

Accuracy of resource selection functions across spatial scales

Carolyn B. Meyer^{1*} and Wilfried Thuiller²

¹Department of Botany, University of Wyoming, Laramie, Wyoming 82071, USA and ²Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Université J. Fourier, BP 53, 38041 Grenoble cedex 9, France

*Corresponding author. Carolyn Meyer, PhD, Department of Botany 3165, 1000 University

Avenue, University of Wyoming, Laramie, WY

82071, USA. Tel.: (307) 766 2923; Fax: (307) 766 2851; E-mail: meyerc@uwyo.edu

ABSTRACT

Resource selection functions (RSFs) can be used to map suitable habitat of a species based on predicted probability of use. The spatial scale may affect accuracy of such predictions. To provide guidance as to which spatial extent or grain is appropriate and most accurate for animals, we used the concept of hierarchical selection orders to dictate extent and grain. We conducted a meta-analysis from 123 RSF studies of 886 species to identify differences in prediction success that might be expected for five selection orders. Many studies do not constrain spatial extent to the grain of the next broader selection order in the hierarchy, mixing scaling effects. Thus, we also compared accuracy of single- vs. multiple-grain RSFs developed at the unconstrained extent of an entire study area. Results suggested that the geographical range of a species was the easiest to predict of the selection orders. At smaller scales within the geographical range, use of a site was easier to predict when environmental variables were measured at a grain equivalent to the home-range size or a microhabitat feature required for reproduction or resting. Selection of patches within home ranges and locations of populations was often more difficult to predict. Multiple-grain RSFs were more predictive than single-grain RSFs when the entire study area was considered available. Models with variables measured at both small and large (> 100 ha) grains were usually most predictive, even for many species with small home ranges. Multiplegrain models may be particularly important for species with moderate dispersal abilities in habitat fragments surrounded by an unsuitable matrix. We recommend studies should no longer address only one grain to map animal species distributions.

Keywords

Fragmentation, predictive accuracy, resource selection, scale, selection order, species occurrence.

INTRODUCTION

A resource selection function (RSF) is defined as any statistical model that is proportional to the probability of use by a species (Manly et al., 2002). RSFs typically relate used and unused sites or used and random sites to environmental variables to predict site use by a species, assuming probability of use is directly proportional to values of the resources in the area. One of the most important applications of RSFs is mapping species distributions to aid in conservation (Araújo et al., 2004), reserve design (Cabeza et al., 2004), population viability analysis, or land management planning (Boyce et al., 2002). RSFs also have been used to assess biodiversity hotspots (Grand et al., 2004), calculate expected extinction rates (Carroll et al., 2004; Epps et al., 2004), guide re-introduction efforts (Harig & Fausch, 2002; Schadt et al., 2002), and predict spread of invasive species (Havel et al., 2002; Thuiller et al., 2005). For any application, the spatial scale of measurement could greatly affect the accuracy of the RSF predictions (Johnson, 1980; Wiens, 1989; Meyer *et al.*, 2004). Although RSFs can be applied to plants or animals, the focus of this paper is on the effect of scale on accuracy of animal RSFs.

When designing a study to develop an RSF for an animal, one must first determine which spatial scale is appropriate for measuring model variables, specifying both grain (resolution) and extent (areal coverage) (Vaughan & Ormerod, 2003). Some studies give no justification for the scale chosen. For others, the decision is often related to one of the four hierarchical selection orders defined by Johnson (1980) that meets the study's objectives. First-order selection is the selection of the geographical range of a species. Within that range, second-order selection determines the home range of an individual or social group. Third-order selection is the use of different habitat patches ('patch' is a contiguous vegetation type) within the home range. Fourth-order selection is use of feeding sites within a habitat patch. For the purposes of this paper, we expanded fourth order

Table 1 The hierarchical scales of selection orders, and example study objectives for each. The mean (bold), SE (in parentheses), and range (in italics) of κ and D_{xy} for resource selection functions of vertebrates^{*} are shown. Only reproductive, latrine, or resting sites were included in the estimates given for κ and D_{xy} at fourth-order selection

Order	Biological level	Scale of used area (optimum grain) within available habitat (spatial extent)	Examples of RSF study objectives	κ†	D _{xy}
0	Species	Geographical ranges within world or parts of world	Assess biodiversity, movement of invasive species, climate change	_	0.88 (0.004) A 0.52–1.00
1	Population	Regions containing populations within geographical ranges	Reserve designs, metapopulation viability analysis, land-use planning, reintroductions	0.43 (0.03) A 0.00-0.83	0.75 (0.03) B 0.36-0.98
2	Individual	Home ranges within regions containing populations	habitat management, conservation of used areas	0.60 (0.05) AB 0.27–0.89	0.80 (0.04) AB 0.54-0.92
3	Individual life requirement at patch scale	Patches within home ranges	habitat management or mitigation of impacts	0.49 (0.07) AB 0.11–0.87	0.67 (0.06) B 0.40-0.85
4	Individual life requirement at local scale	Microhabitats within used patches	Protection or creation of key life-history attributes	0.68 (0.07) B 0.32–1.00	0.74 (0.16) AB‡ 0.35–1.00

*0 order from sample of species of 173 birds (SB) with small (< 100 ha) home range (HR), 214 birds with large (\geq 100 ha) HR (LB), 88 mammals with small HR (SM), 72 mammals with large home range HR (LM), 67 reptiles with small HR (SR), and 43 amphibians with small HR (A). 1st order from 43 SB, 3 LB, 3 SM, 1 LM, 14 A, 13 SR, 3 fish (F). 2nd order from 9SB, 2 LB, 1 SM, 7 LM; 3rd order from 3 SB, 10 LB, 6 LM, 1 reptile with large home range (LR). 4th order from 5 SB, 3 LB, 4 SM, 7 LM, 1 SR, 2 F.

†Within same column, different capital letters indicate significant pairwise differences (P < 0.05) using Tukey's post-hoc comparison test. ANOVA $F_{3,100} = 6.08$, P = 0.001 for κ; $F_{4,714} = 17.08$, P < 0.001 for D_{xy} . Mean prevalence for κ was 0.32, 0.45, 0.44, and 0.44 for orders 1, 2, 3, and 4, respectively. Prevalence for D_{xy} was 0.27, 0.33, 0.50, 0.21, and 0.41 for orders 0, 1, 2, 3, and 4, respectively.

 $Sample size for 4th order D_{xy}$ is very low at n = 4, providing low power to detect differences with other orders.

to include selection of any local feature within a habitat patch to meet life requirements.

We added an additional order to Johnson's (1980) to account for selection of areas used by populations within the geographical range, which some RSF studies address (hereafter referred to as 1st order, changing Johnson's 1st to 0 order, Table 1). Habitat perfectly suitable for individuals may be too fragmented or isolated to support a population or metapopulation (Hanski, 1998), which would only become apparent by assessing selection at the population level. If appropriate, first-order selection could be divided further into population (1st order a) and metapopulation (1st order b) selection orders. If a home range is large, thirdorder selection could be divided further into small landscapes within home ranges (mosaic of patches, 3rd order a), as well as homogeneous patches within landscapes of home ranges (3rd order b).

In a hierarchical analysis, the selection order ideally should dictate the grain (pixel size) used to map presence and the spatial extent of the area to be surveyed and considered available (Wiens *et al.*, 1987; Luck, 2002). For example, in second-order selection the grain for presence should be the seasonal or annual home-range size (area an animal normally travels in day to day activities throughout the period of interest), and the spatial extent for selecting used, unused or random sites should be limited to the area containing the local population of that individual. In fourth-order selection, nest or den sites should be compared to nearby unused sites in the same habitat patch. In other words, the spatial extent should be constrained to the grain of the next lower (broader-scale) selection order to hold conditions at other scales

constant (Table 1). Similarly, the grain size for presence should not be smaller than the grain size of the next higher (finer) order to avoid mixing selection orders and weakening the model. Although commonly done, this means that second-order RSFs should not compare used microhabitat sites or patches inside a home range to unused microhabitat sites or patches that are both inside and outside the home range. Environmental correlates such as percentage of each land cover, mean elevation, or distance to a feature should be measured at the same grain size as presence, although other grains could be added. Although rarely done, comparisons should use a paired or matched statistical design in the RSF if more than one population or patch is evaluated (i.e. discrete choice logistic regression; Manly *et al.*, 2002; Boyce *et al.*, 2003).

If the area considered available is not constrained and encompasses a study area that has a larger spatial extent than the next lower selection order, multiple grains of selection may be influencing the location of a life-history characteristic of interest or individual home range. For example, selection of a raptor's nest site in a relatively large tree (4th order) may be contingent on whether that tree is within a patch that provides enough canopy cover for the young (3rd order) and is near grassland containing food resources available within the birds' home range (2nd order). The potential home range around the prospective nest site may contain all life requirements for an individual but not be used because it is within a landscape that contains habitat amounts too small or isolated to sustain a viable population or is near human activities that disturb the animals (1st order). Finally, if the landscape is outside the geographical range of the species due to climatic or other factors, the tree will not be used (0 order).

Thus, when the spatial extent chosen as available is unconstrained to a large study area, one might expect multiple-grain (hereafter referred to as multigrain) models to perform better at predicting animal locations than a single-grain model. In this paper, multigrain models are defined as models with more than one buffer size (grain) around the used or unused (or random) pixel, with each buffer representing a different hierarchical order. The used 'pixel' is the minimum grain mapped to delineate a used site. The need for such multigrain models may be most pronounced for specialist species living in one habitat type that is fragmented or isolated, especially if they have a moderate to limited ability to disperse between fragments (Noon & McKelvey, 1992; Doak, 2000; Bergman et al., 2004). Metapopulation theory states that size and isolation of a habitat fragment containing a population are important determinants of fragment occupancy for species that have limited dispersal among disparate fragments (Hanski, 1998). The dispersal ability shifts depending on the species tolerance of the matrix surrounding the habitat patches (Ricketts, 2001), and thus poor suitability of the matrix also may increase the importance of multigrain RSFs.

Multigrain models may provide high prediction accuracy and eliminate the need for constraining the available area. Many studies prefer not to constrain the spatial extent and instead randomly sample potential habitat throughout a study area to obtain used and unused sites (Design I in Manly *et al.*, 2002). Multigrain RSFs may be ideal for such studies or mapping of local features such as nests, dens, or even used patch types within home ranges. However, if only one selection order is of interest, multigrain models may not be necessary, or as predictive.

The aim of this paper is to provide some guidance on how to (1) choose the appropriate spatial scale or scales (grain and extent) for developing RSFs for an animal species and (2) assess the accuracy of the final RSF model relative to other studies with similar objectives, information sorely lacking due to the variety of methods used to assess 'accuracy' of RSFs. To achieve our objectives, we compared accuracy of published RSFs having variables measured at different grains and multiple grains for many species with various life-history characteristics. Our specific objectives were to determine (1) if habitat use at certain selection orders is easier to predict than other selection orders, irrespective of the species, and (2) if multiscale RSFs are more predictive than single-scale models, and if so, under what conditions.

METHODS

Comparison of selection orders and multigrain RSFs

We used a meta-analysis approach, obtaining information from 123 published papers for 886 animal species (1070 RSFs) at grains ranging from point locations (nest or roost tree) to 2500 km². Of the 886 species, 341 had RSFs measured at grains finer than the geographical (0 order) grain and 545 were measured only at the geographical grain (2500 km²). The majority of the finer-grain RSFs were logistic regression models (e.g. Augustin *et al.*, 1996; Cowley *et al.*, 2000), although some were discriminant function analyses (e.g. Welsh & Lind, 2002; Woolf *et al.*,

2002) and generalized additive models (GAM; e.g. Suarez-Seoane *et al.*, 2002; Knapp *et al.*, 2003). The geographical-grain RSFs were GAMs (Thuiller *et al.*, 2004). Stepwise approaches were the most commonly used methods to select the final model from a set of candidate models (e.g. Matsuoka *et al.*, 1997; Mitchell *et al.*, 2001), although quite a few used information-theoretical criteria (e.g. Gibson *et al.*, 2004; Suorsa *et al.*, 2005).

Based on the minimum pixel size used to depict presence, we first classified each RSF as characterizing presence at the microhabitat, patch, home range, population, or geographical grain. Microhabitat included conditions at a local site such as a nest, feeding, or resting site. Patch habitat was smaller than the home range, yet larger than microhabitat and often represented characteristics of homogeneous areas within the home range (e.g. patch of large trees or grassland). For the home-range grain, the pixel size (square, circle or 100% minimum convex polygon) must have approximated the estimated size of the home range. We obtained most sizes of home ranges from the published literature, although some were interpolated from regressions of mean body size on home range developed for each taxonomic group (Schoener, 1968; Turner et al., 1969; Harested & Bunnell, 1979; Minns, 1995). The population grain included presence pixels much larger than the home range but less than 2500 km^2 , the pixel size we used for the grain of the geographical range. A 2500 km² pixel is small for the minimum size of discrete parts of the geographical range, but was the best available. We purposely included a variety of taxonomic groups in each grain size to identify generalities across species.

If the spatial extent considered available in a study was constrained according to the criteria in Table 1, we further classified the RSF into a selection order. If extent of an RSF was not constrained and sampling occurred throughout the study area, we recorded whether the RSF was single grain (i.e. measured at the scale of the presence pixel) or was multigrain (at least two grains), measured across additional hierarchical scales of selection. To meet the objective of identifying factors that delineate a geographical range, spatial extents at the geographical grain included large areas discovered or known to have zero probability of use. In contrast, studies at smaller grains had different objectives and generally omitted such habitats from within the study area, such as terrestrial habitat for fish or trees too small for nests.

Used sites and sites randomly selected from available habitat are not mutually exclusive, which may reduce prediction accuracy when both are used in RSFs (Boyce *et al.*, 2002). Nevertheless, we included RSFs developed using random as well as unused sites because mean accuracy in each grain category was nearly identical or often higher than it was for presence/absence RSFs.

We estimated mean prediction accuracy of each grain category of RSF using Cohen's kappa (κ) and Somers' $D_{xy}(D_{xy})$. Both measures are relatively comparable across studies despite changes in species prevalence (Manel *et al.*, 2001), particularly when assessed on calibration data using logistic regressions (McPherson *et al.*, 2004). Except for the geographical grain, the majority of the RSFs were logistic regressions (90%), and classification accuracy was reported mainly for calibration data sets that did not show strong significant trends with prevalence,



Figure 1 Relationship between prevalence (proportion of sites used) and Somers' D_{xy} for 657 generalized additive models that predicted presence of vertebrates at the geographical scale (zero-order selection) using bioclimatic and land cover variables (regression equation is $D_{xy} = 0.93 - 0.18$. prevalence, $r^2 = 0.26$, P < 0.001).

although we did find a significant, slight decrease in accuracy with increasing prevalence in the zero-order GAMs (Fig. 1). We accounted for this decrease in our comparisons.

Kappa and D_{xy} both have a scale ranging from -1 (opposite or negative agreement and correlation, respectively) to 0 (no better than random) to 1 (perfect agreement or correlation). Kappa was calculated using sensitivity, specificity (typically calculated using 0.5 thresholds), and sample sizes provided in published papers using the equation in Fielding and Bell (1997). Somers' D_{xy} , if not reported, was derived from the more commonly reported concordance statistic, c (Harrell, 2001), or from area (AUC) under a receiver operating characteristic curve (AUC and *c* are identical). In some cases, we requested information from authors when data needed to calculate κ were missing from a paper, and we had to supplement grain categories of low sample size with results from a few unpublished graduate theses. Analysis of variance (ANOVA) with Tukey's post-hoc comparison test ($\alpha = 0.05$) was used to compare κ or D_{xv} among grain categories, applying Box-Cox power transformations when necessary to meet test assumptions (Sokal & Rohlf, 1995). We also assessed the magnitude of differences to evaluate biological, rather than statistical significance (Anderson et al., 2000).

Accuracy of RSFs depends on the assumption that values of environmental variables in the model are directly proportional to probability of occupancy by a species (Manly *et al.*, 2002). Unfortunately, factors rarely measured sometimes reduce effectiveness of the RSF for prediction, including resource availability, interactions with other species, historical biogeography, demographic stochasticity, detectability, and rarity of the species (O'Neil & Carey, 1986; Van Horne, 1986; Garshelis, 2000; Manel *et al.*, 2001; Morrison, 2001; Gu & Swihart, 2004). Nonetheless, by looking across many RSFs, general scaling patterns should emerge.

Fragmentation effects

Because we found that RSFs of some species were predicted best at single grains, we investigated the effect of fragmentation and suitability of the surrounding matrix on the need for multigrain models. First, we compared accuracy of RSFs of three studies of passerine birds that included single- and multigrain models (multigrain was less and greater than the home range) in fragmented shrub (Bolger *et al.*, 1997) and forest habitats (Mitchell *et al.*, 2001; Hagan & Meehan, 2002). Each study area contained different levels of unsuitability of the matrix. Second, we assessed the effect of an organism's dispersal ability in fragmented landscapes on accuracy of multigrain vs. single-grain models by comparing RSFs for 17 sedentary and 23 vagile butterfly and moth species. The multigrain models included conditions of fragments in which populations occurred (population grain), as well as the landscape surrounding the fragment (metapopulation grain). The single-grain models included only the fragment conditions.

Comparison of three fixed grain sizes

We also compared RSFs developed within individual studies to qualitatively determine if multigrain models (at least two grains) were often selected as 'best' by authors (criteria used varied with the study) compared to single-grain models. We fixed the boundaries of the grain sizes to three scales commonly addressed by studies because studies comparing biologically determined scales were less available. The three grains were local (< 100 ha), landscape (100-10,000 ha), and regional (> 10,000 ha) scales. One purpose of this exercise was to evaluate if RSFs for species with small home ranges are more predictive when they include grains far beyond the home range where metapopulation dynamics could become important. We were able to use 136 species from our original pool of 886 species for this analysis plus an additional 110 species from 19 other published RSF studies. Furthermore, we added 135 Australian species from an unpublished but comprehensive government document with RSFs (NSW NPWS, 1994), bringing the total to 381. All studies used for this comparison had available area unconstrained to the study area and pixel size varied from point locations to 169 km².

RESULTS

Comparison of selection orders and multigrain RSFs

Among five hierarchical selection orders, mean D_{xy} accuracy of vertebrate RSFs at the geographical order (0-order selection) was highest (0.88), which was $\geq 16\%$ higher than the population-(1st) and patch-level (3rd) orders (Table 1), even when adjusted to match prevalence of the other orders (using regression in Fig. 1). Unfortunately, κ could not be calculated from published studies for the geographical order, but could be averaged over sufficiently large sample sizes for the rest of the selection orders, providing greater power to detect differences among first through fourth orders than D_{xy} (13 < n_{κ} < 133; 4 < $n_{D_{m}}$ < 42). Mean κ of the fourth-selection order was over 50% higher than mean κ of the population-level (1st) order, when fourth order included reproductive, latrine, or resting sites of vertebrates (Table 1). However, fourth-order feeding sites or used sites unassigned to any activity were three times harder to predict on average than dens, nests, latrines, and rest sites ($F_{1,18} = 26.90$,



Figure 2 Mean $(\pm 1 \text{ SE})$ correct classification beyond chance using kappa (κ) of vertebrate RSFs among grain sizes used to depict presence when spatial extent is (1) constrained for each selection order, (2) unconstrained to entire study area and environmental variables are measured at the single scale of the presence pixel, or (3) unconstrained and variables are measured at multigrain scales. Dashed lines show mean D_{xy} (when available) for comparison. For the four groups shown from left to right, grain sizes of environmental variables are (a) microsite at reproductive, latrine, or rest sites (For κ , ANOVA $F_{2.47} = 21.35$, P < 0.001); (b) microsite at feeding or unspecified use sites ($F_{2,15} = 21.41, P < 0.001$); (c) patches smaller than home range areas but larger than microsites ($F_{2,72} = 3.84$, P = 0.026); and (d) areas equal to the home-range size ($F_{2.58} = 0.91$, P = 0.409). From left to right, selection orders, shown by open bars, are 4th, 4th, 3rd, and 2nd order. * = differences in κ are significant (P < 0.05) between two bars underneath the asterisk based on Tukey's post-hoc test (note: multigrain bar for microfeeding sites also was significantly higher than bar of constrained microfeeding sites).

P < 0.001, open-bar microsites in Fig. 2). In general, although not always statistically significant, selection orders based on poorly understood boundaries, such as the boundary of a biologically meaningful 'patch' (3rd order) or of a 'population' (1st order), had lower accuracy than selection orders with more obvious boundaries such as the geographical range (0 order), home range (2nd order), or reproductive site (4th order; Table 1).

Unfortunately, most invertebrate species were sampled at the population (1st) order and could not be compared across selection orders. The mean κ of first-order RSFs was 0.37 (SE = 0.031, n = 71), a value similar to the low mean κ of 0.43 of first-order RSFs for vertebrates (Table 1; $F_{1,131} = 2.06$, P = 0.15). The low classification success of the invertebrates corroborates that it is difficult to predict locations of populations.

In non-hierarchical RSFs of vertebrate species, where available area was not constrained to the pixel size of the next hierarchical level, multigrain models averaged a higher κ than single-grain models (\geq 20%, Fig. 2). The exceptions were RSFs with home range as the pixel size. However, D_{xy} showed the same trend of reduced accuracy in single-grain models even at the home-range grain (D_{xy} was 2.6 times lower, $F_{1,37} = 5.67$, P = 0.005, Fig. 2). Unconstrained multigrain models were quite effective, performing with accuracy similar to constrained hierarchical models, or better in the case of feeding/general-use sites at the microscale (Fig. 2).

For all the RSFs with grains finer than the geographical range, the larger species with home ranges > 100 ha often had the most predictive models (59%), even though they composed the minority (17%) of the RSFs. RSFs of highest accuracy (≥ 0.83 for κ or ≥ 0.93 for D_{xy}) were those that predicted black bear dens (Ursus americanus; Oli et al., 1997), brown bear home ranges (Ursus arctos; Posillico et al., 2004), East Caucasian tur patches within home ranges (*Capra cylindricornis*; Gavashelishvili, 2004), otter patches (Lutra lutra) containing spraints (White et al., 2003), forest patches of lion-tailed macaque (Macaca silenus; Umapathy & Kumar, 2000), brood-rearing patches of lesser scaup (Aythya affinis; Fast et al., 2004), and nests of four large bird species including black kites (Milvus migrans; Sergio et al., 2003), black vultures (Aegypius monachus; Poirazidis et al., 2004), house crows (Corvus splendus; Soh et al., 2002), and merlins (Falco columbarius; Hull Sieg & Becker, 1990). RSFs of smaller species with similarly high accuracy were those that predicted pool use by small-mouth bass (Micropterus dolomieu) and Ouchita mountain (Lythrurus snelsoni) shiners (Taylor, 1997) and areas used by populations of smallmouth salamander (Ambystoma texanum; Kolozsvary & Swihart, 1999), viperine snakes (Natrix maura), dice snakes (Natrix tessellata; Guisan & Hofer, 2003), mountain vizcachas (Lagidium viscacia; Walker et al., 2003), and African pied starlings (Spreo bicolour; McPherson et al., 2004). Notably, nine of these 17 species occurred in fragmented habitats.

Fragmentation effects

Increasing unsuitability of the matrix appears to increase the need for adding broader grains of habitat analysis to RSFs for small birds. RSFs of passerine birds in fragmented habitats were significantly more predictive using multigrain than single-grain models when the matrix contained unsuitable urban development or was composed mostly of young, intensively managed stands (D_{xy} more than doubled; Fig. 3). In contrast, single, local-grain RSFs were as predictive as multigrain RSFs in fragmented forests composed of a variety of more suitable successional stages with abundant medium to mature stands (Fig. 3).

Dispersal ability appeared to affect importance of multigrain RSFs for butterflies and moths in fragmented landscapes. Vagile lepidopterans able to disperse frequently to distant populations had a tenfold higher κ when environmental variables were measured at both the metapopulation grain and the population grain than when measured at only the population grain. In contrast, sedentary butterflies showed less of an increase in accuracy (only 75%) using multigrain RSFs, and the increase was not significant (Fig. 4).

Comparison of three fixed grain sizes

Of 366 species with RSFs developed from candidate variables measured at more than one of three fixed grain sizes (< 100 ha, 100–10,000 ha, > 10,000 ha), the majority (62%) of the RSFs selected as 'best' were multigrain. This was true of many species with home ranges < 100 ha, as well as those with larger home ranges. Multigrain RSFs were best for 72% of reptiles, 89% of



Figure 3 Mean (± 1 SE) classification accuracy (Somers' D_{xy}) of RSFs with environmental variables measured at the single-patch grain of the presence pixel and at multiple grains for three studies of passerine birds. Urban = shrubland habitat in an urban matrix in California (ANOVA $F_{1,32}$ = 5.28, P = 0.028; Bolger *et al.*, 1997); Young = mostly young forest matrix from intensive harvest in the south-east (ANOVA $F_{1,39}$ = 23.76, P < 0.001; Mitchell *et al.*, 2001); Mature = abundant medium age to mature forests fragmented by harvest in Maine (ANOVA $F_{1,36}$ = 0.92, P = 0.344; Hagan & Meehan, 2002). * = significant difference between the two bars.



Figure 4 Fragment-scale accuracy (± 1 SE) of RSFs compared to multigrain (fragment and surrounding landscape) accuracy for moth and butterfly groups of differing mobility (sedentary ANOVA $F_{1,17} = 0.60, P = 0.450$; vagile $F_{1,16} = 32.26, P < 0.001$). * = significant difference between the two bars.

fish, and 62% of bird species with small home ranges and for 51% of birds and 66% of mammals with landscape to regional scale (> 100 ha) home ranges. However, amphibians (48% of best RSFs were multigrain), small mammals (33%), and lepidopterans (43%) had the majority of the 'best' RSFs measured at grains < 100 ha.

DISCUSSION

The effects of scale on biological organisms appear to be partially independent and partially dependent of the size of the organism and area needed to meet habitat requirements. For example, the Earth's macroclimate changes at a broad scale across the planet, strongly affecting the distribution of an organism at the grain of the geographical range in a predictable fashion independent of an organism's size (Guisan & Zimmerman, 2000; Pearson et al., 2004; Guisan & Thuiller, 2005). This became evident when we observed the highest classification accuracy at the 0 order for all species using RSFs with bioclimatic variables, regardless of the animal's size and taxonomic group. Inclusion of land cover variables with the bioclimatic variables did little to improve predictions (Thuiller et al., 2004). However, the distribution of an organism within the geographical range was easier to predict when the scale of measurement matched a grain dependent on the size or life history of the organism such as the home range (2nd order) or a local habitat feature required for reproduction or resting (4th order). In particular, local reproductive sites (nests, dens) of large animals were generally easy to predict, possibly because such trees or logs must be large to accommodate large animals, and large features are rare across the landscape. When features required for reproduction are abundant in the landscape, probably the case for smaller species, fine-grain selection of such sites may be more difficult to detect. Similarly, feeding sites were difficult to predict probably because an animal requires food to be abundant in an area to support individuals. Thus, differentiating feeding or general use sites from available sites at the micrograin was often challenging.

For broader grains, large species require large areas of specific habitat components that may be rare (and thus easy to predict) on the landscape because humans commonly remove or fragment components at that scale. For example, urbanization and roads fragment wolf and bear habitat or increase risk of mortality (Mladenoff *et al.*, 1999; Naves *et al.*, 2003) but may have little effect on small bird or mammal populations contained within a fragment (Umapathy & Kumar, 2000). Notably, small species sometimes had highly predictive RSFs when evaluated at the population grain, probably because human and natural disturbances (fire, hurricanes) fragment their habitat at that scale.

Compared to unconstrained single-grain RSFs, multigrain RSFs applied to an entire study area were more effective at predicting species distributions, as effective as the hierarchical approach using selection orders. The majority of species appear to be responding to habitat patterns at more than one grain (Mackey & Lindenmayer, 2001). Even a number of species with small home ranges < 100 ha (> 33%) were predicted best by adding grains measured at large scales (>100 ha) such as some molluscs (Dunk et al., 2004), rodents (Walker et al., 2003), small birds (Saab, 1999) and fish (Pont et al., 2005). One advantage of using a multigrain RSF and not constraining the available area is that one single equation, rather than multiple hierarchical equations, can be used to map the distribution of a species. It also may eliminate variables that are highly correlated across scales, focusing attention on variables at scales that are most limiting for a species (Meyer et al., 2002, 2004).

A number of RSFs, particularly for small species, did not require inclusion of grains > 100 ha to create the best models.

One reason may be that large grains are less important to small species in unfragmented habitats or fragments with less hostile matrices, as suggested by our comparisons of the three passerine bird studies. Other multigrain bird studies show this same trend (Knick & Rotenberry, 1995; Saab, 1999). Unfortunately, multigrain vs. single-grain RSF comparisons are infrequently conducted for large numbers of other taxa, making it difficult to state whether this result can be generalized to other taxonomic groups.

Before assuming fragmentation increases the importance of multigrain models in other taxa, dispersal ability should be considered. In fragmented landscapes, habitat occupancy by lepidopteran populations was best predicted using multigrain RSFs for strong but not weak dispersers. We expected the opposite that strong dispersers would easily occupy all fragments and not show a matrix or metapopulation effect. Ricketts (2001) similarly found movements of butterfly species with high vagility were more impacted by quality of the matrix and distance to other fragments than were sedentary species. In that study, mobile species decreased their dispersal rates when the matrix was less suitable for crossing (more conifers), whereas sedentary species rarely left the patch. However, when a species was extremely vagile, the matrix became unimportant because all matrix types were suitable for crossing. Most likely many of our 'vagile' species had intermediate levels of mobility, explaining why the matrix and distance to surrounding fragments were still important. Taylor (1997) found similar mobility effects with fish isolated in pools in a drying stream. Pool volume dictated fish presence in the isolated pools far more than did distance of the pool from the downstream confluence. In contrast, fish in stream sections with connected pools and thus greater mobility were predicted best with larger or multigrain RSFs that accounted for pool volume and distance.

Our results should be interpreted with caution because, although we tried to have a mix of different vertebrate taxa of different sizes in each compared category, percentages were not equal. Small mammals were infrequently sampled at multiple scales. Ideally, we should have the same species percentages in each compared category, but such information was unavailable at sufficient sample sizes. Additionally, classification success often was provided in a paper only for scales that produced a strong, predictive model, and success was not tested on independent data. Consequently, accuracy is probably biased upward, which may have reduced our ability to detect significant differences among scales or selection orders. Nevertheless, this is the first study that has compared accuracy across many published studies and provides a baseline to assess the quality of future studies. This study should be repeated when larger sample sizes for each major taxonomic group become available in each grain category and selection order.

Recommendations

In agreement with Vaughan and Ormerod (2003), we recommend that studies should no longer address just one scale to develop a distribution map for a species, even for highly localized species. Use of either nested or multigrain RSFs is recommended. The grain depends on each selection order of interest, and extent should be either constrained to the selection order (with sites compared using discrete choice models) or, if unconstrained, multiple grains around a site should be measured that include the larger hierarchical scales inherent in the study area. The minimum grain selected for the population order is often arbitrary and could be guided by criteria such as the minimum area needed for a viable population based on area-incidence relationships with body size (Biedermann, 2003).

We observed a bias toward sampling invertebrates at the population grain and sampling large vertebrates at home-range or smaller grains. Logistically, sampling the home range of a snail or the habitat of populations of grizzly bears may be difficult, but we consider such endeavours worth pursuing. Finally, more studies should report at least two measures comparable among studies, such as κ or D_{xy} . The threshold-free D_{xy} derived from AUC is often preferred (McPherson *et al.*, 2004; Vaughan & Ormerod, 2005), but both measures will assist comparative meta-analyses such as this one (Fielding, 2002; Guisan & Thuiller, 2005).

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