Research Article

Nest Survival of Clay-Colored and Vesper Sparrows in Relation to Woodland Edge in Mixed-Grass Prairies

TODD A. GRANT,[1] *United States Fish and Wildlife Service, J. Clark Salyer National Wildlife Refuge, Upham, ND 58789, USA*
ELIZABETH M. MADDEN,[2] *United States Fish and Wildlife Service, J. Clark Salyer National Wildlife Refuge, Upham, ND 58789, USA*
TERRY L. SHAFFER, *United States Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND 58401, USA*
PAMELA J. PIETZ, *United States Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND 58401, USA*
GORDON B. BERKEY, *United States Fish and Wildlife Service, J. Clark Salyer National Wildlife Refuge, Upham, ND 58789, USA*
NEIL J. KADRMAS,[3] *University of North Dakota, Department of Biology, Grand Forks, ND 58202, USA*

Abstract

*The quantity and quality of northern mixed-grass prairie continues to decline because of conversion to agriculture, invasion of woody and exotic plants, and disruption of important ecological processes that shape grasslands. Declines in grassland bird populations in North Dakota, USA, have coincided with these largely anthropogenic alterations to prairie habitat. In grasslands of north-central and northwestern North Dakota, woody plants have increased due primarily to fire suppression, extirpation of bison (*Bos bison*), and widescale planting of tree shelter belts. In northern grasslands, effects of woody vegetation on survival of grassland birds are poorly understood, and conclusions are based mainly on studies conducted outside the region. We examined nest survival of clay-colored sparrows (*Spizella pallida*) and vesper sparrows (*Pooecetes gramineus*) relative to the distance nests were located from aspen (*Populus tremuloides*) woodland edges and relative to other habitat features near the nest. Clay-colored and vesper sparrow nest survival was higher for nests located near woodland edges, nests with greater cover of Kentucky bluegrass (*Poa pratensis*), and nests more concealed by vegetation. Vesper sparrow nest survival increased as the percent cover of tall shrubs near the nest increased. Based on video-camera data, the 13-lined ground squirrel (*Spermophilus tridecemlineatus*) was the most common predator of sparrow eggs and young. Thirteen-lined ground squirrels were more common far from woodland edges than near, and this pattern may, in part, explain clay-colored and vesper sparrow nest survival in relation to woodland edges. In contrast to our results, studies conducted in other grassland systems generally report lower nest survival for grassland birds nesting near trees and shrubs. This disparity in results demonstrates the need to identify specific nest predators and their distributions with respect to important habitat features because these data can be important in explaining—and perhaps predicting—patterns of nest predation.* (JOURNAL OF WILDLIFE MANAGEMENT 70(3):691–701; 2006)

Key words

aspen woodland, clay-colored sparrow, edge effects, grassland birds, mixed-grass prairie, North Dakota, vesper sparrow, woody vegetation.

Northern mixed-grass prairie has declined by >70% from historic extent (Samson and Knopf 1994, Samson et al. 2004), and more than 404,000 ha of native rangeland have been converted for agricultural production in North Dakota, South Dakota, and Montana since 1985 (Higgins et al. 2002). The quality of remaining prairie tracts increasingly is diminished by fragmentation, expansion of woody and exotic plants, and loss or misapplication of important ecological processes, especially fire and herbivory (Samson and Knopf 1994). Relative to other systems, fragmentation effects in grasslands are poorly understood (McGarigal and Cushman 2002).

In North Dakota, grassland bird populations have declined in recent decades, while species associated with woody vegetation have increased (Igl and Johnson 1997, Peterjohn and Sauer 1999). Increases in woody plants appear detrimental to the integrity of native prairies (Samson and Knopf 1994, Grant and Murphy 2005) and also to grassland birds as an ecological group (Johnson and Temple 1990, Winter et al. 2000, Bakker et al. 2002, Grant et al. 2004*a*). However, no studies have examined the effects of woody vegetation on nest survival for grassland birds breeding in the northern mixed-grass prairie region.

Predation is the primary source of nest mortality in birds and undoubtedly has influenced the evolution of avian life histories (Ricklefs 1969, Martin 1992). Nest parasitism by brown-headed cowbirds (*Molothrus ater*) also can depress host productivity (Davis and Sealy 2000, Granfors et al. 2001, Burhans et al. 2002). However, relatively few studies have documented nest success and brood parasitism rates or identified important nest predators for songbirds breeding in northern grasslands (but see Pietz and Granfors 2000, Granfors et al. 2001, Davis 2003, Winter et al. 2004).

We studied nest survival for clay-colored and vesper sparrows breeding in grasslands fragmented by expanding aspen woodlands in north-central North Dakota. Following the ecological trap hypothesis of Gates and Gysel (1978), we predicted higher densities but lower nest survival for clay-colored and vesper sparrows breeding near woodland edges. We tested this hypothesis by examining nest survival relative to the distance nests were located from aspen woodland edges. We also examined nest survival in relation to habitat features near nests. To explore the role of nest predation in shaping patterns of nest survival, we identified the most common predators of sparrow eggs and young.

[1] *E-mail: todd_grant@fws.gov*
[2] *Present address: United States Fish and Wildlife Service, Medicine Lake National Wildlife Refuge, Medicine Lake, MT 59247, USA*
[3] *Present address: United States Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, Lewistown, MT 59457, USA*

We then estimated the relative abundances of important nest predators in relation to woodland edges and compared their distributions to observed nest survival of clay-colored and vesper sparrows.

Study Area

We conducted our study on the 23,900-ha J. Clark Salyer National Wildlife Refuge (NWR) in McHenry County, North Dakota, USA (about 48°33′N, 100°33′W). The refuge is within the northern mixed-grass prairie region (Partners in Flight Physiographic Area 37; Fitzgerald et al. 1998). Although classified as northern mixed-grass prairie, the contemporary plant community of our study area was more precisely characterized as parkland (i.e., $\geq$1 aspen grove/km^2; Archibold and Wilson 1980). Aspen parkland in north-central North Dakota could be considered an island or southern extension of the aspen parkland ecoregion, and it comprised about 280,000 ha in Bottineau, McHenry, and Pierce Counties.

Prior to settlement by Europeans, woodland within the region was primarily restricted to riparian and wetland margins and the northeast aspect of sand ridges (Coupland 1961, Grant and Murphy 2005). Extirpation of bison, fire suppression, and planting of tree shelter belts have been implicated in woody plant increases in north-central and northwestern North Dakota (Grant and Murphy 2005). For example, the coverage of aspen woodland on J. Clark Salyer NWR has doubled since European settlement, and remaining grasslands could be lost within 75–130 years (Grant and Murphy 2005).

Study area grasslands were dominated by a needle grass–wheatgrass (*Stipa–Agropyron*) association intermingled with 2 exotic grasses, Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*). Grasslands were interspersed with short ($\leq$1.0 m) brush dominated by western snowberry (*Symphoricarpos occidentalis*), tall (2–3 m) shrub dominated by chokecherry (*Prunus virginiana*) and willow (*Salix* spp.), and aspen woodland. Ranching was the dominant land use on private grasslands adjacent to the refuge. Prescribed grazing by cattle, prescribed fire, and periodic rest have been used to manage grasslands within J. Clark Salyer NWR.

Methods

Nest Monitoring

We searched for nests of grassland birds within the parkland region of J. Clark Salyer NWR in 1997, 1998, and 2002. We searched 3 general grassland areas (e.g., Fig. 1) that were located within 10 km of each other and were mostly surrounded by aspen woodland. To minimize potential dependencies among nests, we generally did not search the same areas in subsequent years (e.g., we only searched 9% of the study area in all 3 years). Nest studies such as ours that do not mark individuals cannot account for potential pseudoreplication resulting from renests or second nests within a year. Substantial renesting or second nest attempts by the same pairs could inflate sample sizes.

At the time of our searches, grasslands had been rested $\geq$2 growing seasons since being burned or grazed; grasslands generally recovered to pretreatment conditions within 2–3 growing seasons following defoliation by grazing or fire (Nenneman 2003). Although we monitored nests of all grassland species using the study area, our focal species were clay-colored and vesper sparrows because 1) they were the 2 most abundant passerine species within the study area, 2) point count data from a previous study (Grant et al. 2004*a*) suggested they could be found nesting both near and far from aspen woodland edges (Fig. 1), and 3) both species were known hosts of parasitic brown-headed cowbirds (Knapton 1994, Jones and Cornely 2002, Shaffer et al. 2003). The 2 species differ in taxonomy, egg crypsis, overall nest survival (Grant et al. 2005), and habitat selection; clay-colored sparrows typically build nests near the ground within the stems of western snowberry and other shrubs, whereas vesper sparrows nest on the ground amid grasses and forbs.

We searched for and monitored nests from about 15 May to 15 July each year. We systematically located nests between 0630 and 1500 hours Central Standard Time (CST) by flushing adult birds from their nests using a 25-m weighted rope pulled through the grass by 2 people. We also located nests fortuitously and by observing behaviors of parents (e.g., carrying food). We marked nests by placing survey flags 3 m to the north and south of each nest, with the top of the flag just above the average height of the vegetation. To estimate nest age, we candled 1–2 eggs in each nest (Lokemoen and Koford 1996) or aged nestlings from voucher photographs of known-age young. We monitored nests every 2–5 days until the nests either fledged young or failed. We classified nests as surviving the interval between visits if at least 1 egg or nestling was alive on the latter visit or if at least 1 young fledged on or before the final visit. Within 1–3 days of predicted fledging, we visited the nest every day to minimize uncertainty in assigning the final nest fate. After finding the nest, our visits rarely lasted more than 5 seconds, and we viewed most nests from 1–3 m away. We used the behaviors of the parents (e.g., alarm calling, carrying food), presence of young near the nest, nestling age at the previous visit, evidence of nest disturbance, evidence of nestling mortality, and presence of feces and feather scales at the nest to classify nests as successful or failed. We excluded nests that probably were abandoned due to researcher disturbance (e.g., nests abandoned during laying with only 1 egg in the nest).

Habitat Measurements

We measured 8 habitat variables known either to predict avian occurrence (Madden et al. 2000, Grant et al. 2004*a*) or productivity in grasslands (Nenneman 2003), or to be essential in monitoring plant succession in northern grasslands (Grant et al. 2004*b*). Following the nesting season (mid-Jul to early Aug), we measured plant community composition of the nest patch using 10-m radius plots centered on each nest (Grant et al. 2004*b*). Beginning at the nest, we established a belt transect, 10-m long $\times$ 0.1-m wide, along a random compass bearing and then placed subsequent transects at 90, 180, and 270 degrees from the first. We classified vegetation within 20 0.5 $\times$ 0.1-m segments of each transect using common plant community associations for the region (Grant et al. 2004*b*), with each plot yielding 80 belt segment records. We estimated percent cover from the frequency with which a cover type occurred within the nest plot (e.g., 10% Kentucky bluegrass cover corresponds to 8 of 80 belt-segments/nest plot classified as Kentucky bluegrass). We used a Global Positioning System (GPS) unit to record the position ($\pm$3–5 m)

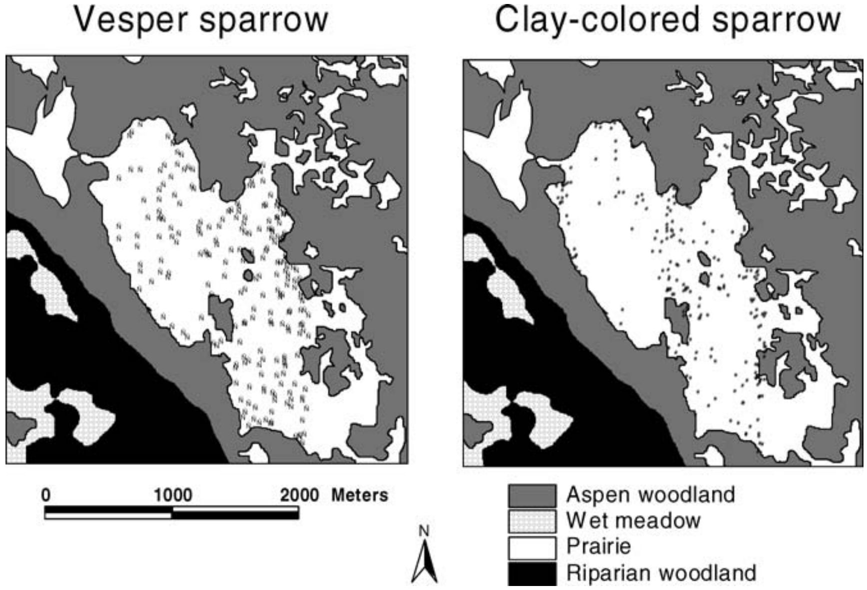

Figure 1. Spatial distribution of nests relative to woodland edges for vesper and clay-colored sparrows in 1997, 1998, and 2002 on J. Clark Salyer National Wildlife Refuge, N.D., USA. Only nests located in 1 of 3 study grasslands are shown here.

of each nest and then used Geographic Information System software to determine the distance (m) from each nest to the nearest aspen woodland edge (digitized on 1:7920 aerial photographs).

In 2002 only, we quantified nest visibility using a circular disk that was 6.3 cm in diameter, and radially divided into 8 equal black and white segments (Davis and Sealy 1998). When we first found the nest, we placed the disk horizontally in the nest and recorded the number of visible segments from a distance of 1 m in each quadrant (NE, SE, SW, NW), and from 1.5 m directly over the nest. The percent of visible segments provided an index of nest visibility (i.e., nests with an index of 100% were completely visible, nests with an index of 0% were completely concealed). We measured visibility only for nests that contained eggs or small young (<4–5 days old).

Explanatory Variables

We investigated the effects of 8 habitat variables on daily survival rates of clay-colored sparrow and vesper sparrow nests. We used the following habitat variables: 1) distance (m) to the nearest woodland edge (DISTANCE), 2) index of nest visibility (VISIBLE; 2002 only), 3) percent cover within 10 m of the nest of brush $\leq$1 m in height (BRUSH), 4) percent cover within 10 m of the nest of tall shrubs >1 m in height (TSHRUB), 5) percent cover within 10 m of the nest of Kentucky bluegrass (KYBLUE), 6) percent cover within 10 m of the nest of smooth brome (BROME), 7) percent cover within 10 m of the nest of native grasses and forbs (NATIVE), and 8) percent cover within 10 m of the nest of native forbs (FORB).

We used the natural log of DISTANCE and arc-sine-square-root transformed values (i.e., arcsin[sqrt(x)]) of BRUSH, TSHRUB, KYBLUE, BROME, NATIVE, FORB and VISIBLE in all analyses. We chose these transformations based on a priori considerations. For instance, we thought it reasonable that distance effects would be more pronounced at smaller distances to edge than at greater distances, suggesting the use of the log transformation. Similarly, we expected effects of the various vegetation components, such as BRUSH, to be greatest when those components were either very sparse or very common. For example, if BRUSH was related to daily survival rate, it seemed reasonable to expect that the effect of increasing BRUSH from zero to 5% would be greater than the effect of increasing brush from 45 to 50%. The arc-sine-square-root transformation accommodates this type of relationship by spreading out values near zero or 1 disproportionately to less extreme values (i.e., those nearer 0.5).

Candidate Models

In an earlier study, we found that occurrence of 15 grassland bird species was strongly affected by proximity to aspen woodland (Grant et al. 2004*a*). Thus, we hypothesized that survival rates of nests might vary in relation to distance between the nest and the nearest aspen woodland edge. This was the primary question that motivated our study. We also hypothesized that vegetation features near the nest might influence nest survival rates. For example, occurrence of clay-colored sparrows increased with coverage of both TSHRUB and BRUSH (Grant et al. 2004*a*), perhaps because these types of sites provide an advantage in terms of nest survival. To examine whether habitat variables were related to daily nest survival rates, we used the information–theoretic approach (Burnham and Anderson 2002) and constructed candidate models consisting of each habitat variable by itself and in combination with all other habitat variables taken one at a time. For example, we considered models including only DISTANCE, NATIVE, or FORB (1-variable models), and models involving DISTANCE and NATIVE, DISTANCE and FORB, and NATIVE and FORB (2-variable models). To keep the number of candidate models manageable, we did not consider models that included 3 variables. In addition, we constructed a global model that included all 7 habitat variables, and we constructed a null model that included no habitat variables. Thus, we constructed 30 models for each species: 7 1-variable models, 21 2-variable models, the global model, and the null model. In a separate analysis, we evaluated the importance of nest visibility measured in 2002 by considering the following 6 candidate models: null model; VISIBLE; DISTANCE; VISIBLE and DISTANCE; VISIBLE and BRUSH; and VISIBLE, DISTANCE, and BRUSH. All candidate models also included a cubic polynomial effect of nest age, based on a previous analysis of these data that looked at temporal effects on nest survival (Grant et al. 2005). Although we were not interested in age effects here, we included them to avoid potential confounding of habitat and temporal effects and to provide accurate estimates of nest success. Grant et al. (2005) found no relationship between year and nest survival; therefore, we did not include an effect of year in our analysis of the same nest data.

Estimating Nest Survival

We used the logistic-exposure method (Shaffer 2004) to fit each candidate model. Logistic-exposure models are similar to logistic regression models in that the daily survival rate for any nest on a given day is modeled as a logistic function of the values of explanatory variables for the nest on that day. We used the GENMOD procedure of SAS Institute (1997) to estimate the regression coefficients in our logistic-exposure models (Shaffer 2004). We then estimated daily survival rates from the resulting logistic function (see Shaffer 2004 for details). We treated each interval between visits to a nest as 1 observation in the analysis. The response variable was whether or not the nest survived the interval.

We evaluated our candidate models with Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson 2002). We used the effective sample size (n; Rotella et al. 2004) when computing AIC_c (i.e., n = total number of days that nests were known to survive + the total number of intervals in which a failure occurred). We used model-averaging to avoid potential effects of model-selection uncertainty (Burnham and Anderson 2002). We examined the average model graphically by plotting nest survival as a function of individual habitat variables while holding other habitat variables at their median values. We defined nest survival as the probability that a nest survived to fledge $\geq$1 young, and we computed nest survival as the product of estimated daily survival rates for each day in the nesting cycle. We assumed nesting cycles of 22 days for clay-colored sparrows and 25 days for vesper sparrows.

Relative Importance of Habitat Variables

Because each habitat variable occurred in the same number of models (8), we were able to assess the relative importance of each variable by summing the Akaike weights (w) across all models in which that variable appeared (Burnham and Anderson 2002). The sum of the Akaike weights can be thought of as a *relative importance value* for a particular explanatory variable. However, when interpreting relative importance values from an observational study like ours, consideration must be given to the range of observed values for each explanatory variable. The true importance of an explanatory variable may not be apparent unless the variable is observed at both low and high values. Therefore, we report descriptive statistics for each habitat variable along with relative importance values.

Identification of Nest Predators

We speculated that songbirds may not share the same suite of nest predators as large-bodied birds (e.g., ducks and prairie grouse) that have been well studied in northern grasslands (Sargeant et al. 1993). In 1998–1999, we used miniature black-and-white cameras (about $4 \times 4 \times 4$ cm) to videotape predation and other activities at grassland passerine nests (for details, see Pietz and Granfors 2000). Average distance between the nest and camera was 21 cm; the camera field of view included the nest and a small surrounding area. Infrared light-emitting diodes (LEDs) mounted around the camera lens provided cryptic illumination at night. Each camera was connected by a 50-m cable to a time-lapse video-cassette recorder (VCR), which recorded continuously at 4–5 images/sec. We visited the VCR daily to change videotapes, check or change batteries, and check nest status. When the nesting attempt was completed, we removed the camera and examined the nest area for signs of fledging or predation. We reviewed videotapes to determine fates of all eggs and nestlings and to identify nest predators.

Mammal Trapping

In 2002–2003, we used live traps and pitfall traps to sample the relative abundance of small-bodied (e.g., shrews, mice and voles, squirrels) and midsized (e.g., raccoons [*Procyon lotor*]) terrestrial vertebrates. We mainly wished to compare mammal communities (especially relative abundances of nest predators) in prairies far from woodlands to those at prairie-woodland edges. We established 3 paired plots in prairie-interior and prairie-woodland edge habitats (i.e., we paired each prairie interior plot with an adjacent prairie-woodland edge plot). We centered prairie-interior plots (>100 m from woodland edges) within grassland patches surrounded by woodland. Prairie–woodland edge plots straddled the transition zone from prairie to woodland, with about half of the plot in each habitat. Each plot included 3 parallel 100-m transects (perpendicular to the woodland–grassland edge) 20 m apart. On each 100-m transect, we used 11 Sherman live traps (1 every 10 m) for capturing small mammals and 6 Tomahawk or Havahart mesh live traps (1 every 20 m) for capturing larger mammals. Each plot also included 1 pitfall transect oriented perpendicular to and in the approximate center of the 3 parallel 100-m live-trap transects. For each pitfall transect, we placed 6 17-L buckets (one every 5 m) buried to ground level with a 25–50 cm tall drift fence running the length of the transect and bisecting the center of each bucket. We drilled small holes in each bucket to drain precipitation.

We sampled each plot once in 2002 (Jul) and 3 times in 2003 (Jun–Aug) using 5-day sample periods. We set and baited live traps and opened pitfall traps to capture mammals during 1600–0800 hours CST. We identified captured animals by species, sex, and age class (juvenile, subadult, adult); each animal was weighed, marked with numbered tags or (for larger mammals) paint, and released. We estimated relative abundance as the total captures/

100 trap-nights by species-group summed across 3 interior or edge plots.

Results

Nest Survival

We monitored the fates of 250 clay-colored sparrow and 246 vesper sparrow nests, resulting in effective sample sizes of 2,442 and 2,701, respectively. The median interval length between nest visits was 3 days for clay-colored sparrows and 2 days for vesper sparrows, and 99% of all intervals were <6 days. Overall nest survival was 0.296 for clay-colored sparrows and 0.449 for vesper sparrows. Brown-headed cowbirds parasitized only 1 (<0.01%) vesper sparrow and 6 (2.4%) clay-colored sparrow nests.

Of 30 habitat models we considered, no model was clearly superior (Table 1). All models included a cubic effect of nest age (see Grant et al. [2005] for a complete discussion of age effects). For both sparrows, we found the most support for a model that included DISTANCE and KYBLUE, followed closely by a model including only DISTANCE (Table 1). However, numerous models had ΔAIC_c values <2, indicating that use of model-averaged parameter estimates was appropriate (Table 2). Based on relative importance values (Table 3), DISTANCE was the variable most associated with clay-colored sparrow and vesper sparrow nest survival. Although percent cover of tall shrubs was near zero (Table 4), it was ranked second in importance for vesper sparrows (Table 3). Percent cover of Kentucky bluegrass also was important for both clay-colored and vesper sparrows (Table 3). Nest survival was highest near aspen woodland edges for both species and declined as the distance from woodland increased (Fig. 2). Nest survival also increased as percent cover of Kentucky bluegrass increased (Fig. 2). Vesper sparrow nest survival increased as percent cover of tall shrubs increased (Fig. 2).

In our analysis of nest visibility, the model for clay-colored sparrows including VISIBLE, DISTANCE, and nest age ranked second-best ($\Delta AIC_c = 1.15$, $w = 0.21$) behind the model that included effects of DISTANCE and nest age ($\Delta AIC_c = 0.0$, $w = 0.37$). For vesper sparrows, VISIBLE occurred in the best model with DISTANCE and nest age ($\Delta AIC_c = 0.0$, $w = 0.25$), and it occurred in the second-best model with nest age ($\Delta AIC_c = 0.18$, $w = 0.22$). For both species, we found higher nest survival for more concealed nests (Fig. 3).

Nest Predators

In 1998 and 1999, we identified 13-lined ground squirrels as the most common predator of eggs and nestlings (Table 5), accounting for 37% of the predation events documented on camera. The 8 other predators identified each accounted for 3% to 17% of the videotaped predation events.

In 2002 and 2003, we captured 2,707 mammals representing 23 species. We report results for 4 species groups observed depredating songbird nests (taken from Table 5). We captured 97% of 13-lined ground squirrels on prairie-interior plots (Table 6). We found that voles were common in both edge and interior plots; meadow voles (*Microtus pennsylvanicus*) were more common in prairie-interior plots, whereas red-backed voles (*Clethrionomys gapperi*) were common only in edge plots. We captured more mice (*Peromyscus* spp.) and raccoons near woodland edges than on prairie-interior plots (Table 6).

Discussion

Effects of Woody Vegetation on Nest Survival

Our data do not support the universal assumption that woody vegetation is detrimental to grassland bird nest survival. Nor did we find support for the ecological trap hypothesis (Gates and Gysel 1978), which describes the paradoxical relationship between bird abundance and nest survival near habitat edges. Following Gates and Gysel (1978), we would predict higher bird abundance but lower nest survival near grassland–woodland edges. In our study, clay-colored and vesper sparrow nest survival was highest near woodland edges and declined as the distance from these edges increased. Survival of vesper sparrow nests also was higher near tall shrubs.

Fragmentation and edge effects associated with woody plant occurrence have received little study in grasslands, especially in mixed-grass prairies. We identified only a few studies that specifically measured potential effects of woody vegetation on breeding grassland bird occurrence, abundance, and/or density in mixed-grass prairies. In a previous study that included our study area, Grant et al. (2004*a*) found that the probability of occurrence decreased for 11 of 15 grassland bird species as percent woodland, tall shrub, or brush cover increased; grasslands became largely unsuitable for 9 species when woodland cover exceeded 25%. The occurrence of only 4 of 15 species (clay-colored sparrow, common yellowthroat [*Geothlypis trichas*], brown-headed cowbird, vesper sparrow) increased as woody vegetation increased on survey plots (Grant et al. 2004*a*). In South Dakota, Bakker et al. (2002) found that the occurrence of Savannah sparrows (*Passerculus sandwichensis*), sedge wrens (*Cistothorus platensis*), grasshopper sparrows (*Ammodramus savannarum*), and western meadowlarks (*Sturnella neglecta*) declined as the extent of woody vegetation surrounding a grassland patch increased, but no grassland species were positively associated with woody vegetation. In Saskatchewan, Davis (2004) reported that occurrence and/or abundance of Baird's sparrows (*Ammodramus bairdii*), grasshopper sparrows, and western meadowlarks decreased as shrub density increased or distance to shrubs decreased, whereas clay-colored sparrow and brown-headed cowbird abundance increased with increasing shrub density. Davis (2005) also reported that grassland specialists such as Sprague's pipit (*Anthus spragueii*), chestnut-collared longspur (*Calcarius ornatus*), and Baird's sparrow located nests in sites where shrubs were sparse. In northwestern North Dakota, Madden et al. (2000) reported that occurrence of Baird's sparrows declined with increased brush coverage (primarily western snowberry); conversely, clay-colored sparrows were more common as brush cover increased. In the mixed-grass prairie in central North Dakota, Arnold and Higgins (1986) reported lower relative densities in shrubby versus nonshrubby plots for grasshopper sparrows, chestnut-collared longspurs, Baird's sparrows, and Savannah sparrows. Clay-colored sparrows and brown-headed cowbirds were the most abundant species in shrubby plots, comprising 57% of the total bird density there (Arnold and Higgins 1986). Results from these previous studies suggested that trees and tall shrubs were detrimental to grassland birds nesting in mixed-grass prairies, but some brush cover was required for nesting by a few grassland species, especially the clay-colored sparrow.

Our study is the first to specifically investigate effects of woody

Table 1. Model selection results for the 11 most-plausible logistic-exposure models of daily survival rate for clay-colored sparrow nests ($n = 250$) and vesper sparrow nests ($n = 246$) on J. Clark Salyer National Wildlife Refuge in N.D., USA, 1997, 1998, and 2002. Models are ranked based on Akaike's Information Criterion for small samples (AIC_c), ΔAIC_c, and Akaike weights (w); AIC_c is based on $Log_e(L)$, which is the value of the maximized log-likelihood function, and the number of parameters in the model (K).

Model[a]	K	$Log_e(L)$	AIC_c	ΔAIC_c	w
Clay-colored sparrow					
AGE + DISTANCE + KYBLUE	6	–386.70	785.39	0.00	0.112
AGE + DISTANCE	5	–387.74	785.50	0.11	0.106
AGE (null model)	4	–389.20	786.41	1.02	0.067
AGE + KYBLUE	5	–388.31	786.64	1.25	0.060
AGE + DISTANCE + FORB	6	–387.35	786.74	1.36	0.057
AGE + DISTANCE + BROME	6	–387.41	786.91	1.52	0.052
AGE + DISTANCE + TSHRUB	6	–387.62	787.27	1.88	0.044
AGE + DISTANCE + NATIVE	6	–387.66	787.35	1.97	0.042
AGE + DISTANCE + BRUSH	6	–387.67	787.37	1.98	0.042
AGE + FORB	5	–388.81	787.65	2.26	0.036
AGE + FORB + KYBLUE	6	–387.84	787.71	2.32	0.035
Vesper sparrow					
AGE + DISTANCE + KYBLUE	6	–329.24	670.50	0.00	0.118
AGE + DISTANCE	5	–330.30	670.62	0.12	0.111
AGE + DISTANCE + FORB	6	–329.32	670.68	0.18	0.108
AGE + DISTANCE + NATIVE	6	–329.34	670.71	0.20	0.106
AGE + DISTANCE + TSHRUB	6	–329.36	670.75	0.25	0.104
AGE + DISTANCE + BRUSH	6	–330.16	672.35	1.85	0.047
AGE + DISTANCE + BROME	6	–330.19	672.40	1.90	0.045
AGE + TSHRUB	5	–331.40	672.83	2.33	0.037
AGE + KYBLUE + TSHRUB	6	–330.65	673.32	2.82	0.029
AGE + FORB + TSHRUB	6	–330.71	673.45	2.95	0.027
AGE (null model)	4	–332.84	673.70	3.20	0.024

[a] AGE = cubic polynomial effect of nest age (days). DISTANCE = natural log of distance (m) to the nearest woodland edge. Other variables represent arcsine-square-root transformed values of percent cover within 10 m of the nest: BRUSH = shrubs $\leq$1 m in height, TSHRUB = shrubs >1 m in height, KYBLUE = Kentucky bluegrass, BROME = smooth brome, NATIVE = native herbaceous plants, FORB = native forbs.

vegetation on nest survival of grassland songbirds nesting in northern mixed-grass prairies. Studies conducted in other grassland systems generally reported lower nest survival for grassland birds associated with woody plants, although few of these studies were specifically designed to address these effects. In shortgrass prairies of Colorado, predation by 13-lined ground squirrels was higher for McCown's longspur (*Calcarius mccownii*) nests near shrubs (With 1994). In tallgrass prairies in North Dakota, nest success of grasshopper sparrows decreased with increasing shrub (Scheiman et al. 2003). In tallgrass prairie patches in Missouri, Winter et al. (2000) found higher predation rates for Henslow's sparrow (*Ammodramus henslowii*) and dickcissel (*Spiza americana*) nests and higher brood parasitism rates for dickcissel nests near shrubby edges, although they found no such effects for nests

Table 2. Model-averaged parameter estimates and standard errors (SE) for 10 variables in relation to daily survival rates of clay-colored sparrow nests ($n = 250$) and vesper sparrow nests ($n = 246$) on J. Clark Salyer National Wildlife Refuge, N.D., USA, 1997, 1998, and 2002.

	Clay-colored sparrow		Vesper sparrow	
Parameter [a]	Estimate	SE	Estimate	SE
INTERCEPT	1.258	0.750	3.894	1.379
AGE	0.003	0.001	0.001	0.001
AGE^2	0.813	0.218	0.345	0.310
AGE^3	–0.087	0.021	–0.045	0.025
DISTANCE	–0.052	0.071	–0.141	0.133
BROME	–0.053	0.127	–0.060	0.148
BRUSH	–0.024	0.069	0.000	0.053
FORB	0.097	0.213	–0.156	0.291
KYBLUE	0.129	0.222	0.132	0.255
NATIVE	–0.025	0.072	–0.079	0.157
TSHRUB	–0.014	0.074	0.451	0.808

[a] AGE, AGE^2 and AGE^3 = linear, quadratic, and cubic effects of nest age (days). DISTANCE = natural log of distance (m) to the nearest woodland edge. Other variables represent arcsine-square-root transformed values of percent cover within 10 m of the nest: BRUSH = shrubs $\leq$1 m in height, TSHRUB = shrubs >1 m in height, KYBLUE = Kentucky bluegrass, BROME = smooth brome, NATIVE = native herbaceous plants, FORB = native forbs.

Table 3. Relative importance of 7 habitat variables for predicting daily survival rates for clay-colored sparrow nests ($n = 250$) and vesper sparrow nests ($n = 246$) on J. Clark Salyer National Wildlife Refuge, N.D., USA, 1997, 1998, and 2002.

	Relative importance value[a]	
Parameter	Clay-colored sparrow	Vesper sparrow
DISTANCE[b]	0.456	0.643
BROME	0.169	0.121
BRUSH	0.152	0.106
FORB	0.192	0.214
KYBLUE	0.302	0.218
NATIVE	0.154	0.194
TSHRUB	0.139	0.252

[a] Σ Akaike weights for models that included the variable. Each variable occurred in 8 of 30 candidate models.

[b] DISTANCE = natural log of distance (m) to the nearest woodland edge. Other variables represent arcsine-square-root transformed values of percent cover within 10 m of the nest: BRUSH = shrubs $\leq$1 m in height, TSHRUB = shrubs >1 m in height, KYBLUE = Kentucky bluegrass, BROME = smooth brome, NATIVE = native herbaceous plants, FORB = native forbs.

Table 4. Descriptive statistics for 8 habitat variables used to model daily survival rates for clay-colored sparrow nests ($n = 250$) and vesper sparrow nests ($n = 246$) on J. Clark Salyer National Wildlife Refuge, N.D., USA, 1997, 1998, and 2002.

	Clay-colored sparrow				Vesper sparrow			
Parameter[a]	Median	Min	Max	IQR[b]	Median	Min	Max	IQR
DISTANCE	62	0	368	104	97	1	452	143
BROME	0	0	93	0	0	0	69	0
BRUSH	36	0	98	45	0	0	85	10
FORB	2	0	45	6	6	0	40	14
KYBLUE	8	0	80	25	0	0	84	6
NATIVE	24	0	100	38	89	1	100	35
TSHRUB	1	0	73	10	0	0	28	0
VISIBLE	12	0	28	8	16	0	35	0

[a] DISTANCE = distance (m) to the nearest woodland edge. Other variables represent percent cover within 10 m of the nest: BRUSH = shrubs ≤1 m in height, TSHRUB = shrubs >1 m in height, KYBLUE = Kentucky bluegrass, BROME = smooth brome, NATIVE = native herbaceous plants, FORB = native forbs. VISIBLE = index to nest visibility measured in 2002 only; $n = 69$ clay-colored sparrow nests and 76 vesper sparrow nests.

[b] Interquartile range is the difference between third and first quartiles.

located near forest edges. In tallgrass prairies in Minnesota, bobolink (*Dolichonyx oryzivorus*) and western meadowlark nests had higher predation rates and clay-colored sparrow and western meadowlark nests had higher parasitism rates near woodland edges (Johnson and Temple 1990; reanalyzed by Johnson 2001). In New York, bobolinks avoided woodland edges and had lower nest success near forest and wooded hedgerow edges (Bollinger and Gavin 2004). In contrast, Vickery et al. (1992) found no relationship between nest survival and distance from forest edges for grassland birds in Maine. Renfrew et al. (2005) found similar densities and survival of Savannah sparrow and meadowlark nests located <50 m and >50 m from woodland edges in Wisconsin. Parasitism of clay-colored sparrow nests by brown-headed cowbirds increased with proximity to cowbird perch sites (mainly shrubs or trees) within remnant tallgrass prairies in North Dakota (Romig and Crawford 1995). Davis (1994) and Davis and Sealy (2000) found higher rates of brown-headed cowbird parasitism on grassland bird nests near potential shrubby perch sites in Manitoba.

In most nesting studies, the mechanisms that could induce edge effects (e.g., nest predation or brood parasitism) either are not identified or are derived mostly from speculation (but see With 1994 and Winter et al. 2000). Furthermore, few avian habitat studies have been able to address why use of certain habitats was or was not adaptive (i.e., in terms of survival and fitness) for species studied (Jones 2001, Davis 2005). Together, Grant et al.'s (2004*a*) study of clay-colored and vesper sparrow habitat use and our study of nest survival and local nest predators may offer insights into these elusive questions. Point count data from 1995–1996 (Grant et al. 2004*a*) indicated that clay-colored and vesper sparrows were more common on plots with greater coverage of woody plants (i.e., infer habitat selection [Fig. 4]). Both species also had higher nest survival near woodland edges. We found that 13-lined ground squirrels were the most important predator of sparrow eggs and young and that they were less abundant near woodland edges than

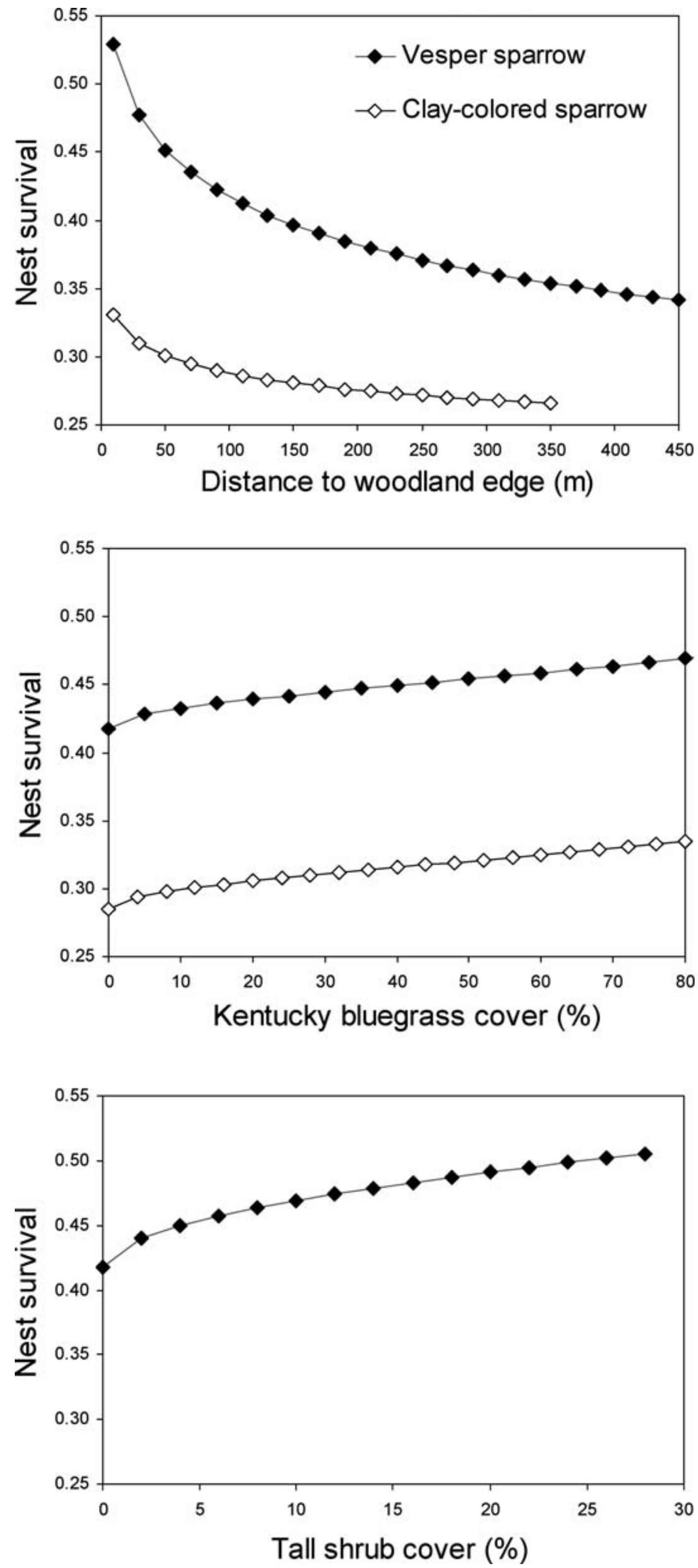

Figure 2. Nest success of vesper and clay-colored sparrows as a function of 1) distance to aspen woodland edge, 2) percent cover of Kentucky bluegrass within 10 m of the nest, and 3) percent cover of tall-shrubs within 10 m of the nest (vesper sparrow only) on J. Clark Salyer National Wildlife Refuge, N.D., USA, 1997, 1998, and 2002.

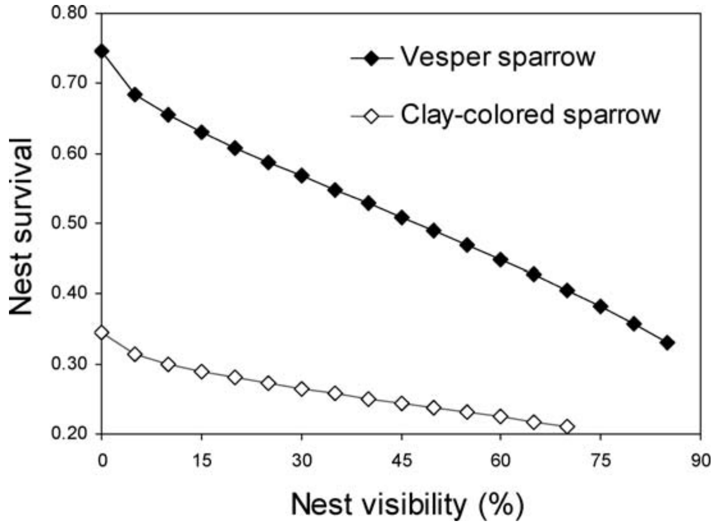

Figure 3. Nest success as a function of nest visibility for vesper and clay-colored sparrows on J. Clark Salyer National Wildlife Refuge, N.D., USA, 2002.

in grassland interiors. Furthermore, nest parasitism rates by brown-headed cowbirds were near zero within our aspen parkland study area, compared to an average of 14% for passerine nests located in treeless grasslands 40 km north of the study site and on other National Wildlife Refuges in the region (T. Grant and R. Murphy, U.S. Fish and Wildlife Service, Upham, N.D., USA, unpublished data), although cowbirds occurred ubiquitously with respect to percent woodland cover (Grant et al. 2004*a*). The coincidence of clay-colored and vesper sparrow nest-site selection, nest survival, and patterns of predation and brood parasitism is intriguing. Did clay-colored and vesper sparrows in our study have higher nest survival, and potentially better fitness, near edges because they are adapted to nesting near woody vegetation? Our data cannot definitively answer this question, but we suggest this as a plausible hypothesis in need of additional study.

Table 5. Number of nest predation events at passerine nests monitored with miniature video cameras on J. Clark Salyer National Wildlife Refuge, N.D., USA, 1998–1999.

Predator	1998	1999	Total%
Deer mouse/white-footed mouse (*Peromyscus* sp.)	1		1
Unidentified vole (*Microtus* sp.) or mouse		2	2
13-lined ground squirrel (*Spermophilus tridecemlineatus*)	3	8	11
American badger (*Taxidea taxus*)	1	2	3
Raccoon (*Procyon lotor*)		1	1
White-tailed deer (*Odocoileus virginianus*)	1	1	2
Hawk (*Buteo* sp.)	1		1
Brown-headed cowbird (*Molothrus ater*)	1	4	5
Plains garter snake (*Thamnophis radix*)	1	1	2
Unidentified predator		2	2
Total predation events[a]	9	21	30
Total nests with cameras	29	35	64

[a] In 1999, 2 different predator species removed/destroyed contents at each of 2 nests. Thus, there were 21 predation events at 19 nests.

Table 6. Total captures/100 trap nights for 3 prairie interior and 3 prairie–woodland edge plots on J. Clark Salyer National Wildlife Refuge, N.D., USA, 2002–2003.

	2002[a]		2003		Total	
Species	Interior	Edge	Interior	Edge	Interior	Edge
Deer mouse/ white-footed mouse	0.78	2.36	1.00	1.85	0.95	1.95
Voles	0.52	1.05	3.05	1.85	2.54	1.69
13-lined ground squirrel	4.40	0	2.77	0.13	3.07	0.11
Raccoon	0	0	0	0.75	0	0.61

[a] Only 1 trapping session in 2002, 3 trapping sessions in 2003.

Studies that examine nest survival relative to woodland edge may produce different results, in part, because of spatial and temporal variation in predator communities. Predation by 13-lined ground squirrels documented at camera-monitored nests on our study area is neither unusual nor universal. For example, 13-lined ground squirrels topped the list of passerine nest predators videotaped on grasslands in central North Dakota (Pietz and Granfors 2000) and on planted grass fields (Conservation Reserve Program) in southwestern Wisconsin (C. A. Ribic, Wisconsin Cooperative Wildlife Research Unit, Madison, Wisc., USA, personal communication). In contrast, raccoons dominated the predator list for pastures in southwestern Wisconsin (Renfrew and Ribic 2003) and no dominance was seen among the 12 predator species identified at nests in western Minnesota grasslands (P. J. Pietz, U.S. Geological Survey, Jamestown, N.D., unpublished data). This variability makes information on local predator communities fundamental to understanding results of research on nest survival.

We caution managers about making broad inferences from studies that lack spatial or temporal replication or that assess only a limited number of species (including our study). Such inferences may not be universally applicable among grassland bird species or among grassland systems. Habitat use patterns differ markedly among species of grassland birds (e.g., Madden et al. 2000, Davis 2004, Grant et al. 2004*a*), so generalizations about the entire group are of dubious value. Generalizations about spatial patterns of nest survival also may have little validity.

Effects of Habitat Features near the Nest

Clay-colored and vesper sparrow nest survival increased as the percent cover of Kentucky bluegrass increased near the nest. Nest survival in 2002 was highest for the most-concealed nests. Winter et al. (2005) also found that nest survival increased with greater nest cover for clay-colored sparrows in tallgrass prairies. The most-concealed nests in our study occurred in native vegetation intermingled with Kentucky bluegrass (vesper sparrow) or in western snowberry with a Kentucky bluegrass understory (clay-colored sparrow). Kentucky bluegrass is an invasive plant now naturalized within mixed-grass prairie, and it often compromises the integrity of native plant communities (Bragg 1995, Grace et al. 2001, Murphy and Grant 2005). Kentucky bluegrass is especially problematic in mesic prairies where this sod-forming grass produces extreme amounts of litter (i.e., dead residual vegetation), which can reduce nesting by some grassland birds (Wilson and

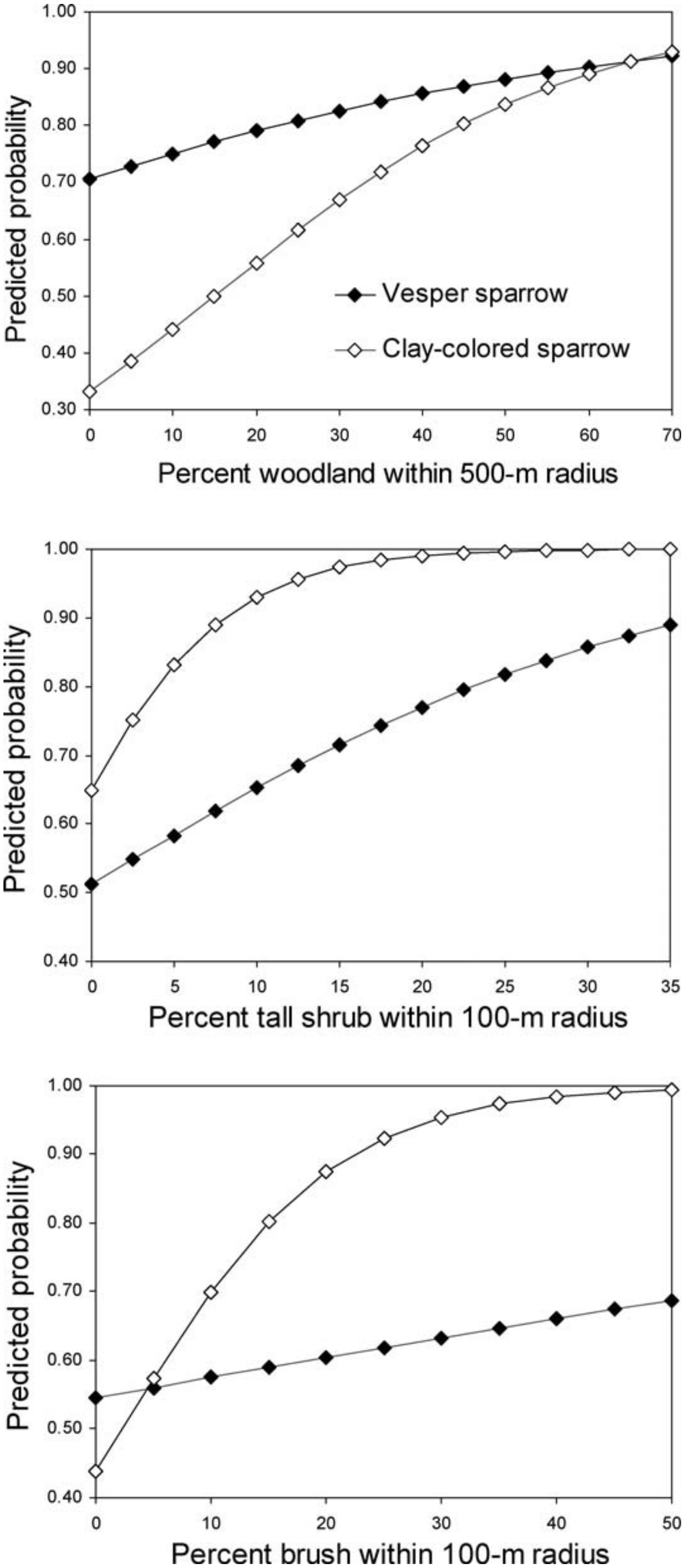

Figure 4. Probability of occurrence of vesper and clay-colored sparrows on 100-m radius point counts as a function of 1) percent aspen woodland cover within a 500-m radius, 2) percent tall shrub cover within 100-m radius, and 3) percent brush cover within 100-m radius on J. Clark Salyer National Wildlife Refuge, N.D., USA, 1995–1996. Incidence curves were adapted from Grant et al. (2004*a*: table 2).

Belcher 1989, Nenneman 2003). Short-stature, native bunch grasses dominated the grasslands we studied, and small amounts of Kentucky bluegrass may have enhanced nest survival by decreasing visibility of nests to potential predators (e.g., Roseberry and Klimstra 1970). Kentucky bluegrass produces more residual vegetation than do many native grasses, especially the year following defoliation by grazing or fire. Some grassland birds, including clay-colored sparrows, can be more abundant on sites with moderate bluegrass cover (Wilson and Belcher 1989, Schneider 1998, Grant et al. 2004*a*).

Management Implications

Despite our findings, we do not recommend management that enhances cover of trees and tall shrubs in northern grasslands. When management includes goals and objectives for prairie restoration or maintenance of grassland bird populations, tall woody plants should be reduced to levels within the range of natural variation defined by major ecological processes (e.g., drought, grazing, fire) characteristic of the region. Because our results differ from those reported in other studies, the need for additional, similar studies of the entire suite of avian species within the mixed-grass prairie and aspen parkland ecoregions, and in other grassland systems is warranted. Where research funds are limiting, we recommend that managers give priority to species exhibiting steep population declines. We also recommend that management designed to benefit populations of grassland songbirds be accompanied by rigorous monitoring programs that provide data to facilitate the kinds of analyses presented here. Monitoring programs should ideally include the identification of specific nest predators, as well as their distributions with respect to important habitat features. These data can be important in explaining, and perhaps predicting, patterns of nest predation. Studies conducted at both patch and landscape scales (Stephens et al. 2003) are needed to assess patterns of nest survival and predation in both fragmented and unfragmented grasslands.

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