequency increases with habitat area, the relationship does not appear to be strong.

Short grass meadow specialists may be especially sensitive to habitat destruction or degradation because of their association with large marshes. Many specialized grassland birds also are area sensitive, and the increasing fragmentation of prairies and other grasslands has been linked to the decline of these species (Herkert 1994a, 1994b; Vickery et al. 1994). Tidal marshes, which may be considered a type of grassland, also have been subject to fragmentation (Niering and Bowers 1966, Bongiorno et al. 1984). Human activities that dissect salt marshes or otherwise reduce their total area may contribute to the decline of short grass meadow specialists. Furthermore, the replacement of short graminoids by *Phragmites* may reduce already limited habitat for these species (Benoit and Askins 1999). Marshes where tidal flow has been restricted by tide gates, dikes, or road construction are especially susceptible to invasion by *Phragmites* (Bongiorno et al. 1984, Roman et al. 1984, Sinicrope et al. 1990). These sites should have high priority for restoration in order to re-establish large expanses of short grass vegetation.

Our results are consistent with the hypothesis that fragmentation of continuous short grass marshes with artificial barriers will not only directly destroy marsh habitat, but also will have a negative effect on the abundance of short grass meadow specialists in the remaining patches of undisturbed habitat. This may apply especially to Seaside Sparrows and Willets, which showed a positive correlation with marsh area even when marshes were considered distinct if they were separated by only 10 m of upland habitat or 30 m of open water. The abundance of more generalist marsh species, including those associated with cattail and *Phragmites*, appears to be less sensitive to habitat fragmentation.

Neither the broad barriers nor the narrow barriers that we used to delineate marshes in separate analyses are likely to inhibit the dispersal of marsh bird species, many of which migrate across great distances. It is more likely that these barriers serve as indicators of habitat edge. In forests and grasslands negative edge effects such as increased rates of nest predation and brood parasitism account for the low density of some species of birds in small habitat patches (Faaborg et al. 1995). Our goal was to determine whether the major edges associated with broad barriers (such as extensive residential areas or forest) and the minor edges associated with narrow barriers (such as railroad tracks and roads) are associated with the occurrence and density of marsh bird species. Our results suggest that both types of edges may be related to the distribution of bird species that are found primarily in short grass meadows. Research on the nest success and survivorship of these species is needed, however, to determine if there is a selective advantage to avoiding smaller marshes.

Marshes can be managed for salt marsh birds by protecting entire marsh systems from development to prevent reduction of the total area of contiguous habitat and by not constructing canals, causeways, and other artificial barriers that divide a large marsh into smaller patches. Where such structures already have been built, marshes can be restored by removing them. Large, continuous marsh systems dominated by short grass meadows should have a high priority for protection and, if necessary, restoration to sustain specialized species of marsh birds.

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