Variogram models reveal habitat gradients predicting patterns of territory occupancy and nest survival among vesper sparrows

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Characterizing landscapes as gradients may help illuminate animal–habitat relationships that are either 1) masked by or 2) impractical to investigate using a purely patch-based perspective. Among other methods, variogram models may reveal these gradients in the environment by quantifying spatial dependence among point samples, yet few analyses of animal-habitat relationships employing variograms have been undertaken. Using vegetation volume measurements from 4-m² plots within breeding vesper sparrow *Pooecetes gramineus* territories, we calculated four territory-scale gradients: 1) mean volume, 2) standard deviation of volume, 3) nugget (a measure of fine-scale variation), and 4) range (an index of patch size). The first two gradients are more commonly employed in animal ecology while the second two were derived using variogram models and are infrequently employed. We next used these gradients in generalized linear models predicting territory occupancy and daily nest survival. We found overwhelming support for employing the range parameter and models indicated 1) birds selected areas with lower average vegetation volume and smaller patch sizes and 2) had lower rates of nest predation in areas with larger patch sizes. While these results indicate a pattern of non-ideal habitat selection, there was no indication that territories which experienced nest predation were selected disproportionately. Our results underscore the utility of 1) variograms among other methods for quantifying gradients in animal habitat and 2) variogram model parameters in investigating the habitat ecology of animals.

Animal–habitat relationships are commonly examined with the view of habitat as a patch mosaic (Forman 1995, Turner et al. 2001). Despite the well-established utility of this 'patch paradigm' (Johnson et al. 1992, Bissonette 1997, Bender et al. 2003), animal ecologists have increasingly examined and employed gradients, continua, and related surface or textural properties of habitat (McGarigal and Cushman 2005, Kupfer et al. 2006, McGarigal et al. 2009, Culbert et al. 2012). Alone or in concert with other conceptual frameworks, these gradients may elucidate animal–habitat relationships and population processes masked when viewing landscapes solely as patches (Kristan 2003, Fischer and Lindenmayer 2006, Lindenmayer et al. 2007, Price et al. 2009).

Among methods for quantifying these gradients, geostatistics offer animal ecologists a toolbox for characterizing habitat using point samples in a continuous field (Isaaks and Srivastava 1989, Rossi et al. 1992, Albright et al. 2011). Geostatistics may be particularly useful in this endeavor when the spatial structure of habitat is not self-evident (Rossi et al. 1992) such as in the absence of sharp transitions between slope aspects or soil types. The primary tool in the geostatistical toolbox is the variogram; a statistical model of the spatial dependence among point samples separated by

increasingly larger distances. Patterns and processes of spatial dependence – either endogenous (e.g. due to social behavior) or exogenous (e.g. due to clustered resources) – in a population response (e.g. abundance) are often of primary interest (Rossi et al. 1992, Monestiez et al. 2006, Certain et al. 2007, Minias et al. 2012). This spatial dependence can also be used to effectively model animal responses when employed as continuous variables in generalized linear models (GLMs; McCullagh and Nelder 1999) describing animal–habitat relationships (Knick and Rotenberry 1995, Mitchell et al. 2001, Marchildon et al. 2011). These studies and others suggest spatial dependence among components of habitat may influence animal responses in ways more pervasive than currently documented. If so, employing gradients of spatial dependence to improve our understanding of animal–habitat relationships – particularly for species of conservation and management concern – is an important undertaking.

In this study, we examined the importance of habitat gradients in territory occupancy and nest survival of the vesper sparrow *Pooecetes gramineus,* a small, ground-nesting songbird (order *Passeriformes*) of relatively dry, open habitats of North America. While classified as a grassland-obligate species (Vickery et al. 1999), the vesper sparrow is one of

many associated with heterogeneous habitats (Benton et al. 2003, Fuhlendorf et al. 2006), preferring to nest in areas of 'patchy' vegetation (Dechant et al. 2000) composed of both relatively open areas of bare ground or shorter vegetation (e.g. grassland, prairie), and taller features with higher canopy cover (e.g. tall annuals, shrubs, forest, fencerows; Finzel 1964, Best et al. 1995, Jones and Cornely 2002, Cunningham and Johnson 2006).

Our study was motivated by 1) the association of vesper sparrows with variable vegetation structure (Dechant et al. 2000) and 2) the difficulty in characterizing the vegetation structure of our study area as a mosaic of patches (Kupfer et al. 2006). Our objectives were to 1) assess the influence of several habitat gradients associated with vegetation volume in the territory occupancy and daily nest survival of vesper sparrows, 2) assess the feasibility of quantifying habitat gradients in our study area via variogram models, 3) compare the predictive ability of variogram model-derived parameters describing vegetation volume relative to more commonly employed measures (i.e. mean and standard deviation), and 4) examine the consistency in gradient–territory occupancy and gradient–nest survival relationships. We expected vesper sparrows to show higher probabilities of territory occupancy and daily nest survival in areas of 1) lower vegetation volume given the high shrub cover of our study area relative to other vesper sparrow breeding habitats (Jones and Cornely 2002) and 2) higher variation in vegetation volume (i.e. higher standard deviation, larger variogram nugget values, and smaller variogram ranges). Implicit in expected relationships with habitat was an expectation of ideal habitat selection (i.e. higher fitness in selected habitat; Arlt and Pärt 2007) and we predicted 1) higher daily nest survival probabilities to be associated with habitat attributes that were important drivers of territory occupancy and 2) successful nests to be in more attractive territories.

Material and methods

Study species

The vesper sparrow winters in the southern US and northern Mexico and breeds in the northern US and southern Canada (Jones and Cornely 2002). With the exception of three US states where populations have increased (Missouri, North Dakota and Washington), significant declines were observed between 1966 and 2009 across most of the US and southern Canada (Sauer et al. 2011). Vesper sparrows are a species of special concern in Washington and Oregon, and a priority focus species in Nevada (Jones and Cornely 2002).

The importance of heterogeneity in vesper sparrow habitat appears tied to several life history requirements, specifically 1) open areas where birds glean invertebrates from low vegetation or scratch for them in litter or bare earth (Jones and Cornely 2002), 2) elevated stems, branches, fence posts, or related structures offering perches for singing males (Best and Rodenhouse 1984), and 3) low, dense vegetation offering nest concealment, thermal cover (Wray and Whitmore 1979, Nelson and Martin 1999), and food items not found in open areas (Best and Rodenhouse 1984, Rodenhouse and Best 1994).

Study area

We conducted our study on private land managed by Lava Lake Land and Livestock, in Blaine County, Idaho, United States (43°29′N, 113°48′W). Two roughly rectangular study sites, Fish Creek and West Fork, were located 2 km apart in sagebrush (*Artemisia* spp.) steppe with elevations ranging from 1680 to 1840 m and dominated by mountain big sagebrush *Artemisia tridentata* ssp. *vaseyana*. When observed at the scale of a songbird territory (generally 0.1–10 ha; Schoener 1968), our study area (and large areas of the intermountain western United States) can be described as a 'sagebrush sea' (Davies et al. 2011) with sagebrush (mean = 1.0 m tall) appearing to be distributed in a generally uniform arrangement among a mixed substrate of bare ground, grasses and forbs (mean = 0.2 m tall). No roads fragmented the study sites and we observed no evidence of large-scale disturbance (e.g. fire) within study site boundaries. The Fish Creek site was 79 ha and the West Fork site was 74 ha. In 2008, we reduced the Fish Creek and West Fork sites to 52 and 54 ha, respectively, due to logistical constraints.

Field measurements and nest monitoring

From mid April to late May 2007 and 2008, we measured the total cover and average height of each plant species using a Daubenmire frame (Daubenmire 1959) within pairs of square 4-m² plots. We centered one plot of each pair at intersections of a 50-m grid system and centered the other plot 2 to16 m away in a random cardinal direction. We also sampled vegetation at each vesper sparrow nest following nest failure or fledging. We sampled 2453 plots during the study duration.

We conducted intensive searches throughout the day for vesper sparrow nests every one to three days from mid-April through late July in both years. We typically located nests when females flushed, though we were assisted by other behavioral cues (Martin and Geupel 1993). We returned to check nests every one to four days and recorded clutch size or the number of nestlings. We assumed a nest was successful (i.e. survived to completion) if it was empty and either 1) nestlings were at least nine days old at the last nest check or 2) vesper sparrows were observed carrying food or alarm-calling in the vicinity of the nest. We assumed nests had been preyed upon when nest contents (eggs or nestlings) disappeared before nestlings were seven days old. We considered nesting attempts in subsequent years to be independent. No reuse of vesper sparrows nests has been reported (Jones and Cornely 2002) and was not observed in our study.

Territory-scale variables

We first condensed our vegetation measurements into the 'effective volume' of vegetation (vegetation volume hereafter, Table 1) which we calculated by summing the product of the height (in cm) and cover (%; 0–100) of all plant species in each plot. We then assumed a 2-ha, nest-centered, circular area (radius = 79.8 m) represented an approximate vesper sparrow territory size and shape (Jones and Cornely 2002) confirmed by observations of banded birds in 2008 (Pollock

Table 1. Territory-scale vegetation variation measured directly in the 2-ha area around vesper sparrow *Pooecetes gramineus* nests, 4-m² field plots within occupied or vacant vesper sparrow territories, or calculated via variogram analyses from plots sampled on Lava Lake Ranch, Idaho, 2007–2008.

Variable	Occupied territories (n = 37)		Vacant territories (n = 37[a])		Successful nests (n = 15)		Failed nests[b] (n = 22)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
MVOL[c] (%)	20.1	0.7	25.0	1.1	19.5	1.3	20.4	0.8
SDVOL[d] (%)	1.59	0.04	1.54	0.05	1.67	0.08	1.52	0.03
NUGGET[e]	0.038	0.010	0.019	0.006	0.038	0.012	0.038	0.016
SILL[f]	0.202	0.020	0.178	0.031	0.240	0.042	0.172	0.018
RANGE[g] (m)	47.6	2.8	59.9	2.6	58.4	4.0	39.9	3.0
GRASSP[h] (%)	49.2	4.1	19.8	2.8	60.2	6.2	42.9	5.1

[a]One vacant territory was omitted due to a small sample of plots.
[b]Failure was due to predation in all nests.
[c]The mean "effective volume" of vegetation across all plots within occupied and vacant territories. This was calculated as the sum of the products of cover (%) and mean height (cm) of all plant species.
[d]The standard deviation of vegetation volume.
[e]The estimated nugget parameter of spherical models fit to variogram clouds of vegetation volume within occupied and vacant territories.
[f]The estimated sill parameter of spherical models.
[g]The estimated range parameter of spherical models.
[h]The proportion of local (4 m²) vegetation in grass at nests or the most central plot within vacant territories.

unpubl.). Using log-transformed vegetation volume values, we calculated the mean and standard deviation of vegetation volume among all plots falling within each territory. We used standard deviation rather than the coefficient of variation as it was less correlated with mean volume ($r = -0.48$ vs -0.61, respectively).

We built empirical variograms from vegetation volume measurements among plots within territories. Empirical variograms (also called sample variograms) are constructed by calculating the variance (γ) among points separated by a range of inter-pair (lag) distances (also called a 'bin'; h);

$$\gamma(h) = \frac{1}{2N(h)} \sum (Z[s_i] - Z[s_j])^2$$

where $N(h)$ is the number of pairs of observations (s_i, s_j) that are in bin h and Z is the value of the point characteristic of interest (Isaaks and Srivastava 1989). To conserve information lost in binning – of concern when modest sample sizes prohibit the recommended minimum of 30 point pairs per bin (Journel and Huijbregts 1978) – the variogram cloud can be calculated from all pairs of points;

$$\gamma(h) = (Z[s_i] - Z[s_j])^2$$

where Z is the observed value at two points (s_i and s_j) separated by the discrete distance h. We used the latter approach; calculating variogram clouds to a lag distance of 113 m (two-thirds the maximum possible distance between plots), as we found modest numbers of pairs (often < 20) within bins even when employing a relatively generous bin width of 10 m.

We fit spherical models to variogram clouds (Müller 1999, Hyun et al. 2012) using iterative generalized least squares (GLS) in the gstat package (Pebesma and Graeler 2013) in R. While the spherical model form is the most widely used semivariogram model, other model forms are available (e.g. exponential or gaussian) and may provide better predictions. Exploratory analysis indicated the exponential model provided modest improvements (mean increase in pseudo-R^2 of 0.04) to predictions in 14% of territories. Thus, for simplicity, we employed only the spherical model

in our analysis. Exploratory analysis indicated no directional patterns in spatial dependence (anisotropy) among plots so we employed a single isotropic model per territory. Three parameters – nugget (n), sill (s), and range (r) – are estimated in a spherical model (Fig. 1), which is defined as

$$\gamma(h;n,s,r) = \begin{cases} n & \text{if } h = 0 \\ n + (s-n)\left(\frac{3h}{2r} - \frac{h^3}{2r^3}\right) & \text{if } 0 < h \le r \\ \sigma^2 & \text{if } h > r \end{cases}$$

The nugget is an indication of microscale variance (between a zero lag distance and the minimum observed lag distance) or measurement error (when lag distances of zero are present). The sill indicates the variance (σ^2) among observed values separated by lag distances beyond the range. The range – the distance at which the sill is reached – is the estimated maximum lag distance of correlation and can be thought of as an index of average patch size (i.e. diameter; Perry et al.
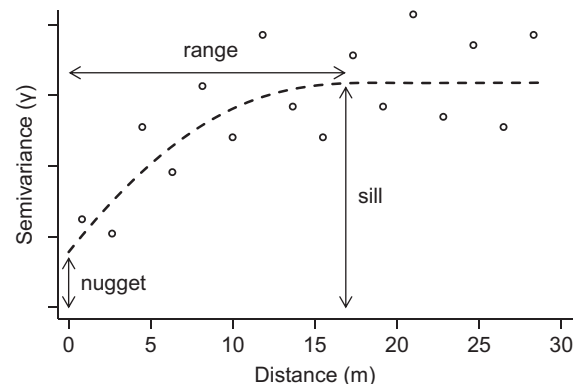

Figure 1. Hypothetical spherical variogram of vegetation volume. The nugget is the (hypothetical) variation at a zero distance separating observations, the sill is the semivariance value beyond the range, and the range is the distance at which the sill value is reached.

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2002) that does not require the classification of the landscape into patches. Patches in our study area can be thought of as relatively continuous areas of vegetation having a similar height and percent cover.

We visually estimated spherical model parameters when GLS failed to fit models. We assessed the fit of GLS variogram models for each territory by employing a leave-one-out cross-validation (Davis 1987) as the objective of fitting a variogram model is to provide the best prediction to spatial features (vegetation plots in our study) and not to fit a variogram model that is the closest possible to variogram values (Goovaerts 1997). We performed cross-validation iteratively by first withholding one plot and using the remaining observations and the spherical model to estimate vegetation volume at the withheld location via ordinary kriging (Davis 1987, Isaaks and Srivastava 1989, Goovaerts 1997). Though several measures of assessing the agreement between true and estimated values are available, we calculated a pseudo-R^2 value for each spherical variogram model as

$$\frac{\sum_{i=1}^{n}(Z[s_i]-\hat{Z}[s_i])^2}{\sum_{i=1}^{n}(Z[s_i]-\bar{Z}[s])^2}$$

where $Z[s_i]$ is the log-transformed vegetation volume measured at location s_i, $\hat{Z}[s_i]$ is the estimated value of Z at location s_i, and $\bar{Z}[s]$ is the mean value of Z from all locations. This pseudo-R^2 value represents the ability of each territory-specific variogram model to independently estimate vegetation volume within the territory. We later employed pseudo-R^2 values from cross-validation in weighting territories in models of territory occupancy and daily nest survival.

Analysis of territory occupancy (see below) required us to calculate variogram model parameters in a sample of available, unoccupied comparison areas ('vacant territories' hereafter) within each unique combination of site and year (site-year hereafter). These areas (also 2-ha circles) were centered on plots ≥ 160 m (twice the radius of estimated territories) from all known nests within each year to avoid spatial overlap. Due to the limited size of our study sites, we employed a number of vacant territories equal to the number of territories.

Territory occupancy

We quantified patterns of vesper sparrow territory occupancy by non-random use wherein we compared occupied to vacant territories (Johnson 1980). This approach assumes vacant territories within each year were both known and available to all birds (or more accurately females, who build nests alone following male territory establishment; Jones and Cornely 2002). While there is potential for false negatives in our use-available design due to some limited use of vacant territories by neighboring females (Keating and Cherry 2004, Johnson et al. 2006), we assumed our search methods allowed for the detection of the vast majority of occupied territories. While few nests within the same year were initiated on the same day, all nests within each year employed in models were concurrently active during at least part of their period of survival (mean = 17.6 days, SE = 1.0).

Statistical modeling

Territory occupancy

We examined territory occupancy using GLMs with a binomial family and a logit error link (a.k.a. logistic regression). We omitted territories that either 1) were re-nesting attempts following predation by rodents or snakes (to avoid the potential effects of previous nest fate on territory occupancy; Peluc et al. 2008) or 2) had uncertain nest fates. In addition to territory-scale habitat gradients, we included a variable describing the local (4 m²) proportion of grass volume at nest sites and the center-most plot of vacant territories. In doing so, we assumed selection for nest-sites was a top–down process preceded by selection for territories. To control for differences in vegetation between years, we centered predictor variables on the mean values observed within each year. This method is suggested for assessing within-subject effects in mixed-effects models (van de Pol and Wright 2009) and is conceptually similar to a conditional (e.g. case-control) logistic regression (Hosmer and Lemeshow 2000) in which years are treated as strata.

Nest survival

We modeled nest survival using logistic exposure models (Shaffer 2004). Logistic exposure is a variant of logistic regression employing a custom link function providing an unbiased daily nest survival estimate by allowing for varying time (exposure) periods between nest visits (Shaffer 2004). To account for other suspected or known influences on nest survival in this species, we included variables in models describing the local (4 m²) proportion of grass volume at the nest site (Pollock 2009) and mean Julian day of the exposure period (Grant et al. 2005) relative to the date of first clutch initiation within years. We did not include effects of year, nest age, or polynomials of exposure period date or nest age (Grant et al. 2005) as they exhibited weak relationships with nest survival in exploratory analyses.

Candidate models

Using all combinations of mean vegetation volume, standard deviation of vegetation volume, variogram nugget and variogram range, we built a candidate set of 15 models of territory occupancy and nest survival. We did not include the variogram sill in models due to a strong correlation with standard deviation of vegetation volume ($r = 0.80$, Table 2). All other variable pairs were correlated at $|r| < 0.5$ and variance inflation factors in global models were < 1.5, thus we assumed multicollinearity was not an issue. To address our second objective of assessing support for variogram model parameters relative to mean or standard deviation, we summed the

Table 2. Pearson correlations (n = 74) among variables employed in models of territory occupancy and daily nest survival among vesper sparrows breeding on Lava Lake Ranch, Idaho, 2007–2008. See Table 1 for variable descriptions.

	MVOL	SDVOL	RANGE	NUGGET	SILL
SDVOL	−0.484				
NUGGET	−0.167	0.313			
SILL	−0.478	0.810	0.209		
RANGE	0.094	−0.104	0.189	0.023	
GRASSP	−0.262	0.258	0.409	0.186	−0.033

weights of models containing each variable as a measure of variable importance (Burnham and Anderson 2002). This method was appropriate as each variable was present in an equal number (eight) of the 15 models.

We considered the pseudo-R^2 of each variogram model as an indication of variogram model quality and used these values to weight models of territory occupancy and nest survival. The homogenization of data quality by weighting observations using sample size, sampling effort, inverse variance of a slope estimate, or another assessment is common in linear modeling (Gurevitch and Hedges 1999, Osenberg et al. 1999, Mech and Zollner 2002). We were, however, concerned that pseudo-R^2 values could be influenced by the number of neighbors and other factors when estimating values via cross-validation (Goovaerts 1997). To adjust for this potential bias ($r = -0.36$, DF = 73, p = 0.01) in the relative quality of models, we first removed the effect of plot number on pseudo-R^2 by retaining the residuals from an OLS model of R^2 predicted by the number of plots. We normalized these residual pseudo-R^2 values for use as observation weights by first scaling the range of values to 0–1. We then centered these values on 1 such that weights had a mean of 1 (SE = 0.03, range 0.5–1.5) and thus did not inflate the sample size (Li et al. 2011). Under this weighting scheme, the poorest-fitting models (pseudo-$R^2 < 0.1$) generally had weights of 0.5–0.6 while the best-fitting models (pseudo-$R^2 > 0.7$) generally had weights of 1.3–1.5. We were also concerned that correlations between this weighting factor and predictor variables in models ($r = 0.13$ to 0.52) could bias results of GLMs. To address this concern, we retained residuals from OLS models of each predictor variable (for use as predictors in GLMs) predicted by observation weights.

Using the candidate model sets of territory occupancy and nest survival, we generated model-averaged parameter estimates iteratively for each variable following Burnham and Anderson (2002, p. 345) by re-weighting those models containing the variable of interest. We examined Moran's I correlograms of residuals (inspecting 2007 and 2008 observations separately) from the most complex models (using 100 m lag intervals) in search of significant residual spatial autocorrelation (Legendre and Legendre 1998) but found none. To address our final objective, we compared parameter estimates from territory occupancy and nest survival models as a preliminary assessment of ideal habitat selection (Pärt et al. 2007) and used a Wilcoxon rank-sum test to compare model-predicted probabilities of territory occupancy (i.e. 'attractiveness') between territories with successful and depredated nests (Misenhelter and Rotenberry 2000) as an additional assessment.

Evaluating models

We evaluated the discriminatory power of GLMs by first generating receiver operating characteristic (ROC) curves (Hanley and McNeil 1982). ROC curves, here constructed using the ROCR package (Sing et al. 2009), indicate the classification sensitivity (true positive rate) versus 1 minus the classification specificity (false positive rate) across a range of cutoff values (0–1). We used the area under the ROC curve (AUC) as an overall measure of discriminatory power (Fielding and Bell 1997). In addition to AUC calculated from all observations, we also calculated leave-one-out cross-validated AUC values by iteratively refitting models using a single, withheld observation and then predicting the response of the withheld observation using the fitted model.

Results

We located 73 vesper sparrow nests in 2007–2008 (47 in 2007, 26 in 2008) of which 23 nests in 2007 and 12 nests in 2008 were known or suspected re-nesting attempts following predation of apparent first nests. After removing a 2008 nest with an unknown fate, we retained a set of 37 nests (24 in 2007, 13 in 2008), 15 of which were successful. All 22 unsuccessful nests were due to predation. Predation occurred during incubation (13 nests) and nestling stages (9 nests) in proportions (59% and 41%, respectively) approximately equal to stage duration (60% and 40%, respectively; Wray et al. 1982, Jones and Cornely 2002). All territories had at least two-thirds of their area within study area boundaries. Vegetation volume was highly correlated with shrub height and cover ($r = 0.59$ and 0.67), but less correlated with herb height and cover ($r = 0.44$ and 0.15), indicating a greater contribution of shrubs to overall vegetation volume.

Each territory contained a mean 23.4 vegetation plots (SE = 1.1, range = 12–36) separated by a mean minimum distance of 4.5 m (SE = 0.3). Of the 74 occupied or vacant territories, spherical models were fit to 65 (88%), while model parameters were visually-estimated for nine territories. Cross-validated agreement (pseudo-R^2) between vegetation volume observed in plots and kriging estimates (including those with visually-estimated parameters) had mean pseudo-R^2 of 0.39 (SE = 0.03, range 0.01–0.90).

Occupied territories had overall lower vegetation volume and larger variogram ranges than vacant territories (Table 1, Fig. 2A, D). Sums of model weights indicated that these two variables were the most important among territory-scale measures of vegetation volume (Table 3). With the exception of one unsupported model ($\Delta AIC_C = 13.9$; Table 4, model 3), all models of territory occupancy had AUC values > 0.8, indicating good to excellent discrimination of occupied and vacant territories (Table 4). The most predictive variable was the local proportion of vegetation in grass and a model with only this variable (not included in the candidate model set) had an AUC of 0.834 ($\Delta AIC_C = 12.438$). The best territory occupancy model employing variogram model parameters (Table 4, model 7) had over 20 times the support of the best model without them (Table 4, model 1).

Higher probabilities of daily nest survival were associated with larger variogram ranges (Fig. 2H), a higher local proportion of vegetation in grass, and later exposure periods (Table 1, Table 3). Sums of model weights indicated greater importance of the variogram range relative to the three other gradients of vegetation volume (Table 3). All models of nest survival built from the complete set of territories and most competitive ($\Delta AIC_C < 4$) cross-validated models had an AUC greater than 0.7, indicating fair discrimination of periods in which nests survived (or fledged) from periods in which nests were depredated (Table 4). The best nest survival model employing a variogram model parameter (Table 4, model 4) had over 70 times the support of the
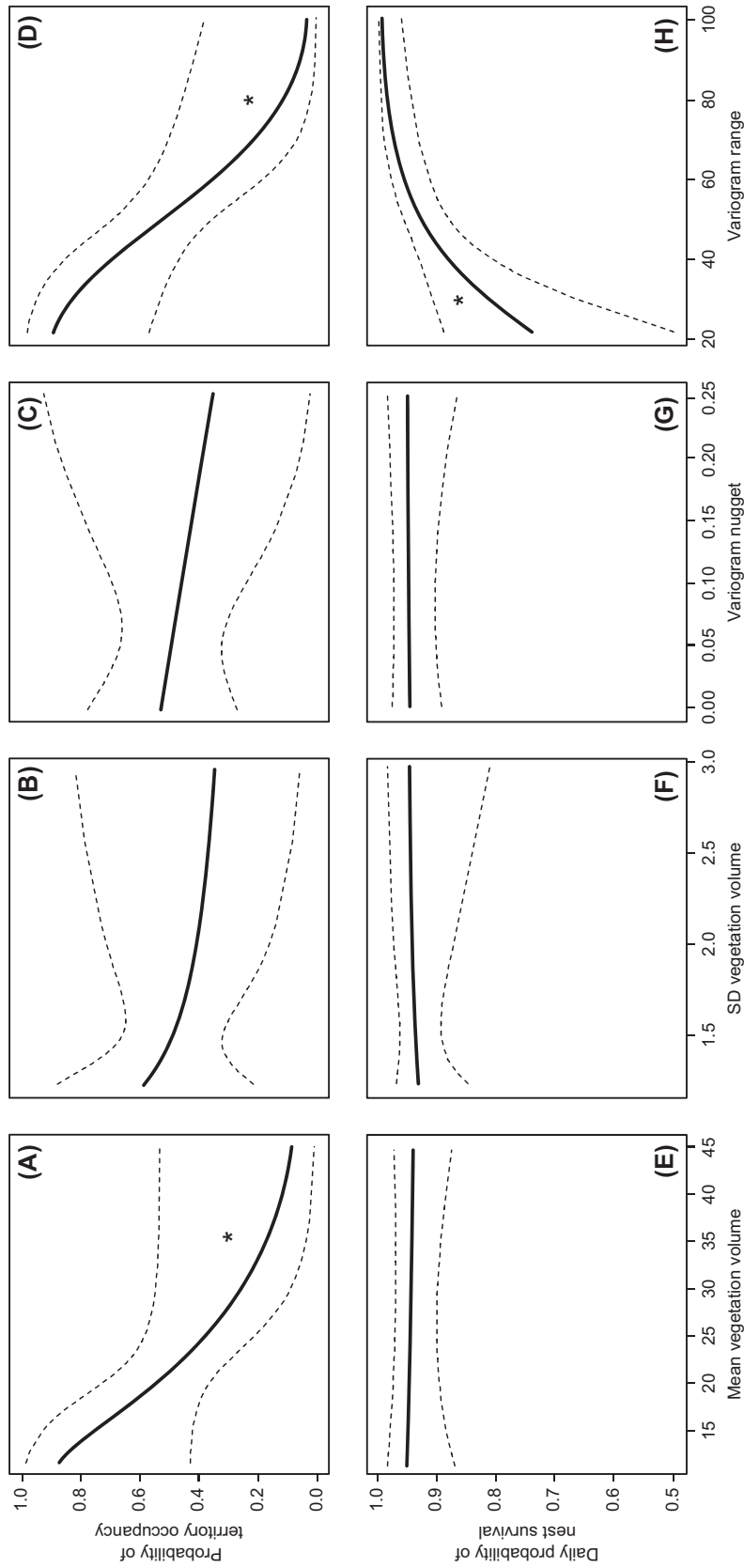
Figure 2. Relationships between four habitat gradients describing vesper sparrow vegetation volume within territories and the probability of territory occupancy and daily probability of nest survival. Measurements are from Lava Lake Ranch, Idaho, USA 2007–2008. Dashed lines indicate 95% confidence intervals around mean linear relationships and asterisks indicate intervals did not include zero. Variables had means of 0 during modeling (see text for more details) but were re-centered on their mean values for presentation. Mean and standard deviation (SD) of vegetation volume axes were back-transformed to their original scale of measurement.

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Table 3. Model-averaged parameter estimates in models of territory occupancy and daily nest survival among vesper sparrows breeding on Lava Lake Ranch, Idaho, 2007–2008. Parameter estimates with 95% confidence intervals that did not include zero are indicated in bold. See Table 1 for variable descriptions.

Variable	Territory occupancy			Daily nest survival		
	Mean	SE	Σw_i[a]	Mean	SE	Σw_i
MVOL	**−3.759**	**1.718**	0.936	−0.472	1.200	0.303
SDVOL[b]	−1.702	1.347	0.391	0.293	1.390	0.253
NUGGET	−4.728	10.440	0.233	−0.092	4.565	0.254
RANGE	**−0.074**	**0.027**	0.930	**0.064**	**0.023**	0.602
GRASSP	**0.084**	**0.022**	—[c]	**0.036**	**0.013**	—[c]
DATE	—	—	—	**0.074**	**0.033**	—[c]

[a]Sum of weights among models containing the variable.
[b]Log-transformed prior to modeling.
[c]Variable included in all models.

best model without one (Table 4, model 2). Predicted probabilities of territory occupancy were slightly higher for successful nests (Fig. 3; mean 0.80, SE = 0.04) than for those with depredated nests (mean = 0.70, SE = 0.05). However, this difference was not significant ($W = 131$, p = 0.31).

Discussion

By using habitat gradients calculated across territories or estimated from variogram models, we were able to effectively model components of vesper sparrow breeding ecology in an area of generally uniform vegetation height and cover characteristic of the 'sagebrush sea'. We found relationships between territory occupancy and habitat gradients to be consistent with our expectations for mean vegetation volume and the variogram range but inconclusive for standard deviation of vegetation volume and the variogram nugget. Relationships between nest survival and territory-scale
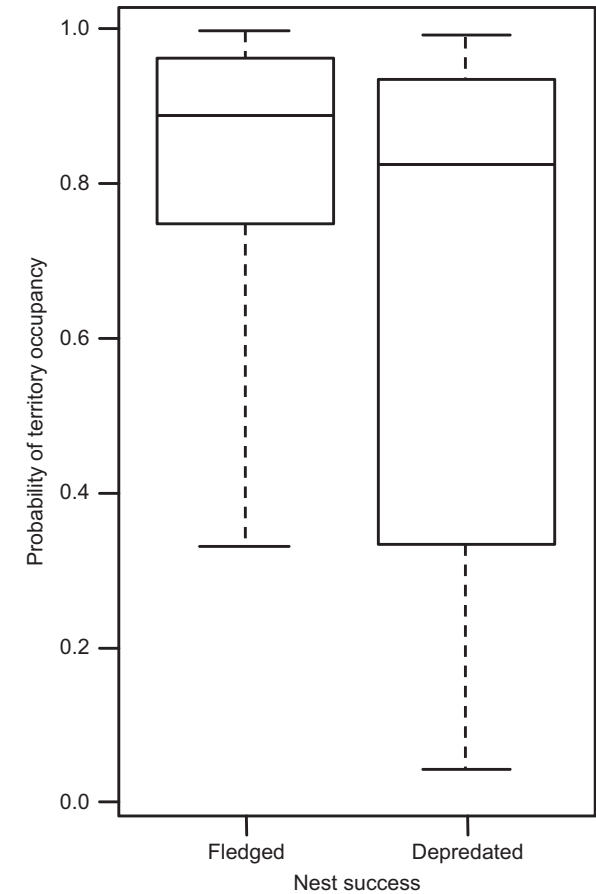

Figure 3. Probabilities of occupancy among vesper sparrow territories fledging young and those depredated on Lava Lake Ranch, Idaho, USA 2007–2008. The probability of territory occupancy is the model-predicted index of 'attractiveness' of each territory. Lines within boxes indicate median values, bottoms and tops indicate first and third quartiles, respectively and whiskers indicate ranges.

Table 4. Candidate model sets of vesper sparrow territory occupancy and daily nest survival on Lava Lake Ranch, Idaho, 2007–2008. For each model, k is the number of fitted parameters, ΔAIC_C is the difference in AIC_C between the best and given model, w_i is the relative weight of the model given the model set, AUC is the area under the receiver operating characteristic (ROC) curve (a measure of model accuracy for binary responses) and CVA is the leave-one-out cross-validated AUC. The most-supported (lowest AIC_C) model for each set is indicated in bold. See to Table 1 for variable descriptions.

#	Model	Territory occupancy				Daily nest survival			
		k[a]	ΔAIC_C	w_i	AUC	CVA	k[b]	ΔAIC_C	w_i	AUC	CVA
1	MVOL	3	6.648	0.015	0.885	0.859	4	9.216	0.004	0.707	0.645
2	SDVOL	3	14.171	0.000	0.838	0.816	4	8.796	0.005	0.705	0.640
3	NUGGET	3	13.940	0.000	0.839	0.797	4	9.393	0.004	0.703	0.607
4	RANGE	3	4.918	0.035	0.888	0.858	4	**0.000**	**0.384**	**0.769**	**0.721**
5	MVOL + SDVOL	4	8.314	0.006	0.885	0.852	5	11.175	0.001	0.705	0.627
6	MVOL + NUGGET	4	7.613	0.009	0.888	0.850	5	11.361	0.001	0.707	0.596
7	MVOL + RANGE	4	**0.000**	**0.411**	**0.914**	**0.883**	5	1.663	0.167	0.769	0.707
8	SDVOL + NUGGET	4	15.413	0.000	0.854	0.801	5	10.973	0.002	0.706	0.597
9	SDVOL + RANGE	4	7.069	0.012	0.888	0.846	5	2.174	0.129	0.771	0.703
10	NUGGET + RANGE	4	7.221	0.011	0.885	0.840	5	2.176	0.129	0.768	0.703
11	MVOL + SDVOL + NUGGET	5	9.632	0.003	0.892	0.844	6	13.383	0.000	0.705	0.584
12	MVOL + SDVOL + RANGE	5	0.720	0.286	0.920	0.885	6	3.893	0.055	0.768	0.676
13	MVOL + NUGGET + RANGE	5	2.364	0.126	0.912	0.868	6	3.816	0.057	0.771	0.692
14	SDVOL + NUGGET + RANGE	5	9.422	0.004	0.885	0.833	6	4.367	0.043	0.772	0.688
15	MVOL + SDVOL + NUGGET + RANGE	6	3.261	0.080	0.917	0.863	7	6.091	0.018	0.773	0.671

[a]Models of territory occupancy included a variable describing the local-scale (4 m²) proportion of vegetation volume in grass.
[b]Daily nest survival models included the proportion of vegetation in grass and the mean day of the exposure period relative to the first recorded nest initiation date within the year.

habitat gradients were inconclusive with the exception of the variogram range which showed a pattern counter to our expectation.

Consistent with the importance of nest predation and parasitism in shaping life-history traits (Martin 1995), grassland birds typically show a preference for larger areas of grassland or similar open vegetation (Helzer and Jelinski 1999, Davis and Brittingham 2004, Ribic et al. 2009). While area-dependence has also been document in vesper sparrows nesting in grass or shrublands within a forested matrix (Vickery et al. 1994), higher probabilities of occupancy we observed in territories with smaller variogram ranges (i.e. having smaller patches of relatively continuous vegetation volume) is consistent with higher abundance (Noson et al. 2006) and higher rates of occupancy (Vickery et al. 1994) along 'patchiness' gradients measured by the number of cover type changes (e.g. shrub-to-bare) along line transects within nesting areas. The general consensus is vesper sparrows select these 'patchier' areas as they offer improved food availability, thermal conditions, and concealment from predators (Rodenhouse and Best 1994, Dechant et al. 2000).

Extending to the local scale, the pattern we detected of territory occupancy associated with smaller patches is consistent with the observed adjacency of 75% of nests to single clumps of vegetation in one study (Nelson and Martin 1999). Based on temperature profiles, the most thermally-favorable incubation conditions in this study were inferred for nests with structure and arrangement of vegetation allowing higher direct morning but lower afternoon sun exposure (Nelson and Martin 1999). Smaller patch sizes are also likely favored for reduced predation risks to adults (e.g. by prairie falcons *Falco mexicanus*; Lima and Valone 1991) by providing improved access to protective cover. This pattern is echoed by strategies for predator evasion interpreted from 1) the uncommon observation of foraging vesper sparrows > 50 m from protective cover during the breeding season (Rodenhouse and Best 1994) and 2) the use of trees or shrubs by the majority of wintering vesper sparrows flushed from open areas at distances ≤ 32 m from cover (Pulliam and Mills 1977).

While few studies have examined the nesting success or daily nest survival of vesper sparrows, one at the scale of the nest site (Wray and Whitmore 1979) similarly found higher rates of nest success associated with greater vertical vegetation density; a measure often associated with grass cover and height (Green and Anthony 1989, Fletcher and Koford 2002). Also consistent with patterns we identified are the higher rates of nest predation among other grassland birds in smaller areas of grassland or closer to grassland-forest or grassland-shrub ecotones (Johnson and Temple 1990, Winter et al. 2000, Herkert et al. 2003, Bollinger and Gavin 2004). An exception is the higher rate of nest predation among prairie-nesting vesper sparrows with distance from woodland edges (Grant et al. 2006). Grant et al. (2006) inferred this pattern was most strongly linked to the abundance of a prairie-associated ground squirrel *Ictidomys tridecemlineatus*; a relative of the suspected nest-depredating ground squirrel *Urocitellus columbianus* in our study area.

Examples of nest predation relative to ecotones between grassland and non-grassland are useful in interpreting the influence of patch sizes on nest survival in our study. However, we 1) reiterate that our study was motivated in part by the lack of clear patch structure in our study area and 2) note that structural variation in sagebrush steppe vegetation communities is quite different from that described in other grassland bird studies. Likewise, while patch sizes inferred from variogram ranges are in familiar distance units (m), due to our sampling resolution (in 4-m² plots) and extent (2 ha territories), these distances are not in most cases directly comparable to 1) habitat area in other studies of grassland birds nor to 2) distances between nests and abrupt habitat discontinuities (e.g. forest-field ecotones) measured in the field or from imagery.

Ecological traps (Battin 2004, Robertson and Hutto 2006) and other variants of non-ideal selection (Pärt et al. 2007, Sadoti and Vierling 2010) have been the focus of avian research in grasslands, agricultural areas, and other open habitats (Best 1986, Shochat et al. 2005), though with overall little attention given to vegetation-associated habitat gradients in these areas (Winter and Faaborg 1999). While adaptive habitat selection in our study is indicated by higher probabilities of territory occupancy and nest survival associated with higher relative grass volume at nest sites and is suggested by the somewhat greater attractiveness of successfully-fledging territories, non-ideal selection is indicated by 1) higher probabilities of territory occupancy associated with lower vegetation and smaller patches, yet 2) higher probabilities of nest survival in territories with larger patches, and 3) little influence of vegetation volume on nest survival. While our results reiterate the importance of investigating both habitat selection and fitness (van Horne 1983), the inclusion of measures more closely reflecting territory selection (e.g. settlement patterns or site fidelity) and fitness (e.g. fecundity or annual survival) will undoubtedly improve our understanding of complex animal–habitat relationships in this and other species (Battin 2004, Bock and Jones 2004, Robertson and Hutto 2006, Chalfoun and Martin 2007). Likewise, further inquiry at finer or coarser scales may better illuminate perceptions and risks associated with habitat selection (Shochat et al. 2005, Chalfoun and Martin 2007, Thompson 2007).

In recommending future approaches to quantifying habitat gradients, we acknowledge that while the spatial density and varied distances between field-sampled plots in our study were well-suited to variogram modeling, improvements are certainly possible. For example, similar habitat characteristics quantified at higher spatial resolutions via light detection and ranging (LiDAR) could improve geostatistical modeling of habitat gradients (Vierling et al. 2008), particularly when adequate field data are unavailable or impractical to collect. These data or others derived from remotely-sensed sources describing continuous habitat characteristics across a surface may be used to measure additional ecologically-relevant metrics via textural analysis or related approaches (McGarigal et al. 2009, Culbert et al. 2012). These approaches to quantifying habitat gradients are applicable to birds in sagebrush steppe much as they are to other animal taxa in other habitats.

In conclusion, we found convincing support for models of vesper sparrow breeding ecology by including habitat gradients measured by variogram model parameters in our

analysis. The results of our study provide further evidence that employing both an often-overlooked geostatistical tool and multiple ecological components can augment our understanding of how species perceive and respond to their environment. This understanding can assist managers in the prioritization of conservation areas or in the creation or modification of habitat for species of conservation concern. When appropriate field-collected or remotely-sensed data are available – particularly in areas that defy classification as patch mosaics – we encourage the application of geostatistics or other methods of quantifying habitat gradients to help illuminate animal–habitat relationships.

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