

Habitat selection at multiple scales¹

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Abstract: Habitat selection is the disproportionate use of available conditions and resources, and involves responses in space and time to perceived risks and rewards. It frequently depends on the scale of measurement, often in non-linear ways that preclude simple extrapolation across scales. More critically, animals often select different habitat components at different scales, and species vary in their scales of selection. Although multi-scaled research on habitat selection has proliferated, synthesis of this work has been impeded by imprecise terminology and arbitrarily defined analytical scales. Here, we review key concepts and findings and evaluate future prospects opened up in part by new technologies that enable novel and more efficient data collection. Innovative measurement, combined with novel analytical approaches, permits habitat selection to be investigated across a broad continuum of scales. By linking habitat selection to fitness as a function of scale, use-of-habitat assessments can be more effective. The fitness costs and benefits of habitat selection change with scale; the scales of habitat selection may inform us of limiting factors. We outline how reward/risk ratios can be used to assess the fitness implications of habitat selection across scales.

Keywords: continuum, fitness, hierarchy, limiting factors, resource selection, scale.

Résumé : La sélection d'habitats est l'utilisation disproportionnée des conditions et ressources disponibles et elle implique des réponses dans l'espace et le temps aux risques et récompenses anticipés. Elle dépend fréquemment de l'échelle de mesure, souvent de façon non linéaire, ce qui exclut la simple extrapolation à travers les échelles. Plus important encore, les animaux sélectionnent souvent différentes composantes d'habitat à des échelles différentes et les espèces varient dans leurs échelles de sélection. Bien que beaucoup de recherche multi-échelle ait été effectuée sur la sélection d'habitats, la synthèse de ce travail a été entravée par l'utilisation de terminologie imprécise et d'échelles analytiques définies arbitrairement. Nous passons ici en revue les concepts et découvertes clés et évaluons les perspectives futures rendues possibles en partie grâce aux nouvelles technologies qui permettent une collecte de données nouvelle et plus efficace. Des mesures novatrices, combinées à de nouvelles approches analytiques, permettent d'étudier la sélection d'habitats à travers un large continuum d'échelles. En reliant la sélection d'habitats à la valeur adaptative en fonction de l'échelle, nous suggérons que l'utilisation d'évaluations de l'habitat puisse être plus efficace. Les coûts et bénéfices pour la valeur adaptative changent avec l'échelle de sélection d'habitats; les échelles de sélection d'habitats peuvent ainsi nous informer sur les facteurs limitants. Nous décrivons comment les ratios récompense/risque peuvent être utilisés pour évaluer les implications de la sélection d'habitats pour la valeur adaptative à travers les échelles.

Mots-clés : continuum, échelle, facteurs limitants, hiérarchie, sélection des ressources, valeur adaptative.

Introduction

Ecologists have devoted more attention to habitat selection—the disproportionate use of resources or conditions by living things—than to any other branch of our discipline. Habitat selection differs from use or association; it implies choice, and is commonly measured as use relative to availability or as use *versus* non-use. Understanding habitat selection is more crucial than ever. Habitat loss is the primary driver of species imperilment and extinction (Wilcove *et al.*, 1998; Venter *et al.*, 2006), and habitat protection is

frequently incorporated into endangered species recovery planning and legislation. Examining habitat selection is one way to assess the importance of habitat to species conservation, but making such assessments is not always straightforward, even for well-studied species. We see 2 main obstructions to understanding habitat selection: First, the conceptual hurdles that obscure our knowledge of habitat selection and its underlying dynamics at multiple scales; and second, the practical limitations on sampling that stem, in part, from these conceptual issues.

Habitat selection research is poised to overcome both the major conceptual obstacles and the practical sampling issues that have encumbered its progress. We suggest that the linkages among habitat selection, scale, and fitness

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are central to this advance. A more mature and integrated framework is at hand, and can be facilitated in part by a refinement of terminology and sophistication of approaches. Here, we discuss developments in understanding habitat selection at multiple scales and outline the path forward.

Selection and scale

Ecologists now recognize that habitat selection is an inherently scale-sensitive process. Whereas an animal eating the leaves of a plant is *using* that plant part, that individual plant, that patch, that vegetation community, landscape, population range, species range, and so on, the animal may be *selecting* habitat at only one or a few of these levels. Detecting the most informative scale of analysis is therefore pivotal to understanding habitat selection (Dayton & Tegner, 1984). Choice of scale may not be intuitive (Bowyer & Kie, 2006) and is frequently driven by logistics rather than concept. Consider habitat selection in its simplest form: an animal encounters some habitat unit and either accepts or rejects it. The researcher must decide on the scale of that unit: the available habitat. As Allen and Hoekstra (1992) noted, “In ecology, looking for the right thing is easier than looking for the right size.”

The literature has focussed on spatial scale, but temporal scale—the duration and resolution of observations in time—not only merits attention (Orians & Wittenberger, 1991; Folt, Nislow & Power, 1998; Fortin, Fryxell & Pilote, 2002; Hobbs, 2003; Vistnes & Nellemann, 2008), but in some circumstances may be more important than spatial scale (Fahrig, 1992). The differences between seasonal and daily decisions, for example, can outstrip the implications of spatial decisions like choosing home ranges and feeding sites. Conditions such as forage availability and predation risk can be as variable in time as they are across space. Ultimately, spatial and temporal scales are linked, both conceptually and practically (Wiens, 1989; Bissonnette, 1996; Figure 1). Their relationship depends on the mobility and behaviour of organisms. The potential distance travelled per

unit time, and thus the available habitat encountered, differs greatly between a sloth and a pronghorn.

Size matters: scale is now part and parcel of habitat selection investigations. Following Johnson (1980) and responding to observations that selection occurs at some scales and not others, studies of habitat selection are now routinely conducted at multiple rather than single scales, often cast as a nested hierarchy (Table I). Apart from the essential species-specific information, what generalizations can we draw from hundreds of these studies?

First, habitat selection measured at one scale is often insufficient to predict habitat selection at another scale. As a result, studies conducted at multiple scales provide a fuller characterization of habitat use patterns than do those conducted at single scales and tend to explain more of the observed variation (Poizat & Pont, 1996). Because ecological patterns cannot always be reliably “scaled up” or “scaled down”, studies conducted at single scales may incorrectly extrapolate selection for particular features across scales (Wiens, 1989; Schneider, 1994). Indeed, some debates (Jenkins, 1982; Nudds, 1982) can be traced to differences in scale.

Second, detecting habitat selection depends on the scales of measurement and analysis (Schneider & Piatt, 1986; Becker & Beissinger, 2003; Garcia & Oritz-Pulido, 2004; Morin *et al.*, 2005). Failure to detect selection at a given scale does not discount it at others. Similarly, because the densities of conspecifics vary with scale (Mayor & Schaefer, 2005), the density-dependence of habitat selection can also depend on scale (Morris, 1987a). For example, Oatway and Morris (2007) showed that habitat selection by meadow voles in enclosures was density-dependent at broad, but not fine, scales. Studies at different scales easily lead to different conclusions, but there is no single correct or “characteristic” scale at which to undertake research (Wiens, 1989; Levin, 1992; Schneider, 1994).

Third, animals may select different habitat components at different scales (Bergin, 1992; VanderWerf, 1993; Apps *et al.*, 2001; Johnson *et al.*, 2002a; Mosnier *et al.*, 2003; Anderson *et al.*, 2005). One explanation for such scale-dependence is variation in the distribution and spatial structure of habitat components on the landscape (Boyce *et al.*, 2003; Anderson *et al.*, 2005; Mayor *et al.*, 2007). For instance, selection by muskoxen (*Ovibos moschatus*) was consistent across scales in the relatively homogeneous environment of the arctic tundra (Schaefer & Messier, 1995a), but selection by elk (*Cervus canadensis*) was scale-dependent in the more structured landscape of the Rocky Mountains (Boyce *et al.*, 2003). Alternatively, selection of different habitat components at different scales is to be expected if limiting factors vary with scale. For example, the fitness derived from habitat elements could drive the scales at which they are selected; if the chief limiting factor cannot be overcome at the broadest scale, it may continue to propel habitat selection at progressively finer scales (Rettie & Messier, 2000; see below).

Fourth, different species select habitat at different scales (Roland & Taylor, 1997). Predators, for instance, might be expected to range widely and thereby to select habitat at broader scales than those of their prey (Hostetler

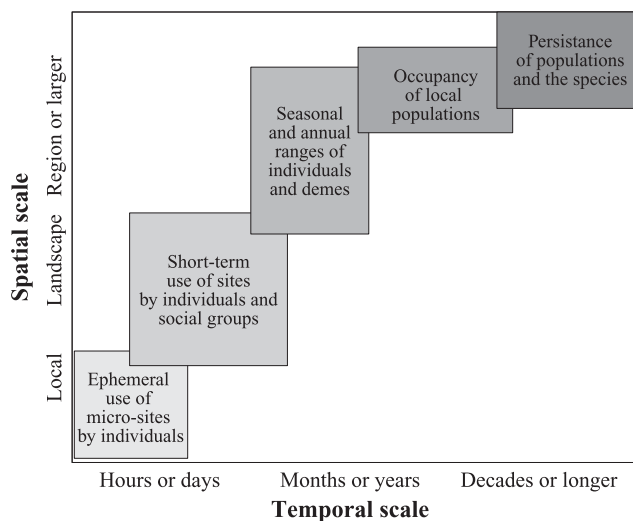


FIGURE 1. The link between spatial and temporal scales of habitat selection. The spatial units reflect organism mobility; the axis units would be appropriate for a long-lived, wide-ranging species like caribou.

& Holling, 2000). Fisher and Volpe (in review) refuted this suggestion, showing that body size alone best explains the dominant scale of habitat selection among terrestrial mammals, with larger animals selecting at broader scales. The scales at which animals interact with their environment can, however, diverge sharply from expectations based on body size (Lima & Zollner, 1996) or human preconceptions (Bowyer & Kie, 2006). Identifying the scales at which animals perceive habitat or weigh availability can help dispense with biases stemming from the “normal”, often arbitrary, scales at which humans perceive landscapes (Manning, Lindenmayer & Nix, 2004). More recently, Wheatley and Johnson (2009) estimated that 70% of scales employed in wildlife-habitat studies were chosen arbitrarily, not tied to biologically relevant levels such as home range size. The consequences of organisms selecting at different scales for community assembly may be far reaching (Purves & Law, 2002). To illustrate, species coexistence with few resources can be facilitated by “coarse-grained” foragers responding to dispersed resources, while “fine-grained” species respond to localized resources (Ritchie & Olff, 1999).

Scale can serve as both a help and a hindrance to forming generalizations regarding habitat selection. For instance, the diverse phenomena of predation, migration, distribution, gregariousness, movements, dispersal, energetics, foraging, and diet can all be considered forms of habitat selection operating at different scales (Orians, 1991; Travis & Dytham, 1999; Brown, 2000). Indeed, the recognition that different natural selection pressures can occur at different scales may be the greatest lesson learned regarding scales of habitat selection. Empowered by the concept of scale, habitat selection has been touted as a unifying paradigm for ecology: an evolutionary strategy, source of speciation, and mechanism of population regulation and community assembly (Morris, 2003). Scale is ultimately a shared feature of interacting individuals, populations, and communities.

Selection, scale, and terminology

As a subdiscipline matures, conceptual unification of the rapidly expanding literature depends on consistent and specific terminology. “Scale” has been used to describe a

TABLE I. Types of “scales” in studies of habitat selection.

Type of scale	Examples	Comments	Key references
Causal levels	Ultimate and proximate	Ultimately, habitat selection is the behavioural response to fitness costs and benefits; proximately, it is the response to perceivable environmental stimuli and cues to fitness.	Hildén, 1965; Hutto, 1985; Morris, 2003
Organizational levels	Species, subspecies, ecotype, population, group, individual	Habitat selection occurs at the individual level, but its effects can be measured as disproportionate use of habitat at any organizational level.	Bradshaw <i>et al.</i> , 1995
Environmental or geographic levels (in space)	Biome, ecoregion, forest patch, tree species, trees; Watershed, stream order, reach, riffle/pool, microsite	These levels are independent of focal species’ (or organisms of that species’) perception and represent hierarchical levels of the structural environment.	Danell, Edenius & Lundberg, 1991
Environmental or geographic levels (in time)	Disturbance cycle (<i>e.g.</i> , burn frequency), seasonal cycle, tidal cycle, lunar light cycle, daily light cycle, environmental pulse	These levels are independent of focal species’ (or organisms of that species’) perception and represent hierarchical levels of the temporal environment.	Kotler & Brown, 1988
Behavioural levels (in space)	Species range, population range, home range or territory, travel route, feeding area, feeding or nesting site	These levels are dependent on focal species and derived from observations of the distribution or movements of individuals. Johnson’s (1980) 4 selection “orders” are an example.	Johnson, 1980; Schaefer & Messier, 1995a
Behavioural levels (in time)	Multi-annual forage cycle (<i>e.g.</i> , snowshoe hare), population abundance cycle, generation time, annual breeding/birthing cycle, travel time, feeding bout, bite	These levels are dependent on focal species and derived from observations of the temporal patterns or movements of individuals.	Revilla <i>et al.</i> , 2004
Spatial scales	10^7 m to 10^{-2} m 10^7 m ² to 10^{-2} m ² 10^7 m ³ to 10^{-2} m ³	Explicit sizes between the spatial grain and extent of analysis, pattern, or process. Measured in units of distance, area, or volume. Patch size, perceptual range, and movement distance are examples that could be expressed as measurable spatial scales.	Schneider & Piatt, 1986; Holland, Bert & Fahrig, 2004; Mayor <i>et al.</i> , 2007
Temporal scales	Century, decade, year, day, hour, minute, second	Explicit sizes between the temporal grain and duration of analysis, pattern, or process. Causal and organizational levels can also be examined temporally. Temporal scales of selection correspond in magnitude to spatial scales of selection such that broader-scale decisions tend to be less frequent (Figure 1).	Orians & Wittenberger, 1991; Fortin, Fryxell & Pilote, 2002

variety of related concepts (Table I). While ecologists generally agree on the meanings of *grain* (smallest level spatial or temporal resolution), *extent* (largest area or duration of investigation), and *scope* (the ratio of extent to grain), terms such as *micro-scale* and *macro-scale* require specific reference points. Johnson's (1980) 4 specific "orders" of selection (species range, home range, feeding site, food items) might have served as a standard for multi-scale habitat selection studies. In practice, individual researchers have more often defined study-specific hierarchical levels, likely due to the variety of research questions and taxa under investigation. Such levels are defined relative to hierarchically organized terms or concepts rather than by strict spatial or temporal dimensions. Comparison of studies, and hence synthesis, would be facilitated by explicit specification of grain and extent of both analyses and habitat selection itself. Such basic quantitative information is often impossible to glean from the literature (Folt, Nislow & Power, 1998). Wheatley and Johnson (2009) advocated distinguishing between multi-scale studies—those that simply vary the grain and extent—and multi-design studies, which investigate different questions in different ways at different scales.

We concur with Hodges (2008) that flexible use of ecological terms helped to advance our science, especially in its early stages. The explosion of interest in ecological scaling (Schneider, 2001) has no doubt benefited from the multifaceted use of "scale". Nevertheless, we also believe the field is sufficiently mature to move to refinement of terminology. Calls for more consistent wording are legion in ecology, including "habitat" (Hall, Krausman & Morrison, 1997) and "scale" (Dungan *et al.*, 2002). While no single definition of "scale" is possible, it is possible to qualify the term with consistent and appropriate modifiers (Table I), a move toward improved understanding in habitat selection research. The terms we propose in Table I are aimed at distinguishing hierarchical levels from spatial and temporal scales. When investigating habitat selection at multiple levels, investigators should indicate the spatial scales represented by those levels. Conversely, when studying selection across spatial scales, reference should be made to associated levels or biological importance of those scales.

Hierarchical habitat selection and limiting factors

Analysis at multiple scales leads to manifold interpretation—each conclusion correct, but none by itself necessarily providing the complete picture (Wiens, 1989). At the same time, however, not all scales are equally informative or pertinent. How can we infer relative importance among scales of habitat selection? Habitat selection depends, of course, on "habitat". Frequently, habitat is deemed as dwelling space or little more than topography and vegetation, presumably because these features can readily be quantified and mapped. In its full sense, however, habitat encompasses the biotic and abiotic resources and conditions that govern the survival, reproduction, and presence of a population (Caughley & Gunn, 1996), an indication that parasites, predators, mutualists, and competitors may also be regarded as habitat for many species. Ecologists already

have a term for such demographic constraints: population-limiting factors.

While habitat selection consists of choices made by individuals, it is often most practically measured at the population level. In many cases, proxies for demography such as density may serve as adequate indicators of habitat quality (Bock & Jones, 2004). Indicators of habitat quality from demography and selective behaviour can become decoupled, however, when the cues that animals use to assess quality habitat are inaccurate. Animals take cues on habitat condition not just from the environment, but in response to the behaviour of conspecifics (Danchin *et al.*, 2004). Cues can misinform animals and ultimately be detrimental to fitness, such as in the case of ecological traps (Schlaepfer, Runge & Sherman, 2002).

Nevertheless, the evaluation of habitat through studies of habitat selection is enhanced when tied to demographic responses like survival and recruitment, thereby linking behaviour to fitness (Van Horne, 1983; Pulliam & Danielson, 1991; Gill, Norris & Sutherland, 2001). In a landmark paper, Rettie and Messier (2000) proposed that, across spatial scales, population-limiting factors and habitat selection can be linked—a logical connection given the broad definition of habitat above. Organisms are hypothesized to select resources (or avoid some unfavourable condition) in an attempt to overcome the chief limitation at each level; if unable to do so, they continue to select that resource at successively lower levels (*i.e.*, more local) levels. The scales of habitat selection should thus reveal an ordered list of limiting factors; the broadest scales are deemed most relevant (Rettie & Messier, 2000). Dussault *et al.* (2005) elaborated: they proposed that animals should make trade-offs among multiple factors when their effects occur at the same scales. The idea appears to unite a growing number of studies, for instance, suggesting predator avoidance may trump foraging decisions (Bowers & Dooley, 1993; Folt, Nislow & Power, 1998; Dussault *et al.*, 2005; Gustine *et al.*, 2006) because the risk of predation is a stronger constraint on fitness than temporary energy shortages.

The Rettie–Messier hypothesis relies upon hierarchy theory. Where nested processes occur, those happening at broader scales occur more slowly and thus constrain lower-level processes (Senft *et al.*, 1987; Allen & Hoekstra, 1992; Figure 1). Multi-scale studies of habitat selection have been construed as a hierarchy at least since Johnson (1980) recommended a nested multi-level framework for analyses. Yet the common observation of selection at multiple scales does not necessarily imply hierarchical selection, that selection at broader scales constrains selection at finer scales. The hierarchy of limiting factors depends on hierarchical constraints among scales, a condition not immediately apparent and rarely tested (but see Harvey & Weatherhead, 2006; Searle *et al.*, 2006). If fine-scale selection is not restricted by habitat selected at coarser scales, it is unclear why selection for the most important limiting factors should occur at coarse scales. Indeed, this "top-down" view of selection decisions is opposed by "bottom-up" suggestions of selection propagating to larger scales, such as when fine-scale animal decisions are exhibited as broader landscape level patterns. (Allen & Starr, 1982; O'Neill, Johnson & King,

1989; Kotliar & Wiens, 1990). Criticism of the hierarchy concept's utility as a theory (*e.g.*, Jagers op Akkerhuis, 2008) may be particularly applicable to habitat selection research. Hierarchy theory is "more a conceptual framework than a predictive theory" (O'Neill, Johnson & King, 1989); application of the Rettie–Messier (2000) idea has been limited. If selection among scales is not hierarchically constrained, the optimal scales of selection may be determined not by ordered importance of limiting factors but by the characteristic scales (*i.e.*, patch sizes) of resources or risks. (Anderson *et al.*, 2005, Mayor *et al.*, 2007).

Scales of selection, rewards, and risks

Habitat selection depends on the balance between rewards and risks. Such a balance may change with life stage. For instance, Werner and Gilliam (1984) proposed that as fish grow, they are increasingly able to forage in riskier habitats. Large individuals can forage more efficiently, have more resources available to them, and may be less susceptible to predation because fewer predators are large enough to prey upon them. Other species might show the opposite pattern: larger individuals may become easier to detect and at greater risk. In either case, we can anticipate that growing animals adjust habitat selection as rewards and risks change; selection may also change as the rewards and risks change with scale.

The fitness of organisms may be greatly influenced by the scales at which they select habitat. Consider costs. At larger scales, animals may remain in sub-optimal habitat even when better habitat is available due to the energetic costs and associated predation risks of dispersing or emigrating long distances (Morris, 1987b; 1992; Folt, Nislow & Power, 1998). When predation risks are more variable at broader *versus* finer scales, optimally foraging animals should have more variable vigilance, giving-up densities, and quitting harvest rates (Brown, 1999). At finer scales, costs involve time lost moving through sub-optimal habitat patches when it could be spent exploiting those or other patches. The benefits of habitat selection may also depend on scale. In a landscape exhibiting positive spatial autocorrelation, fitness rewards from long-distance movements are expected to be more variable than from short movements. Not surprisingly, organism movement is characteristically conservative (Keeling, Wilson & Pacala, 2000).

Because habitat selection depends on scale, and selection depends on the ratio of reward to risk, it follows that the ratio of reward to risk should also depend on scale. We provide a mathematical demonstration (Appendix I; following Schneider, Norris & Gregory, 2008); Searle, Stokes, and Gordon (2008) provided an experimental one. They overlaid maps of resource density and predation risk to show that forager behaviour can depend on the trade-off between these factors, and that this behaviour is influenced by multiple scales. Significant questions remain: At what scales do selection decisions most affect fitness? Does the ratio of risk to reward increase with spatial scale as risks become more important predictors of habitat selection at broad scales? More practically, can we predict habitat use by identifying the scale domains at which the risk/reward

ratio is relatively small, and correspondingly the scales at which it is large?

Detecting the response to risks and rewards across scales

While studies of habitat selection conducted at multiple scales have proliferated in recent years, most consider only 2 or 3 scales. Availability of new types of data expands the range of scales at which habitat selection can be practically measured. Spatially referenced environmental data such as land cover have opened the door to multi-scaled analyses, particularly at broader scales. Biotelemetry, like high-resolution GPS telemetry, is simultaneously pushing our perceptions of animal locations to finer grains and larger extents. Some devices are equipped with video cameras to capture continuous habitat images from the animals' viewpoint (Remington *et al.*, 2007). Data logging equipment provides detailed information on environmental variables such as temperature, light, and salinity, especially in aquatic and marine systems. The coupling of these devices with Geographical Information Systems helps facilitate species-habitat modeling. Cooke (2008) provides a review of telemetry and logging techniques relevant to different habitat types.

To identify the range of scales over which selection occurs and the changing balance of risks and rewards, we recommend an explicitly spatial approach that represents selection on a continuum of spatial scales. Continuum-based approaches can identify the dominant or characteristic scales of selection, as Fisher and Volpe (*in review*) have proposed. The choice of methods is expanding (Figure 2). Holland, Bert, and Fahrig (2004) developed a technique based on species abundance in varying-sized focal patches to determine characteristic scales of habitat association. In principle, resource selection functions (predictive models of selection) can incorporate decision rules across an array of measurement scales (see Boyce, 2006). Three recent approaches (path tortuosity, first passage times, movement rate frequencies) employ movement data of individuals to distinguish scales of selection where animal movements change across scales. In each case, animal behaviour is quantifiably different from what we would expect of a non-selective organism.

First, fractal measures of path tortuosity offer a quantitative yardstick with which the spatial scale of habitat selection can be identified. Fractal methods characterize the spatial structure of movement paths, and they allow comparison to a benchmark such as a correlated random walk (Crist *et al.*, 1992; With, 1994; Wiens *et al.*, 1995; Mårell, Ball & Hofgaard, 2002; Nams & Bourgeois, 2004). Mobile foragers, such as most vertebrates, increase the turning frequency when successful, thus staying within patches of high resource value. Consequently, the scales at which movements are more tortuous indicate scales of selection. Similarly, patterns of time spent foraging or first passage times reveal the scales at which animals concentrate their search effort (Fauchald & Tveraa, 2003; Frair *et al.*, 2005; Pinaud & Weimerskirch, 2005). Increased variance in time spent at particular scales indicates selection at those scales.

Method	Hypothetical result	Interpretation	Reference
Fractal		Selection at scales where tortuosity of actual path exceeds correlated random walk (CRW).	Nams, 2005
First passage time		First passage time (FPT) across a circle is more variable with patchy (selective) animal movement when compared with a correlated random walk (CRW)	Fauchald & Tveraa, 2003
Movement frequency		Differentiate between fine scale intra- and coarse scale inter-patch movements. Breakpoint in model shows scale of change in movements.	Schaefer & Messier, 1995b; Johnson <i>et al.</i> , 2002a
Variogram		Selection at scales where semivariance of used habitat is lower than that of available habitat.	Schaefer & Mayor, 2007
Coarse-graining		Selection at scales where Blocked quadrat variance (BQV) of used habitat is lower than BQV of available habitat.	Mayor <i>et al.</i> , 2007

FIGURE 2. Approaches for investigating habitat selection on a continuum of spatial scales.

Another measure is the frequency distribution of movements (Sibly, Nott & Fletcher, 1990; Schaefer & Messier, 1995b; Johnson *et al.*, 2002b). A “broken stick” in the logarithmic frequency of movement lengths or rates reveals scale domains for identifying patches or modes of selection.

These methods extend the concept of habitat selection from a location- or area-based definition of disproportionate use of available habitat to a path- or individual-based measure of disproportionate use. The degree of habitat selection is measured by the degree to which movements are disproportionately tortuous or result in time spent in excess of that from a random path. Sharp changes in frequency

of movements can differentiate ranges of scale for further analysis of selection. Each of these methods, however, assumes that tortuous movements represent habitat selection rather than resistance to movement through the landscape. State-space models, which couple models of dynamic movement processes to those of observation likelihood (Patterson *et al.*, 2008) are a promising avenue to infer scales of habitat selection from movement data.

Another set of methods include lag-based and coarse-graining methods applied to point-referenced locational data on a grid. These approaches are readily applied to spatial characterization of environmental variables. For

example, Lichstein *et al.* (2002) applied autocorrelation and autoregressive models of bird counts to identify scales of aggregation and related these to aggregative scales of habitat variables. Mayor *et al.* (2007) assessed habitat selection as a reduction in variance in used relative to available sites across a continuum of spatial scales. Reduction of the difference (or the ratio) of variances indicates habitat selection, assuming organisms consistently select favourable habitat. Variograms characterize semivariance among paired sample locations at various lags (Matheron, 1960). Because locations selected by animals are expected to be more similar than those available, comparison of variograms of used and available habitat reveals scales of habitat selection. Likewise, coarse-graining measures such as blocked quadrat variance (Greig-Smith, 1952) can characterize habitat selection as the reduction in variance of used relative to available habitat types across block sizes.

Conclusion

The scale-dependence of habitat selection, once regarded as an impediment to generalization, now serves as a mode of quantifying habitat selection and an avenue toward synthesizing patterns across study areas, populations, and species. Yet if cross-scale habitat selection is to succeed as a unifying concept, we require greater capacity to quantify animal interactions at multiple scales. Our success in defining habitat importance depends on measurement, which in turn depends on scale; our success in conceptualization depends on synthesis of results, which in turn depends on minimizing ambiguity of terms. Animals balance fitness concerns by scale-specific habitat decisions—an area ripe for multi-scaled research. The linkage of habitat selection to fitness as a function of scale can guide such efforts. Recent advances in quantifying scale-dependent pattern make it possible to apply the concept of scale-explicit risk/reward to the study of habitat selection.

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APPENDIX I. Scale dependent reward/risk and habitat selection.

We expect observed correlation of numbers (N) with habitat (H) to be some positive function of reward (g) relative to risk (μ).

$$r(N, H) = f(g/\mu) \quad [1]$$

In the absence of habitat selection, the association with habitat is unrelated to reward and risk.

$$\frac{d(r(N, H))}{d(g/\mu)} = 0 \quad [2a]$$

When habitat selection is operating we expect the association with habitat to increase as reward rises relative to risk. Conversely, the association with habitat decreases as reward falls relative to rising risk.

$$\frac{d(r(N, H))}{d(g/\mu)} > 0 \quad [2b]$$

We thus define habitat selection as an increase in habitat association with an increase in the ratio of reward to risk (Schneider, Norris & Gregory, 2008). By substitution of [1] into [2b] we have:

$$\frac{df(g/\mu)}{d(g/\mu)} > 0 \quad [3]$$

Applying the chain rule, we obtain the change in habitat association with change in scale:

$$\frac{d(r(N, H))}{dL} = \left(\frac{df(g/\mu)}{d(g/\mu)} \right) \left(\frac{d(g/\mu)}{dL} \right) \quad [4]$$

Because [2b] and [3] have the same sign, the correlation with habitat $r(N, H)$ as a function of spatial scale L has the same sign as the change in reward/risk with spatial scale. Thus, reward/risk will increase with scale if association with habitat increases with spatial scale.