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Review

Factors limiting our understanding of ecological scale

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ARTICLE INFO

Article history:

Received 24 January 2008

Received in revised form

22 October 2008

Accepted 23 October 2008

Published on line 9 December 2008

Keywords:

Domain

Extent

Grain

Multi-scale

Scale

Wildlife-habitat modeling

ABSTRACT

Multi-scale studies ostensibly allow us to form generalizations regarding the importance of scale in understanding ecosystem function, and in the application of the same ecological principles across a series of spatial domains. Achieving such generalizations, however, requires consistency among multi-scale studies not only in across-scale sample design, but also in basic rationales used in the choice of observational scale, including both grain and extent. To examine the current state of this science, here we review 79 multi-scale wildlife-habitat studies published since 1993. We summarize rationales used in scale choice and also review key differences in scale-specific experimental design among studies. We found on average that 70% of the observational scales employed in wildlife-habitat research were chosen arbitrarily with no biological connection to the system of study, and with no consideration regarding domains of scale for either dependent or independent variables. Further, we found it common to change either both grain and extent, or the entire suite of independent variables across scales, making cross-scale extrapolations and generalizations impossible. We discuss these sampling limitations by clarifying the differences between multi-scale versus multi-design studies, including the distinction between spatial versus scalar observations, and how these may differ from the commonly cited “orders of resource selection”. We conclude by reviewing both existing and suggested alternatives to reduce the arbitrary nature of observational-scale choice prevalent in today’s literature.

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doi:10.1016/j.ecocom.2008.10.011

1. Introduction

Most ecologists now agree that scale is important when acquiring and interpreting ecological data. Scalar aspects of ecological observation and analysis have become common over the last two decades, and now figure prominently in prioritizing research objectives (Levin, 1992), designing organism-centered sampling methods (Wiens, 1989), and extrapolating process from observed patterns (Turner et al., 1989; Turner, 2005). These ideas have inspired a growing number of “multi-scalar analyses” intent on describing ecological phenomena at more than one observational scale. Unfortunately, increased interest in ecological scale has not resulted in new or innovative understanding of basic questions in scalar ecology. We still lack the ability to predict ecological phenomena across observational scales, which ultimately hinders our progress interpreting observed patterns into known mechanisms and processes. We argue that this inability stems from arbitrary and inconsistent cross-scale study design. To demonstrate this, we review and summarize a large sample of peer-reviewed literature that focuses on the application of scaling principles to wildlife-habitat models. We examine the rationale used by researchers to choose observational scales; evaluate the most commonly used approaches to multi-scale ecological studies; and from this, we summarize some limitations in scale research that require innovation and improvement.

Why use more than one observational scale? Most ecologists likely consider this question rhetorical, but approaches to and interpretations of multi-scale analyses suggest otherwise. The impetus for multi-scale studies should be twofold. First, the same ecological process might show different patterns if observed at different scales. If we study a system at an inappropriate scale, we may not detect its actual dynamics, but may instead identify patterns that are artifacts of scale (Wiens, 1989). The inability to distinguish emigration from mortality in many live-capture studies, for instance, is an artifact of trapping-grid scale. Second, not all aspects of an animal’s biology can be observed using one observational scale. For example, different observational scales often are required to quantify local foraging movements versus natal dispersal movements. These are practical sampling reasons for using multiple observational scales, but there is also a fundamental theoretical reason that receives almost no attention: namely, the ability to *predict* patterns and processes across scales. Because ecological data are always limited, the ability to scale up or scale-down in our predictions is crucial, particularly in conservation and management of wide-ranging species. But, despite a growing number of scale-focused studies, empirical support for ecological scaling techniques remains elusive.

Why are we still largely unable to extrapolate across scales (Levin, 1992; Heuvelink, 1998; Peters and Herrick, 2004)? There are arguably several reasons, the most notable in the literature being the varied definitions of scale (e.g. Dungan et al., 2002), but perhaps the most elementary involve basic study design, and specifically the rationales used in choosing observational scales. Every scalar study

must begin with the selection of a relevant scale, defined in ecological contexts as “the spatial or temporal dimension of an object or process, characterized by both grain and extent” (Turner et al., 1989; Gustafson, 1998; Dungan et al., 2002; also see Schneider, 2001). The constituents of grain and extent are the fundamentals of how we observe ecological systems; grain referring to the finest level of spatial resolution available in a data set, and extent to the physical size or duration of an ecological observation (Turner et al., 1989). Ideally, these both are selected based on relevant information regarding a species’ biology, or grain of perception (Wiens, 1989), but often this is unknown and scalar references are arbitrary. With rare exception the number of scales employed is limited, meaning much weight rests upon rationales used in scale selection. Therefore, it is important to clarify rationales employed in selecting observational scales. If choices are largely arbitrary, published results may reflect scale artifacts and, by examining irrelevant or redundant scales of observation, may entirely miss true scalar processes. Patterns observed across scales will form the bases of hypotheses exploring underlying processes (Swihart et al., 2002), so an important distinction is whether these are derived from arbitrary/anthropocentric versus biological/organism-centered study designs. Similarly, it is worth examining whether cross-scalar experimental designs are consistent among studies. Both of these factors largely define our ability to produce scalar extrapolations and generalizations within the “science of scale” (Goodchild and Quattrochi, 1997).

2. Choice of observational scale

To quantify how observational scales have been chosen for study, we reviewed all multi-scale articles from a sample of journals that publish scalar studies: Landscape Ecology, Journal of Wildlife Management, and Journal of Applied Ecology. Our focus was on wildlife-habitat research: because study taxa are mobile and range over multiple scales, this field of study has produced more multi-scale studies than most, including the geographical sciences. It is from these studies that scalar insights will be generalized into the broader ecological literature. We used Web of Science to search for articles identifying “spatial” or “scale” in their abstract; then, we chose those claiming to have employed >1 observational scale. We analyzed each paper and determined the rationale for selecting the number and dimensions of each spatial scale. We considered choice of scale non-arbitrary if the authors provided a link between scale (grain or extent) and some aspect of the organism’s biology (e.g. movement parameters, home range, dispersal area, foraging distance, etc.), even if cited from previous research. If authors chose a scale because they “felt it to be representative...” or “considered it a good compromise...” we scored these as arbitrary. We noted taxonomic class and field of study (population or community). In total, we reviewed 79 multi-scale wildlife-habitat studies published between 1993 and 2007. We summarized trends in choice of scale over time and among taxonomic and research sub-disciplines (i.e. population versus community ecology).

Table 1 – Articles included in this review, listed chronologically within each taxonomic group. The proportion of non-arbitrary observational scales represents the number of scales selected using biological rational divided by the total number of scales used within each study.

Field of study	Proportion of non-arbitrary observational scales	Citation
Birds		
Community	0	Naugle et al. (1999)
	0	Powell and Steidl (2002)
	50	La Sorte et al. (2004)
	0	Cleary et al. (2005)
	0	Dunford and Freemark (2005)
	0	James et al. (2006)
	50	Koper and Schmiegelow (2006)
	0	Huettmann and Diamond (2006)
	67	Coreau and Martin (2007)
	0	Thogmartin and Knutson (2007)
Population	40	Baker et al. (1995)
	0	Squires and Ruggiero (1996)
	33	Moen and Gutierrez (1997)
	0	Steeger and Hitchcock (1998)
	0	Dellasala et al. (1998)
	0	Hall and Mannan (1999)
	0	Thome et al. (1999)
	100	Miller et al. (1999)
	20	Daw and DeStefano (2001)
	0	Thompson and McGarigal (2002)
	20	Fuhlendorf et al. (2002)
	0	Meyer et al. (2002)
	14	Hatten and Paradzick (2003)
	100	Whittingham et al. (2005)
	0	Driscoll et al. (2005)
	50	Manzer and Hannon (2005)
	50	Blakesley et al. (2005)
	0	Graf et al. (2005)
	0	Bayne et al. (2005)
	25	Miles et al. (2006)
	0	Mahon and Martin (2006)
	0	Sharp and Kus (2006)
	0	Li et al. (2006)
	100	Manning et al. (2006)
	100	Graf et al. (2007)
Reptiles/amphibians		
Community	0	Welsh and Lind (2002)
	0	Martin and McComb (2003)
	0	Price et al. (2005)
	0	Fischer et al. (2004)
Population	0	Russell et al. (2004)
Invertebrates		
Community	0	Duffield and Aebisher (1994)
	0	Cowley et al. (2000)
	0	Fleishman et al. (2003)
	0	Chust et al. (2004)
	0	Schweiger et al. (2005)
	0	Yaacobi et al. (2007)
Population	0	Lesna et al. (1996)
Mammals		
Community	50	Wallace et al. (1995)
	50	Gabor et al. (2001)
	100	Johnson et al. (2004a)
	50	Holloway and Malcolm (2006)

Table 1 (Continued)

Field of study	Proportion of non-arbitrary observational scales	Citation
Population	8	Bowyer et al. (1996)
	0	Pedlar et al. (1997)
	0	Taylor et al. (1999)
	33	Bowers and Dooley (1999)
	0	Terry et al. (2000)
	0	Zimmerman and Glanz (2000)
	100	Schaefer et al. (2000)
	25	Apps et al. (2001)
	67	Bond et al. (2002)
	67	Chamberlain et al. (2003)
	0	Weir and Harestad (2003)
	50	Gosselink et al. (2003)
	100	Johnson et al. (2004b)
	100	Atwood et al. (2004)
	33	Lopez et al. (2004)
	67	Apps et al. (2004)
	67	Wheatley et al. (2005)
	0	White et al. (2005)
	100	Anderson et al. (2005)
	50	Said and Servant (2005)
	33	Wallace and Crosthwaite (2005)
	100	Fisher et al. (2005)
	100	Gustine et al. (2006)
	14	Watrous et al. (2006)
	33	Telesco and Van Manen (2006)
	50	Slauson et al. (2007)
	0	Limpert et al. (2007)
	0	Benson and Chamberlain (2007)

Additionally, we compared and summarized the experimental design employed for each study.

The majority of studies we reviewed (Table 1) were premised on arbitrary choice of scale (Fig. 1). Over the 14-year review period, only 29% (± 5 S.E.M.) of the observational scales we examined had a biological rational for their use. Although variation around each annual mean was relatively high, in no single publication year did >50% of the scales have direct biological links to the species being studied. The number of multi-scalar studies has generally increased over time, with a peak in 1995 and 2004 (Fig. 1). When viewed by taxonomic class, the majority of scalar studies have been completed on birds and mammals (Table 2), with mammalogy showing the highest proportion of non-arbitrary scale choice, though still only 45% on average. Most scale work has been done at the population versus the community level and the majority of observational scales (approximately 60–80%) were chosen arbitrarily (Table 3). Regardless of publication year or field of study, using arbitrary scales of observation clearly is pervasive (Fig. 1).

How might the choice of observational scale affect our understanding of ecological scale? Most studies justify at least one observational scale anchored to something biological (home range or core areas, etc.), and then arbitrarily choose one larger and one smaller scale (i.e. 2/3 arbitrary = ~70%; the average finding of this review). With data deficiencies common in ecology, some might argue all we can do is arbitrarily select scales. Eventually, however, patterns from these studies must drive process-focused hypotheses-based

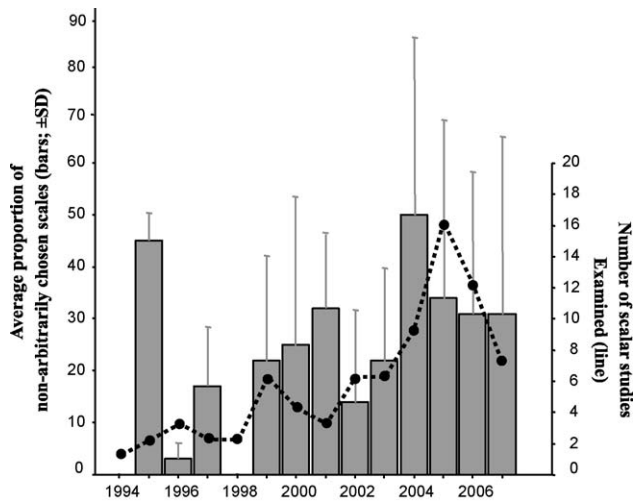


Fig. 1 – Average proportion of non-arbitrary scales used in scalar ecology studies (bars, left y-axis), and the number of studies examined for each year (dotted line, right y-axis). A total of 79 studies were reviewed from the journals Landscape Ecology, Journal of Wildlife Management, and Journal of Applied Ecology taken from issues published between 1993 and 2007.

research. Absent from this literature is concern whether arbitrarily chosen scales are even on different scale domains (Wiens, 1989) than others employed in the same study. Currently, existing scale research is poised to proceed to this stage on patterns that might largely be artifacts of scale alone, from studies principally employing either anthropocentric or arbitrary scales of observation. Arbitrary scale choice will inhibit our ability to make cross-scale predictions, which essentially is the primary reason for doing multi-scale analyses.

3. Cross-scalar predictability

Cross-scalar predictability should be the paramount question in scalar ecology, but is missing from almost all multi-scale studies we reviewed. This is not a new concept. Wiens (1989), for example, clearly outlined why the identification of “domains of scale” is key to our understanding of ecological systems. He contends if the scale spectrum is not continuous (i.e. every change in scale does not bring with it changes in patterns and processes), there may be domains of scale over which patterns and processes are predictable. That is, if we can predict how observations will change among domains (the space between known break-points), we may be able to extrapolate observations among scales. For instance, rather than measuring animal density in ten 30-ha forests, we might only measure density in ten 2-ha forests, and then scale up. The logistical implications are striking, but the theoretical implications carry even more weight: points where pattern and process change along a scale continuum likely identify key shifts in ecological processes. Why is this not a primary objective of multi-scale studies? Based on our literature

Table 2 – Total counts and proportion of non-arbitrary spatial scales employed among different taxonomic groups for scalar ecology studies done over the last 2 decades. A total of 79 studies were reviewed from the journals Landscape Ecology, Journal of Wildlife Management, and Journal of Applied Ecology taken from issues published between 1993 and 2007.

Year	Taxa			
	Birds	Herps	Inverts	Mammals
1994			1	
1995	1			1
1996	1		1	
1997	1			1
1998	2			
1999	4			2
2000			1	3
2001	1			2
2002	4	1		1
2003	1	1	1	3
2004	1	2	1	5
2005	8	1	1	6
2006	8			4
2007	3		1	3
Total count	35	5	7	32
Proportion of non-arbitrary scales (±S.E.M.) (%)	23 ± 6	0	0	45 ± 7

review, we submit this happens from researchers confounding spatial and scalar approaches, combined with a misconception between orders of selection (Johnson, 1980) and scales of observation.

Table 3 – Total counts and proportion of non-arbitrary spatial scales employed between two fields of research for scalar ecology studies done over the last two decades. A total of 79 studies were reviewed from the journals Landscape Ecology, Journal of Wildlife Management, and Journal of Applied Ecology taken from issues published between 1993 and 2007.

Year	Field of research	
	Community	Population
1994	1	
1995	1	1
1996		3
1997		2
1998		2
1999	1	5
2000	1	3
2001	1	2
2002	2	4
2003	2	4
2004	4	5
2005	4	12
2006	4	8
2007	3	4
Total count	24	55
Proportion of non-arbitrary scales (±S.E.M.) (%)	17 ± 6	34 ± 5

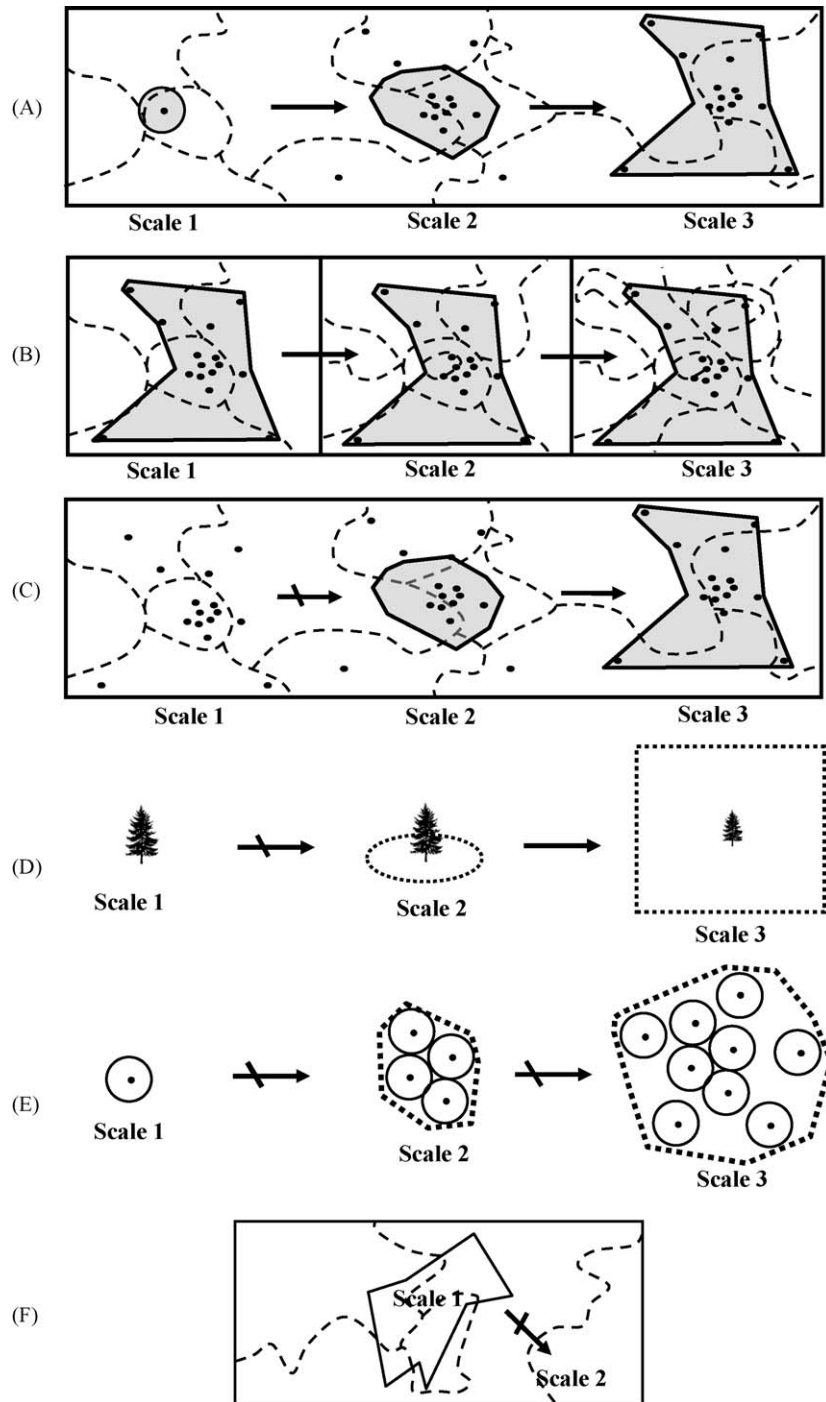


Fig. 2 – A summary of commonly used sampling approaches to “multi-scalar” studies in ecology. Broken arrows denote inappropriate multi-scalar comparisons explained below. (A) Multi-scalar extent approach: a truly scalar approach where habitat structure is summarized around animal locations (black dots) at varying spatial extents (gray areas) and grain is held constant. In this approach, the variation associated with habitat structure at multiple scales is captured, and can thus be legitimately compared among scales. In this example, the same habitat variables are quantified around a single point (scale 1), then around a cluster of points (e.g. kernel-based core area; scale 2), then around a home range (e.g. MCP; scale 3). (B) Multi-scalar grain approach: Similar to (A) above; a true scalar approach where only grain is altered to make changes in scale, but extent is held constant. (C) Mixed spatial-scalar approach: in this approach, scale 1 is examined by comparing the proportion of points falling within different habitat polygons to a random distribution of points. Larger scales are then examined using the same methods as (A) above. Though purported as multi-scalar (3 scales), this approach in fact only examines 2 scales: the smallest “scale” is not scalar; it is spatial: no variation in habitat structure is captured at the smallest “scale”. (D) Multi-scalar nest-trees: commonly used to evaluate nest sites at multiple scales, this approach is similar to (B) above, whereby non-scalar metrics (e.g. DBH, nest height, aspect, and nest type) of individual nest trees are

4. Spatial versus scalar observations

Ecologists must clearly distinguish between *spatial* and *scalar* observations. This distinction exists in various forms (e.g. Pickett et al., 1994; Stern, 1998; Dungan et al., 2002), but in practice the two are used interchangeably creating an ambiguity that has sobering implications for scalar sampling design, analysis, and interpretation. *Spatial* sampling deals with x–y locations in space, and observations generally consist of patch occupancy, distance-to, or time-budget measurements quantifying observational variation irrespective of grain or extent. Unless initially quantified as zero, variation in *spatial* observations will not change with changes in extent. However, an object's referenced position in space most likely will vary with changes in grain; but this would then represent a *scalar* sampling design.

A *scalar* sampling design deals with changes in either grain or extent: to make scalar inferences, changes in one cannot accompany changes in the other, and independent variables must remain consistent across scales (e.g. Fig. 2A and B). If grain and extent are changed simultaneously, one cannot decouple the importance of each if patterns change among observational scales. Often when this design is employed (e.g. Dellasala et al., 1998; Terry et al., 2000; Zimmerman and Glanz, 2000; Gabor et al., 2001; Chamberlain et al., 2003; Lopez et al., 2004; Mahon and Martin, 2006; Benson and Chamberlain, 2007), it is the smallest scale that is *spatial* rather than *scalar* (e.g. Fig. 2C). For instance, measurements of habitat proportions within core areas or home ranges are common in multi-scale studies (Apps et al., 2001; Gosselink et al., 2003; Wheatley et al., 2005; among others). But, when scaling down to individual animal locations (often termed micro-site or foraging scales; Moen and Gutierrez, 1997; Welsh and Lind, 2002; Zimmerman and Glanz, 2000), a tendency exists to switch from habitat proportions to proportion of locations within habitats (e.g. Chamberlain et al., 2003), the latter denoting a change from *scalar* to *spatial* sampling (e.g. Fig. 2C). Similarly, nest-sites often are used as focal points for multi-scale studies, whereby habitat proportions are summarized around each nest. Although “nests” versus “landscapes” are treated as separate scales, individual nests often are described in both non-spatial and non-scalar terms (e.g. nest height, tree diameter, slope, aspect, etc.; Fig. 2D) without reference to any particular grain or extent (e.g. Squires and Ruggiero, 1996), and are not scales in and of themselves. Because both grain and extent are changed simultaneously among

observations, or are not referred to at all, these types of designs prevent cross-scale comparisons or generalizations. They are in effect multi-*design* studies, not multi-scale studies, and are only partially relevant to scalar ecology.

Problems can still manifest when grain or extent are controlled across observational scales. For instance, using multiple replicates of the same plot size to scale up and quantify habitat over larger scales (e.g. Fig. 2E; Hall and Mannan, 1999; Weir and Harestad, 2003; Cleary et al., 2005) is not a valid multi-scalar approach. Such techniques simply capture average habitat variation at a single extent from several equal-sized plots, effectively masking changes in variation among scales (i.e. the metric of interest). In a related sense, quantification of used-versus-available habitat must be done using similar extents for both used and available habitat, such that variation associated with *smaller* core areas (used habitat) is not compared directly to variation associated with arbitrarily defined, *larger* study areas (available habitat; Fig. 2F). Because we expect different variance structures associated with each change in extent (e.g. the modifiable area unit problem, or MAUP; Openshaw, 1984), different extents cannot be compared directly in this respect.

5. Orders of selection versus observational scales

One of the most-cited papers in multi-scalar wildlife-habitat studies is Johnson's (1980) article on resource use-versus-availability and orders of resource selection. Most authors use this context when describing their choice of observational scale, from micro-site (4th-order selection) to landscape-scale (1st or 2nd-order selection). Johnson (1980) presents some statistical methodology to account for how used versus available resources can be quantified. In doing so he also presents a hierarchical method to define and rank resources used at different orders of selection. Johnson (1980) argues this hierarchy would have a unifying nature for habitat-use studies, allowing disparate studies to become comparable once organized within the hierarchy.

Though we agree with this in theory, Johnson's hierarchical approach largely has been misinterpreted as a scalar approach, or a method to choose relevant scales and their associated independent variables. Many studies citing this work conceptualize observational scales and selection orders as the same things, perhaps because higher-order selection originally was defined in more spatial terms (i.e. actual food items at a feeding site; 4th-order selection; Johnson, 1980, p. 69). The result of this

measured at the smallest “scale”, then larger scales are evaluated by quantifying different habitat variables (usually landscape metrics such as patch size, patch type by area, etc.) at larger scales. Scale 1, the smallest “scale” in this approach, is in fact non-scalar, and is often also non-spatial. (E) Invariant plot size: this approach attempts to quantify habitat characteristics over increasingly larger areas, beginning at a single animal point location and progressively including larger numbers of points over larger areas. However, to cover larger areas inclusive of several points, multiples of the same plot size are used, effectively only quantifying habitat variation at a single scale. (F) Compositional-type analysis: habitat within a “used area” (e.g. a core area; scale 1) is compared to habitat available throughout the study area (scale 2), effectively comparing habitat and its associated variability quantified at two different scales; the core-use area (smaller scale) to the study area (larger scale). This approach is only scalar if used- and available-habitat plots are equal in size such that increases/decreases in scale are applied equally to both.

misconception is that higher selection orders are sampled spatially and are in fact also non-scalar, whereas lower orders of selection are sampled within and in reference to defined spatial extents (e.g. home ranges, plot sizes, study areas, etc.). Unlike lower orders of selection, many third- or fourth-orders of selection in wildlife-habitat studies entirely lack a spatial grain or extent (e.g. Squires and Ruggiero, 1996; Moen and Gutierrez, 1997; Steeger and Hitchcock, 1998; Hall and Mannan, 1999; Terry et al., 2000; Zimmerman and Glanz, 2000; Gabor et al., 2001; Chamberlain et al., 2003; Lopez et al., 2004; Sharp and Kus, 2006; among others). Failure to identify a grain or extent results in an operational inability to generalize across scales, because no common across-scale data are measured. Scaling up or down is impossible. This removes nothing from the validity of these studies in other respects, but they are not examining ecological scale, merely observing different phenomena in different ways within the same study (i.e. multi-design studies).

Orders of selection are conceptually useful, particularly in logic used to compare seemingly disparate resource-use studies, but they arguably encourage researchers to change both grain and extent, and the suite of variables observed among scales in their sample designs. When viewed strictly in scalar terms as multiple extents or grains, the focus then becomes changing only scale and not the independent variables measured among scales. Only then can we observe how the same variables change with changes in scale, and only then can we identify relevant domains of scale.

6. Solutions

How can we choose relevant scales of observation in the absence of organism-centered clues to scalar starting points? Methods for scale selection do exist, but most require organism data a priori. For example, first-passage time, defined as the time required for an animal to cross a circle with a given radius, can be a measure of how much time an animal uses within a given area, which will be scale dependent. A plot of variance in first-passage time versus spatial scale can reveal the scale at which the animal concentrates its search effort (Fauchald and Tveraa, 2003) and perhaps perceives habitat structure. Similarly, frequency-based methods such as kernel densities (e.g. Seaman and Powell, 1996) can be used to define focal areas within which habitat structure likely influences an animal's behavior and thus, from the size of these focal areas, can define starting points for observational scale. Movement analyses also can help determine biologically relevant observational scales. Curve-fitting models of movement distances (e.g. Sibley et al., 1990; Johnson et al., 2002) can suggest small versus large scales in reference to a study animal's behavior, or examination of walk parameters (e.g. random, Levy flight, etc.; but see Edwards et al., 2007) can suggest both grain (focal areas) and extent (movement distances in-between). All of these, however, require detailed animal data at the onset which is not generally available.

In the absence of available animal data, how might we proceed to identify a justifiable observational scale? How big

should the trapping grid be, or how far around a sampling transect should we quantify habitat structure? The most relevant clues in these situations are direct examination of variability associated with habitat structure per se among scales. Natural scalar breaks in average habitat values and their associated variation can give strong clues towards how an animal might *have* to perceive habitat structure. There might be clear breaks in the habitat-scale continuum within which animals are forced to cope, and which may help structure habitat-use hypotheses including choice of biologically relevant scales. This may suggest domains of scale within which changes in sampling extent will not generate significant changes in habitat structure. For example, homogeneous or monotonically scaling habitat proportions, or large average gaps between suitable patch types, if known, can suggest both a starting and end point for scale choice based on habitat scaling alone. At the least, this may help rule out redundant scales where one should not expect new habitat relationships to form relative to other (similar) scales. The same logic can be used to interpret existing habitat models in scalar contexts. If a significant habitat model is found at one scale and not another, is this because the animal is in fact responding to habitat at that scale, or does that scale simply represent the grain and extent for which a given habitat variable inherently shows the least variation? Our interpretation is always the former, and never the latter (but see Johnson et al., 2004a), even though sophisticated techniques to examine within-plot mean and variance are well established in the literature (see Dale et al., 2002). A simple examination of the independent variables' cross-scale variation could give additional credence not only to the rationale behind choice of observational scale, but also to the final interpretation of statistically significant habitat models.

From this review three main ideas arise as suggestions to improve research in ecological scale. First, ecologists wishing to incorporate scale must be judicious to clarify multi-scale from multi-design studies. A simple examination of the literature on the number of multi-scale studies is misleading; many of these change both grain and extent, or the whole suite of independent variables among scales, which violates a truly scalar approach. These studies do not investigate scale per se, but rather ask different questions using different methods about different processes among what are misinterpreted as different scales (also see Mayer and Cameron, 2003). Second, ecologists must decide a priori whether they can truly ask scalar questions using relevant scales of observations, or whether they are simply guessing at scale and fishing for scalar patterns irrespective of either; (a) the spatial grain and extent of hypothesized life history traits of an organism; or (b) an examination of the habitat-scale continuum to identify potential scale domains of habitat parameters hypothesized to be important to the study species. Rather than obfuscate the potential importance of scale through arbitrary study design, research efforts might best be directed in full to a single scale until a more informed rationale for multi-scale study can be generated. Lastly, we must clarify exactly why we employ multiple scales of observation: it should always be to improve our abilities in cross-scalar predictability, and to

determine at what scales certain processes are relevant and among what scales we see breaks in these processes. To do this, however, requires consistent sampling of similar independent variables across different scales of observation.

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