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Extending utility of hierarchical models to multi-scale habitat selection

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Abstract

Aim: Characterizing animal habitat selection is central to ecology and conservation, and understanding selection across multiple spatial scales is a particular priority for research. However, the ability of selection models to capture multi-scale response has been limited by the dual analytical hurdles of cross-scale collinearity and overlapping landscapes. The aim of this study was to overcome these limitations using a novel, spatially hierarchical approach.

Location: North America's northern Great Plains (U.S.A. and Canada).

Methods: We developed a novel adaptation of the occupancy modelling framework that integrates animal response conditionally across scales. We then compared outcomes to those from a traditional multi-scale model. We illustrated our approach using the breeding distribution of two North American grassland songbirds of conservation concern, Sprague's Pipit *Anthus spragueii* and Chestnut-collared Longspur *Calcarius ornatus*.

Results: Our model successfully captured bird response to local habitat within a broader landscape context, even when habitat associations occurred in opposite directions across scale. Probabilities of occupancy were more strongly affected by local conditions when landscape context was favourable than when it was unfavourable. The traditional multi-scale approach extended problems of scale into spatial predictions by over-estimating occurrence where conditions were locally favourable but regionally unsuitable.

Main conclusions: The spatially hierarchical approach provides an integrated model of habitat selection across scales by allowing broader landscape context to shape local response to conditions. For grassland songbirds, our application enabled targeting that could enhance the expected benefits of conservation when compared to the traditional approach.

KEYWORDS
Anthus spragueii, *Calcarius ornatus*, conservation planning, grassland songbirds, habitat selection, multi-scale occupancy

1 | INTRODUCTION

The study of habitat selection is a central focus of ecology that informs wildlife management and conservation (Boyce & McDonald, 1999; Manly, 2002). Habitat selection is a hierarchical process, with animals making movement decisions ranging from long-distance dispersal or migration to microscale selection of nesting or foraging sites (Hutto, 1985; Johnson, 1980; Wiens, 1973). Models of selection therefore are highly sensitive to scale, which includes the resolution of sampling (grain) and the size of the study area (extent; Dungan et al., 2002; Boyce, 2006; Mayor, Schaefer, Schneider, & Mahoney, 2007). Grains that are too large for animal or habitat data will miss patterns at finer scales, whereas extents that are too small constrain the order of selection captured and restrict inference (Boyce, 2006; Johnson, 1980).

Biologists often want to identify ecologically important scales of selection and to understand how relationships with habitat change across scale. Understanding scales of selection can be particularly important for conservation management applications. For example, the United States Endangered Species Act (ESA, 1973) is the country's strongest conservation law. It mandates that critical habitat for endangered species must be identified and protected but does not specify scale. Ignoring how variables across scales influence habitat suitability could lead to inappropriate or ineffective legal designations. Because of its known importance, multi-scale analysis is commonly included in species–habitat studies (Mayor, Schneider, Schaefer, & Mahoney, 2009). However, two major obstacles have plagued attempts to characterize selection across scales: (1) cross-scale collinearity and (2) the problem of overlapping landscapes around fine-scale survey data.

1.1 | Collinearity

Collinearity among predictors is a common challenge facing habitat models (Dormann et al., 2013), which is compounded in multi-scale studies (Battin & Lawler, 2006). Habitat attributes are almost always autocorrelated in space, meaning that local-scale variables show a strong relationship with similar measures at broader scales (Figure 1a; Purtauf, Thies, Ekschmitt, Wolters, & Dauber, 2005). Frequently, researchers address collinearity by dropping all but the single “best” variable from a highly correlated cross-scale group. While this does reduce collinearity within predictors, it is not desirable because potentially important information is lost from other scales. Further, ecological variables can behave in unpredictable and often unintuitive ways across scale, making selection of a single best scale a non-trivial task that has profound implications for model interpretation (Wheatley, 2010).

Another common approach when dealing with cross-scale collinearity is to model animal response separately at several scales and then compare model likelihoods (Lawler & Edwards, 2006). This approach, too, can be misleading because variables modelled at any one scale may still include substantial information from latent cross-scale

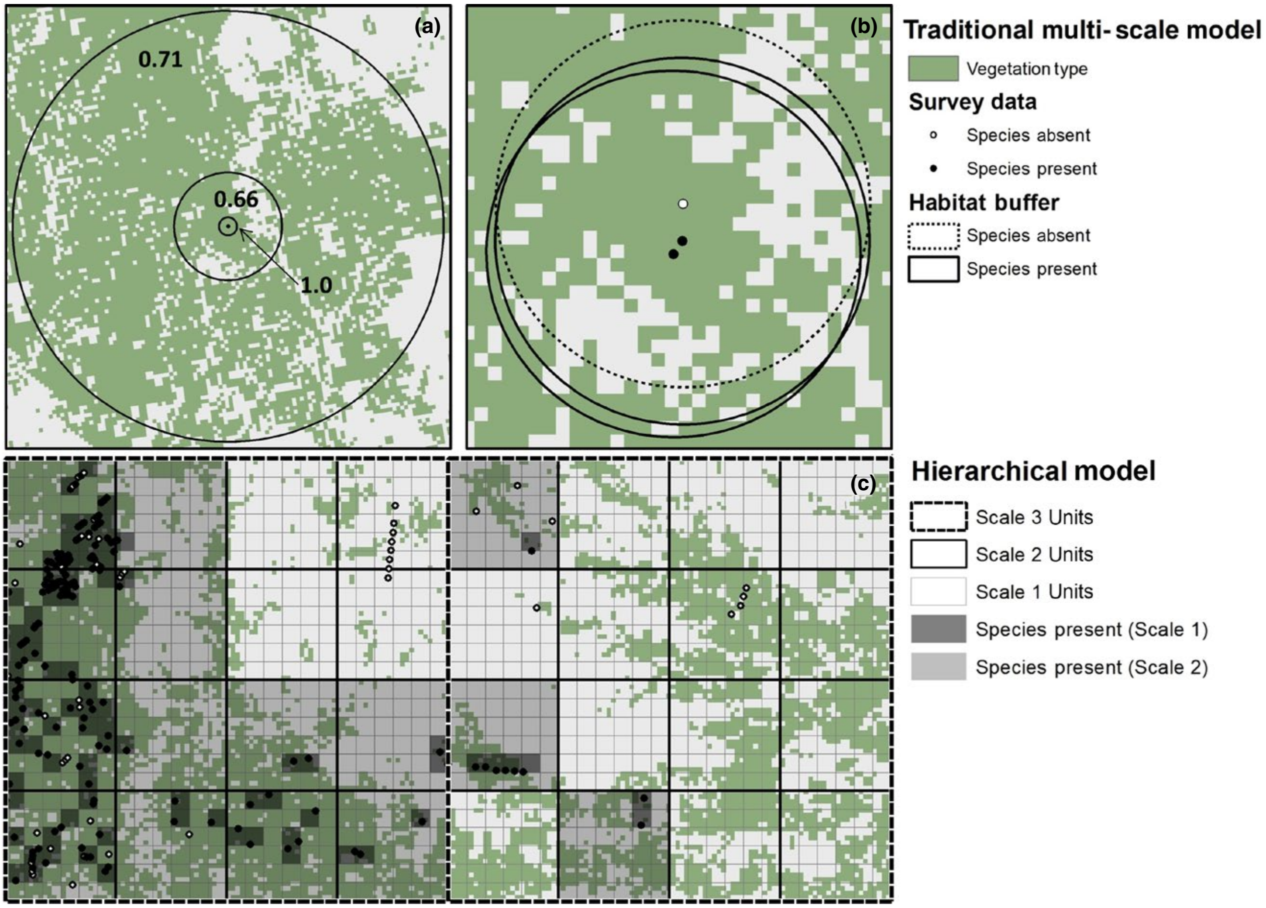

FIGURE 1 Common problems facing studies of habitat selection at multiple scales compared with a spatially hierarchical approach. (a) Concentric buffers often lead to cross-scale collinearity in habitat covariates. Numbers indicate proportional cover of a vegetation type in each buffer. (b) Overlapping landscapes result from clustering of survey points and artificially decrease variability in the predictor. (c) Two occupied broad-scale units from the spatially hierarchical sampling frame. Shading indicates observed occupancy at intermediate and fine scales. [Colour figure can be viewed at wileyonlinelibrary.com]

correlations (Battin & Lawler, 2006; Cushman & McGarigal, 2002; Mahon, Martin, & Lemay, 2008). For example, Bakermans and Rodewald (2006) reported that availability of insect prey was not related to *Empidonax virescens* (Acadian Flycatcher) abundance in riparian forests of central Ohio, despite a known importance of prey to territory selection and reproductive success. Broader scales of analysis revealed that birds were avoiding more urbanized areas that also happened to have higher than average insect abundance (Bakermans & Rodewald, 2006). In this case, the broad-scale correlation between insect abundance and land use was likely confounding observed patterns of local selection. Without the broad-scale analysis, the results of this study could have led managers to disregard an important component of habitat quality for this species.

1.2 | Overlapping landscapes

Although broad-scale processes like land use or climate gradients almost certainly influence distributions of many species, the ability to detect their effects is often limited by sampling constraints. Survey data are typically clustered at a relatively fine scale, leading to an increasingly high degree of overlap in surrounding landscapes as scale of analysis increases (Figure 1b). Use of habitat data from overlapping landscapes equates to pseudoreplication in most modelling frameworks and can result in non-independence of residuals (Eigenbrod, Hecnar, & Fahrig, 2011; Zuckerberg et al., 2012), artificially narrow confidence intervals (Legendre, 1993) and diminished statistical power from reduced variability in predictors (Eigenbrod et al., 2011).

Ecologists have used three basic strategies to mitigate the problem of overlap, none of which is entirely satisfactory (Zuckerberg et al., 2012). Some researchers proactively design sampling to minimize clustering and overlap (Eigenbrod et al., 2011), whereas others thin data by removing overlapping sites a posteriori (Koper & Schmiegelow, 2006). The first approach reduces the efficiency of data collection and the second results in information loss and wasted sampling effort. Most frustrating perhaps is that the elimination of overlap does not necessarily remove autocorrelation in the data, and neither method guarantees statistical independence (Zuckerberg et al., 2012). A third approach controls for autocorrelation directly by modelling it and removing its effect (Dormann et al., 2007; Thogmartin & Knutson, 2007). However, because autocorrelation can reflect latent biological or environmental processes (Keitt, Bjørnstad, Dixon, & Citron-Pousty, 2002; McIntire & Fajardo, 2009), its removal can actually obscure patterns of interest.

1.3 | Spatially hierarchical models

Hierarchical models represent an elegant solution to the problems of collinearity and overlapping landscapes in studies of multi-scale habitat selection. In a hierarchical model, parameters are related to one another through a joint probability that reflects the dependence among them (Gelman, Carlin, Stern, & Rubin, 2004). This framework provides the basis for the rapidly growing field of occupancy modelling, which has already supplied myriad novel and innovative ways to analyse biological data. Occupancy modelling was first developed as a method to integrate imperfect detection in survey data as a nested process within species distribution models. It differs from standard logistic regression because it estimates probability of occupancy (ψ) rather than probability of occurrence (Lele, Merrill, Keim, & Boyce, 2013; MacKenzie et al., 2006). Occupancy is then separated from probability of detection (p) by parameterization through repeated sampling in time or space (MacKenzie et al., 2006). The structure of occupancy models is naturally hierarchical, wherein the detection process is constrained by the occupancy state. For example, if a species is absent, it cannot be detected no matter how high the probability of detection. Occupancy models have already been extended to address diverse ecological questions including habitat selection (MacKenzie et al., 2002), species abundance and diversity (Royle, 2004), spatial replicates (Kery & Royle, 2008), multiple observers (MacKenzie et al., 2006), multiple detection methods (Nichols et al., 2008) and multi-scale occupancy (Mordecai, Mattsson, Tzilkowski, & Cooper, 2011; Nichols et al., 2008; Pavlacky, Blakesley, White, Hanni, & Lukacs, 2012).

This paper extends the spatially hierarchical occupancy framework pioneered by Nichols et al. (2008), Pavlacky et al. (2012) and Mordecai et al. (2011) to incorporate a multi-scale habitat selection process. Nichols et al. (2008) were the first to apply an occupancy model hierarchically across two spatial scales, separating species use of sample units from presence at individual survey sites. Pavlacky et al. (2012) used this multi-scale framework to effectively account for non-independence of spatially replicated monitoring data, but did not include habitat covariates. Mordecai et al. (2011) applied a two-scale model to analyse distribution of *Seiurus motacilla* (Louisiana Waterthrush) in the south-eastern U.S.A. Although these authors did associate habitat with distribution across scales, variables were each measured at only one scale. Here, we extend their approach by scaling habitat variables along with occupancy and relating them across multiple, nested scales. Our method represents a novel adaptation of the occupancy modelling framework that addresses some of the most common problems facing studies of multi-scale habitat selection.

The hierarchical structure of occupancy modelling allows for conditional integration of multi-scale covariates, which reduces collinearity and overlapping landscapes and clarifies interpretation of species–habitat relationships across scale (Figure 1c). Cross-scale collinearity is reduced because the dependence among scales is modelled explicitly through a joint probability. Because occupancy is also hierarchical in space, habitat covariates at broad scales are related to landscape occupancy at the same scale prior to integration across scales; thus, landscapes have no need to overlap (Figure 1c). Here, we applied the spatially hierarchical framework to investigate how variables of known local importance scale up to broader extents and how patterns at broad extents constrain local selection. To illustrate model application, we analysed the breeding distribution of two at-risk grassland songbird species in the northern Great Plains of North America and compared results to those from traditional multi-scale logistic regression.

2 | METHODS

2.1 | Modelling framework

Our application of spatially hierarchical models uses a consistent set of variables to estimate integrated response to habitat across scales. We conducted analyses in Program R (R Development Core Team, 2013) and estimated model parameters with JAGS (Plummer, 2003) through package R2JAGS (Su & Yajima, 2012).

Traditional models of habitat selection seldom include the same covariate measured at different scales because collinearity violates model assumptions and confuses interpretation. The separation of scales of analysis into different levels of a hierarchical model allows us to overcome these limitations. Further, this framework provides a method of gaining additional information from the same data and does not require additional sampling. Our model is spatially hierarchical where occupancy at finer scales is conditional on occupancy at broader scales. The parameter ψ represents broad-scale occupancy and can be interpreted as the proportion of broad-scale units that are occupied in the study region. The parameters for finer-scale occupancy correspond to species presence conditional on presence in the scale(s) above. Intermediate-scale occupancy (θ) is conditional on ψ and local occupancy (ϕ) is conditional on θ and ψ. The conditional product $\psi|\theta|\varphi$ corresponds to local-scale occupancy. Within each level, habitat covariates can be included in logistic regression to estimate level-specific probability of occupancy. The model for nested units of three scales *i*, *j* and *k* (Figure 1) is specified as:

Broad-scale process model in unit *i*:

$$X_i \sim \text{Bernoulli}\,(\psi)$$
$$\text{logit}(\psi) = \beta_0 + \beta_x \times \text{covariate}_{x\ldots}$$

Intermediate-scale observation model in unit *i,j*:

$$Y_{ij} \sim \text{Bernoulli}\,(X_i \times \theta)$$
$$\text{logit}(\theta) = \alpha_0 + \alpha_y \times \text{covariate}_{y\ldots}$$

Fine-scale observation model in unit *i,j,k*:

$$Z_{ijk} \sim \text{Bernoulli}\,(Y_{ij} \times \phi)$$
$$\text{logit}(\phi) = \delta_0 + \delta_z \times \text{covariate}_{z\ldots}$$

where *X*, *Y* and *Z* are the latent occupancy state at broad-, intermediate- and fine-scale levels, respectively, and can be either occupied (1) or not occupied (0). Covariates are measured at the scale of occupancy in each level.

2.2 | Case study: grassland songbirds in the North American Great Plains

Scale-dependent habitat selection is well recognized in migratory songbirds (Battin & Lawler, 2006; Hutto, 1985; Wiens, 1973). To demonstrate application of our multi-scale modelling approach, we analysed the breeding distribution of two grassland songbird species of high conservation concern in the northern Great Plains of the U.S.A. and Canada. Sprague's Pipit *Anthus spragueii* (Audubon, 1844; herein "pipit") is a grassland specialist that breeds in relatively moist, native mixed-grass prairie (Davis, Robbins, & Dale, 2014). Chestnut-collared Longspur *Calcarius ornatus* (Townsend, 1837; herein "longspur") shares a similar breeding distribution but prefers grassland with sparser cover (Hill & Gould, 1997; Lipsey & Naugle, in press). Both species have been declining across North America more than 3% annually since 1966 (Sauer et al., 2014) and are federally Threatened in Canada (COSEWIC, 2009; Environment Canada, 2012). The International Union for Conservation of Nature lists the pipit as globally Vulnerable and the longspur as Near-Threatened (IUCN, 2014).

2.2.1 | Data preparation

We assembled songbird data from 32,204 point counts from 2007 to 2012 in a study region that includes the northern Great Plains of the U.S.A. and Canadian prairie provinces (Lipsey et al., 2015; see Appendix S1 in Supporting Information). Data were collected or compiled by Alberta Fisheries and Wildlife Management Information System, the North American Breeding Bird Survey, the Bird Conservancy of the Rockies, Environment Canada, the Canadian Wildlife Service, Montana Natural Heritage Program, the University of Montana and the University of Manitoba. Surveys were at least 200-m apart and were not repeated. We superimposed an arbitrary, hierarchically nested lattice across the study region with cells corresponding to three spatial scales of analysis (Figure 1c). We used scales defined by the standard U.S. cadastral system (White, 1983) because these form the basis of land ownership and management in the region. The scales included 2.6-km^2 (section), 93-km^2 (township) and 1,492-km^2 (quadrangle; Figure 1c). Each unit at the finest scale of analysis (2.6-km^2) contained from 0 to 10 individual survey points. Due to processing limitations, we excluded 1,134 survey points that fell in units containing >10 points. We selected these for exclusion based on date, keeping the most recent.

2.2.2 | Occupancy

Observed patterns of species occupancy represented the dependent variable in each level of analysis. We translated occupancy across scales using simple presence/absence: if a species was observed in a given survey, the fine-, intermediate- and broad-scale cells containing the survey point were each considered to be occupied (Figure 1c). Species were absent only if all surveys in the unit were non-detections. Units containing no surveys were treated as missing data and predicted under the Bayesian framework. Because the number of surveys per fine-scale unit varied from 0 to 10, those containing fewer surveys faced a risk of non-detection or false absence from insufficient sampling. We corrected for this by including a fourth parameter to the model (*p*) to estimate species availability for detection in individual surveys. To control for sampling effort across fine-scale units, we also included the number of surveys (0–10) as a covariate in the fine-scale observation model. We used uninformative, uniform priors constrained between −10 and 10 for all parameters. We ran three chains without thinning for a total of 102,000 Markov chain Monte Carlo iterations. The first 2,000 iterations were discarded as burn-in. Model convergence was determined through the Gelman–Rubin diagnostic.

The use of a multi-year dataset greatly improved spatial coverage compared to data from any single year. However, the inclusion of multiple breeding seasons violates the assumption of closure and p therefore refers only to availability for detection in a survey given that the cell has been occupied at any time during sampling. When survey data from multiple years occur within the same cell, this parameter accounts for annual differences in true occupancy. Similarly, when multiple survey points from the same year fall within the same cell, p accounts for non-detections in an occupied cell. This is desirable because our intended scope of inference was to evaluate general patterns of occupancy across the breeding distribution within the 5-year time frame.

2.2.3 | Habitat metrics

We included two habitat metrics as model covariates across scales: proportion grassland and Normalized Differential Vegetation Index (NDVI). Grassland amount is a crucial component of habitat for both study species because it provides resources important throughout their life history (Davis et al., 2014; Hill & Gould, 1997). We derived a binary layer of grassland from 30-m land cover products created by Agriculture Agri-Food Canada (2001) and level II of the Multi-Resolution Land Characteristics Consortium 2011 National Land Cover Dataset (Homer et al., 2015). We calculated proportional variables using an aggregated mean of the binary layer at each relevant spatial scale.

We included NDVI because vegetation biomass is an important habitat factor for grassland birds, eliciting strong selection responses that are variable across bird species (Fisher & Davis, 2010). NDVI allows remote detection of live green plant canopies, where higher values correspond with greater fractional vegetation cover and leaf area in the sampled pixel (Carlson & Ripley, 1997). We used remotely sensed NDVI from moderate resolution imaging spectroradiometer data sampled at a 250-m resolution for July (LP DAAC, 2014), July is approximately the peak of vegetative growth in the region and allows good biomass discrimination (Wang, Rich, Price, & Kettle, 2005). Because survey locations from multiple years often fell into the same fine-, intermediate- or broad-scale sampling unit of the hierarchical model (Figure 1), we used averaged NDVI values across the full 5-year time frame (2007–2012). To control for the variability in NDVI caused by non-grassland vegetation like wetland or woodland, we included an interaction term between grassland amount and NDVI. To facilitate Bayesian parameter estimation and allow direct comparison of coefficients, we standardized all habitat covariates by centring on the mean and scaling by standard deviation.

2.2.4 | Comparison with traditional approach

To compare performance of spatially hierarchical models with a traditional multi-scale approach, we fit models for each species and each scale using standard logistic regression (Hosmer & Lemeshow, 2000) and the same set of survey data used in hierarchical model estimation. We calculated habitat covariates with concentric rectangular buffers around survey locations, corresponding to the scales used in hierarchical models (2.6, 93 and 1,492-km^2). We used the same habitat covariate layers used in spatially hierarchical models, including grassland amount and July NDVI averaged across the 5-year time frame. We determined the level of cross-scale collinearity among predictors using Pearson correlation coefficients (r). We fitted logistic regression models and then used Akaike's information criterion (AIC; Anderson, Burnham, & Thompson, 2000) and Akaike weights (Wagenmakers & Farrell, 2004) to identify the most predictive scale individually for each covariate (Boyce, 2006). Finally, we fit full models for each species that included the two covariates at their selected scale(s) and their interaction. To allow comparison of coefficients between hierarchical and traditional models, we standardized covariates by centring on the mean and scaling by standard deviation.

We compared strength of model fit to the original dataset by calculating area under the receiver operating curve (AUC; Metz, 1978) for each species and method. To assess how well model predictions matched observed patterns of distribution, we compared them to data from the Breeding Bird Survey (BBS; Sauer et al., 2014). We used the R package OPTIMALCUTPOINTS (Lopez-Raton, Rodriguez-Alvarez, Suarez, & Sampedro, 2014) to identify probability surface cut-points for each model that maximized both sensitivity and specificity of predictions and used these to create maps of predicted distribution for each species. To evaluate models, we overlaid them with known BBS distribution and calculated proportion of overlap by area.

3 | RESULTS

3.1 | Model description

Observed proportion of occurrence ranged from 0.29–0.31 to 0.23–0.25 for pipits and longspurs, respectively, across scales. The effective sample size was 16,000–300,000 for the pipit model and 12,000–290,000 for the longspur model. The Gelman–Rubin diagnostic indicated convergence at all levels of each model ($.00010 > \hat{R} > .0012$). For full model outputs, see Appendix S2.

3.2 | Scale

By nesting species responses across scale, spatially hierarchical models identified the importance of environmental factors operating over multiple scales in shaping species distributions (Table 1). By contrast, highly overlapping buffers in traditional models (Figure 1b) limited results to consideration of only fine-scale variables. Cross-scale collinearity in traditional concentric buffers (Figure 1a) was extremely high for both habitat metrics (r = .79–.90 and r = .92–.97 for proportion grassland and NDVI, respectively), necessitating the choice of a single scale for inclusion in models. For both species, predictor variables measured at the finest scale had by far the best fit (Table 2). We therefore used fine-scale metrics for covariates in traditional models.

TABLE 1 Coefficients showing response of two grassland songbird species to habitat covariates in central North America, 2007–2012, comparing traditional single-scale logistic regression and three nested levels of a spatially hierarchical model. Covariates were standardized by centring on the mean and scaling by standard deviation. Bold type indicates coefficient significance at $p < .05$ (traditional model) or Bayesian confidence interval that does not overlap zero (spatially hierarchical model). Scales include broad (1,492-km^2), intermediate (93-km^2) and fine (2.6-km^2)

	Traditional	Spatially hierarchical		
	Fine	Broad	Intermediate	Fine
Sprague's Pipit				
Intercept	**−1.63**	−0.07	**0.33**	**−0.40**
Grassland	**1.37**	0.24	**1.10**	**0.54**
NDVI	**0.28**	0.13	**0.50**	**0.33**
Grass × NDVI	**0.36**	**0.36**	**0.41**	0.00
Chestnut-collared Longspur				
Intercept	**−2.01**	**−0.43**	0.06	**−0.66**
Grassland	**1.16**	**1.15**	**0.73**	**0.14**
NDVI	**−0.14**	0.05	**0.32**	**−0.22**
Grass × NDVI	**0.14**	**0.79**	0.07	**−0.19**

3.3 | Occupancy

Estimates of occupancy from spatially hierarchical models (ψ, θ and ϕ) indicated that species were widely distributed within the study region and that this pattern was relatively consistent across scales (Table 3). In general, about half (34%–58%) of sample units at any scale were predicted to be occupied by each species. Birds were most patchily distributed below the intermediate scale (93-km^2). Survey-level availability for detection was comparable and high for both species (.65–.67), suggesting that if a species was detected in a fine-scale unit (2.6-km^2) at least once during the 5-year time frame, it was likely to be detected in other surveys within that unit.

3.4 | Sprague's Pipit habitat

Nested habitat metrics across scales allowed us to characterize how species' response to local habitat varied with the broader landscape context (Table 1; Figure 2). Grassland was the primary factor shaping distribution of pipits across scales, and grass availability at intermediate scales (93-km^2) was particularly important (Table 1). Pipits were also positively associated with high NDVI at all scales, and there was a positive interaction between grassland and NDVI at broad and intermediate scales, indicating that the positive relationship with NDVI occurred only when grassland amount was also high (Table 1). Pipits' response to local habitat increased when landscape context was favourable, and traditional models were unable to capture this difference. For example, the hierarchical model predicted that occupancy for pipits in a high-quality local site (100% grass cover) was up to three times greater (0.6 vs. 0.2) when the landscape also contained a high proportion of grass (Figure 2a,b). Fine-scale grass cover was estimated to be four times more influential in the traditional model compared to the hierarchical model when landscape context was poor (probability of occurrence .9 vs. probability of occupancy .2; Figure 2).

3.5 | Chestnut-collared longspur habitat

Habitat relationships for longspurs were similar to those for pipits as both showed multi-scale selection for grassland cover. However, longspurs responded most strongly to grass at the broadest scale whereas

TABLE 2 Parameter estimates (β_i), standard error (SE_i), log likelihood ($\text{Log}[L_i]$), Akaike's information criterion (AIC_i), difference in AIC versus top model ($\Delta[AIC_i]$) and Akaike weights ($w_i[AIC]$) for traditional logistic regression models of individual predictor variables across three spatial scales for Sprague's Pipit (A) and Chestnut-collared Longspur (B). Grassland is proportion of grassland land cover and NDVI is mean Normalized Differential Vegetation Index. Scales include broad (1,492-km^2), intermediate (inter.; 93-km^2) and fine (2.6-km^2). Each model was fitted individually with a given species, variable and scale. Sample size for all models was $n = 31{,}070$. All models were highly significant ($p < .0001$)

(A)						
	β_i	SE_i	$\text{Log}(L_i)$	AIC_i	$\Delta(AIC_i)$	$w_i(AIC)$
Grassland						
Fine	3.04	.044	−12,871	25,746	0	1.00
Inter.	3.18	.043	−13,238	26,481	735	0.00
Broad	2.60	.038	−14,140	28,284	2,538	0.00
NDVI						
Fine	−0.0004	−.00001	−14,693	29,390	0	1.00
Inter.	−0.0004	−.00001	−14,734	29,472	82	0.00
Broad	−0.0004	−.00001	−14,897	29,797	407	0.00
(B)						
Grassland						
Fine	3.08	.058	−11,890	23,784	0	1.00
Inter.	3.52	.050	−11,963	23,931	147	0.00
Broad	2.48	.068	−12,394	24,792	1,008	0.00
NDVI						
Fine	−0.0005	−.00001	−13,111	26,226	0	1.00
Inter.	−0.0005	−.00001	−13,179	26,361	135	0.00
Broad	−0.0005	−.00001	−13,380	26,764	538	0.00

TABLE 3 Occupancy estimates for two species at three nested spatial scales and availability for detection (*p*) at survey points within occupied fine-scale units in central North America, 2007–2012. Scales include broad (ψ; 1,492-km^2), intermediate (θ; 93-km^2) and fine (ϕ; 2.6-km^2)

	Sprague's Pipit			Chestnut-collared Longspur		
	Mean	95% Lower	95% Upper	Mean	95% Lower	95% Upper
ψ	0.48	0.41	0.56	0.40	0.32	0.48
θ	0.58	0.54	0.62	0.51	0.46	0.57
ϕ	0.40	0.37	0.43	0.34	0.31	0.37
p	.65	.64	.66	.67	.66	.68

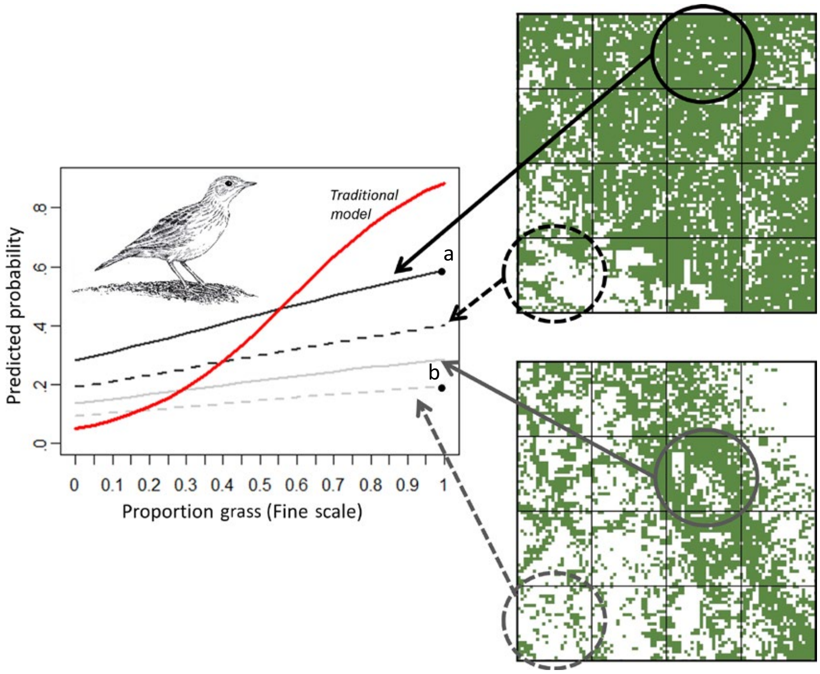

FIGURE 2 Response of Sprague's Pipit (*Anthus spragueii*) to fine-scale (2.6-km^2) grassland amount depends on landscape context in central North America, 2007–2012. Red line shows probability of occurrence from traditional, logistic regression models using local-scale habitat data. Black lines show predicted probability of occupancy in a broad-scale landscape (1,492-km^2) with high grass cover (100%), grey lines show probability of occupancy in a landscape with low grass cover (10%). Solid lines show probability of occupancy with high grass cover (100%) at the intermediate scale (93-km^2), and dashed lines show probability of occupancy with low intermediate-scale grass cover (30%). Models were estimated with above-average Normalized Differential Vegetation Index (0.75) at all scales. A suitable local site would be three times more likely to be occupied in the high-grass landscape (a) than the low-grass landscape (b). [Colour figure can be viewed at wileyonlinelibrary.com]

pipits were more closely associated at the intermediate scale (Table 1). Longspurs' relationship with NDVI is another example of the importance of landscape context in habitat selection. Locally, longspurs selected low NDVI and the traditional model suggested a weak negative relationship (Table 1; Figure 3). However, the hierarchical model revealed that longspurs selected productive grassland landscapes at broad scales and only selected for dry patches within these landscapes (Table 1; Figure 3). For example, a site with a locally low NDVI of 0.3 would have four times the probability of occupancy for longspurs if it was within a high-NDVI landscape (.4 vs. .1; Figure 3a,b). The traditional model was unable to account for broad-scale NDVI and produced estimates of high occurrence in dry landscapes that exceeded estimates of occupancy from hierarchical models by as much as three times (Figure 3).

3.6 | Spatially explicit example

Models had moderate fit for both species and overall fit was comparable between the hierarchical and traditional approaches (hierarchical model AUC = 0.77 for both species, traditional model AUC of 0.78 and 0.77 for pipit and longspur, respectively). Predicted distributions from hierarchical models more closely matched BBS distributions than those of traditional models for both species. For pipits, the hierarchical prediction had more overlap with BBS (80%) than that of the traditional model (75%). Improvement for longspurs was even more marked (96% vs. 84%; Figure 4).

4 | DISCUSSION

Spatially hierarchical models offer a deeper, more integrated understanding of multi-scale habitat selection than traditional approaches. Nested relationships adjust response to local habitat according to the broader landscape context. For instance, pipits were up to three times more likely to occupy the same habitat inside versus outside a high grassland landscape (Figure 3a,b). The traditional modelling approach could not capture this variability and instead linked occurrence only to locally

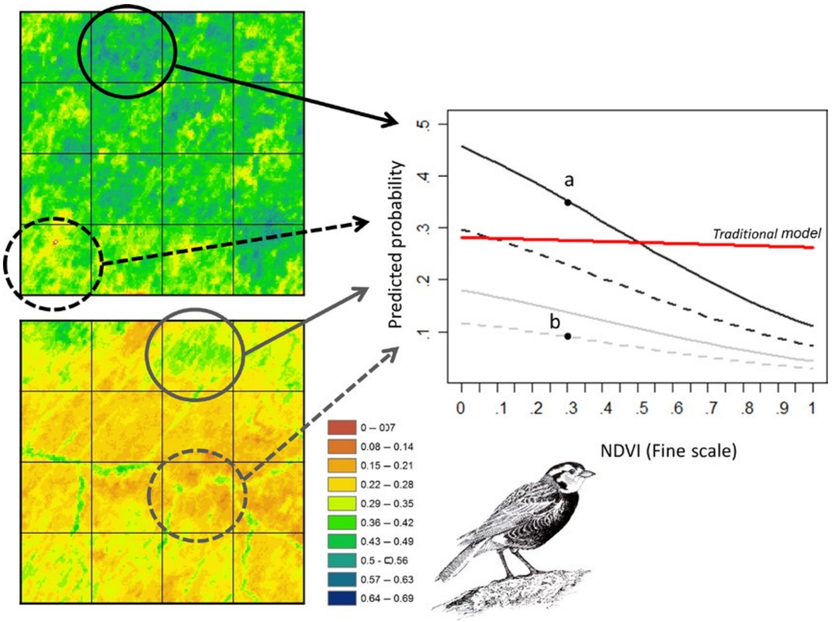

FIGURE 3 Response of Chestnut-collared Longspur (*Calcarius ornatus*) to fine-scale (2.6-km^2) Normalized Differential Vegetation Index (NDVI) depends on landscape context in central North America, 2007–2012. Red line shows probability of occurrence from a traditional logistic regression model using fine-scale data. Black lines show predicted probability of occupancy in a broad-scale landscape (1,492-km^2) with above-average NDVI (0.75), and grey lines show probability of occupancy in a landscape with below-average NDVI (0.4). Solid lines show probability of occupancy with above-average NDVI (0.7) at the intermediate scale (93-km^2), and dashed lines show probability of occupancy with below-average intermediate-scale NDVI (0.3). Models were estimated with above-average grassland cover (60%) at all scales. A suitable fine-scale site would be four times more likely to be occupied in the high-NDVI landscape (a) than the low-NDVI landscape (b). [Colour figure can be viewed at wileyonlinelibrary.com]

favourable habitats regardless of landscape context. Moreover, effect of habitat at multiple scales became cumulative when the direction of response was consistent. Conditionally integrated responses revealed that changes in local conditions had a stronger influence on occupancy in suitable landscapes, which were already more likely to be occupied. For pipits, local conditions could affect probability of occupancy by as much as 30% in high grassland landscapes versus only 10% in grass-poor landscapes (Figure 3). In this case, the spatially hierarchical approach enables targeting that could greatly enhance the expected beneficial outcomes of grassland conservation or restoration for songbirds.

Many studies of habitat selection include multiple scales, such as a recent method developed by DeCesare et al. (2012) called scale-integrated resource selection functions (SRSF). These authors show that a single SRSF can be used to simultaneously predict habitat suitability at three scales and demonstrate how inclusion of multiple scales can affect critical habitat designations under ESA. The approach is similar to the one presented here, except that in DeCesare et al. (2012), probability of use at each scale is estimated separately prior to integration. Without the joint probability distribution of a hierarchically nested structure, collinearity remains a concern in SRSF and variables at each scale must be assumed to be independent. By contrast, our spatially hierarchical approach is capable of capturing complex nested patterns of response, even when variables are highly correlated across scale(s).

Spatially hierarchical models were uniquely able to capture selection when it occurred in opposite directions across scales (Thogmartin & Knutson, 2007; Wheatley, 2010). Longspurs occupied grassland landscapes with high NDVI but locally selected sites with less biomass (Table 3). Measured traditionally at a single scale, these responses were contradictory and strength of longspurs' local preference for low NDVI was diluted by landscape associations. Sign changes in response to habitat across scale have been reported for other species but never modelled explicitly. In one example, the influence of moisture in prairie hardwood transition forests on *Hylocichla mustelina* (Wood Thrush) was negative at local and landscape scales but positive at intermediate scales (Thogmartin & Knutson, 2007). Authors interpreted findings as selection for dry patches within wet landscapes but were unable to model this nested response in an integrated fashion.

We identified important spatial scales of selection that are orders of magnitude broader than those previously recognized for grassland songbirds. Few studies measure response to habitat in landscapes >1000-ha, and even fewer consider much broader scales (e.g., 80,000-ha; Thogmartin, Knutson, & Sauer, 2006). Cross-scale collinearity limited our traditional models to a single scale of analysis for habitat metrics and over-emphasized the importance of local variables. Despite the importance of landscape context in hierarchical models, overlapping buffers in the traditional approach biased model selection heavily towards local scales.

Management of ecosystems often manifests at human administrative scales. For example, agricultural land sales, conversions, restorations and other management in the northern Great Plains occur at the scale of a section, or one square mile. It is an advantage of the spatially hierarchical approach that its conditional cross-scale integration can assess and identify wildlife responses to changes at such

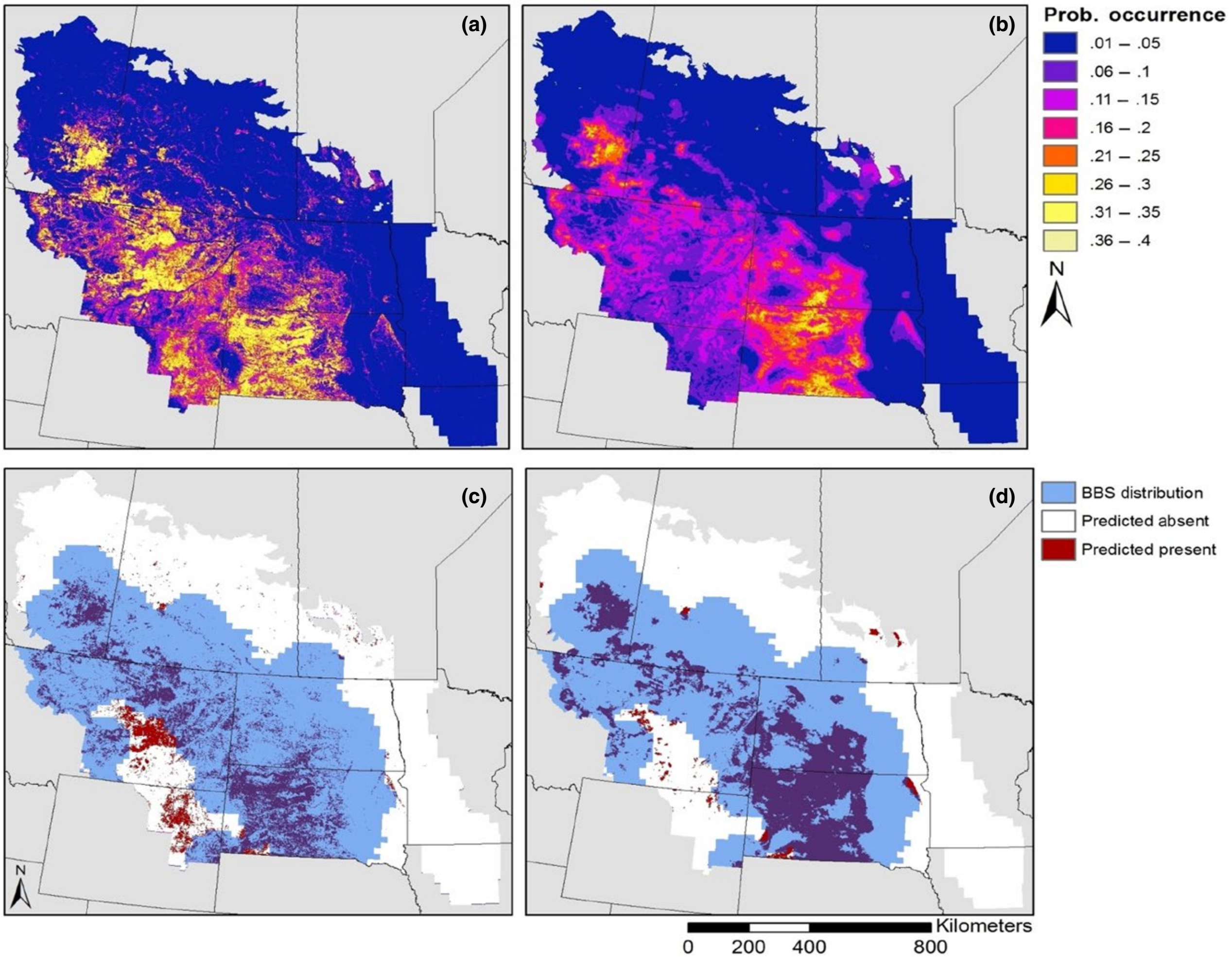

FIGURE 4 Spatial predictions from traditional logistic regression (a, c) and spatially hierarchical models (b, d) for Chestnut-collared Longspur (*Calcarius ornatus*) distribution in central North America, 2007–2012. Continuous predicted probability surfaces shown in a and b. Optimal cut-points of 0.24 and 0.13 were used for traditional and hierarchical models, respectively, to generate predicted distributions (c, d). Observed distribution from the Breeding Bird Survey (BBS; Sauer et al., 2014) shown in transparent blue on top of predictions in c and d. Map projection: Albers Conic Equal Area. [Colour figure can be viewed at wileyonlinelibrary.com]

anthropologically relevant scales. Of course, inference from hierarchical models could be even further strengthened by incorporating biologically derived scales of analysis (Wheatley & Johnson, 2009). We commend recent techniques that use count (Bellier, Monestiez, Certain, Chadoeuf, & Bretagnolle, 2012) and movement data (Frair et al., 2005) to characterize the spatial scales of animal perception and movement. Including animal-centric scales as levels within a spatially hierarchical model would promise great advances in our understanding of species–habitat relationships.

The inherent problem of scale in traditional habitat modelling extends into spatially explicit predictions used to guide real-world conservation decisions. We demonstrate that traditional models may overpredict occurrence where conditions are locally favourable but regionally unsuitable. For example, maps of traditional output for longspurs wrongly identified the south-west part of our study region as a priority for conservation (Figure 4a,b). Longspurs are in fact so rare in the south-west that BBS excludes it from the species range (Figure 4c,d). This xeric region was largely unoccupied by longspurs because locally favourable conditions were not embedded within more productive landscapes as identified by NDVI. Had this map been used to inform conservation, actions that would be better placed in the north and east could be wasted in the south-west.

The problem of scale is one of the greatest obstacles to understanding species–habitat relationships. Anthropocentric bias in sampling biological communities and associated environmental attributes can distort our perception of habitat selection and limits the utility of habitat-based models in ecology and conservation. The spatially hierarchical approach presented here reduces anthropocentric bias by providing a more holistic measure of species' response that is less sensitive to scale(s) of sampling. Further, our approach helps maximize the information extracted from a given set of occupancy data without requiring new investments of time or resources in the field. Advantages extend beyond methodological considerations to include tractable conservation applications. Conditional integration of animal response across scales enables targeting of management within landscapes that will amplify beneficial outcomes of conservation.

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BIOSKETCH

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AUTHOR CONTRIBUTIONS

M.K.L., D.E.N. and P.M.L. conceived the ideas; M.K.L. compiled data; M.K.L. and J.J.N. performed the analyses; M.K.L. and D.E.N. led the writing, which was commented on and improved by all the authors.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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