

BREEDING BIRD TERRITORY PLACEMENT IN RIPARIAN WET MEADOWS IN RELATION TO INVASIVE REED CANARY GRASS, *PHALARIS ARUNDINACEA*

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Abstract: Invasive plants are a growing concern worldwide for conservation of native habitats. In endangered wet meadow habitat in the Upper Midwestern United States, reed canary grass (*Phalaris arundinacea*) is a recognized problem and its prevalence is more widespread than the better-known invasive wetland plant purple loosestrife (*Lythrum salicaria*). Although resource managers are concerned about the effect of reed canary grass on birds, this is the first study to report how common wet meadow birds use habitat in relation to reed canary grass cover and dominance. We examined three response variables: territory placement, size of territories, and numbers of territories per plot in relation to cover of reed canary grass. Territory locations for Sedge Wren (*Cistothorus platensis*) and Song Sparrow (*Melospiza melodia*) were positively associated with reed canary grass cover, while those for Common Yellowthroat (*Geothlypis trichas*) were not. Only Swamp Sparrow (*M. georgiana*) territory locations were negatively associated with reed canary grass cover and dominance (which indicated a tendency to place territories where there was no reed canary grass or where many plant species occurred with reed canary grass). Swamp Sparrow territories were positively associated with vegetation height density and litter depth. Common Yellowthroat territories were positively associated with vegetation height density and shrub cover. Song Sparrow territories were negatively associated with litter depth. Reed canary grass cover within territories was not associated with territory size for any of these four bird species. Territory density per plot was not associated with average reed canary grass cover of plots for all four species. Sedge Wrens and Song Sparrows may not respond negatively to reed canary grass because this grass is native to wet meadows of North America, and in the study area it merely replaces other tall lush plants. Avoidance of reed canary grass by Swamp Sparrows may be mediated through their preference for wet areas where reed canary grass typically does not dominate.

Key Words: breeding birds, Common Yellowthroat, riparian, Sedge Wren, Song Sparrow, Swamp Sparrow

INTRODUCTION

Wet and sedge meadows in the Upper Midwestern United States have been reduced to less than 1% of their former extent (Reuter 1986, Sampson and Knopf 1994, Hoffman and Sample 1995, Noss et al. 1995). Like prairies and wetlands, wet meadows have been lost through conversion to agriculture and urbanization, but changes in hydrology caused by river development have also contributed to habitat loss. A major threat to remaining wet meadows is invasion of reed canary grass (*Phalaris arundinacea* L.), which has become a problem in wetlands and wet meadows throughout much of temperate North America (Galatowitsch et al. 1999, Pavoglio and Kilbride 2000). Reed canary grass is native to North America but has become aggressively invasive in many wetland systems throughout the Upper Midwest and Northwest (Merigliano and Lesica 1998,

Galatowitsch et al. 1999, Lavoie et al. 2005). Introgression with introduced cultivated strains or changes in nutrient loading and hydrology of wetlands may be contributing to reed canary grass aggressiveness (Maurer et al. 2001, Green and Galatowitsch 2002, Lavoie et al. 2005).

Compared to mesic prairies, wet and sedge meadows of the Upper Midwestern United States typically have lower diversity of plant and avian species (e.g., Curtis 1959, Hoffman and Sample 1988, Mossman and Sample 1990). Where reed canary grass now dominates, plant diversity is even lower (Galatowitsch et al. 1999, Cochrane and Iltis 2000, Bernthal and Willis 2004). The invasiveness of reed canary grass and its tendency to form apparent monocultures is widely recognized, yet there are no published studies documenting the effects of reed canary grass on wildlife, and birds in particular. Present consensus among resource managers and

wetland biologists in the Upper Midwest is that reed canary grass is of little value to wildlife and its invasion reduces bird use of wet meadows (i.e., Steinauer 1999, Groshek 2000). However, some grassland species such as Sedge Wrens (*Cistothorus platensis* Latham), and occasionally Henslow's Sparrows (*Ammodramus henslowii* Audubon), have been observed in reed canary grass dominated grasslands (D. Sample, Wisconsin Department of Natural Resources, pers. comm.).

We examined bird use of riparian wet meadow habitat in relation to reed canary grass coverage. We made three predictions under the assumptions that greater reed canary grass cover reduces habitat quality and breeding songbirds in wet meadows select habitat according to an ideal free distribution (Fretwell and Lucas 1970, Fretwell 1972). If reed canary grass reduces habitat quality in ways birds can detect, and if birds can discern reed canary grass from other wet meadow plants, 1) we expected that territories would be placed to "avoid" areas with relatively high reed canary grass cover. The bird species we focused on breed and feed within their territories. If reed canary grass negatively influences resources (i.e., food) that birds require, 2) we expected a positive relationship between territory size and the amount of reed canary grass cover within a territory, because birds would require a larger area to meet their resource needs. Finally, at the site level, if sites with greater reed canary grass cover have fewer necessary resources they would support fewer bird territories, 3) we expected an inverse relationship between number of territories at a site and the amount of reed canary grass cover on a site.

METHODS

Study Area

Thirteen riparian wet meadow sites were selected in the Driftless Region (the area not glaciated during the Paleozoic; Curtis 1959) of southeastern Minnesota and southwestern Wisconsin (Figure 1). In the Driftless area of Minnesota and Wisconsin, natural wet meadows not dominated by reed canary grass are rare (Minnesota County Biological Survey 1996a, 1996b, Cochrane and Iltis 2000, EMK pers. obs.). We did not consider wet meadows that were hayed or grazed because haying and grazing can change habitat structure as well as influence bird behavior, productivity, and community composition (i.e., Popotnik and Giuliano 2000, Renfrew and Ribic 2001). Because we wanted to find wet meadows that were not disturbed, but still repre-

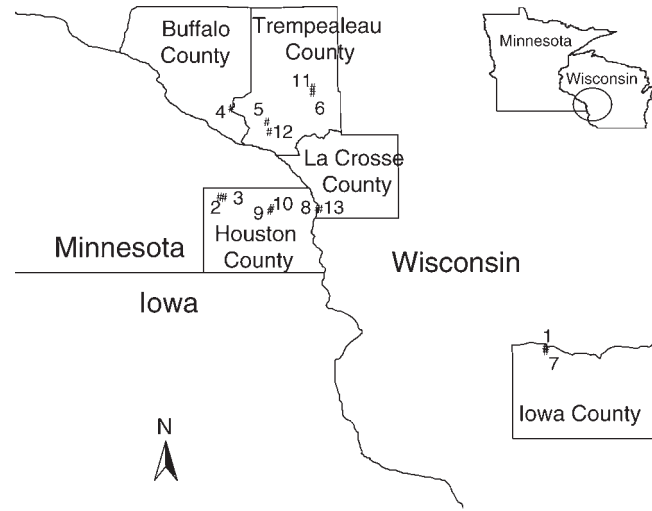


Figure 1. Locations of study sites in southeastern Minnesota and southwestern Wisconsin. Numbers depict locations of sites listed in Table 1. Because of the small scale of the graphic, several sites do not show up as distinct dots, but are indicated by site numbers.

sented a wide range of reed canary grass infestation (and no detailed GIS data were available to assist with this), we relied on our knowledge of the area, interviews with resource managers and landowners, and extensive searches of the study area for potential study sites. Twelve sites were located in 2001. An additional site with little reed canary grass was grazed by cattle in early 2001, so we did not sample it until 2002 (when it was not grazed). Sites were large enough to accommodate bird surveys (≥ 4.5 ha, range 4.5–16.5 ha, average = 10.6 ha), and represented a full range of reed canary grass prevalence: five sites were dominated by native wet-meadow/grassland vegetation, three sites had a mixture of native vegetation and reed canary grass, and five sites were dominated by reed canary grass.

Bird Surveys

Spot mapping surveys (Vickery *et al.* 1992, Bibby *et al.* 1997) were conducted between 06:00 and 10:30 from mid-May through mid-August. Six to eight and eight to nine surveys were conducted on each site in 2001 and 2002, respectively. The number of surveys per site was fewer in 2001 because logistic issues delayed sampling that year, two sites were flooded mid-season (thereby preventing one scheduled survey), and bird activity was low in early August 2001. For each site, weekly surveys involved one observer, who walked slowly along grid lines (see below), mapping bird locations, recording behaviors and movements, and when possible, recording sex and age. Observers varied the corner

of the survey grid where they started and the direction in which they walked the grid for each survey. The amount of time spent in each plot was proportional to plot size with approximately 925 m of grid line walked per hour. All observers had at least two years of experience in surveying breeding wet meadow birds of the Upper Midwest before this project. As spot mapping methods require familiarity with study plots, all surveys of a given plot were completed by a single observer. Analytically then, observer effects were inextricable from plot effects [and plot effects were accommodated in data analyses (see following)].

To aid in spot mapping, each study site was marked with color-coded, numbered PVC poles (i.e., points) at 50-m intervals to create a grid. Shape and size of plots varied because grids were placed to maximize use of an area. A surveyor's level was used to ensure grid lines were straight and a 50-m tape was used to measure the distance between points. Points in each grid were used as sampling locations for vegetation. The Universal Transverse Mercator coordinates of each point were collected from all grids with a global positioning system (PLGR +96, Rockwell International Corporation, Cedar Rapids, IA). Grid point locations in 2001 and 2002 differed by less than 5 m, but data were collected in reference to grid location each year.

We focused on four bird species: Sedge Wren, Common Yellowthroat (*Geothlypis trichas* L.), Swamp Sparrow (*Melospiza georgiana* Wilson), and Song Sparrow (*M. melodia* Latham). These species are primarily monogamous, and thus allowed reasonable estimation of territories based on singing male detections, simultaneous singing male detections, and observations of male-female pair interactions. These species also were common enough to provide adequate sample sizes for analyses. Sedge Wrens are a species of concern in the Upper Midwest (Knutson et al. 2001, U.S. Fish and Wildlife Service 2002). While Red-winged Blackbirds (*Agelaius phoeniceus* L.) were ubiquitous, their polygynous mating system makes mapping territories very difficult (Yasukawa and Searcy 1995). Other bird species were present and noted but because they were not as common, small sample sizes precluded full analyses.

Vegetation Sampling

Vegetation was sampled both years at every grid point at each study plot. Sampling was conducted in early to mid-August in 2001 and 2002 (i.e., after completion of bird surveys). If vegetation around the point had been trampled prior to vegetation

sampling, vegetation was sampled at a similar, untrampled area within 5 m of that point. All plant species within a 2 m radius of the sampling point were identified and percent cover of each plant species was estimated. The percent cover summed over all species could exceed 100% because the canopy of plants overlapped. Percent cover of grasses and sedges combined, forbs, shrubs, tree, litter, water, snag and downed wood were similarly estimated. Vegetation height density was estimated with the Robel technique (Robel et al. 1970). Four Robel pole readings, taken from roughly the four cardinal directions, were averaged. Three litter depth measurements (to the nearest mm) were taken from three haphazard locations within 2 m of the sampling point with a small metric ruler and averaged. Litter depth was measured from the ground surface to the top of the dead and down herbaceous vegetation layer. We also estimated a reed canary grass dominance variable, as the percent cover of reed canary grass divided by the total cover of plant species present other than reed canary grass at a sample point. Thus, reed canary grass dominance varied between zero and one (rounded to the nearest tenth) with one indicating a reed canary grass monoculture and zero indicating no reed canary grass.

Data Analyses

Delineation of bird territories occurred after the field season ended and was based on a number of criteria from mapped bird detections. Each observer interpreted field data from sites they had surveyed (because territory delineation required familiarity with sites). To reduce observer bias, several criteria were used to define how territories were delineated (following) and the study director cross-checked maps from weekly surveys with estimated territory delineations. Territories were defined primarily from detections of singing males. At least three consecutive weeks of detections of a singing male in a localized area was deemed a territory. Usually other information was also present to give us further confidence in territory existence and locations such as: a) at least one survey with simultaneous detection with a different male near-by (simultaneous singing or aggressive chasing), b) observation of the focal male interacting with a female and displaying some courtship or nest protective/maintenance behavior (carrying nest material or fecal sacs), and c) observation of a weakly flying fledgling in the vicinity. Bird locations and territories were first estimated in reference to grid points using paper maps and then transferred to geographic informa-

tion systems format by digitizing in ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA) (*sensu* Witham and Kimball 1996). As a frame of reference for digitizing, we used grid points overlaid upon U.S. Geological Survey digital ortho-quarter quadrangle aerial photographs of study sites.

We recognize that territories were estimated, and that there was bird activity outside of plotted territories; however, because bird observations were collected over many weeks during intense survey efforts and these observations still did not meet our criteria for a territory, we feel comfortable that they probably do not constitute territories. Furthermore, any territories established and then abandoned by floating individuals between the times of our surveys would not be occupied long enough for successful breeding.

We compared used to unused habitat, rather than used to available habitat, to avoid reliance on overlapping use categories (see Thompson and Taylor 1990) and because apparently unused habitat was readily demarcated. Because the desired analytical unit was a territory, we constructed “null-territories” to sample the areas of plots that were not classified as territories. “Null-territories” were ovals with average size and aspect ratio similar to those estimated from territories for each species on each plot each year. Null territories were randomly placed sequentially in a plot until no more null territories could be fitted (without overlapping a territory or existing null territory), ignoring territories of species other than the one for which we generated the null territories. Thus, null territories for each species (each plot and each year) overlapped the territories of other species. We developed an extension in ArcView 3.2 (available from Tim Fox, USGS, Upper Midwest Environmental Sciences Center) to automate the estimation of null-territory sizes and aspect ratios and randomly place these null-territories in each plot. Null-territories were allowed to border both null and used territories because used territories often shared borders. Comparing used vs. null territories (unused areas) avoided scaling issues that result from comparing the smaller extents of territories to the larger extent of study plots. An important criticism of comparing used to unused habitat is that more intensive sampling might show unused habitat to be used. We believe this issue is trivial in our situation for the reasons previously stated.

To estimate habitat characteristics for territories and null-territories, we estimated inverse-distance-weighted surfaces for six potential predictor variables for each plot each year. Inverse distance

weighting is a method of interpolating for unknown areas the values derived from known point locations, and is done as a weighted moving average based on weights that are inversely proportional to the square of the distance between point locations (Bonham-Carter 1996, Johnston *et al.* 2001). Surfaces were estimated using Geostatistical Analyst extension in ArcGIS 8.1 (Environmental Systems Research Institute, Redlands, CA). In any interpolation, the number of neighboring grid points used in estimating the surface influences the spatial pattern of habitat variable estimates. To best reflect conditions at a plot each year, creation of these surfaces was supervised by the technician familiar with each plot. The technician was not told how many neighboring points were used to create surface estimates (between three and nine), but was asked to choose the surface best representing coverage of a variable at the plot. Surfaces were created for both years because vegetation cover and height, and reed canary grass dominance can shift between years (because of weather, duration and depth of spring flooding and, in the case of one plot, a spring burn), and grid locations differed slightly between years. Finally, ArcView shapefiles of territories and null territories for each bird species were joined with habitat variable surfaces and the average for each habitat variable within each territory and null territory was estimated using ArcMap 8.1 Spatial Analyst (zonal statistics). To reduce estimation error, we did not extend the boundary of each inverse distance surface past the outermost points on a grid, and any territories or null-territories that fell outside of the plot boundary (50 m from the outermost points of each grid) were not included in analyses of habitat variable associations with territory presence. However, estimates for territories and null-territories that were partially within the inverse-distance-weighted surface were included.

We did not conduct the analyses based on habitat variable estimates from each grid point within territories and null territories because the number of sample points per territory (or null-territory) ranged from 0–4 (e.g., Figure 2). We also did not use a simple average of the habitat variables at points and attribute them to territories for the same reason.

Territory Presence and Reed Canary Grass. Nine *a priori* habitat models were compared for each species. Habitat variables included percent reed canary grass cover, index of reed canary grass dominance, vegetation height density, percent cover

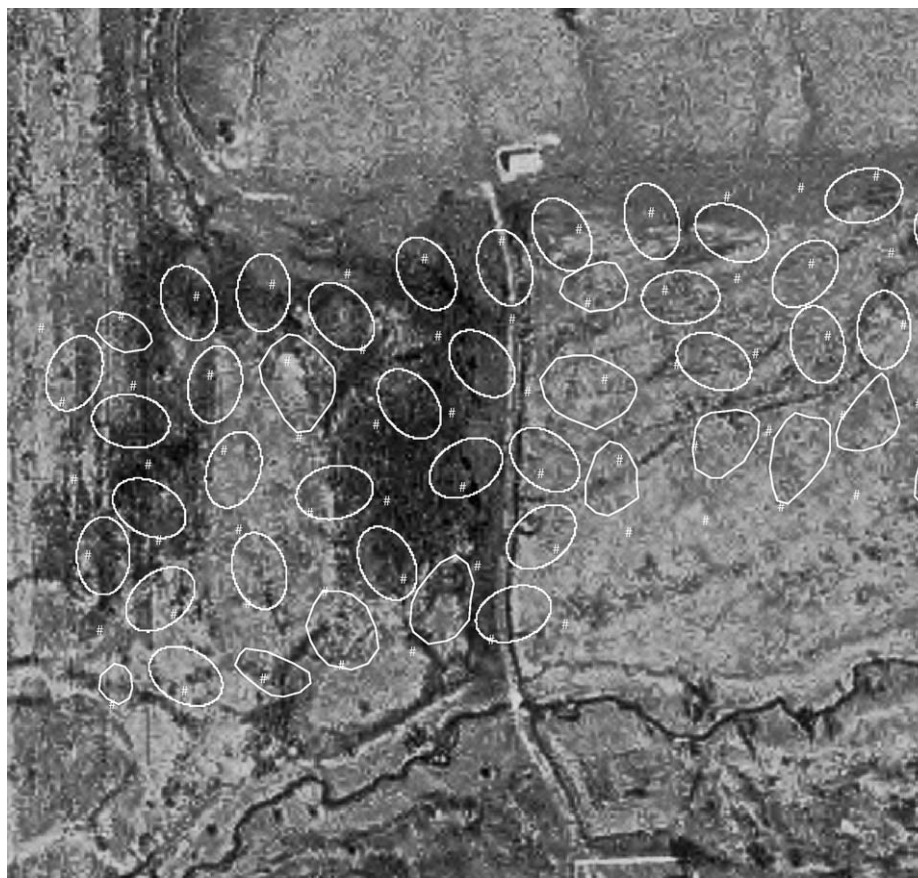


Figure 2. An example of a study site depicting the grid of habitat sampling points and estimated Swamp Sparrow (*Melospiza georgiana*) territories (irregular ovals) and null-territories (regular ovals). On this plot (and this particular year) for this species, the maximum number of grid points in a territory was two, but on other plots, for this and other species, territories were larger and could encompass up to four grid points.

of forbs, percent cover of shrubs, and average litter depth. We were interested primarily in the reed canary grass variables – both alone and in combination with other structure variables. Also, shrub cover, litter depth, and vegetation height density can influence bird habitat selection of these species (i.e., Rising 1996, Mowbray 1997, Guzy and Ritchison 1999, Herkert et al. 2001); we examined these variables alone, with each other, and in combination with reed canary grass variables and forb cover.

For each species, territory presence was modeled as functions of habitat predictors using logistic models with random effects corresponding to plot and plot*year. Plot and plot*year effects were presumed distributed conditionally as normally-distributed random variables (on the logit or link scale) with variances σ_s^2 and $\sigma_{s(yr)}^2$ respectively; inter-annual correlation at the plot scale was coarsely addressed by nesting year effects for a given site within the site. Because the importance of plot, year and plot*year effects were expected to be

species dependent, we fitted intercept only models with combinations of these random effects using SAS nonlinear mixed modeling procedure (NLMIXED; SAS 2003); for each species, the “best” of these intercept or base models was included in all habitat models for the given species (where ‘best’ is defined in the following paragraph). Likelihoods were estimated over group-specific random effects using adaptive Gaussian quadrature (ADQ; Pinheiro and Bates, 1995), and were maximized using a trust region optimization algorithm (Moré and Sorensen 1983).

For each species, model fit and associated parameter estimates were assessed using Akaike weights, a derivative of the Akaike’s Information Criterion (AIC; Akaike 1973, Burnham and Anderson 2002). Model AIC weights vary from 0–1, with larger weights indicating greater weight of evidence in favor of the given model being the best for the purposes of representing the (finite) information in the data (Burnham and Anderson 2002). Model-averaged covariate estimates, with 95% model-

averaged, large-sample confidence intervals, were derived after Burnham and Anderson (2002)

Territory Size and Reed Canary Grass. Associations between log-territory size and percent reed canary grass cover were estimated using linear mixed models, with year and plot as random variables. Territory size was estimated in ArcView 3.2, and then log transformed. The explanatory variable (average percent reed canary grass cover by territory) was estimated from inverse distance weighted surfaces. We adjusted for inter-annual correlation within plots by nesting years within plots. We did not adjust for temporal correlation within territories because, unlike plots, territory locations did not remain constant across years. Linear mixed models were fitted using restricted maximum likelihood and SAS linear mixed modeling procedure (MIXED; SAS 2003).

Territories Density and Reed Canary Grass. The association between territory density per plot and average percent reed canary grass cover per plot was assessed using a negative binomial count assumption. Average percent reed canary grass was derived from vegetation sampling points per plot per year. Temporal correlation within plots was addressed using generalized estimating equations (GEEs; Liang and Zeger 1986); variation in plot size was addressed by treating log[plot area (ha)] as an offset variable. Counts for Swamp Sparrows and Song Sparrows were highly correlated across years (Swamp Sparrow $r = 0.97$, Song Sparrow $r = 0.93$). Consequently, the association between territory density and reed canary grass cover for those species was assessed using only 2002 data. Models of territory density were fitted using SAS generalized linear modeling procedure (GENMOD; SAS 2003).

RESULTS

Mean percent reed canary grass cover at study plots ranged from approximately 7%–90% (Table 1). Although the mean number of plant species detected on a per point basis and the number of plant species detected on the plot tended to decrease as the percent cover of reed canary grass increased, no study plot was a pure monoculture of reed canary grass. Thirty-one percent of all points (470 points out of 1530) had $\geq 90\%$ reed canary grass cover, and of these, 85% (398 points) had at least one other plant species present, often with greater than 50% cover. At the five plots with the greatest average cover of reed canary grass, 8%–35% of the sample points were not dominated by reed canary grass and 17–75 other plant species were present.

Common Yellowthroat was the most abundant bird species both years, followed by Sedge Wren (Table 2). Common Yellowthroats were the only species detected at all plots both years, whereas the Sedge Wrens, Swamp Sparrows, and Song Sparrows were not detected on at least one plot each year. Estimated average territory sizes were similar among species but appeared smaller for all species in 2002 than 2001.

Territory Presence and Reed Canary Grass. The model with percent reed canary grass, vegetation height density, percent shrub cover, and litter depth covariates was among the competing models for all four bird species (Table 3). Three models, all with a single covariate (reed canary grass dominance, vegetation height density, or percent shrub cover) were not supported for any of the species.

Reed canary grass cover was positively associated with territory placement for Sedge Wrens and Song Sparrows and negatively associated with territory placement for Swamp Sparrows (Table 4). The estimated associations were slight for Sedge Wrens and Song Sparrows and Swamp Sparrows – 1.4% and 0.8% increases and a 1.3% decrease in the odds of a territory with each increment (10% cover) in percent reed canary grass cover, respectively. While the association between Swamp Sparrow territory placement and RCG appeared slight, the corresponding association with reed canary grass *dominance* appeared biologically significant – an 80% decrease in odds of a territory for each increment (steps of 0.01) increase in reed canary grass dominance.

Vegetation height density, litter depth, and shrub cover also were associated with territory placement. Swamp Sparrow and Common Yellowthroat territories were positively associated with vegetation height density. Odds of territory occurrence increased for Swamp Sparrows and Common Yellowthroats with each decimeter increase in vegetation height density. Swamp Sparrow territories were positively associated with litter depth (1.8% increase in odds for each cm increase of litter depth), whereas Song Sparrow territories also were negatively associated with litter depth (1.5% decrease in odds for each cm increase in litter depth). For Common Yellowthroats, percent shrub cover also was positively associated with territory placement (1.6% increased odds for each 10% increment increase in shrub cover).

Territory Size, Territory Density, and Reed Canary Grass. Territory sizes did not appear strongly associated with average percent reed canary grass cover within territories (Table 5). As Log-territory

Table 1. Vegetation characteristics of riparian wet meadow study sites in southeastern Minnesota and southwestern Wisconsin, 2002. Sites are in order of increasing mean percent reed canary grass (RCG) cover. Means and standard deviations, in parentheses, were estimated from all points in each plot. Percent cover of reed canary grass = %RCG, and vegetation height density = VHD.

Site	No. of sample points	No. of points RCG dom. ^a	Mean VHD (m)	Mean litter depth (mm)	Mean no. of plant species /point	Total no. of plant species ^b	Mean percent cover					
							RCG	All grass and sedge	Forb	Shrub	Litter	Tree
1	80	4	0.8 (0.31)	41.2 (16.9)	14.6 (4.80)	98	7.6 (21.8)	84.6 (10.0)	76.5 (11.1)	48.8 (30.5)	96.9 (10.26)	0.2 (2.28)
2	77	3	0.9 (0.25)	64.8 (35.45)	10.9 (4.49)	114	20.2 (26.39)	88.0 (16.78)	85.6 (10.57)	4.3 (9.65)	95.8 (11.96)	6.8 (23.53)
3	72	13	0.9 (0.26)	13.6 (7.97)	13.7 (12.68)	86	25.0 (36.00)	89.6 (11.80)	73.8 (20.06)	13.8 (21.11)	87.9 (12.88)	1.5 (9.44)
4	67	0	0.6 (0.16)	55.9 (28.45)	12.7 (2.49)	77	25.2 (26.35)	99.5 (2.08)	75.5 (12.34)	3.0 (8.12)	96.1 (5.76)	0
5	59	9	0.9 (0.34)	95.5 (45.70)	12.7 (2.49)	83	27.8 (29.07)	89.0 (8.65)	76.3 (17.31)	22.1 (29.16)	95.4 (8.37)	2.2 (8.32)
6	53	24	1.1 (0.31)	90.3 (40.06)	10.4 (14.90)	63	48.5 (46.26)	97.0 (5.75)	60.9 (31.01)	10.4 (20.66)	98.1 (3.98)	3.7 (16.53)
7	79	38	0.9 (0.35)	61.9 (39.70)	5.1 (3.20)	57	55.2 (41.05)	82.3 (23.75)	57.0 (35.29)	3.6 (10.78)	87.8 (20.37)	0.8 (5.04)
8	47	21	0.7 (0.23)	9.9 (4.43)	6.6 (3.27)	53	64.6 (20.34)	86.1 (17.96)	44.1 (27.29)	4.1 (14.19)	82.3 (21.00)	2.3 (13.32)
9	33	24	1.1 (0.26)	55.3 (25.8)	5.6 (3.32)	42	72.4 (31.43)	84.8 (19.86)	45.4 (32.70)	6.4 (19.17)	92.2 (17.55)	3.6 (15.37)
10	89	58	0.9 (0.25)	53.6 (20.83)	5.7 (3.50)	75	72.9 (29.75)	95.4 (5.85)	35.1 (31.46)	1.5 (8.06)	97.7 (9.43)	0.3 (3.18)
11	40	29	1.3 (0.33)	74.0 (28.76)	5.1 (3.36)	43	75.4 (29.90)	92.6 (7.85)	39.7 (27.55)	1.3 (5.70)	95.1 (9.70)	0.5 (3.20)
12	40	33	1.1 (0.27)	75.9 (48.13)	6.3 (5.04)	45	79.4 (28.33)	91.8 (10.35)	43.9 (33.73)	2.5 (9.27)	85.5 (26.50)	0
13	64	59	1.1 (0.30)	31.2 (14.82)	2.3 (1.20)	17	89.8 (18.04)	90.3 (16.40)	42.0 (32.83)	2.6 (12.75)	97.9 (8.83)	0

^a Number of points where reed canary grass had the highest percent cover.

^b Number of plant species detected on a site with cover > 5% on at least one sample point.

Table 2. Estimated number of bird territories and average territory size in m² (10th and 90th percentiles) on riparian wet meadows in southwestern Minnesota and southeastern Wisconsin, 2001–2002.

Species	Number of territories		Range number of territories per plot		Territory size (m ²)			
	2001	2002	2001	2002	2001		2002	
					Mean	P(p10, p90)	Mean	(p10, p90)
Sedge Wren Common	115	164	0–27	0–33	1560	(736, 2790)	1366	(430, 2487)
Yellowthroat	323	322	17–46	5–43	1499	(611, 2601)	1294	(399, 2152)
Swamp Sparrow	205	179	0–33	0–57	1627	(746, 2840)	1383	(513, 2357)
Song Sparrow	113	127	0–34	2–28	1773	(1056, 2677)	1264	(489, 2454)

size varied within and across plots, R^2 values may be estimated for both spatial scales. At the territory scale, R^2 estimates were $\leq 2\%$ for all species, while, at the plot scale, R^2 estimates were $\leq 2\%$ and 12% for Common Yellowthroat and Song Sparrow (both years). Plot-scale R^2 estimates varied from 2001–2002 for Sedge Wren and Swamp Sparrow (6% and 67%, and 10% and 43%, respectively). Some fraction (possibly large) of the variation in plot-scale R^2 values may have arisen from imprecision in the corresponding plot-scale variance estimates. Average reed canary grass cover at plots was not clearly associated with the number of territories in plots for any of the four common breeding species (Table 5).

DISCUSSION

Results of this study contradict popular notions that birds avoid areas with high reed canary grass

cover. We examined three hypotheses concerning how reed canary grass may negatively affect breeding birds in wet meadows, and found evidence of a negative effect only for Swamp Sparrow territory placement. Evidence for a slight positive response to reed canary grass cover or dominance was found for Sedge Wren and Song Sparrow territory placement. However, lack of an observed association of reed canary grass with territory size or the number of territories on a plot for all four study species indicates that sites with a range of reed canary grass cover may provide similar habitat – or that we could not discern a response in terms of habitat use with our methods. If reed canary grass reduced habitat acceptability and perhaps suitability, one would have expected birds to place territories to avoid high reed canary grass cover, or to increase territory size in areas with higher reed canary

Table 3. Territory presence model information for Sedge Wren, Common Yellowthroat, Swamp Sparrow, and Song Sparrow in riparian wet meadows of southwestern Minnesota and southeastern Wisconsin, 2001–2002. Abbreviations include number of model parameters (k; including random terms ^a), covariate terms [%RCG = percent cover of reed canary grass; %Forb = percent cover of forbs; VHD = mean vegetation height density; Litter = mean litter depth, %Shrub = percent cover of shrub, RCGDOM = reed canary grass dominance index), and model weights (w_i).

Model	Sedge Wren			Common Yellowthroat			Swamp Sparrow			Song Sparrow		
	k	AIC	w_i	k	AIC	w_i	k	AIC	w_i	k	AIC	w_i
Base ^a	3	13.2	0.00	5	19.2	0.00	3	43.6	0.00	4	9.4	0.01
%RCG, VHD												
%Shrub, Litter	7	0.6	0.36	9	2.2	0.18	7	0.0	0.55	8	0.0	0.39
RCGDOM, VHD,												
%Shrub, Litter	7	8.1	0.01	9	1.7	0.22	7	0.4	0.45	8	2.9	0.09
%RCG	4	0.0	0.60	6	22.4	0.00	4	34.8	0.00	5	10.2	0.00
RCGDOM	4	8.7	0.01	6	22.9	0.00	4	36.6	0.00	5	11.3	0.00
VHD, %Forb,												
%Shrub, Litter	7	10.5	0.00	9	0.0	0.52	7	14.0	0.00	8	5.0	0.03
VHD	4	14.4	0.00	6	13.5	0.00	4	25.1	0.00	5	11.1	0.00
%Forb, %Shrub,												
Litter	6	8.8	0.01	8	5.74.3	0.06	7	27.7	0.00	8	3.0	0.09
%Shrub	4	8.9	0.01	6	17.45.7	0.03	4	43.4	0.00	5	8.5	0.00
Litter	4	10.9	0.00	6	17.4	0.00	4	25.6	0.00	5	0.1	0.39

^a Base models included year-specific intercepts, random site effects and, for Common Yellowthroat and Song Sparrow models, random year-site effects; the variance of year-site effects was allowed to vary by year in the Common Yellowthroat models.

Table 4. Model averaged conditional odds ratios for potential predictors of territory placement. For each species the variables represented are: %RCG = percent cover of reed canary grass; RCGDOM = reed canary grass dominance index, VHD = mean vegetation height density, %Shrub = percent cover of shrub, %Forb = percent cover of forbs, Litter = mean litter depth. CI = confidence interval. Confidence intervals that exclude one indicate evidence of association with the listed covariate. Confidence Intervals were estimated under a large sample assumption.

Parameter	Sedge Wren		Common Yellowthroat		Swamp Sparrow		Song Sparrow	
	Odds ratio	(95% CI)	Odds ratio	(95% CI)	Odds ratio	(95% CI)	Odds ratio	(95% CI)
%RCG	1.014	(1.005–1.018)	1.002	(0.996–1.007)	0.987	(0.980–0.994)	1.008	(1.001–1.016)
RCGDOM	2.300	(0.926–5.715)	1.347	(0.651–2.786)	0.176	(0.070–0.443)	1.990	(0.784–5.056)
VHD	0.895	(0.399–2.007)	2.279	(1.195–4.347)	4.502	(1.126–9.536)	0.816	(0.346–1.925)
%Shrub	0.989	(0.973–1.004)	1.016	(1.006–1.026)	1.001	(0.985–1.016)	1.010	(0.999–1.027)
%Forb	0.999	(0.990–1.008)	1.001	(0.994–1.008)	1.004	(0.995–1.012)	1.002	(0.996–1.011)
Litter	1.007	(0.999–1.014)	1.005	(0.998–1.011)	1.018	(1.010–1.056)	0.985	(0.976–0.995)

grass cover (resulting in fewer territories in plots with higher reed canary grass cover).

Reed canary grass is native to North America (Marten 1985), and in the Upper Midwestern United States wet meadows are typically dominated by tall lush grasses and sedges (Reuter 1986). That reed canary grass now dominates such areas may not have changed the structure of the vegetation to a degree that deters Sedge Wrens, Common Yellowthroats, and Swamp and Song Sparrows; however, it is difficult to determine how well our study plots with low reed canary grass cover encapsulate historical plant community conditions because no records of plant species composition exist for wet meadows before European settlement of the area.

Others have noted breeding bird use of reed canary grass in wet meadows, grassy waterways, and roadsides in the Upper Midwest (Mossman and Sample 1990, Bryan and Best 1991, Camp and Best 1994, Renfrew and Ribic 2001, Benson 2003). Sedge Wrens are denizens of tall, rank, grassy vegetation (Herkert et al. 2001), thus, a slight preference for areas with higher reed canary grass cover does not seem unusual. Common Yellowthroats and Song Sparrows occur in thick vegetation in a wide range of habitats often associated with shrubby vegetation (Rising 1996, Guzy and Ritchison 1999). For Common Yellowthroats, we found evidence of

a strong association with vegetation height density and weak association with percent cover of shrubs, but no such associations were found for Song Sparrows. Because Common Yellowthroats and Song Sparrows are found in a wide variety of open habitats, we may not expect reed canary grass to deter them from using open wet meadow habitat. Only Swamp Sparrows appeared to place territories to avoid areas with high reed canary grass cover and dominance. This relationship was probably related to site wetness rather than to reed canary grass dominance, per se. Swamp Sparrows typically are associated with standing water and robust emergent wetland vegetation such as cattail (*Typha* spp., Mowbray 1997). Similar to findings of Greenberg (1988) in northwest Pennsylvania, Swamp Sparrow territories in our study tended to be in or near the wetter areas of plots, which often had cattail or dogwood (*Cornus* spp.) and relatively low levels of reed canary grass. Swamp Sparrows did nest in plots with high reed canary grass cover and several territories occurred in areas with high reed canary grass cover (> 80%). Furthermore, the size and number of Swamp Sparrow territories did not appear to be influenced by reed canary grass cover.

The breeding bird responses to invasive wet meadow/wetland plants have been examined for common reed (*Phragmites australis* Cav.) and purple

Table 5. Estimated associations (with 95% confidence intervals) between reed canary grass cover (RCG; units) and log-territory size and mean reed canary grass cover at the plot level and territory density. Territory density estimates represent effect multipliers, with null value of one.

Species	RCG and log-territory size		RCG and territory density	
	Estimate	(95% CI)	Estimate	(95% CI)
Sedge Wren	0.0004	(-0.0015, -0.0008)	0.9956	(0.9774, 1.0094)
Common Yellowthroat	0.0004	(-0.0002, 0.0010)	1.0023	(0.9920, 1.0020)
Swamp Sparrow	-0.0009	(-0.0018, 0.00003)	1.0185	(0.9956, 1.0115)
Song Sparrow	-0.0008	(-0.0017, 0.0002)	1.0048	(0.9851, 1.0102)

loosestrife (*Lythrum salicaria* L.). Similar to reed canary grass in our study, presence of many bird species is not affected by dominance of common reed (Benoit and Askins 1999). Purple loosestrife-dominated areas in Saginaw Bay, Michigan, on Lake Huron, had higher bird densities but lower bird diversity than other vegetation types (Whitt *et al.* 1999). Benoit and Askins (1999) and Whitt *et al.* (1999) noted that common reed and purple loosestrife frequently occur in dense monocultures with little or no open water or other shorter vegetation. They hypothesized that lack of habitat heterogeneity may contribute to lower avian diversity in monocultures of invasive plants in wetlands. In our study, reed canary grass formed tall lush stands, often with other tall lush wet meadow plants (tall sedges [*Carex* spp.], goldenrod [*Solidago* spp.], rice cut-grass [*Leersia orizoides* (L.) Swartz], common mint [*Mentha arvensis* L.]) and few points were in true monotypic stands of reed canary grass. Openings and patches of shorter vegetation were uncommon in our study plots, and are not typical for wet meadows in the study area, regardless of plant species dominance (unless such plots are grazed). Furthermore, wet meadows in this region typically do not have a diverse bird community (Hoffman and Sample 1988, Mossman and Sample 1990). Although there are no records of the plant species composition in the study area before European settlement, Curtis (1959) indicated that tallgrass prairie and sedge meadow historically occurred in the area. Increased dominance of reed canary grass may not have changed the vegetative structure to a degree that would drastically affect the bird community of wet meadows in the study area.

While it appears that the riparian wet meadow bird community in this study may not respond to reed canary grass invasion, we could not directly monitor avian productivity. It is possible that reed canary grass may function as an ecological trap (Schlaepfer *et al.* 2002) if those birds with territories in higher reed canary grass cover had lower productivity. For example, Lloyd and Martin (2005) found that while Chestnut-collared Longspurs (*Calcarius ornatus* Townsend) do not avoid an exotic grass (crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.]) in shortgrass prairie, they have lower reproductive success in crested wheatgrass than in native prairie.

Two estimates of arthropod food resources for nesting birds in our wet meadow plots were not affected by reed canary grass. Arthropod abundance and biomass were not reduced in areas with higher reed canary grass cover (Meier 2004). Although the arthropod community composition may differ along

a reed canary grass cover gradient (Meier 2004), arthropod orders recognized as important in grassland bird diets (Coleoptera, Araneae, Orthoptera, and Lepidoptera; Wiens 1974, Wiens and Rotenberry 1979), were not common on any of our plots, whereas Diptera, Homoptera, Hemiptera, and Hymenoptera were abundant (Meier 2004).

Even though reed canary grass may not severely affect the breeding bird community, its negative effect on other native plant species has been documented (Barnes 1999, Galatowitsch *et al.* 1999, Cochrane and Iltis 2000, Bernthal and Willis 2004). Reed canary grass is still promoted as a forage grass (e.g., <http://www.uwex.edu/ces/crops/reedcang.htm>; Volesky 1998) or a planting for wastewater treatment (Springman *et al.* 1995), and its competitive abilities may be enhanced by nutrient loading from upland agricultural sources (Green and Galatowitsch 2002, Maurer *et al.* 2003). Therefore, reed canary grass is likely to pose a problem for maintaining or restoring plant diversity in vanishing riparian wet meadows and wet meadows in other hydrologic settings in the Upper Midwestern United States.

The analytical approaches we used may be refined further. For example, interest in whether territory placement was associated with reed canary grass cover appeared to require the selection of a spatial equivalent to a territory. These "null" territories may be defined by size, variation in size, shape, variation in shape, location, and combinations of these and other characteristics. While the effect of this uncertainty in definition was not explored, we believe that acknowledgment of this uncertainty in our models would have led to increased error estimates and confidence limit widths. Other analytical concerns include whether area assigned to null territories included area that, for reasons unrelated to reed canary grass cover, were unsuitable for territories. In some cases, this information was known and controlled for. For example, the four species of birds examined in this study do not use open water areas, and such areas within plots were excluded from analyses. Another concern is that we assumed that territories were selected as functions of the averages of reed canary grass and other habitat descriptors. However, birds may be responding to more than averages; they may, for example, be responding to heterogeneity within a given spatial area (Freemark and Merriam 1986, Krüger and Lindstrom 2001).

Our methods appear most appropriate in situations where locating nests is not prudent. Such situations include where habitat is delicate enough that investigation would create noticeable and

enduring paths to nests (which may, in turn, increase access to nests by predators), pose safety concerns (e.g., as with studies conducted within some swamps), or create logistic challenges. Typical investigations of nesting habitat use involve measuring features at nest sites and comparing those to features of random points that are assumed to be unused. However, those random sites may actually occur in a territory of the same species (if not the same individual pair) and may be used for another essential activity such as foraging. Also, because we used spot mapping to delineate territories, the location of territories was not known until after the breeding season, so estimating where used and unused areas of plots were located and sampling habitat accordingly during the appropriate time frame was not possible. This situation may be encountered in other investigations. Sampling habitat on a regular grid allows relative ease of sampling and relocating sampling points in successive years if necessary. Lastly, this approach also provides an appealing, conjoint means of visualizing bird and habitat data.

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