ASSOCIATIONS OF WINTERING BIRDS WITH HABITAT IN SEMIDESERT AND PLAINS GRASSLANDS IN ARIZONA

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Abstract—We studied associations with winter habitat for seven species of birds, one species-group (eastern and western meadowlarks combined), and total sparrows at seven sites in the semidesert and plains grasslands of southeastern Arizona from 1999–2001, sampling with mist-nets and survey-transects. We measured structure and composition of vegetation, assessing vegetative differences among sites, and modeled associations between indices of avian abundance and six vegetative variables using generalized linear models. For all vegetative variables, there were significant differences among sites. Numbers of northern harriers (*Circus cyaneus*) were positively associated with total number of sparrows. Indices of abundance for individual species of birds were statistically correlated with various measures of structure and composition of vegetation. In particular, grasshopper (*Ammodramus savannarum*) and vesper (*Pooecetes gramineus*) sparrows were negatively associated with amount of bare ground; horned larks (*Eremophila alpestris*) were negatively associated with vertical grass density; Baird's sparrows (*A. bairdii*) were negatively associated with shrub density; meadowlarks (*Sturnella magna* and *S. neglecta* combined) were positively associated with native grass. Our results suggest that these species would benefit from management of habitat that affects the vegetative characteristics associated with their abundance.

Resumen—Estudiamos las asociaciones de hábitat invernal de siete especies de aves, un grupo de *Sturnella magna* y *Sturnella neglecta* juntos, y el número total de gorriones en siete sitios en los pastizales semiáridos y de planicies del sureste de Arizona de 1999 hasta 2001 mediante muestreos con redes de niebla y conteos en transectos. Medimos la estructura y composición de la vegetación, evaluando las diferencias entre sitios, y modelamos la asociación entre los índices de abundancia de aves y seis variables vegetales usando modelos lineales generalizados. Para todas las variables vegetales, hubo diferencias significativas entre sitios. Los números de *Circus cyaneus* estuvieron positivamente asociados con el número total de gorriones. Los índices de abundancia para especies individuales de aves estuvieron estadísticamente correlacionados con varias medidas de estructura y composición de vegetación. En particular, los gorriones *Ammodramus savannarum* y *Pooecetes gramineus* estuvieron negativamente asociados con la cantidad de suelo desnudo; *Eremophila alpestris* estuvieron negativamente asociados con la densidad vertical de pastos; *Ammodramus bairdii* estuvieron negativamente asociados con la densidad de arbustos; *Sturnella magna* y *S. neglecta* juntos estuvieron positivamente asociados con pastos nativos. Nuestros resultados sugieren que estas especies se beneficiarían del manejo de hábitat que afecta las características vegetales asociadas con su abundancia.

The grasslands of the southwestern United States and northwestern Mexico, including the semidesert and plains grasslands of southeastern Arizona, support a distinct assemblage of birds during the breeding season and short-distance migrants from northern prairies during the winter. Little was known about the breeding ecology of this semidesert grassland avifauna until the last few decades, and even less is known about their winter (nonbreeding) ecology. Many grassland species have shown significant declines in populations rangewide (Peterjohn and Sauer, 1999) and are species of conservation concern (Latta et al., 1999; United States Fish and Wildlife Service, 2008; Berlanga et al., 2010). It is possible that limitations of resources in winter, in addition to loss and degradation of winter habitat, may be among the causes of declines in populations, and winter survivorship may be a driving factor of trends in populations (Herkert and Knopf, 1998; Vickery et al., 1999). There is a growing body of literature on use of habitat by grassland birds during the nonbreeding season (Desmond et al., 2005;

Kelly et al., 2006; Agudelo et al., 2008; Macías-Duarte et al., 2009; Panjabi et al., 2010). Given these declines in populations, potential influence of the nonbreeding season on populations of grassland birds, and lack of information regarding requirements of wintering birds for habitat, additional research on winter ecology and requirements of grassland birds for habitat is needed to inform programs for conservation (J. M. Ruth, in litt.; Herkert and Knopf, 1998; Vickery et al., 1999; Vickery et al., 2000).

In general, semidesert and plains grasslands exhibit structural simplicity and limited structural heterogeneity (Merola-Zwartjes, 2005). What little vertical vegetative structure is available (shrubs, trees, and patchy bunch-grass) can be very important in influencing avian communities. Vegetative structure, density and presence-absence of shrubs or trees, percentage of grass cover, height of grass, presence or absence of native (or exotic) species of grass, and amount of bare ground are known to be correlated with abundance of wintering grassland birds (Bock et al., 1986; Bock and Bock, 1992; Kelly et al., 2006; Agudelo et al., 2008; Macías-Duarte et al., 2009).

We present results of a correlative study of associations of wintering grassland birds with habitat using seven sites throughout the semidesert and plains grasslands of southeastern Arizona and provide multisite, multiyear models of associations of birds with habitat. Nonbreeding birds may use a broader range of habitats or tolerate a broader range of characteristics than during the breeding season (Igl and Ballard, 1999). Our objective was to determine which variables of vegetative structure and composition were correlated with the indices of abundance of seven species of grassland birds, one species-group (i.e., meadowlarks), and total sparrows inhabiting these grasslands of southeastern Arizona in winter.

MATERIALS AND METHODS—Semidesert grasslands, interspersed with plains grasslands, extend from southeastern Arizona, southern New Mexico, and parts of western and trans-Pecos Texas south along the Mexican plateau to Mexico City (McClaran and Van Devender, 1995; Brown et al., 2007). We selected seven study sites nonrandomly that were representative of the types of upland grassland of southeastern Arizona (McClaran and Van Devender, 1995), in terms of vegetative characteristics and range of management activities (including ungrazed sites and sites employing a range of grazing regimes). The sites were in the Sonoita, San Rafael, and Altar valleys in Santa Cruz and Pima counties, which support the largest remaining, relatively undeveloped grassland landscapes in southeastern Arizona. These sites (Fig. 1) were: 1) Audubon Appleton-Whittell Research Ranch (Audubon), 3,200 ha administered by the National Audubon Society; 2) Babocomari Ranch (Babocomari), two pastures totaling 3,923 ha on a family-owned cattle ranch; 3) Buenos Aires National Wildlife Refuge (Buenos Aires), 46,000 ha administered by the United States Fish and Wildlife Service; 4) Davis Pasture (Davis), 1,560-ha pasture administered by the Bureau of Land Management as part of the Las Cienegas National Conservation Area; 5) Hilton Pasture

(Hilton), 2,920-ha pasture administered by the Bureau of Land Management as part of the Las Cienegas National Conservation Area; 6) Diamond C Ranch (Diamond C), seven pastures, each 36–93 ha, on a family-owned cattle ranch; and 7) San Rafael Valley (San Rafael), two pastures totaling 1,348 ha administered by the United States Department of Agriculture Forest Service, Coronado National Forest. Sites supported a variety of native annual and perennial bunchgrasses, exotic lovegrasses (*Eragrostis*), semi-shrubs, succulents, sparse shrubs, and low trees (McClaran and Van Devender, 1995).

We sampled study sites for birds three times during the winter field-season (January–March) each year in 1999, 2000, and 2001. Given similarities in plumage and life-history and behavioral differences among species of birds, we used mist-net plots and survey-transects to sample birds. Rappole et al. (1998) and Wang and Finch (2002) suggested that a combination of mist-netting and other surveying methods is useful in addressing some biases associated with each individual method. We used flushing transect-surveys to sample species that were relatively easy to identify when flushed: northern harriers (*Circus cyaneus*); horned larks (*Eremophila alpestris*); Sprague's pipits (*Anthus spragueii*); vesper sparrows (*Pooecetes gramineus*); eastern and western meadowlarks (*Sturnella magna* and *S. neglecta*) combined. We employed a flush mist-netting protocol (Gordon, 2000a) to sample savannah sparrows (*Passerculus sandwichensis*), grasshopper sparrows (*Ammodramus savannarum*), and Baird's sparrows (*A. bairdii*), species that are difficult to identify using transect or area-search methods (Desmond, 2004; Macías-Duarte et al., 2009; Panjabi et al., 2010). A similar flush mist-netting protocol developed by Chandler and Woodrey (1995) has been used to estimate relative abundance or relative density in wintering Henslow's sparrows (*Ammodramus henslowii*; Bechtoldt and Stouffer, 2005; Johnson et al., 2009; Palasz et al., 2010).

We randomly located six mist-net plots on each site except Hilton using the protocols developed by Gordon (2000a). On each plot, eight nets (30-mm mesh), each 2.6 × 12.0 m, were erected in a line ca. 100-m long. Mist-net plots on Audubon and Buenos Aires were those used by Gordon (2000a, 2000b) in 1996–1999. We sampled each study site three times during winter each year; all six plots on a site were sampled during a single day (0830–1700 h Mountain Standard Time). We varied the order in which plots were sampled, ensuring that each was sampled once in the morning, once mid-day, and once in the afternoon. After setting up mist-nets, 15–30 volunteers walked around the outside of the plot and lined up along the 300-m boundary at one end of the plot (C-D-E-F or G-H-I-J in Fig. 2); at a signal, they walked toward the nets, flushing birds in front of them and into the nets. We immediately removed birds from nets, placed them in cloth or nylon-mesh bags, and repeated the protocol on the opposite end of the plot. We identified birds captured to species, banded them with federal leg bands, and released them at the site of capture.

We located six avian survey-transects on each site (most 1,000 m in length; due to size of pasture, one 900-m transect on Buenos Aires and two 700-m, one 800-m, and two 900-m transects on Diamond C). We placed the first transect perpendicular to and at a random starting point along a low-traffic, unpaved road or dirt track within the site. Minimum distance between starting points of transects was 300 m, but 90% of transects were >500 m apart. We marked transects at 100-m intervals with flagged, painted rebar. Two teams of three
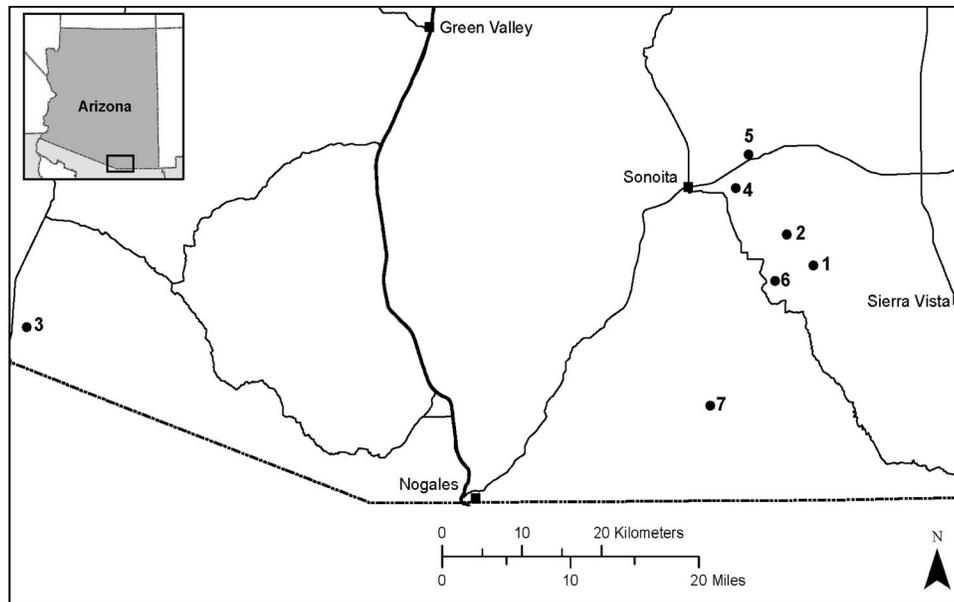
Fig. 1—Study sites in southeastern Arizona where associations of wintering birds with habitat were assessed: 1) Aububon Appleton-Whittell Research Ranch, 31°35′–37′N, 110°29′–32′W, elevation 1,450–1,540 m; 2) Babocomari Ranch, 31°37′–39′N, 110°31′–36′W, elevation 1,430–1,525 m; 3) United States Fish and Wildlife Service Buenos Aires National Wildlife Refuge, 31°31′–36′N, 111°28′–33′W, elevation 1,050–1,115 m; 4) Davis Pasture, Bureau of Land Management Las Cienegas National Conservation Area, 31°40′–42′N, 110°35′–37′W, elevation 1,410–1,495 m; 5) Hilton Pasture, Las Cienegas National Conservation Area, 31°41′–45′N, 110°34′–37′W, elevation 1,390–1,455 m; 6) Diamond C Ranch, 31°34′–37′N, 110°32′–35′W, elevation 1,475–1,575 m; 7) San Rafael Valley, Coronado National Forest, 31°26′–30′N, 110°37′–40′W, elevation 1,505–1,590 m.

individuals conducted surveys of birds along transects. One person was responsible for walking along the marked transect and recording all observations; the other two walked parallel to and on either side of the central person in a regular sweeping pattern from 5–20 m from the marked transect and back. Care was taken to avoid double-counting. We identified birds to species when possible; if not, we assigned birds to a category, such as *Ammodramus* or meadowlarks. We sampled each transect three times each winter, conducting surveys from 0800–1200 h Mountain Standard Time and varying the order so each transect was surveyed once in early morning, once in mid-morning, and once in late morning.

We characterized structure and composition of vegetation on each transect and mist-net plot once each winter (1999–2001). There was little growth of grass during the winter, and no site experienced heavy grazing in winter. So, little change occurred in structure over the winter months. We took most measurements of vegetation at 25-m intervals along transects, resulting in 28–40 observations/transect, depending on length of the transect. For mist-net plots, we walked a transect (path depicted in Fig. 2 by dashed lines from D to A to H, reversing course down the dotted line through the middle of the plot, and then from E to B to I) sampling at 25-m intervals until 40 samples were obtained.

We used pole-measurements to evaluate vertical density of grass and structure and composition of vegetation. These involved using a wooden dowel (6-mm diameter), marked every decimeter along its length for 1 m (Wiens, 1969). We took measurements from a point at ca. 650 mm to the right and perpendicular to the transect-line every 25 m by placing the pole vertically touching the ground. The observer recorded the number of contacts with vegetation in each decimeter (Wiens, 1969), identified the species of grass touching the pole, and estimated the number of total contacts by species (or genus if necessary). Few contacts occurred above 4–5 decimeters.

We estimated densities of shrubs and trees using point-centered quarter measurements (Bonham, 1989) at both ends and midpoint of transects and at both ends of mist-net plots (the midpoints between H-I and D-E, Fig. 2). At each point, we visually divided the surrounding area into four quadrants defined by the transect-line and an imaginary perpendicular line through the point. In each quadrant, we identified the nearest plant in each of several categories (succulent, semi-shrub <1 m in height; shrub from 1–2 m in height; shrub or tree >2 m in height). We recorded the distance from the central point using distance categories (0–5 m; >5–15 m; >15–30 m; >30–50 m; >50–100 m; >100–200 m; >200 m).

Of the avian species present on sites, sample sizes were adequate for analysis of seven species, meadowlarks (*Sturnella*), and total sparrows. For species recorded from mist-nets (savannah, grasshopper, and Baird's sparrows), we indexed avian abundance using total number of distinct individuals of a species captured during a season on each mist-net plot (i.e., recaptures were excluded), summed across all mist-net plots for the total number of individuals per site per year. For species recorded from transects (northern harrier, horned lark, Sprague's pipit, vesper sparrow, and meadowlarks), we used maximum number of individuals of that species recorded during a season on each transect, summed across all transects for an index of relative abundance (=total number of individuals) per site per year (Johnson, 2008). Under an assumption of closure, the maximum number is closer to the
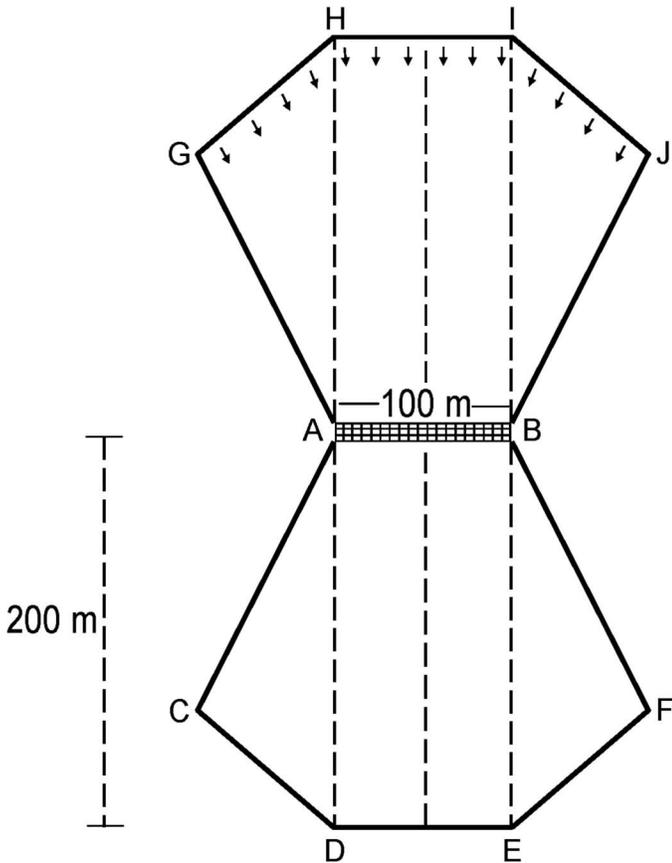
FIG. 2—Diagram of mist-net plot. Each 7-ha hourglass-shaped plot was composed of ca. 100 m of mist-nets (eight nets, 2.6 × 12 m, 30-mm mesh) strung across narrowest part of plot (A to B); flushing zones on both sides of the mist-nets were defined in the field by a series of flagged, painted rebar placed 200 m in perpendicular distance from mist-nets with angled wings on either end (C-D-E-F and G-H-I-J).

true but unknown abundance than means or medians. We also calculated total number of sparrows recorded on a transect (summing all observations of sparrows to obtain the maximum recorded during a season on each transect). We pooled counts of eastern and western meadowlarks because they are difficult to distinguish when not singing or calling and when in the hand (Pyle, 1997); both occur in southeastern Arizona in winter. We assigned species to three general categories based on the literature and our experience in the field: open-grassland specialist, requiring extensive grassland landscapes with few or no shrubs, or grassland generalist, showing tolerance for a broader range of grassland types that may or may not include shrubs; solitary-foraging, largely-flocking, or intermediate-flocking species; (in one case) species of raptor.

Based on information in the literature concerning vegetative characteristics that might be of relevance relative to the avian species evaluated, we calculated seven variables from vegetative measurements previously described. We then computed Pearson correlation coefficients for all pairs of these variables. In cases of absolute correlations ≥0.70, we retained the variable thought to be most biologically relevant and discarded the other. Based on these criteria, one variable (i.e., variation in vertical density of grass) was eliminated from further consideration, and the

following six were retained for use in models: 1) shrub density–density of large shrubs (>1 m in height) in shrubs per hectare calculated by summing the calculations of point-centered quarter density for medium (1–2 m) and tall (>2 m) shrubs; 2) vertical grass density–measured as contacts with grass in 1-dm intervals of height along a vertical pole (Wiens, 1969) and calculated by summing total number of contacts on pole in first (lowest), second, third, and fourth decimeters at a sampling point and averaging across points on plot; 3) bare ground–amount of bare ground, based on percentage of points on plot that had no contact with vegetation anywhere on vertical pole; 4) protected foraging space–divided number of contacts on vertical pole in first (lowest) decimeter interval by sum of contacts in first and second decimeter intervals, averaging across points on plot with low values indicating greater openness at ground level (fewer contacts with vegetation) and more vegetation above (i.e., more protected foraging space); 5) standing dead litter–amount of standing dead litter present and calculated by summing total number of contacts with standing dead-litter on vertical pole in all decimeter intervals at a point and averaging across points on plot; 6) native grass–proportion of identified species of grass that are native and calculated by summing total number of contacts with native grass on vertical pole in all decimeter intervals at a point, dividing by sum of total number of all contacts with grass, and averaging across points on plot (by definition, site with higher proportion of native grasses had lower proportion of exotic grasses).

We modeled relationships between indices of avian abundance and vegetative variables using generalized linear models (McCullagh and Nelder, 1989) as implemented in SAS/STAT version 9.2 (SAS Institute Inc., 2008). Because the dependent variable was birds counted and we expected there would be contagion of birds (e.g., flocking and group-foraging) for many species, we assumed a negative binomial distribution (White and Bennetts, 1996) for our generalized linear models and used the log-link function. We applied an information-theoretic approach to selection of models and estimation of parameters (Burnham and Anderson, 2002).

Using total number of individuals per site per year for each avian species or group as the dependent variable, we constructed a global model containing the six vegetative variables and then a standard set of candidate-models with various combinations of the six variables to represent conditions we judged might be associated with avian abundance (Appendix). We used Akaike's Information Criterion with correction for small sample size and overdispersion ($QAIC_c$) to rank candidate-models by how well they were supported by the data (Burnham and Anderson, 2002). We computed model-weights w_i, where w_i is weight of evidence in favor of model i being the best model in the candidate-set. The best model had the smallest value of $QAIC_c$; we considered additional models with $\Delta QAIC_c \leq 2$ to be well supported top models (Burnham and Anderson, 2002). We estimated model-parameters (i.e., the beta coefficients) for the variables using SAS Proc Genmod (SAS Institute Inc., 2008). The beta coefficient is a value representing the magnitude and direction of the effect of a covariate (e.g., a vegetative variable) on the dependent variable (e.g., abundance of an avian species). So, for example, a negative beta-coefficient for shrub density means that numbers of birds are inversely proportional to shrub density. In contrast, a positive beta-coefficient for shrub density

TABLE 1—Comparisons of vegetative measurements (means with 1 *SD* in parentheses) for sites in southeastern Arizona using analysis of variance ($F_{6,227}$; all $P < 0.001$). For each site, data ($n = 36$) pooled across mist-net and transect plots (except Hilton for which there were no mist-net plots and $n = 18$), and across years. Means with same letter within a variable were not statistically different ($P > 0.05$; Tukey's comparisons).

			Variable			
Site, statistic	Shrub density	Vertical grass density	Native grass	Protected foraging space	Standing dead litter	Bare ground
Audubon	2.05 (3.42)b	4.52 (1.28)bc	0.72 (0.24)c	0.67 (0.08)b	39.06 (23.69)ab	0.14 (0.09)c
Babocomari	2.97 (6.50)b	3.43 (0.90)d	0.77 (0.21)c	0.78 (0.06)a	15.31 (10.78)c	0.26 (0.08)ab
Buenos Aires	24.53 (30.57)a	4.92 (1.40)b	0.43 (0.24)d	0.63 (0.07)b	26.53 (21.80)bc	0.13 (0.07)c
Davis	0.37 (0.10)b	3.72 (1.46)cd	0.95 (0.11)ab	0.75 (0.07)a	20.78 (15.23)c	0.24 (0.12)ab
Hilton	0.82 (0.57)b	2.85 (1.22)d	0.98 (0.04)a	0.78 (0.12)a	18.06 (17.84)c	0.31 (0.16)a
Diamond C	0.95 (0.67)b	3.05 (1.00)d	0.99 (0.04)a	0.78 (0.11)a	21.36 (19.10)c	0.19 (0.12)bc
San Rafael	0.46 (0.61)b	7.61 (2.10)a	0.84 (0.17)bc	0.66 (0.07)b	50.33 (33.94)a	0.06 (0.05)d
F-value	18.1	46.2	41.8	23.2	11.8	23.9

means that numbers of birds are directly proportional to shrub density. We considered a variable to have a statistically significant association with avian abundance when 95% confidence limits for the parameter-estimate did not include zero; otherwise, we concluded there was no statistical evidence for an association between the variable and avian abundance.

To minimize the number of variables in the set of candidate-models, we initially determined whether the standard set of models needed to include year, site, or both for individual species by constructing three simple models for each species with variables year, site, or both and ranking these models based on $QAIC_c$. If 95% confidence limits on parameter-estimates for the variable(s) in the best of the three models did not cover zero, then we considered the variable(s) in that model to be associated with avian abundance and included them in all of the standardized bird-vegetation candidate-models for that species.

When data from transects were used for species, we included length of transect as a covariate to account for effort. Finally, for northern harriers, we included an additional candidate-model with total number of sparrows as a covariate. We assessed vegetative differences among sites using a one-way analysis of variance and Tukey's multiple-comparison procedure (Ott, 1988).

RESULTS—At the site-scale, comparisons of the vegetative variables among sites indicated that there were significant differences among sites in all six variables (Table 1). Buenos Aires had significantly higher densities of shrubs and significantly lower proportions of native grass than did all other sites. San Rafael had higher vertical grass density, more standing dead litter, and less bare ground than did all the other sites. Diamond C, Davis, and Hilton had the highest proportions of native grass. Audubon, Buenos Aires, and San Rafael had more protected foraging space than did other sites.

Tables 2 and 3 provide a summary of avian abundance for species sampled using mist-net plots and for species sampled using survey-transects, respectively. They demonstrate the variation among sites and years that is addressed for appropriate avian species or groups in the models.

Tables 4 and 5 present top models for seven species, meadowlarks combined, and total sparrows. For each species or group, Table 4 provides the best model along with all top models ($\Delta QAIC_c \leq 2$). For each species or group, Table 5 includes parameter-estimates and their 95% confidence limits for all variables in the top models. For some variables in top models, the confidence limits of the estimate (Table 5) included zero, meaning there was not statistical evidence of association with avian abundance. We describe results only for those variables in these top models where confidence limits of parameter-estimates did not include zero.

For northern harriers (raptor), abundance was best (lowest $QAIC_c$) explained by the model that included only total number of sparrows (a positive association). For all the models that included vegetative variables, $\Delta QAIC_c > 4$.

For horned larks (open-grassland specialist; largely-flocking species), four models had $\Delta QAIC_c$ values ≤ 2. Abundance was best explained by the model including vertical grass density (negative association), site, and year. Among the top four models, variables consistently associated with numbers of horned larks were vertical grass density, site, and year.

Five models for Sprague's pipits (open-grassland specialist; solitary-foraging species) had $\Delta QAIC_c$ values ≤ 2. Abundance was best explained by the model including native grass (negative association), year, and site. Year and site were consistently associated with numbers of Sprague's pipits in the top five models, and native grass was included in four of the five top models.

For vesper sparrows (grassland generalist; intermediate-flocking species), five models had $\Delta QAIC_c$ values ≤ 2. Abundance was best explained by the model including bare ground (negative association) and site. Among the top five models, the only variable consistently associated with numbers of vesper sparrows was site; bare ground was included in four of the five top models. Although not included in the best model, protected foraging space

TABLE 2—Number of distinct individual birds captured on six mist-net plots at each of six sites in southeastern Arizona sampled three times each winter, 1999–2001.

Year	Site						Total
	Audubon	Babocomari	Buenos Aires	Davis	Diamond C	San Rafael	
Savannah sparrow							
1999	2	2	12	0	0	6	22
2000	20	17	11	0	19	4	71
2001	0	34	48	60	33	1	176
Grasshopper sparrow							
1999	52	27	79	19	25	87	289
2000	74	7	43	8	58	36	226
2001	3	0	12	17	10	1	43
Baird's sparrow							
1999	14	8	6	7	0	26	61
2000	5	6	1	13	3	14	42
2001	10	4	10	14	3	8	49

(negative association) was included in two of the five top models, suggesting that abundance may have been greater in areas with more openness at ground level and overlying protective vegetation.

Four models for savannah sparrows (grassland generalist; intermediate-flocking species) had $\Delta QAIC_c$ values $\leq$ 2. Abundance was best explained by the model including native grass (negative association) and year, and these were the variables consistently associated with numbers of savannah sparrows in the top four models.

TABLE 3— Number of birds recorded at seven sites in southeastern Arizona, calculated as the sum of the maximum number of individuals recorded on six transect plots at each site sampled three times each winter, 1999–2001.

Year	Site							Total
	Audubon	Babocomari	Buenos Aires	Davis	Hilton	Diamond C	San Rafael	
Northern harrier								
1999	4	4	3	0	4	2	7	24
2000	5	6	6	3	3	5	8	36
2001	4	4	5	7	4	4	8	36
Horned lark								
1999	33	149	83	140	94	127	162	788
2000	20	74	37	417	55	32	25	660
2001	64	358	55	529	436	77	23	1,542
Sprague's pipit								
1999	1	4	0	1	0	3	1	10
2000	0	3	0	0	0	1	0	4
2001	0	3	1	7	2	1	2	16
Vesper sparrow								
1999	10	2	95	1	44	34	13	199
2000	127	20	75	1	66	24	6	319
2001	27	23	76	16	6	24	3	175
All sparrows								
1999	43	41	229	9	80	58	204	664
2000	363	78	244	26	107	165	241	1,224
2001	53	66	244	101	23	97	98	682
Meadowlarks								
1999	7	10	12	8	16	51	53	157
2000	33	14	13	9	14	14	26	123
2001	21	28	19	21	10	20	82	201

Table 4—Best model (lowest QAIC$_c$) and top models (ΔQAIC$_c \leq 2$) for seven species of birds, one species-group, and total sparrows in southeastern Arizona, showing variables in each model, log-likelihood value [log(L)], number of parameters (K), minimum QAIC$_c$, ΔQAIC$_c$, and Akaike weight (w_i). Length of transect was included as a covariate in all models for species or groups that used data from transects, which included all except savannah, grasshopper, and Baird's sparrows.

Model	log(L)	K	Minimum QAIC$_c$	ΔQAIC$_c$	w_i
Northern harrier ($n = 126$)					
All sparrows	−110.57	4	295.52	–	0.66
Horned lark ($n = 126$)					
Vertical grass density, site, year	9,333.49	12	−19,622.68	–	0.28
Vertical grass density, shrub density, site, year	9,334.58	13		0.19	0.26
Vertical grass density, shrub density, protected foraging space, site, year	9,335.08	14		1.67	0.12
Vertical grass density, protected foraging space, site, year	9,333.86	13		1.70	0.12
Sprague's pipit ($n = 126$)					
Native grass, site, year	−57.73	12	116.65	–	0.18
Native grass, standing dead litter, site, year	−56.20	13		0.41	0.15
Standing dead litter, site, year	−58.02	12		0.76	0.13
Native grass, vertical grass density, site, year	−56.73	13		1.23	0.10
Native grass, bare ground, site, year	−56.83	13		1.39	0.09
Vesper sparrow ($n = 126$)					
Bare ground, site	1,007.03	10	−1,589.33	–	0.17
Protected foraging space, site	1,006.67	10		0.58	0.13
Bare ground, native grass, site	1,007.80	11		1.17	0.10
Bare ground, protected foraging space, site	1,007.72	11		1.30	0.09
Bare ground, shrub density, site	1,007.63	11		1.44	0.08
Savannah sparrow ($n = 108$)					
Native grass, year	230.82	5	−496.70	–	0.29
Native grass, vertical grass density, year	231.26	6		1.26	0.15
Native grass, bare ground, year	231.04	6		1.76	0.12
Native grass, standing dead litter, year	230.95	6		1.94	0.11
Grasshopper sparrow ($n = 108$)					
Bare ground, protected foraging space, year, site	650.16	11	−1,125.97	–	0.26
Bare ground, year, site	648.37	10		0.67	0.18
Bare ground, shrub density, year, site	649.53	11		1.11	0.15
Bare ground, standing dead litter, year, site	649.10	11		1.87	0.10
Baird's sparrow ($n = 108$)					
Shrub density, vertical grass density, site	−59.72	9	130.43	–	0.35
Shrub density, standing dead litter, bare ground, site	−58.55	10		0.26	0.30
Shrub density, site	−61.98	8		1.81	0.14
All sparrow species ($n = 126$)					
Protected foraging space, bare ground, site, year	6,179.25	13	−9,333.25	–	0.48
Protected foraging space, site, year	6,176.75	12		1.30	0.25
Meadowlark species ($n = 126$)					
Native grass, standing dead litter, site	315.51	11	−570.98	–	0.29
Native grass, standing dead litter, vertical grass density, site	316.42	12		0.73	0.20
Native grass, vertical grass density, site	314.78	11		1.38	0.15

The models for grasshopper sparrows (open-grassland specialist; solitary-foraging species) included four with ΔQAIC$_c$ values ≤ 2. Abundance was best explained by the model including bare ground (negative association), protected foraging space (negative association), year, and site; however, evaluation of parameter estimates provided no evidence of statistically important association between protected foraging space and numbers of grasshopper sparrow. Among the top four models, variables consistently associated with numbers of grasshopper sparrows were bare ground, year, and site.

For Baird's sparrows (open-grassland specialist; solitary-foraging species), three models had ΔQAIC$_c$ values $\leq$ 2. Abundance was best explained by the model including

TABLE 5—Parameter-estimates (i.e., beta coefficients) and their 95% confidence limits for variables included in top models by species. Parameter-estimate is from the highest-scoring model in which that variable appears; in all cases, relationship (positive or negative) between avian abundance and vegetative variable was the same in all top models in which that variable was included.

Model variable	Parameter-estimate $\pm$ SE (95% confidence limits)
Northern harrier	
All sparrows[a]	0.009 $\pm$ 0.003 (0.003, 0.016)
Horned lark[b]	
Vertical grass density[a]	−0.452 $\pm$ 0.097 (−0.642, −0.261)
Shrub density	−0.016 $\pm$ 0.010 (−0.036, 0.004)
Protected foraging space[c]	−1.650 $\pm$ 1.633 (−4.851, 1.552)
Sprague's pipit[b,d]	
Native grass[a]	−2.665 $\pm$ 1.161 (−4.940, −0.390)
Standing dead litter	−0.021 $\pm$ 0.014 (−0.047, 0.006)
Vertical grass density	−0.205 $\pm$ 0.164 (−0.527, 0.116)
Bare ground	1.881 $\pm$ 1.539 (−1.135, 4.898)
Vesper sparrow[b]	
Bare ground[a]	−2.957 $\pm$ 1.319 (−5.542, −0.372)
Protected foraging space[a,c]	−4.375 $\pm$ 2.186 (−8.659, −0.091)
Native grass	1.119 $\pm$ 0.904 (−0.652, 2.890)
Shrub density	0.011 $\pm$ 0.011 (−0.011, 0.034)
Savannah sparrow[d]	
Native grass[a]	−1.434 $\pm$ 0.673 (−2.752, −0.115)
Vertical grass density	−0.116 $\pm$ 0.119 (−0.350, 0.117)
Bare ground	−1.499 $\pm$ 2.261 (−5.930, 2.933)
Standing dead litter	0.005 $\pm$ 0.010 (−0.014, 0.025)
Grasshopper sparrow[d]	
Bare ground[a]	−4.760 $\pm$ 1.645 (−7.984, −1.536)
Protected foraging space[c]	−2.925 $\pm$ 1.544 (−5.951, 0.102)
Shrub density	−0.032 $\pm$ 0.023 (−0.078, 0.013)
Standing dead litter	0.006 $\pm$ 0.005 (−0.004, 0.017)
Baird's sparrow[b]	
Shrub density[a]	−0.166 $\pm$ 0.054 (−0.273, −0.060)
Vertical grass density[a]	−0.141 $\pm$ 0.066 (−0.270, −0.011)
Standing dead litter[a]	−0.012 $\pm$ 0.005 (−0.023, −0.002)
Bare ground	0.272 $\pm$ 1.259 (−2.196, 2.740)
All sparrows[b]	
Protected foraging space[a,c]	−4.064 $\pm$ 1.273 (−6.559, −1.569)
Bare ground[a]	−1.831 $\pm$ 0.804 (−3.407, −0.256)
Meadowlark species[b]	
Native grass[a]	1.164 $\pm$ 0.475 (0.233, 2.095)
Standing dead litter[a]	−0.010 $\pm$ 0.004 (−0.017, −0.003)
Vertical grass density	−0.086 $\pm$ 0.064 (−0.211, 0.039)

[a] Variable considered to have a significant association with abundance of the species or group when 95% confidence limits of parameter-estimate did not cover zero.

[b] Estimates based on separate parameter-estimates for each site; site was significant in explaining abundance for this species.

[c] Negative parameter-estimates indicate positive association between indices of bird abundance and amount of protected foraging space (i.e., abundance greater in areas with more openness at ground level and overhanging protective vegetation).

[d] Estimates based on separate parameter-estimates for each year; year also important in explaining abundance.

shrub density (negative association), vertical grass density (negative association), and site. Among the top three models, variables consistently associated with numbers of Baird's sparrows were shrub density and site; vertical grass density and standing dead litter (negative association) were each included in one of the three top models.

Two models for total number of sparrows had $\Delta QAIC_c$ values ≤ 2. Abundance of sparrows was best explained by the model including protected foraging space (negative association), bare ground (negative association), year, and site. Among the two top models, variables consistently associated with total numbers of sparrows were site and protected foraging space, meaning abundance was greater in areas with more openness at the ground level and overhanging protective vegetation. Bare ground was included in one of the two top models.

For meadowlarks (open-grassland specialist; intermediate-flocking species), three models had $\Delta QAIC_c$ values ≤ 2. Abundance was best explained by the model including native grass (positive association), standing dead litter (negative association), and site. Among the three top models, variables consistently associated with numbers of meadowlarks were native grass and site; standing dead litter was included in two of the three top models.

DISCUSSION—Variation among our sites is indicative of the range of vegetative structure and composition in the semidesert and plains grasslands of southeastern Arizona. Variation is influenced by multiple interacting factors including the patchy distribution and amount of precipitation, abiotic factors (e.g., soil, slope, and aspect), long-term history of management (e.g., planting of exotic grasses and past grazing regimes), fire, and current grazing regimes or cattle-exclusions. For example, although we do not have similar documentation from all sites, exotic lovegrasses were planted on Audubon in the 1940s and 1950s (Bock et al., 1986) and on Buenos Aires in the 1970s (Geiger and McPherson, 2005); not surprisingly, these were two of the sites with the lowest proportions of native grass.

Precipitation is an important factor affecting vegetation and, therefore, wintering birds in desert grasslands (Macías-Duarte et al., 2009). Precipitation in our study region is local and patchily distributed (L. Kennedy, pers. comm.). Grazing also affects vegetation and birds. Four of the five grazed sites (Babocomari, Davis, Hilton, and Diamond C) showed the expected pattern of lower vertical grass density, more bare ground, and less standing dead litter than the two ungrazed sites (Audubon and Buenos Aires; Saab et al., 1995; Bock and Bock, 1999; Merola-Zwartjes, 2004). However, the pattern was reversed on San Rafael (a grazed site), which had greater vertical grass density and less bare ground than the currently ungrazed sites (Audubon and Buenos Aires) and more standing dead litter than did Buenos Aires. Finally, the

scope of inference for avian associations with habitat in this study is limited to the range of values of the vegetative variables at our sites. This can be important for grassland species that may respond differently to a variable at opposite ends of the spectrum (Ruth, 2000).

The results of this study add to a limited body of knowledge about wintering ecology of grassland birds. The relevance of the six vegetative variables we selected was supported by the results. All six variables were incorporated in top models for multiple species; three were included in the best model for at least one species or group of species, and three were included in the best model for two or more species or groups of species.

Five species were open-grassland specialists, and two were grassland generalists. Since the end of the nineteenth century, desert grasslands in southern Arizona have experienced notable increases in the distribution and density of scrubby trees and shrubs, including mesquite (*Prosopis*), juniper (*Juniperus*), burroweed (*Isocoma tenuisecta*), and snakeweed (*Gutierrezia*; Bahre, 1995). Lehmann lovegrass (*Eragrostis lehmanniana*), the dominant exotic grass on our sites, was imported from southern Africa in 1932 to reseed degraded rangelands and control erosion throughout southeastern Arizona (Bahre, 1995). Previous studies suggest that open-grassland specialists would find higher shrub densities and exotic grasslands less habitable and that grassland generalists would show either positive associations with shrub density or tolerance for a shrub component (i.e., no association; Pulliam and Mills, 1977; Bock et al., 1986; Lima and Valone, 1991).

Of the five open-grassland specialists in our study, only meadowlarks showed a negative association with exotic grasses (positive association with native grass). Although other studies (primarily from the breeding season) indicate a mixed response of meadowlarks to exotic grasses, our results are consistent with findings that eastern meadowlarks in southeastern Arizona in winter were more abundant on sites with native rather than exotic grasses (Bock et al., 1986). Based on personal observations involving calls and behavior, eastern meadowlarks comprised most of the meadowlarks tabulated in this study. The surprising positive association of Sprague's pipit with exotic grasses in our results is contrary to what has been documented for the breeding season (Robbins and Dale, 1999; Merola-Zwartjes, 2005; S. L. Jones, in litt.). Although we discerned some statistical evidence for associations between abundances of open-grassland specialists and proportion of native and exotic grasses, other studies (primarily in the breeding season) show no consistent preference for native or exotic grasses in the other open-grassland specialists we analyzed (horned larks, Baird's sparrows, and grasshopper sparrows). However, Bock et al. (1986) found wintering grasshopper sparrows more abundant in native-grass sites in Arizona. The limited association of open-grassland specialists with

native and exotic grass could be explained if vegetative structure is more important than species-composition of grasses in habitat selected by grassland birds (Davis and Duncan, 1999). This is certainly the case in our results, where vertical grass density, bare ground, standing dead litter, and shrub density were included in the best models for open-grassland birds.

Of the five open-grassland specialists in our study, only Baird's sparrow showed a negative association with shrub density; this is consistent with what has been reported for this species during the breeding season (Green et al., 2002; Dechant et al., 2002) and the nonbreeding season (Desmond et al., 2005; Panjabi et al., 2010). There was no evidence of associations with shrub density for the other four open-grassland specialists. This was surprising for Sprague's pipit because other studies reporting on wintering Sprague's pipits (Desmond et al., 2005; Macías-Duarte et al., 2009; Panjabi et al., 2010) have shown negative responses to shrub cover. Although we found some statistical evidence for associations between abundances of open-grassland specialists and shrub density, other studies reported mixed results for many open-grassland specialists with respect to associations with shrub density during the nonbreeding season (Lima and Valone, 1991; Desmond et al., 2005; Agudelo et al., 2008; Macías-Duarte et al., 2009; Panjabi et al., 2010). Our study did not show evidence of associations with shrub density for either of the two grassland generalists (vesper and savannah sparrows), which may indicate a tolerance for shrubs in their winter habitat. Although Pulliam and Mills (1977) documented positive associations of wintering vesper and savannah sparrows with shrub or tree cover, our results are not particularly surprising given the mixed findings reported for these species regarding associations between avian abundance and shrub density during the nonbreeding season (Lima and Valone, 1991; Bock and Bock, 1992; Desmond et al., 2005; Macías-Duarte et al., 2009; Panjabi et al., 2010).

There are several possible reasons for the lack of strong associations between avian indices and various vegetative variables in our study. Of course, lack of evidence for positive or negative associations does not mean that no association exists; rather, our data do not provide such evidence. In addition, with regard to shrub density, our study was designed primarily to document the associations of wintering grassland birds with various characteristics of vegetation in remaining open-grassland habitats, so shrub densities on all but Buenos Aires were extremely low. Avian associations with shrub densities at different spatial scales or higher densities of shrubs than those present on our sites may have yielded different results (Desmond et al., 2005). However, one likely reason for the lack of correlation between avian indices and shrub density is the ability of grassland birds to use a broader range of habitats in winter than during the breeding season. Igl and Ballard (1999) found that, although

grassland species were most abundant during the nonbreeding season in structurally simple habitats that resembled their breeding habitats (grassland and shrub-grassland), they were observed in a broader range of habitats during the nonbreeding season than previously described. In fact, several studies have found wintering grassland birds in habitats with more woody vegetation than preferred during the breeding season (Emlen, 1972; Hutto, 1992; Igl and Ballard, 1999).

Three species were solitary foragers, one was a largely-flocking species, and three were intermediate-flocking species. Previous studies have suggested that more bare ground and lower densities of grass attract flocking species because they permit the detection of approaching predators, one of the benefits of a flocking strategy (Pulliam and Mills, 1977; Grzybowski, 1983*a*, 1983*b*; Lima and Valone, 1991). In comparison, solitary foragers rely on a strategy of hiding to avoid predators and, therefore, would respond negatively to more bare ground and positively to grass (Pulliam and Mills, 1977). Consistent with these studies, our one largely-flocking species (horned lark) showed a negative association with vertical grass density, a finding similar to those of other studies that found negative associations of occurrence or abundance of horned larks with grass cover in the nonbreeding season (Bock and Bock, 1992; Desmond et al., 2005; Macías-Duarte et al., 2009, Panjabi et al., 2010), but in contrast to results of Agudelo et al. (2008). In addition, one of the three solitary-foraging species (grasshopper sparrow) showed a negative association with bare ground; similarly, other studies in the nonbreeding season have demonstrated a positive relationship of occurrence or abundance of grasshopper sparrows to grass cover or height of grass (Desmond et al., 2005; Macías-Duarte et al., 2009; Panjabi et al., 2010). However, Baird's sparrow, also a solitary forager, showed the opposite (negative) association with vertical grass density than that suggested and indicated by literature on responses to grass cover and height of grass in the nonbreeding season (Desmond et al., 2005; Macías-Duarte et al., 2009; Panjabi et al., 2010). We had considered vesper sparrow as a species somewhat inter-mediate between solitary foragers and largely-flocking species (Panjabi et al., 2010). However, the negative associations of abundance of vesper sparrows with bare ground and positive association with protected foraging spaces are more consistent with the literature regarding solitary-foraging species. In fact, Pulliam and Mills (1977) observed that, although vesper sparrows sometimes occur in small flocks with other sparrows while wintering in Arizona, they generally occur as single individuals.

There are additional factors that influence foraging strategies and avian abundance. All species in our study with the exception of the northern harrier forage on the ground. Ground foragers require sufficient space to forage at ground level, and it is reasonable to think that areas supporting vegetative structure that deters such movements would be avoided. Consistent with this concept, abundance of Baird's sparrows and meadowlarks showed a negative association with standing dead litter; abundances of horned larks and Baird's sparrows also were negatively associated with vertical grass density. This suggests that, for some species in winter, higher vertical grass density and more standing dead litter may present obstacles to foraging.

The northern harrier preys substantially on grassland birds (Preston, 1990; MacWhirter and Bildstein, 1996). Preston (1990) found that birds comprised as much as 42% of the diets of northern harriers and that abundance of the species was significantly associated with biomass of prey but not vegetative cover. Consistent with the life history of the northern harrier, we found that its abundance was positively associated with total number of sparrows, and there was no evidence of associations with vegetative variables.

Our study did not address all factors that may be associated with abundance of wintering grassland birds. One promising explanatory variable is seed-resources (Ginter and Desmond, 2005; Desmond et al., 2008). In addition, long-term, broad-scale studies are required to address the substantial spatial and temporal variation in abundance and distribution of grassland birds (Knopf, 1996). Demographic studies looking at survival would address the limitations of using avian abundance as an indicator of good habitat (Van Horne, 1983; Bock and Jones, 2004).

Information about habitat required by species of conservation concern is needed to better manage grasslands in the Southwest. Sprague's pipit, grasshopper sparrow, and Baird's sparrow are of international or regional concern for conservation (United States Fish and Wildlife Service, 2008; Berlanga et al., 2010) on their breeding and wintering grounds, and horned larks and eastern meadowlarks are of concern because, although still common, their populations have shown steep declines (Berlanga et al., 2010). Grassland management affecting the complex, interrelated factors that influence vegetative structure and composition in southeastern Arizona can include decisions regarding grazing (inten-sity, season, and frequency), prescribed fire, and restora-tion and manipulation of habitat. Our results suggest that some of the avian species we studied will benefit from management that controls encroachment of shrubs (Baird's sparrow), minimizes the amount of bare ground (grasshopper and vesper sparrows), controls the amount of standing dead litter (Baird's sparrow and meadow-larks), avoids high vertical density of grass (Baird's sparrow and horned lark), and promotes native grasses or controls exotic grasses (meadowlarks). It is beyond the scope of our study to make specific recommendations for management; however, some observations can be made based on other literature. Fire is a strong ecological force

in semidesert grasslands and can maintain relatively shrub-free grasslands, reduce litter and other fine fuels, and reduce grass cover (McPherson, 1995; Bock and Block, 2005). In semidesert grasslands, land is primarily used as rangeland; grazing by domestic cattle is widely recognized as having impacts on vegetative structure and composition. Under some conditions, grazing is known to reduce litter, reduce cover and height of grass, affect amount of bare ground, influence proportions of native and exotic grasses, and influence densities of shrubs (McClaran and Van Devender, 1995; Merola-Zwartjes, 2005). Whether grazing or fire will benefit or negatively impact the number of wintering birds will depend on the particular combination of management-practices and other factors such as climate (Saab et al., 1995). It also is possible to manually remove shrubs and exotic grasses and restore or plant native grasses; however, these efforts are usually limited to small areas and, typically, are not practicable at broader scales. We encourage researchers and managers to work together to design studies and adaptive management-plans to evaluate these suggestions and to address additional questions about the habitat that is important for wintering grassland birds.

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APPENDIX—Global model and standard set of candidate-models used to evaluate the association of avian abundance with explanatory variables. Preliminary models were evaluated to determine whether to include year, site, or both in models for each species.

Global model: shrub density, vertical grass density, bare ground, protected foraging space, standing dead litter, native grass

Standard candidate-models:

- shrub density
- vertical grass density
- bare ground
- protected foraging space
- standing dead litter
- native grass
- vertical grass density, native grass
- vertical grass density, shrub density
- vertical grass density, standing dead litter
- vertical grass density, protected foraging space
- shrub density, bare ground
- bare ground, protected foraging space
- bare ground, native grass
- bare ground, standing dead litter
- native grass, standing dead litter
- bare ground, shrub density, standing dead litter
- vertical grass density, standing dead litter, native grass
- vertical grass density, shrub density, protected foraging space

Additional candidate-model (for northern harrier only): total sparrow numbers