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# Determining the spatial scale for conservation purposes – an example with grizzly bears

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## ABSTRACT

This study suggests procedures for determining the spatial scale for conservation guidelines for animals, giving an illustration with an analysis of grizzly bear habitat selection. Bear densities were sampled by identifying hairs at bait stations in British Columbia. Habitat variables were measured using remote sensing. Spatial scale was changed by varying the window size over which the variables were averaged. First, the spatial pattern of bears was studied, measuring the patchiness in bear densities at a variety of spatial scales, by calculating the correlation in bear densities between adjacent windows. This was repeated for the habitat variables. Finally, the overall interaction between bears and habitats was analysed, measuring the strength of habitat selection at different spatial scales. There are three domains of scale: at 2–4 km, bears and habitats are patchy, at 5–10 km, bears select for habitats, and at 40+ km, habitats are patchy and bears select for habitats. At scales of 40+ km, bears selected for: (i) higher slopes, or (ii) higher slopes, and some combination of more avalanche chutes, fewer roads and trees, higher elevations, and less logged land. Within 15 km areas, bears selected for 6 km areas that are either at higher elevations, or at higher elevations and had fewer trees. The relationship of conservation guidelines at different spatial scales should be determined by measuring and comparing hierarchical to non-hierarchical selection. The scales that bears select for habitats roughly correspond to the scales used in present grizzly bear conservation plans in British Columbia.

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## 1. Introduction

One of the cornerstones to animal conservation is understanding the relationship between animals and habitat. It is difficult to study this experimentally, especially for large animals, and thus we often measure habitat selection, assuming that it implies conservation value. One complication is that animals may not view habitats at the same spatial scales that biologists do. Thus a key question is what is the appropriate spatial scale for conservation guidelines. A first step to addressing this would be to answer the following questions:

(i) at which scales are populations most patchy, (ii) at which scales are habitats most patchy, and (iii) at which scales do animals select habitats most strongly? Habitat selection studies that incorporate spatial scale typically address the last question only.

Such studies have to make several choices. The first is which spatial scales to use for measuring habitat – whether to use biologically relevant scales (Loyn et al., 2001; Luck, 2002a) or arbitrarily chosen scales at equidistant spatial intervals (Mitchell et al., 2001; McGrath et al., 2003). The second is which scales to use for measuring animal use—whether to use

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just one fixed spatial scale (Mitchell et al., 2001; Hatten and Paradzick, 2003), or to vary animal scale with habitat scale (McLoughlin et al., 2002). The final choice is how to relate the habitat variables at different scales – whether to combine habitat variables from all spatial scales into one relationship (Apps et al., 2004), whether to produce a uniquely different model for each scale (Hatten and Paradzick, 2003), or whether to use all variables at each scale in order to compare strength of selection across scales (McGrath et al., 2003).

We suggest that the following choices be made. First, habitats should be measured at many spatial scales, spread out equidistantly over a wide spatial range. They should not be restricted to biologically relevant scales because it is often difficult to measure these. For example, one common scale that has been used is home range size (McLoughlin et al., 2002; Zabel et al., 2003). However some animals use multi-scaled hierarchical home ranges, and some animals do not even have asymptotic home ranges (Gautestad and Mysterud, 1995). It takes little extra effort to analyse additional spatial scales – the largest effort is gathering the data and initially setting up the analysis algorithms. Furthermore, it is important to both measure and compare, hierarchical versus non-hierarchical selection.

Second, animal use should be analysed at the same scales that habitat data are. A biological reason for doing this, is if an animal perceives a certain area of land as one piece of habitat, then you would expect a similar use throughout that area. Differences in use throughout that area would be due to other factors, not the type of habitat. A statistical reason, is that variation among animal use among small areas is composed of two parts: variation within large areas, and variation among large areas – but we are only interested in variation among large areas. The variation within large areas would decrease the power of our tests.

Third, our measure of selection should be comparable among spatial scales. Thus all variables should be included in each model at each scale, and precision and accuracy should not vary with scale. For example, if habitat and animal data gathered at small spatial scales are averaged for the larger scales, then the number of samples used to calculate the means in each window increases with window size. This decreases sampling error, increasing precision. Furthermore, sampling errors in independent variables create a bias in linear models (Neter et al., 1996), and the bias would change with spatial scale. These effects of sampling errors should be removed in the analysis. These issues have not been discussed before.

We illustrate these issues in an analysis of spatial scale of habitat use of grizzly bears (*Ursus arctos*). Grizzly bears select habitats at various spatial scales, but it is not known which scales are most important, and which should be used in conservation. At landscape scales, larger than individual home ranges, bears avoid roads (Archibald et al., 1987; Apps et al., 2004), select against forest (Mace and Waller, 1997a), but for the amount of deciduous vegetation (Mace et al., 1999). Within home ranges, bears still avoid roads and human habitation (Clevenger et al., 1992, 1997), but habitat use changes throughout the season. During spring and early summer, bears in mountainous areas use riparian areas and forest openings that are free of snow (McLellan and Hovey, 1993) and avalanche chutes (McLellan and Hovey, 2001). As berries begin to ripen in mid summer, bears move to areas with high berry

concentrations such as natural burns (Zager et al., 1983), logged areas (Zager et al., 1983; Waller and Mace, 1997), and upper elevation forests (Hamer et al., 1991; Mace et al., 1996). Most of these studies have analysed grizzly bear habitat selection for the purpose of directing conservation effort, but they have focused on predicting bear abundance, not which are the most appropriate scales to use in conservation guidelines.

These studies do not give a scientific basis for choice of scale for conservation guidelines. For example, in British Columbia, residence of 25% of the North American grizzly bear population (Banci et al., 1995), the spatial scales used in conservation plans have been based on planning needs and expert perceptions of pertinent scales of importance for grizzlies (Kootenay Inter-Agency Management Committee, 1997), not on the results of specific scientific studies. The purpose of our study is to measure the appropriate spatial scale for conservation guidelines of grizzly bears. We do this by finding at which scales grizzly bear populations are most patchy, at which scales are their habitats most patchy, and at which scales do grizzly bears respond to their habitats most strongly. We then analyse habitat selection parameters at those scales.

## 2. Methods

### 2.1. Field methods

Our study area was located in south-eastern British Columbia, Canada (51° Lat, 117° Long), and was dominated by the Selkirk Mountains, with many peaks exceeding 2400 m. The majority of the area was forested. Western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) typically characterised low elevation forests, while Englemann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) forests were dominant above about 1400 m. Treeline was at 2000 m.

Habitat use data were collected as part of a population estimation study that used hair capture and DNA profiling as the individual mark in a mark-recapture design (Woods et al., 1999; Mowat and Strobeck, 2000). This sampling method has been used to estimate population size for several large areas of British Columbia and Alberta (Woods et al., 1999; Mowat and Strobeck, 2000; Poole et al., 2001). This technique samples a large number of different bears over thousands of square kilometres, and although the sampling design is largely chosen around the constraints of population estimation, it is also useful in examining habitat selection.

The bear population was sampled between June 19 and August 14 of 1996. Mean density of bears was 0.0266 (95% c.i. of 0.0227–0.0317) bears/km<sup>2</sup> (Mowat and Strobeck, 2000). The 9866 km<sup>2</sup> study area was partitioned into 8 × 8 km cells with every second cell sampled in a checker board fashion. One capture site was installed in each of 76 cells for approximately 10 days. Capture sites were baited with rotten meat, and barbed wire was used to catch hair from bears. DNA profiling of the hairs was used to identify individuals and species. Each site was visited once at the end of the 10-day trapping session and removed. The next site was installed elsewhere in the same cell with the stipulation that new sites be at least 1 km from all previous sites. Further details on field and lab methods can be found in Mowat and Strobeck (2000) and Woods et al. (1999). The animals were handled in accor-

dance with the principles and guidelines of the Canadian Council on Animal Care.

## 2.2. Habitat variables

We chose habitat variables (Table 1) that were readily available from existing databases, that were accessible and inexpensive, that would directly relate to future GIS modelling endeavours, and that were perceived to be important to grizzly bears. An ArcInfo® Geographic Information System (GIS) was used to convert data from each variable to a grid with a 50 × 50 m cell size. These values were then averaged to produce habitat values for windows of different sizes in our analyses. The averaging also caused the resulting habitat variables to be normally distributed.

## 2.3. Overall strategy of analysis

Our interest was in analysing grizzly bear habitat use at different spatial scales. We did this in several steps. First, we studied the spatial pattern of grizzly bear densities by themselves, measuring the patchiness in bear densities at a variety of spatial scales. Then we did the same thing for the habitat variables. Then we studied the overall interaction between grizzly bears and habitats, measuring the strength of habitat selection at a variety of spatial scales. Finally, using those spatial scales at which grizzly bears show the strongest selection, we did a more detailed analysis of habitat selection.

## 2.4. Spatial scales

At each spatial scale of interest we defined windows of a fixed size, distributed throughout the study site. We calculated average values for bear density and habitat variables within each window, and varied spatial scale by varying the window size over which the variables were averaged. This differs from the methods traditionally used in geospatial statistical analyses (Rossi et al., 1992), such as variograms and correlograms. There, one calculates various statistics using windows of fixed sizes, but varying the lag distances between windows. Instead, we varied window size. We did this because it better describes what we mean when we consider how animals respond to habitats at different spatial scales. For example, if bears respond to habitats at a spatial scale of 4 km, this

means that they respond to habitat type in a 4 × 4 km area (i.e. a 4 km window) rather than to a small block of habitat 4 km away (i.e. a lag distance of 4 km). Thus, whenever we refer to a window size, or a spatial scale, we will refer to the length of one side.

We calculated window means differently for large and small scales. For larger spatial scales (3–40 km) we used square windows spaced 1/4 window-width apart, covering the whole study site. The overlapping of the windows minimised variation due to window placement. For smaller scales (0.5–7 km) we used round windows centred on bear sampling sites. These windows were placed this way in order to avoid missing data, because most small randomly located windows contained no bear sampling sites, and those that did had usually one, located anywhere inside the window. The overlap in ranges of spatial scales between the large and small scales (an overlap in the range of 3–7 km) gave a check that the two techniques were giving similar results.

The analyses used all windows that were completely in the study area. To avoid violating the assumption of independence caused by the overlapping of windows, we used an effective sample size based on the number of non-overlapping windows in the study site. For the larger scales this calculation was the number of windows divided by 16, but for the smaller scales this calculation involved an iterative process where a window was selected, then all windows overlapping with that one were removed, then the next closest non-overlapping window was chosen, etc, until all windows were gone. This whole process was carried out 10 times, starting with different initial windows.

At each window size the analysis incorporated patterns over the whole range of spatial scales, from that size up to the whole study area. For example, bears may select for specific forage at a small scale, prefer more open coverage at a medium scale, and avoid human disturbance at a large scale. All of these behaviours affect bear density at a small scale, and in order to isolate the effects at one specific spatial scale, we need to remove the effects of the larger scales.

Thus we also carried out analyses where we removed the effects of larger scales, by calculating deviations from means of larger windows. This is analogous to partitioning the sums-of-squares in an analysis of variance (Sokal and Rohlf, 1995; Neter et al., 1996). Our aim was to have a 2× range for each spatial scale – for example, values in 1 km windows were

**Table 1 – Habitat parameters analysed and the sources of the data**

Habitat parameters	Units	Source
Elevation	Meters	TRIM <sup>a</sup>
Slope	Percentage	TRIM
Distance to water	Meters	TRIM
Distance to roads <sup>b</sup>	Meters	TRIM
Distance to human development	Meters	TRIM cultural, and private land
Logged land	Proportion of area	B.C. Forest Cover Mapping and Forest Development Plans
Treed land	Proportion of area	Landsat unsupervised classification
Avalanche chutes	Proportion of area	Landsat unsupervised classification and Forest Cover Mapping

In the analysis, the negative of the distance parameter was used. The areas were transformed to a proportion of the window area.

a TRIM represents “Terrain Resource Information Management” (Balsler, 1987), a public access GIS data source.

b This includes all roads, but most roads in the study site were secondary logging roads

subtracted from the means of 2 km windows (for notation, this was called the 1–2 km spatial scale) – this removed all patterns at spatial scales larger than 2 km.

This use of deviations from a local mean has a couple of benefits. First, it models the hierarchical manner in which it has been suggested (Johnson, 1980; Hutto, 1985; Sallabanks, 1993) that animals select habitats – that animals first select home ranges, and then select habitats to use within those home ranges. In other studies using radio-tracking data, hierarchical selection has been analysed by first measuring home range selection, by comparing home range habitats to habitats in the overall study area; then by measuring habitat use within home ranges, by comparing habitat use of individual animals to habitats available in each home range (Aebischer et al., 1993; Sallabanks, 1993).

The second benefit is that using local deviations minimises the effects of autocorrelations – since deviations from a local mean are less autocorrelated than deviations from an overall mean.

One potential problem when analysing habitat use at different spatial scales is that sampling error changes with spatial scale, since the number of samples used to calculate the means per window, increase with window size. Sampling errors typically create a bias in linear models, and the bias changes with spatial scale. We removed the effects of sampling errors (Laws, 1997; Appendix A), thus eliminating this potential problem.

## 2.5. Spatial patterns in bear density

In order to find the scales of patchiness in bear densities, we calculated the correlation in bear densities between adjacent windows. If there is patchiness at only one spatial scale, then correlation should be positive when windows are smaller than patches, negative when windows are approximately patch size, and zero when windows are larger than patch size. However if there is patchiness over a range of scales, then there would be positive correlations over that range. This analysis is similar to correlograms, as used in geospatial statistical analyses (Rossi et al., 1992), except that we varied window size instead of lag distance. “Scale” refers to the width of two windows, since correlation would peak when two windows are inside a patch.

We carried out the procedures differently for large and small scales, since we had to use different types of windowing procedures. For larger spatial scales (4–80 km), with the square windows, we used vertical or horizontal pairs, centred anywhere on the study site. For smaller scales (1.5–20 km), with the round windows centred on bear sampling sites, we used pairs of windows in any orientation. All possible pairs of windows that were completely in the study site, and that contained bear sampling sites, were used.

Note that patchiness in sampling sites does not affect our results. This is because only windows that contained bear sampling sites were used, and because our measure of bear density was unbiased with respect to the numbers of sites.

In order to estimate confidence intervals in the correlations we used a bootstrapping technique (Efron and Tibshirani, 1991). To avoid violating the assumption of independence, for the size of the bootstrapped samples we

used the numbers of independent pairs of windows (non-overlapping), not the total numbers of pairs (overlapping).

For a measure of bear density we used the proportion of sites visited by grizzly bears within the window.

## 2.6. Causes of bear patchiness

We also tested whether patchiness in bear populations was caused by the same individual bears being found throughout each patch. We did this by estimating the similarity in individuals between pairs of windows – i.e., to see if the same bears tended to use the same patch. For example, a peak in similarity at small scales but not the larger ones would suggest that the small-scale patchiness is due to grouping, but that the larger scale patchiness is not.

To test for this, we used the identifications of individual bears (by DNA profiling) and calculated a variation of Jaccard’s Coefficient of species similarity (typically used in comparing communities; Krebs, 1999):

$$S = \frac{\# \text{ bears common to both}}{\# \text{ of individual bears in both}} \quad (1)$$

This similarity measure ranges from 0, when completely different bears are found in each window, to 1, when exactly the same bears are found in both windows.

## 2.7. Spatial patterns in habitats

We measured the scales of patchiness in habitats in a similar manner as the bear densities, using the same setup of pairs of windows. This was done for each habitat variable separately, and all together. As a measure of overall correlation between habitats of adjacent windows, we used the square root of the mean of correlations squared (we did not use canonical correlation because estimates of it are inflated by low sample sizes, and in our situation, sample size changes with spatial scale). Thus heterogeneity is shown by a peak and drop in correlation as spatial scale increases.

## 2.8. Habitat selection

We analysed the overall interaction between grizzly bears and habitats by measuring the strength of habitat selection at a variety of spatial scales. Unlike the previous analyses, at each spatial scale, each data point contains measurements of both bears and habitats from one window, and we want to know how they correspond. Thus, rather than comparing adjacent windows, we analysed the relationship between bear density and habitat within the same windows (of different varying window sizes). “Scale” refers to the width of one window.

We used general linear models in which our independent variables were the habitats of the windows, and the response was bear density. In order to isolate the effects of the different habitat variables we carried out an interactive step-wise regression, and at each step considered the relationships among the habitat variables themselves. The strength of the overall relationship between bears and habitat, as modelled by the regression, was measured by a multiple correlation, with error estimates of it by the Fisher  $z$  and Hotelling  $z^*$  transformations (Sokal and Rohlf, 1995; Neter et al., 1996).

In order to see how these variables relate to each other, we considered their 'Tolerance'. This measures how independent one variable is from the others together and is estimated by  $1 - R^2$  of that variable against the rest of the habitat variables (Pedhazur, 1982). Tolerance ranges from 0, meaning that the variable is completely correlated with a linear combination of the others, to 1, meaning that is completely unrelated to all the others.

The computer programs to select the pairs of windows and calculate variance–covariance matrices were written in Mathematica (Wolfram, 1999), with the resulting matrices analysed with the statistical package SYSTAT (Wilkinson et al., 1999).

### 3. Results

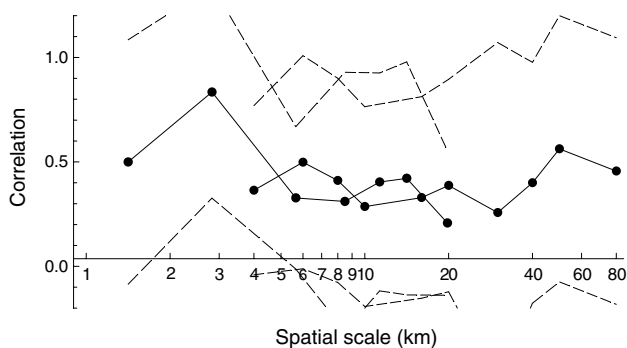
We monitored hair snares in 76 cells, approximately 5 times each, between June 19 and August 14, 1996, and retrieved hair from 109 individual bears 134 times. Of the 381 sites, 23% successfully snared grizzly bear hair. As many as 5 bears left hair at a site; some multiple visits were females with cubs (data presented in Mowat and Strobeck, 2000).

#### 3.1. Spatial patterns in bear density

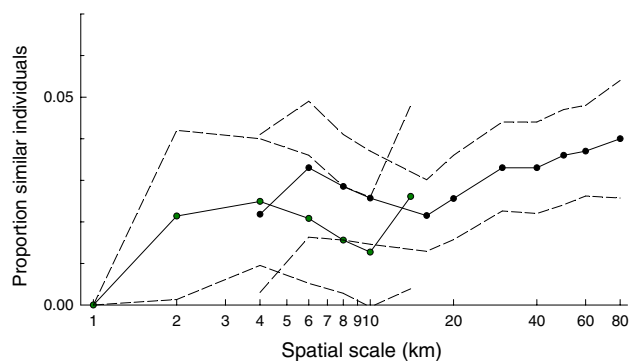
Correlations in bear density between pairs of windows decreased from 3 to 4 km (Fig. 1), suggesting that there is patchiness in bear density at small spatial scales (size 3–4 km). The confidence interval is too broad to tell if there are any significant patterns at larger spatial scales.

The patchiness in bear distributions at small scales is not due to the spatial distribution of sampling sites, because the analysis compares bear density only for pairs of windows that contain sampling sites.

We tested if it might be due to individual bears using sites that are close together. The similarity in individual bears between pairs of habitat windows (Fig. 2) shows two important features. First, we do not see the peak at the small scale that we saw in the bear patchiness results (Fig. 1). Second, similarities are extremely low at all scales – the largest is at a scale of 80 km, where it is still only 0.04. Thus only 0.04 of the bears found in areas 40 km apart are common to both



**Fig. 1 – Patchiness in bear density over a range of spatial scales. The values represent correlations in bear density between adjacent windows. Spatial scale is the width of a pair of adjacent windows. The dashed lines represent 90% confidence intervals. The larger the correlation the stronger the patchiness at that scale. Patchiness peaks at 3 km.**



**Fig. 2 – Similarity in bear distributions between pairs of windows, at varying distances. Values represent the proportion of bears that are the same between pairs of windows; a 1 represents all the same bears, and a 0 completely different ones. Spatial scale is the width of a pair of adjacent windows. Dashed lines represent 90% confidence intervals.**

areas. At smaller scales the similarity is even lower – 0.02 of the bears found in areas 1 km apart are common to both areas. Thus the patchiness in bear numbers is not because of the same individual bears using sites close together, nor due to a grouping behaviour (e.g., family groups at small scales, or sub-populations at larger scales).

#### 3.2. Spatial patterns in habitats

Correlations in habitat variables between pairs of windows decreased from 2 to 4 km, then increased at 20 km (Fig. 3). This suggests that there is patchiness in habitat variables at small (2–4 km) and intermediate-large spatial scales (20–80+ km).

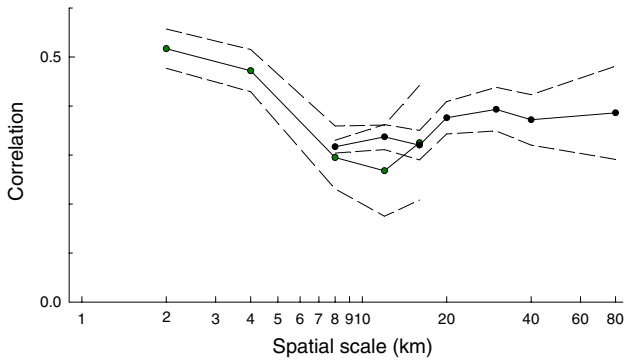
#### 3.3. Bear habitat selection

Bears select habitat variables differently, depending on spatial scale (Fig. 4), but overall, bears select most strongly for habitats at two distinct spatial scales: 4–8 and 40+ km (Fig. 5), with selection being strongest at the large scale of 40+ km. We will thus concentrate our more detailed analysis at these two spatial scales. Bias due to selection of bear sampling sites is minimal (Appendix B).

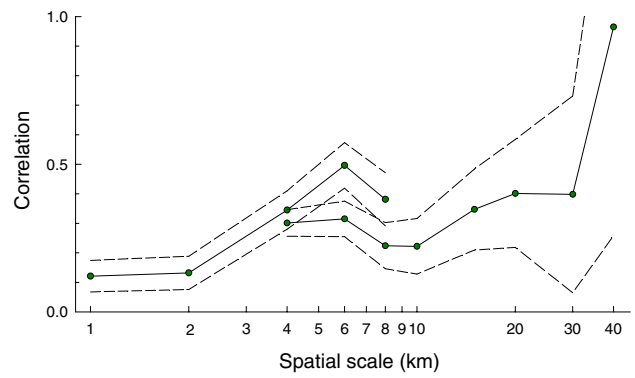
Note that Fig. 5 shows selection with effects at larger scales removed. For example, the peak at 6 km means that within  $15 \times 15$  km windows (approximately  $2 \times$ ), bears select for areas of size  $6 \times 6$  km – i.e., hierarchical selection. In order to answer the question of which scale best predicts bear distribution and habitat relationships over the whole study area, this analysis was also carried out without removing effects at larger spatial scales (Fig. 6). The increased correlation at large scales shows that windows of size  $40 \times 40$  km are most useful in predicting bear density from habitat information, over the whole study area.

##### 3.3.1. Large spatial scale – 40+ km

Elevation, slope, roads, logged, trees, and avalanche chutes all individually correlate with bear density (Table 2), and many



**Fig. 3 – Patchiness in habitats at various spatial scales.** The values represent correlations in all habitat variables between adjacent windows. Spatial scale is the width of a pair of adjacent windows. Dashed lines represent 90% confidence intervals. The larger the correlation the stronger the patchiness at that scale. The left line in each graph shows data from windows centred at bear sampling sites, while the right line shows data from windows in a grid pattern. Note the increased habitat patchiness at small and large scales.



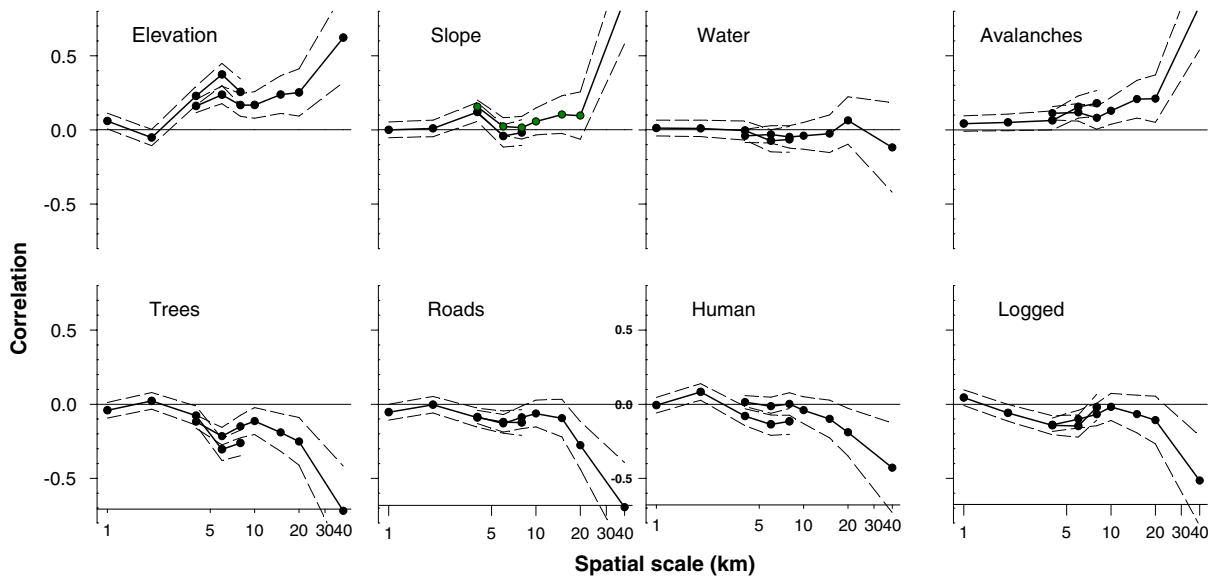
**Fig. 5 – Localised habitat selection at various spatial scales.** It is localised, or hierarchical, in that deviations from a local mean of about 2x window size, instead of from the global mean, are used. The values represent correlations between grizzly density and all habitat variables within windows of that size. Spatial scale is the width a window. The larger the correlation the stronger the selection at that scale. Habitat selection peaks at 4–8 and 40+ km. The values represent correlations between grizzly density and all habitat variables within windows of that size. Dashed lines are 90% confidence intervals. Left set of lines is based on windows centred on bear sampling sites, and right set is from regularly spaced windows.

correlate with each other (Table 3). Thus we carried out an interactive step-wise regression, and at each step considered the relationships among the habitat variables themselves.

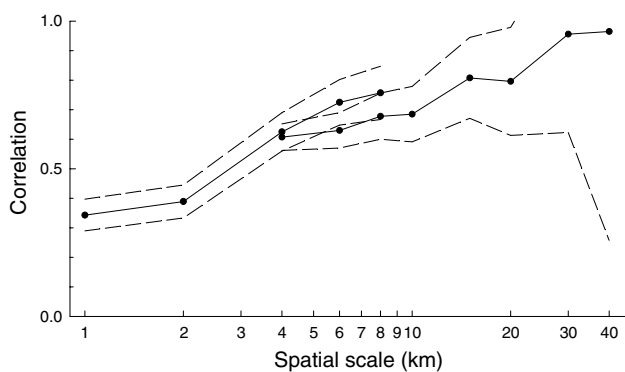
Water has the highest tolerance, 0.47 (Table 2), showing that it is the most independent of the rest of the habitat variables. The other seven have very low tolerances, showing that they are related to each other, with elevation, slope, logged, trees and avalanche chutes being the most related. Six of

these interrelated variables also correlate strongly with bear density (Table 2).

When we control for the effect of slope (the variable with the strongest relationship to bear density; Table 2), then the relationships between bear density and each of the other hab-



**Fig. 4 – Localised habitat selection at various spatial scales—individual habitat variables.** It is localised in that deviations from a local mean of about 2x window size, instead of from the global mean, are used. The values represent correlations between grizzly density and each habitat variable within windows of that size. Spatial scale is the width a window. Dashed lines are 90% confidence intervals. The larger the correlation the stronger the selection at that scale. The left line in each graph shows data from windows centred at bear sampling sites, while the right line shows data from windows in a grid pattern. A positive correlation shows selection for that habitat variable and a negative correlation shows selection against it.



**Fig. 6 – Habitat selection over the whole study site, at various spatial scales. This shows which scale best predicts bear distribution:habitat relationships over the whole study site. Values represent correlations between grizzly density and all habitat variables within windows of that size. Spatial scale is the width a window. The larger the correlation the stronger the selection at that scale. Habitat selection is highest at 40+ km, thus windows of size 40+ km are most useful in predicting bear distribution and habitat relationships. Dashed lines are 90% confidence intervals. Left set of lines is based on windows centred on bear sampling sites, and right set is from regularly spaced windows.**

itat variables in that group of six disappear. This shows that none of them has any effect on bear density that is statistically different from, or larger than, the effect of slope. On

the other hand, if we control for all of the other five variables together (elevation, roads, logged, trees, avalanche chutes), then the partial correlation for bear density vs slope still remains significant. This means that the relationship between bear density and slope is more than just due to slope being correlated with these other habitat factors that bears might select.

We can conclude that over the whole study site, bears select for 40 km areas on the basis of:

- (i) slope-bears prefer higher slopes, or
- (ii) slope, and some combination of more avalanche chutes, fewer roads and trees, higher elevations, and less logged land.

3.3.2. *Intermediate spatial scale*

The analysis at this scale used means taken from 6 × 6 km windows. In addition, in order to remove effects from larger scales, deviations were taken from 15 × 15 km windows rather than from global means. Thus this measured hierarchical selection.

Bear density is most correlated with elevation and trees (Table 2), and also significantly correlated (but less so) with avalanche chutes, logged, and humans. The smaller tolerances for elevation and trees show that these variables are related to each other, but the rest of the variables are quite independent of each other.

Controlling for elevation, the significant relationship between bears and trees disappears. But controlling for trees, then there is still a significant relationship between bears

**Table 2 – Correlations of individual habitat variables with bear density, at the 40+ and 6–15 km spatial scales**

Habitat	40+ km scale			6–15 km range of spatial scales		
	Correlation	P-value <sup>a</sup>	Tolerance <sup>b</sup>	Correlation	P-value <sup>a</sup>	Tolerance <sup>b</sup>
Elevation	0.62	0.01	0.08	0.37	0.001	0.39
Slope	0.88	0.00	0.07	−0.04	0.57	0.77
Water	−0.12	0.66	0.47	0.07	0.32	0.89
Roads	−0.70	0.003	0.17	0.12	0.10	0.69
Human	−0.43	0.10	0.22	0.14	0.06	0.78
Logged	−0.52	0.04	0.13	−0.15	0.05	0.80
Trees	−0.72	0.002	0.08	0.30	0.001	0.42
Avalanche chutes	0.84	0.001	0.11	0.16	0.04	0.73

a P-value measures the significance level for a non-zero correlation.

b Tolerance measures how independent that variable is from all of the rest of them.

**Table 3 – Correlations of individual habitat variables against each other, at the 40+ km spatial scale**

	Slope	Elevation	Water	Roads	Human	Logged	Tree	Avalanche chutes
Slope	1							
Elevation	0.83	1						
Water	0.00	−0.30	1					
Roads	0.75	0.79	−0.18	1				
Human	0.55	0.66	−0.19	0.78	1			
Logged	−0.65	−0.84	0.47	−0.68	−0.46	1		
Tree	−0.60	−0.68	0.27	−0.76	−0.56	0.64	1	
Avalanche chutes	0.83	0.59	0.05	0.72	0.62	−0.37	−0.52	1

and elevation. Thus within 15 km areas, bears select for 6 km areas that are at either: (i) at higher elevations, or (ii) at higher elevations and have fewer trees. We cannot tell which it is, or if the second, how much bears select for elevation vs trees. Bear density is not related to the other seven variables. Overall, bears select for habitats much less strongly at this scale than at the 40+ km scale (an  $R$  of 0.38 vs 0.88 at 40+ km).

## 4. Discussion

### 4.1. Spatial scale

Processes in ecological systems change with spatial scale, but they do not always change smoothly. Wiens (1989) proposed that there are regions (called 'domains') of scale, within which patterns do not change, and these domains are separated by sharp transitions as different processes become important at larger scales vs smaller scales. In our study we saw patterns at three distinct spatial scales. Since the relationships between bears and habitat are qualitatively different in each of these regions, this suggests that these are distinct domains, and that therefore different aspects of bear biology are important in each.

However, we see an interesting and unexpected feature in our results. Bear densities and habitats are patchy at all spatial scales ranging from 1 to 80 km, and there is significant non-hierarchical habitat selection at all scales. There are various ways this could occur.

First, different categories of bears (e.g., ages, sexes, individuals) could respond at different spatial scales. This is possible, because males and females have different home range sizes, and females with small cubs select habitat in order to avoid males (Nagy and Haroldson, 1989; Mace and Waller, 1997b), likely because strange males will kill cubs (Swenson et al., 1997).

Second, bears could change their scale of patchiness over time. This too is possible, because grizzly bears tend to be confined to snow-free greened-up areas early in spring, with their choices increasing as the season progresses (Jonkel, 1987; McLellan and Hovey, 1993); they also increase home range size when mating (Dahle and Swenson, 2003).

Finally, the idea of the domains being distinct, might be too simplistic-while there are some aspects of bear:habitat biology that are more important at some spatial scales, there might be other aspects that change continuously with spatial scale. That is, that grizzly bears might actually view their world at a continuum of spatial scales. Analogously, Hoffman and Wiens (2004) discovered that tenebrionid beetle species richness and some habitats variables showed positive covariance at all spatial scales. Perhaps the distinctness of domains of scale needs more tests.

### 4.2. Conservation applications

We highlight several useful principles for evaluating the choice of scale in forest-use guidelines. First, it is important to identify the main domains using the behaviour of the animals themselves, before carrying out more detailed analyses in those domains. When doing this a wide range of spatial scales should be used. This is typically not done – many stud-

ies of the spatial scale aspects of animal:habitat relationships have either used naturally occurring divisions of spatial scale (e.g. Diffendorfer et al., 1995; Mace et al., 1996; Chapin et al., 1997), or have arbitrarily chosen a few specific spatial scales to study (e.g. Bowers et al., 1996; Pedlar et al., 1997; Timoney, 1999). For example, Apps et al. (2004) developed predictive functions of grizzly bear distribution north of our study site, testing 3 specific spatial scales (diameters of 5, 13 and 22 km). However we found that habitat selection increased sharply at larger scales than they tested (at 40+ km; Fig. 5). Perhaps Apps et al. (2004) would have found stronger or different predictive equations had they tested a larger spatial scale.

Second, the study should allow comparisons of strength of selection across the different spatial scales. This is difficult when different types of data are used – for example, some studies measure habitats selection by using locations of individual animals at a small scale, vs whole home ranges at a large scale. Even when the data is collected in the same way, the analysis must ensure that results can be compared – we had to remove the effects of sampling variation (Appendix A) because they depended on spatial scale.

Third, measuring habitat patchiness helps in assessing the applicability of predictive models of distribution, to other study sites. The best way to test them is to use independent data sets (e.g. Luck, 2002b) – but often these are not available. In our study, the question is, do grizzly bears in other areas select habitat at the same spatial scales? The underlying biological question is whether selection at these scales is inherent, or is it a result of the spatial distribution of habitats? The habitat patchiness results helps us to answer this. Bears selected most strongly at scales of 6 and 40 km, however habitats were patchy only at the 40 km scale. Thus selection at 6 km was likely not caused by habitat spatial distribution, but at 40 km it might have been.

Finally, studies include both hierarchical and non-hierarchical selection. For example, grizzly bears selected for areas of width 6 km that are at higher elevations than the surrounding 15 km, but bears did not show a peak in non-hierarchical selection at that scale. Other animals have also been shown to select hierarchically: caribou select types of patches depending on the type of landscape they are in (Johnson et al., 2004) and eagle owls select nest sites after selecting home range sites (Martinez et al., 2003). Other animals have also been shown to select non-hierarchically: mule deer selected for patch size at small scales but not at larger scale (Kie et al., 2002). Vaughan and Ormerod (2003) stressed that distribution models for conservation should include spatial hierarchies. However no previous study has measured both types of scalar selection, nor compared them.

It is important to both measure and compare, hierarchical versus non-hierarchical selection, for two reasons. First, ignoring hierarchical selection might lose important information. Grizzly bears in our study did not show non-hierarchical selection at 6 km – one might conclude that selection at this scale is unimportant, if hierarchical selection was ignored.

Second, the type of selection determines how to relate conservation guidelines at different spatial scales. If non-hierarchical selection is most important, then guidelines at the smaller scale can be independent of where the smaller units are located. However, if animals select hierarchically

then conservation guidelines should be defined in the context of the larger scale. For example, within 40 km areas, bears select for areas of locally high altitude. Guidelines for habitat preservation based on altitude should thus be based on the altitude of surrounding areas. This is an important topic that has not been previously addressed.

#### 4.3. Grizzly bear conservation

Present grizzly bear conservation plans in British Columbia consider guidelines at the stand level (2500 ha on the average) and multiple landscape unit level (200,000 ha on the average), but the choice of scale has been based on planning needs and expert perceptions of pertinent scales of importance for grizzlies (Kootenay Inter-Agency Management Committee, 1997). Grizzly bears in our study area selected for habitats at two distinct spatial scales: at 4–8 km (1600–6400 ha) and 40+ km (160,000+ ha), which roughly correspond to the “stand” and “multiple landscape unit” levels used in conservation plans.

It is clear that our large scale results support the relevance of the “multiple landscape unit” level in conservation, but it is less clear how our intermediate scale results relate to the “stand” level. This is because there are two different types of results at the intermediate spatial scale. Windows of size 4–8 km are most useful in predicting bear density within 15 × 15 km areas (e.g. Fig. 5), but not over the whole study site (e.g. Fig. 6). It is not clear which of these types of analyses is most useful for conservation guidelines, and more research is needed to clarify the situation. It would be useful for future studies to explore the nature of hierarchical selection. For example, we measured selection within a 2 × width area. With a larger sample size, it would be useful to vary the sizes of larger areas – and do this for a varying sizes of core areas.

An analytical approach emphasising scale as in this study may provide justification for choosing appropriate conservation scales and serve to identify habitat parameters most suited for consideration at those scales.

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### Appendix A. Removing the effects of observation error

At each spatial scale, our measures of animal density and habitat vary due to two components: natural variability through space, and observational error. Using type I linear models in such a situation can create a bias (Sokal and Rohlf, 1995; Neter et al., 1996). Even worse, the observational error

changes with spatial scale (more samples taken from larger windows), causing the bias to change with scale. For example, the measure of bear density, the proportion of sites visited by bears, is more variable at smaller scales because there are fewer sites in smaller windows. This might decrease the estimated correlation between windows.

The bias can be adjusted if the observation error can be calculated separately (Rayner, 1985). We removed the effect of observational error by an adaptation of the methods of Laws (1997).

Suppose for windows of a certain size, we calculate mean bear densities in each window based on  $n_B$  samples, and calculate habitat values based on  $n_H$  samples.

Suppose  $\bar{B}_i$  = mean bear density in the  $i$ th window;  $\sigma A_B^2$  = variance in bear density among windows;  $\sigma W_B^2$  = variance in bear density among samples within a window;  $\sigma A_{BH}$  = covariance of bear densities and habitat values among windows; then the variance among mean bear densities is given by

$$\text{Var}(\bar{B}_i) = \sigma A_B^2 + \frac{\sigma W_B^2}{n_B} \quad (2)$$

and a similar relationship exists for the habitat means. This shows that the variance among mean bear densities is inflated by the observational error (the second term). Of course, the more samples we have in each window (larger  $n_B$ ), the smaller the effect of observational error.

However, the covariance among bear and habitat values is given by

$$\text{Cov}(\bar{B}_i, \bar{H}_i) = \sigma A_{BH}. \quad (3)$$

This means that the covariance among bear and habitats is not affected by the observational error. Consequently, the estimated correlation between bears and habitats is biased downwards, because the variances are inflated but the covariance is not. If we now increase spatial scale, the numbers of samples per window increases, decreasing the effect of observational error, resulting in an increase in the correlation – and this increase is simply due to the effects of scale on sampling error, not due to any biological relationship.

We can remove the effect of the observational error by first estimating it; in each window, the observational error term is the standard error squared. For an overall estimate of the term, we used the mean of the standard errors within each window. We then subtracted this from the overall estimated variance, to get an estimate for the variance among windows. We did this for bear densities and all habitat variables.

Note that this procedure does not transform the means, but the variance–covariance matrix. We then used the transformed variance–covariance matrix in subsequent analyses.

### Appendix B. Hair capture station habitats

One potential problem in our analysis at smaller spatial scales was that the bear sites were placed nonrandomly within each 8 × 8 cm cell. They were placed where the technicians thought bears were most likely to be found (this was done because the primary focus in the study was estimating bear density (Mowat

and Strobeck, 2000), while measuring habitat use was secondary). Thus it is important to know how this affects our analysis.

For each spatial scale sampled, we measured overall habitat differences between bear sampling sites and the study area, as follows:

$$\frac{1}{n} \sqrt{\sum \left( \frac{b_i - s_i}{s_i} \right)^2}, \quad (4)$$

where  $n$  is the number of habitat variables (here,  $n = 9$ );  $b_i$ , mean of the  $i$ th habitat variable at bear sampling sites;  $s_i$ , mean of the  $i$ th habitat variable over the whole study area.

This is the mean Euclidean distance between the habitats of the bear sampling sites and the whole study site, but standardised in order to combine habitats with very different scales. The measure ranges from 0 to 1.

Habitats of bear sampling sites differed most from the whole study site at a spatial scale of 1 km, with the effect decreasing at larger scales. The bear sites primarily differed in that the slope was shallower, there was more water, more of the area was logged, and there were more avalanche chutes. Habitats in windows of size 4 km, or larger, around each bear site were effectively the same as those found throughout the study site. Thus this biased placement should have little effect at scales 4 km or larger.

The biased placement at scales below 4 km strengthened some of our results. The biased analysis effectively uses a subset of more preferred habitats, and within those, compares those habitats that bears used vs did not use. This would make it more difficult to detect habitat selection – making our results more conservative. We kept the smaller spatial scales in our analysis because while the bias made the reasons for nonsignificant habitat selection at small spatial scales less certain, it made the significant patchiness in bear density more certain.

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