Hierarchical multi-grain models improve descriptions of species’ environmental associations, distribution, and abundance

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Abstract. The characterization of species’ environmental niches and spatial distribution predictions based on them are now central to much of ecology and conservation, but implicitly requires decisions about the appropriate spatial scale (i.e., grain) of analysis. Ecological theory and empirical evidence suggest that range-resident species respond to their environment at two characteristic, hierarchical spatial grains: (1) response grain, the (relatively fine) grain at which an individual uses environmental resources, and (2) occupancy grain, the (relatively coarse) grain equivalent to a typical home range. We use a multi-grain (MG) occupancy model, aided by fine-grain remotely sensed imagery, to simultaneously estimate species–environment associations at both grains, conduct grain optimization to measure response grain, and apply this analysis framework to an example species: a medium-sized bird (Tockus deckeni) in a heterogeneous East African landscape. Based on home range analysis of movement data, we calculate an occupancy grain of 1 km for T. deckeni. Using a grain optimization procedure across 32 grains from 10 to 500 m, we identify 60 m as the most strongly supported response grain for a suite of environmental variables, slightly coarser than opportunistic behavioral observations would have suggested. Validation confirms that the accuracy of the optimized MG occupancy model substantially exceeds that of equivalent single-grain (SG) occupancy models. We further use a simulation approach to assess the potential impacts of accounting for the multi-scale structure of species’ environmental requirements on estimates of population size. We find that the more strongly supported MG approach consistently predicts a minimum population size in the study landscape that is much lower than that provided by the SG model. This suggests that SG approaches commonly used in conservation applications could lead to overly optimistic abundance and population estimates, and that the MG approach may be more appropriate for supporting species conservation goals. More generally, we conclude that multi-grain approaches of the sort presented, and increasingly enabled by growing high-resolution remotely sensed data, hold great promise for offering a more mechanistic framework for assessing the appropriate grain(s) for population monitoring and management and enable more reliable estimates of abundances and species’ distributions.

Key words: hierarchical models; occupancy models; response grain; spatial grain; spatial scale; species distributions; species–environment relationships.

INTRODUCTION

The relationship between species occurrence and environmental factors lies at the heart of ecology and remains a key challenge for the field. Understanding species–environment associations is linked to both theoretical and practical objectives, from answering foundational questions about species’ ecological niches, to tracking the spread of invasive species, understanding and predicting the impacts of global change, prioritizing sites for conservation, and informing management decisions (Johnson 1924, Booth et al. 1988, Austin et al. 1990, Ferrier et al. 2002, Gray 2005, Kremen et al. 2008, Belmaker and Jetz 2011, Matthews et al. 2011, Frishkoff and Karp 2019). Because natural environments are structured in space and time, and an organism’s perception of its environment is shaped by its biophysical characteristics, species perceive and respond to environmental heterogeneity at specific spatial scales (Kolasa 1989, O’Neill et al. 1989, Wiens 1989, Wiens and Milne 1989, Kotliar and Wiens 1990, Wu and Loucks 1995). The concept of a limited set of scales at

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which organisms most strongly respond to environmental factors has been variously referred to as “domains of scale” (Wiens 1989), “characteristic scales” (Urban et al. 1987, Wu 1999), the “scale of ecological phenomena” (Dungan et al. 2002), and “intrinsic scale” (Wu and Li 2006). We recognize two primary spatial grains at which species characteristically respond to their environment. We use the term “occupancy grain” to denote the grain roughly equivalent to a species’ typical home range, and “response grain” to denote the grain at which an individual uses environmental resources.

Empirical evidence from diverse taxa and ecological settings indicates that species–environment relationships vary with spatial scale. In riparian and pitch-pine–scrub-oak forests, landscape composition within 1,000–1,200 m of sampling locations explained substantially more variation in bird occurrence than environmental factors within shorter distances (Saab 1999, Grand and Cushman 2003). Roland and Taylor (1997) found that four dipteran parasitoids responded to forest structure at different spatial extents ranging from 53 to 850 m, while Holland et al. (2004) observed distinct, unimodal relationships between abundance and amount of forest cover within 20–2,000 m for nine species of deadwood-boring beetles. Similar patterns have also been recorded in aquatic and marine systems: Harig and Fausch (2002) found that cutthroat trout depended on several stream and pool variables, but was not strongly associated with factors within larger drainage basins. In Caribbean marine protected areas, adult abundance in most reef fish groups was most strongly associated with seagrass cover within 1 km (Grober-Dunsmore et al. 2007).

These studies demonstrate the pervasiveness of scale-dependence in species–environment associations and illustrate two primary types of scale-dependence: across grains, a species may respond differently to the same environmental factor, and/or to different sets of environmental factors. Thus in order to obtain reliable inferences about species’ ecological niches and accurately predict their distributions, researchers must conduct analyses (1) using environmental factors and (2) at multiple spatial grains (MG), meaningful to the species of interest (Meentemeyer and Elgene 1987, Wiens 1989, Levin 1992, Wu 1999, Chalfoun and Martin 2007, Connor et al. 2018). The consequences of a mismatch between the grain of analysis and the grain of a species’ response to its environment may include the failure to measure responses to spatial variation or specific variables (de Knegt et al. 2010); a decrease in the amount of variation explained by environmental predictors (McIlroy and Purves 2011); and erroneous extrapolation of processes or patterns to larger or smaller grains (Miller et al. 2004). These might ultimately lead to misinformed or misplaced conservation and management actions, particularly if the variables in question affect species’ response in a hierarchical manner, as is the case for, e.g., land cover and climate (Newbold 2018, Graham et al. 2019). Despite well-established ecological theory and abundant empirical support, no consensus exists regarding the appropriate grains at which analyses should be performed, nor an optimal approach for selecting them (but see Holland et al. 2004, Nams 2005, Schooley 2006, Schaef er and Mayor 2007).

Occupancy models allow estimation of occupancy while accounting for imperfect detection (MacKenzie et al. 2002, Tyre et al. 2003) and typically include two model components: one addressing the ecological process where the imperfectly observed (latent) state process of occupancy is modeled, and a second addressing the observation process, which is conditioned on the state process (Royle and Kéry 2007). Replicate samples and environmental covariates are used to jointly estimate model parameters, accounting for dependence and collinearity across model components (Battin and Lawler 2006, Nichols et al. 2008). This hierarchical, yet flexible, formulation makes occupancy models ideal for addressing MG species–environment relationships. Nichols et al. (2008) extended occupancy models to accommodate detections from complementary sampling devices. By adding another component to a standard occupancy model, Nichols et al. (2008) introduced a parameter that could be used to estimate occurrence at an additional spatial scale. Mordecai et al. (2011) implemented this approach to estimate the probability that Louisiana Waterthrush (Seiurus motacilla) occupied a stream reach during a sampling period, and were available for detection during at least one sample. Pavlacky et al. (2012) analyzed occurrence data for Lark Sparrows (Chondestes grammacus) and Brown Creepers (Certhia americana) collected at two spatial scales, treating small-scale occupancy as an estimate of individuals present, but unexposed to sampling (i.e., rare or cryptic species).

In these studies, each component of the model was associated with a spatial footprint of a particular sampling method, such as the effective detection distance of a camera trap (Nichols et al. 2008) or a point count (Mordecai et al. 2011). In contrast, here we aim to identify the spatial grains that are biologically important for a particular species. We extend the multi-grain (MG) occupancy modeling framework to measure the spatial grains at which species–environment associations occur, and estimate these relationships at these grains. First, we review ecological theory regarding the spatial grains at which resource selection likely occurs. Second, we construct a MG occupancy model based on the theoretical structure of species–environment associations. Third, we develop a grain optimization procedure to empirically identify biologically relevant grains for the study species. We then apply this approach to a rich data set for the Von der Decken’s Hornbill (Tockus deckeni), a resident bird in a heterogeneous East African savanna landscape.

Ecological theory recognizes that, for a resident species, the selection of habitat and resources is nested, both hierarchically and spatially, within a home range (Johnson 1980, Morris 1992, Meyer and Thuiller 2006). Thus, we define the first, coarse component of our MG model...
as “MG occupancy”, the probability that a coarse spatial unit contains or overlaps an occupied home range (Fig. 1, “Occupancy process”). We operationalize MG occupancy at a species’ occupancy grain, the grain equivalent to the size of a typical home range, and expect that detections and non-detections across replicate samples indicate whether a spatial unit intersects an occupied home range. We then define a second, finer component of our MG model, “MG use”, as the probability that an individual uses the resources in a fine spatial unit within an occupied home range (Fig. 1, “Use Process”). We operationalize MG use at a species’ finest resolvable response grain and expect that detections and non-detections at this grain reveal spatial variation in the use of environmental resources by a resident individual (conditional on occupancy at the coarse grain). Each model component thus captures distinct, yet complementary, species–environment associations (Johnson 1980, Orians and Wittenberger 1991, Pribil and Picman 1997, Morris 2003).

Historically, sound capture of cross-scale species–environment associations has been hindered by lack of reliable measurements of environmental variation across scales. Advances in remote sensing now permit continuous acquisition of environmental characteristics that can be aggregated across different extents and grains (Bush et al. 2017). Recent satellite missions, such as Landsat 8, Sentinel-1, Sentinel-2, ICESat-2, MODIS, SRTM, ASTER, GEDI, Quickbird, and others, enable accurate capture of environmental and climatic data (Zarnetske et al. 2019) at spatial grains from 0.6 m (Quickbird) to 1 km (MODIS), and coarser. Here, we take advantage of these novel opportunities afforded by remote sensing technology, paired with occupancy modeling, to identify

![Diagram](image-url)

**Fig. 1.** The hierarchically and spatially nested processes of occupancy (ψ) and use (θ). Occupancy represents the probability that a coarse spatial unit intersects an occupied home range. This process operates at a spatial grain equivalent to a species’ typical home range size, and is imperfectly observed through sampling of coarse sites. Use represents the probability that a species intensively uses the environmental conditions within a fine spatial unit (given that the containing coarse site lies within an occupied home range). This process operates at a grain equivalent to the species’ response grain, and is imperfectly observed through sampling of fine sites. The processes of occupancy and use are linked, both hierarchically and spatially; for example, fine spatial units suitable for use, but contained within coarse spatial units unsuitable for occupancy, are insufficient to support the species’ occurrence. Similarly, coarse spatial units that do not contain fine spatial units suitable for use are also inadequate for occurrence. The observation process accommodates the potential for the species to be incorrectly undetected during surveys of fine sites due to land cover, variation in vocalization, and other factors. The parameter p is probability of detection.
the spatial grains at which species–environment associations occur. Specifically, to identify a species’ response grain in practice, we propose a grain optimization procedure (McGarrigal et al. 2016), aided by fine-grain remotely sensed data, in which (1) a study extent is divided into spatial units at which a species might perceive and respond to environmental heterogeneity (Leblond et al. 2011), (2) the strength of the association between species occurrence and environmental conditions is assessed, and (3) these steps are repeated at many grains (finer than the typical home range), culminating in (4) identification of the spatial grain at which the strongest multi-variate relationships occur. Applying this approach to our study system, we set the grain for MG occupancy at 1,000 m, approximately equal to the diameter of a typical *T. deckeni* home range (as calculated from GPS tracking data; see Materials and Methods). During surveys, we observed *T. deckeni* differentiate among environmental resources at very fine grains. For example, hornbills used complex vegetation surrounding seasonal water flows, selectively foraged within shrub canopies, and preferentially used narrow shrubland-grassland edges. Based on these observations, we expected *T. deckeni*’s response grain, and thus the optimal grain for MG use, to be 10 m or finer (see Methods).

Materials and Methods

Study area and environmental data

All field work was conducted at Mpala Research Centre (MRC), a 20,000 ha research conservancy located in Laikipia, central Kenya that varies from 1,600 to 2,000 m in elevation. Rainfall typically peaks during long (April–May) and short (October–November) rainy seasons, with considerable spatial variability. Mean annual precipitation varies from 400 to 700 mm, that the area may be considered a mosaic of arid and semiarid land cover (McClanahan and Young 1996). Common vegetation includes Acacia-dominated savanna on sandy “red” and poorly drained, clay “black cotton” soils, narrow riparian zones, and arid bushland.

We developed 19 predictor variables related to key environmental factors in determining bird spatial distributions: land cover, vegetation density (i.e., proportion of ground covered by vegetation), vegetation vertical structure, topography, proximity to resources critical to *T. deckeni*, and climate (MacArthur 1964, Cody 1981, Storch 2002, Benitez-López et al. 2010). We generated a land cover classification from high-resolution Quickbird imagery of MRC and derived the proportion of land cover types in which *T. deckeni* was repeatedly observed: areas with very dense shrubs (*prop_closedshrub*); areas with sparse shrubs and dense herbaceous vegetation (*prop_grass*); areas with some shrubs and sparse herbaceous vegetation (*prop_openshrubwherb*); and areas with sparse shrubs and dense herbaceous vegetation (*prop_openshrubwherb*). We also derived a land cover heterogeneity metric (lcchet). We calculated the Normalized Difference Vegetation Index (NDVI; Rouse 1974), which has been linked to plant photosynthetic activity (Asrar et al. 1984), and extracted the brightness (KTB) and moisture (KTW) eigenvectors of a Tasseled Cap transformation (Crist et al. 1984). We fused data from vegetation plots, Tasseled Cap variable eigenvectors, and NDVI texture to predict an index of vegetation structure (SCI) across MRC. We derived topographic variables of elevation (elev) and slope (slope), topographic complexity (TCI), and annual direct solar radiation (TAI) from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM). Finally, we interpolated long-term mean annual precipitation (precip) across the study area using rain gauge data and topographic variables. For a more comprehensive description of the methods used to derive these variables, please see Appendix S1: Section 1.

Study species and detection/ non-detection data

The Von der Decken’s Hornbill (*Tockus deckeni*) is a medium-sized (125–225 g) omnivorous bird that typically occurs in adult pairs or small family groups, consumes primarily invertebrates and fruits, and is found in moderately open to closed savanna.

During July 2012–January 2016, we conducted surveys for *T. deckeni* within 75 1 × 1 km sampling sites at MRC. Sampling sites were distributed across precipitation and elevation gradients, and among major land cover types, in a stratified random arrangement (Fig. 2). Each 1-km cell was surveyed approximately bimonthly during morning (06:30–10:30) and afternoon (15:30–18:30) periods. The sampling effort of an individual survey was required to meet (1) a spatial requirement to search at least 10% of the cell area, and (2) a temporal requirement to search for a minimum of 30 minutes. Because we endeavored to balance (1) searching at least 10% of a 1 × 1 km cell during each survey with (2) searching the entire 1 × 1 km cell across multiple surveys, survey routes were not identical. Any adult *T. deckeni* detected during a survey was followed for up to 15 consecutive locations. We recorded each location at which a bird was observed using distance-and-bearing methods: distance was measured by a rangefinder with uncertainty ± 1 m, and bearing was measured by a compass with uncertainty ± 1°. Only adult *T. deckeni* were recorded.

This sampling design is equivalent to a spatially nested and replicated, within-season version of the robust design (Pollock 1982, MacKenzie et al. 2003, Nichols et al. 2008), with coarse sampling sites (1 × 1 km grid cells) subsampled by finer “primary” sites (searched spatial units), each with multiple “secondary” sampling occasions (individual surveys). Repeated secondary sampling occasions (surveys) are required to account for the probability of a species’ detection at the fine primary
In addition, models based on the robust design (see Occupancy models) typically assume that spatial units are closed to changes in occupancy status over the study period. We thus selected a study period that balanced the requirement for repeated surveys with the assumption of closure. The selected study period, April–December 2014, includes one short and one long rainy season and the typical *T. deckeni* breeding and fledging cycle (roughly April–July), but excludes the major dry season (roughly January–March). Within this period, we assumed that coarse spatial units were closed to changes in occupancy, and fine spatial units were closed to changes in use.

In our sampling methods, spatial uncertainty arises from (1) the accuracy of GPS unit used to record the observer’s position, and the precision of (2) the compass bearing and (3) the distance to the observed bird (Wieczorek et al. 2004). We used the well-established point-radius methods of (Wieczorek et al. 2004) to calculate the median spatial uncertainty across all observations (B: 4.6 m) were considered detections. Spatial units within the searched area, but further from a detection than the median distance traveled by *T. deckeni* during a minimum survey (C: 500 m), were considered non-detections. If no individuals were detected during the survey, all searched spatial units were considered non-detections.

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**Fig. 2.** Converting surveys of 1-km cells into detections and non-detections. During April–December 2014, we performed approximately 500 surveys within 75, 1,000 × 1,000 m sampling sites distributed across Mpala Research Centre (MRC), located in central Kenya (see lower left inset). For visualization purposes, we summarize our sampling effort at the spatial grain of 100 m. *N* indicates the total number of surveys conducted in each spatial unit (100 × 100 m grid cell) during the study period (see color bar). During each survey, observers searched a 1 × 1 km grid cell for *Tockus deckeni* for a minimum of 30 minutes (see upper right inset). The total area searched during the survey is defined by the survey route (dashed gray line) and A, the median distance at which *T. deckeni* were first detected in the field (44 m). When an observer detected the species, searched spatial units within the median spatial uncertainty across all observations (B: 4.6 m) were considered detections. Spatial units within the searched area, but further from a detection than the median distance traveled by *T. deckeni* during a minimum survey (C: 500 m), were considered non-detections. If no individuals were detected during the survey, all searched spatial units were considered non-detections.
between T. deckeni occurrence and environmental factors: 10 m.

We laid a grid of 10 × 10 m over MRC and converted our survey data into detections and non-detections at this grain (Fig. 2, inset). We calculated the median distance at which T. deckeni were first detected during the study period (44 m), buffered each survey route by this distance, and considered the resulting buffer as the area searched by an individual survey. Since the ability to account for the probability of a species’ detection requires repeated visits to the same location, we considered only 10-m grid cells that were surveyed at least three times during the study period. A 10-m grid cell that was both searched three times and at least 75% covered by a detection buffer was considered a detection. Consequently, all detections outside the searched area (i.e., outside of the 44-m buffered survey route) and in grid cells not considered sufficiently surveyed were discarded. On average, approximately only two T. deckeni observations from an individual survey were counted as detections and used in hierarchical occupancy models (Appendix S1: Fig. S1), thus minimizing temporal and spatial dependence of observations. While using only first detections would have further reduced temporal dependence, it would also reduce the available observations to the extent that modeling occupancy and use could not be implemented. Finally, we estimated the median distance (287 m) traveled by T. deckeni during the minimum survey duration (30 minutes). To avoid false negatives in non-detection data, we established a conservative minimum distance (500 m) between detections and non-detections in searched areas where T. deckeni was detected. All 10-m grid cells within the area searched during a survey in which no T. deckeni were detected were considered non-detections. All 10-m grid cells within the searched area where T. deckeni was detected, but at least 500 m from a detection, were also considered non-detections.

**Home range analysis**

During 2013–2014, we attached data-logging GPS tracking devices (constructed by the Technical Workshop at the University of Konstanz, Germany) to adult male T. deckeni for which tag weight (10.5–14.5 g) did not exceed 5% of body mass (n = 19). Tags were attached via backpack harness constructed of 5 mm teflon ribbon, crossed across the breast, and sealed with heat shrink tubing. All capture, handling, and attachment procedures were approved by the Yale University Institutional Animal Care and Use Committee (IACUC protocol no. 2013-11568). For each tagged individual with sufficient data (n = 15), we used a nonparametric, fixed-radius, kernel density approach (Getz and Wilmers 2004, Getz et al. 2007) implemented in the R package adehabitatHR (Calenge 2006) to determine the isopleth bounding 97.5% of relocations. Median home range size across 15 tagged T. deckeni was 1.36 km2.

**Occupancy models**

We describe the MG extension to the state-space formulation of single-grain (SG) occupancy models using notation following MacKenzie et al. (2002) and Royle and Kéry (2007). The parameter \( \psi_i \) represents a species’ occupancy of coarse spatial unit \( i = 1, \ldots, n_i \). We set the grain for MG occupancy approximately equal to T. deckeni’s median home range size (1 km², or one 1,000 × 1,000 m grid cell; see Home range analysis). Thus, \( \psi_i \) may be interpreted as the probability that coarse grid cell \( i \) substantially overlaps an occupied home range. The parameter \( \theta_j \) represents use by a species of fine grid cell \( j = 1, \ldots, n_j \), given that \( j \) lies within an occupied home range. This definition is statistically indistinguishable from those in other occupancy models constructed at grains smaller than a typical home range (see Bailey et al. 2014, Tingley et al. 2016). Given that the spatial uncertainty of all detections was approximately 4.6 m, we set the grain for MG use (i.e., the finest possible response grain for T. deckeni) to 10 m. The parameter \( p_k \) represents the probability that a species will be detected in fine spatial unit \( j \) during sampling occasion \( k = 1, \ldots, n_k \) given both occupancy of the containing coarse spatial unit and use of \( j \). This formulation of the MG model assumes that (1) the occupancy status of coarse spatial unit \( i \) applies across all \( j \) and \( k \) and there are no changes in the occupancy status over the course of the study, (2) the use status of fine spatial unit \( j \) applies across all \( k \), and (3) false detections do not occur (i.e., all individuals identified as T. deckeni are identified correctly). While the temporal extent of the survey overlaps the typical T. deckeni breeding and fledging cycle, assumption (1) is unlikely to be violated because only adult birds were recorded and included in the model.

The detections and non-detections across all \( k \) for a given \( j \) are represented as vectors of 1s (detections) and 0s (non-detections). We construct a set of probabilistic arguments to estimate the likelihood of these “detection histories.” Consider an example coarse spatial unit \( i = 1 \) and two of its component fine spatial units, \( j = 1 \) and \( j = 2 \). Fine spatial unit \( \{i = 1, j = 1\} \) has a detection history of 000000, while fine spatial unit \( \{i = 1, j = 2\} \) has a detection history of 010010. This combination of detection histories indicates that coarse unit \( i = 1 \) is occupied. The likelihood of the detection history for \( \{i = 1, j = 1\} \) can be written as

\[
\psi_1 \theta_1 \prod_{k=1}^{6} (1 - p_k) + \psi_1 (1 - \theta_1)
\]

where the left-hand term represents occupancy at coarse unit \( i = 1 \), use at fine unit \( j = 1 \), and no detections of the species within \( k = 6 \) surveys, while the right-hand term \( \psi(1 - 0) \) represents occupancy at coarse unit \( i = 1 \) but no use of fine unit \( j = 1 \). The likelihood of the detection history for \( \{i = 1, j = 2\} \) can be expressed as
\[
\psi_1 \theta_1 \times (1 - p_1) \times p_2 \times (1 - p_3) \times (1 - p_4) \times p_5 \times (1 - p_6)
\]

such that the observed variation in the use of \( i = 1, j = 2 \) among \( k \) is solely due to false non-detections.

The model likelihood is then proportional to the product of similar probabilities for all spatial units, which is maximized to yield maximum likelihood estimates of \( \psi, \theta, \) and \( p \). To estimate the influence of environmental factors on \( T. \) deckeni detection, use, and occupancy, we included a suite of non-collinear environmental variables \((m = 1, \ldots, m_n)\) we expected to be biologically relevant for \( T. \) deckeni at fine and coarse spatial grains (based on previous SDMs for this study system at select spatial grains; see Mertes and Jetz 2018). We included typical covariates affecting detection probability, such as time of day and season, in early model runs; however, these variables were not significant and were thus excluded from the final model. We also included an indicator variable \( w_m \) for each covariate, which takes the value of 1 if its associated predictor variable is included in a model, and 0 if not (George and McCulloch 1997, Kuo and Mallick 1998). Thus, MG occupancy, MG use, and MG observation may be written as

\[
\logit(\psi_i) = a_0 + w_{a1} \alpha_{1, \text{elev}_i} + w_{a2} \alpha_{1, \text{lcchet}_i} + w_{a3} \alpha_{3, \text{NDVI}_i} + w_{a4} \alpha_{4, \text{precip}_i}
\]

\[
\logit(\theta_{ij}) = w_{p1} \beta_{1, \text{dist2water}_{ij}} + w_{p2} \beta_{2, \text{KWT}_{ij}} + w_{p3} \beta_{3, \text{prop_grass}_{ij}} + w_{p4} \beta_{4, \text{SCI}_{ij}} + w_{p5} \beta_{5, \text{shrubprop}_{ij}} + w_{p6} \beta_{6, \text{TAI}_{ij}}
\]

\[
\logit(p_{ijk}) = \delta_1 \text{elev}_{ijk} + \delta_2 \text{propclosedshrub}_{ijk}
\]

To ensure that total prior uncertainty remained constant regardless of the number of parameters in an individual model, we set a prior for the total variance of all covariate parameters in each model component with a Gamma distribution and shape and inverse scale parameters \((3.29, 7.8)\), resulting in an approximately Uniform(0,1) marginal distribution for each parameter (Link and Barker 2006, Hooten and Hobbs 2015). We used vague, Uniform(0,1) priors for detection covariates, and Bernoulli(0.5) priors for indicator variables (see Grain optimization procedure).

We fit MG models to \( T. \) deckeni detection and non-detection data using Markov chain Monte Carlo (MCMC) methods implemented in OpenBUGS (see Data S1: OpenBUGS code for MG occupancy model) via the package R2OpenBUGS (Sturtz et al. 2005) in the R statistical environment (available online).\(^2\) For each model, we ran three independent Markov chains for 60,000 iterations, discarding the first 10,000 as burn-in. To circumvent computer memory and storage limits, we retained every other sample for analysis. While “thinning” may slightly reduce the precision of posterior parameter estimates (but see Zuur et al. 2002), we minimized thinning \( (2\times, \text{compared to common rates of } 40-100\times; \text{Link and Eaton [2012]}) \) and report parameter estimates with appropriate precision (see Table 1). Based on inspection of trace plots, the Brooks-Gelman-Rubin statistic (Gelman and Rubin 1992), and Geweke’s diagnostic (all diagnostic values within two standard deviations of a normal distribution; Geweke 1991), there was no evidence that models failed to converge.

We used a separate set of detections derived from movement data (GPS locations with estimated speed <0.1 m/s and estimated spatial error ≤5 m) and 10-m grid cells with no detections (not used to fit models) to assess model performance. We used three validation metrics: area under the receiver operating curve (AUC), a general index of predictive performance; the True Skill Statistic (TSS), a joint evaluation of omission and commission errors; and the Continuous Boyce Index (CBI; see Boyce et al. 2002, Hirzel et al. 2006), a frequency ratio under model-predicted vs. random expectations similar to \( k \)-fold cross validation. AUC is the most common statistic used to evaluate occurrence models in ecology (Porfírio et al. 2014), but has both advantageous properties (it is unaffected by prevalence and threshold-independent) and undesirable ones (it equally weights errors of omission and commission). CBI, on the other hand, considers how much model predictions differ from a random distribution of observed presences and allows for unreliable (or no) absence data (Boyce et al. 2002, Hirzel et al. 2006). TSS accounts for errors of both omission and commission and the likely outcome from random guessing. For comparison, we also constructed SG occupancy models at 10, 60, and 1,000-m grains with identical predictor variables, fit SG models to \( T. \) deckeni detection data using the package hSDM (Vieilledent et al. 2014), and performed identical convergence diagnostics and accuracy assessments.

**Grain optimization procedure**

To identify \( T. \) deckeni’s response grain, and thus the appropriate grain for MG use, we fit 32 models that varied only in the grain at which MG use was constructed \((10-500 \text{ m})\). When aggregating detection histories to coarser analysis grains, we used only detections and non-detections from surveys on different days. To investigate how \( T. \) deckeni’s environmental associations change across grains, we measured the posterior mean of the indicator variable for each environmental covariate at each analysis grain. All indicator variables have prior distributions of \( w_m \sim \text{Bernoulli}(0.5) \): equal probability of being included in the model in an individual MCMC sample or not (Royle and Dorazio 2008). A posterior mean close to 1 indicates that its associated covariate strongly influences the modeled response (O’Hara and Sillanpaa 2009, Hooten and Hobbs 2015). We

\(^2\)https://www.r-project.org/
calculated the Bayes Factor (BF) for each indicator variable from its prior mean (0.5) and posterior mean as

\[ BF_{\text{inclusion}} = \frac{w_m(\text{data})}{1 - w_m(\text{data})} \]

This quantity is equivalent to the posterior odds ratio and may be interpreted as the strength of support for the inclusion of the associated covariate in the model (Jeffreys 1961, Des H.V. Smith et al. 2011). BFs > 3 are considered “substantial” evidence for a variable’s inclusion in a model, BFs between 10 and 150 are “strong” to “very strong”, and BFs > 150 are “decisive” (Jeffreys 1961, Kass and Raftery 1995, O’Hara and Sillanpaa 2009, Jarosz and Wiley 2014). As a minimum criterion for identifying T. deckeni’s response grain, we required that a majority of BFs indicate at least “substantial” support, and the majority of accuracy metrics indicate comparatively high predictive accuracy.

**Estimating population size**

To explore how considering species–environment relationships at multiple spatial grains may inform occurrence predictions, we used a simulation approach to estimate the number of occupied T. deckeni home ranges across MRC. For the SG case, we used the most accurate SG occupancy model at T. deckeni’s occupancy grain (1 km). For the MG case, we used our final MG model, with MG occupancy at T. deckeni’s occupancy grain (1 km) and MG use at T. deckeni’s identified response grain (60 m).

First, we used our testing data to identify threshold values of probability of occupancy and use that minimized the false negative rate (the number of sites with observed detections that were predicted to be unsuitable). Specifically, we selected the probabilities of occupancy and use that achieved 90% sensitivity in their respective model or model component (Pearson et al. 2004, Liu et al. 2005). We derived a biologically realistic frequency distribution of T. deckeni home range sizes from our movement data, and estimated their radii (assuming a circular shape). We then randomly selected a location within MRC, randomly drew a home range radius, and buffered the selected location by the selected radius.

Under the SG approach, we accepted a home range if its mean SG occupancy met or exceeded the SG occupancy threshold value. Under the MG approach, we accepted a home range if its mean probability of use met or exceeded the MG use threshold value and its mean probability of occupancy met or exceeded the MG occupancy threshold value. We continued placing reasonably overlapping (≤20%, the maximum overlap observed among tracked individuals) territories in this manner until insufficient area remained to place another realistically sized home range, and repeated this process 999 times under each approach.

**RESULTS**

Of the 100,000 finest spatial units (10 × 10 m grid cells) across Mpala Research Centre (MRC) that were searched at least three times during the study period, our example species, Tockus deckeni, was detected at least once in ~6,000 (Fig. 2). At an intermediate grain (100 m), T. deckeni were detected at least once in 290 of 4,000 spatial units. At the coarsest possible grain considered in our grain optimization procedure (500 m), 97 out of ~4,000 spatial units saw at least one detection. We used these detection histories in single-grain (SG) and multi-grain (MG) hierarchical occupancy models to investigate T. deckeni’s environmental associations across a wide range of analysis grains.

We found compelling evidence that T. deckeni responds most strongly to its environment at a grain of 60 m. T. deckeni use was most strongly influenced by environmental covariates at grains 50–140 m (Fig. 3). In addition, at the 10, 60, and 100 m grains, BFs for at least one covariate exceeded 1,000 (all BFs were subsequently truncated at 350 in visualizations). At 60 m, BFs for four covariates in MG use exceeded the threshold for “strong” evidence (Jeffreys 1961, Kass and Raftery 1995, O’Hara and Sillanpaa 2009, Jarosz and Wiley 2014). At 60 m, the majority of accuracy metrics (AUC and CBI) were at or near their cross-grain maximum (Fig. 3). We therefore identify 60 m, rather than our hypothesized 10 m, as T. deckeni’s response grain, and thus the optimal grain for MG use. Posterior medians and 95% Bayesian credible intervals (CBIs) for MG use and occupancy covariates at our hypothesized (10 m) and identified (60 m) response grains are reported in Table 1.

Given the seemingly small disparity between 10- and 60-m grains, even small differences in posterior parameter estimates among these two constructions of MG use are of note. Most dramatically, the association between T. deckeni occurrence and the proportion of grassland cover (prop_grass) is positive when MG use is constructed at 10 m, but negative at 60 m. Vegetation structure (SCI) has a strongly positive, significant relationship with T. deckeni occurrence at 10 m, but not at 60 m. Conversely, NDVI is a significant predictor of T. deckeni occupancy of coarse spatial units when MG use is constructed at 10 m, but is not significant when the grain of MG use is 60 m. Finally, while the association between T. deckeni occurrence and shrubprop is significant in MG use in both final MG models, this relationship is much stronger in MG use at 60 m than 10 m.

At both 10 and 60 m, MG use achieved higher predictive accuracy than equivalent SG occupancy models (Fig. 4). In contrast, the accuracy of MG occupancy (AUC = 0.89 and CBI = 0.45–0.55) when MG use was constructed at both 10 and 60 m was similar to that of equivalent SG occupancy models (AUC = 0.87, CBI = 0.65). Given the True Skill Statistic, MG use and MG occupancy models (TSS = 0.45–0.6) consistently
outperformed SG occupancy models (TSS = 0.2–0.4) in predicting T. deckeni occurrence at fine and coarse grains (see Fig. 4).

Across MRC, the extent of fine spatial units predicted to be used by T. deckeni is much larger than that of coarse spatial units predicted to contain occupied home ranges (Fig. 4). That is, predicted use of environmental resources by T. deckeni is much more widespread than predicted occupancy. We infer that the environmental factors most strongly associated with T. deckeni use, proximity to water, dense shrub vegetation, and low exposure (see Table 1), are widely available at fine grains,

Table 1. Estimated parameters for use levels of final MG models.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>MG occupancy (1 km), MG use (60 m)</th>
<th>MG occupancy (1 km), MG use (10 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median 2.5% 97.5%</td>
<td>Median 2.5% 97.5%</td>
</tr>
<tr>
<td>$a_{\text{elev}}$</td>
<td>$-0.62$ $-1.53$ $-0.01$</td>
<td>$-0.45$ $-1.58$ $0.26$</td>
</tr>
<tr>
<td>$a_{\text{lechert}}$</td>
<td>$0.31$ $-0.14$ $0.78$</td>
<td>$0.31$ $-0.27$ $0.75$</td>
</tr>
<tr>
<td>$\alpha_{\text{NDVI}}$</td>
<td>$0.44$ $-0.06$ $0.95$</td>
<td>$0.90$ $0.34$ $1.58$</td>
</tr>
<tr>
<td>$\alpha_{\text{precip}}$</td>
<td>$0.17$ $-0.55$ $0.96$</td>
<td>$0.19$ $-0.47$ $1.15$</td>
</tr>
<tr>
<td>$\beta_{\text{dist2water}}$</td>
<td>$-2.00$ $-3.35$ $-1.03$</td>
<td>$-0.80$ $-0.97$ $-0.64$</td>
</tr>
<tr>
<td>$\beta_{\text{KTw}}$</td>
<td>$-1.19$ $-2.40$ $-0.14$</td>
<td>$-1.71$ $-2.66$ $-0.85$</td>
</tr>
<tr>
<td>$\beta_{\text{prop_grass}}$</td>
<td>$-0.54$ $-1.20$ $0.01$</td>
<td>$0.15$ $0.03$ $0.27$</td>
</tr>
<tr>
<td>$\beta_{\text{SCI}}$</td>
<td>$0.21$ $-0.55$ $0.96$</td>
<td>$1.22$ $0.84$ $1.69$</td>
</tr>
<tr>
<td>$\beta_{\text{shrubprop}}$</td>
<td>$1.67$ $0.51$ $3.19$</td>
<td>$0.20$ $0.04$ $0.34$</td>
</tr>
<tr>
<td>$\beta_{\text{TAI}}$</td>
<td>$-1.16$ $-2.53$ $-0.35$</td>
<td>$-1.09$ $-1.69$ $-0.56$</td>
</tr>
</tbody>
</table>

Notes: Shown are posterior median estimates and 95% Bayesian confidence intervals (CBIs) for all parameters in the two final MG models. MG occupancy ($\sigma$) is constructed at 1 km, while MG use ($\beta$) is constructed at 60 m (gray) or 10 m (white). See Appendix S1: Table S1 for further information on each environmental variable. Variables for which the CBI does not overlap zero are shown in boldface type.
while the factors associated with home range occupancy, elevated NDVI, long-term mean annual precipitation, and lower elevation, are relatively uncommon at coarse grains. The general locations of less-suitable areas are broadly similar among MG use and MG and SG occupancy predictions, likely because several environmental variables in MG use are related to variables in MG and SG occupancy (for example, shrub density and NDVI, or KTW and mean annual precipitation). Thus, the distribution of *T. deckeni* across MRC appears to be limited by the mosaic of environmental conditions required to support a home range, rather than the amount of high-quality foraging patches or complex vegetation.

The portion of MRC predicted to be suitable for *T. deckeni* occupancy under the SG approach is approximately 185 km², while only ~110 km² are predicted to be suitable for both MG use and occupancy (Fig. 5). This discrepancy results in a substantially lower estimate of the number of occupied *T. deckeni* home ranges across MRC under the MG approach (median number of home ranges = 86) vs. the SG approach (median number of home ranges = 103).

**DISCUSSION**

Occupancy modeling provides a general, flexible framework for investigating questions about species’ spatial distributions when occurrence data are affected by imperfect detection, while recent advances in remote sensing uniquely allow cross-scale capture of species–environmental associations (Pettorelli et al. 2016, Anderson 2018). Here, we extended occupancy modeling methods and utilized remotely sensed imagery to address enduring questions about the spatial grain(s) at which species–environment relationships operate, constructing a multi-grain (MG) hierarchical model based on the structure of species–environment associations expected from ecological theory. The primary contribution of this study is the application of grain optimization to measure the spatial grains at which a species responds most strongly to its environment. We also extend this scale-conscious analysis framework to estimate population size across an example study landscape.

At each of 32 analysis grains, we used indicator variables to vary the environmental covariates in the use and occupancy processes of our MG model among MCMC samples, Bayes Factors (BFs) to evaluate the probability that each covariate should be included in the model (Jarosz and Wiley 2014), and an independent data set and three accuracy metrics to assess model predictive accuracy (AUC, CBI, and TSS). Our evaluation criteria indicated that our example study species, *Tockus deckeni*, responded both strongly and relatively similarly to the environmental variables in MG use across a narrow range of grains (40–150 m). At other grains, performance metrics for MG use either substantially decreased...
(indicator variables, BFs, CBI) or varied inconsistently (AUC) across grains. This pattern of strong, relatively consistent responses in MG use along a limited range of spatial grains, surrounded by abrupt transitions (or erratic variation), matches the expected results when species–environment associations are structured as scale domains and a sufficient range of spatial scales has been sampled (Wiens 1989, Wheatley and Johnson 2009, Lechner et al. 2012). This finding supports our proposal that MG occupancy models may be used to measure species’ response grains. Even if occurrence processes operate exactly as proposed by ecological theory, they are not likely to be perfectly independent at their respective response grains (Huston 1999). However, in our MG model, interference from species–environment associations at other grains, which may prevent conclusive identification of response grains when using single-grain (SG) methods (Orians and Wittenberger 1991, Rotenberry and Wiens 1991, Pribil and Picman 1997, Johnson et al. 2002), is less likely to confound parameter estimates and detection of response grains. Similarly, as we varied the grain of MG use by a factor of 50, posterior

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**Fig. 5.** Population estimates are lower under a multi-grain (MG) vs. single-grain (SG) approach. Top panels show areas that meet suitability thresholds under SG (left) and MG (right) approaches, overlaid by an example simulation in which suitable home ranges are placed across MRC to capacity. In the SG approach (left), the suitable area comprises all spatial units (1 km) for which the SG model (1 km) achieved 90% sensitivity. In the MG approach (right), the suitable area comprises all units (60 m) for which both MG occupancy (1 km) and MG use (60 m) achieved 90% sensitivity. Unsuitable areas are shown in light gray. The bottom panels show the predicted *T. deckeni* population of MRC, estimated from 1,000 simulations under SG (left; median = 103 home ranges) and MG (right; median = 86) approaches.
estimates of parameters in MG occupancy remained relatively stable. This outcome suggests adequate separation among the use and occupancy processes of the MG model, and their associated processes. Overall, our MG model effectively characterized two distinct, yet complementary sets of species–environment relationships that lead to the observed spatial distribution of our study species. 

The multiple sets of environmental requirements implemented in the MG model also lead to lower population size estimates across the study landscape. For example, our final MG use highlighted fine spatial units (60 m) containing patches of complex vegetation near water sources. However, in order to be considered suitable in MG home range placement simulations, such patches also had to occur within a coarse spatial unit (1 km) that satisfied complementary sets of environmental requirements (e.g., at low or intermediate elevations and containing productive vegetation during most of the year). The MG approach thus filters “more suitable” from “less suitable” spatial units using multiple sets of criteria and at multiple grains, and highlights only the spatial units where suitable conditions overlap. Consequently, fewer spatial units in the study landscape were suitable under MG vs. SG criteria, and lower population size estimates resulted from MG vs. SG simulations. While the MG approach clearly induces stronger spatial and environmental constraints, we argue that these constraints produce a more informed characterization of individuals’ space and niche requirements, and thus likely a more accurate assessment of how many home ranges are likely to be distributed across a landscape.

Over all grains considered for MG use, T. deckeni was most strongly associated with linear distance to the closest permanent water body (dist2water) at grains between 50–150 m, vegetation and soil moisture (KTW) at grains finer than 200 m, and density of individually delineated shrub canopies (shrubprop) at grains between 40–100 m. These variables likely identify vegetation patches, such as those located near rivers and seasonal water flows (“luggas”), which supply important food resources, as well as the large trees required for nesting cavities. We repeatedly observed T. deckeni foraging along the edges of open, grassy areas (“glades”); this strategy is captured by large BFs for proportion grassland land cover (prop_grass) at grains between 120–180 m, and incoming solar radiation (TAI) at grains between 60 and 140 m. Together, these variables approximate favorable growing conditions for grassland plants, and thus also areas likely to contain T. deckeni prey such as grassland insects, as well as insects that inhabit or consume the dung of large herbivores (Kemp 1976, Lack 1987, Young 2015). At 60 m, a sufficient proportion of these species–environment relationships are maximized, meeting our first criterion for identifying a species’ response grain. Our second criterion for identifying a response grain was also met when the majority of the predictive accuracy metrics (AUC, CBI, and TSS) were maximized for the MG use model constructed at 60 m. In comparison, the SG model we built at the 60-m grain scores lower on two of three accuracy metrics: AUC (MG use 60 m = 0.89, SG 60 m = 0.81) and TSS (MG use 60 m = 0.55, SG 60 m = 0.48). In addition, the SG model elides both the theoretical and quantitative differences in species–environment associations that are clearly apparent in our MG models.

These results provide a clear example of the value of performing grain optimization; that is, evaluating the relationship between occurrence patterns and potential environmental predictor variables across a wide range of biologically reasonable scales (McGarigal et al. 2016). Even though the response grain we selected a priori for T. deckeni (10 m) was based on years of detailed observations, and the response grain revealed by grain optimization (60 m) was not radically different, estimated species–environment associations varied substantially between these grains. For example, grassland cover (prop_grass) was positive and significant in MG use at 10 m, but negative and nearly significant in MG use at 60 m. This pattern is consistent with frequently observing adult T. deckeni forage along the edges of glades. At the 10 m grain, these observations fall into 10 × 10 m grid cells with a relatively high proportion of grassland cover, but at the 60-m grain, these observations fall into 60 × 60 m pixels that lie mostly in adjacent shrubland. Had we not performed grain optimization, we would have incorrectly inferred that the relationship observed at 10 m influenced T. deckeni use of fine spatial units within an occupied home range. Indeed, extending a relationship that is apparently confined to very fine spatial grains across the entire study extent may have contributed to the lower AUC and CBI of MG use at 10 m.

Our formulation of the MG model assumes (1) no changes in the occupancy status within coarse spatial units and (2) no changes in the use status within fine spatial units over the study period. We are confident that assumption 1 is unlikely to be violated in our system, because only adult birds were recorded, and adult T. deckeni maintain fairly stable home ranges. We acknowledge that assumption 2 may not be upheld in all circumstances (e.g., the use status of a fine spatial unit might change between dry and rainy seasons) and is more likely to be violated when finer spatial units are considered. Violation of assumption 2 could potentially lead to overestimation of the probability that an individual uses the resources in a given spatial unit, underestimation of the probability of detection, and biased parameter estimates (Rota et al. 2009). However, bias associated with violations of the closure assumption is minimal when the number of sample occasions is relatively low (Otto et al. 2013). In this study, we attempted to balance assumption 2, the assumption of closure for use of fine-grain sites, with the assumption of spatial and temporal independence of observations shared by all occupancy models. Specifically, we attempted to balance the availability of repeated observations, with a study period...
during which closure for use of fine-grain sites could reasonably be expected. We selected a period (April–December 2014) that contains relatively consistent environmental conditions (two rainy seasons, separated by a short gap) and includes only one reproductive cycle (for a species that may live for 10 yr in the wild; see Kemp and Woodcock [1995]). Further thinning data (i.e., by retaining only first observations from surveys) reduced data available from a period during which fine-grain closure could be reasonably assumed, such that modeling occupancy and use could not be achieved. Instead, we implemented several spatial and temporal filters to minimize spatiotemporal dependence among observations, resulting in retaining, on average, only two detections from any individual survey (Appendix S1: Fig. S1).

Several recent studies have explored alternate approaches to resolving scale dependence issues in species distribution and occupancy modeling. For example, (Dorazio 2014) jointly modeled data from both opportunistic observations and planned surveys while accounting for imperfect detection. (Renner et al. 2015) proposed that point process models offer a natural way to analyze presence-only data, and demonstrated a framework for selecting pseudo-absence (i.e., quadrat) locations. (Koshkina et al. 2017) constructed an integrated, inhomogeneous point process model that simultaneously uses presence-only and site occupancy data. While such approaches offer exciting advances in understanding and predicting species distributions, their recognition of the hierarchical structure of species–environment relationships is limited. The approach we present here addresses this hierarchy, which is well-established in ecological theory (Kolasa 1989, O’Neill et al. 1989, Wiens 1989, Wiens and Milne 1989, Kotliar and Wiens 1990, Wu and Loucks 1995, Wu 1999, Wu and Li 2006). We also explicitly calculate the spatial grain(s) important to a species of interest, itself a potentially significant quantity for basic ecology and management purposes.

A grain optimization procedure may be applied to any species when replicate survey data are available and home range residency is consistent across the closure period. Indeed, this approach is ideal for poorly studied species, for which information on potential grains of response or occupancy are lacking. Our findings also have broad conservation and management implications due to the ubiquity, explicit or implicit, of spatial scale in sampling designs, species distribution models, abundance estimation, and understanding and forecasting the effects of environmental stressors on species occurrence or abundance. First, landscape suitability assessments (e.g., for siting a reserve or corridor) will be more accurate when their spatial resolution aligns with the response grain of the target species. Second, monitoring efforts typically have a characteristic sampling unit, such as a quadrat, plot, or trap array; matching the sampling unit to a response grain improves the chances of capturing environmental relationships that are biologically relevant to the species of interest. The modeling and grain optimization approach we present enables the identification of appropriate grains for either of these purposes. Third, our MG home range distribution simulations offer managers a readily applicable framework for estimating the population size of a territorial species within a given landscape. Finally, we demonstrate that disentangling sets of species–environment relationships reveals discrepancies in the distributions of critical environmental factors at different spatial grains. Such cross-scale interpretations may be of particular use in suitability assessments for species of conservation concern, e.g., by distinguishing between sites that meet a species’ ecological requirements at multiple grains and sites that provide limited environmental support. In summary, we suggest that the MG models demonstrated here, with necessary modifications for landscape features and species-level attributes, may be generalized to a range of taxa, systems, and spatial scales, as a tool for identifying biologically meaningful spatial grains for analysis, conservation, and management.

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**DATA AVAILABILITY**

Movement data are available on Movebank at https://doi.org/10.5441/001/1.cp97k9j1. Detection histories and site grid data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cz8w9gj0f. OpenBUGS code that comprises the authors’ hierarchical, multi-grain occupancy model is available in Data S1 and on Zenodo at: http://doi.org/10.5281/zenodo.3612779.