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Scales of selection and perception: landscape heterogeneity of an important food resource influences habitat use by a large omnivore

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Variation in food abundance and distribution influences animal foraging behavior, but response is contingent on the amount of resource heterogeneity detected, which is consistent with environmental 'grain' size. Large mammals presumably perceive their surroundings at broad spatial scales, but the importance of landscape-level food resource properties for habitat use is generally less understood. We evaluated the role of heterogeneity of Canada buffaloberry *Shepherdia canadensis*, defined by fruit distribution and variability in patch quality (fruit density), in grizzly bear *Ursus arctos* habitat selection by comparing patch- and landscape-level foraging strategies (resource use). Our objectives were to: 1) identify the spatial scale at which grizzly bears select buffaloberry fruit resources; 2) determine whether patch- or landscape-level foraging strategies explain resource use; and 3) assess the importance of resource heterogeneity in structuring habitat selection. Buffaloberry patch and landscape variables were combined with GPS radio-telemetry data from eight collared grizzly bears in west-central Alberta, Canada, to fit resource selection functions (RSFs). We found that a spatial scale of 1887 m, corresponding to an average travel distance for bears over 5.5 h, was the most supported scale for buffaloberry use. Landscape-level foraging strategies generally had more support than those of the patch-level, with spatial heterogeneity of buffaloberry patches best explaining grizzly bear selection for fruit resources. Bears selected for areas with a wider distribution of buffaloberry fruit and greater variability in patch quality, thus providing both a higher probability of shrub encounter and greater contrast between resource patches. A negative interaction between distribution and variability, however, indicated a tradeoff where use of areas with a more widespread fruit distribution decreased when variability in resource quality was high. These results demonstrate the influence of food resource heterogeneity on animal habitat use and emphasize the value in considering spatial scale in studies of animal–resource interactions.

Environmental heterogeneity influences animal behavior (Wiens and Milne 1989, Crist et al. 1992, With 1994) with selection for food resources depending partly on how the properties of those resources vary in space (Heinrich 1979). The response of an animal to variation in food abundance and distribution is contingent on the amount of resource heterogeneity that it detects in its surroundings, which is consistent with its environmental 'grain' (Levins 1968). Optimal foraging theory proposes that animals will seek to acquire food resources at the lowest energetic cost, thereby maximizing efficiency and fitness (Charnov 1976). This assumes that animals have perfect knowledge of the heterogeneity of these resources (Rapport 1991); however, this information is typically incomplete (Pyke 1984) as it is constrained by their grain size. Generally, grain size increases with body size (With 1994, Ritchie 1998, Mech and Zollner 2002), suggesting that large mammals would perceive their environment at a relatively broad spatial scale beyond that of the local patch.

As experimental scales should be dictated by the organism and phenomenon of study (Wiens et al. 1986, Addicott et al. 1987), examination of selection for food resources (Nielsen et al. 2010) should therefore not only consider local supply, but also incorporate landscape-level resource estimates to better reflect the amount of environmental heterogeneity large mammals perceive. Grizzly (brown) bears *Ursus arctos* are habitat generalists with a diverse, omnivorous diet (Hamer et al. 1991, Mattson et al. 1991, McLellan and Hovey 1995, Munro et al. 2006) that enables them to adjust their foraging behavior based on annual and seasonal food availability (Jonkel and Cowan 1971, Bunnell and Tait 1981, Deacy et al. 2017). Resource abundance and distribution therefore affect habitat use (Jonkel and Cowan 1971, Nielsen et al. 2004a, 2010), and accounting for this heterogeneity by acknowledging their grain size could provide valuable insight into the landscape factors most relevant for habitat selection.

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Resource selection functions (RSFs) are statistical tools for evaluating animal habitat selection that estimate relative probability of use given particular environmental site characteristics (Manly et al. 2002). RSF models that have been developed for grizzly bears previously (Nielsen et al. 2002, Moe et al. 2007, Goldstein et al. 2010, Peters et al. 2015) have mainly evaluated the effects of environmental variables, such as habitat cover type and elevation, measured at the local patch-level. Questions of spatial scale, which are essential for testing the influence of environmental heterogeneity, have been largely overlooked in the context of grizzly bear habitat selection, although these have been investigated for other animals such as ungulates (Boyce et al. 2003, Anderson et al. 2005). The few studies that have directly considered scale have focused on the extent of the landscape available for bear use (Nielsen et al. 2004a, Ciarniello et al. 2007), rather than the spatial scale at which properties of the resource units themselves were estimated. Grizzly bear habitat selection models also seldom incorporate food resource attributes as explanatory variables, despite food-probability models often explaining bear selection more effectively than those that are habitat-oriented (Nielsen et al. 2003). Buffaloberry occurrence in particular, along with that of a few other key food items, significantly predicts bear foraging activity (Nielsen et al. 2010). Spatial variation of food resources appears to be more influential for grizzly bear habitat use than temporal availability (Mangipane et al. 2018); however, the importance of food resource heterogeneity relative to other food properties has not been explored, although it has been demonstrated to strongly affect grizzly bear foraging behavior (Searle et al. 2006).

Canada buffaloberry *Shepherdia canadensis* (L.) Nutt. is one of the primary fruit resources for grizzly bears in the Canadian Rocky Mountains, where it comprises a major component of their summer and early fall diet (Munro et al. 2006). The fruit is especially crucial during hyperphagia, when bears increase their food consumption to build body fat reserves in preparation for winter denning (Nelson 1980). Grizzly bear selection for buffaloberry has been assessed using predictions of shrub occurrence (Nielsen et al. 2003, 2010), but given the dioecious habit of this species and that only female plants bear fruit, occurrence does not correspond to the availability of the food resource itself. Although local density of grizzly bears is correlated with buffaloberry fruit abundance (Nielsen et al. 2017), selection for buffaloberry fruit resources has not been fully examined. An understanding of seasonal habitat use of this important resource is valuable for informing the conservation and management of grizzly bear populations (Boyce et al. 2002), including the threatened population in the province of Alberta (ASRD 2010).

The focus of this paper is to evaluate the role of landscape-level food resource heterogeneity in grizzly bear selection for buffaloberry patches by comparing patch- and landscape-level foraging strategies. Buffaloberry heterogeneity as defined here reflects both fruit distribution and variability in patch quality, represented by fruit density, which are properties that contribute to spatial heterogeneity (Kotliar and Wiens 1990). We know that buffaloberry heterogeneity is significantly related to the heterogeneity of conifer forest canopy (Denny and Nielsen 2017), but the implications of these shrub (resource) patterns for bears have not yet been studied.

Our objectives were therefore to: 1) identify the spatial scale at which grizzly bears select buffaloberry fruit resources; 2) determine whether patch- or landscape-level foraging

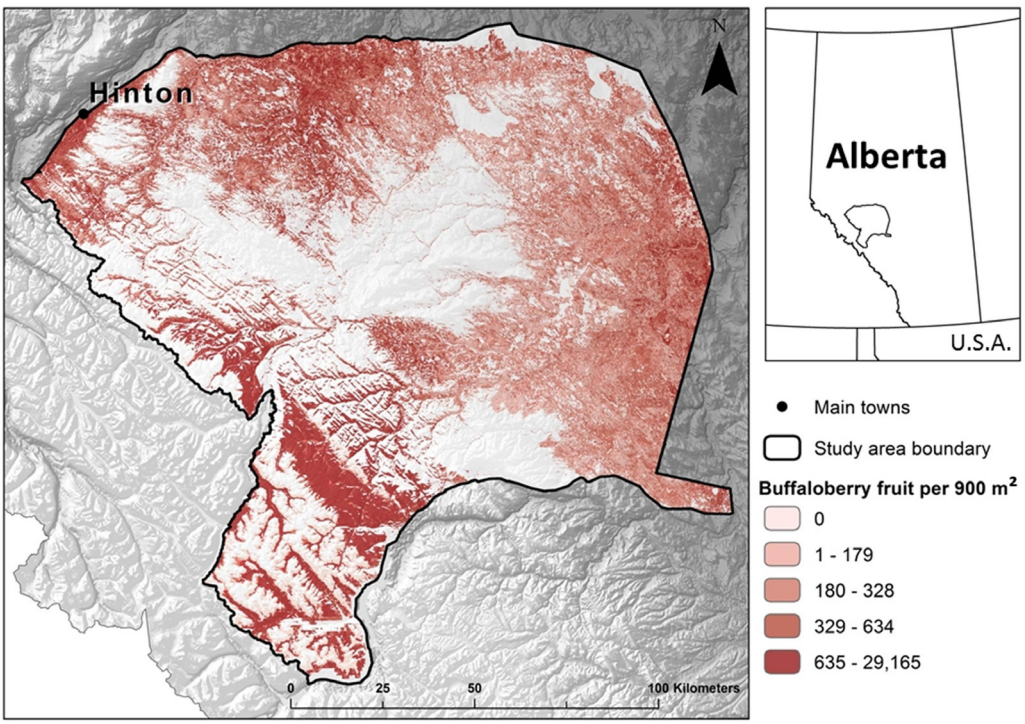


Figure 1. Location of the study area near Hinton, Alberta, Canada (53°24′41″N, 117°33′50″W) defined by a buffaloberry fruit density model (fruit/900 m²) by Nielsen et al. (2017). Fruit density is symbolized based on quantile classification.

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strategies explain resource use; and 3) assess the importance of resource heterogeneity in structuring habitat selection. We hypothesize that: 1) landscape-level foraging strategies will be more supported than those of the patch-level because grizzly bears perceive their surroundings at spatial scales beyond that of the patch, in accordance with their environmental grain; and 2) the heterogeneity of the food resource (buffaloberry) will further explain grizzly bear resource selection because changes in food availability influence foraging behavior.

Methods

Study area

We defined the study area by the spatial extent of a buffaloberry fruit density model (see Nielsen et al. 2017 for details of the modelling approach) that covered 19 952 km^2 of managed, conifer-dominated forest located near the town of Hinton (53°24′41″N, 117°33′50″W) in the Rocky Mountains foothills of west-central Alberta, Canada (Fig. 1). Elevation ranges from approximately 850–3200 m with dominant tree species being lodgepole pine *Pinus contorta*, white spruce *Picea glauca* and trembling aspen *Populus tremuloides*. Active natural resource extraction and human activity related to the forestry, mining, and energy (oil and gas) industries, along with recreational use, have produced a variety of anthropogenic disturbances and early seral forests.

Grizzly bear habitat selection and GPS radio-telemetry dataset

Grizzly bears involved in this study were captured for the fRI Research Grizzly Bear Program (Hinton, Alberta) using either aerial darting or culvert traps (Cattet et al. 2003), and fitted with Followit (Lindesberg, Sweden) iridium satellite-based GPS radio collars. Capture and handling protocols followed guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) and were approved by Animal Care Committees at both the University of Alberta and the University of Saskatchewan, and by Alberta Environment and Sustainable Resource Development. We obtained a total of 7783 GPS radio-telemetry locations recorded at a 30-min frequency from eight collared bears (four female, four male) monitored during fruit ripening of buffaloberry between 1 August and 15 September 2016. This temporal period has been linked to an increase in the utilization of fruit resources by grizzly bears in the study region, which comprise on average 49.7% of their diet during this timeframe (Munro et al. 2006), although this depends on availability in a given year. The 2016 season was characterized by high buffaloberry fruit production in the area (T. Larsen, pers. comm.), suggesting it would be a suitable year to examine

Table 1. Eight candidate hypotheses and associated foraging strategies describing grizzly bear selection for buffaloberry fruit resources at the patch- and landscape-levels.

Foraging hypothesis	Spatial scale	Model variable	Variable explanation	Foraging strategy
1. Null	–	random intercept term for bear identity	–	• selection for buffaloberry is random as bears move through their environment • bears will utilize resource patches of any quality when they encounter them
2. Local resource quality	patch	fruit density (30-m pixel)	local 'quality' of resource patch	• bears will select for areas of higher local patch quality regardless of surrounding patch attributes
3. Proximity	patch	Euclidean distance to nearest buffaloberry patch	immediate accessibility of resource	• bears will opportunistically utilize the closest resource patch to their current location
4. Local resource quality and proximity	patch	fruit density (30-m pixel) + Euclidean distance to nearest buffaloberry patch	local 'quality' of resource patch + immediate accessibility of resource	• bears will select for higher quality resource patches from those closest to their current location
5. Landscape resource quality	landscape	mean fruit density (1887-m radius)	average 'quality' of resource patches at the landscape-level	• bears will select for areas of higher average patch quality at the landscape-level
6. Variability	landscape	standard deviation of fruit density (1887-m radius)	amount of contrast between adjacent resource patches	• bears will select for areas with greater variability in patch quality • higher contrast facilitates assessment of patch quality and ability to identify high-quality patches (cue for exploitation)
7. Distribution	landscape	proportion of the landscape with buffaloberry fruit present (1887-m radius)	broader distribution of resource	• bears will select for areas where the resource is more widespread • increased probability of encountering a patch of any quality
8. Heterogeneity	landscape	standard deviation of fruit density * proportion of the landscape with buffaloberry fruit present (1887-m radius)	interaction between the amount of contrast between adjacent resource patches and the broader distribution of resource	• bears will select for areas where the resource is more widespread and there is greater variability in patch quality

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bear use of this resource given the inter-annual variation in fruiting phenology (Krebs et al. 2009).

We only considered crepuscular (twilight) and diurnal (daylight) locations recorded between 6 a.m. and 10 p.m. in our analysis as this represents the typical daily foraging period for bears in this area during summer months (Munro et al. 2006). We determined crepuscular and diurnal periods by consulting sunrise, sunset, and civil twilight tables for Hinton, Alberta, for the month of August, 2016 (NRCC 2017). GPS radio-telemetry data from collared animals are compatible with a used-available RSF study design, as no information is available regarding true absences (Boyce et al. 2002). We delineated a seasonal home range per bear by calculating minimum convex polygons (MCPs) that effectively encompassed all the GPS points ('used' locations) of each individual. We generated random points within every MCP at a density of 10 points km^{-2} of home range to represent 'available' locations for each bear, resulting in a total of 70 498 random points. All spatial analyses were performed in a GIS (ArcMap ver. 10.3.1, ESRI 2015).

Spatial scale and fruit resource properties

We derived two patch-level and three landscape-level buffaloberry variables using the buffaloberry fruit density model (Nielsen et al. 2017). The first patch-level variable was local fruit density, estimated at a 30 × 30 m (900 m^2) pixel resolution. Euclidean distance to the nearest pixel occupied by buffaloberry was the second, which was calculated for all points to indicate direct proximity to a resource patch. Local elevation, also estimated per 900 m^2, was obtained as a third non-resource patch-level variable.

To determine the most appropriate spatial scale for the three landscape-level variables, we first calculated mean fruit density, standard deviation (SD) of fruit density, and proportion of the landscape with buffaloberry fruit present within a series of 32 circular moving 'windows'. Radii corresponded to grizzly bear travel distances at successive 30-min increments based on an average movement rate for bears in the study region of 343 m h^{-1} for the month of August (Graham and Stenhouse 2014). Spatial scales ranged from 172 m to 5488 m, which represented travel distances for periods from 30 min to 16 h, in accordance with the diurnal and crepuscular timeframe. We extracted values for the patch-level variables and the landscape-level variables measured at each spatial scale and compared 'used' and 'available' locations per bear following a type III resource selection function study design (Manly et al. 2002).

The addition of random effects into population-level RSF models can both address the spatio-temporal autocorrelation (Gillies et al. 2006) that usually affects these data (Boyce et al. 2002, Nielsen et al. 2002) and control for differences in the number of GPS locations recorded per individual (Bennington and Thayne 1994). These advantages have contributed to the increased application of mixed-effects logistic regression models, a type of generalized linear mixed model (GLMM) (Skrondal and Rabe-Hesketh 2004), in studies of animal resource selection (Gillies et al. 2006, Hebblewhite and Merrill 2008, Koper and Manseau 2009). We fit a mixed-effects logistic regression model, with a random intercept for bear identity, per scale using the lme4 package (Bates et al. 2015) in R (ver. 3.3.2 <www.r-project.org>) for each of the three landscape-level buffaloberry variables to assess the influence of spatial scale on bear habitat use. These were global models intended to investigate population-level effects, rather than individual-level responses, and 'used' and 'available' locations for all bears were grouped. We included local elevation as a fixed effect predicted to influence buffaloberry fruiting phenology, which depends on temperature (Krebs et al. 2009, Laskin 2017), and specified it as a quadratic term because we expected grizzly bears would select for intermediate elevations where shrubs are typically more productive (Hamer and Herrero 1987). We extracted odds ratios from all model outputs and examined these as a function of spatial scale for the three landscape-level buffaloberry variables to visualize changes in effect size. Spatial scales were ranked per buffaloberry variable using Akaike information criterion (AIC) (Akaike 1974, Burnham and Anderson 2002) and then compared across variables to identify the most supported scale overall (Supplementary material Appendix 1).

Comparison of patch- and landscape-level foraging strategies

We developed eight a priori candidate hypotheses describing grizzly bear selection for buffaloberry based on fruit resource properties proposed to influence foraging strategies at the patch- and landscape-levels (Table 1). Patch-level hypotheses suggested bears would prioritize the local quality of the resource and direct proximity to a patch, while those of the landscape-level focused on the average quality of the resource, variability in patch quality, and fruit distribution. In particular, the resource heterogeneity hypothesis considered an interaction between variability in patch quality and

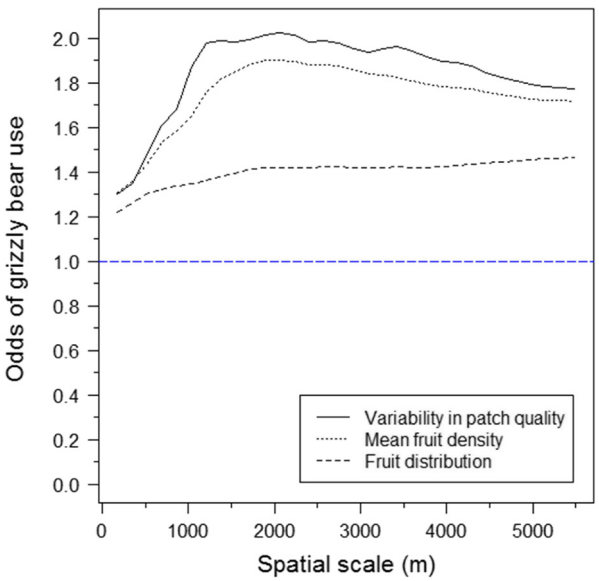


Figure 2. Effects of variability in buffaloberry patch quality (standard deviation of fruit density), mean fruit density, and fruit distribution (proportion of the landscape with buffaloberry fruit present) on the odds of grizzly bear use (selection) of a site, across spatial scales (moving window radii) from 172 m to 5488 m. Dashed blue line represents an odds ratio of 1 which would indicate no effect of the explanatory variables.

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fruit distribution, where it was hypothesized that greater contrast between patches could promote selection for areas with a widespread fruit distribution by facilitating the assessment of patch quality. We fit a mixed-effects logistic regression model representing each hypothesis to the set of 'used' and 'available' locations. Multicollinearity among explanatory variables was evaluated to ensure that Kendall rank correlation coefficients did not exceed a threshold of |0.7| and variance inflation factors for linear terms were < 5. We tested variable transformations using AIC and consequently applied $\log_{10}$-plus-one transformations to all variables except elevation and distance to nearest patch. After determining the final model structures, we compared support for the eight hypotheses with AIC. Coefficients were also used to predict effects of both individual variables and interaction terms on the relative probability of grizzly bear use of a site.

Results

Spatial scale and fruit resource properties

A spatial scale of 1887 m (window radius), corresponding to an average travel distance for bears over 5.5 h, was the most supported scale overall for grizzly bear habitat selection (Supplementary material Appendix 1) and was used for all consecutive models. Effects of mean fruit density, variability in patch quality, and fruit distribution on bear habitat selection were positive and fluctuated in strength with spatial scale (Fig. 2). Variability in patch quality demonstrated the strongest individual effect on bear use, although that of mean fruit density was similar. Fruit distribution had the weakest effect, the strength of which continued to increase gradually but did not peak over the range of scales examined.

Table 2. Comparison of the eight candidate foraging hypotheses describing grizzly bear selection for buffaloberry fruit resources at the patch- and landscape-levels. Standardized beta (β) coefficients for model variables are displayed with standard errors in square brackets and odds ratios italicized. Dashes indicate where variables are not applicable.

Foraging hypothesis	Spatial scale	Intercept	Elevation	Elevation^2	Local fruit density (30 m)†	Distance to patch	Standard deviation (SD) of fruit density (1887 m)†
Heterogeneity	landscape	–1.64 [0.42] *0.19*	4.51 [0.19] *91.07*	–4.83 [0.20] *0.01*	–	–	0.51 [0.05] *1.66*
Variability	landscape	–1.75 [0.43] *0.17*	4.26 [0.18] 70.59	–4.62 [0.19] *0.01*	–	–	0.70 [0.02] *2.01*
Landscape resource quality	landscape	–1.75 [0.43] *0.17*	4.77 [0.19] *117.63*	–5.08 [0.20] *0.01*	–	–	–
Proximity	patch	–1.56 [0.38] *0.21*	3.92 [0.17] *50.59*	–4.26 [0.18] *0.01*	–	–0.50 [0.02] *0.61*	–
Local resource quality and proximity	patch	–1.56 [0.39] *0.21*	3.92 [0.17] *50.53*	–4.25 [0.18] *0.01*	–0.09‡ [0.01] *1.00*	–0.50 [0.02] *0.61*	–
Distribution	landscape	–1.53 [0.40] *0.22*	4.55 [0.19] *94.21*	–4.97 [0.20] *0.01*	–	–	–
Local resource quality	patch	–1.40 [0.38] *0.25*	3.45 [0.16] *31.55*	–4.00 [0.18] *0.02*	0.11 [0.01] *1.12*	–	–
Null	–	–1.45 [0.20] *0.23*	–	–	–	–	–

Foraging hypothesis	Proportion of landscape with buffaloberry fruit (1887 m)†	SD * Proportion (interaction) (1887m)†	Mean fruit density (1887 m)†	ΔAIC
Heterogeneity	0.15 [0.04] *1.16*	–0.16 [0.03] *0.86*	–	0.00
Variability	–	–	–	25.43
Landscape resource quality	–	–	0.64 [0.02] *1.90*	80.49
Proximity	–	–	–	348.01
Local resource quality and proximity	–	–	–	350.01
Distribution	0.35 [0.02] *1.42*	–	–	749.29
Local resource quality	–	–	–	1053.64
Null	–	–	–	2010.65

†Log_{10}-plus-one transformation applied
‡Coefficient presented as 100 times its original value

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Comparison of patch- and landscape-level foraging strategies

Landscape-level foraging strategies were generally more supported than those of the patch-level, the highest ranked of which was proximity to patch. The heterogeneity hypothesis was most supported overall and represented all of the model weight (Table 2). For this hypothesis, variability in patch quality demonstrated a strong positive effect on grizzly bear habitat selection with a one standard deviation increase in variability raising the odds of bear use by 66%, compared to 16% for an equivalent increase in fruit distribution (Table 2). The relative probability of bear use was predicted to increase more than six-fold between areas of no variability in patch quality and those with an average landscape-level variation of 400 fruit per 900 m^2, the latter representing the approximate yield of an average shrub in a typical season (Fig. 3). Probability of habitat use gradually increased 1.5-fold from a landscape with no buffaloberry to one completely occupied by shrubs (Fig. 4). The interaction between variability in patch quality and fruit distribution was substantially supported over the individual variability and distribution hypotheses (ΔAIC scores of 25.4 and 749.3, respectively). Although within the heterogeneity hypothesis these two variables were positively related to bear habitat use, their interaction was negative, indicating decreased use of areas with a more widespread fruit distribution when variability in patch quality was high (Table 2). The relative probability of bear use was predicted to remain low across most observed levels of fruit distribution until the variability in patch quality exceeded about 100 fruit per 900 m^2 (2.0 on a $\log_{10}$-transformed scale; Fig. 5). Relative probability of bear use appeared highest at moderate fruit distributions and high variability in patch quality, demonstrating a tradeoff between these two factors. Predictions were constrained to conditions found within the study area (Fig. 5) after further inspection revealed that extreme tradeoffs could not occur, since both very low fruit distribution and very high variability in patch quality was not possible (Fig. 6). Overall, habitat selection was highest in the upper foothills and subalpine regions of the study area (Fig. 6).

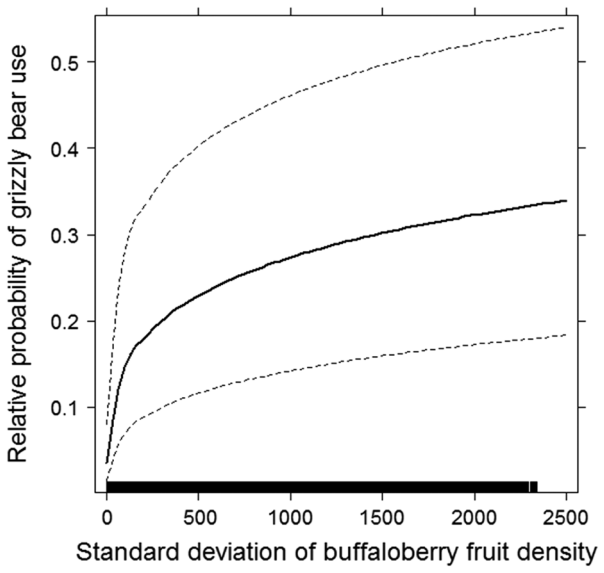


Figure 3. Predicted effect of the variability in buffaloberry patch quality (standard deviation of fruit density; fruit/900 m^2), estimated at a spatial scale of 1887 m (window radius), on the relative probability of grizzly bear use (selection) of a site, based on the heterogeneity foraging hypothesis which was most supported in AIC comparison. Dashed lines indicate 95% confidence intervals.

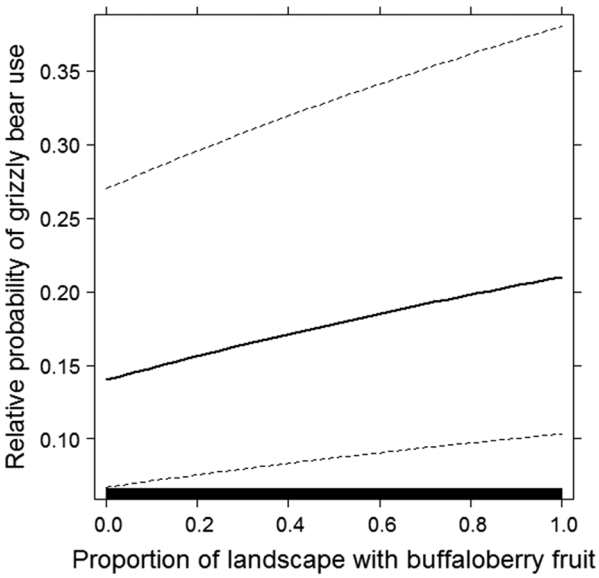


Figure 4. Predicted effect of buffaloberry fruit distribution (proportion of the landscape with buffaloberry fruit present), estimated at a spatial scale of 1887 m (window radius), on the relative probability of grizzly bear use (selection) of a site, based on the heterogeneity foraging hypothesis which was most supported in AIC comparison. Dashed lines indicate 95% confidence intervals.

Discussion

We observed that buffaloberry heterogeneity best explained grizzly bear selection for fruit resources. Bears selected for areas with a wider distribution of buffaloberry fruit and greater variability in patch quality, thus providing both a higher probability of shrub encounter and greater contrast between resource patches. Landscape-level foraging strategies were more supported than those of the patch-level, pointing to the large environmental grain of grizzly bears. Specifically, bears were most influenced by buffaloberry properties estimated at a spatial scale of 1887 m or 1.89 km (window radius) which corresponds to an average travel distance over 5.5 h, suggesting they may synthesize information on environmental conditions they encounter while moving through their home range. A similar scale of 1.69 km was used to measure average buffaloberry fruit supply when comparing this to the local abundance of bears (Nielsen et al. 2017).

Variability in patch quality emerged as an especially meaningful landscape-level buffaloberry property, based on its inclusion in the two most supported hypotheses. This implies that contrast between adjacent resource patches promotes selection by facilitating the assessment of quality and enabling bears to more efficiently identify high-quality patches. Even the addition of a modest amount of variability, equivalent to the fruit yield of an average shrub, was

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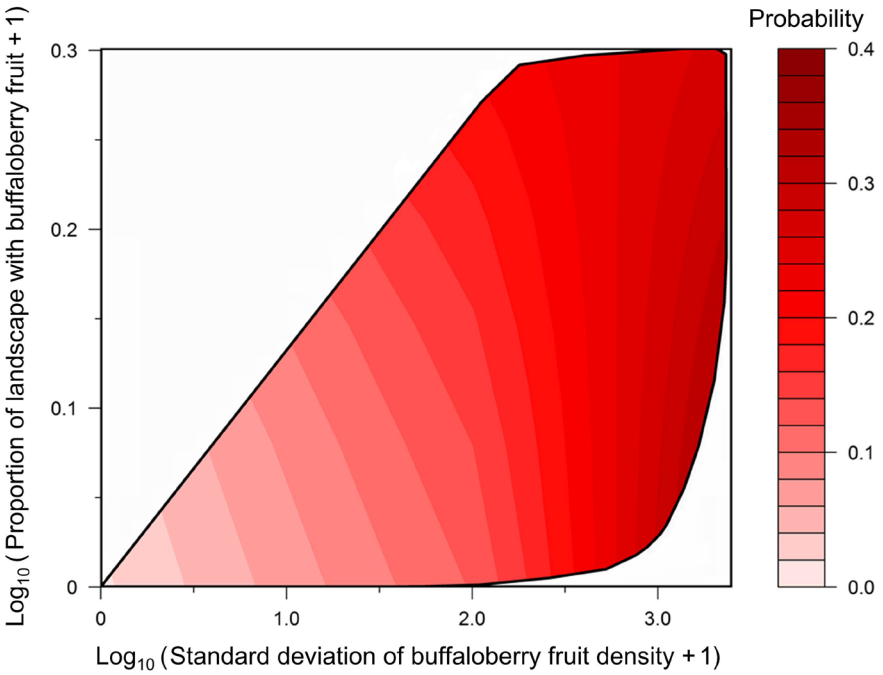


Figure 5. Predicted effect of the interaction between variability in buffaloberry patch quality (standard deviation of fruit density) and fruit distribution (proportion of the landscape with buffaloberry fruit present) on the relative probability of grizzly bear use (selection) of a site, based on the heterogeneity foraging hypothesis which was most supported in AIC comparison. Axes displayed with $\log_{10}$-plus-one transformed values to reflect variable transformations in the model. Predictions were constrained to conditions found within the study area by generating a minimum convex polygon representing data for all 'used' and 'available' locations in the model.

shown to increase bear habitat use (Fig. 3). Less support was found for the landscape resource quality hypothesis, which highlighted areas with a broad distribution of high-quality buffaloberry patches that were thus characterized by greater landscape homogeneity. Grizzly bear utilization of buffaloberry resources may therefore be contingent not only on locating high-quality patches, but also recognizing them as such, suggesting contrast could act as a cue for exploitation.

The positive effect of landscape variability on grizzly bear habitat selection is also likely related to their generalist habit (Hamer et al. 1991, Mattson et al. 1991, McLellan and Hovey 1995, Munro et al. 2006) and distinct habitat needs for different diel activities (Munro et al. 2006). Fruit density is a function of environmental and demographic factors that influence shrub growth and fruit production, such as local canopy cover (Hamer 1996, Nielsen et al. 2004b) and density (Johnson and Nielsen 2014). Greater variability in fruit density suggests the presence of a broader range of site types and increased environmental heterogeneity, which promotes plant species richness (Kreft and Jetz 2007). A higher diversity of complementary food resources, which affect local bear abundance (Nielsen et al. 2017), could provide animals with the opportunity to substitute these more readily and optimize macronutrient intake (Coogan et al. 2014). Landscape heterogeneity may thus contribute to grizzly bear foraging success by facilitating dietary flexibility, and helping to buffer against inter-annual fluctuations in the productivity of key food species (Krebs et al. 2009).

Previous work has also found food resource heterogeneity to be important for grizzly bear foraging behavior (Searle et al. 2006) and habitat use (Mangipane et al. 2018). Searle et al. (2006) conducted feeding trial experiments where the spatial arrangement of patches was manipulated and residence times of resource patches examined. Surrounding spatial context in the patch hierarchy was shown to affect residence time, with models accounting for this broader heterogeneity 34-times more supported than those limited to the patch-level.

The combination of both fruit distribution and variability in patch quality in the heterogeneity hypothesis suggests that bears respond to multiple aspects of their food resources simultaneously, implying that they compromise between different foraging strategies (Table 1) when selecting resources (Senft et al. 1987). This adaptability may be particularly necessary in our study area where anthropogenic disturbance caused by resource extraction is prevalent (Gaulton et al. 2011), requiring that bears navigate a dynamic environment. The interaction between variability in patch quality and fruit distribution was important to include, as the heterogeneity hypothesis received considerably more support than either of the individual hypotheses. Contrary to our expectations, the interaction was observed to be negative; this may relate to the elevation gradient and associated geographic separation of areas with a widespread fruit distribution and those with high variability in fruit density, which were restricted to high elevations in the west. Fruit distribution presumably demonstrates greater control over grizzly bear resource selection in the low-lying eastern portion, but its effect may decline with proximity to the mountains as it is overwhelmed by the comparatively stronger influence of variability. Bears in our study area may thus face a tradeoff between selecting for fruit distribution and variability in patch quality, partly due to the effect of terrain on buffaloberry properties.

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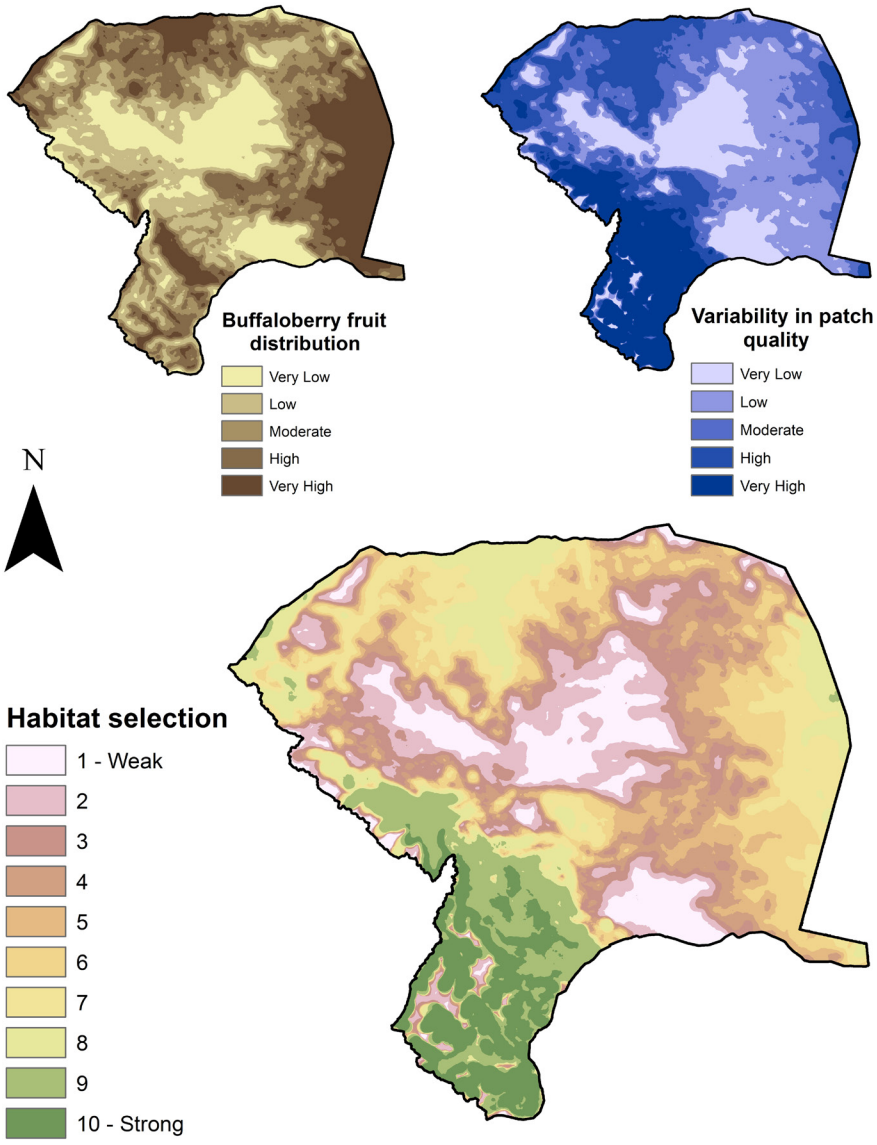


Figure 6. Buffaloberry fruit distribution (proportion of the landscape with buffaloberry fruit present), variability in buffaloberry patch quality (standard deviation of fruit density), and grizzly bear habitat selection based on the heterogeneity foraging hypothesis for the study area near Hinton, Alberta, Canada (53°24′41″N, 117°33′50″W). Elevation was not included as a variable in prediction of habitat selection to focus on the effects of buffaloberry properties. Symbolization is based on quantile classification for ease of display; however, areas with 'very high' variability in patch quality, in particular, may be over-represented due to a low frequency of extremely high values.

Our findings suggest human activities that shift the distribution and quality of food resources and generate landscape heterogeneity could promote grizzly bear habitat selection. Forest harvesting, for example, has been found to increase bear habitat use (Nielsen et al. 2004a, Stewart et al. 2013) through the creation of canopy openings which foster the growth of various food plants (Nielsen et al. 2004b, Munro et al. 2006) and significantly affect understory heterogeneity (Denny and Nielsen 2017). The effects of disturbance on food resource heterogeneity are not straightforward to predict, however, as they depend on a number of factors including initial site conditions and disturbance type. Proposed developments should therefore be evaluated on an individual basis to anticipate possible consequences for landscape patterns of food resources and bear foraging behavior, as well as mortality risk (Boulanger and Stenhouse 2014).

Conclusions

These results emphasize the value in considering environmental heterogeneity and spatial scale in studies of animal-resource interactions. Landscape-level estimates of resource properties should be incorporated into resource selection frameworks, especially for large-bodied, vagile species which typically perceive and respond to their surroundings at broad spatial scales. We recommend that researchers test the sensitivity of habitat selection to resource spatial scale, as we have here, to determine that which is most appropriate prior to proceeding with further analysis. This step will contribute to reducing the error associated with adopting an arbitrary experimental scale (Wiens 1989), as the conventional patch-level focus may obscure the factors affecting animal space use (Morrison et al. 2006). Accurately representing the level of

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spatial perception of study organisms will reflect the influence of food resource heterogeneity and ensure valid conclusions regarding foraging behavior to inform the conservation and management of wildlife species at risk.

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Supplementary material (available online as Appendix wlb-00409 at <www.wildlifebiology.org/appendix/wlb-00409>). Appendix 1.

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