

Grain-dependent functional responses in habitat selection

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Abstract

Context Spatial scale is an important consideration for understanding how animals select habitat, and multi-scalar designs in resource selection studies have become increasingly common. Despite this, examination of functional responses in habitat selection at multiple scales is rare. The perceptual range of an animal changes as a function of vegetation association, suggesting that use, selection and functional responses may all be habitat- and scale-dependent.

Objectives Our objective was to determine how varying grain size affects our interpretation of functional response in habitat selection and to elucidate scalar and landscape effects on habitat selection.

Methods We quantified the functional response of GPS-collared, female white-tailed deer (*Odocoileus virginianus*, $n = 18$) in Riding Mountain National Park, Canada, to different habitat types. Functional responses were quantified at multiple spatial scales by regressing proportion of habitat used against proportion of habitat available at different buffer radii (ranging from 75–1000 m radius) surrounding used (telemetry) locations and available points within the individual's seasonal home range. We examined how functional responses changed as a function of grain by plotting grain size against the slope of the functional response.

Results We detected functional responses in most habitat types. As expected, functional responses tended to converge towards 1 (use proportional to

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availability) at large buffer sizes; however, the relationship between scale and functional response was typically non-linear and depended on habitat type.

Conclusions We conclude that a multi-scalar approach to modelling animal functional responses in habitat selection is important for understanding patterns in animal behaviour and resource use.

Keywords Functional response · Grain · Habitat selection · Perceptual range · Scale-dependence · Spatial memory · White-tailed deer · Ungulates

Introduction

Interpretation of space-use patterns of animals is intimately linked to our understanding of animal movements through distinct habitat types or vegetation associations. The arrangement of habitat will directly influence how habitat selection processes are detected and interpreted (Wiens et al. 1993). Landscapes are by their nature heterogeneous, and therefore organisms cannot always obtain an optimal combination of resources within their home range (Orians and Wittenberger 1991). As such, individuals may select resources proportionally to availability (act as fine-grained foragers sensu MacArthur and Levins 1964), or select resources disproportionately (coarse-grained foragers), depending on whether the proportion of a habitat type in a home range equals the proportion of time spent within it. However, individuals may simultaneously be fine- or coarse-grained foragers depending on the relative availability of the resource in question. How availability affects the use of habitats by animals is referred to as the functional response in habitat selection (hereafter ‘functional response’; Mysterud and Ims 1998), which has been detected in a variety of taxa including ungulates (Osko et al. 2004; Godvik et al. 2009; Herfindal et al. 2009; Morellet et al. 2011; Beyer et al. 2013; Leclerc et al. 2014; van Beest et al. 2015), bears (Mauritzen et al. 2003), birds (Gillies and St Clair 2010; Deville et al. 2013), and elephants (Roever et al. 2012).

How scale affects animal resource selection is a question of fundamental importance in ecology (Wiens 1989; Levin 1992; Wheatley and Johnson 2009). Modifying the scale of analysis has been shown to affect patterns in resource selection (Boyce et al. 2003; Anderson et al. 2005; Meyer and Thuiller 2006;

Ciarniello et al. 2007; Leblond et al. 2011, Laforge et al. 2015) as well as the detection of interspecific competition (Whittaker and Lindzey 2004) and sexual segregation (Bowyer et al. 1996). Spatial scale in ecology can be defined by two components, extent and grain (Hobbs 2003). When dealing with decisions made by individuals, extent is the area deemed available to the animal and is typically defined by the framework established by Johnson (1980). Grain can be defined either as the minimum mapping unit for habitat data (Thompson and McGarigal 2002; Hobbs 2003) or as the area surrounding used and available telemetry points defining availability (Meyer and Thuiller 2006; Laforge et al. 2015). We use the latter definition here, and use ‘resolution’ to describe the former. Multi-scalar studies of functional responses in habitat selection are rare, and usually consider the extent component of scale (Herfindal et al. 2009).

Incorporating grain into studies of habitat selection and associated functional responses may deepen our understanding of how animals select for sites based on neighbouring habitat. Traditional methods of quantifying habitat at the resolution of the data are sensitive to changes in the resolution of the data and risk generalizing potentially distinct habitats based on differences in their ecological context. Integrating grain size into analyses of functional responses is important for understanding the scale at which an animal might perceive its environment. Animals may be selecting for patches as opposed to points (Rettie and McLoughlin 1999), making the consideration of ‘landscape context variables’ sensu Leblond et al. (2011) vital to the study of animal space use. The relationship between scale and functional response is also likely to depend on habitat type and behaviour. Habitat type is known to affect vigilance behaviour in mule deer (*Odocoileus hemionus*; Altendorf et al. 2001) and red deer (*Cervus elaphus*; Jayakody et al. 2008), suggesting that habitat composition can affect the size of the perceptual range of individuals (Olden et al. 2004). For example, animals are likely to have a smaller perceptual range when travelling in enclosed habitats such as forest compared to open habitats, where detection of predators becomes more important at larger spatial scales. Incorporating grain into the analysis of functional responses also allows for the inclusion of resources not traditionally considered in functional response studies, namely measures of habitat diversity and linear features such as roads and streams (but see Beyer et al. 2013).

Functional grain has been shown to be important in animal mobility (Romero et al. 2009) and morphology (Turlure et al. 2010). Baguette and Van Dyck (2007) suggested that changes in functional grain encompassing different patch sizes and configurations would alter how animals perceive, and ultimately disperse through their environment. To our knowledge, no studies have yet examined how modifying grain size affects interpretation of functional responses in habitat selection.

Our goal was to examine functional responses at multiple grain sizes for various habitat types for white-tailed deer (*Odocoileus virginianus*) in Riding Mountain National Park, Manitoba, Canada, and the surrounding agricultural matrix. We produced seasonal home ranges for 18 female white-tailed deer and quantified functional response at multiple grain sizes by regressing the proportion of habitat that an animal used against the proportion of habitat available to the individual computed at different buffer radii surrounding used (telemetry) locations and available points within the individual's seasonal home range. We plotted the slope of the functional response as a function of grain size. We hypothesized that if individuals select habitat differently depending on grain size, the functional response would also change as a function of grain. Because use and availability overlap the least at smaller grain sizes of analysis, we predicted that functional responses would be strongest and most evident at smaller grains and weaken as grain size increased. Patch size in most landscapes varies as a function of vegetation type, as landscapes are naturally heterogeneous. Animal movement behaviour is likely influenced by patch size and functional grain of the landscape (Baguette and Van Dyck 2007; Romero et al. 2009), as well as by perceptual range, which is known to vary by vegetation type (Olden et al. 2004). We therefore predicted that functional grain would interact with patch size and perceptual range to affect the shape of the function generated when plotting the functional response slope against scale across different habitat types.

Methods

Study area

The study area was located in southwest Manitoba, Canada (51°N, 100°W; Fig. 1). The area contained

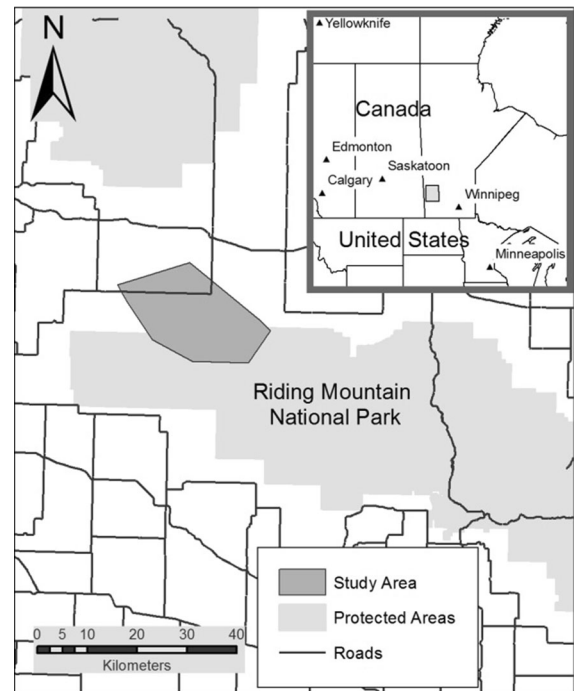


Fig. 1 Riding Mountain National Park, MB, Canada and the surrounding agricultural region. White-tailed deer telemetry data were collected in the *dark shaded area*

two distinct habitats: the forest-dominated area within Riding Mountain National Park (RMNP) and the surrounding agricultural matrix. RMNP is a 2974 km² protected area that consists of eastern deciduous forest, northern boreal forest and rough fescue grasslands with areas of wetland (Rowe 1972; Caners and Kenkel 2003). Higher elevations in the park are dominated by spruce (*Picea* spp.), pine (*Pinus banksiana*) and aspen (*Populus tremuloides*). The area surrounding the park is intensively managed for the production of annual cereal and oilseed crops, perennial forage crops and as cattle pasture (Brook 2010), interspersed with deciduous forest, wetland and grassland.

The area is populated by a large diversity of wildlife species. During the study period, it was estimated that there were 2700 elk (*Cervus canadensis*), 2500 moose (*Alces alces*) and a large population of white-tailed deer (Brook and McLachlan 2006). Predators in the area include wolves (*Canis lupus*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*).

Data collection and habitat variables

Adult female white-tailed deer ($n = 18$) were captured via a net gun fired from a helicopter (Cattet et al. 2004) in February 2006 and fitted with GPS tracking collars. Collars were active for one year and recorded locations at 2–4 h intervals. Stationary collars had a mean overall accuracy of 15.0 m (Brook 2008). Individuals were captured in the agricultural area north of RMNP and in the north of the park but were free to enter or exit the park at any point along the boundary. A total of 20,799 locations were collected, with a mean of 452 (SD = 317.5) locations per animal per season.

We created seasonal 95 % minimum convex polygon (MCP) home ranges (Osisko et al. 2004; van Beest et al. 2010) for each white-tailed deer ($n = 46$ deer seasons). MCPs are frequently used in habitat selection studies as it is considered a simple, unambiguous and objective method to delineate all areas used and available to individuals (Godvik et al. 2009; Herfindal et al. 2009). By constructing 95 % MCPs we removed used locations at the outer edge of the seasonal home ranges. This was done because visits to the edges of home ranges are typically exploratory movements and as such habitat use of ungulates can differ substantially from habitat use within the home range (Börger et al. 2006; van Beest et al. 2011). We also objectively defined season length based on differences in movement rate over time as measured for the same collared female white-tailed deer as presented in van Beest et al. (2013). To better reflect availability and to include habitat just outside the 95 % home range, we buffered 95 % MCPs by 327 m (the mean distance travelled between successive GPS fixes). Within each individual's home range we generated random points equal to the number of GPS fixes. Telemetry points located in lakes were removed ($n = 15$) and lakes were excluded when generating random points, since lakes were not deemed habitat useable by white-tailed deer. We also removed all telemetry locations located outside the buffered home ranges.

We quantified several environmental covariates at the resolution of the data and in concentric buffers around used and available points to analyse the effect of changing grain on functional response (Fig. 2). We used an existing landcover-vegetation map developed from 30 m resolution Landsat 5 satellite imagery (Geobase: <http://www.geobase.ca>). We used buffers

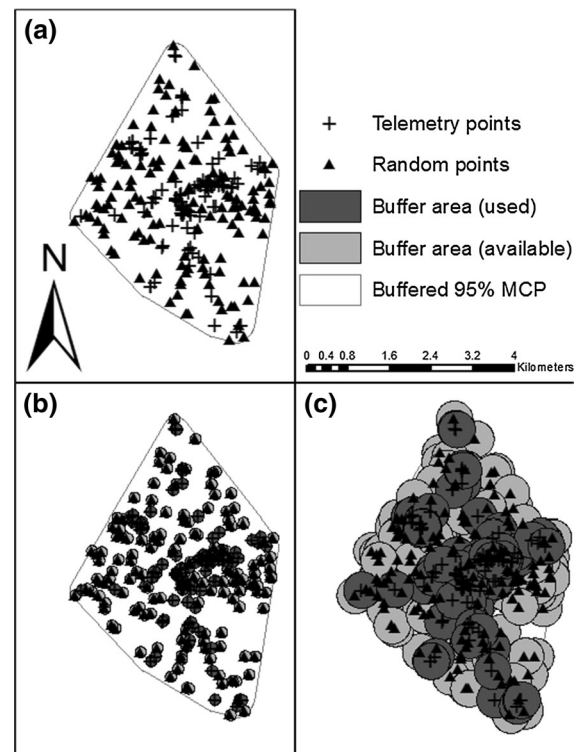


Fig. 2 Example of how use and availability were quantified for a single white-tailed deer in Riding Mountain National Park, MB (2006–2007). In **a** no buffers were added and used and available resources were quantified only at the resolution of the raster dataset (i.e., single pixel, 30 m × 30 m). Here, functional response was quantified using the proportion of used versus the number of available points in each habitat type. In **b** buffers with a radius of 150 m were added to used and available locations and functional responses were quantified using the mean of the proportion of habitat in the buffers. In **c** buffers are increased to 500 m in radius

with radii of 75, 150, 327, 500, 750 and 1000 m using ArcMap (ArcGIS 10, ESRI Redlands, California, USA) and Geospatial Modelling Environment (Beyer 2012). We chose grain sizes to reflect a continuum of scales, with 75 m being the smallest size to reasonably capture any meaningful surrounding habitat on a raster map with a 30 m resolution, and the maximum size approaching the mean diameter of white-tailed deer seasonal home ranges for this population. The 327 m buffer was chosen as it was the mean distance travelled by white-tailed deer between GPS fixes. Field validation on the landcover map was performed in 2011 and showed that 84 % of validated points were accurate, with the majority of misclassified points being due to changes in agricultural cropland (Dugal et al.

2013). Within each buffer, we calculated the proportion of forest, annual cropland, perennial cropland, grassland and wetland as well as density of streams and unpaved roads ($\text{m} \times \text{ha}^{-1}$). We used Simpson's Diversity Index as a measure of landscape heterogeneity, because it was most descriptive of white-tailed deer habitat use in RSF modelling for this population (Laforge et al. 2015).

Quantifying functional responses

We quantified functional responses for each resource type by regressing, for each seasonal home range, the use of the resource against its availability (Mysterud and Ims 1998, Morellet et al. 2011). At the resolution of the data (i.e., for the finest level of analysis where buffers were not used), this was simply the proportion of points used and available. We were therefore unable to model linear features or diversity at this scale. For buffers, values corresponded to mean proportion of the habitat type (or simple mean for linear features and diversity) across all available and used buffers. Since we had several seasonal home ranges for each individual deer, our methods corresponded to a repeated measures analysis. We therefore used mixed effects linear regression (R package lme4; Bates et al. 2015) to quantify functional responses in habitat selection with individual fitted as a random intercept to account for any patterns in the model residuals owing to repeated observation of the same individual but also to account for unbalanced observations among individuals (Pinheiro and Bates 2000).

A beta coefficient for availability (slope) of one corresponds to no functional response (use remains proportional to availability as availability changes), a slope of zero indicates constant use of a resource and a slope different than one and zero indicates a functional response in habitat selection. A slope greater than one indicates a positive functional response, where selection of the resource increases with increasing availability, a slope between 0 and 1 indicates a negative functional response (where use of a resource increases with increasing availability but selection decreases). A negative slope would indicate that use of the resource declines with increasing availability. To determine the effect of changing grain of analysis on functional response, we then estimated the slope and standard error of the functional responses at each grain of analysis and plotted slope against scale for each

habitat type using generalized additive modeling (R package mgcv, Wood 2015).

Results

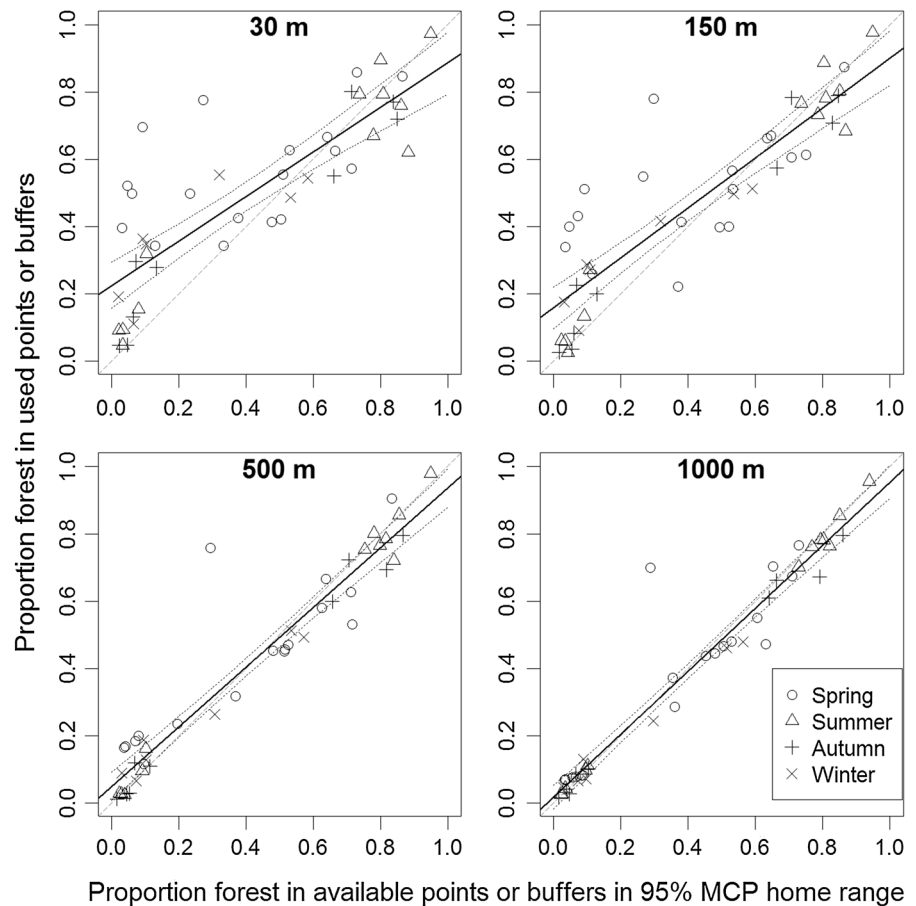
We detected a clear relationship between grain size and the strength of the functional responses. As grain size increased, the slope of the functional response typically approached 1, as shown for relative use of forest (Fig. 3). Of the eight habitat types examined, six had 95 % confidence intervals (CI) for the slope of the functional response that did not overlap the 95 % CI of the slope of the response at one or more other grain sizes, suggesting significant differences in functional response as a function of grain (Fig. 4). Functional responses were most evident at small and intermediate grain sizes; however, selection estimates at smaller grains were also associated with larger standard errors (Fig. 4).

White-tailed deer displayed unique functional responses dependent on habitat type and grain size (Fig. 4). White-tailed deer showed a strongly negative functional response in relative use of forest and both types of crop at small buffer sizes, but as grain size increased, the slope of the functional response weakened and approached one. The functional response in relative use of wetland cover was also negative at small grain sizes, but became positive (proportionally more use as availability increased) at large grains. Stream density had a positive functional response at small grain sizes, which saturated towards one as grain size increased. Functional response of grasslands was weak across all grain sizes, whereas road density and Simpson's Diversity displayed a positive functional response at intermediate grain size and a negative response at large grain sizes (Fig. 4).

Discussion

We found a significant effect of grain size on the interpretation of white-tailed deer functional responses. The strongest functional response was either detected at the smallest grain (five habitat types) or at intermediate grains (three habitat types)—providing moderate support for our first prediction that the smallest grains would result in a larger functional response. The functional response to all habitat types

Fig. 3 Functional responses of adult female white-tailed deer across four seasons ($n = 46$ deer seasons) to forest habitat at four grains of analysis in Riding Mountain National Park, 2006–2007. The *black line* is the slope of the functional response, with a 95 % confidence envelope represented by dotted lines. A slope of 1 would represent a proportional increase in use with increasing availability (represented by a *dashed line*); whereas a slope of 0 would indicate constant use of the resource



displayed a tendency to saturate at 1 as grain size approached the seasonal home range size of white-tailed deer. The response of white-tailed deer to each habitat type displayed a unique relationship between functional response and grain size (in support of our second prediction). These results suggest that our interpretation of functional responses in habitat selection is dependent on the grain at which habitat is quantified.

Animal habitat selection is based on trade-offs, with individuals typically having to balance the acquisition of optimal forage with the risk of predation (Sih 1980). In ungulates, this involves balancing foraging bouts in more productive open habitats where predation risk is higher against ruminating and resting in covered forest habitats (Myserud et al. 1999). Hence, as availability of profitable foraging (open) habitats increases, we should see an increase in their use; however, due to time budgets, we would not expect a constant increase. Therefore, the functional

response is expected to be between constant and proportional use, termed the ‘real world trade-off hypothesis’ by Godvik et al. (2009). Our results suggest that changing the scale at which observations are made affects the interpretation of this trade-off, and as such underscore the importance of examining scale in functional response studies.

Despite the acceptance of the importance of scalar processes to the examination of animal habitat selection (Wiens 1989; Levin 1992), they have rarely been examined in the context of functional responses. Herfindal et al. (2009) found that home range size was an important factor in functional response at both the home range- and landscape-level of selection; however, they did not consider how the relative abundance of different habitat types affects functional response. Functional response can vary across selection orders (Herfindal et al. 2009), therefore varying grain size for different resources may encompass different levels of selection on continua of scales. Habitat selection, and

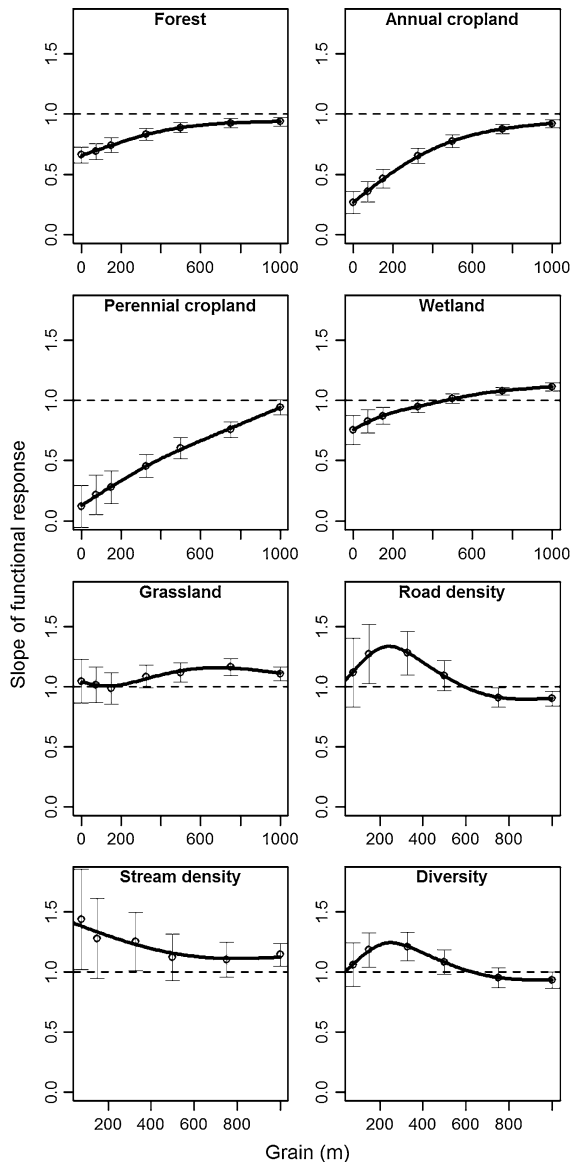


Fig. 4 Slope and 95 % confidence intervals for functional responses across several grains of analysis for adult female white-tailed deer ($n = 18$) in Riding Mountain National Park, 2006–2007. Dashed line indicates a slope of one (proportional use at that grain)

as a result functional response, is influenced not only by the composition of habitats but also by their configuration (Stubblefield et al. 2006; Radford and Bennett 2007). Functional grain of analysis has also been shown to be important when analysing landscape connectivity and animal dispersal (Baguette and Van Dyck 2007; Galpern and Manseau 2013). As such, the inclusion of grain size in functional response studies is

important for two reasons. Firstly, it incorporates patch size and landscape heterogeneity into the analysis, which are important factors in habitat selection studies (Rettie and McLoughlin 1999). Secondly, it allows for the inclusion of habitat types surrounding an individual location, which may have an impact on resource selection patterns. For example, an individual may choose to forage in open habitats that are near closed habitats as potential refuge from predators.

White-tailed deer displayed a positive functional response to roads that was highest at intermediate (327 m) scales, suggesting that as the density of unpaved roads increased in their seasonal home ranges, white-tailed deer selected for areas within 327 m of roads. Moose have been shown to select for roads at intermediate scales (Rempel et al. 1997) while avoiding them at small scales (Dussault et al. 2007). By contrast, elk (*Cervus canadensis*) have been shown to avoid roads at the landscape scale and select for roads at smaller scales due to their association with edge habitat (reviewed by Anderson et al. 2005). Beyer et al. (2013) found a functional response to road crossings in moose. Our results show that there is an interaction between scale of observation and functional response in how ungulates select habitat surrounding roads.

The interaction between buffer size and functional response varied by habitat type, indicating a change in how animals respond to scale across habitats. To navigate across landscapes, animals use cues from the landscape (either via environmental gradients or navigational beacons; Fagan et al. 2013) and by means of spatial memory. Animal behaviour varies as a function of habitat (Altendorf et al. 2001; Jayakody et al. 2008); therefore, how an animal travels through a landscape will be directly affected by the composition and configuration of that habitat. An animal's perceptual range is not fixed, but varies across both habitat types (Olden et al. 2004) and functional grain (Baguette and van Dyck 2007), influencing the scale at which habitat selection decisions are made and subsequently the spatial scale of the functional response.

Conclusions

We have shown that the functional response in habitat selection of white-tailed deer is contingent upon the spatial scale of investigation. Is there a 'best' scale at

which to make conclusions about functional responses? Animals face different pressures at different scales, often simultaneously. Habitat management likewise occurs on many spatial scales, with the establishment of protected areas or policies on hunting quotas occurring at broad spatial scales, to fencing on individual farms which occur on small scales. As such, prescribing an ideal scale for any analysis (or indeed, even for a single resource) may not be possible nor advisable. By contrast, functional responses are likely to be most ecologically relevant at scales at which selection is known to be highest. Future studies could incorporate a multi-grain resource selection function approach (Laforge et al. 2015) to determine what grain sizes are most relevant for each habitat type and incorporate them into studies of functional responses.

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References

- Altendorf KB, Laundré JW, López González CA, Brown JS (2001) Assessing effects of predation risk on foraging behavior of mule deer. *J Mammal* 82:430–439
- Anderson DP, Forester JD, Turner MG, Frair JL, Merrill EH, Fortin D, Mao JS, Boyce MS (2005) Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecol* 20:257–271
- Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecol* 22:1117–1129
- Bates D, Maechler M, Bolker B and Walker S (2015). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-8, <http://CRAN.R-project.org/package=lme4>
- Beyer HL (2012) Geospatial modelling environment (Version 0.7.2.1). (Software). URL: <http://www.spatial ecology.com/gme>
- Beyer HL, Ung R, Murray DL, Fortin M-J (2013) Functional responses, seasonal variation and thresholds in behavioural responses of moose to road density. *J Appl Ecol* 50:286–294
- Börger L, Franconi N, Ferretti N, Meschi F, De Michele G, Gantz A, Coulson T (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am Nat* 168:471–485
- Bowyer RT, Kie JG, Van Ballenberghe V (1996) Sexual segregation in black-tailed deer: effects of scale. *J Wildl Manag* 60:10–17
- Boyce MS, Mao JS, Merrill EH, Fortin D, Turner MG, Fryxell J, Turchin P (2003) Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421–431
- Brook RK (2008) Elk-agriculture Conflicts in the Greater Riding Mountain Ecosystem: Building Bridges Between the Natural and Social Sciences to Promote Sustainability. University of Manitoba, Winnipeg Manitoba, Canada (PhD Dissertation)
- Brook RK (2010) Habitat selection by parturient elk (*Cervus elaphus*) in agricultural and forested landscapes. *Can J Zool* 88:968–976
- Brook RK, McLachlan SM (2006) Factors influencing farmers' concerns regarding bovine tuberculosis in wildlife and livestock around Riding Mountain National Park. *J Environ Manag* 80:156–166
- Caners RT, Kenkel NC (2003) Forest stand structure and dynamics at Riding Mountain National Park, Manitoba, Canada. *Community Ecol* 4:185–204
- Cattet M, Caulkett N, Wilson C, Vendenbrink T, Brook RK (2004) Intranasal administration of xylazine to reduce stress in elk captured by net gun. *J Wildl Dis* 40:562–565
- Ciarniello LM, Boyce MS, Seip DR, Heard DC (2007) Grizzly bear habitat selection is scale dependent. *Ecol Appl* 17:1424–1440
- Deville A-S, Grémillet D, Gauthier-Clerc M, Guillemain M, Von Houwald F, Gardelli B, Béchét A (2013) Non-linear feeding functional responses in the Greater Flamingo (*Phoenicopterus roseus*) predict immediate negative impact of wetland degradation on this flagship species. *Ecol Evol* 3:1413–1425
- Dugal CJ, van Beest FM, Vander Wal E, Brook RK (2013) Targeting hunter distribution based on host resource selection and kill sites to manage disease risk. *Ecol Evol* 3:4265–4277
- Dussault C, Ouellet J-P, Laurian C, Courtois R, Poulin M, Breton L (2007) Moose movement rates along highways and crossing probability models. *J Wildl Manag* 71:2338–2345
- Fagan WF, Lewis MA, Auger-Méthé M, Avgar T, Benhamou S, Breed G, LaDage L, Schlägel UE, Tang W, Papastamatiou YP, Forester J, Mueller T (2013) Spatial memory and animal movement. *Ecol Lett* 16:1316–1329
- Galpern P, Manseau M (2013) Finding the functional grain: comparing methods for scaling resistance surfaces. *Landscape Ecol* 28:1269–1281
- Gillies CS, St Clair CC (2010) Functional responses in habitat selection by tropical birds moving through fragmented forest. *J Appl Ecol* 47:182–190
- Godvik IM, Loe LE, Vik JO, Veiberg V, Langvatn R, Mysterud A (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90:699–710

- Herfindal I, Tremblay J-P, Hansen BB, Solberg EJ, Heim M, Sæther B-E (2009) Scale dependency and functional response in moose habitat selection. *Ecography* 32: 849–859
- Hobbs NT (2003) Challenges and opportunities in integrating ecological knowledge across scales. *For Ecol Manag* 181:223–238
- Jayakody S, Sibbald AM, Gordon IJ, Lambin X (2008) Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. *Wildl Biol* 14:81–91
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71
- Laforge MP, Vander Wal E, Brook RK, Bayne EM, McLoughlin PD (2015) Process-focussed, multi-grain resource selection functions. *Ecol Mod* 305:10–21
- Leblond M, Frair J, Fortin D, Dussault C, Ouellet J-P, Courtois R (2011) Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. *Landscape Ecol* 26:1433–1446
- Leclerc M, Dussault C, St-Laurent M-H (2014) Behavioural strategies towards human disturbances explain individual performance in woodland caribou. *Oecologia* 176:297–306
- Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73:1943–1967
- MacArthur R, Levins R (1964) Competition, habitat selection, and character displacement in a patchy environment. *Proc Natl Acad Sci USA* 51:1207–1210
- Mauritzen M, Belikov SE, Boltunov AN, Derocher AE, Hansen E, Ims RA, Wiig Ø, Yoccoz N (2003) Functional responses in polar bear habitat selection. *Oikos* 100:112–124
- Meyer CB, Thuiller W (2006) Accuracy of resource selection functions across spatial scales. *Divers Distrib* 12:288–297
- Morellet N, Van Moorter B, Cargnelutti B, Angibault J-M, Lourtet B, Merlet J, Ladet S, Hewison AJM (2011) Landscape composition influences roe deer habitat selection at both home range and landscape scales. *Landscape Ecol* 26:999–1010
- Mysterud A, Ims RA (1998) Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435–1441
- Mysterud A, Larsen PK, Ims RA, Østbye E (1999) Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? *Can J Zool* 77:776–783
- Olden JD, Schooley RL, Monroe JB, Poff NL (2004) Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *J Anim Ecol* 73:1190–1194
- Orians GH, Wittenberger JF (1991) Spatial and temporal scales in habitat selection. *Am Nat* 137:S29–S49
- Osko TJ, Hiltz MN, Hudson RJ, Wasel SM (2004) Moose habitat preferences in response to changing availability. *J Wildl Manag* 68:576–584
- Pinheiro JC, Bates DM (2000) *Mixed-effects models in S and S-Plus: statistics and computing*. Springer, New York
- Radford JQ, Bennett AF (2007) The relative importance of landscape properties for woodland birds in agricultural environments. *J Appl Ecol* 44:737–747
- Rempel RS, Elkie PC, Rodgers AR, Gluck MJ (1997) Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. *J Wildl Manag* 61:517–524
- Rettie WJ, McLoughlin PD (1999) Overcoming radiotelemetry bias in habitat-selection studies. *Can J Zool* 77:1175–1184
- Roever CL, van Aarde RJ, Leggett K (2012) Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant. *Ecography* 35:972–982
- Romero S, Campbell JF, Nechols JR, With KA (2009) Movement behaviour to landscape structure: the role of functional grain. *Landscape Ecol* 24:39–51
- Rowe JS (1972) *Forest regions of Canada*. Information Canada, Ottawa
- Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041–1043
- Stubblefield CH, Vierling KT, Rumble MA (2006) Landscape-scale attributes of elk centers of activity in the central Black Hills of South Dakota. *J Wildl Manag* 70:1060–1069
- Thompson CM, McGarigal K (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). *Landscape Ecol* 17:569–586
- Turlure C, Schtickzelle N, Baguette M (2010) Resource grain scales mobility and adult morphology in butterflies. *Landscape Ecol* 25:95–108
- van Beest FM, Mysterud A, Loe LE, Milner JM (2010) Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *J Anim Ecol* 79:910–922
- van Beest FM, Rivrud IM, Loe LE, Milner JM, Mysterud A (2011) What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J Anim Ecol* 80:771–785
- van Beest FM, Vander Wal E, Stronen AV, Brook RK (2013) Factors driving variation in movement rate and seasonality of sympatric ungulates. *J Mammal* 94:691–701
- van Beest FM, McLoughlin PD, Mysterud A, Brook RK (2015) Functional responses in habitat selection are density dependent in a large herbivore. *Ecography Early View*. doi:10.1111/ecog.01339
- Wheatley M, Johnson C (2009) Factors limiting our understanding of ecological scale. *Ecol Complex* 6:150–159
- Whittaker DG, Lindzey FG (2004) Habitat use patterns of sympatric deer species on Rocky Mountain Arsenal, Colorado. *Wildl Soc Bull* 32:1114–1123
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Wiens JA, Stenseth NC, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. *Oikos* 66:369–380
- Wood, SN (2015) mgcv. R package version 1.8-6, <http://CRAN.R-project.org/package=mgcv>