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RESEARCH ARTICLE

Predicting species-habitat relationships: does body size matter?

Erica F. Stuber · **Lutz F. Gruber** · **Joseph J. Fontaine**

Abstract

Context Allometric scaling laws are foundational to structuring processes from cellular to ecosystem levels. The idea that allometric relationships underlie species characteristic selection scales, the spatial scales at which species respond to landscape features, has recently been investigated, however, supporting empirical evidence is scarce.

Objectives Lack of pattern can be explained by inaccurate estimation, low power, confounding factors, or absence of a relationship. In this paper, we evaluate the relationship between body size and species characteristic selection scales after overcoming limitations of previous study designs.

Methods We conducted 1328 avian point counts across the state of Nebraska using the robust sampling design to account for imperfect detection. We used Bayesian latent indicator scale selection with N-mixture models to estimate species' characteristic selection scales of six habitat features for 86 species. We propagated the uncertainty associated with assigning characteristic scales to a model of the relationship between body size and characteristic spatial scales.

Results Species characteristic scales varied across habitat predictors, and varied in the uncertainty associated with selecting single characteristic scales. After propagating uncertainty our results do not support a relationship between species' body size and the spatial scales at which they respond to landscape features.

Conclusions As species abundance integrates birth, death, immigration, and emigration processes, each of which are influenced by ecological processes manifesting at various scales, we question whether a general allometric relationship should be expected. Our results suggest that selection may act on responses to specific environmental features, rather than responses to spatial scale per se.

Keywords Allometry · Bayesian latent indicator scale selection · BLISS · Multi-scale · Scale of response · Species characteristic scale

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Introduction

It is increasingly apparent that the scale at which individuals perceive and interact with their environment shapes the response of species to ecological conditions (Wiens 1976; Johnson 1980; Fahrig 2001). Indeed, the notion that particular spatial scales may best describe specific species-habitat relationships is substantiated across a wide range of taxa (Roland and Taylor 1997; Saab 1999; Mowat 2006; Nams et al. 2006), and is formally termed the species characteristic selection scale (SCSS) (Holland et al. 2004). The SCSS framework postulates that within a species ecological conditions measured at a particular spatial scale can best-predict species' responses, whereas conditions measured at other spatial scales may poorly predict species' responses (Robinson 1950). As such, mismatches between the scale at which we consider species to respond to environmental conditions, and the true scale of the ecological processes affecting the species can contribute to incorrect inference (Henebry 1995; Keitt et al. 2002). Despite the potential importance of SCSS in shaping our understanding of everything from species richness and community dynamics (Levin 1992; Rahbek and Graves 2001; Whittaker et al. 2001) to conservation and management practices (Razgour et al. 2011), the underlying processes generating SCSS remain largely unknown (Miguet et al. 2016). A lack of a formal understanding of the processes driving SCSS limits our ability to develop a more predictive or hypothesis-testing framework for identifying SCSS, and thus increases the risk of mismatches between what we think we know and the true scale of the ecological processes affecting a species (Jackson and Fahrig 2015).

Body size is among a species' most apparent characteristics (LaBarbera 1989) with pervasive effects on population, community, and ecosystem processes via its functional link to individual requirements and performance (Calder 1984). For example, size-dependent metabolism can constrain population dynamics through the scaling relationship between size and individual rates of birth, growth, and death (Savage et al. 2004; West et al. 1997). The distribution of body sizes within a population can subsequently moderate a population's ability to respond to disturbance. Additionally, individual-level resource requirements, which scale with body size, can constrain population size at carrying capacity such that

abundance typically declines with increasing body size (Damuth 1981; Allen et al. 2002; Savage et al. 2004). Given the correlation between body size and other scale dependent species-specific traits such as metabolic rate, dispersal, and home range size (Peters 1986; West et al. 1997; Jenkins et al. 2007), it is not surprising that allometric scaling is increasingly invoked as a means to further our understanding of SCSS (Thornton and Fletcher 2014; Jackson and Fahrig 2015).

There are two obvious mechanisms that could underlie an allometry of SCSS. First, an allometry of SCSS could derive from size-dependent metabolic rate (West et al. 1997). Larger species have larger energetic demands that necessitate a larger area over which to collect resources (Peters 1986). Thus, a neighborhood scale with the resources necessary to support the energetic requirements of a population could explain species abundance. Second, the scale at which a species interacts with the landscape may be related to perceptual range, which is related to body size through sensory organs and mobility (Wiens 1989; Doak et al. 1992; Crist and Wiens 1994; With and Crist 1996; Zollner 2000). Larger species may respond to environmental conditions across a larger spatial scale because either they perceive the environment at larger scales (Mech and Zollner 2002), or because they are able to move farther to satisfy daily, seasonal, or annual requirements (Perry and Garland 2002).

Despite an apparent expectation for an allometry of SCSS, most studies have returned equivocal or largely null results (Hostetler and Holling 2000; Holland et al. 2005; Cunningham and Johnson 2006; Desrochers et al. 2010; Fisher et al. 2011; Thornton and Fletcher 2014). For example, none of the 22 individual avian studies analyzed in a meta-analysis demonstrated a statistically significant relationship (Thornton and Fletcher 2014). Although the repeated failure to find a relationship may suggest body size is not important in understanding the scalar relationship between species and their environment, it may also reflect issues of study design. For example, many analyses of SCSS have small sample sizes (12 beetle species: Holland et al. 2005; 6 mammal species, Fisher et al. 2011; meta-analysis of 22 avian studies: mean = 19 bird species, Thornton and Fletcher 2014), leading to relatively low power to detect the relationship of interest. This issue is further compounded when there

is a lack of variation in body sizes among species considered. In birds, the taxa with the largest number of studies performed, the average difference between the smallest and largest species considered is only 315 grams (meta-analysis of 22 avian studies: Thornton and Fletcher 2014). Combined with low sample sizes, the lack of variation in body sizes greatly reduces the statistical power of a study, likely obscuring relevant biological patterns. Finally, one of the biggest issues facing studies of SCSS is a lack of standardized methodology for choosing appropriate landscape variables and spatial scales to consider when postulating a SCSS. Species are presumably responsive to any number of land cover classifications; yet for logistical reasons, most studies limit their analyses to only a few cover types which are often averaged (among avian studies the median number is 3: Thornton and Fletcher 2014). Species clearly affiliate with different land cover types at different spatial scales (e.g., Hinsley et al. 1995; Naugle et al. 2000; Jorgensen et al. 2014), and the inclusion or exclusion of particular land cover classifications in an analysis may even alter the scale at which a species associates with any other landscape types (Stuber et al. 2017). Similarly, variation in the number of scales considered for each land cover type can play a large role in influencing the choice of a SCSS (Jackson and Fahrig 2015), and thus the potential strength of the relationship between body size and SCSS. When the number of scales considered is small, the risk of inappropriately assigning a scale to a species is high. Indeed, variation in the scales considered between different investigations has led to inconsistencies in the SCSS selected for the same species, indicating the potential for error that may further obscure relevant biological relationships (Thornton and Fletcher 2014).

Given the theoretical support for the presence of a relationship between body size and SCSS, coupled with recent meta-analyses suggesting sampling design may ultimately obscure the relationship (Thornton and Fletcher 2014), there is a need for a more comprehensive approach to explore the allometry of SCSS. Here we attempt to overcome the limitations of previous investigations by considering the relationship between body size and SCSS for 86 species representing three orders of magnitude in body size (min: 6 g, max: 6023 g). Using an analytical method (Bayesian latent indicator scale selection; BLISS) demonstrated to outperform other common SCSS

selection techniques (Stuber et al. 2017), we consider the potential for six land cover types, acting at nine candidate spatial scales (500 m–20 km radii) to reflect the specific SCSS for each of the 86 species. In considering the relationship between body size and SCSS across species, we did not average the scales of response for multiple habitat predictors, rather we included the intraspecific variation. Using error propagation, we then investigated the ability of body mass to predict SCSS while accounting for a measure of species mobility.

Methods

Data collection

We recorded the abundance of Nebraska breeding bird species (Table 1) from April-July of 2016 across Nebraska, USA using a point count sampling method (Blondel et al. 1981; Buckland et al. 2001) with up to 4 replicate samples to account for imperfect detection (e.g., the 'robust' sampling design; Pollock 1982). We performed surveys during maximum vocalization times between 15 min before sunrise and 10h00 (Ralph and Sauer 1995). During surveys, we recorded every individual seen or heard during a 3-min period within 500 m of the observer. We conducted surveys at a total of 544 survey point locations. Not all points were surveyed 4 times due to inclement weather (including fog, drizzle, prolonged rain, and wind greater than 20 km/h; n = 1328 total surveys performed).

We investigated the influence of six land cover types, row crop, Conservation Reserve Program grasses (CRP), small grain, non-CRP grassland, woodland, and wetland land cover, which are expected to influence bird abundance at multiple spatial scales (Patterson and Best 1996; Bakker et al. 2002; Van Buskirk and Willi 2004; Cunningham and Johnson 2006; Kelsey et al. 2006; Winter et al. 2006; Renfrew and Ribic 2008; Thompson et al. 2014). The proportion of each land cover type within nine spatial scales surrounding each survey point (500 m, 1000 m, 2000 m, 3000 m, 4000 m, 5000 m, 10 km, 15 km, and 20 km radii) were derived from a 30 m resolution spatially-explicit land cover product developed by the Rainwater Basin Joint Venture for the state of Nebraska, which was updated in 2015 (Bishop et al.

Table 1 Parameter estimates for the relationship between body size and SCSS accounting for species' average mobility

	β (95% CI) equal propagation	β (95% CI) proportional propagation
Intercept	3.52 (3.42, 3.63)	3.44 (3.33, 3.54)
Body mass	0.03 (− 0.003, 0.070)	0.04 (− 0.001, 0.07)
Mobility	− 0.005 (− 0.025, 0.015)	− 0.001 (− 0.02, 0.02)
CRP	− 0.016 (− 0.018, − 0.014)	0.05 (0.047, 0.059)
Grain	− 0.04 (− 0.042, − 0.038)	0.022 (0.017, 0.029)
Grass	− 0.02 (− 0.023, − 0.019)	0.075 (0.070, 0.081)
Woodland	0.033 (0.031, 0.036)	0.126 (0.12, 0.13)
Wetland	0.054 (0.052, 0.057)	0.136 (0.13, 0.14)

Error propagation was performed by sampling the posterior distributions of BLISS scale estimates equally across species (Equal Proportion) and in proportion to species' prevalence in the dataset (Proportional Propagation). Mean estimates (β) and uncertainty (95% credible interval (CI)) are presented based on 5000 samples of the posterior distribution. The Intercept represents the row crop land cover type; all other land cover estimates represent differences from the Intercept

2011). We chose the six spatial scales because they range from the minimum point count sampling unit, to substantially larger than expected breeding territory sizes represented in our sample of species (Jackson and Fahrig 2012).

Statistical analysis

We modeled the relative abundance of 86 bird species using a standard Bayesian N-mixture model, which combines a Poisson model for the latent ecological process governing the distribution of species abundance on the landscape with a conditional Binomial model for the observation process regulating how many birds are counted at a given location using our repeated-measures design (Royle et al. 2007). Our sampling design enabled us to model the key quantity of interest, relative abundance, while correcting for imperfect detection of individuals (Tyre et al. 2003; Royle et al. 2005), which is often ignored in studies of spatial scaling relationships.

We assumed a closed population for each site within each year (Royle 2004), and we included year, and the linear and quadratic effects of six land cover types as fixed effects (centered on the grand-mean) in the linear predictor for the ecological process. Our linear predictor for detection probability included date, time of survey and its quadratic effect, cloud cover, wind speed, and temperature all centered on the grand mean and scaled to 1SD, and observer identity (total 8) as a random effect to account for among-individual differences in surveyor ability (Kendall et al. 1996; Diefenbach et al. 2003).

Because the composition of land cover variables may influence abundance relationships at different spatial scales, we incorporated multiple possible spatial scales using Bayesian latent indicator scale selection (BLISS), a model selection approach to flexibly select the single best-performing spatial scale for each predictor variable after evaluating all possible combinations of spatial scales (Stuber et al. 2017). Briefly, the nine spatial scales represent candidate scales that entered the standard N-mixture model as latent variables with each land cover predictor appearing in the model at any of the potential scales. Similar to typical MCMC sampling of coefficient estimates, at each iteration of the reversible-jump MCMC sampling procedure used in BLISS, a possible spatial scale for each predictor is sampled. At each iteration, the model included all land-cover variables available in the study; however, at each iteration, each predictor could take a different spatial scale proportional to the predictor's probability, which allows for predictor-specific identification of the most important spatial scales (see Stuber et al. 2017 for full details). By using an independent latent scale indicator for each predictor, BLISS allows each predictor to be estimated at different spatial scales, and the reversible-jump procedure avoids collinearity between spatial scales of predictor variables. Furthermore, BLISS outperforms the most common spatial scale selection procedures currently used to identify spatial scales with the highest predictive performance (Stuber et al. 2017).

BLISS was demonstrated to be accurate in identifying true scales of effect, and returning unbiased, precise coefficient estimates of predictor variables through simulation studies under a range of commonly encountered ecological and sampling scenarios (e.g., variation in spatial and temporal replication, between-scale and between-predictor collinearity; Stuber et al. 2017). Extending the simulation study of Stuber et al. (2017) to consider between-predictor correlations of rho = 0.7, 0.8, and 0.9 indicated that the ability of BLISS to accurately predict the appropriate scale degraded at rho = 0.9 (data not shown). Because the highest correlations between our predictor variables were approximately rho = 0.8, where BLISS performs well, we retained all land cover variables for analysis.

Analyses were performed in JAGS (Just Another Gibbs Sampler; Plummer 2003) via the R programming environment (R 3.1.1 package rjags; Plummer et al. 2015) using zero-mean, normally distributed priors with large variance for fixed effects and discrete uniform priors for the nine candidate spatial scales. We used the maximum observed counts at each survey site as the initial starting values for MCMC sampling and visually inspected trace plots to confirm convergence. We ran each posterior simulation for 50,000 iterations, to attain convergence, with a burn-in period of 10,000. Models that failed to converge were run longer until they were assessed to converge (posterior distributions based on 50,000 iterations after thinning). We considered the spatial scales with the highest posterior probabilities to be the SCSS for each land cover predictor for each species, but also propagated model uncertainty for further analyses (described below).

We constructed a separate linear mixed model to estimate the relationship between the SCSS of land cover variables (log-transformed) estimated from BLISS and included species' average female body mass and species' mobility as fixed effects (both log-transformed; package "lme4": Bates et al. 2014). For all species, we retrieved adult female body mass from Dunning (1984). We used the distance between species' breeding and wintering distribution centroids based on species distribution data compiled by Bird-Life International and Handbook of the Birds of the World (Bird species distribution maps of the world 2016), calculated with the Haversine formula (Sinnott 1984), as a proxy for species' mobility as this is expected to relate to the maximum spatial scale at which individuals of a species may perceive environmental cues. The Haversine formula determines the great-circle distance between two points (here, centroids of breeding and wintering distributions) on the surface of a sphere given their latitude and longitude. Species average female body size and mobility were not correlated in our species set.

We used this meta-model to estimate the relationship between species' size and mobility, and species' SCSS estimated with BLISS. To account for uncertainty in the selection of a single SCSS (e.g., each predictor variable has a full posterior distribution of possible SCSSs), for each species and land cover variable we subsampled 5000 draws from the posterior distribution of the scale indicator variable generated by BLISS (e.g., 30,000 data points per species). When there is a high degree of uncertainty in selecting a single SCSS (e.g., low posterior probability in the best-performing scale), error propagation becomes important in subsequent meta-models that rely on model estimates as inputs. When posterior probability in the best single spatial scale is high, then using a point estimate (e.g., a single value for SCSS rather than the posterior distribution of model estimated SCSS) in subsequent meta-models will return similar results as an analysis accounting for model uncertainty (i.e., because there is low uncertainty). Results can potentially diverge in models accounting for uncertainty versus not accounting for uncertainty when the selection of a single SCSS is ambiguous. We used a linear model with species as a random effect to analyze the relationship between species' body mass and mobility (fixed effects), accounting for the land cover predictor type, and the spatial scale predicting abundance using the posterior sample to propagate uncertainty in SCSS. The regression formula for our meta-model was $log(scale_i) = \beta_0(Crop) + \beta_1(CRP) + \beta_2(Grass) + \beta_3(Grain) + \beta_4(Wetland) + \beta_5(Woodland) + \beta_6 log(bodymass_i) + \beta_7 log(1 + mobility_i) + \gamma_{species_i} + \varepsilon_i$ where there was one data point i for each combination of species and land cover predictor, $\gamma_{species_i}$ represented zero-mean normally distributed random effects, and ε_i were independent and normally distributed error terms. We did not incorporate phylogenetic relatedness into our analysis because we aimed to test the general hypothesis that SCSS increases with body size regardless of whether variation is due to phylogenetic history per se (e.g.,

following the metabolic theory of ecology within birds), and no phylogenetic signal was detected in previous analyses in birds (Thornton and Fletcher 2014).

We simulated 5000 draws from the joint posterior distributions of the meta-model parameters using non-informative priors (package "arm"; Gelman et al. 2015). We extracted the mean and 95% credible intervals (CI) around the mean (Gelman and Hill 2007), which represent the parameter estimate and its uncertainty. Additionally, we ran the same analysis where the error propagation of SCSS uncertainty (e.g., the posterior distribution subsampling procedure) was performed in proportion to the prevalence of the species in our dataset (e.g., rare species had proportionally fewer posterior distribution samples) as we expect prevalence to impact our ability to characterize a SCSS (see Supplementary Data for data used to fit equal error propagation and proportional error propagation models).

Results

Prevalence of the 86 bird species in the analyzed dataset ranged from a minimum of three survey sites having at least one detection (Blue-gray Gnatcatcher, *Polioptila caerulea*; Great-tailed Grackle, *Quiscalus mexicanus*; Say's Phoebe, *Sayornis saya*; and Western Wood Pewee, *Contopus sordidulus*) to a maximum of 465 of sites having at least one detection (Western Meadowlark, *Sturnella neglecta*) (see Supplementary Appendix 1).

Bayesian latent indicator scale selection

We estimated the posterior probabilities of nine candidate spatial scales for each of six land cover predictors for 86 species and present the estimated posterior probability of the single scale with the most posterior probability (e.g., the designated SCSS; Supplementary Appendix 2). Species varied in the amount of uncertainty associated with selecting a single SCSS for each predictor such that posterior probability was often distributed among multiple candidate scales, rather than a majority of posterior probability being assigned to a single scale. Of the 86 species modeled, 16 species had greater than 0.50 probability in a single spatial scale (e.g., an absolute

Fig. 1 Posterior distributions of the spatial scales (in km) of six ▶ land cover predictors: row crop, CRP, grassland, small grain, woodland, and wetlands for Lark Buntings (*LARB* top- high average posterior probability in a single scale) and Chipping Sparrow (*CHSP* bottom- low average posterior probability in a single scale) breeding in Nebraska as estimated by Bayesian latent indicator scale selection

majority in a single scale) for row crop, 23 species for CRP, 15 species for grassland, 14 species for small grain, 17 species for woodland, and 15 species for wetland (Supplementary Appendix 2). Only 14 species had high posterior probabilities (i.e., greater than 0.95) in a single scale for at least one land cover predictor (Supplementary Appendix 1), indicating unambiguous evidence for selecting a single best-performing spatial scale for that predictor. On average, species had a 0.35 probability in their most probable spatial scales across predictor variables (sd = 0.17), indicating weak evidence in support of selecting a single best-performing spatial scale (see Fig. 1 for example of species with high and low average spatial scale posterior probabilities).

Relationship between SCSS, body size, and mobility

In the equal error propagation meta-model, species had, on average, smaller SCSSs designated for CRP, small grain, and grassland compared to row crop (Intercept; Table 1), and larger SCSSs designated for woodland and wetland predictors than for row crop. Under proportional error propagation (i.e., rare species given less weight in the meta-model), on average, the row crop predictor had the smallest designated SCSSs (Table 1). After propagating the uncertainty in model selection to subsequent linear regression modelling, neither body size, nor mobility predicted the SCSS explaining relative abundance across 86 species (Fig. 2). Conducting proportional error propagation did not alter the analysis (Table 1).

Discussion

By sampling a large number of species, spanning a wide range of body size, and characterizing SCSS over numerous candidate spatial scales we present a
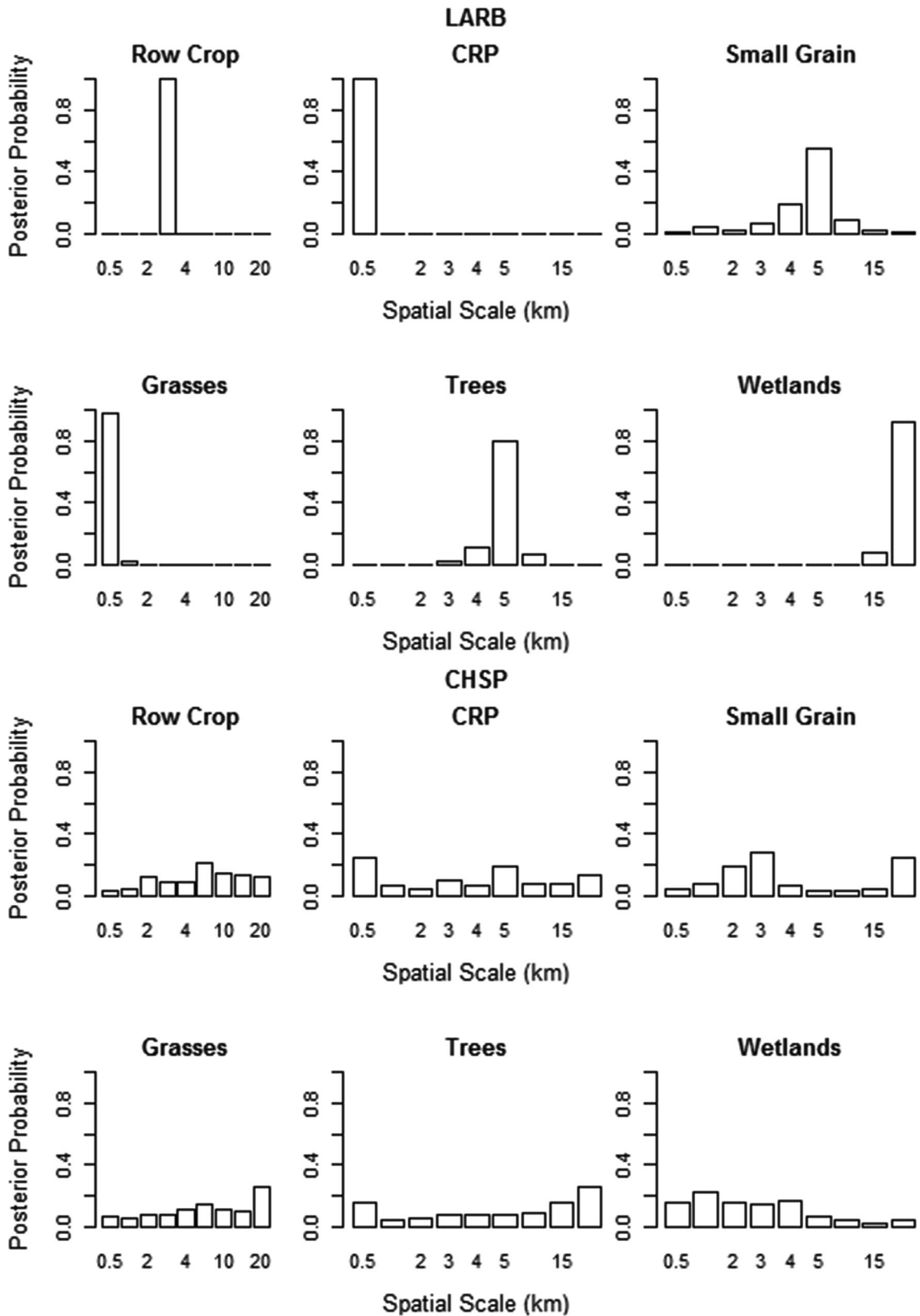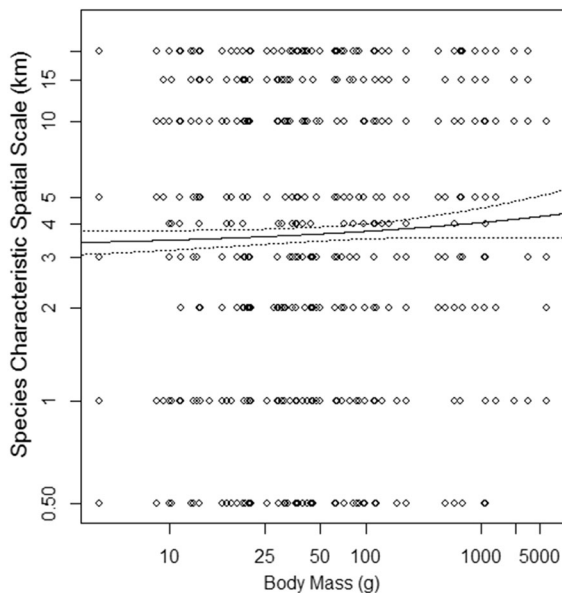
Fig. 2 Estimated relationship between species average female body mass and Bayesian latent indicator scale selection of species characteristic selection scale. The regression is given with 95% credible intervals based on equal error propagation with species' mobility held at the mean. Open circles represent species characteristic selection scales defined as the single scale with the highest posterior probability for each land cover type within species

comprehensive examination of evidence suggesting that neither body size nor species' mobility explain variation in SCSS across multiple land cover types. Although the traditional, sometimes arbitrary approach of haphazardly selecting spatial scales at which to conduct investigations is slowly being replaced by multi-scale, and optimized multi-scale studies (Wheatley and Johnson 2009; Holland and Yang 2016), a predictive framework for making selections remains elusive. Because only 25% of multi-scale studies optimize the selection of spatial scales (reviewed in: McGarigal et al. 2016) there is much still to be learned from optimizing multi-scale investigations. Indeed, methods for optimizing scale selection are continually evolving, and traditional model selection approaches (e.g., AIC), improperly applied in multi-scale studies have been demonstrated to indicate false scales of effect with disconcerting frequency (Stuber et al. 2017). Previous multi-scale studies based on small sample sizes and limited variation across predictors have suggested an allometry of SCSS (Holland et al. 2005; Fisher et al. 2011; 22 citations investigated within Thornton and Fletcher

2014 meta-analysis), which has spurred continued scientific interest in determining the existence of a biological relationship (Thornton and Fletcher 2014; Jackson and Fahrig 2015); however, even after accounting for the potential spurious effects of rare species in our analysis, we were unable to predict the spatial scale at which to measure habitat relationships based on species' body size or mobility alone. Although we can hypothesize a relationship between body size and the spatial scale at which a species associates with the landscape based on sound theoretical foundations such as energetic requirements and mobility (Jenkins et al. 2007; Hendriks et al. 2009), our study adds to those demonstrating no statistical relationship (Hostetler and Holling 2000; Desrochers et al. 2010; 22 avian studies analyzed in: Thornton and Fletcher 2014). The largest and smallest species included in our sample had characteristic spatial scales across the full spectrum of candidate scales, including the smallest and largest. This was also true for the most localized and furthest-moving species considered, indicating that neither size nor mobility were systematically related to the size of the spatial scale best predicting species' response. Our study encompassed substantial variation in body size, mobility, and spatial scales, as well as a substantial sample of species in a continuous landscape, which is important for correctly identifying SCSS given the expected weak relationship (Thornton and Fletcher 2014), but like many others we did not detect an allometric relationship.

Given the preponderance of theoretical support for an allometry of SCSS, why have we, and so many others failed to find a relationship between body size and SCSS? One possibility is the complexity of the relationship between species abundance and the environment within which a species is found. The presence of individuals at a given location is the product of a multitude of individual decisions as well as the realization of multiple hierarchically linked ecological processes that act over varying time scales including birth, death, immigration, and emigration (Wu 2006; Miguet et al. 2016). For example, population fecundity, one component of population abundance, is shaped by resource availability over short time scales (e.g., during the breeding season) and small spatial extents (e.g., within the breeding habitat), whereas we expect immigration to be influenced by longer-term, and larger spatial processes (Miguet et al.

2016). Hierarchy theory suggests that processes can be better-understood if both lower and higher level dynamics are considered in context. For example, lower level individual dynamics occurring on relatively fast time scales collectively contribute to abundance, but may average out at higher levels, while higher level meta-population dynamics may constrain possible abundance values (Wu and Loucks 1995). The concatenation of multiple hierarchical processes, associated with multi-scale influences, each with potentially wide variation in SCSS, may result in a single response variable (i.e., abundance) that contains substantial noise obscuring the presumed biological relationship between body size and SCSS. Similarly, our measure of mobility, the distance between wintering and breeding range centroids, may better-reflect larger-scale responses such as species occurrence at a location rather than abundance, which may be predicted by local movements (Holling 1992). Indeed, if abundance at a location were to be broken down into its constituent processed (e.g., births, deaths, immigration, emigration) and investigated at the level of these processes, a pattern may emerge. However, characteristics of aggregate processes, such as those leading to abundance, may be the result of non-linear interactions, or supervenient properties where reductionist decomposition is not advisable (Holling 1992; Wu 2007). While we expect this avenue for future research to be fruitful, the current body of evidence does not support the hypothesis that the spatial scale of biological response (abundance) scales with species' body size. Although we focused our analysis on a single level of the hierarchy, we demonstrate multi-scale patterns within species due to relationships between abundance and land cover predictors manifesting at different spatial scales. Patchiness of abiotic environmental conditions likely influences the distribution of resources on the landscape, which in turn can shape the distribution of consumers (Wu and Loucks 1995). Because different abiotic and vegetative processes manifest at process-specific characteristic scales (Wu 2006), or ranges within which processes are scale-invariant (Holling 1992), it is unsurprising that consumers also display relationships with resource parameters at different spatial scales. Characteristic scales of consumer response to resource distribution or physical environmental properties should reflect an interaction between the characteristic scales of resources or

abiotic conditions and the species' relevant grain size of observation (Kolasa et al. 2012). Identifying the biological variables indicating perceptive ability, or perception of environmental characteristics is necessary to create a predictive framework for multi-scale studies.

In postulating an allometry of SCSS it is assumed that because larger species move farther to satisfy resource requirements (Perry and Garland 2002) they are more likely to perceive and associate with the environment at larger scales (Mech and Zollner 2002). Although selection may act to affect the relationship between body size, mobility, and the scale of environmental perception, ecological conditions may ultimately constrain our ability to measure the outcome through the metric of population abundance. Indeed, a lack of an allometry of SCSS may be evidence supporting the energy equivalence rule (EER). Although evidence is equivocal, EER predicts that the energy available to populations in a community is independent of body size (Damuth 1981). The prediction of equal population energy use is based on the cancelling effects of opposing relationships between population density and body size (slope approximately -0.75), and metabolic rate and body size (slope approximately $+0.75$) either because of energetic or non-energetic mechanisms (Blackburn et al. 1993). Under the EER, where energy use is equivalent across populations in a community, we would not expect the predicted relationship between SCSS and metabolic rate, and thus between body size and SCSS. One amendment to the EER suggests that the -0.75 slope relationship for population density and body size only holds for energy-limited populations (e.g., at the tail of an abundance distribution), and a quantile regression of abundance rather than of average abundance may be more appropriate to understand such relationships between size and abundance (Blackburn et al. 1993; Marquet et al. 1995). Furthermore, this approach ignores that allometric relationships may vary with diet, age, or phylogeny; it may be that there is no general allometric relationship.

Given the complexity of the interactions affecting how a species relates to its environment and how much variation is expected in SCSS, should we really expect a species to have a single SCSS at all? Is selection acting on species' response to habitat characteristics or species' response to spatial scales? Does SCSS vary with population size, environmental quality, or

intraspecific variation in population traits? All are open questions. The current SCSS paradigm, which seeks to define a 'single' characteristic scale for each species limits our understanding of the potential underlying variation. Although our results do not suggest a size-dependent ecological process underlying between-species differences in spatial selection scale for abundance, we demonstrate clear evidence that species are responding to different habitat composition factors independently at different scales. A noteworthy example being the ring-necked pheasant (*Phasianus colchicus*), which is responding to the proportion of woodland at a relatively large scale (10 km) and the proportion of grassland at a much smaller scale (1 km). RNEP are non-migratory, with low mobility, which may suggest two distinct ecological processes governing population distribution, rather than multi-scale hierarchical habitat selection in individuals' settlement decisions. For example, the configuration of woodland may be associated with edge effects in grassland birds (Fletcher et al. 2003; Bollinger et al. 2004), while the amount of grassland might be related to patch size, regulating carrying capacity (Ribic et al. 2009). As such, it is not biologically appropriate to assume that the effects operate at the same scale. Most previous studies investigating spatial scale relationships with species abundance or occupancy are often limited to a single habitat parameter (e.g., Holland et al. 2004; Holland et al. 2005; Cunningham and Johnson 2006; Buler et al. 2007; Garcia and Chacoff 2007; Bergman et al. 2012), constrain multiple predictors to the same scale (e.g., Seavy et al. 2009), or average the spatial scales selected when multiple predictors are evaluated (e.g., Thornton and Fletcher 2014). Such practices may limit our ability to reveal important species-habitat relationships. Future studies may benefit from considering the influence of multiple, possibly independent, habitat predictors on species abundance. In particular, we caution that a SCSS determined from a study considering only a single habitat parameter should not necessarily be extrapolated to other habitat parameters (but see Martin and Fahrig 2012).

Developing a predictive framework for determining the spatial scale at which to conduct investigations or carry-out management actions is valuable from both fundamental and applied perspectives. Such a framework would add to our understanding of ecological processes regulating biological responses and increase the accuracy and efficiency of conservation and management actions. The study of spatial scaling of biological responses is still young, and while a predictive framework is being developed, it may behoove investigators and conservation practitioners alike to determine the species' spatial scale of selection prior to conducting investigations such that relevant data collection may be applied at appropriate spatial scales to address the questions at hand. The continued, systematic compilation of scale-optimized studies will certainly help to uncover systematic relationships between species traits and ecological factors that shape species characteristic scales of selection.

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