

Habitat variables explain Loggerhead Shrike occurrence in the northern Chihuahuan Desert, but are poor correlates of fitness measures

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Abstract Conservation efforts should be based on habitat models that identify areas of high quality and that are built at spatial scales that are ecologically relevant. In this study, we developed habitat models for the Loggerhead Shrike (*Lanius ludovicianus*) in the Chihuahuan Desert of New Mexico to answer two questions: (1) are highly used habitats of high quality for shrikes in terms of individual fitness? and (2) what are the spatial scales of habitat associations relevant to this species? Our study area was Fort Bliss Army Reserve (New Mexico). Bird abundance was obtained from 10 min point counts conducted at forty-two 108 ha plots during a 3-year period. Measures of fitness were obtained by tracking a total of 73 nests over the 3 years. Habitat variables were measured at

spatial scales ranging from broad to intermediate to local. We related habitat use and measures of fitness to habitat variables using Bayesian model averaging. We found a significant relationship between bird abundance and measures of fitness averaged across nesting birds in each plot (correlation up to 0.61). This suggests that measures of habitat use are indicative of habitat quality in the vicinity of Fort Bliss. Local- and intermediate-scale variables best explained shrike occurrence. Habitat variables were not related to any measures of fitness. A better understanding of the factors that limit individual bird fitness is therefore necessary to identify areas of high conservation value for this species.

Keywords Loggerhead Shrike · Chihuahuan Desert · Habitat use · Habitat quality · Fitness · Multi-scale habitat associations · Image texture

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Introduction

Wildlife habitat models are widely used for conservation planning, specifically for identifying critical habitat for some species. Habitat models are most useful for conservation and management if they can be used to identify not only which habitat is occupied, but also which habitat is of high quality (i.e., contributing to high fitness). However, habitat variables

that influence habitat use (e.g., abundance or occurrence) are not always good predictors of individual bird fitness and vice versa (Winter et al. 2005, 2006). The potential for obtaining information about habitat quality as a model outcome depends on two things: first, it depends on the relationship between measures of habitat use and measures of fitness, and second, it depends on the ability to identify the spatial scale(s) of habitat associations. Here, we attempted to model avian habitat quality in terms of individual bird fitness and to assess multi-scale habitat associations for the Loggerhead Shrike (*Lanius ludovicianus*) in the Chihuahuan Desert of New Mexico.

Species habitat models are most commonly based on measures of habitat use such as species abundance or occurrence. The problem is that these measures of habitat use are not necessarily an indicator of high habitat quality in terms of high individual fitness (Van Horne 1983; Battin 2004; Johnson 2007). Under the ideal-free distribution (Fretwell and Lucas 1969) individuals of a species are predicted to select habitats of high quality until the quality has declined due to the influx of individuals. At this point the higher quality habitat approximates the suitability of habitats of lower quality, and lower quality habitats are selected. Density of individuals is higher in high quality habitat because it can support more individuals than lower quality habitat. A population of Prothonotary Warblers (*Protonotaria citrea*) occupying a region of flooded and dry areas (Petit and Petit 1996) functioned in an ideal-free way, with both higher density of nests and higher nest success in flooded areas than in dry areas. In fact, in a meta-analysis of the relationship between avian abundance and productivity, more than 70% of the studies examined reported a positive relationship between abundance or density and measures of habitat quality (Bock and Jones 2004). However, there are some instances where populations do not operate in an ideal-free way, i.e., where high densities of a species are found in habitats of low quality where individual fitness is poor. In the Chihuahuan Desert of New Mexico, for example, the Black-throated Sparrow (*Amphispiza bilineata*) experiences low reproductive success in habitats that host high densities (Pidgeon et al. 2003). Similarly, in a Maine sandplain, Savannah Sparrow (*Passerculus sandwichensis*) has higher reproductive success at lower densities (Vickery et al. 1992). Finally, a study of the Red-

backed Shrike (*Lanius collurio*) in Belgium found that individuals occurred, but did not always reproduce successfully when essential resources were missing from their territories (Titeux et al. 2007). The potential existence of a negative relationship between measures of habitat use such as abundance or probability of occurrence and measures of fitness poses an important challenge for conservation. If habitat relationships for a species of concern are not correctly discerned, management efforts and resources may be invested in lower quality habitats that do not meet the goal of maximizing long-term population viability. Characterizing the relationship between habitat use and measures of fitness is thus a critical first step in developing and applying wildlife habitat models for conservation.

A second important factor to consider in development of habitat models is the spatial scale(s) of habitat associations. Birds respond to habitat at a number of spatial scales, from the scale of the geographical range, to the scale of the territory, and ultimately to the scale of nest and foraging sites (Hutto 1985). In the northern Chihuahuan Desert, for example, the abundance and occurrence of many bird species is related to broad-scale variables such as the length of shrubland/grassland edge, the number of patches, or grassland cover abundance within 1 to 2 km (Gutzwiller and Barrow 2001, 2002, 2008). In Wisconsin, wooded cover up to 1200 m from pastures was negatively associated with abundance of four species of grassland passerines (Renfrew and Ribic 2008). At finer spatial scales (e.g., within patches of habitat), vegetation composition and structure, indicative of good forage or nest sites, also influence species distribution (Cody 1981). Abundance of the Dickcissel (*Spiza americana*) for example, is positively correlated with vertical vegetation cover and percent forb abundance (Patterson and Best 1996). The Grasshopper Sparrow, on the other hand, is more abundant in areas of lower vertical cover (Patterson and Best 1996). These examples demonstrate that habitat features from broad to fine spatial scale may be necessary for explaining patterns of habitat use in birds.

Measures of avian fitness may also be influenced by the interaction of habitat variables at multiple spatial scales, i.e., vegetation composition and structure in the vicinity of the nest (Martin 1993) and beyond. For example, in the Mixed Grass Prairie of

southeastern Alberta, the nest success of the Sharp-tailed Grouse (*Tympanuchus phasianellus*) is related to habitat characteristics measured at multiple spatial scales from broad (1600 m from the nest) to local (within 50 m of the nest; Manzer and Hannon 2005). In a shrub steppe habitat, nest success of Brewer's Sparrow (*Spizella breweri*) is related to habitat attributes (e.g., potential nest shrub density and shrub cover) at both the scale of the territory and the nest (Chalfoun and Martin 2007). At a local scale, Loggerhead Shrike had lower reproductive success in the edge vegetation along fence lines than in pastures (Yosef 1994). These studies demonstrate that habitat features influence fitness not only locally, but also beyond the immediate vicinity of the nest.

Habitat variables associated with the location of nests and those associated with measures of nest success may differ, as was shown in a recent study of habitat associations of two species of warblers (Yellow-rumped Warbler (*Dendroica coronata*) and Black-poll Warbler (*D. striata*)) and one species of sparrow (White-throated Sparrow (*Zonotrichia albicollis*)) in Newfoundland, Canada (Dally et al. 2008). The same was true for three species of grassland birds (Clay-colored Sparrow (*Spizella pallida*), Savannah Sparrow (*Passerculus sandwichensis*), and Bobolink (*Dolichonyx oryzivorus*)) in Minnesota and North Dakota (Winter et al. 2005, 2006). These results emphasize that the way in which habitat influences not only habitat use, but also fitness, needs to be understood for making well informed management decisions.

The overarching objective of our study was to model Loggerhead Shrike habitat use and fitness measures in the northern Chihuahuan Desert of New Mexico, a semi-arid ecosystem, for the purpose of predicting hotspots of high productivity. Specifically, we ask: (1) what is the relationship between abundance, a measure of habitat use, and nest-based measures of fitness?, and (2) what is the contribution of habitat variables measured at different spatial scales for explaining patterns of habitat use and nest-based measures of fitness?

We selected the Loggerhead Shrike to address our research questions for two reasons: it responds strongly to habitat structure, and it is a species of conservation concern. Loggerhead Shrikes require tall perches for hunting (Craig 1978), open areas for foraging, and shrubs for nesting (Brooks and Temple 1990; Yosef 1996; Pruitt 2000). This requirement for

interspersed shrubs and open areas partly explain its recent population decline. Desert and shrub steppe habitat is thought to have been the primary habitat of the species prior to settlement by Europeans (Cade and Woods 1997). During the late nineteenth and early twentieth century the range of the Loggerhead Shrike expanded into the East and upper Midwestern US as forested land was cleared for agriculture (Cade and Woods 1997). During the early twentieth century, farms included a large proportion of grass pasture, with hedgerows providing hunting perches and nest sites (Novak 1989 cited in Pruitt 2000). As farming practices subsequently changed to include large planted monocultures, hedgerows were removed. During the same time period, forest succession occurred, and farms were converted to suburbs. All of these changes resulted in habitat loss, and as a result, the range of the species contracted (Yosef 1996; Cade and Woods 1997), and the Loggerhead Shrike has recently experienced substantial population declines (Cade and Woods 1997). In the United States, the Loggerhead Shrike was designated as a Migratory Nongame Bird of Management Concern in 1987 by the United States Fish and Wildlife Service, and is listed as threatened or endangered in 14 of the 48 continental United States (Pruitt 2000). In Canada, the species is considered threatened in the West and endangered in the East (Pruitt 2000). In New Mexico, part of the species' former stronghold, the population trend is now negative, and the Loggerhead Shrike is designated a Species of Conservation Concern (New Mexico Partners in Flight. 2007). Given its status, understanding the relationship between habitat use and measures of fitness is important for conservation of the species.

Methods

Study area

Our study was conducted on 282,500 ha of McGregor Range of the Fort Bliss Army Reserve in the Chihuahuan Desert of New Mexico (Fig. 1). The climate is hot and dry with average minimum and maximum temperatures ranging from 11 to 19°C and 30 to 35°C, respectively, for the May–July period, and monthly precipitation ranging from 13 to 44 mm for the same months (Western Regional Climate Center

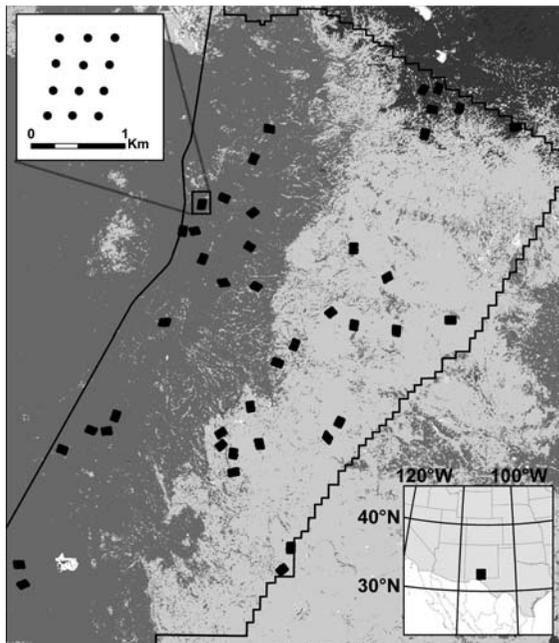


Fig. 1 Representation of the study area located in southern New Mexico, USA (see *bottom right* insert). The *black irregularly shaped rectangles* represent the location of the 42 sampling plots. The *different shades of grey* (from lightest to darkest, respectively) indicate grasslands, shrublands, and open woodlands (classes obtained from the SW-REGAP landcover data). The *top-left* insert zooms on one of the 42 108 ha plot, and shows the location of the 12 grid points (3×4) located 300 m apart

2005). Elevation and soil types (including sand, loam, gravel, limestone, and sandstone) determine different habitat types, including two grasslands (black grama (*Boutela eriopoda*) and mesa grassland), four shrublands (dominated by creosote bush (*Larrea tridentata*), mesquite (*Prosopis sp.*), sandsage (*Artemisia filifolia*), or whitethorn (*Acacia constricta* and *A. neovernicosa*), and one pinyon-juniper (*Pinus edulis*-*Juniperus sp.*) dominated habitat.

Data

Bird data

We used an existing dataset to measure habitat use and fitness of the Loggerhead Shrike. The data were acquired during the 1996, 1997 and 1998 breeding seasons at 42 sampling plots (108 ha, Fig. 1) (Pidgeon 2000). Each sampling plot consisted of a 12-point grid with points located 300 m apart.

Trained observers conducted 10-min point counts and recorded each bird heard or seen within a 150 m radius of each grid point 4–5 times during each breeding season. Plot-level abundance was calculated by summing the counts across the 12 points for a given visit.

The interior 54 ha (600×900 m) of each study plot was also intensively searched for nests. Nest search protocol included (1) searching all large shrubs (the most suitable nest habitat for this species), and (2) conducting alternating systematic and random searches in smaller shrubs and *Yucca sp.* We mapped search zones to assure uniform plot coverage. Shrike behavioral cues were also useful in finding nests. This protocol allowed us to find all nests located within the extent of the 42 study plots. A total of 73 Loggerhead Shrike nests across the 3 years (17 in 1996, 31 in 1997, and 25 in 1998) were found and monitored every 2–3 days. The nest data provided nest-based measures of fitness (average clutch size, total number of nestlings that fledged (hereafter number of fledglings) and nest success (whether a nest produced at least one fledgling or not)). We grouped the data into two stages for subsequent nest success analysis: (1) egg laying and incubation, and (2) nestling stage, and recorded whether or not each stage was completed successfully. Nest success was quantified as a binary variable (0 or 1). The length of the observation interval for each stage was noted, and used to model nest success using the logistic exposure approach (Shaffer 2004) (see statistical analysis section below).

Habitat variables

We measured habitat variables for each nest and grid point at three spatial scales: a broad scale of 1 km that characterized the ecological context surrounding territories, an intermediate spatial scale of 10.89 ha that corresponded to the size of an average Loggerhead Shrike territory (Yosef 1996), and a local scale that captured habitat features in the vicinity (<50 m) of each nest and grid point (Table 1).

Broad-scale measures of habitat were based on the Southwest ReGAP classified satellite imagery (U.S. Geological Survey National Gap Analysis Program 2004), which was created using Landsat Enhanced Thematic Mapper Plus (ETM+) imagery acquired between 1999 and 2001 (Lowry et al. 2005). We

Table 1 List of variables used for fitting mixed-effects models at the broad-, intermediate-, and local-scales

Spatial scales	List of measured variables
Broad	Percent grassland
	Edge density (i.e., density of shrubland/ woodland vs grassland edges)
	Patch richness (i.e., total number of cover types)
Intermediate	Mean NDVI
	Contrast of NDVI
	Angular second moment of NDVI
Local	Elevation
	Foliage height diversity
	Potential nest shrub density (i.e., all shrubs except tall spiny ones)
	Grass percent cover
	Forb percent cover

calculated landscape indices in a 1 km radius buffer centered at each nest and grid point, because variables measured at this spatial scale have been shown to be associated with Loggerhead Shrike occurrence in the Chihuahuan Desert (Gutzwiller and Barrow 2001, 2002). We calculated patch richness by counting the number of habitat classes present in each buffer, and then reclassified the image into grasslands and woody vegetation (shrublands and pinyon juniper woodlands). We quantified the percent grassland as an estimate of foraging habitat, and grassland-woody vegetation edge density as an estimate of the amount of suitable nest habitat and perch availability. All landscape indices were calculated in Fragstats (MacGarigal et al. 2002).

Intermediate-scale measurements were obtained by quantifying image texture in a 10.89 ha area centered at each nest or grid point. Image texture quantifies variability in pixel values in a user-defined neighborhood. This allows analysis of a landscape at a scale that is biologically meaningful, e.g., the average home range size of a species of interest. Image texture measures are useful in predicting avian distribution patterns, e.g., bird occurrence in Maine (Hepinstall and Sader 1997), group size of Greater Rheas (*Rhea americana*) in Argentina (Bellis et al. 2008), and bird species richness in the northern Chihuahuan Desert (St-Louis et al. 2006, 2009), and have successfully discriminated habitat use by two morphs of White-throated Sparrow (*Zonotrichia*

albicollis) in New York (Tuttle et al. 2006). The Normalized Difference Vegetation Index (NDVI) from a June 1996 Landsat TM image was used as the basis of the texture measure because previous analysis has shown that this measure performs better at predicting bird species richness than texture based on other bands or combinations of bands from the electromagnetic spectrum in the same ecosystem (St-Louis et al. 2009). We used second-order contrast (i.e., a measure of variability) and angular second moment (i.e., a measure of homogeneity) to quantify texture (Haralick et al. 1973). We also calculated mean NDVI as an estimate of plant productivity. Image texture measures were calculated in ENVI 4.4 (ITT Visual Information Solutions).

Local-scale measures of habitat included forb and grass cover, foliage height diversity (FHD) and shrub density. Percent cover was averaged across four 1 m² circles located within a random distance (0–5 m) of each nest or grid point, in the four cardinal directions. FHD was measured at each nest and grid point by counting the number of plant species that touched each 25-cm section of a vertical pole (3 m) placed at random distances (0–5 m) along each of the four cardinal directions. Point or nest-specific FHD was then calculated using the Shannon's diversity formula ($H = -\sum_{j=1}^S p_j \ln p_j$; where p_j is the proportion of hits in a given section of the pole and S is the total number of sections). We calculated shrub density using the point-center quarter method (PCQ) (Cottam and Curtis 1956), and used a correction factor to account for our truncated search radius of 50 m (Warde and Petranka 1981). The distance to the nearest suitable nest substrate within 50 m was measured in four quadrants around each nest or grid point. Suitable nest substrates included shrub species that typically have strong branches and attain a height of at least 1 m (e.g., *Artemisia filifolia*, *Atriplex canescens*, *Condalia ericoides*, *Flourensia cenura*, *Prosopis glandulosa*, *Rhus* sp, but not *Accacia* sp., *Larrea* sp, or *Fouquieria*. *Yucca torreyi* and *Y. elata* were also included as suitable; Pidgeon, pers. obs.).

We estimated the elevation at each grid point from a 10 m resolution digital elevation model. We averaged the habitat measures (including landscape indices, texture, and elevation) obtained at the 12 grid points to obtain plot-level measures of habitat characteristics.

Statistical analyses

Abundance as an indicator of habitat quality

We used Spearman's rank correlation to evaluate the relationship between bird abundance and measures of fitness. We averaged the two highest counts per plot from the 4–5 annual visits to obtain a measure of bird abundance for the 1996, 1997, and 1998 breeding seasons, respectively. We felt this measure was more representative of the distribution of breeding birds, and would avoid inclusion of individuals that might be transitory, not holding territories. We summarized the nest data for each year as follows: total number of eggs produced within a plot, total number of fledglings, and total number of successful nests (i.e., number of nests where at least one egg hatched). For a given year, we considered all plots where at least one adult shrike was detected, resulting in a sample size of 32, 26, and 23 plots out of 42 in 1996, 1997, and 1998, respectively.

Multi-scale analysis of habitat associations

We used Bayesian model averaging to evaluate bird-habitat associations. We first converted bird abundance and the number of nests per plot into presence-absence data because Loggerhead Shrikes occurred at less than 65% of the plots, and the data were significantly overdispersed based on a Chi-square test ($P < 0.05$). This test assumes that the standard deviation divided by the mean of the data follows a Chi-square distribution.

We used mixed-effect logistic regression models in a Bayesian model averaging framework to relate bird and nest occurrence to variables measured at the (A) broad-, (B) intermediate-, and (C) local-scale, and (D) a combination of the above (Table 1). We accounted for the repeated nature of the data (i.e., the fact that plots were surveyed 3 years) by including plot as a random effect in these models. To perform the Bayesian model averaging, we fitted all possible combinations of variables (restricting the models to contain no more than five explanatory variables to avoid overfitting our data), selected a subset of variables best supported by the data using the Occam's window criterion (Madigan and Raftery 1994), and used an approximation to Bayes factors (Link and Barker 2006) to calculate posterior probabilities for the models (i.e., the probability that each

model is the true one). The Occam's window approach allows selecting a subset of models best supported by the data. We chose this modeling averaging approach rather than AIC weights because it is more conservative, i.e., AIC weights tend to favor more complex models (Link and Barker 2006). We calculated the posterior probabilities that each variable coefficient is different from zero by summing up the posterior probabilities of the models in which the variable is present. A high probability thus indicates high confidence that the coefficient is different than zero. All statistical analyses were conducted in R 2.7.0 (R Development Core Team 2008).

The relationship between nest success and the habitat variables measured at the three spatial scales was estimated using the logistic exposure approach (Shaffer 2004), where each nest could be represented by 1 or 2 data points, representing stages in the nesting cycle (i.e., (1) egg laying through incubation, (2) nestling). For each stage, the length of each observation interval (in days) was used as an input variable in the model. The logistic exposure approach assumes that the probability of surviving an interval depends on the interval length. We used linear models with Gaussian distribution to estimate the number of fledglings and clutch size as a function of habitat variables. These response variables were square root transformed to allow modeling using a Gaussian distribution. We combined the 3 years for the analysis but incorporated a fixed effect for year. We also included a random effect for plot when analyzing both the number of fledglings and clutch size because multiple nests occurred at the same plot. We fitted models with all possible combination of variables for nest success, clutch size, and number of fledglings.

We tested the significance of the best fitted models (based on BIC) for measures of habitat use and measures of fitness using log-likelihood ratio tests. We tested for spatial autocorrelation in the model residuals using semi-variograms with 95% confidence envelopes.

Results

Summary of habitat use and fitness data

Shrike occurred at 32, 26, and 23 plots out of 42 in 1996, 1997, and 1998, respectively. Out of the 73

nests, more than 50% succeeded across the three breeding seasons (40 nests), with an average clutch size of 4.57 and an average of 2.23 fledglings. Nest height averaged 1.21 m. The height at which successful and unsuccessful nests were located did not differ significantly (F -test, $P > 0.05$). Close to 75% of the nest failures, or 33% of the total number of nests, can be attributed to depredation. Moreover, successful and unsuccessful nests were located over-all in the same set of shrub species.

Abundance as an indicator of habitat quality

We calculated Spearman's correlation using plot-level data for the 3 years separately to evaluate whether abundance reflects high habitat quality (represented by individual bird fitness). We found a positive correlation between abundance and most nest-based measures of fitness ranging from 0.39 to 0.61 (Table 2). These findings are evidence that, for the Loggerhead Shrike in our study area, abundance is positively associated with habitat quality.

Multi-scale analysis of habitat associations

We fitted all possible combinations of variables within each spatial scale to evaluate (1) if bird occurrence, nest occurrence, and measures of fitness were associated with the habitat variables that we measured, and

Table 2 Spearman's correlation coefficients of the relationship between bird abundance and (1) number of nests per plot, and (2) nest-based measures of fitness summarized at the plot level

	Loggerhead Shrike abundance		
	1996 ($n = 32$)	1997 ($n = 26$)	1998 ($n = 23$)
Number of nests	0.43*	0.39*	0.53*
Total number of eggs produced	0.41*	0.42*	0.41*
Total number of fledglings	NS	0.46*	0.52*
Total number of successful nests	NS	0.47*	0.61*

We used only the plots for which at least one shrike was detected during the point counts in a given breeding season. The resulting number of plots used in the analyses is indicated below year. NS indicates when the correlation was not significant at the 0.05 level

* P -value between 0.01 and 0.05

(2) which spatial scale(s) had the strongest influence. However, none of the habitat variables predicted clutch size, number of fledglings, or nest success. Habitat variables at different spatial scales were significantly related to both bird and nest occurrence. For both bird and nest occurrence, all models that were best supported by the data (and used in the model averaging) were significant (Table 3). Local-scale and intermediate scale variables resulted in similar fit for bird occurrence, with BIC values very close to each others. Models that contained variables from multiple scales were slightly better than single-scale models but the difference in BIC was not substantial.

Intermediate- and broad-scale variables provided very similar model fit for explaining the occurrence of nests. A combination of variables from multiple scales did not improve the models obtained using intermediate-scale variables alone.

Bayesian model averaging identified the habitat variables that are most strongly (relatively to other variables) associated with patterns of bird and nest occurrence at each spatial scale, according to the posterior probabilities. At the broad scale, Loggerhead Shrike occurrence was positively associated with proportion of grassland (Table 4). Loggerhead Shrikes were more likely to occur in areas where the proportion of grassland in the surrounding 1 km landscape was high. Nests were also more likely to occur where patch richness was low, but the posterior probability of that coefficient is not very large, signaling this relationship is not especially strong.

At the intermediate spatial scale, NDVI mean was most strongly associated with Loggerhead Shrike occurrence. Shrikes were more likely to occur at plots with low NDVI mean, whereas nests were more likely to occur in low NDVI contrast areas.

At the local scale, Loggerhead Shrike occurrence and nest occurrence were most strongly related to foliage height diversity, and both were most likely to occur at sites where foliage height diversity was low.

When we fitted models using all possible combinations of variables from all three spatial scales, we found that the posterior probabilities for the broad-, intermediate-, and landscape-scale variables were low in most cases. This reflects that, as seen in Table 3, the best supported models were often very similar across the three scales in terms of their explanatory power.

Because of the lack of a significant relationship between nest-based measures of fitness and habitat

Table 3 Model statistics for the best logistic models (those having minimum BIC) from a suite of models fitted at each spatial scale for explaining the occurrence of adults and nests of Loggerhead Shrike. Bayesian Information Criterion (BIC) values can be used for comparing model fit across scales

Response	Scale	Variables included in the best model	BIC	χ^2	<i>P</i> -value
Shrike occurrence	Broad	Proportion of grassland Edge density	152	12.8	0.002
	Intermediate	Mean NDVI	140	19.4	0
	Local	Foliage height diversity Forb cover	142	22.9	0
	All scales	Grass cover Elevation	138	27.1	0
Nest occurrence	Broad	Patch richness	154	6.6	0.010
	Intermediate	Contrast of NDVI	150	11	0.001
	Local	Foliage height diversity	156	4.9	0.027
	All scales	Contrast of NDVI	150	11	0.001

The χ^2 statistics and resulting *P*-values were used for evaluating the overall model significance. No models fitted to explain nest-based measures of fitness were significant

Table 4 Posterior probabilities (in percent) obtained using a Bayesian model averaging approach for evaluating the relative contribution of the variables within each spatial scale individually (left) or combined (right) for explaining patterns of bird and nest occurrence. The signs of the model averaged coefficients are also presented in parenthesis

Scale	Variable	Individual scales		All scales together	
		Shrike occurrence	Nest occurrence	Shrike occurrence	Nest occurrence
Broad	Proportion Grasslands	72 (+)	14 (+)	32 (+)	30 (+)
	Edge density	41 (–)	43 (–)	7 (+)	5 (–)
	Patch richness	40 (–)	61 (–)	9 (+)	7 (–)
Intermediate	NDVI mean	85 (–)	30 (–)	29 (–)	14 (–)
	NDVI con	24 (–)	60 (–)	28 (–)	36 (–)
	NDVI asm	19 (+)	33 (+)	11 (+)	23 (+)
	Elevation	11 (+)	7 (–)	50 (–)	50 (–)
Local	Foliage height diversity	100 (–)	65 (–)	15 (–)	5 (–)
	Potential nest shrub density	41 (+)	23 (–)	8 (+)	9 (–)
	Forb cover	48 (+)	16 (+)	27 (+)	4 (+)
	Grass cover	10 (–)	15 (+)	67 (+)	43 (+)

The posterior probabilities and coefficients were obtained after fitting all possible combination of variables at each spatial scale (i.e., 15 models for the local- and intermediate-scales, 7 models for the broad-scale, and 1023 when different scales were combined). The Occam's window was used for selecting a subset of models best supported by the data

variables at any of the three scales considered, we could not conduct BMA for the fitness data.

Discussion

Habitat models are essential tools for conservation planning. The potential discrepancy between

measures of habitat use and measures of habitat quality was highlighted in the seminal paper by Van Horne (1983) and many studies that followed confirmed the need for caution in using habitat models that are based on measures of habitat use (i.e. data on occurrence or abundance) alone (Vickery et al. 1992; Pidgeon et al. 2003; Bock and Jones 2004; Pidgeon et al. 2006). Thus one general

consideration when using habitat models is to understand the nature of the relationship between measures of habitat use such as abundance and measures of fitness. Another consideration is to understand if habitat variables that explain habitat use are the same as those explaining measures of fitness.

We found positive correlations between Loggerhead Shrike habitat use and nest-based measures of fitness. The shrike, in our study area, is thus among the majority of species for which there is a positive relationship between habitat use and measures of habitat quality (Bock and Jones 2004). It is not clear, however, how the correlation between use and fitness in the Loggerhead Shrike compares to this metric in other species. The strength of correlations we found (0.39 to 0.61) suggests that factors other than habitat are responsible for an equal amount of the variation in the relationship between use and fitness. Moreover the variables that explained Loggerhead Shrike abundance were not related to any of the measures of nest success we estimated. This discrepancy in habitat associations between measures of abundance and measures of fitness suggests that caution is warranted when using measures of habitat use as indicators of habitat quality in the Chihuahuan Desert. Similar patterns were revealed in a study of three grassland bird species in North Dakota and Minnesota (USA), where the factors that influenced density were clearly different than factors influencing habitat quality (Winter et al. 2006). Substantial changes in the landscape over the last 150 years may be implicated in the moderate correlation that we found between abundance and measures of fitness, but the mechanism is unclear. Changes in landcover (e.g., from desert grasslands to desert shrubs) were precipitated, for example, by heavy livestock grazing in the late nineteenth century (Dick-Peddie 1993). Relatively rapid changes in landcover may impair the ability of birds to adapt, and contribute to failure to discriminate good quality habitat from poor quality habitat (Bock and Jones 2004), as appears to be the case for the Black-throated Sparrow (*Amphispiza bilineata*) in the same ecosystem (Pidgeon et al. 2003, 2006).

In our northern Chihuahuan Desert study area multiple scale models were not substantially better than single-scale models for characterizing Loggerhead Shrike habitat use. We found that variables measured at different scales had similar explanatory

power. However it is not clear that this is true in other areas of Loggerhead Shrike range. Intermediate-scale variables were often better, or at least as good, as the variables measured at the local and broad spatial scales for explaining bird and nest occurrence. Image texture calculated within an 11×11 pixels window around the point counts has the potential to capture elements of bird habitat that integrate both the resolution of the central pixel (30 m) and the extent of the window (330 m). Using image texture, on one hand, local, *per-pixel* habitat characteristics such as proportion of green vegetation (e.g., shrubs) can be depicted by NDVI. Additionally, among-pixel differences in photosynthetically active vegetation cover are depicted by quantifying the variability in pixel values within a given window. Given Loggerhead Shrikes' requirement for a mixture of open areas and shrubs (Brooks and Temple 1990; Yosef 1996; Pruitt 2000) it seemed that image texture quantified at the scale of the point count was appropriate for monitoring the habitat of this species. In our models, however, birds and nests were more likely to occur in areas with low NDVI heterogeneity (e.g., contrast) and low mean NDVI, than in areas of high heterogeneity. Given our experience in the field, we intuitively expected the opposite, because low heterogeneity in image texture translates to low vertical diversity in vegetation. Although in many ecosystem Loggerhead Shrikes prefer open grasslands with only a few scattered shrubs, this species does occur and nest in a variety of habitats in our study area, from shrubland-dominated habitats to open grasslands. Sites with lower heterogeneity include areas with relatively high diversity of forbs and grasses (personal observation), and perhaps associated high abundance of prey species. Short vegetation may also enhance hunting efficiency. In South Carolina, Loggerhead Shrikes are associated with areas that contained a high proportion of short grass around the nest sites (Gawlik and Bildstein 1990). On the other hand, Prescott and Collister (1993) found that shrikes avoided areas of short grass and that occupied sites contained a higher proportion of tall grass. These results suggest that there may be a tradeoff between high prey availability (higher in tall grass) and high foraging efficiency (higher in low grass). The relationship between image texture and the probability of shrike occurrence may also be an artifact of the sampling scheme. The sites with the highest texture,

i.e., pinyon-juniper habitat, are the high-elevation sites where shrike occurrence is very rare. This may have skewed the relationship between shrike occurrence and habitat heterogeneity. In our study, shrikes were also less likely to occur in areas of high edge density between woody vegetation and grassland. In contrast, in the Chihuahuan Desert of Big Bend National Park, boundary types did not significantly explain shrike habitat use (Gutzwiller and Barrow 2008).

Our results suggest that perches and nest shrub availability are not limiting factors for Loggerhead Shrikes on Fort Bliss Army Reserve. Shrikes appear to spend time in areas that provide the most foraging opportunities. The naturally low shrub density in grass-dominated areas of our study area appears to be sufficient to fulfill Loggerhead Shrikes' requirements for perches and nest sites, and in fact the negative association of shrikes with edge density of shrubs and grasses suggests they may avoid areas where many shrubs and small trees are present (e.g., pinyon-juniper habitat). It is also important to mention that we might have obtained different insights into habitat use if we had looked at factors that explained abundance. However, the nature of our data did not allow analysis of habitat factors associated with abundance per se given the low number of birds at each plot.

Perhaps the most striking result from our study is the lack of a relationship between habitat variables and nest-based measures of fitness. This suggests that we failed to measure key elements that determine variation in habitat quality. Neither clutch size, number of fledglings, or nest success was significantly related to the broad-, intermediate-, or local-scale habitat variables that we measured. These results are in accordance with recent findings of habitat associations of the Red-backed Shrike in Italy, where none of the ecological factors associated with shrike territory at the broad- or local-scales predicted the number of young fledged (Brambilla et al. 2009). One of the main causes of nest failure for the Loggerhead Shrike in our study system was predation. The predation rate corresponds to the rate found in some other studies (e.g., Yosef (2001) reported that 32% of the nests were depredated in a 3-year long study conducted in south central Florida, USA). While we did not measure predators directly, we did measure factors known to influence predation rates, such as

vegetation structure (Martin 1993). If the habitat surrounding the nests (as captured by the broad-, intermediate-, and landscape-scale variables we measured) did not affect nest success, it is possible that some characteristics of the nest location (e.g., nest shrub species, nest height) may have increased predation risks. However, in our study system, neither nest shrub species or nest height appeared to have influenced nest predation. This finding is similar to those of Woods and Cade (1996) in which the type of shrub, or location of the nest in the shrub, did not discriminate successful and unsuccessful nests.

Our failure to identify relationships between habitat variables and measures of fitness has several other possible explanations. Because we measured habitat variables during the breeding season, for example, we did not assess habitat related to females' pre-laying condition, a main determinant of clutch size (Haywood and Perrins 1992) (e.g., quality of forage habitat before the breeding season, severity of the previous winter). Other factors, such as inclement weather during the nesting period, may also explain the measures of fitness that we examined. In southwestern Oklahoma, USA, low Loggerhead Shrike fledgling numbers were attributed to inclement weather (e.g., high precipitation and wind followed by drought) in two breeding seasons (Tyler 1992). In two shrubsteppe sparrow species reproductive success was higher in wetter years than dryer years, and within-year variability in precipitation also affected the reproductive success of Sage Sparrows (*Amphispiza belli*) (Rotenberry and Wiens 1991).

The objectives of this paper were to evaluate whether Loggerhead Shrike abundance, a measure of habitat use, is a good proxy for quality habitat, and to evaluate how habitat variables measured at different spatial scales relate to habitat use and to nest-based measures of fitness. Our results suggest that bird abundance is a significant, but not strong proxy for Loggerhead Shrike habitat quality. We also found that habitat variables including high proportion of grasslands, low edge density, low NDVI contrast and mean, and low foliage height diversity were associated with Loggerhead Shrike adult and nest occurrence. However, none of the habitat variables measured explained the variability in nest-based measures of fitness. Our results highlight both the complexity of understanding what constitutes high quality breeding habitat, and the complexity of

characterizing these factors using measurable habitat variables.

We present a promising approach, the use of image texture, for incorporating within-habitat variability in models of abundance and occurrence of wildlife species. This approach can be applied to other ecosystems as well where within-habitat variability plays an important role in defining patterns of species distribution.

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