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Process-focussed, multi-grain resource selection functions

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ABSTRACT

Like most aspects of ecology, the process of habitat or resource selection scales in space as well as time. However, scaling questions have generally focused on extent including size of study area and home ranges that dictate availability of resources. Grain of analysis (size of resource units used) is generally restricted to questions of methodology as opposed to functional ecology. Most often, grain is adopted as a point, unit, or patch that is common in size to all habitat resources used and available; however, in the process of habitat selection, it is feasible that individual animals may opt to select for different resources at different grains. For example, animals may use units of vegetation association at a finer grain when feeding or resting compared to when moving through habitat. Here we introduce and evaluate the 'multi-grain resource selection function', or MRSF. We generated MRSFs for a case study of GPS-collared white-tailed deer (*Odocoileus virginianus*; $n = 14$) at Riding Mountain National Park, Manitoba, Canada. We created models across two seasons and extents and varied the radius around used and available points within which resource types were measured, and compared models to evaluate the relative importance of resource variables at different grains. We hypothesized that resource selection would vary with grain and that RSFs computed using multiple grains would be more predictive than models computed using a single grain as they better incorporate the space of influence on decision making in different habitat areas. We found that models of animals using grains of different sizes for different resource types were characterized by comparatively lower AIC scores. We conclude that scaling grain can and should be considered in models of resource selection, and that animals make decisions on resource selection at multiple grains. The MRSF, like analyses incorporating individual effects, density dependence, and functional responses, brings us closer to incorporating process, rather than only patterns, into the study of resource and habitat selection.

1. Introduction

The concept of scale is central to the study of how animals interact with their environment (Levin, 1992; Wheatley and Johnson, 2009; Wiens, 1989). Scale of analysis has been shown to affect resource selection patterns (Anderson et al., 2005; Boyce et al., 2003; Ciarniello et al., 2007; Leblond et al., 2011; Meyer and Thuiller, 2006), interspecific competition (Whittaker and Lindzey, 2004), and detection of sexual segregation (Bowyer et al., 1996). Survival and reproduction may be affected by various scale-sensitive mechanisms (Bowyer and Kie, 2006) and depend on scale of analysis. Scale, however, has two key components – extent and grain (Hobbs, 2003) – that in different ways may influence animal behaviour, habitat, resource, and home range use.

In the study of habitat selection, extent is studied by modifying the area deemed available to organisms and is typically defined by the framework established by Johnson (1980). Johnson (1980) defined four hierarchical orders of selection made on increasingly shorter time scales, ranging from the geographic range of the species to the selection of food items during foraging. Most models of habitat selection are conducted at either the 2nd or 3rd order, which define establishment of a home range and use of resources within that home range, respectively. Grain can be defined as the minimum mapping unit of landscape data (resolution or pixel size for raster data, Hobbs, 2003; Thompson and McGarigal, 2002), or sometimes, as is the case here, as the size of an area surrounding

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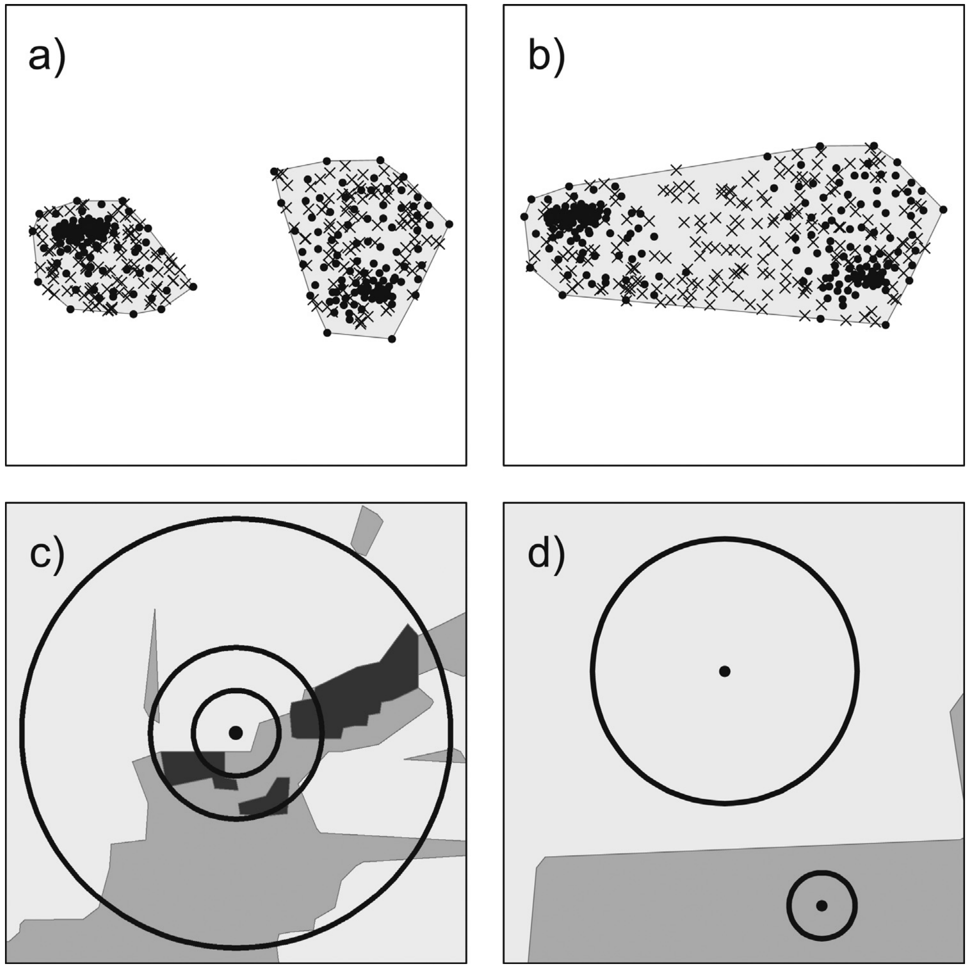

Fig. 1. Conceptual diagram to illustrate the various components of scale. In RSFs, used points (•) are contrasted against available points (×). (a) Within-home-range extent (third order selection *sensu* Johnson's (1980) selection orders) is where random points are generated within the home ranges of individuals to analyse how individuals use space within their home ranges. (b) Landscape extent (second order *sensu* Johnson (1980)), where random points are generated throughout the study area to determine factors influencing the location of home ranges over a landscape. (c) Example of multiple grain sizes. Buffers of increasing radius are generated around a telemetry relocation on the landscape. Larger buffers incorporate greater landscape context. (d) An example of how the perceptual range of an individual (the grain at which resource selection decisions are made) can vary as a function of habitat type, with open habitats (light grey) resulting in a larger perceptual range than an enclosed habitat such as forest (dark grey).

points of observation within which ecological data are considered (Anderson et al., 2005; Meyer and Thuiller, 2006; Fig. 1).

Habitat selection is known to change continuously across spatial scales (Wiens, 1989), resulting in different domains of habitat selection depending on scale of analysis. Wiens (1989) defined a domain of habitat selection as a range of scales over which ecological patterns are similar, and Thompson and McGarigal (2002) proposed that habitat can be viewed as a spectrum which shifts in response to changing scale. It should, therefore, be possible to identify thresholds in selection domains by examining a continuum of spatial scales, with those thresholds representing scales where the relative abilities of different factors to limit fitness change (Rettie and Messier, 2000; Schaefer and Mayor, 2007). Altering extent modifies what resources are deemed available to individuals, whereas changing grain size modifies how a selected (or available) resource is defined and subsequently perceived (the grain at which decisions are made) by an animal (e.g., 'landscape-context variables', *sensu* Leblond et al., 2011).

Despite acknowledging the importance of scale on the process of habitat selection, most researchers on the subject typically approach the study of scale from the perspective of examining statistical hierarchies as opposed to examining underlying mechanisms behind patterns. It is reasonable to expect the scale at which an animal responds to its environment to vary as a function of habitat type and behaviour. For example, vigilance behaviour by prey animals has been shown to vary by habitat type (e.g., mule deer [*Odocoileus hemionus*], Altendorf et al., 2001; and red deer [*Cervus elaphus*], Jayakody et al., 2008)—suggesting that a change in the size of the perceptual range of an individual across habitats should affect behaviour. An animal travelling through or feeding in an enclosed habitat such as in forest will be selecting habitat on a smaller scale (incorporating a smaller area around them in making resource use and movement decisions) than an individual travelling or foraging in open habitats, where vigilance and consideration of cover become increasingly important at larger spatial scales. As such, different habitat types should be selected at different grains depending on the animal's perceptual range. This idea is not new: Morris (1987) argued that individuals may be either coarse-grained or fine-grained foragers (*sensu* MacArthur and Levins, 1964) depending on the scale examined. However, incorporating this insight into contemporary models of habitat selection is lacking.

Considering the context of a resource unit can have a profound effect on resource selection. For example, white-tailed deer (*Odocoileus virginianus*) are large herbivores that are known to select for edge habitat (Williamson and Hirth, 1985). By modelling