

Postfledging Movement Behavior and Habitat Use of  
Adult Female Saltmarsh Sharp-tailed Sparrows

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B.S., University of Montana, 2001

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APPROVAL PAGE

Master of Science Thesis

Postfledging Movement Behavior and Habitat Use of  
Adult Female Saltmarsh Sharp-tailed Sparrows

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## THESIS ABSTRACT

The findings presented in these two chapters represent the first explicit postfledging movements and habitat use for adult female Saltmarsh Sharp-tailed Sparrows. Female sparrows varied considerably in their use of total space, but appeared to move consistently during the postfledging period in the distance between relocations and the distance to from relocations to their nest. Movement behavior was best predicted by models incorporating the amount of artificial ditch and natural channel margins, but we were unable to demonstrate preferential use of these features within female home ranges.

This study also identified a shift in habitat use from the nesting period (as reported in other studies) to the postfledging period. Even in such a relatively simple system as salt marshes, individual females demonstrated different preferential use of individual habitat components. The overall pattern of habitat use, however, was strikingly different from that previously described for Saltmarsh Sharp-tailed Sparrows during other periods of their life. This new suite of microhabitat components that describes postfledging habitat use consists of relatively tall and structurally varied vegetation, at locations relatively close to the marsh edge, and with relatively greater amounts of bare ground and *S. alterniflora* (tall form). Previous attempts to estimate Saltmarsh Sharp-tailed Sparrow population size in Connecticut have been hindered by a lack of knowledge concerning the home range size, movement patterns and habitat use of this species. These data should facilitate the creation of demographic models that could provide valuable insight into conservation actions and into the processes that regulate Saltmarsh Sharp-tailed Sparrow populations.

## **Chapter 1: Postfledging movement behavior of adult female Saltmarsh Sharp-tailed Sparrows**

### **INTRODUCTION**

For effective conservation and management we need comprehensive knowledge of a species' biology at all life stages (Fletcher et al. 2006). Relatively little is known about the postfledging needs and movement behavior of birds (Vega Rivera et al. 1998; Lang et al. 2002) and few species have been studied in detail during this life stage. Nonetheless, previous studies have reported high fledgling mortality during the first several days after leaving the nest (Naef-Daenzer et al. 2001) and throughout the subsequent weeks (e.g., Woolfenden 1978, Sullivan 1989, King et al. 2006; Berkeley et al. 2007). Juvenile survival may not have the greatest impact on population growth rates (reviewed in Sæther and Bakke 2000; Murphy 2001; Fletcher et al. 2006), but local management actions may be more able to positively influence this life history period.

Most post-fledgling studies have solely examined fledgling survival (K. Wells, unpublished data), and few studies have examined the detailed actions of the attending parents during the dependency period (King et al. 2006). Moreover, nearly half of the published postfledging studies have examined postfledging ecology in forests and upland prairie habitats and some species (e.g., Wood Thrush, *Hylocichla mustelina*) have been disproportionately represented in the postfledging literature (K. Wells, unpublished data). To broaden our understanding of the postfledging period, we need space use data collected in a variety of species across a diversity of landscapes. Such data will allow us to document the range and sources of influence



on both parental and juvenile postfledging movement behavior. Furthermore, documenting the movement capabilities of individuals can allow us to: 1) identify population structures; 2) measure the ability of a species to colonize newly-created and restored areas (Hanski 1998); 3) document the possible impact of fragmentation (Grubb and Doherty 1999).

The cost to attending adults during the dependency period is not trivial and can reduce survival (Wheelwright et al. 2003), delay future reproductive attempts (McGillivray 1983), and may influence how both parents and offspring move through the landscape (Vega Riviera et al. 2000; Bayne and Hobson 2001). A species' movement behavior, breeding success, and mortality rates can vary greatly among habitat patches of different sizes (Winter et al. 2006), and the effects of fragmentation and patch size on postfledging movements are poorly understood (Strong and Bancroft 1994). During the dependency period the young become increasingly independent of their attending parent(s) for decisions regarding resource selection and direction of movement.

The Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*) is an obligate saltmarsh breeding species of the U.S. Atlantic coast, with more than half of the total population projected to nest in southern New England (Dettmers and Rosenberg 2000). In this species, males are non-territorial and do not provide any parental care (Woolfenden 1956; Greenlaw and Rising 1994). Female Saltmarsh Sharp-tailed Sparrows are also non-territorial with overlapping home ranges and will often nest within several meters of each other (Greenlaw and Rising 1994; JMH personal observation). These ground nests are quite vulnerable to daily tidal flooding and the

near-monthly new and full moon tides that can briefly submerge tidal marshes (Lewis 1920; Greenberg et al. 2006).

The primary objective of this study was to quantify the movements of adult female Saltmarsh Sharp-tailed Sparrows during the postfledging stage, and to investigate the relationship between space use and: 1) water margin features; 2) body weight; 3) marsh size; and, 4) time of season. Saltmarsh Sharp-tailed Sparrows spend more time foraging from exposed muddy surfaces (e.g., the margins of tidal water features) than any other microhabitat in the marsh (Post and Greenlaw 2006), which are most commonly found along ditches and channels. Hence, we hypothesized that the presence of ditches and channels within the home range of females could explain their movement patterns. Larger individuals may require greater area to obtain necessary resources (McNab 1963), and marsh size could be a proxy for habitat quality (*cf.*, Zarette et al. 2000), forcing females in poor quality marshes to also travel farther. Lastly, females may be more likely to wander farther from their nesting area towards the end of the breeding season as their chances of reproducing again that year diminish. We specifically chose Saltmarsh Sharp-tailed Sparrows for this study because changes in space use may be more difficult to detect in species with: 1) more attending adults (since the costs and consequences of postfledging care would be spread across more individuals; 2) territorial behavior that may inhibit movement beyond the defended area; and, 3) few postfledging studies have examined extreme habitat specialists.

## METHODS

### *Study Area*

This study was conducted at six salt marshes along a ~ 25 km stretch of Long Island Sound in Connecticut (Figure 1), roughly between the towns of Guilford (New Haven County) and Old Saybrook (Middlesex County). The predominant vegetation at all sites consisted of *Spartina patens*, *S. alterniflora*, *Juncus gerardii*, and *Distichlis spicata* (Chapter 2). The invasive species *Phragmites australis* was present at all six sites to varying degrees but was largely confined to the edges and drier upper portions of the marshes.

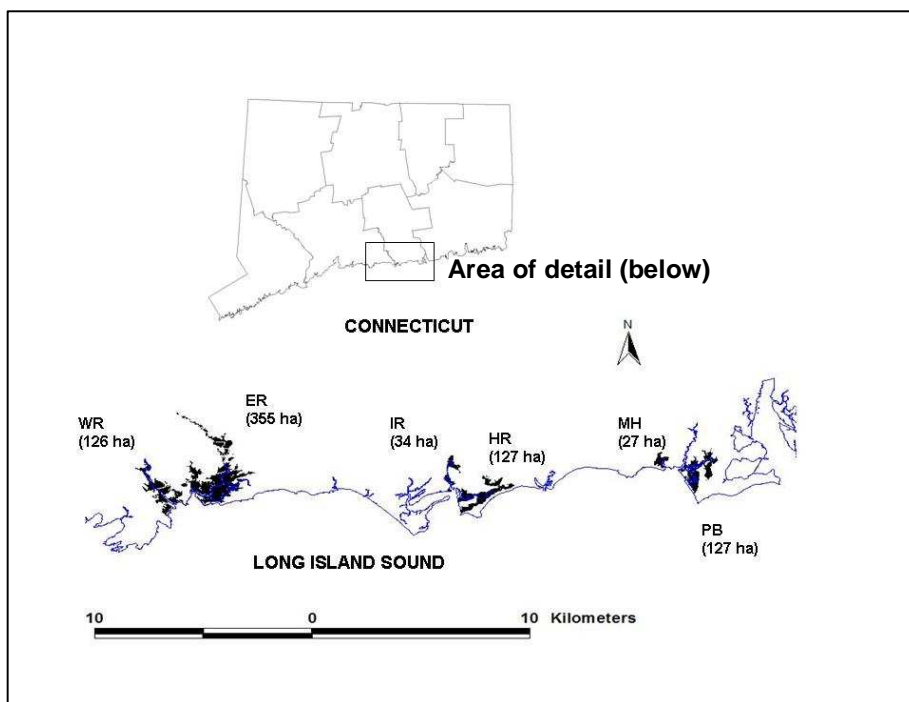


Figure 1. Salt marshes (with sizes in ha) with radio-transmitted adult female Saltmarsh Sharp-tailed Sparrows in 2006 and 2007: West River (WR), East River (ER), Indian River (IR), Hammock River (HR), Mud & Hagar Creek (MH), and Plum Bank Wildlife Management Area (PB).

Pervasive landscape features in salt marshes are artificial drainage ditches and natural channels (e.g., streams and rivers). All of the marshes in our study and > 90% of marshes in New England were ‘ditched’ prior to the 1940s, largely to reduce standing water and facilitate mosquito control (Bourn and Cottam 1950). In our study marshes ditches were dug parallel to one another at roughly 30-40 m intervals. These ditches often extend for hundreds of meters in a perfectly straight line, but ditch layout can be highly variable (Figure 2).



Figure 2. West River Marsh aerial photo (left; from The University of Connecticut’s Center for Land Use Education and Research (<http://www.clear.uconn.edu>) with a natural channel (curvy line running from top to bottom through the middle of the marsh), artificial ditches (straight lines radiating to left and right), and Long Island Sound visible in the extreme lower right corner. Close-up (right) of an artificial ditch at mid-tide near a similar point where the box is centered in the left photo.

### *Nest Searching and Monitoring*

Data were collected between May and September in 2006 and 2007.

Beginning in late May each year we searched for nests every 3-10 days and continued to search for nests throughout the season. Marshes were systematically searched by walking back and forth at closely-spaced intervals and constant speed to ensure that nests throughout each marsh were found. We discovered nests by flushing females, observing female nesting behavior (e.g., food carrying), and opportunistically.

Once found, nests were marked 5 m away with a short utility flag and monitored every 3-5 days until failure or fledging occurred. Starting on the day prior to expected fledging, all nests were checked daily. When nests were found empty, we searched the surrounding area for drowned nestlings and observed the female for up to two hours for food provisioning behavior. We considered young to have fledged if young were present up until at least the day prior to expected fledging, and we did not find drowned nestlings around the nest.

We aged nestlings either by witnessing hatching (day 0) or based on Woolfenden's (1956) descriptions of known-age Saltmarsh Sharp-tailed Sparrow nestlings. Female sparrows were captured at their nest during the nestling stage, generally, one or two days prior to expected fledging. After capture we took basic morphological measurements and weighed females to ensure that radio transmitter weight was  $\leq 3\%$  of body weight. We attached a USGS aluminum band, a site-specific color band, and a radio transmitter. For most females ( $n = 21$  of 23) we also attached radio transmitters at this time to the largest nestling in their nest as part of another study. Because we generally attached radios immediately prior to fledging,

we had few radio-marked females with unsuccessful nests and hence we excluded data from these females for this study.

### *Radio Attachment and Tracking*

We attached radio transmitters (.51 g, Model BD-2N; Holohil Systems Ltd., Ontario, Canada) using two methods: a figure-8 harness (Rappole and Tipton 2007) using elastic beaded thread with a 42 mm harness loop (see Naef-Daenzer 2007), and attaching transmitters to the synsacrum with glue (Loctite 422, Loctite Corporation, USA). Females (n = 2 of 5) were able to forcefully remove glued transmitters from themselves or their nestlings (n = 4 of 4) so we attached all subsequent transmitters using the figure-8 harness. We used the same transmitter body in both years, but in 2007 we increased the antenna diameter from 0.18 to 0.56 mm in response to females bending and/or breaking-off their antennas which reduced signal strength. We trimmed the heavier antenna to just-over tail length so that the weight of the total transmitter package remained approximately the same as the previous year.

We tracked sparrows on foot using Model R-1000 receivers (Communication Specialists, Inc., Orange, California) commencing the day after transmitter attachment to allow individuals to become accustomed to the presence of the transmitter. We used a systematic sampling regime to locate each radio-tagged bird once daily between 0530 and 2030. We scanned for radio signals before entering marshes to approximate the location of all radio-marked birds. Because Saltmarsh Sharp-tailed Sparrows are agile runners (Hill 1968; Greenlaw and Rising 1994), radio-tagged birds were approached at a brisk walk until they either flushed or were

seen in the vegetation, and a GPS point was taken with (horizontal precision  $\leq 4$  m with Wide Area Augmentation System (WAAS) enabled; Garmin Etrex, Garmin International, Inc. Olathe, Kansas). This method for finding marked adult birds has advantages over the standard triangulation method used often in telemetry studies (White and Garrott 1990), because it allows one to record the bird's exact location rather than placing the bird in the center of an error polygon (Findholt et al. 2002). We attempted to vary the direction from which we approached radio-tagged birds each day so as to avoid systematically driving birds in one direction.

Sparrows were tracked until their transmitters fell off or failed, until they were depredated, or until they moved beyond our range of detection. We only included female sparrows that were detected at least three d in our analysis. Once a sparrow went missing, we continued to search for it for 3 d over a 10-ha area centered on the last known location.

### *Model Building*

We used an information-theoretic approach (Burnham and Anderson 2002) to compare a set of *a priori* models, and we tested these models against three dependent variables: 1) minimum convex polygon [MCP] size; 2) mean distance from relocation sites to the female's nest; and, 3) mean distance moved between consecutive days. For each dependent variable we tested a global model and 4 single-variable models that included the following explanatory variables: (a) marsh size (calculated using the Connecticut Department of Environmental Protection and Office of Long Island Sound Programs (1995) Tidal Wetlands GIS Coverage in ArcView); (b) capture

weight; (c) median tracking date (expressed as days since January 1); and, (d) cumulative ditch and channel margin length (square root transformed to meet normality assumptions) within a female's MCP. The lack of natural channels in most female home ranges ( $n = 12$ ) precluded analyzing the length of natural channel margins as a separate explanatory variable.

Saltmarsh Sharp-tailed Sparrows are known to forage extensively in exposed muddy substrate (Post and Greenlaw 2006). Measuring the area of exposed muddy surfaces along water features from aerial photos is not reliable, due to the presence of overhanging vegetation and the limited picture resolution (JMH personal observation), especially for water features  $< \sim 2$  m. To index the amount of muddy surface available to females, therefore, we delineated the edges of artificial ditches and natural channels from true color coastal imagery viewed over the internet from The University of Connecticut's Center for Land Use Education and Research (<http://www.clear.uconn.edu>) in ArcView with the ECW plug-in (ER Mapper, San Diego, California). Since sparrows generally forage along the margins of ditches and channels, we marked the edges of water feature wider than  $\sim 2$  m by tracing both boundaries of the feature. For features less than  $\sim 2$  m wide we simply drew a single line down the middle of the feature.

Movement data were measured using the Animal Movement (ver. 1.1; Hooge and Eichenlaub 1997) and XTools extensions (DeLaune 1997) in ArcView 3.3 (Environmental Systems Research Institute, Redlands, California), and analyzed with SAS 9.1 (SAS Institute Inc., Cary, North Carolina), as were all other data. We tested for correlation between the mean distance from locations to the nest and mean



distance between consecutive relocations and days since fledging occurred using sequential Bonferroni corrections (Rice 1989).

Estimates of space use, including home range estimators are sensitive to the number of measurements used (Harris et al. 1990; White and Garrott 1990). Therefore, we investigated the impact of this potential nuisance variable (the number of measurements used; hereafter referred to as subsample size) on all dependent variables. The variable was differed slightly depending on the dependent variable being tested. For models describing MCP size and the mean distance from the bird to the nest the number of relocations was the subsample size. For models of the mean distance between consecutive relocations we used only the number of measurements between consecutive days; we excluded adjacent pairs of locations separated by a day when the bird was not located. We ran each of the above 5 models with and without sample size included as an additional explanatory variable.

We calculated Akaike's information criterion (Akaike 1973) with small sample size correction (Hurvich and Tsai 1989), and used Akaike weights ( $w_i$ ) to compare the relative likelihood of each candidate model. For each dependent variable we created: 1) a confidence model set that included any model with an  $\Delta AIC_c < 4.0$ ; 2) averaged parameter estimates for any variable occurring in the confidence set of models; 3) weighted unconditional standard errors from those estimates (Burnham and Anderson 2002); and, 4) a composite model (Burnham and Anderson 2002). We evaluated the assumptions of models by visual examination of residuals vs. predicted value plots and normality tests (Shapiro and Wilk 1965) of residuals.

### *Water Feature Margin Length Measurement and Comparison*

Since ditches and channels are common features within salt marshes, we investigated whether we could distinguish their presence in a female's MCP compared to a random area within the same marsh. For each female sparrow we selected a random area within the same marsh that matched the size of her calculated MCP using the AlaskaPak extension (U.S. Department of Interior 2002) for ArcView. We disregarded any random area that overlapped roads or that contained > 50% non-salt marsh areas (e.g., forests), and selected another random area. We then separately compared the cumulative margin lengths of artificial ditches (paired *t*-test) and natural channels (Wilcoxon matched pairs signed-rank test due to extreme non-normality) between a female's MCP and that in the corresponding random area to determine whether the lengths differed from that expected by chance.

## **RESULTS**

Over two years, 23 female Saltmarsh Sharp-tailed Sparrows that successfully fledged young were followed for at least 3 days ( $\bar{X} = 12.7 \pm 5.0$  days). Eight females (35%) were radio-tracked until suspected radio expiration (mean days tracked = 17.9), 12 (52%) disappeared before expected radio failure (mean days tracked = 10.9 d), one (4%) was depredated 14 d post-deployment, and two (9%) shed their radios (5 and 10 d post-deployment). The recovered radio of the depredated female was chewed, covered in mud, and yet still produced reasonable telemetric output. We suspect that she was killed by a mammal, because the chewed-up remains were found on the ground in the marsh beneath very dense vegetation near the entrance to a hole.

All data are presented for  $n = 23$  individuals, with mean  $\pm$  SD given unless otherwise explicitly stated. We removed two females from the movement portion of the analysis that exhibited extreme movement behavior unlike that of the remaining females. The removal of these two females did not change the composition of the composite model for each of the three dependent variables quantifying movement behavior. Two females initiated a second nest 14 and 17 d after their first brood fledged, 69 and 30 m away from their previous nests, respectively. We truncated the data for these two individuals at the point when they initiated their second clutches, so all postfledging movement data for all birds followed a single successful reproductive attempt.

During the first day following a fledging event females were usually quite conspicuous while delivering food to fledglings. Based on observations of radio-tagged females repeatedly carrying food to separate areas, we infer that fledglings likely did not stay together after leaving the nest, and we never observed multiple fledglings together. Consequently, they occupied a much larger area than if they had remained together, which made observing fledglings (and the behavior of the attending female) much more difficult. After the first day post-fledging, due to the dense marsh vegetation, and cryptic behavior of fledglings and females it was not possible to ascertain if dependent young were still alive, even when they were radio-transmitted, without physically searching and finding the fledging in the vegetation.

Female MCP size following their chicks fledging ranged from 0.14 to 1.06 ha ( $\bar{X} = 0.51 \pm 0.29$  ha, median = 0.40 ha). Minimum convex polygon size was significantly correlated with the mean distance from relocations to the nest site and

with the mean distance between consecutive relocations ( $r = 0.61$ ,  $p = 0.002$ , and  $r = 0.48$ ,  $p = 0.021$ , respectively). In general, the mean daily distance moved between relocations remained fairly stable (Figure 3). Distances between relocations and to the nest were generally less than 100 m. Within individuals, we did not detect any significant trends in the distance between consecutive locations (range of  $r = -0.41$  to  $0.76$ ), and overall there was no relationship between mean distance between consecutive daily relocations and days post-fledging ( $r = -0.21$ ,  $p = 0.344$ ). The mean distance between a female's consecutive relocations during the postfledging period was significantly correlated with the mean distance between the female's location and her nest ( $r = 0.71$ ,  $p = 0.0002$ ).

There was no evidence that females moved away from the nest following the fledging of their young (Figure 3), and there was no relationship between mean distance from the nest and days post-fledging ( $r = -0.14$ ,  $p = 0.529$ ). We did not detect any movements of radio-tagged birds moving between marshes. Examining each female separately, we detected no individuals with a significant trend in their distance located each day from their nest.

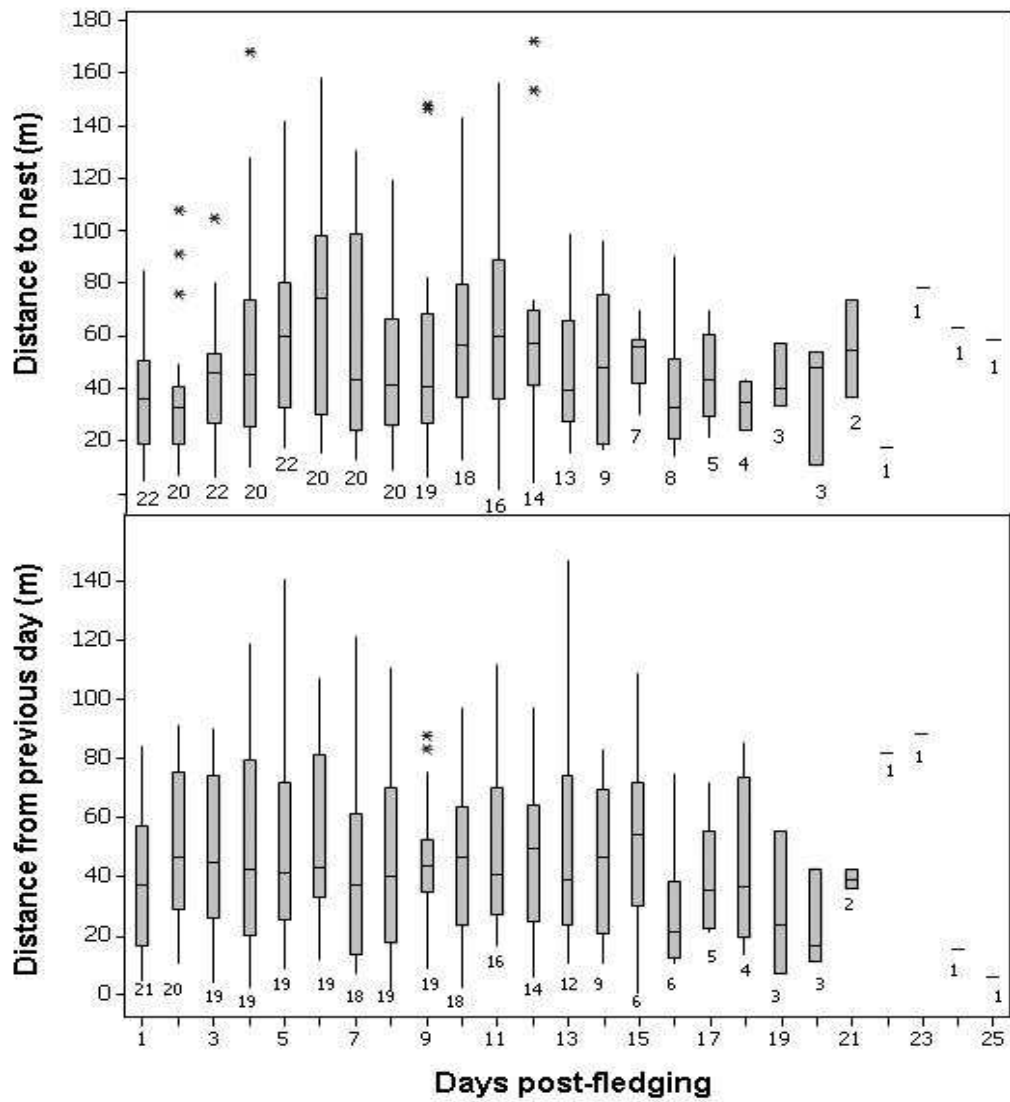


Figure 3. Box plots of the distances from daily relocation sites to the nest (top panel) and distances between observations on consecutive days (bottom panel) for all female Saltmarsh Sharp-tailed Sparrows during the postfledging period. Asterisks indicate observations falling beyond 1.5 times the inter-quartile range. Subsample sizes for each day are given below the boxes and vary slightly between the two panels for a given day since we were unable to locate every female each day.

### *Model Performance*

Female space use and movement rates were best predicted by models that incorporated the length of natural channel and artificial ditch margins (Table 1). The same two models were selected as either the first or second best explanation for each dependent variable (Table 2). Models containing only the length of water feature margins best explained MCP size ( $w_i = 0.76$ ) and mean distance between relocations ( $w_i = 0.41$ ). A similar model also containing the nuisance variable, subsample size, was the best explanation of the mean distance from relocation sites to the nest ( $w_i = 0.58$ ). These were the only models to fall within the confidence model set ( $\Delta AIC_c < 4.0$ ) for each dependent variable, and together their combined Akaike weight was  $> 0.95$  for MCP and the mean distance between relocations, and  $0.81$  for mean distance between relocations and the nest. The remaining variables (weight, marsh size, and date) all had little explanatory power for any of the dependent variables (individual variable Akaike weights  $< 0.09$  in all cases).

Table 1. Composite model with all variables that were included in the confidence model set ( $\Delta AIC_c < 4.0$ ) for each dependent variable: minimum convex polygon, mean distance to nest, and mean distance between consecutive daily locations.

Dependent Variable	Parameter		
	Intercept Mean $\pm$ SE	Days tracked Mean $\pm$ SE	Margin length Mean $\pm$ SE
Minimum Convex Polygon	-137.69 $\pm$ 1186.51	15.87 $\pm$ 24.3	415.56 $\pm$ 78.46
Mean Distance to Nest	36.14 $\pm$ 15.72	-0.88 $\pm$ 0.64	2.34 $\pm$ 0.75
Mean Distance Between Consecutive Daily Locations	37.91 $\pm$ 13.52	-0.4 $\pm$ 0.35	1.1 $\pm$ 0.49

Table 2. Comparison of models created to explain the variation in MCP size, mean distance between relocations and the nest, and mean distance between consecutive daily locations of female sparrows during the postfledging period. All models with Akaike weights  $\geq 0.001$  are included. Models included in the confidence set are indicated with \* ( $\Delta AIC_c < 4.0$ ). The number of variables (k) in each model includes the intercept and error term. For models describing home range size and mean distance to the nest, subsample size equals the number of radio relocations for an individual. For models describing mean distance between two consecutive relocations, subsample size equals the number of measurements made between pairs of relocations on consecutive days.

Dependent Variable	Explanatory variables	K	$\Delta AIC_c$	$w_i$
Minimum Convex Polygon	*Margin length	3	0.00	0.755
	*Margin length + subsample size	4	2.32	0.237
	Margin length + capture weight + marsh size + median tracking date	6	9.46	0.007
	Margin length + capture weight + marsh size + median tracking date + subsample size	7	13.06	0.001
Mean Distance To Nest	*Margin length + subsample size	4	0.00	0.575
	*Margin length	3	0.85	0.376
	Median tracking date	3	8.18	0.010
	Capture weight	3	8.23	0.009
	Marsh size	3	8.44	0.008
	Margin length + capture weight + marsh size + median tracking date + subsample size	7	8.48	0.008
	Margin length + capture weight + marsh size + median tracking date	6	9.41	0.005
	Median tracking date + subsample size	4	10.61	0.003
	Capture weight + subsample size	4	10.93	0.002
Marsh size + subsample size	4	10.95	0.002	
Mean Distance Between Consecutive Daily Locations	*Margin length	3	0.00	0.410
	*Margin length + subsample size	4	0.03	0.404
	Marsh size	3	4.19	0.050
	Capture weight	3	4.41	0.045
	Median tracking date	3	4.66	0.039
	Marsh size + subsample size	4	6.74	0.014
	Capture weight + subsample size	4	7.17	0.011
	Median tracking date + subsample size	4	7.20	0.011
	Margin length + capture weight + marsh size + median tracking date	6	7.97	0.008
	Margin length + capture weight + marsh size + median tracking date + subsample size	7	8.18	0.007

### *Water Feature Margin Comparisons*

Female minimum convex polygons and equivalently-sized random areas within the same marshes contained similar amounts of both artificial ditch and natural channel margins. Twelve minimum convex polygons did not contain any natural channels, while nine random areas also lacked measurable natural channels. Two minimum convex polygons and three random areas did not contain any artificial water features. We failed to detect a significant difference in the length of artificial ditches or natural water features between the minimum convex polygons and random areas (paired  $t_{22} = -0.63$ ,  $p = 0.538$ , and Wilcoxon matched pairs,  $S = 23.50$ ,  $p = 0.325$ , respectively) (Figure 4). Minimum convex polygons contained significantly greater lengths of artificial ditch margins than natural channel margins ( $\bar{X} = 127 \pm 99$  m, and  $\bar{X} = 48 \pm 74$  m, respectively; Mann-Whitney  $t$  approximation,  $t = 685.0$ ,  $p = 0.003$ ). The equivalently-sized random areas also matched this pattern of significantly greater lengths of artificial ditch margins than natural channel margins ( $\bar{X} = 117 \pm 92$  m, and  $\bar{X} = 71 \pm 107$  m, respectively; Mann-Whitney  $t$  approximation,  $t = 638.5$ ,  $p = 0.036$ ).



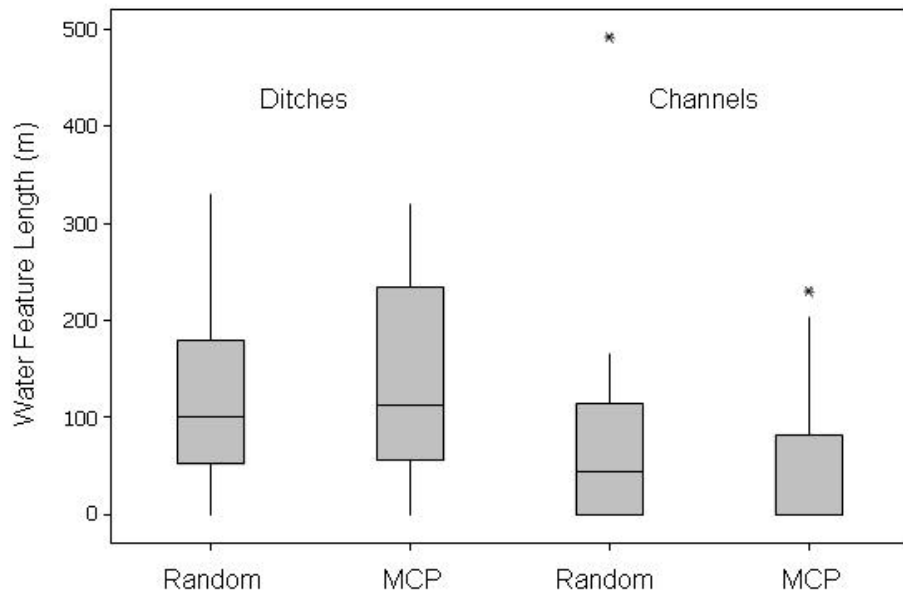


Figure 4. Comparison between artificial ditch and natural channel lengths measured within a female sparrow's calculated MCP ( $n = 23$ ), and within paired random areas ( $n = 23$ ) of equal size within the same marsh. Female home ranges and random areas both contained significantly greater lengths of ditch margins. There was no significant difference in the length of ditch or channel margins among female home ranges and the corresponding random areas. Asterisks represent values beyond 1.5 times the inter-quartile range.

## DISCUSSION

There was substantial variation in the total amount of space female Saltmarsh Sharp-tailed Sparrows used during the postfledging period. Females, on average, used 0.51 ha during the period they were radio-tracked, but our estimates ranged from 0.14 to 1.06 ha. These estimates are similar to previous breeding season estimates produced from non-telemetric methods. Based on observations of banded birds Woolfenden (1956) estimated that females occupied 0.4 ha and Greenlaw and Rising (1994) reported a mean of 1.1 ha (range 0.4 – 3.1 ha). Both of these estimates were

produced by observing individuals during the summer, but without knowing the stage of reproduction these females were in. Our intent was to quantify space use during the postfledging period, and hence we attached radios at the end of the brooding phase. Combined with the few number of individuals who wore radios > 1 day during the brooding phase (n = 5), it is difficult to say how and if individual space use changes throughout the reproductive cycle, but space use is known to change in other species through the breeding period (Stenger and Falls 1959; Fink 1990).

Following their chicks fledging, the distance from a female's locations to her nest and between consecutive relocations were fairly consistent, with no change in either distance in relation to the number of days since fledging had occurred. This result was perhaps surprising for a number of reasons. The flight and movement capabilities of fledglings should steadily increase after they leave the nest, and some studies have reported fledglings moving increasingly away from the nest (Berkeley et al. 2007). If we are correct that Saltmarsh Sharp-tailed Sparrows fledglings behave independently of one another after leaving the nest then they should move further apart over time. We would expect this increased separation between fledglings to result in the attending female traveling greater distances with each passing day. This pattern of increased female movement over time was not apparent from our data, possibly because we were unable to follow the majority of female sparrows until radio expiration, and because of the low number of females we were radio-tracking towards the end of suspected battery life when this increased movement pattern should be most prevalent.

Female space use and movement rates were best predicted by models incorporating the length of natural channel and artificial ditch margins. These features are abundant in most of the salt marshes occurring throughout the range of the Saltmarsh Sharp-tailed Sparrow. Less than 10% of remaining marshes remain unditched (Bourn and Cottam 1950) throughout their range. Channels and ditches, and the associated vegetation, are important foraging sites for Saltmarsh Sharp-tailed Sparrows (Greenlaw and Rising 1994; Post and Greenlaw 2006), and are important predictors of micro-habitat use (Chapter 2). Since ditches generally run parallel to each other at fixed intervals, they may occur in such configuration within marshes as to preclude individuals from moving in such a way to maximize their use of these features. To move between ditches females would have to traverse the areas between them.

Although we rationalized that space use would be influenced by the availability of water feature margins we found no evidence to support this hypothesis. The lengths of channel and artificial ditch margin did not differ between female home ranges and random areas of similar size. At the scale of female Saltmarsh Sharp-tailed Sparrow home ranges it appears that these margins are incorporated randomly into female space use, and are not a result of preference. It is likely that the best models predicting mean distance to the nest and the mean distance between consecutive daily locations simply reflect the increase in ditch margin with increased marsh area.

There is considerable evidence for many groups of animals that a species' home range size increases with body size (Harestad and Bunnell 1979). This increasing space has been attributed to a host of possible factors including increasing

energy requirements (McNab 1963). Our modeling approach, however, found little relative support for differences in movement behavior based on body size differences between females. Considering that the weight of females in our study covered a narrow range, it is possible that our movement behavior metrics were not sensitive enough to detect differences due to body weight, or over the scale that we made measurements it had little effect on movement behavior. If smaller habitat patches have less abundant food supplies (*cf.*, Zarette et al. 2000), then female sparrows may have to increase their use of space to find adequate amounts of food, or lead their fledglings farther distance from their nest than females in larger marshes with more abundant food resources.

Benoit and Askins (2002) reported a decrease in sparrow density in small marshes compared to larger ones, but we found no evidence to suggest that female sparrows use space or move differently with respect to marsh size. A large proportion of the radio-tagged females ( $n = 12$ ; 52%), however, went missing prior to expected radio failure. Some of these females may have disabled their radio or been depredated, but it is likely that some of them made substantial movements away from their last known location. We searched 10 ha centered on the last known location for a missing female, and in marshes  $< 30$  ha (e.g., Indian River and Mud & Hager Creek) we feel confident that we would have detected any females still within these marshes with working radios. Thus, females with working radios who prematurely disappeared from small marshes likely left the marsh altogether, as has been reported elsewhere for this species (DiQuinzio et al. 2001).

We did not detect inter-marsh movements, however, and radio-tagged birds were never observed to cross large within-marsh features (e.g., roads and railroad tracks) in the interior of our largest study marshes. These features running through the marsh were always raised on berms a minimum of 3 m above the marsh. Attesting to their willingness to move, though, we frequently observed birds flying distances > 100 m across river mouths. If adults show unwillingness to cross these elevated landscape features then they would likely serve as a barrier to fledgling movement. However, movement across undesirable habitat during the postfledging period is poorly understood and highly variable between species (Desrochers and Hannon 1997; Bayne and Hobson 2001). For females to move out of these marshes, we hypothesize that the movements must be occurring at dawn, dusk, or during the night when they are known to migrate (Greenlaw and Rising 1994).

In conclusion, we provide the first information on postfledging movements by adult female Saltmarsh Sharp-tailed Sparrows. Females varied considerably in their use of total space (0.14 to 1.06 ha), but overall distances moved were consistent throughout the postfledging period. Movement behavior was best predicted by models incorporating the amount of artificial ditch and natural channel margins, but we were unable to demonstrate preferential use of these features within female home ranges. We were hampered in our investigation of the postfledging period by the majority of females that went missing prior to expected radio-expiration. These females may have finished providing care for fledglings or they may have lost their fledglings from mortality. However, the frequency at which attending adults move from the natal area during the post-breeding period may not necessarily correspond

with nesting breeding success (Arlt and Pärt 2008). Understanding how fledgling Saltmarsh Sharp-tailed Sparrows move during the postfledging period, and the relation of these movements to those of the attending female, may offer the best understanding of movement behavior of the females during this time.

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## Chapter 2: Postfledging Habitat Use by Adult Female Saltmarsh Sharp-tailed Sparrows

### INTRODUCTION

A temporally changing environment (Warnock and Takekawa 1995) or one that has been unduly influenced by anthropogenic disturbance (Misenhelter and Rotenberry 2000) may make the identification of fitness-maximizing habitat more difficult for individuals. Humans are altering ecosystems at a rate never before seen in human history (Wilcove et al. 1998; Millennium Ecosystem Assessment 2005), and wetlands in particular are being degraded and disappearing due to human alteration and habitat destruction (Balmford and Bond 2005). Anthropogenic disturbance in New England has destroyed many historic salt marshes (Tiner 1984): as much as 30% in Connecticut (Rozsa 1995) and up to 80% in other localized areas (Bertness et al. 2002). The remaining salt marshes continue to face serious threats from urbanization, degradation, and invasive species (e.g., *Phragmites australis*) Bertness et al. 2002; Zedler and Kercher 2004). Much of the physical manipulation and degradation of salt marshes resulted from the extensive grid ditching that is ubiquitous in northeastern U.S. coastal marshes. This alteration occurred beginning in the late nineteenth century to 'improve' salt marshes for agricultural production (haymaking of *Juncus gerardii* and *Spartina patens*), and later for mosquito control (Bourn and Cottam 1950).

Individual organisms should select for habitat that improves their chances of survival and reproductive success, but doing so can create conflicts during the breeding and post-breeding periods when parents must balance their needs with those of their offspring (Spencer 2002). The needs of an individual may change their habitat preference throughout their life history (Vega Rivera et al. 1998; Pagen et al. 2000;

King et al. 2006), so it can be particularly important to identify the needs and preferences of the life stage targeted by management and conservation actions.

Females Saltmarsh Sharp-tailed Sparrows provide all of the parental care and have over-lapping home ranges while males are also non-territorial (Woolfenden 1956; Greenlaw and Rising 1994), hence females should not be constrained to specific areas by territory boundaries. The young fledge from their nest 8-11 days after hatching (DeRagon 1988; Greenlaw and Rising 1994), and are incapable of flight. They are likely to be particularly vulnerable to predation and drowning at this stage, as numerous studies have recorded high levels of postfledging mortality for other passerines (e.g., Woolfenden 1978, Sullivan 1989, Naef-Daenzer et al. 2001; King et al. 2006; Berkeley et al. 2007). Understanding patterns of habitat use at this time, therefore, may be particularly important. Saltmarsh Sharp-tailed Sparrows occur exclusively in salt marshes throughout their life cycle, making them particularly vulnerable to changes in marsh vegetation and physical structure.

Saltmarsh Sharp-tailed Sparrows breeding habitat consists primarily of *S. patens* and other high-marsh associated plants (Reinert and Mello 1995; Brawley et al. 1998; Shriver 2002), with little *P. australis* (Benoit and Askins 1999). At the 1-m scale nests are placed in *S. patens* with a deep thatch layer (Gjerdrum et al. 2005). These ground nests are quite vulnerable to daily tidal flooding and on a monthly basis especially the spring tides that typically submerge tidal marshes (Lewis 1920; Greenberg et al. 2006). At the 1-ha scale nests are more common in areas that are away from the edge of the marsh and composed of *J. gerardii* (Gjerdrum et al. 2008).

Adults tend to be found in areas where there is deep thatch away from the marsh edge (Gjerdrum et al. 2008).

Does habitat selection by female sparrows remain constant from the nesting to the postfledging period? If so, we would expect females to be found in areas away from the marsh edge, in areas dominated by *J. gerardii*. However, little attention has been paid to Saltmarsh Sharp-tailed Sparrow use of artificial ditches and natural water channels (e.g., rivers) in habitat selection studies. Sparrows frequently use these ditches and channels as movement corridors (Greenlaw and Rising 1994; JMH personal observation) and predominantly forage from muddy substrate (Post and Greenlaw 2006). Since, the majority of salt marshes (~ 90%) within the breeding range of Saltmarsh Sharp-tailed Sparrows (central Maine to Virginia; Greenlaw and Rising 1994; Hodgman et al. 2002) were grid-ditched before 1938 (Bourn and Cottam 1950) these water features are ubiquitous in their habitat. Saltmarsh Sharp-tailed Sparrows have likely declined throughout their range (Greenlaw and Rising 1994).

We investigated the habitat use of Saltmarsh Sharp-tailed Sparrows (*Ammodramus caudacutus*), during the postfledging period after a successful nesting attempt. This study differs from all previous approaches to quantifying Saltmarsh Sharp-tailed Sparrow habitat use, at all life history stages, because we followed radio-tagged individuals of known sex and reproductive status. Furthermore, we performed habitat measurements at the actual locations where these individuals were visually observed. Our objectives here were to identify components of salt marshes that best predict the specific locations used by adult female Saltmarsh Sharp-tailed Sparrows during the postfledging period. We compared vegetative cover at locations used and

available to female sparrows and proximity of these locations to artificial ditches, natural channels, and the marsh edge.

## **METHODS**

We collected data at five salt marshes along a ~ 25 km section of Long Island Sound in Connecticut (Figure 1), between the towns of Guilford (New Haven County) and Old Saybrook (Middlesex County). Individual salt marshes ranged in size from 27 ha (Mud-Hagar Creek Marsh) to 355 ha (East River Marsh) and were composed of numerous public and private properties.

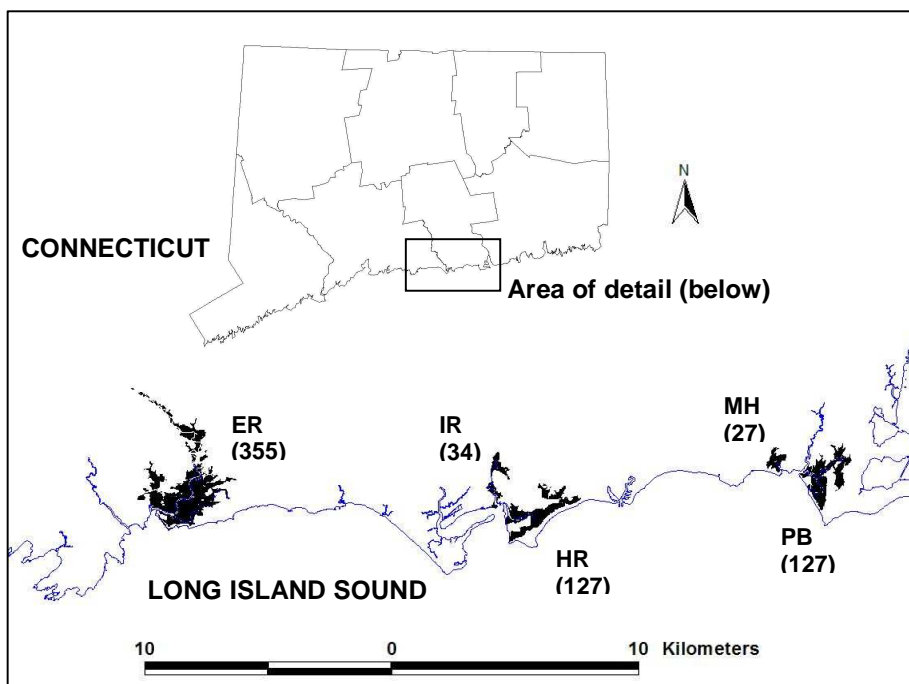


Figure 1. Salt marshes (with size in hectares) where we measured habitat used and available to radio-transmitted adult female Saltmarsh Sharp-tailed Sparrows during the postfledging period: East River (ER), Indian River (IR), Hammock River (HR), Mud-Hagar Creek (MH), and Plum Bank Wildlife Management Area (PB).

### *Nest Searching and Monitoring*

Female Saltmarsh Sharp-tailed Sparrows build well-camouflaged ground nests in salt marshes. We distributed nest searching activities evenly across the marshes by dividing marshes into grids and searching for nests in a systematic manner. Only portions of the largest marshes were searched, as we did not have complete access to certain marshes and were constrained by private property boundaries. We searched individual sections no more frequently than every 3 days to minimize our impact on nesting birds. Discovered nests were marked with a utility flag placed 5 m away and were initially monitored every 3-5 days. We estimated nestling age by witnessing hatching (day 0) or based on Woolfenden's (1956) descriptions of different aged nestlings, and checked nests daily starting two days prior to the expected fledging date (day 10). Nestlings were banded on day 5 or occasionally later. When individual nestlings were missing we intensively searched the area around the nest to determine whether drowning, predation, or fledging had occurred. We considered young to have fledged from a nest, when they were present up until the day prior to expected fledging and females appeared to be attending to fledged young (e.g., food carrying) hiding in the dense vegetation.

### *Radio Attachment and Tracking*

We captured female sparrows at their nests with two-paneled mist nets, generally 1-2 days prior to the date on which their young were expected to fledge. We took basic morphological measurements (e.g., wing and tarsus length) and attached a

USGS aluminum band and a site-specific color band. We attached radio transmitters (model 0.51 g, BD-2N; Holohil Systems Ltd., Carp, Ontario), using the Rappole and Tipton (1991) figure-8 harness method using elastic beaded thread with a 42 mm harness loop (Naef-Daenzer 2007). For most females (n = 10 out of 12) we also attached a radio transmitter to her single largest nestling for a separate study.

We radio-tracked female sparrows on foot with Model R-1000 handheld receivers (Communication Specialists, Inc., Orange, California) starting the day after transmitter attachment. Before we entered marshes, we scanned for the location of all radio-marked birds. After approximating the locations of individuals we approached each bird quickly on foot and flushed it from the vegetation. Most saltmarsh vegetation was short (< 0.5 m), which, allowed us to quickly pinpoint the location of flushing females. They generally flushed at a distance of 4-10 m with a detectable increase in signal strength when females flew into the air. In marshes with multiple radio-marked birds we varied the order in which we relocated individuals and approached each bird from a direction that would avoid unknowingly flushing individuals not yet located. We recorded a GPS location directly over the spot where the bird was first seen with a Garmin Etrex (Garmin International, Inc. Olathe, KS), and marked the location with a uniquely numbered utility flag.

Physically finding and flushing individuals has a number of advantages over a traditional triangulation-based search strategy. The researcher is better able to record the exact location of the animal, as opposed to placing the animal in the middle of an error polygon created through triangulation (Saltz 1994; Findholt et al. 2002). This increased precision in recording animal locations can lead to improved estimates of



microhabitat conditions at points actually used by the animal, especially at the small spatial scales as in this study.

We found and recorded the location of each individual once daily. For missing birds we searched an area of approximately 10 ha centered on the last known location, for three consecutive days after disappearance. One female initiated a second nest after successfully fledging her first brood. Since our focus here is on postfledging habitat selection, we truncated her data set to include only her habitat use prior to the initiation of her second clutch.

#### *Habitat Analysis-Used vs. Available*

To minimize our impact on radio-tagged females and to reduce the chance of disturbing fledglings hiding in the vegetation near to a female's location, we recorded vegetation characteristics after radio-tracking had ceased for an individual. We centered a 1-m<sup>2</sup> quadrat over each location where a female had been found. We always placed two opposite corners of the quadrat on a line between compass-determined north and south. We followed the same basic sampling protocols used in previous studies (Gjerdrum et al. 2005, 2008; Humphreys et al. 2007) to facilitate comparison. Within each quadrat we estimated the percent cover of each plant species and bare ground to the nearest percent. We estimated vegetation height as the mean height of the individual plant stem closest to each of the corners. Thatch height was measured at the center of the quadrat. All vegetation data were collected during July and August 2007.

To assess the habitat available to each female, we quantified vegetation characteristics at a number of random points equal to the number of points recorded for that female. We generated random points within a one hectare circle around each female sparrow's nest using the AlaskaPak extension (U.S. Department of Interior 2002) for ArcView 3.3 (Environmental Systems Research Institute, Redlands, California). We choose a 1 ha circle based on the approximate maximum home range size of previous estimates of space use by radio-transmitted females (Chapter 1). Random points were located in the field with a GPS unit. We discarded and replaced points that fell outside of the marsh boundary or within a permanently flooded area. None of the random locations overlapped locations actually used by females (*cf.*, Thomas and Taylor 2006). For analysis we removed one location available for each of two females, due to incomplete recording of vegetation characteristics.

In ArcView, we used true color coastal aerial imagery (University of Connecticut Center for Land Use Education and Research; <http://www.clear.uconn.edu>) processed over the internet with the ECW plug-in (ER Mapper, San Diego, California) to map artificial and natural water features. We used the Connecticut Department of Environmental Protection and Office of Long Island Sound Programs (1995) Tidal Wetland Coverage layers for ArcView to delineate marsh boundaries. For all points where vegetation was sampled we calculated the distance to the nearest marsh edge, artificial ditch, and natural channel using the Nearest Feature Extension v3.8b (Jenness 2004). The edges of small water features (< 2 m wide) can be difficult to distinguish from aerial photos because they are often obscured with vegetation. For water features < 2 m wide, therefore, we drew a line

down the center of the feature. For features  $> 2$  m wide we marked the edges of the water feature by tracing both boundaries of the feature, and measured distance to the nearest line.

### *Statistical Analyses*

We used a combination of methods to compare habitat used by, and available to, females. We examined the normality of the data using Shapiro-Wilk normality tests ( $\alpha = 0.05$ ; Shapiro and Wilk 1965). For each variable we pooled the individual sparrow's mean values and conducted two-sided Mann-Whitney (using the  $t$  approximation) or  $t$ -tests, as needed, to measure differences between used and available habitat features. We calculated Cohen's  $d$  (Cohen 1988), a measure of effect size and the degree of distribution overlap between habitat variables in used and available locations. We used Cohen's  $d$  and traditional  $p$  values of  $\geq 0.8$  and  $0.05$ , respectively, as indication of significance when comparing variable means among locations used and available to females. A Cohen's  $d$  value of  $\geq 0.8$  indicates the two distributions overlap by less than 50% (Cohen 1988). For  $t$ -tests we assumed that both samples came from populations with equal variances unless the Folded F statistic ( $F'$ ) produced by SAS suggested otherwise, where we then used a correction for unequal variances (Satterthwaite 1946).

We also used a simple vote count procedure to compare habitat availability to habitat used for each female sparrow separately. For each individual we conducted  $t$ -tests or two-tailed Mann-Whitney tests (using the  $t$  approximation), if data significantly deviated from normality, to compare the sites she used to those available

to her. We then counted the number of females detected using significantly more or less of a given habitat variable. For each variable, we counted the number of females whose mean from occupied locations was greater or lesser than the mean for available habitat. We used sign tests with these numbers to detect deviation from the expected ratio of 1:1. For individual variable sign tests we excluded females if both their locations used or available did not contain any measurable amount. All statistical analyses were performed with SAS 9.1 (SAS Institute Inc., Cary, North Carolina).

### *Model building*

To compare locations actually used by female sparrows to those available to them we also used an information-theoretic approach (Burnham and Anderson 2002) to compare models selected *a priori* using logistic regression. We based our models on 1) the results of previous habitat selection studies for Saltmarsh Sharp-tailed Sparrows, 2) our own hypotheses about how these sparrows use their habitat based on extensive observation, and 3) a framework designed to tease apart differences in use of artificial ditch and natural water channel margins.

From our initial set of candidate models, we used the Hosmer and Lemeshow (1989) goodness-of-fit statistic to ensure that models were appropriate to compare using logistic regression. We were unable to compare models that resulted in complete or quasi-separation for some individuals (Appendix 1). Separation problems occur when the maximum likelihood algorithm fails to converge on a single coefficient estimate, and is often a result of small sample size (Allison 1999). We also tested for multicollinearity by running all candidate models as linear regression

models and calculating variance inflation factors (Montgomery and Peck 1992). We used 5.0 as our cutoff for removing variables that caused unacceptably high multicollinearity.

Due to different sample sizes across individuals we fitted models to each female sparrow's data separately (Thomas and Taylor 2006) and then calculated Akaike's information criterion (AIC) for each model (Akaike 1973), using the small sample size correction ( $AIC_c$ ; Hurvich and Tsai 1989). We then summed  $AIC_c$  scores for each model across all females and used Akaike weights ( $w_i$ ), based on  $\Delta\sum AIC_c$  to assess the relative likelihood of each model (Gervais et al. 2003; Glenn et al. 2004; Zielinski et al. 2004). Since our best (lowest  $\sum AIC_c$  score) model received > 90% of the Akaike weights, we created a weighted average of parameter estimates using parameter estimates for that model from all individuals. For weights, we used the inverse of the standard error for each individual parameter estimate (Zielinski et al. 2004) to account for differences in the quality of those parameter estimates caused by the unequal amounts of information collected for individuals.

We also compared the  $\sum AIC_c$  approach for final model selection to a much simpler method of ranking all models for each female (from the lowest to highest  $AIC_c$  score) and computing a mean ranking for each model across individuals. In effect, this gives each individual bird a single vote for the order of best-fitting models, regardless of the size of their dataset. We noted the numbers of times that a particular model fell within the confidence set ( $\Delta AIC_c < 4.0$ ) of the best model for each individual.

## RESULTS

### *Used vs. Available Vegetation*

We detected 22 species of salt marsh plants at 170 locations used by 12 female Saltmarsh Sharp-tailed Sparrows, and at 168 matched random locations. Five plant types (Figure 2) constituted the majority of the vegetation recorded at both used (77% of all coverage) and available (91% of all coverage) locations: *S. patens*, *S. alterniflora* (both tall and short forms), *D. spicata*, and *J. gerardii* (Figure 2). Additional species of plants included *Iva frutescens*, *Lonicera sempervirens*, and the invasive species *P. australis*. Locations used by five individuals contained *P. australis* ( $n = 5$ ,  $\bar{X} = 5.1 \pm 1.7\%$ ).

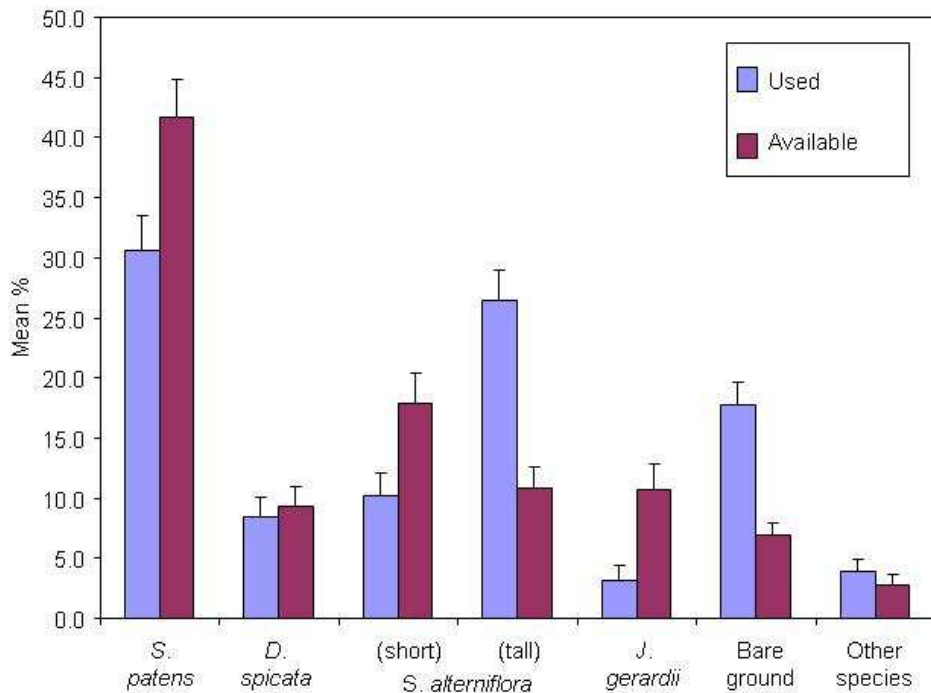


Figure 2. The mean (+ SE) percent vegetation cover and bare ground for 1-m<sup>2</sup> locations used ( $n = 170$ ) and available ( $n = 168$ ), combined for all twelve female sparrows during the postfledging period.

Examining each female's habitat use, relative to what was available (Figure 3) showed contrasting resource selection by different birds for five of the twelve variables tested. Some individuals used microhabitats containing disproportionately high amounts of *D. spicata* and tall *S. alterniflora*, while others used locations with disproportionately low amounts. Seventy-five percent of individuals were located closer to the marsh edge than expected based on available locations, but most variables did not have such a strong unidirectional pattern of selection. For example, only twenty-five percent of females used vegetation that was disproportionately tall, and that contained relatively high amounts of tall *S. alterniflora* and bare ground. Using sign tests, we detected significant departure from the 1:1 ratio for mean vegetation height ( $M = 4$ ,  $p = 0.0386$ ), standard deviation of vegetation height ( $M = 4$ ,  $p = 0.0386$ ), tall form *S. alterniflora* ( $M = 5$ ,  $p = 0.0063$ ), and distance to marsh edge ( $M = -4$ ,  $p = 0.0386$ ) (Figure 4).

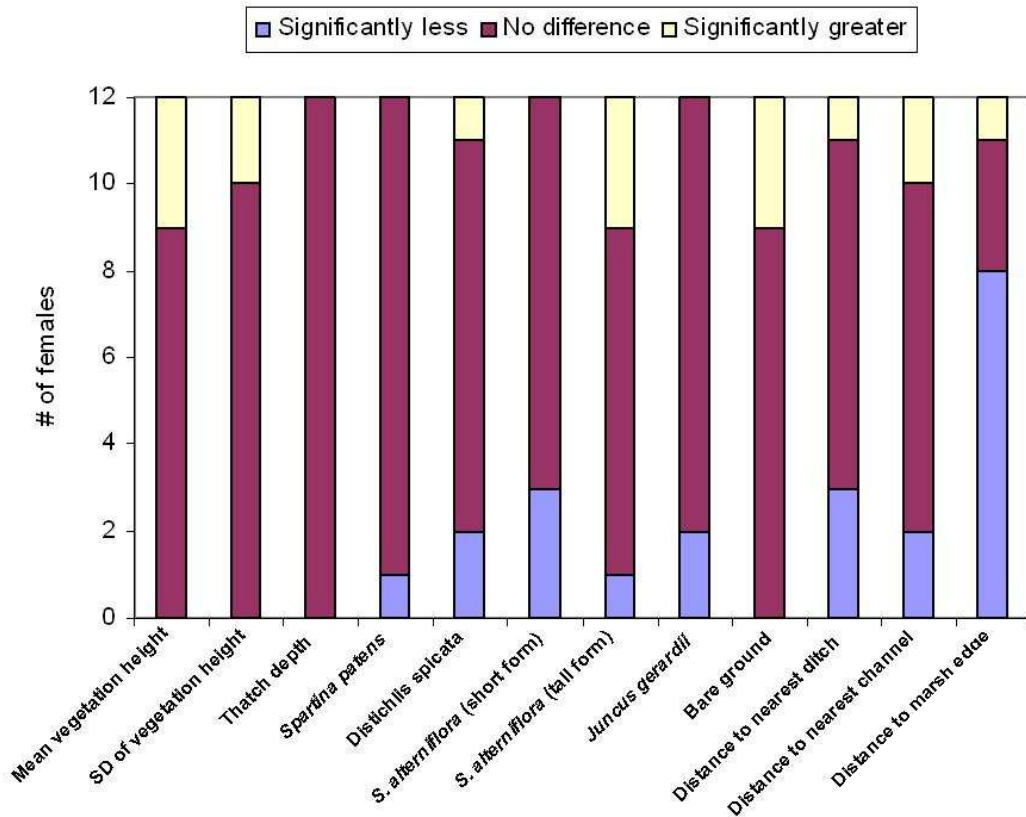


Figure 3. A comparison of habitat used and available to female sparrows. Bars represent a given habitat feature compared to number of females detected at locations with significantly greater or lesser amounts of a given habitat feature compared to available locations.

Both sign tests (Figure 4) and two-sided tests of means (Table 1) detected broad patterns of habitat use, even though individual comparisons (Figure 3) showed apparently opposing patterns of resource selection by different individuals. A disproportionate number of females were found at locations with taller vegetation and greater standard deviation of vegetation height, more *S. alterniflora* (tall form), and were located closer to the marsh edge than random locations. These results were generally supported by the two-sided tests, except that distance to the marsh edge was



not significantly different from random locations. In addition, two-sided tests revealed that females used locations with disproportionate amounts of bare ground.

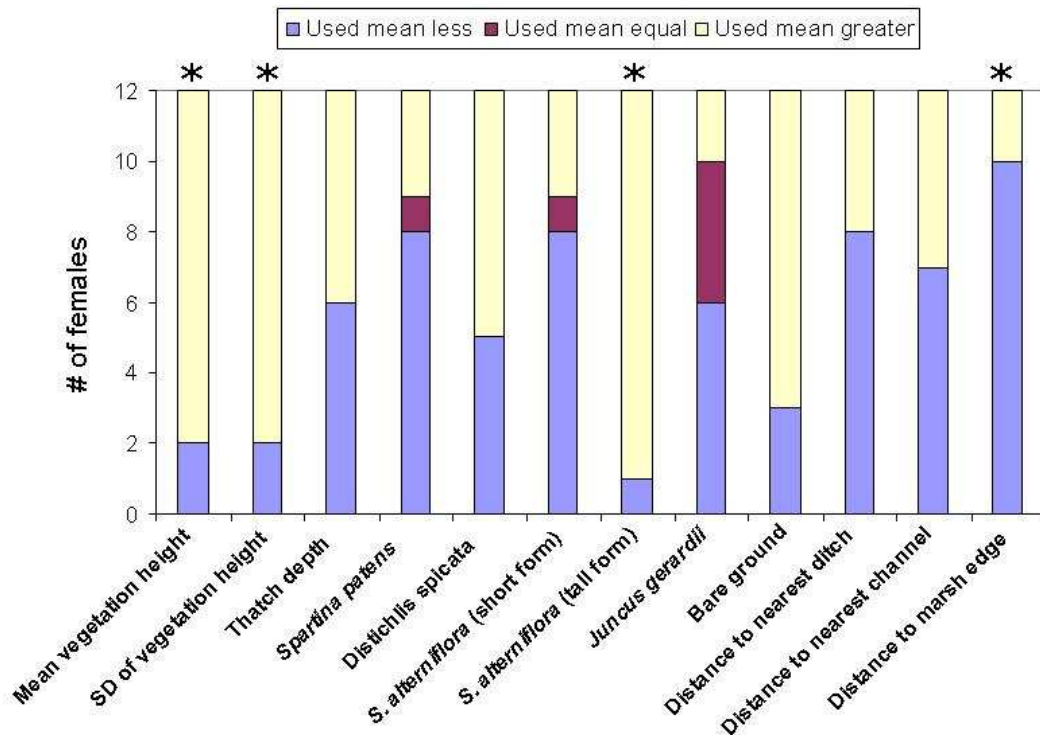


Figure 4. Sign tests detected non-random habitat use for mean and standard deviation of vegetation height, % *S. alterniflora* (tall form), and proximity to marsh edge. An asterisk above the column denotes a significant departure from the expected 1:1 ratio if females were using habitat randomly. For some individuals (in red) the mean values for some variables were equal to zero for both used and available sites. Data for these cases were not included in the sign test for those variables.

Table 1. Two-sided comparisons of the mean variable level for individuals between locations used (n = 12) and available (n = 12) using either two-sample t-tests or the Mann-Whitney tests where appropriate. The Cohen's *d* values for these four tests were all > 0.8, indicating that the distributions of used and available distributions overlapped by less than 50% (Cohen 1988).

Variable	Used	Available	Test Statistic	P value	Cohen's   <i>d</i>
	SE	SE			
Mean vegetation height (cm)	39 ± 5	30 ± 1	$t = 109.0$	0.028	0.82
SD of vegetation height (cm)	19 ± 2	14 ± 1	$t_{22} = -2.1$	0.048	0.86
Thatch depth (cm)	8 ± 1	6 ± <1	$t_{22} = -1.51$	0.145	0.62
% <i>S. patens</i>	31 ± 5	41 ± 5	$t_{22} = 1.25$	0.224	0.51
% <i>D. spicata</i>	7 ± 1	9 ± 3	$t_{22} = 0.59$	0.564	0.24
% <i>S. alterniflora</i> (short form)	8 ± 4	16 ± 4	$t = 178.0$	0.122	0.59
% <i>S. alterniflora</i> (tall form)	28 ± 5	11 ± 3	$t_{22} = -3.08$	0.005	1.26
% <i>J. gerardii</i>	4 ± 2	11 ± 5	$t = 168.5$	0.278	0.62
% Bare ground	17 ± 3	7 ± 1	$t_{14.4} = -3.34$	0.005	1.36
Distance to nearest ditch (m)	16 ± 4	14 ± 1	$t = 165.0$	0.411	0.16
Distance to nearest channel (m)	36 ± 8	43 ± 7	$t_{22} = 0.69$	0.494	0.28
Distance to marsh edge (m)	93 ± 15	126 ± 15	$t_{22} = 1.54$	0.139	0.63

#### *Female Habitat Model Selection*

Model selection using the simple approach of ranking all models within each individual ( $\Delta AIC_c$ ) and computing a mean ranking, compared well to the method of ranking models using all individuals based on  $\Delta \Sigma AIC_c$  (Table 2). Both methods ranked models similarly (n = 22,  $\rho = 0.86$ ,  $p = < 0.0001$ ). The model with the best mean rank among individuals was the second best model selected using  $\Delta \Sigma AIC_c$ . The best model selected using  $\Delta AIC_c$  was included in the confidence set of models ( $\Delta AIC_c < 2.0$ ) for 42% of sparrows.

Table 2. Comparison of two model ranking procedures used to compare a suite of *a priori* models in their ability to separate locations used and available to females Saltmarsh Sharp-tailed Sparrows using logistic regression: 1) model comparison via  $\Delta\sum AIC_c$  tabulated from all individuals, and 2) comparison by ranking models (mean rank) via  $\Delta AIC_c$  within individuals only. For each individual we also noted the number of times a particular model was included in the confidence set ( $\Delta AIC_c < 4.0$ ) for the best model (# CI). We based these models on our observations of Saltmarsh Sharp-tailed Sparrow habitat use, and on the hypothesized relationships between habitat variables measured in our study.

Model	$\sum AIC_c$	$\Delta\sum AIC_c$	$w_i$	Mean Rank	# CI
Distance to nearest channel + distance to marsh edge	387.3	0	0.93	7.3	8
Distance to nearest ditch + distance to marsh edge	392.3	5.1	0.07	6.5	6
<i>S. patens</i> + distance to marsh edge	401.6	14.3	<0.01	8.7	6
Distance to nearest channel + SD of vegetation height + distance to marsh edge	404.6	17.3	<0.01	9.3	4
Distance to nearest ditch + SD of vegetation height + distance to marsh edge	412.1	24.8	<0.01	10.2	4
Bare ground + distance to nearest ditch + <i>S. alterniflora</i> (tall form) + distance to marsh edge	414.2	27.0	<0.01	10.0	3
Distance to nearest channel + <i>S. alterniflora</i> (tall form)	422.8	35.5	<0.01	9.5	4
Bare ground + distance to nearest channel + <i>S. alterniflora</i> (tall form)	429.3	42.0	<0.01	11.7	3
Bare ground + distance to nearest channel	430.8	43.5	<0.01	11.1	2
Distance to nearest channel	435.1	47.8	<0.01	10.4	3
Distance to nearest channel + distance to nearest ditch	443.7	56.4	<0.01	12.3	2
Distance to nearest channel + <i>S. patens</i>	449.7	62.4	<0.01	14.3	1
Mean vegetation height + bare ground + <i>S. alterniflora</i> (tall form)	457.1	69.8	<0.01	12.8	2
Bare ground + distance to nearest ditch + <i>S. alterniflora</i> (tall form)	457.5	70.2	<0.01	11.7	3
Distance to nearest ditch + <i>S. alterniflora</i> (tall form)	460.9	73.7	<0.01	11.8	2
Bare ground + <i>S. alterniflora</i> (tall form)	465.0	77.7	<0.01	10.4	3
Bare ground + distance to nearest ditch	466.8	79.5	<0.01	10.9	2
Mean vegetation height	479.1	91.8	<0.01	13.6	2
Distance to nearest ditch	479.2	92.0	<0.01	12.3	2
Distance to nearest ditch + <i>S. patens</i>	494.0	106.7	<0.01	14.8	2
Mean vegetation height + <i>S. patens</i>	497.4	110.2	<0.01	17.3	1
SD of vegetation height	499.3	112.0	<0.01	16.3	1

The best model ( $w_i = 0.926$ ) discriminating between areas used by female Saltmarsh Sharp-tailed Sparrows and areas available to them contained the variables describing the distance to natural water features and the distance to the marsh edge (Table 3). Distance to the marsh edge (Figure 5) occurred in the 6 models with the lowest  $\Delta AIC_c$ , even though it was only included in 8 of 22 (36.4%) candidate models. The second best model ( $\Delta AIC_c = 5.067$ ,  $w_i = 0.074$ ) was similar to the best model (Table 2) except that the variable for the distance to the nearest natural channel (Figure 6) was replaced with the distance to the nearest artificial ditch (Figure 7).

Table 3. Weighted average parameter estimates and standard errors of variables appearing in the model with the lowest  $\sum AIC_c$ . Parameter estimates from each female were weighted with the inverse of the standard error of the parameter to adjust for differences in precision between individuals.

Parameter	Weighted Estimate	SE
Intercept	3.78	0.23
Distance to nearest natural channel	-0.01	0.02
Distance to marsh edge	-0.04	0.01

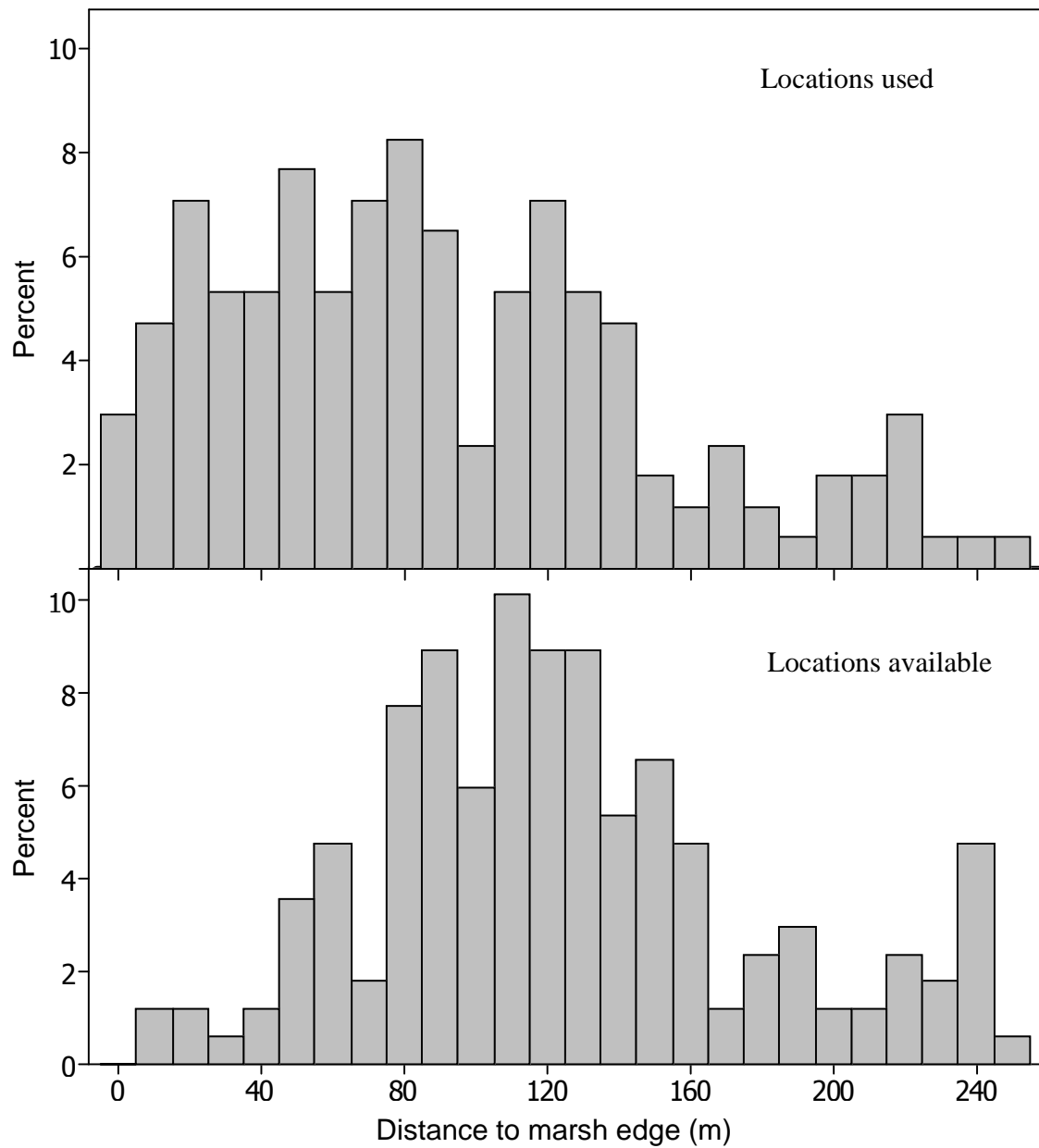


Figure 5. The proximity of all female locations used ( $n = 170$ ; top) and available ( $n = 168$ ; bottom) to the nearest marsh edge. The variable distance to marsh edge occurred in all models with Akaike weights ( $w_i$ )  $> 0.0001$ . On average, females were located 33 m closer to the marsh edge than random locations available to them (Table 1).

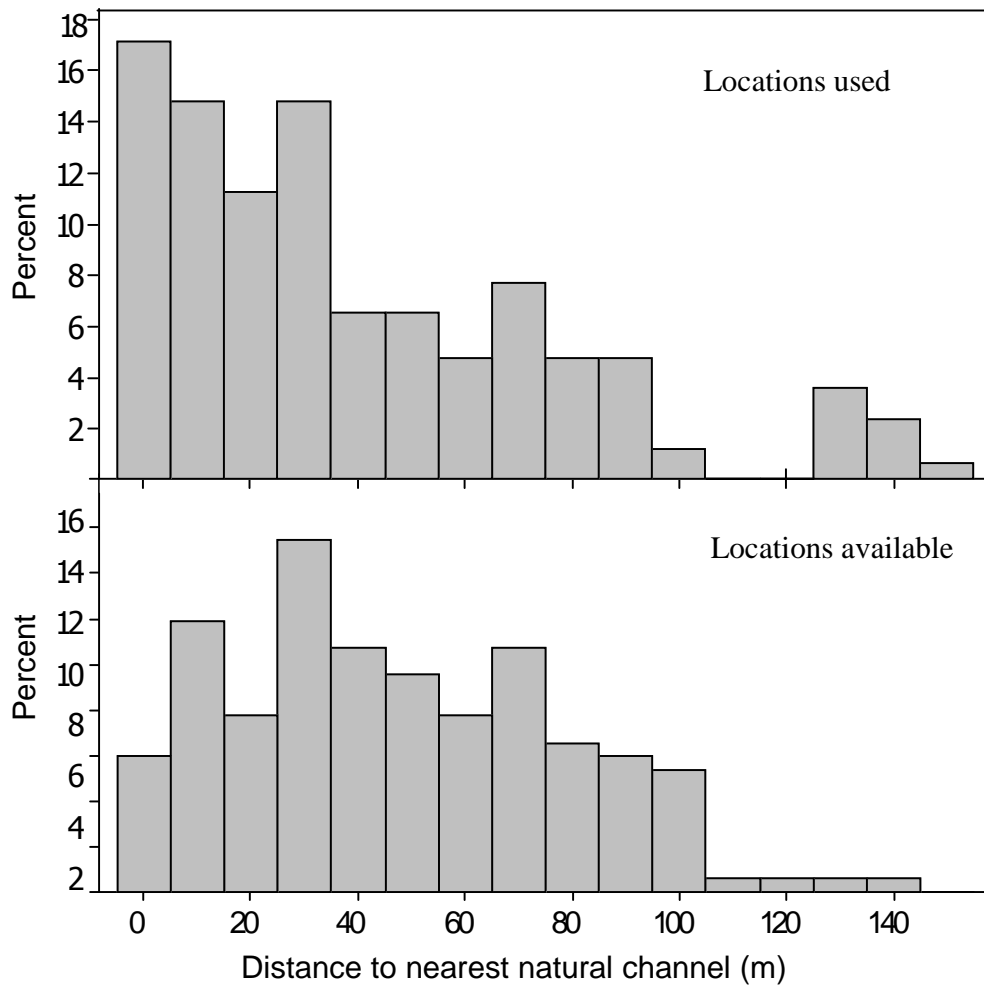


Figure 6. The proximity of all female locations used (n = 170; top) and available (n = 168; bottom) to the nearest natural water channel. This variable, along with distance to the marsh edge, composed the best model explaining female habitat use during the post-fledging period.

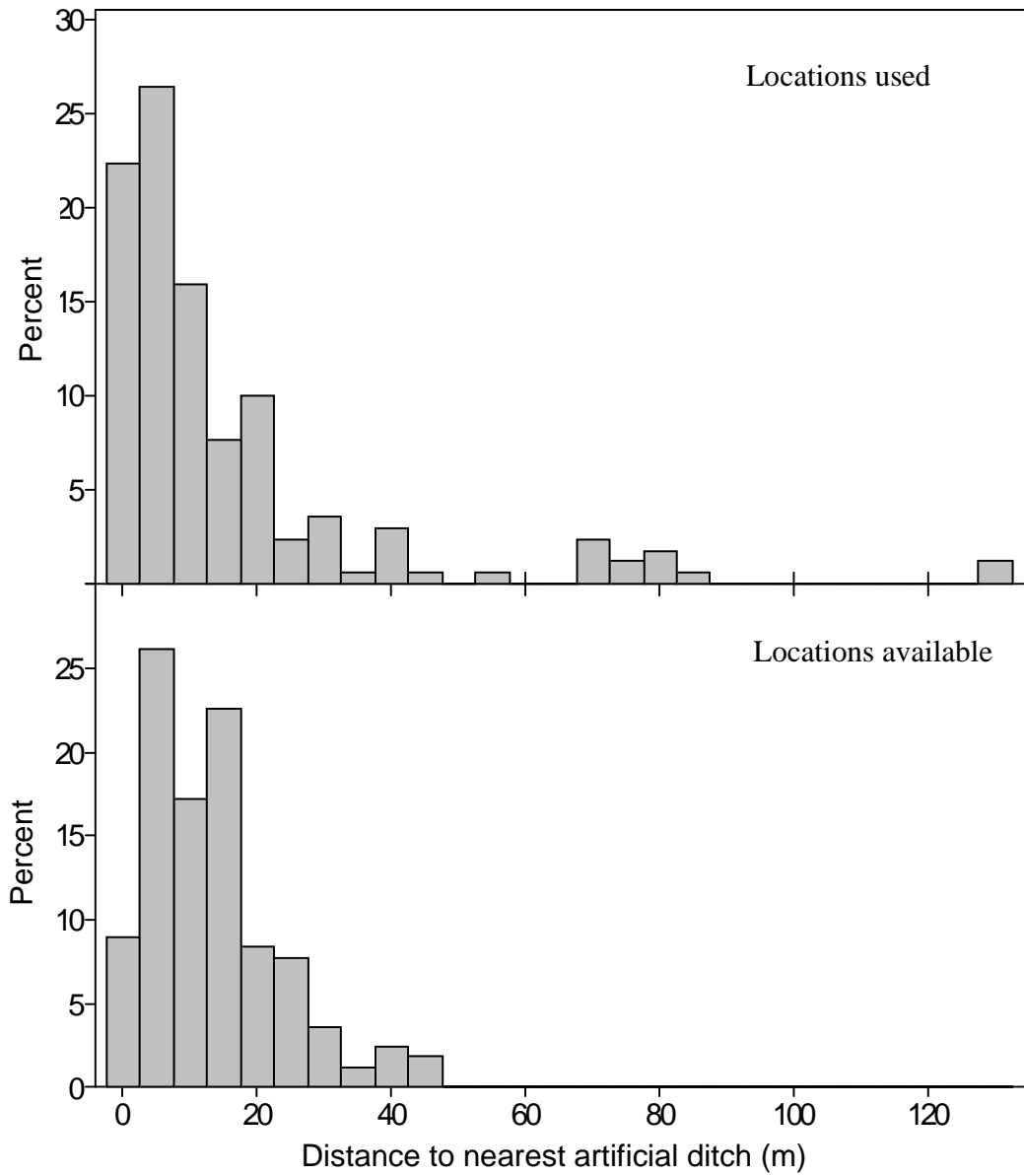


Figure 7. The proximity of all locations used (n = 170; top) and available (n = 168; bottom) to the nearest artificial ditch. The second best-supported model included this variable along with distance to the marsh edge.

## DISCUSSION

Female Saltmarsh Sharp-tailed Sparrows used locations in the postfledging period that were closer to channels and ditches, and to the marsh edge than expected by chance. Ditches and channels are abundant in most of the salt marshes occurring throughout the range of the Saltmarsh Sharp-tailed Sparrow, where less than 10% of marshes remain un-ditched (Bourn and Cottam 1950). The use of artificial and natural water features by Saltmarsh Sharp-tailed and Seaside Sparrows (*Ammodramus maritimus*) has been noted elsewhere (Woolfenden 1956; Greenlaw and Rising 1994; Post and Greenlaw 1994). Post and Greenlaw (2006) reported that Saltmarsh Sharp-tailed Sparrows disproportionately used muddy shallow pools and spent a greater amount of time foraging by probing or gleaning from the mud surfaces, including those of ditch and channel margins, than any other feeding method. Their results match our observations of frequently flushing sparrows from the areas around these water features. If female sparrows are using the areas adjacent to and within these water features for their greater foraging value then they may not discriminate between ditches and channels, even though ditches tend to be narrower and have steeper edges. They may simply be attracted to the amount of exposed mud and other micro-habitat components related to ditches and channels.

Saltmarsh Sharp-tailed Sparrow habitat use is likely to be more appropriately described by a combination of variables and the relationships among them. A significantly disproportionate number of females were found in locations with relatively tall vegetation and high standard deviation of vegetation height, and greater amounts of tall form *S. alterniflora* and bare ground (Table 1). Individually, these



habitat components performed poorly in model selection, which is supported by our observations of movement behavior and habitat use of sparrows. For example, at low tide river beds offer huge expanses of available muddy substrate for foraging, but we rarely saw sparrows foraging greater than a few meters from the vegetation lining the margins of these features. Tall *S. alterniflora* juxtaposed with bare ground is commonly found along the ditch and channel margins, and collectively these conditions may offer additional benefits beyond good foraging areas.

We offer an addition to the foraging hypothesis, based upon our data presented here and on observations of marked birds during the postfledging period. Tall vegetation and the relative openness of ditch and channel margins may serve as a refuge for recently fledged sparrows, which are unable to fly when they leave the nest, and are likely incapable of powered flight during the first week after fledging (Figure 8; JMH personal observation). They are vulnerable to predation during this period, and the tall *S. alterniflora* may mask their movements and position from aerial predators better than shorter vegetation. The spacing of large *S. alterniflora* stems (Figure 9) also allows sparrows to move and quickly run without disturbing the vegetation (JMH personal observation). *Spartina patens* stands tend to be quite short with densely packed stems and birds are forced to either run on top of these stands or plow their way through them, which causes the vegetation to move and exposes their presence. Pushing through this dense vegetation would make moving (especially for non-flighted fledglings) more energetically challenging and it is also much easier to follow a young bird trying to run through these stands (JMH personal observation).



Figure 8. Photo of a wing from a Saltmarsh Sharp-tailed Sparrow chick nine days after hatching, and taken approximately 20 hrs before fledging occurred. Fledglings leave the nest on foot before they are able to undertake powered flight.

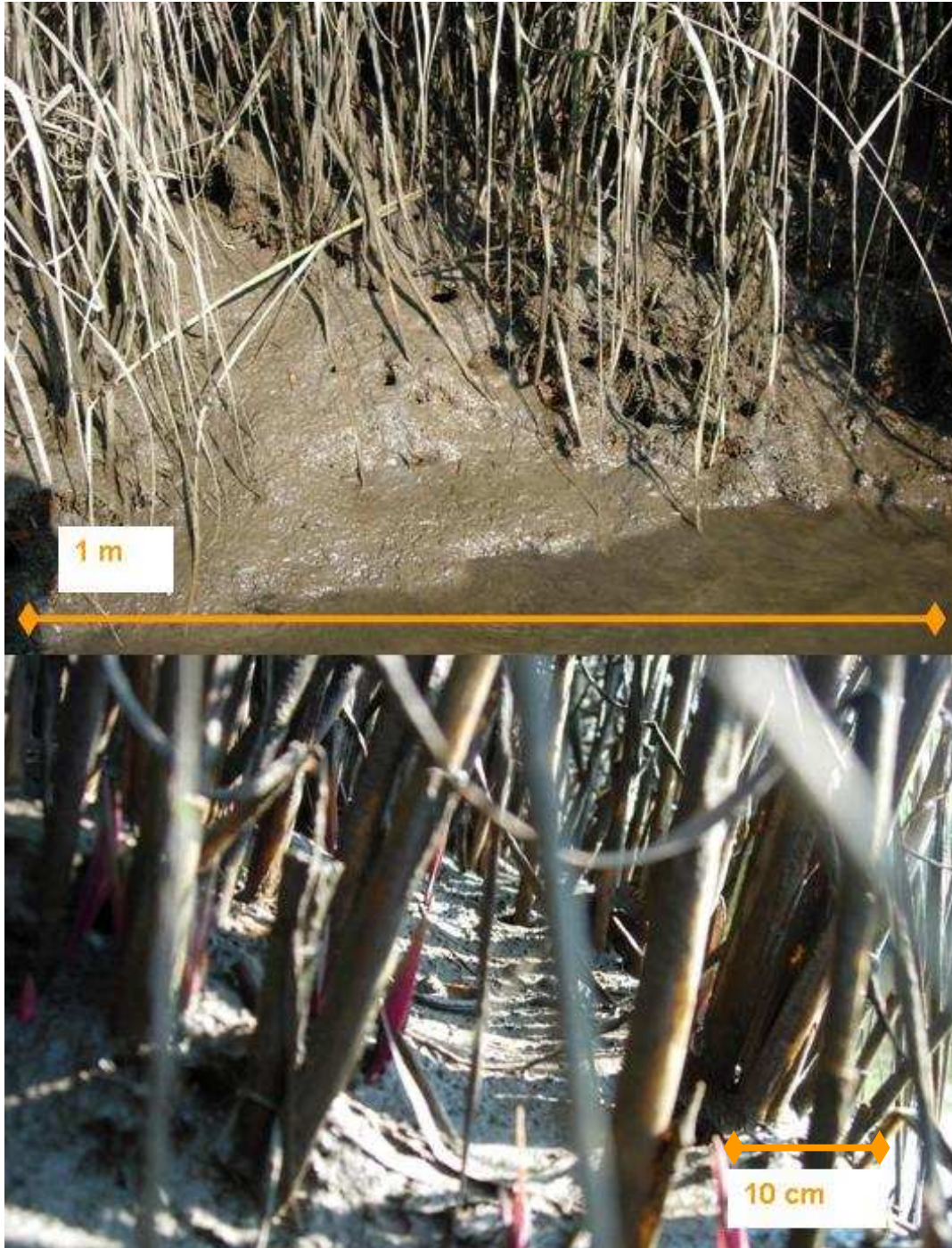


Figure 9. Representative photos of tall form *S. alterniflora* monoculture stands from several meters away (left) and up close from ground level (right). These tall stands may offer concealment from above, provide access to muddy surfaces for probing and gleaning, and individual plant stems are spaced far enough apart to allow sparrows to quickly and easily chase after prey or run from disturbance.

Moving closer to the marsh edge may also be an important behavioral adaptation to reduce the risk of drowning during flooding events. Proximity to the marsh edge occurred in all models with Akaike weights  $> 0.0001$ , and 75% of female sparrows were generally found at locations significantly closer to the marsh edge than were random locations. Marshes experience predictable low-level flooding with both daily high tidal events, although the water level in the high marsh during these times may not be appreciably different. However, marshes experience extensive flooding every 26-28 days during the lunar cycle and from extreme weather events that can submerge extensive portions of the marsh. Flooding has long been noted as an important cause of nest failure for *Ammodramus* spp. (Lewis 1920; Greenberg et al. 2006) sometimes resulting in  $\geq 60\%$  of all nest loss (DeRagon 1988; Gjerdrum et al. 2005). Moving towards the relatively higher elevations of the marsh edge perhaps reduces the probability of fledglings drowning. These tall stands may also offer important protection from drowning. We have observed fledged sparrows clinging to the top of *S. alterniflora* (tall form) stands, afloat in the vegetation during extreme flooding events, although most flighted individuals simply move to the marsh edge at these times (Greenlaw and Rising 1994; JMH personal observation).

These telemetry results are particularly striking because, when occurrence patterns are averaged across the entire breeding season, females are more common farther from the marsh edge (Gjerdrum et al. 2008). Nests were also more common further from the marsh edge, and in areas with relatively abundant *J. gerardii* which tends to be found at higher elevations. This combination of results suggests that females may place nests away from marsh edges in dense relatively high vegetation

(e.g., *J. gerardii* and *S. patens*) to minimize both predation from upland predators and flooding risk. Females may then move towards the marsh edge with their fledglings to take advantage of the higher ground and even greater reduced flooding risk once their young are mobile enough to escape predation and use tall vegetation fringing the marshes.

It is clear that a species' habitat preferences may change with age (Vega Rivera et al. 1998; Pagen et al. 2000; King et al. 2006) or even in the presence of predators (Martin 1988) or competitors (Fretwell and Lucas 1970; Diamond 1978). Berkeley et al. (2007) monitored the movements and habitat use of fledgling Dickcissels (*Spiza americana*). Adult nesting habitat consisted entirely of restored grasslands, but fledglings also used soybean and corn fields, other types of grasslands, and occasionally wetlands. This change in habitat use from the nesting to the post-breeding period has also been reported in Ovenbirds (*Seiurus aurocapilla*) where fledglings use areas with fewer trees and greater understory density than nesting sites (King et al. 2006). Similar changes in habitat use between the nesting and postfledging periods has also been reported in Wood Thrush (*Hylocichla mustelina*; Vega Rivera et al. 1998), Botteri's Sparrows (*Aimophila botterii*; Jones and Bock 2005), and a number of other migrating songbird species (Pagen et al. 2000; Marshall et al. 2003). Appropriate habitat management for any species should consider the specific life stage being targeted by management or conservation actions, and adjust their goals accordingly.

In conclusion, our study has identified a shift in Saltmarsh Sharp-tailed Sparrow habitat use from the nesting to the postfledging period. Even in a relatively

simple system with few plant species (Bertness and Ellison 1987), individuals demonstrated different preferential use of individual habitat components and an overall pattern of habitat use strikingly different from that previous described for Saltmarsh Sharp-tailed Sparrows. We have provided the first explicit postfledging descriptions of adult female Saltmarsh Sharp-tailed Sparrows habitat use. We have identified a new suite of microhabitat components that describes postfledging habitat use as a function of relatively tall and structurally varied vegetation, relatively close to the marsh edge, and with relatively greater amounts of bare ground and *S. alterniflora* (tall form).

## APPENDIX 1

Individual models that resulted in quasi and/or complete separation for some individuals. Separation problems occur when the maximum likelihood algorithm fails to converge on a single coefficient estimate, and is often a result of small sample size (Allison 1999). Models failing to reach convergence are not appropriate to compare using logistic regression, since a maximum likelihood estimate does not exist for the parameter causing separation issues.

Models:

- 1) *D. spicata* + SD of vegetation height + thatch depth
- 2) *D. spicata* + *J. gerardii*
- 3) Bare ground + *D. spicata* + *J. gerardii* + *S. patens* + *S. alterniflora* (short form) + *S. alterniflora* (tall form) + thatch depth
- 4) *J. gerardii* + *S. patens*
- 5) Bare ground + *S. patens* + distance to marsh edge
- 6) Bare ground + mean vegetation height + distance to nearest ditch + *S. alterniflora* (tall form) + distance to marsh edge
- 7) Bare ground + mean vegetation height + distance to nearest channel + *S. alterniflora* (tall form) + distance to marsh edge
- 8) Bare ground + distance to nearest ditch + *S. alterniflora* (tall form) + distance to marsh edge
- 9) *J. gerardii* + distance to marsh edge

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