On the Modifiable Areal Unit Problem and kernel home range analyses: the case of woodland caribou (*Rangifer tarandus caribou*)

by

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B.Sc., University of Guelph, 2003

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Supervisory Committee

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Abstract

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There are a myriad of studies of animal habitat use that employ the notion of “home range”. Aggregated information on animal locations provide insight into a geographically discrete units that represents the use of space by an animal. Among various methods to delineate home range is the commonly used Kernel Density Estimation (KDE). The KDE method delineates home ranges based on an animal’s Utilization Distribution (UD). Specifically, a UD estimates a three-dimensional surface representing the probability or intensity of habitat use by an animal based on known locations. The choice of bandwidth (i.e., kernel radius) in KDE determines the level of smoothing and thus, ultimately circumscribes the size and shape of an animal’s home range. The bounds of interest in a home range can then be delineated using different volume contours of the UD (e.g., 95% or 50%). Habitat variables can then be assessed within the chosen UD contour(s) to ascertain selection for certain habitat characteristics.

Home range analyses that utilize the KDE method, and indeed all methods of home range delineation, are subject to the Modifiable Areal Unit Problem (MAUP) whereby the changes in the scale at which data (e.g., habitat variables) are analysed can alter the outcome of statistical analyses and resulting ecological inferences. There are two components to MAUP, the scale and zoning effects. The scale effect refers to changes to the data and, consequently the outcome of analyses as a result of aggregating data to coarser spatial units of analysis. The aggregation of data can result in a loss of

fine-scale detail as well as change the observed spatial patterns. The zone effect refers to how, when holding scale constant, the delineation of areal units in space can alter data values and ultimately the results of analyses. For example, habitat features captured within 1km^2 gridded sampling units may change if instead 1km^2 hexagon units are used.

This thesis holds there are three “modifiable” factors in home range analyses that render it subject to the MAUP. The first two relate specifically to the use of the KDE method namely, the choice of bandwidth and UD contour. The third is the grain (e.g., resolution) by which habitat variables are aggregated, which applies to KDE but also more broadly to other quantitative methods of home range delineation

In the following chapters we examine the changes in values of elevation and slope that result from changes to KDE bandwidth (Chapter 2) UD contour (Chapter 3) and DEM resolution (Chapter 4). In each chapter we also examine how the observed effects of altering each individual parameter of scale (e.g., bandwidth) changes when different scales of the other two parameters are considered (e.g., contour and resolution). We expected that the scale of each parameter examined would change the observed effect of other parameters. For example, that the homogenization of data at coarser resolutions would reduce the degree of difference in variable values between UD contours of each home range.

To explore the potential effects of MAUP on home range analyses we used as model population 13 northern woodland caribou (*Rangifer tarandus*). We created seasonal home ranges (winter, calving, summer, rut and fall) for each caribou using three different KDE bandwidths. Within each home range we delineated four contours based on differing levels of an animal’s UD. We then calculated values of elevation and slope

(mean, standard deviation and coefficient of variation) using a Digital Elevation Model (DEM) aggregated to four different resolutions within the contours of each seasonal home range.

We found that each parameter of scale significantly changed the values of elevation and slope within the home ranges of the model caribou population. The magnitude as well as direction of change in slope and elevation often varied depending the specific contour or season. There was a greater decrease in the variability of elevation within the fall and winter seasons at smaller KDE bandwidths. The topographic variables were significantly different between all contours of caribou home ranges and the difference between contours were in general, significantly higher in fall and winter (elevation) or calving and summer (slope). The mean and SD of slope decreased at coarser resolutions in all caribou home ranges, whereas there was no change in elevation. We also found interactive effects of all three parameters of scale, although these were not always as direct as initially anticipated. Each parameter examined (bandwidth, contour and resolution) may potentially alter the outcome of northern woodland caribou habitat analyses.

We conclude that home range analyses that utilize the KDE method may be subject to MAUP by virtue the ability to modify the spatial dimensions of the units of analysis. As such, in habitat analyses using the KDE careful consideration should be given to the choice of bandwidth, UD contour and habitat variable resolution.

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Dedication

I dedicate this thesis to my Baba, Mary Kilistoff. I love you very much. I am sorry my life path has kept me away for so long but now I'm coming home.

Co-Authorship Statement

This thesis is a combination of three scientific manuscripts of which I am lead author. The original idea of analysing the effect of kernel density bandwidth and resolution on the values of topographic variables in home range analyses was first proposed by both Dr. Dennis Jelinski and Dr. Trisalyn Nelson. This idea was later built upon by myself and Dr. Dennis Jelinski to focus specifically on home range analyses of northern woodland caribou and to include the analysis of utilization distribution contour. Access to the caribou data was provided by Mark Williams of the BC Ministry of Forests, Lands and Natural Resource Operations. I performed all data preparation, data analysis, interpretation of results and writing. Dr. Trisalyn Nelson provided guidance with respect to statistical analyses. Dr. Dennis Jelinski provided editorial comments and suggestions.

1 Introduction

In spatial ecology, scale has two main components: Grain and extent (Meentemeyer and Box 1987, Wiens 1989). Grain is the minimum resolution of the data; for example, the pixel size in remote sensing imagery, quadrant size in studies of plant ecology, or, from an animal perspective, the minimum mapping unit at which habitat variables are assessed (e.g., Thompson and McGarigal 2002). Extent, which is inversely related to grain, is the scope or domain of the data and is often defined as the size of the study area or the time period for which a landscape or population process occurs. That these scale-based data can be "modified" is the crux of the Modifiable Areal Unit Problem (Openshaw and Taylor 1979, Openshaw 1984, Fotheringham and Wong 1991). Specifically, MAUP refers to the impact that the choice of areal unit (in terms of size and shape) has on results of statistical analyses as a consequence of varying scale. There are two main components to MAUP. The first component, the scale issue, refers to the changes that occur in spatial data when it is aggregated to coarser spatial units (e.g., when remotely sensed data is resampled from a grid resolution of 30x30m to one of 50x50m). This process tends to average out the fine-scale detail in the data and in thematic landscape data can result in, for example, the loss of small or rare landscape classes (Turner et al. 1989, Gottschalk et al. 2011). The second component of MAUP, the zoning issue, refers to the number of different ways (holding grain constant) that spatial units can be delineated in space. For example, if rectangular sampling units are used (e.g., 100x500m), differences in variable values measured may occur when these units are oriented in a north-south direction versus an east-west direction due to the anisotropic nature of some landscape patterns (Dungan et al. 2002). The changes that occur in data as a result of both the scale and zoning aspects of MAUP can lead to spurious statistical results as well as inferences (Fotheringham and Wong 1991, Jelinski and Wu 1996, Dark and Bram 2007).

Whilst MAUP was well known to geographers (e.g., Openshaw and Taylor 1979, 1981), ecologists were largely unaware of the issue until publication of Jelinski and Wu's (1996) paper, as evidenced by the 214 Web of Science citations and 375 in Google Scholar. In other words, ecologists now recognize MAUP as an important issue needing attention when dealing with spatial data that are modified, typically by aggregation. This attention includes analysis of landscape pattern including use of landscape metrics (Wu 2004) and land-use/land-cover change (Buyantuyev et al. 2010), analyzing species-habitat relationships (Li et al. 2006, Schooley 2006, Lechner et al. 2012), modelling patterns of species distribution (Hui et al. 2009, Lassueur et al. 2006, Pandit et al. 2010), abundance (Hui et al. 2009) and diversity (Foody 2004).

Home range analyses, for which there are a myriad of studies on an extraordinarily wide range of animals, are subject to a range of issues related to MAUP but have been largely overlooked. The concept of an animal's home range (HR) was described by Burt (1943:351) as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young". Kernohan et al. (2001: 126) suggested a more explicit definition of home range as "the extent of area with a defined probability of occurrence of an animal during a specified time period". These time periods can be spatially decomposed and quantified by applying Utilization Distributions (UDs), which takes the form of a 2-D probability density function representing the probability of occurrence, or relative amount of time spent by an animal in a defined area within its home range (Van Winkle 1975, Seaman and Powell 1996, Millspaugh et al. 2006). Estimations of the UDs has garnered significant attention within the context of both parametric (e.g., Jenrich-Turner, Jenrich and Turner 1969; Dunn estimator, Dunn and Gipson 1977) and non-parametric methods (e.g., fourier series smoothing, Anderson 1982; harmonic mean, Dixon and Chapman 1980).

Worton, in two seminal works (1987, 1989), introduced Kernel Density Estimation (KDE) as a non-parametric and non-mechanistic technique for estimating HR's and UDs. In addition to providing less biased estimates of HR size than other methods (Worton 1995), the KDE is able to identify multiple centers of activity (Kernohan et al. 2001), and generates a direct estimate of an animal's UD (Worton 1987, Kernohan et al. 2001). Home ranges are created using the KDE by interpolation of point location data, say, as provided by radio-collar data (e.g. Rupp and Rupp 2010). A kernel is placed over every location and the density of locations within each kernel is determined (the radius of which is the bandwidth). A gridded (raster) surface, the Utilization Distribution (UD), is then produced by averaging the densities of all overlapping kernels at each location resulting in a surface representing the probability or intensity of use by an animal. Methods based on the UD such as KDE thus provide more information than simple delineation of an animal's home range (Anderson 1982).

In those home range analyses that use the KDE method, there are three potential ways that MAUP may significantly affect the results. These include, (1) the choice of bandwidth, or smoothing parameter, when creating the home range, (2) the contours delineated within the home range that identify specific areas of use based on variable

Utilization Distributions, and, (3), the grain at which habitat variables are analyzed (e.g., resolution or grid cell size of remotely sensed data).

While in the following chapters the specifics of these three issues will be described in more detail, the basic issues remain to be discussed in brief as follows. First, the choice of kernel bandwidth will determine the degree of smoothing applied to the data and, therefore, the size and shape of the area delineated as an animal's home range (Seaman and Powell 1996, Seaman et al. 1999, Gitzen and Millspaugh 2003, Fieberg 2007). Coarse-scale bandwidths (i.e. large) assign distant animal locations more influence and can potentially over-estimate home range size (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001), whereas fine-scale bandwidths cause nearby locations to have more influence on the UD resulting in smaller estimates and potentially under-estimating home range size (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001). Therefore, as a result of changes in the size and shape of a home range and hence the nature of habitat (e.g., type or composition) or resources (e.g., forage, water, refuge from predators) found within, there is an implication that selection of bandwidth has the potential to impact analyses of those variables and resulting inferences (Marzluff et al. 2004, Harris and Chen 2005).

Secondly, similar to bandwidth, the UD contour at which analyses are conducted will also determine the size (geographic extent) and shape of the area included in home range analyses. Contours of the UD identify areas with a specified probability or level of use by an animal. The outer bounds of a home range is typically delineated using the 95% contour (e.g., Belant and Follman 2002, Brown et al. 2003, Berger and Gese 2007, Rayl et al. 2014). Investigations into more concentrated areas generally use the 50%

contour to delineate what is termed the ‘core area’ of an animal’s home range (e.g., White et al 1996, Dickson and Beier 2002, Metsaranta and Mallory 2007, Webb et al. 2007). Selection of a specific UD contour will determine not only the size and shape of each area associated with a specific level of use, but, similar to bandwidth, could change the values or habitat or resource variables used in any analysis. For example, Hébert and Weladji (2013) found significant differences in the coniferous forest stand characteristics (e.g., tree height, ground cover and lichen biomass) associated with low (95%), medium (75%) and high (50%) use intensity levels (i.e., contours of the UD) within woodland caribou home ranges in Newfoundland.

Third, studies using UD-delineated home ranges to assess habitat or resource variables will often do so with the use of rasterized habitat or resource data (e.g., Rettie and Messier 2000, Wittmer et al. 2007, Wilson et al. 2012). The grain (e.g. the resolution) of this data might be determined by the source of the data (e.g., Landsat, 30m; Marzluff et al. 2004, Johnson and Gillingham, 2008) or may be aggregated to coarser resolutions to, for example, match the resolution of other variables used in an analysis (e.g., Kie et al. 2002, Roger et al. 2007, Bremset et al. 2009). The aggregation of data to coarser resolutions can impact the heterogeneity/variance present in each dataset and, in turn, possibly alter the outcome of any statistical analyses performed (Jelinski and Wu, 1996; Dark and Bram 2007).

The overall goal of this study is to assess the potential effect of MAUP on home range analyses with respect to choice of bandwidth and contour in KDE as well as the grain at which habitat variables are analysed. To illustrate the issues, we use home ranges created using high frequency GPS telemetry data collected for 13 woodland caribou (*Rangifer tarandus*) of the Level Kawdy herd found in northern British Columbia (Figure 1.1). Woodland caribou in BC are the focus of a number of studies which aim to further our understanding of their movement and habitat use in order to aid in the effective management and conservation of this species (e.g. Terry et al. 2000, Fortin et al. 2008, Leblond et al. 2011). While previous research has investigated the effect of scale on the outcome of woodland caribou habitat analyses (e.g. Apps et al. 2001, Johnson et al. 2002, Leblond et al. 2011), few have done so using the parameters of scale assessed in this study (i.e., bandwidth, contour and resolution). Seasonal habitat selection by caribou is, in part, driven by topography including elevation and slope (Poole et al. 2000, Culling and et al. 2005, Gustine et al. 2006, DeCesare et al. 2012) and, as such, it is these variables that we use to assess the effect of scale in woodland caribou home range analyses. Specifically, we address how choice of bandwidth, contour and resolution change the values of topographic variables commonly used in home range analyses of woodland caribou, namely elevation and slope. To investigate the impact of MAUP, we created seasonal home ranges for each caribou using three different bandwidths and delineated four different contours within each home range. Caribou home ranges were then coupled with elevation and slope data from a Digital Elevation Model (DEM) aggregated to four different resolutions. We hypothesised that changes in each variable examined (bandwidth, contour, resolution) would have individual as well as combined impact on values of elevation and slope (e.g., the value of topographic variables within a home range will vary depending on the bandwidth used in KDE, and the degree to which they vary will differ depending on the resolution of the data).

The use of smaller bandwidths in KDE will decrease the total amount of area encompassed by each home range and each contour within a home range. Therefore, depending on the original topography in each contour (i.e., at the largest/original bandwidth examined), as well as the topography of adjacent contours, we expected that changes in topographic variables as bandwidth decreased would vary depending on contour and that, similarly, differences in elevation and slope between contours would vary depending on bandwidth.

Areas that are more variable with steeper slopes, in general, should be characterized by a greater decrease in slope values as DEM resolution increases, relative to areas that are less topographically variable (Zhang and Montgomery 1994, Wolock and McCabe 2000). In other words, with respect to slope in particular, the topography of the area in which the effect of aggregation is analysed will likely affect the degree to which topographic values change at coarser resolutions. In home range analyses this area (in terms of size and shape) is dictated by the bandwidth used in KDE and the UD contour at which analyses are performed. We therefore hypothesized that changes in both the KDE bandwidth and UD contour would change the observed effect of aggregating DEM resolution on topographic values in caribou home ranges. Conversely, because increasing resolution should, hypothetically, homogenize values of elevation and slope (Thieken et al. 1999, Wolock and McCabe 2000, Thompson et al. 2001), different resolutions should also impact the effect of bandwidth, as well as contour. In other words, we expected that, as a result of the homogenization of elevation and slope at coarser resolutions, there would be less observed change in these topographic values between home ranges created using different KDE bandwidths or within each home range when compared between contours.

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2 The Modifiable Areal Unit Problem and caribou (*Rangifer tarandus*) home range delineation: effects of bandwidth choice in Kernel Density Estimation

2.1 Abstract

The notion of home range is fundamental to the study of animal habitat use. The Kernel Density Estimation (KDE) method is commonly used by researchers to delineate an animal's home range based on known locations. One of the most critical parameters in KDE is bandwidth choice. The choice of bandwidth in KDE determines the level of smoothing applied to an animal's location data and as a result determines both the size and shape of the resulting home range. In consequence, selection of bandwidth has the potential to impact an animal's home range and equally the habitat variable of interest within. Home range analyses that use the KDE method are thus subject to what is known as the Modifiable Areal Unit Problem (MAUP) by virtue of having a modifiable bandwidth. MAUP refers to how changes to the size and shape of spatial units of analysis can alter the outcome of statistical analyses. There are two components to MAUP: The scale and the zoning effect. The scale effect refers to the changes to data that occur as a result of aggregating data to coarser spatial units of analysis. The zoning effect refers to the multitude of ways (when holding scale constant) that areal units of analysis can be delineated in space. Home range analyses are also subject to MAUP as a result of the choice of contour (i.e. delineation within the home range representing higher levels of use) and grain (e.g., resolution) at which habitat variables are measured.

We examined the degree to which the values (mean, standard deviation and coefficient of variation) of topographic habitat variables (elevation and slope) change within the seasonal home ranges of northern woodland caribou (*Rangifer tarandus*) as a result of bandwidth choice in KDE. We also determined how the choice of contour within each home range and resolution of topographic variables alter the observed changes in elevation and slope that occur with changes in bandwidth. We created seasonal home ranges for each caribou and determined the change in topographic values ($\bar{x}$, SD and CV of elevation and slope) at three different bandwidths (h_{ref}, $0.8h_{ref}$ and $0.6h_{ref}$) within four contours (25, 50, 75 and 95%) of each home range at four DEM resolutions (25, 75, 125 and 175m). We found that values of elevation and slope changed for all contours of caribou seasonal home ranges as KDE bandwidth decreased. When finer KDE bandwidths were used the topographic values decreased within the contours of certain seasons while they increased in others. The degree to which topographic values changed varied within each season between different contours as well as between seasons within specific contours. The change observed in topographic values with different bandwidths could potentially affect analyses of caribou habitat use and or preference, and further investigations should be conducted to determine to what degree of impact such analyses may undergo.

2.2 Introduction

The concept of an animal's home range was described by Burt (1943:351) as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young". Since then ecologists make use of the notion of an animal's home range to assess, for example, spatial overlap between individuals (e.g., Horner and Powell 1990), habitat selection (e.g., Metsaranta and Mallory 2007) and to determine seasonal movement patterns (e.g., Walton et al. 2001). The Kernel Density Estimation (KDE) method of Worton (1987, 1989) is widely used in home range analyses to identify the outer geographic bounds as well as areas of differing levels of use within an animal's home range (Kernohan et al. 2001, Laver and Kelly 2008). Kernel-based home range estimates are based on a density estimate calculated from a set of recorded locations (e.g., GPS locations) that can be interpreted as an animal's utilization distribution (UD; e.g., Dickson and Beier 2002, Fischer and Gates 2005, Hébert and Welaji, 2013).

Home range analyses that make use of the KDE method are potentially subject to the Modifiable Areal Unit Problem (MAUP) (Gehlke and Biehl 1934, Openshaw 1984). MAUP arises when spatial data are modified such that the results differ when the same analysis is applied to the same data. There are two main components to MAUP in terms of aggregation schemes. The first component is the scale effect whereby spatial units of analysis are aggregated into larger areal units and data values (e.g., mean) change as a result of this aggregation. The second component is the zoning effect where the scale of analysis is held constant (i.e., the spatial dimensions of the units), but the shape of the aggregation units is modified (for example, where data aggregated into 1 km^2 grid cells are re-arranged into 1 km^2 hexagons). Changes in data (e.g., decrease in variance) resulting from the use of different scales or zoning configurations can lead to spurious statistical results and ecological inferences (Jelinski and Wu 1996, Dark and Bram 2007).

The creation of the UD surface using the KDE approach, and the subsequent home range delineation, is subject to MAUP by virtue of having a modifiable kernel bandwidth. This ultimately determines not only the geographical extent and shape of a home range, but also the UD values within that home range (Seaman and Powell 1996, Seaman et al. 1999, Gitzen and Millspaugh 2003, Fieberg 2007).

Bandwidth selection is one, if not the most critical, choice when using KDE to create home ranges (Worton 1995, Seaman and Powell 1996 Seaman et al. 1999, Kernohan et al. 2001, Hemson et al. 2005, Kie et al. 2010). Fine-scale bandwidths (i.e., small bandwidths) cause nearby animal locations to have a strong influence on the resulting KDE surface (Worton, 1989, Seaman and Powell 1996, Kernohan et al. 2001), whereas coarse-scale bandwidths (i.e., large bandwidths) assign a greater influence to distant animal locations. The net result of using coarse-scale bandwidths is a smoothing of "peaks" and "valleys" of the distribution, thus providing a more general representation of an animal's UD (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001). From a MAUP perspective, bandwidths that are too fine can lead to an underestimation of home range size, whilst coarse-scale bandwidths can overestimate home range area (Kernohan et al. 2001). Therefore, by modifying the extent, as well as shape, of an animal's home range, the choice of bandwidth in KDE can influence the delineation and subsequent analyses of habitat or resource variables associated with the home range (Marzluff et al. 2004, Harris and Chen 2005).

Within home range studies there are a number of bandwidth techniques. These techniques include the use of algorithms such as Least Squares Cross Validation (LSCV) (e.g., Red deer (*Cervus elaphus*), La Morgia et al. 2011; caribou (*Rangifer tarandus*), Fischer and Gates 2005, Schindler et al. 2006, Metsaranta and Mallory 2007, Schmelzer and Otto 2003), the reference method (h_{ref}) (e.g., Roe deer (*Capreolus capreolus*), Börger et al. 2006a) and scaled-h_{ref} (e.g., caribou, Wilson et al. 2012, Rayl et al. 2014), or, instead of an algorithm, a static bandwidth size (e.g., caribou, Hébert and Weladji 2013). Many studies base bandwidth selection on the recommendations of Worton (1995) or

Seaman et al. (1996, 1999) (e.g. Morrow et al. 2001, Belant and Follmann 2002, Bontandina et al 2002, Kobler et al. 2008). However, the performance of a particular bandwidth can change with for example, different sample sizes (Fieberg 2007, Fieberg and Börger, 2012) or spatial distribution patterns (Gitzen et al. 2006, Downs and Horner 2008). Furthermore, in a recent review by Laver and Kelly (2008), they found that 48% of the 84 studies employing KDE did not report the bandwidth method used.

Despite the numerous investigations into bandwidth selection (e.g. Jones et al. 1996, Seaman and Powell 1996, Seaman et al. 1999, Horne and Garton 2006), little is known about the potential impact of selected KDE parameters (e.g., bandwidth) on home range delineation, statistical results and subsequent inferences (Gitzen et al. 2006, Fieberg 2007). In other words, how might the Modifiable Areal Unit Problem (MAUP) impact the values and analysis of habitat or resource variables within home ranges delineated using KDE?

In addition to bandwidth, two other components of scale within home range analyses that utilize KDEs might also impact the observed values and spatial patterns of habitat variables, namely, 1) the choice of contour (delineated within each home range based on different levels of probability of the UD), and, 2) the grain (e.g. resolution) at which habitat variables are assessed. Contours delineated based on values of an animal's utilization distribution are used to identify and assess areas within a home range of differing probability or intensity of use (e.g., Barg et al. 2005, Webb et al. 2007, Ryder et al. 2007). The choice of contour, similar to bandwidth, will determine the geographic extent (in terms of size and shape) of area that is analysed within a home range. Thus contour choice will also determine the habitat features there within, potentially changing the outcome and inferences of home range analyses (e.g., Börger et al 2006a). The grain (e.g. resolution) at which habitat variables within a home range are assessed can also change variable values (e.g., the mean or variance) and potentially alter the outcome of statistical analyses. The aggregation of habitat data to larger spatial units has the potential to average out the fine scale detail of data and change the measured values and spatial patterns (Bowyer et al. 1996, Boyce 2006).

The overall objective of this study was to determine how bandwidth selection alters home range analyses when viewed through the lens of the MAUP, whereby changes in the size and shape of a home range as a result of the bandwidth used in KDE alters the measured habitat variables there within. In addition, we assessed how the change in habitat values that occurred with the use of different bandwidths varied depending on the choice of UD contour, as well as data resolution. To meet our objectives we used topographic variables, namely elevation and slope, within the home ranges of northern woodland caribou (*Rangifer tarandus*) in British Columbia, Canada. Northern caribou are located throughout north central and western BC, and undertake altitudinal migrations to subalpine and alpine habitats during calving and summer to avoid predation by wolves (Bergerud et al. 1984, Bergerud and Page 1987, Johnson et al. 2004). They use low elevation pine forests in winter to forage on lichens by cratering, especially on south facing slopes (Bergerud et al. 1984, Bergerud and Page 1987). The seasonal home range of northern caribou is therefore, in part, driven by elevation and slope (Poole et. al. 2000, Culling and Culling 2005, Gustine et al. 2006, DeCesare et al. 2012), and these two variables are frequently included in studies investigating caribou habitat use (e.g., Poole et al. 2000, Johnson et al. 2004, Culling and Culling 2005, Jones et al. 2007, Leblond et al. 2011). Furthermore, because the temporal scales of analyses may affect the observed habitat use patterns of caribou (Börger et al. 2006a, Basille et al. 2012, van Beest et al. 2013), our analyses includes a seasonal component.

To determine how the use of different bandwidths in KDE change the measured values of elevation and slope within caribou home ranges we used high frequency GPS telemetry data from 13 female caribou of the Level Kawdy herd in northern British Columbia (Figure 2.1). Using KDE we created seasonal home ranges for each caribou and assessed the change in values of elevation and slope (mean, standard deviation and coefficient of variation) that occurred as we decreased bandwidth size. All changes in topographic values were assessed within the context of four different UD contours at four different Digital Elevation Model (DEM) resolutions. The changes in values of topographic variables at each decrease in KDE bandwidth were then used to assess the following:

1. The magnitude and direction of change within each seasonal contour at each DEM resolution.
2. The difference between contours within a season in terms of the magnitude of change in values.
3. The difference between each season in terms of the magnitude of change in values.
4. For each seasonal contour, the difference, in terms of magnitude of change in values, between each of the four DEM resolutions.

We hypothesized that the use of different bandwidths in KDE would result in significant changes in the values of elevation and slope measured within northern caribou seasonal home ranges. Furthermore, we expected that the observed change in topographic values (magnitude and direction) would vary depending on the resolution of those variables, as well as the specific contour and season in which they were assessed. In other words, depending on the topography within a specific contour, as well as the topography of adjacent contours, we expected that the observed changes in values of elevation and slope as bandwidth decreased would vary between contours within caribou seasonal home ranges. In addition, we expected that the homogenization of topographic values at coarser DEM resolutions (Thieken et al. 1999, Wolock and McCabe 2000, Thompson et al. 2001) would decrease the observed differences in topographic values at each change in bandwidth.

2.3 Methods

2.3.1 Caribou data

We used GPS telemetry data obtained from 13 northern woodland caribou of the Level Kawdy herd, British Columbia (58° N, 131° W) (Figure 2.1) equipped with ATS G2110E radio-collars (Advanced Telemetry Systems, ATS, Isanti, MN). Collars for these 13 caribou were deployed in October 2011 (eight caribou) and March 2012 (five caribou). The transmission rate of collars was one per day with the exception of a period between March 3rd-9th (2012) where transmission rate was five-to-six per day for eight of the caribou as identified in Table 2.1.

Telemetry data for the 13 caribou was categorized into the following seasons: Winter, calving, summer, rut and fall. There are a variety of methods employed to separate caribou location data into seasons including some investigators who us pre-determined, (and somewhat arbitrary) dates for each season (e.g., Poole et al. 2000, James et al. 2004, Said et al. 2005, Wittmer et al. 2007). However, these dates may vary between herds, between years within a particular herd and even between individuals within a herd (Hatler 1986, Culling et al. 2005, Jones et al. 2007).

The dates of each season for individual caribou for this analysis were determined based on distinct shifts in values of net displacement, elevation and slope. Net displacement is a measure of the distance of a particular recorded caribou location from a point of origin and has been used by some authors to aid in identifying seasons for wolves (Lesmerises et al. 2012), moose (Dettki and Ericsson, 2008) and caribou (Courbin et al. 2009). For our purposes, the point of origin was the first recorded GPS location for each caribou. We plotted values of net displacement against time (Julian day) and overlaid the values of elevation and slope extracted at each caribou location from a 25m resolution digital elevation model (DEM). We used these plots of net displacement and dates identified by other authors (e.g., Poole et al 2000, Culling et al. 2005, Jones et al. 2007) as guidelines to identify seasons for each caribou based on distinct shifts in location coupled with distinct shifts in elevation and slope. Distinct shifts in location were identified as a sharp directional increase or decrease in values of net displacement. These shifts were both preceded and followed by relatively stable values of net displacement and accompanied by a change in the range of elevations and/or slopes occupied by a caribou.

Selected season dates varied for each caribou (Table 2.1). We were not able to identify a distinct calving season for two of the caribou (D030457 and D030465). Therefore only four seasons were subsequently analyzed for these two caribou. In addition, we identified two separate winter locations for caribou D030468. All other caribou migrated to a well-defined wintering area between Dec 4th and Jan 19th where they remained until the spring whereupon they travelled to calving areas. However, D030468 migrated to its winter area on Dec 20th, remained there until Jan 24th, and then traveled approximately 87 km to a secondary wintering grounds where it remained until spring. We therefore analyzed not one, but two, sets of winter locations for D030468 separately in all further analyses.

2.3.2 Kernel Density Estimation

2.3.2.1 Home range delineation

Utilization distributions and home ranges for each of the thirteen Level Kawdy caribou were produced using fixed kernel density estimation (Worton 1989) in the ArcGIS 9.3 (ESRI 2008) extension Home Range Tools (HRT, Rodgers et al. 2007). KDE is a non-parametric probability density function used to estimate an animal's home range or UD based on known locations of that animal. A kernel (probability density function) is placed over each observation (e.g., radio-telemetry location) and a density estimate for that location is then determined based on the average of the calculated densities that overlap at that point. The estimated probability density function, $\widehat{f_h}(x)$ of an unknown UD is calculated using:

$$\widehat{f_h}(x) = \frac{1}{nh^2} \sum_{i=1}^{n} K\left[\frac{x - X_i}{h}\right]$$

where *n* is the number of locations, *K* is the kernel function used (e.g., bivariate normal/Guassian, Epanechnikov), *h* is the smoothing parameter or bandwidth of the kernel, *x* is the *x, y* location at which the estimate is calculated and *X* represents the *x, y* coordinates of the *n* locations in the dataset (Silverman 1986, Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001).

To investigate the effect of bandwidth selection, we created three home ranges per caribou for each season using different proportions (1.0, 0.8, and 0.6) of the reference bandwidth (h_{ref}). The reference method selects a bandwidth based on sample size and the standard deviation of each observed *x,y* location (Worton 1989, Gitzen 2006):

$$h_{ref} = n^{-1/6}\sqrt{\frac{s_x^2 + s_y^2}{2}}$$

where s_x^2 and s_y^2 are estimates of the variances of the point locations in the *x* and *y* direction respectively (Worton, 1995). As a result, h_{ref} is appropriate for unimodal data (i.e., have one center of activity) that are normally distributed in bivariate space (Worton 1989, 1995). However, animal location data are typically not “normally” distributed (Blundell et al. 2001, Downs and Horner 2008, Kie et al. 2010) and often have multiple modes (centers of activity) (Seaman and Powell 1996, Seaman et al. 1999, Börger et al. 2008). In these cases h_{ref} tends to produce a bandwidth value that is too large and over-smoothens the data (Kie et al. 2010). To overcome this issue, using a proportion of the reference bandwidth (scaled-h_{ref}) is recommended (Rodgers et al. 2011) as it can produce less biased estimates of home range size (Worton 1995). The proportions of h_{ref} used in this study (1.0, 0.8 and 0.6) were deemed representative of the range of scaled- h_{ref} values used in the literature (e.g., Bertrand et al. 1996, Kie et al. 2002, Berger and Gese 2007, Jaques et al. 2009).

The number of locations used to create each seasonal home range ranged from 16 to 168 (Table 2.1). This number was occasionally lower (see Table 2.1) than that recommended by Seaman et al. (1999) (minimum 30, > 50 preferred) and Girard et al. (2002) (30-100 for seasonal home ranges). This is due to a collar transmission rate of one per day and the inherently short nature of some seasons (e.g., calving). Although not all caribou seasonal home ranges met the recommended minimum number of locations, they did meet the minimum of one location per day as recommended by Girard et al. (2002). In addition, despite the presence of spatial autocorrelation in the seasonal subsets of location data for our caribou, as indicated by values of the Swihart and Slade index (Swihart and Slade 1985a) > 0.6, and Schoener index (Schoener 1981) >2.4 or <1.6 (Swihart and Slade 1985b, Rogers and Kie 2011), all recorded locations were used as recommended by De Solla et al. (1999), Blundell et al. (2001) and Fieberg (2007). The Rut home range produced for D030470 was approximately 3.3km^2, which was deemed too small in relation to other home ranges and thus excluded from any further analysis.

2.3.2.2 Contour delineation

Each cell in a gridded (rasterized) surface produced by the KDE method contains a probability/density value that represents the estimation of an animal’s UD (Worton 1987, Kernohan et al. 2001). An animal’s home range is then determined by the area that includes a fixed percentage of the estimated UD volume (termed volume contours or isopleths (Kernohan et al. 2001). Typically, the outer bounds of an animal’s home range is delineated using a 95% volume contour of the UD and core use areas are frequently delineated using the 50% contour (Laver and Kelly 2008). To investigate the effect of contour selection on changes in values of slope and elevation with decreasing bandwidth, four contours were delineated within each home range: The 25, 50, 75 and 95% volume contours of the UD. The 50 and 95% contours were selected based on their common use in the home range literature (as discussed previously), and the 25 and 75% contours were selected as (roughly) logical mid-points between the other two contours. All subsequent values and change in values of slope and elevation were calculated within the context of each of the four contours of a home range.

2.3.3 Topographic data

To assess how resolution affects the observed change in values of slope and elevation with decreasing bandwidth, we used a 25m Digital Elevation Model (DEM), then aggregated it to three additional resolutions (75, 125, and 175m). All subsequent analyses were performed at each of the four resolutions. We resampled the DEM using bilinear interpolation. This method assigns the new, coarser-resolution cell, a value based on the weighted average of the nearest four cells (Wu et al. 2005). This resampling method was selected over other methods such as nearest neighbour and cubic convolution firstly due to its common usage (e.g., Chaubey et al. 2005, Descleé et. al. 2006, Bader and Ruijten 2008, Kerns et al. 2009) and secondly because the actual method used has less impact than the act of resampling itself (Rees 2000, Wu et al. 2005, Wu et al. 2008). Slope (%) values were calculated at each resolution (i.e., they were not calculated at the original 25m DEM and then resampled to coarser resolutions) in the spatial analyst extension of ArcGIS 9.3 (ESRI 2008). We then calculated the summary statistics, namely mean ($\bar{x}$), standard deviation (SD), and coefficient of variation (CV) of slope and elevation, within each of the four contours of all home ranges.

2.3.4 Statistical analysis

2.3.4.1 Magnitude and direction of change

All statistical analyses were performed in SPSS (IBM 2013). We used pairwise multiple comparisons to determine whether the $\bar{x}$ of elevation or slope within each contour of a home range were significantly different at each successive decrease in bandwidth ($h_{ref} – 0.8h_{ref}$ and $0.8h_{ref} – 0.6h_{ref}$) and the overall change in bandwidth ($h_{ref} – 0.6h_{ref}$). Pairwise comparisons were conducted using the Games-Howell (Games and Howell 1976) or Tukey-Kramer (Tukey 1953, Kramer 1956) methods and were performed in the context of each contour/season for individual caribou at each of the four resolutions. The Games-Howell method is recommended in unbalanced designs (i.e., unequal sample sizes between groups) when variances are unequal (Keselman and Rogan 1978, Jaccard et al. 1984, Rafter et al. 2002, Ruxton and Beauchamp 2008). However, in unbalanced designs when variances are equal, the Games-Howell method can inflate the Family-Wise Error Rate (Rafter et al. 2002) and be less powerful than the Tukey-Kramer method (Jaccard et al. 1984, Rafter et al. 2002), which is the recommended alternative in these cases (Dunnett 1980a, Hayter, 1984, Rafter et al. 2002).

Values of elevation and slope within each contour were not normally distributed (Kolmogorov-Smirnov test $p<0.05$). However, transformations were not applied to the data for two reasons. First, both pairwise comparison methods (Games-Howell and Tukey-Kramer) use the studentized range distribution and are robust to non-normal data (Petrinovich and Hardyck 1969, Ramseyer and Tcheng 1973, Jaccard et al. 1984). Second, if the mean-variance relationship is not maintained after a transformation is applied, this can inflate type I error rate (McArdle and Anderson 2004). Variance homogeneity was assessed using the Brown-Forsythe (1974) modification of Levene's test (Lev_{med}), which uses the median instead of the mean of the data and is more robust when data are non-normal (Conover et al. 1981, Day and Quinn 1989). When results of Lev_{med} indicated variances were homogeneous, the Tukey-Kramer pairwise comparison method was used, otherwise the Games-Howell procedure was used.

The results of the above pairwise comparisons that were significantly different ($p<0.05$) in $\bar{x}$ elevation or slope between bandwidths were then used to calculate the mean change in $\bar{x}$ ($\bar{x}_{\Delta\bar{x}}$), SD ($\bar{x}_{\Delta SD}$), and CV ($\bar{x}_{\Delta CV}$) for each season/contour/resolution. In other words, for each season/counter, we determined the $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ of elevation and slope at the three decreases in bandwidth at each of the four resolutions. The $\bar{x}$ change in values of elevation and slope for each scenario were then used (as detailed in the following section) to assess differences between seasons, as well as the interactive effect of contour or resolution on changes in topographic values with decreasing bandwidth.

To assess whether values of elevation and slope were consistently higher or lower within a particular contour/season at each decrease in bandwidth (i.e., direction of change) we used the Exact Binomial Test of Proportions. This test is recommended for use specifically in the analysis of 2x1 contingency tables with small (<100) sample sizes (Richardson 1994). Also, because sample sizes were small (in our case ≤14) we used the exact form of this test, whereby p values are not estimated asymptotically but are instead calculated based on the exact distribution of the test statistic (Mehta and Patel 2011). All other analyses (next section) were performed on the absolute and/or directional values of $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$. However, directional $\bar{x}_{\Delta}$ values for a particular contour/season were only assessed in further analyses if the binomial test of proportions indicated a significantly higher proportion of change in one direction ($p<0.05$).

2.3.4.2 Pairwise comparisons of descriptive metrics

The $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ (hereafter referred to as the 'descriptive metrics' when discussing all three) of each contour/season/resolution at each successive ($h_{ref} - 0.8h_{ref}$ and $0.8h_{ref} - 0.6h_{ref}$) and overall change in bandwidth ($h_{ref} - 0.6h_{ref}$) were used to further explore the effects of the following parameters

1. *Contour choice*: We compared the descriptive metrics of elevation and slope between the contours within each season.
2. *DEM resolution*: We compared the descriptive metrics of slope and elevation within each contour/season between each of the four resolutions (25, 75, 125 and 175m).
3. *Season*: We compared the descriptive metrics of slope and elevation within each contour/resolution between each of the five seasons (winter, calving, summer, rut and fall).

All above comparisons of $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ were performed using either the Tukey-Kramer, Games-Howell or T3 procedures for pairwise multiple comparisons. Normality of the descriptive metrics were tested using the Shapiro-Wilk test (Shapiro and Wilk 1965). Homogeneity of variances was tested using either the Levene's (Lev_{mean}; Levene 1960) or the Brown-Forsythe (1974) modification of Levene's test (Lev_{med}). The Lev_{med} method is appropriate for samples with non-normal distributions, however, especially for small sample sizes, it has reduced power (higher Type II error rates) if distributions are in fact normal (O'Brien 1978, Games et al. 1979). Where the distribution of both samples was normal (Shapiro-Wilk, $p<0.05$), the $\mathrm{Lev}_{\mathrm{mean}}$ method of testing variance homogeneity was used. If the results of the $\mathrm{Lev}_{\mathrm{mean}}$ or $\mathrm{Lev}_{\mathrm{med}}$ tests indicated variances were homogeneous, the Tukey-Kramer pairwise comparison method was used, otherwise the Games-Howell method was used. In cases where variance homogeneity could not be accurately assessed due to small sample sizes and/or differences in the distribution of each sample (i.e., one sample normally distributed and the other not), Dunnett's (1980b) modification (T3) of Tamhane's (1979) pairwise comparison procedure was used. Similar to the GH method, the T3 method can be used when variances are not homogeneous but is typically considered to be less powerful than the GH method (Rafter et al. 2002). Although it is less powerful than the GH method, the T3 method has not been found to have the same inflated Type I error rate that the GH method does (liberal) in cases where variances are in fact homogeneous (Jaccard et al. 1984, Rafter et al. 2002).

2.4 Results

As bandwidth decreased we found no significant differences in the descriptive metrics between each of the four resolutions (25, 75, 125, 75m). However, the total number of significant differences found for each seasonal contour decreased at coarser resolutions (Tables B.1 and B.2, Appendix B). In addition, the results of other comparisons (e.g., comparing the descriptive metrics between contours of a season) were not significant at all resolutions examined. To illustrate our findings we have reported the results at the finest resolution for which significant differences were found. Further detailed results including, for example, 95% confidence intervals of pairwise comparisons, as well as the resolutions at which significant results were found, are reported in Tables B.5 – B.8 (Appendix B).

2.4.1 Range and proportion of differences between bandwidths

Elevation

As bandwidth decreased $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ of elevation ranged up to 44.2m (±36.1m), 33.4m (±27.2m) and 0.0 3 (±0.02) respectively (Table 2.2). The maximum observed change in elevation was 129.6m (Mean), 88.0m (SD) and 0.08 (CV). As bandwidth decreased, the mean elevation also decreased within a significant proportion (p) of caribou home ranges in all contours of the winter (p = 0.83-1.0) and the 25% contour of the calving ranges (p = 0.89) (Figure 2.2). In contrast, mean elevation increased at finer bandwidths in the 95% contour of the summer (p = 0.83-0.92), fall (p = 0.83-0.9) and rut (p = 0.89-0.9) ranges ($p<0.05$). Both SD and CV of elevation were typically lower ($p<0.05$) at finer bandwidths in the fall (all contours, p = 0.0.83-1.0), winter (50, 75, 95%, p = 0.83-1.0), and rut (25, 95%, p = 0.83-1.0).

Slope

As bandwidth decreased, the $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ of slope (%) within a contour/season ranged up to 3.3% (±2.8%), 2.5%(±0.5%) and 0.12 (±0.17) respectively (Table 2.3). The maximum observed change in slope was 9.7% (Mean), 8.2% (SD) and 0.42 (CV). As bandwidth decreased there was a significantly higher proportion of caribou home ranges in the winter (75% and 95% contours, p = 0.84-0.92), calving (95% contour, p = 0.90-1.0), rut (25% and 95% contours, p = 0.83-1.0) and fall (50, 75 and 95% contours, p = 0.83-1.0) that showed a decrease in mean slope ($p<0.05$) (Figure 2.3). A similar pattern emerged with respect to changes in the SD of slope (p = 0.83-0.92,

$p<0.05$) with the exception of the 95% and 25% contours of the calving and rut home ranges respectively. At finer bandwidths the CV of slope was also lower in a significant proportion of the caribou home ranges ($p<0.05$) of the winter (25% and 75% contours, p = 0.83-1.0), calving (95%, p = 0.89-1.0), summer (75%, p = 0.89), rut (25%, p = 1.0) and fall (25%, p = 0.8) seasons.

Elevation and slope

The contours of each season in which a significant proportion of caribou showed the same directional change in topographic values did not do so consistently at each decrease in bandwidth or at each resolution examined. Of those directional changes that were consistent at all three bandwidths, most occurred in the fall and winter (79%) and in the outer two contours of home ranges (70%). A similar pattern emerged with respect to resolution whereby directional changes that were significant at all four resolutions were typically in the fall and winter ranges and in the outer two contours of home ranges for both elevation (71% and 87%) and slope (75% and 77%).

2.4.2 Difference between contours

Within each season the descriptive metrics of slope and elevation were significantly higher within certain contours ($p<0.05$) (Figures 2.4 and 2.5). These differences between contours varied by season, the specific change in bandwidth, as well as DEM resolution.

Elevation

As bandwidth decreased, differences in $\bar{x}_{\Delta SD}$ of elevation between contours were found in all seasons ($p<0.05$) (Figure 2.4). Whereas, significant differences in $\bar{x}_{\Delta \bar{x}}$ between contours were found only in the fall and rut season, and differences were found in $\bar{x}_{\Delta CV}$ in the winter, fall and rut ranges (p<0.05). The amount of change in $\bar{x}$, SD and CV of elevation was frequently higher within the outer contours of a season (75% of all differences), and it was generally higher within the 95% contour relative to one or more inner contour (70% of all sig differences). Winter was the only season where differences in $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ were consistently higher within the 95% contour relative to one or more other contours at all three changes in bandwidth. In other seasons, differences in the change in elevation values were typically only found to be significant at one decrease in bandwidth (Table B.5, Appendix B).

Slope

As bandwidth decreased, significant differences (p<0.05) between contours in $\bar{x}_{\Delta\bar{x}}$ of slope were found in the fall, in $\bar{x}_{\Delta SD}$ in the calving, summer and fall ranges, and in $\bar{x}_{\Delta CV}$ in winter and summer ranges (Figure 2.5). The $\bar{x}_{\Delta\bar{x}}$ and $\bar{x}_{\Delta SD}$ in the fall ranges were higher in the outer counters relative to inner contours (p<0.05). Whereas, $\bar{x}_{\Delta SD}$ in the summer and calving ranges was higher within the 50% contour, and $\bar{x}_{\Delta CV}$ in the winter and summer ranges was higher in the 25% contour.) Only contours within the summer ranges differed in terms of changing slope values at the initial decrease in bandwidth (h_{ref} -0.8 h_{ref})., while all other differences between contours were found at the second (0.8 h_{ref} -0.6 h_{ref}) and overall change in bandwidth (h_{ref} -0.6 h_{ref}) (Table B.6, Appendix B).

2.4.3 Difference between seasons

As bandwidth decreased, the change in slope and elevation values within each contour varied between seasons (p<0.05) (Figures 2.6 and 2.7). Significant differences in the descriptive metrics of slope and elevation between seasons were not consistent in all resolutions or changes in bandwidth.

Elevation

As bandwidth decreased, the descriptive metrics of elevation were typically higher in the contours of the fall (50, 75 and 95%) and winter (95%) ranges (56% and 32% of all differences respectively) (Figure 2.6). Seasons differed more frequently with respect to $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ (40% and 44% of differences) and within the 95% contour (56% of all differences). Approximately half of the differences found between seasons (52%) were at the initial decrease in bandwidth (h_{ref} -0.8h_{ref}). With the exception of $\bar{x}_{\Delta\bar{x}}$ between the 50% contour of the summer and winter ranges, only those differences found between the 95% contour of seasons were significant at more than one resolution (Table B.7, Appendix B).

Slope

As bandwidth decreased, the descriptive metrics of slope were consistently lower within the contours of the winter home ranges relative to other seasons (63% of all differences) (Figure 2.7). Seasons with a higher amount of change in slope values varied depending on the specific value ($\bar{x}$, SD or CV), contour and change in bandwidth. Some 60% of differences between seasons were found at the initial decrease in bandwidth (h_{ref} - 0.8h_{ref}). Differences between seasons were not consistent at each resolution (Table B.8, Appendix B). Most were found to be significant at only one resolution, with the exception of comparisons between the fall and winter ranges.

2.5 Discussion

Ecologists often use Kernel Density Estimation (KDE; Worton 1989) to delineate animal home ranges in order to analyse wildlife habitat associations (Laver and Kelly 2008). Bandwidth selection within KDE is an important criterion because of its effects on home range size (Jones et al. 1996, Seaman and Powell 1996, Gitzen et al. 2006). Coarse scale (i.e., large) bandwidths can over-smooth location data by assigning distant locations more weight and thus potentially over-estimate home range size (Worton, 1989, Seaman and Powell 1996, Kernohan et al. 2001). Conversely, fine-scale (i.e., small) bandwidths assign nearby locations more weight and can lead to an under-estimation of home range size (Worton, 1989, Seaman and Powell 1996, Kernohan et al. 2001). Despite the potential for error in estimating in home range size, there is a dearth of research on how bandwidth choice changes the characteristics or values of habitat variables measured within a home range and inferences thereof (Börger et al. 2006b, Fieberg 2007).

We used the Modifiable Areal Unit Problem (MAUP; Gehlke and Biehl 1934, Openshaw 1984) as an analytical framework to assess the impact of changing bandwidth on analysis of topographic habitat variables within northern woodland caribou home ranges created using KDE. We also determined how the observed changes in topographic values at different bandwidths varied depending on the contour and DEM resolution at which they were assessed. Our results indicated that bandwidth affects values of slope and elevation within the seasonal home ranges of northern caribou, and also that the degree to which values change (in terms of magnitude and direction) can vary depending on the specific season and contour.

The implications of our results in home range analyses could vary depending on the hierarchical scale (*sensu* Johnson 1980) at which habitat selection is assessed. Home ranges can be used to identify habitats or resources that are either used within the greater landscape (2nd order selection; e.g., Rettie and Messier 2000, McLoughlin et al 2007) or available to an individual (3rd order selection; e.g., Dickson and Beier 2002, Mosnier et al 2003,). The impact on selection analyses will in part depend on the direction of change in topographic values (i.e., increase or decrease) that occurs with the use of different bandwidths. For example, within 2nd order selection analyses, a decrease in the variability of topographic values within the home range could result in an apparent increase in selection for certain elevations or slopes within the greater landscape (Mayor et al. 2007, Witt et al. 2012). Conversely, apparent selection within the home range (3rd order) could decrease as a result of this lower variability in values (Boyce et al. 2003, Ciarniello et al. 2007). In the Level Kawdy caribou home ranges it was typically the fall and winter ranges that showed a consistent pattern in terms of the direction of change in topographic values at smaller bandwidths. In winter ranges all values of elevation and the mean and SD of slope were generally lower (in one or more contour) at smaller bandwidths. A similar pattern emerged in the fall with the exception of mean elevation which increased in the 95% contour of most caribou home ranges at smaller bandwidths. This decrease in the variability of topographic values could have implications for both 2nd and 3rd order selection analyses in both of these seasons. For example, the winter ranges of northern caribou are typically found in areas of lower elevation with gentler slopes relative to other seasons (Wood 1996, Jones et al. 2007, Culling et al. 2005). The decrease in variability of slope and elevation within these home ranges could lead to an increase in apparent selection for specific topographic values at the landscape level (2nd order) while at the same time decrease apparent selection within the home range (3rd order).

The implications of our findings for habitat selection analyses will also depend on the magnitude of change in topographic values. As bandwidth decreased the amount of change in topographic values varied within a season between contours as well as within a particular contour between seasons. For example, changes in elevation were typically lower in the calving ranges (44% of all differences) and higher in the fall and winter ranges (56%and 32% of all differences respectively). Changes in slope values were also typically higher in the fall (38% of all differences). However, contrary to trends observed for elevation, changes in slope were frequently lower in winter (63% of all differences) and higher in the calving ranges (31% of all differences). The increased topographic values in certain seasons may be, in part, the result of larger changes in the extent of analysis (i.e. contour/home range size) at smaller bandwidths. The variability of a particular habitat feature is expected to increase when there is an increase in the spatial extent owing to increased heterogeneity with space (Wiens 1989, Dungan et al. 2002).

Home ranges in the fall were significantly larger than those in the other seasons and subsequently had a greater decrease in contour area (i.e. km^2) when smaller bandwidths were used in KDE (see Table B.3, Appendix B). This larger change in contour size in the fall home ranges may have contributed to the greater change in topographic values relative to other seasons. Similarly, in the fall, there was a higher amount of change in topographic values in the outer (75 and 95%) contours relative to inner (25 and 50%) contours. There was also a larger decrease in size (i.e., km^2) in the outer versus inner contours of the fall home ranges (see Table B.4, Appendix B). The greater topographic variability within home ranges of the fall at h_{ref} or, conversely, significantly lower variability at $0.6h_{ref,}$ especially within the outer contours, could affect

2nd or 3rd order analyses for this season. In terms of the impact on 3rd order selection, the use of larger bandwidths (e.g. h_{ref}) would increase the topographic variability within the fall season and at the same time potentially increase what is apparent selection for certain elevations and slopes within the home range. For example, Witt et al. (2012) found that the increased heterogeneity of the landscape at their largest scale of analysis increased apparent use of hemlock patches by white-tailed deer (*Odocoileus virginianus*).

Seasonal variations in caribou home range size have been found in other herds, as well as in other regions/ecotypes (e.g., Chicowski 1993, Stuart-Smith et al 1997, Brown et al. 2003, Ferguson and Elkie 2004, Metsaranta and Mallory 2007). Consistent with the findings of Stuart-Smith et al. (1997), Brown et al. (2003) as well as Metsaranta and Mallory (2007), the home ranges of the Level Kawdy herd were significantly larger in the fall and winter and smaller in calving and summer (Table A.1, Appendix A). However, Cichowski (1993) and Ferguson and Elkie (2004) found that woodland caribou summer ranges were larger than those in winter. Therefore, while a greater effect of changing bandwidth may be expected in seasons where caribou have larger home ranges, the specific seasons in which this occurs may not be consistent in different investigations (i.e., of different herds or regions).

The greater decrease in contour size (e.g., in the fall) may have led to some of the observed variation in descriptive metrics (e.g., $\bar{x}_{\Delta\bar{x}}$) between different seasons or contours. However, the topography of the area occupied by each seasonal home range also likely led to some of the variation in the effect of bandwidth. The effect that a change in the extent of analysis (e.g., KDE bandwidth/home range size) has on the values of a particular variable will depend, in part, on the heterogeneity of that variable within the landscape. The effect will also depend on the scale at which that heterogeneity/variability remains similar (i.e., domains of scale) or conversely changes (i.e., threshold; Wiens 1989, Wheatley 2010). Changes in extent that remain within a particular variable's scale domain will see little difference in variable values (e.g., Turner et al. 1989). Conversely, more change will be observed if the new analysis extent passes a scale domain threshold above or below which the patterns of the variable change significantly (Turner et al. 1989, Wiens 1989, Wu and Loucks 1995). This could in part explain the lower observed change in slope (all contours) and elevation (25, 50 and 75% contours) in winter relative to other seasons. Northern caribou winter ranges are characterized by areas of lower elevation and gentler slopes relative to other seasons (Wood 1996, Jones et al. 2007, Culling et al. 2005; Tables A.3, Appendix A). Due to the lower topographic variability within the winter ranges, the changes in contour (and home range) size that occurred with decreasing bandwidth likely did not pass a scale threshold of slope or elevation within the landscape. However, change in the variability (SD and CV) of elevation was higher in the 95% contour of winter compared to other seasons (e.g. calving, rut and summer) and all other contours within the winter ranges (depending on the specific change in bandwidth). Therefore, the lower amount of change observed at smaller bandwidths in the inner contours of winter is likely due to lower variability in topography. Whereas the 95% contour (at the outer bounds of caribou winter ranges) is likely found in an area where the scale domain of patterns in topography (specifically elevation) changes, thus a decrease in contour size resulted in a larger decrease in values of elevation as this scale threshold was passed (Turner et al. 1989, Wiens 1989, Wu and Loucks 1995). This decrease in elevation in the 95% contour for winter could indicate that the use of larger bandwidths (and potentially the delineation of home ranges using the 95% contour) includes areas within the winter home range that are significantly different from the area actually selected for by caribou. Thus habitat selection analyses of winter ranges may be more impacted by the use of larger bandwidths because of the inclusion of greater heterogeneity in elevation within the 95% contour.

2.5.1 Bandwidth Selection

We found that the values of slope and elevation in the home ranges of northern caribou changed with the use of different bandwidths in KDE, and that the amount of change observed varied with season and contour. Analyses of the effect of changing bandwidth on topographic variables were done using different proportions of the reference bandwidth (scaled- h_{ref}; Worton 1995). However, there are a number of other bandwidth methods available to researchers, such as Least Squares Cross Validation (LSCV: Silverman 1986), Biased Cross Validation (BCV: Scott and Terrell, 1987) and solve-the-equation plug-in methods (e.g., Sheather and Jones 1991). Each method differs in terms of its ability to estimate and characterize an animals' UD and home range, with some being more appropriate for certain distribution types (Silverman 1986, Worton 1989) spatial patterns (Gitzen et al. 2006, Downs and Horner 2008) or sample sizes (Seaman et al. 1999) of location data. The appropriate bandwidth method may also vary depending on the specific research objectives (Kernohan et al. 2001, Gitzen et al. 2006). Choice of one method over another can therefore result in the under- or over-estimation of home range size depending on the characteristics of the data. For example, LSCV, which is commonly recommended (Seaman and Powell 1996, Seaman et al. 1999, Powell 2000) and widely used (e.g. Fisher and Gates 2005, Webb et al. 2007, Kerston and

Marzluff 2010), has been criticised for its tendency to under-estimate home range size and create disjointed representations of an animal’s space use especially when location data are highly clustered (Blundell et al 2001; Gitzen et al 2006). The reference method, which is also commonly employed (e.g. Börger 2006a, Rayl et al. 2014) is appropriate when location data are normally distributed in space, otherwise it has a tendency to over-smooth the data and produce larger estimates of home range size (i.e., over-estimates) (Kie et al. 2010). In accordance, researchers wishing to use the reference method often use a proportion of h_{ref} (i.e., scaled-h_{ref}, Worton 1995). Therefore, if the characteristics of location data (e.g. spatial pattern, sample size) differ between seasons then the use of a specific bandwidth method may over-estimate home range size for one season and under-estimate for another.

Home range size, movement rates and distribution patterns of woodland caribou have been shown to vary seasonally (e.g. Cichowski 1993, Stuart-Smith et al. 1997, Ferguson and Elkie 2004). Differences in seasonal movement rates have been attributed to differences in the availability, abundance and patchiness of resources in the landscape, as well as trade-offs between foraging and vigilance for predators (Johnson et al, 2001, 2002, Mayor et al. 2009). Thus, relative seasonal movement rates can vary between herds or geographic locations possibly as a result of having to respond to different environmental, landscape or resource conditions and spatial patterns. Home range size, as previously discussed, also varies seasonally. The findings of this study are consistent with those of Stuart-Smith et al. (1997) as well as Metsaranta and Mallory (2007), whereby the fall and winter home ranges were larger than those in summer and calving, whereas Chichowski (1993) found that summer ranges were large than those in winter.

In addition, as was the case in this study, sample sizes used to create home ranges vary seasonally due to differences in the length of certain seasons. As a result of differences in home range size, movement patterns and sample size, the use of one bandwidth method within a study to delineate all seasonal home ranges may perform well (i.e. accurate delineation) for some seasons while it may over- or under-estimate home range size in others. As demonstrated here, changes in the size of caribou home ranges can significantly change the values of elevation and slope measured within each home range. Therefore, differences in the performance of a particular bandwidth between seasons could potentially, for example, increase topographic variability measured within the home ranges of one season, while at the same time decreasing it in the home range of another season. Researcher would therefore benefit from the use of more than one bandwidth in home range analyses as recommended by Worton (1995) as well as Bowman and Azzalini's (1997).

2.5.2 Effect of DEM resolution

The aggregation of data to coarser resolutions may result in a loss of fine scale detail and homogenization of data values (Turner et al. 1989, Parody and Milne 2005). The effect of aggregating thematic land cover data in wildlife-habitat studies has been extensively studied (e.g., Karl et al. 2000, Betts et al. 2006, Li et al. 2006, Guisan et al. 2007, Stickler and Southworth 2008, Carter et al. 2010, Gottschalk et al. 2011, Song et al. 2013). However, investigations into the effect of aggregation on topographic data in habitat analyses have been little explored despite the importance of topography to a number of species, as well as its frequent inclusion in analyses of habitat associations (e.g., black-tailed deer (*Odocoileus hemionus columbianus*), Bowyer et al. 1998; cougars

(*Puma concolor*) Dickson et al. 2005; and grizzly bears (*Ursus arctos*), Ciarniello et al. 2007). On the other hand, in studies of hydrology, the effect of changing DEM resolution on topographic values is much better understood. In general, these studies have found a decrease in slope values at coarser resolutions (Thompson et al. 2001, Wu et al. 2008) and a decrease in the correlation between elevation values at fine and coarser resolutions (Usery et al. 2004).

We expected that as a result of changes in topography (e.g. homogenization or decrease in slope) the change observed in topographic values at smaller bandwidths would be significantly different (i.e. less change) when measured at coarser resolutions. The DEM resolutions examined in this study (25, 75, 125 and 175) were selected as a representative sample of a range of resolutions used in other studies of home range (e.g., 30m: Boyce et al. 2003, McCorquodale 2003; 50m: Rupp and Rupp 2010, van Beest et al. 2010; 80m: Bowyer et al. 1998; 90m: Barbknecht et al. 2011; 100m: Gibeau 1998, Jiang et al., 2010, Acevedo et al. 2011; 150m: Rupp and Rupp 2010; 200m: Rohner and Demarchi, 2000). Contrary to expectations, no significant differences were found in $\bar{x}_{\Delta}$values between resolutions for any seasonal contour. However, the number of significant differences that occurred within each seasonal contour at smaller bandwidths (i.e., the number of caribou) decreased at coarser resolutions (Tables B.1 and B.2, Appendix B). Therefore, while the use of coarser resolutions did not significantly alter the mean change in topographic values (e.g., $\bar{x}_{\Delta\bar{x}}$) observed for a particular contour/season, it did change the values enough in the contours of some individual caribou that differences between bandwidths (e.g., $\bar{x}$ elevation) were no longer significant. In addition, other comparisons (e.g. between seasons) were not always significant at each DEM resolution examined. For example, while the change in SD of elevation was higher in the 95% contour of winter relative to calving at all resolutions, it was typically only significantly higher in contours of the fall at one of the resolutions examined (see Table B.7, Appendix B). This could potentially impact analyses that, for example, use coarser topographic data to compare caribou habitat selection between seasons (e.g. 90m: Ryder et al. 2007).

2.6 Conclusions

The results of this study indicate that the summary statistics for slope and elevation within the contours of northern caribou seasonal home ranges can change significantly depending on the bandwidth used. This observed change could have implications for other analyses of woodland caribou habitat selection. For example, potentially decreasing apparent selections within a home range if there is a decrease in the variability of topographic values at smaller bandwidths (Boyce et al. 2003, Ciarniello et al. 2007). Further analyses should be conducted to determine how and to what degree the observed change in topographic values will in fact alter the outcome of caribou habitat selection analyses. It would also be useful to extend these analyses to other species.

We concur with the recommendations of Worton (1995) and Bowman and Azzalini (1997) that studies using KDE to delineate home ranges should use multiple bandwidths to determine if, and to what degree, bandwidth choice impacts their findings. Kertson and Marzluff (2010), for example, used three different bandwidth methods (plug-in, LSCV, and h_{ref}) to assess resource use (distance to water, % clearcut and regenerating forest, and slope) within cougar home ranges. While the use of different bandwidths did not significantly affect the outcome of cougar resources use models, it did, however, change the relative importance of the variables within each model (Kertson and Marzluff 2010).

In this study the observed change in topographic values varied between seasons as well as between contours. Therefore, bandwidth choice may affect the outcome of habitat selection analyses to a greater or lesser degree in certain seasons (e.g. fall) or within a season if using, for example, Johnson's (1980) method of hierarchical habitat use (e.g., 2nd vs 3rd). The performance of a particular bandwidth (e.g. LSCV) may depend on caribou distribution patterns and movement rates which can change seasonally, and this seasonal variation may also vary between herds (e.g. Cichowski 1993, Stuart-Smith et al. 1997, Ferguson and Elkie 2004). In addition, the changes in values of elevation and slope within a home range may depend on the topography of the area in which the home range is located, which can also vary seasonally and between herds (e.g., Jones et al. 2007). As such, analyses into the impact of bandwidth on caribou habitat selection should be conducted on additional herds over multiple years. In addition, although topography is important to habitat selection of woodland caribou, other habitat characteristics are also important (e.g. land or vegetation cover such as pine-lichen woodland; Johnson et al. 2004) and the potential impact of bandwidth choice on these factors should be examined.

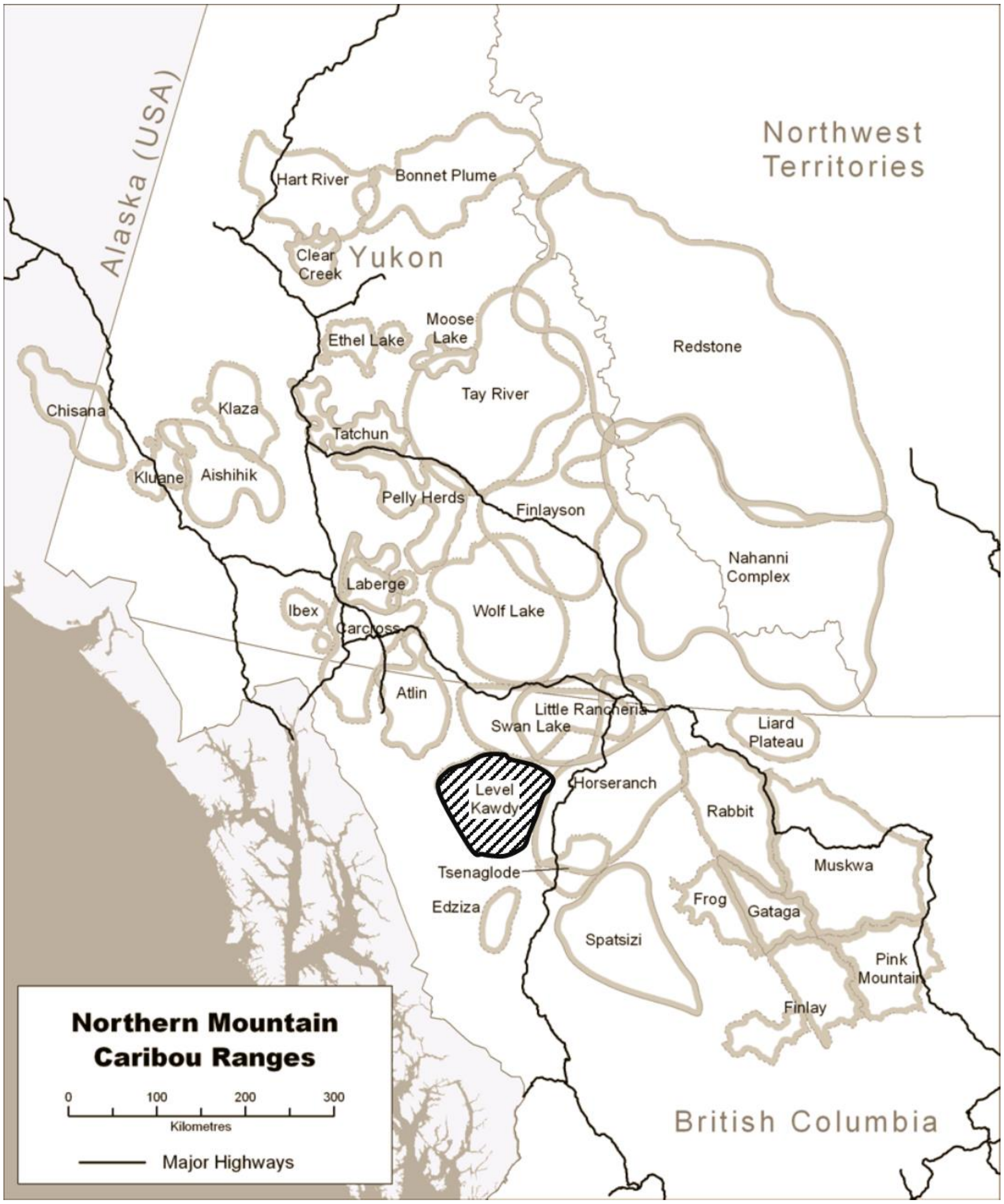

Figure 2.1 Ranges of Northern woodland caribou herds (*Rangifer tarandus caribou*) in western Canada. (reproduced from: Environment Canada, 2012)

Table 2.1 Selected season dates for each caribou and sample sizes used to create seasonal home ranges.

	Season														
	Winter			**Calving**			**Summer**			**Rut**			**Fall**		
Caribou	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**
D030452	Dec 27	May 4	119	May 23	Jun 15	23	Jul 5	Sep 11	69	Sep 12	Oct 24	41	Oct 25	Dec12	49
D030453	Dec 13	Apr 30	168	May 24	Jul 11	46	Jul 12	Sep 9	59	Sep 11	Oct 10	29	Oct 21	Dec25	66
D030457	Dec 23	Apr 10	142	n/a	n/a	n/a	May 22	Sep 6	104	Sep 14	Oct 20	37	Oct 21	Dec 12	53
D030460	Dec 27	Apr 16	90	May 24	July 1	39	Jul 2	Aug 22	52	Sep 12	Oct 22	41	Oct 23	Dec3	42
D030461	Jan 11	Apr 18	131	May 27	Jun 24	26	Jun 26	Sep 5	72	Sep 6	Oct 20	44	Oct 22	Dec7	47
D030462	Jan 17	Apr 24	130	May 22	Jul 6	46	Jul 17	Aug 26	39	Aug 27	Oct 19	53	Oct 21	Dec 5	44
D030464	Dec 20	Apr 28	164	May 27	Jul 11	46	Jul 22	Sep 11	52	Sep 12	Oct 22	38	Oct 23	Dec20	59
D030465	Jan 12	Apr 27	133	n/a	n/a	n/a	May 30	Sep 11	103	Sep 15	Oct 11	27	Oct 12	Dec7	57
D030466	Dec 28	May 10	130	May 30	Jun 25	27	Jun 26	Sep 13	77	Sep 14	Oct 16	33	Oct 17	Dec 10	53
D030468	Dec 21	Jan 24	36	May 13	Jun 16	35	Jun 18	Aug 25	69	Sep 7	Oct 17	39	Oct 18	Dec 13	55
	Feb 3	Apr 21	75												
D030470	Jan 19	Apr 28	101	May 24	Jun 8	16	Jun 10	Aug 11	61	Aug 12	Oct 25	70	Oct 26	Nov 27	33
D030471	Dec 23	Apr 16	148	May 22	Jul 9	35	Jul 13	Aug 29	31	Sep 7	Oct 22	32	Nov 10	Dec 6	26
D030490	Dec 4	May 5	148	May 21	Jun 17	28	Jul 3	Sep 10	67	Sep 15	Oct 20	36	Oct 21	Nov 24	35

Table 2.2 Range of descriptive metrics as well as maximum (absolute and directional) differences in the elevation (m) with successive (h_{ref} – 0.8h_{ref} and 0.8h_{ref} - 0.6h_{ref}) and overall (h_{ref} - 0.6h_{ref}) changes in bandwidth.

Elevation Variable	Direction of Change	Successive changes in bandwidth						Overall change in bandwidth					
		Range						Range					
		$\overline{x}_{\Delta low}$	(±SD)	-	$\overline{x}_{\Delta high}$	(±SD)	max	$\overline{x}_{\Delta low}$	(±SD)	-	$\overline{x}_{\Delta high}$	(±SD)	max
MEAN	**Absolute**	4.9	(4.5)	-	23.7	(25.2)	78.7	8.2	(8.5)	-	44.2	(36.1)	129.6
	Increase	2.8	(2.1)	-	30.8	(26.3)	78.7	2.1	(0.5)	-	55.7	(33.7)	129.6
	Decrease	5.6	(5.0)	-	28.5	(17.3)	59.7	7.6	(4.2)	-	42.4	(42.3)	95.8
SD	**Absolute**	3.6	(2.8)	-	20.0	(19.2)	65.3	8.3	(9.6)	-	33.4	(27.2)	88.0
	Increase	0.3	(0.3)	-	12.1	(12.7)	32.5	1.5	(1.0)	-	18.3	(21.1)	42.6
	Decrease	3.9	(2.7)	-	21.5	(19.4)	65.3	9.2	(5.4)	-	38.7	(26.8)	88.0
CV	**Absolute**	<0.01	(<0.01)	-	0.02	(0.02)	0.06	0.01	(<0.01)	-	0.03	(0.02)	0.08
	Increase	<0.01	(<0.01)	-	<0.01	(<0.01)	0.02	<0.01	(<0.01)	-	0.01	(0.01)	0.03
	Decrease	<0.01	(<0.01)	-	0.02	(0.02)	0.06	<0.01	(<0.01)	-	0.03	(0.02)	0.08

Table 2.3 Range of descriptive metrics as well as maximum (absolute and directional) differences in the slope (%) with successive (h_{ref} – $0.8h_{ref}$ and $0.8h_{ref}$ - $0.6h_{ref}$) and overall (h_{ref} - $0.6h_{ref}$) changes in bandwidth.

Slope Variable	Direction of Change	Successive change in bandwidth						Overall change in bandwidth					
		Range						Range					
		$\overline{x}_{\Delta low}$	(±SD)	-	$\overline{x}_{\Delta high}$	(±SD)	max	$\overline{x}_{\Delta low}$	(±SD)	-	$\overline{x}_{\Delta high}$	(±SD)	max
MEAN	**Absolute**	0.3	(0.2)	-	2.8	0.3	8.5	0.7	(0.7)	-	3.3	(2.8)	9.7
	Increase	0.1	(0.1)	-	4.0	(1.2)	5.9	0.2	((0.1)	-	6.0	(1.4)	7.8
	Decrease	0.4	(0.3)	-	2.5	(4.0)	8.5	0.7	(0.3)	-	2.5	(4.0)	9.7
SD	**Absolute**	<0.1	(<0.1)	-	2.5	(0.5)	8.2	0.6	(0.6)	-	2.3	(1.2)	8.1
	Increase	0.1	(0.1)	-	1.8	(0.8)	2.8	<0.1	(<0.1)	-	2.1	(1.2)	3.7
	Decrease	0.1	(0.1)	-	2.2	(1.4)	8.2	0.5	(0.5)	-	2.9	(2.0)	8.1
CV	**Absolute**	0.02	(0.01)	-	0.12	(0.11)	0.28	0.04	(0.04)	-	0.12	(0.17)	0.42
	Increase	<0.01	(<0.01)	-	0.12	(0.11)	0.28	<0.01	(<0.01)	-	0.14	(0.16)	0.29
	Decrease	0.01	(<0.01)	-	0.11	(0.06)	0.24	0.23	(0.02)	-	0.20	(0.20)	0.42

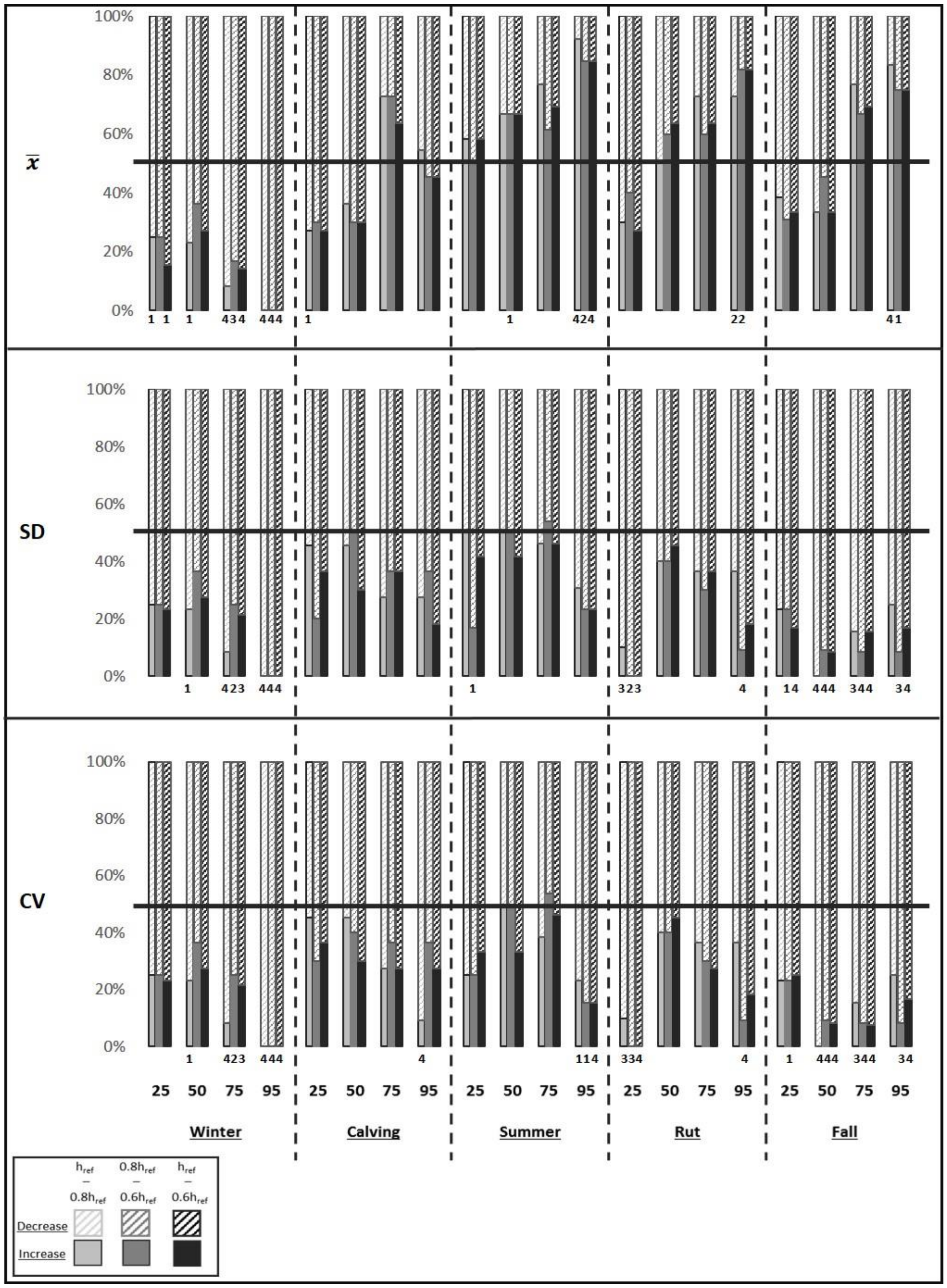

Figure 2.2 Proportion of increases vs. decreases in mean, SD and CV of elevation (m) with each change in bandwidth in the four contours (25, 50, 75 and 95%) of the five seasonal home ranges (winter, calving, summer, rut and fall).

$^{1, 2, 3, 4}$ indicates the number of resolutions at which significant differences were found using the exact binomial test of proportions (*p*<0.05).

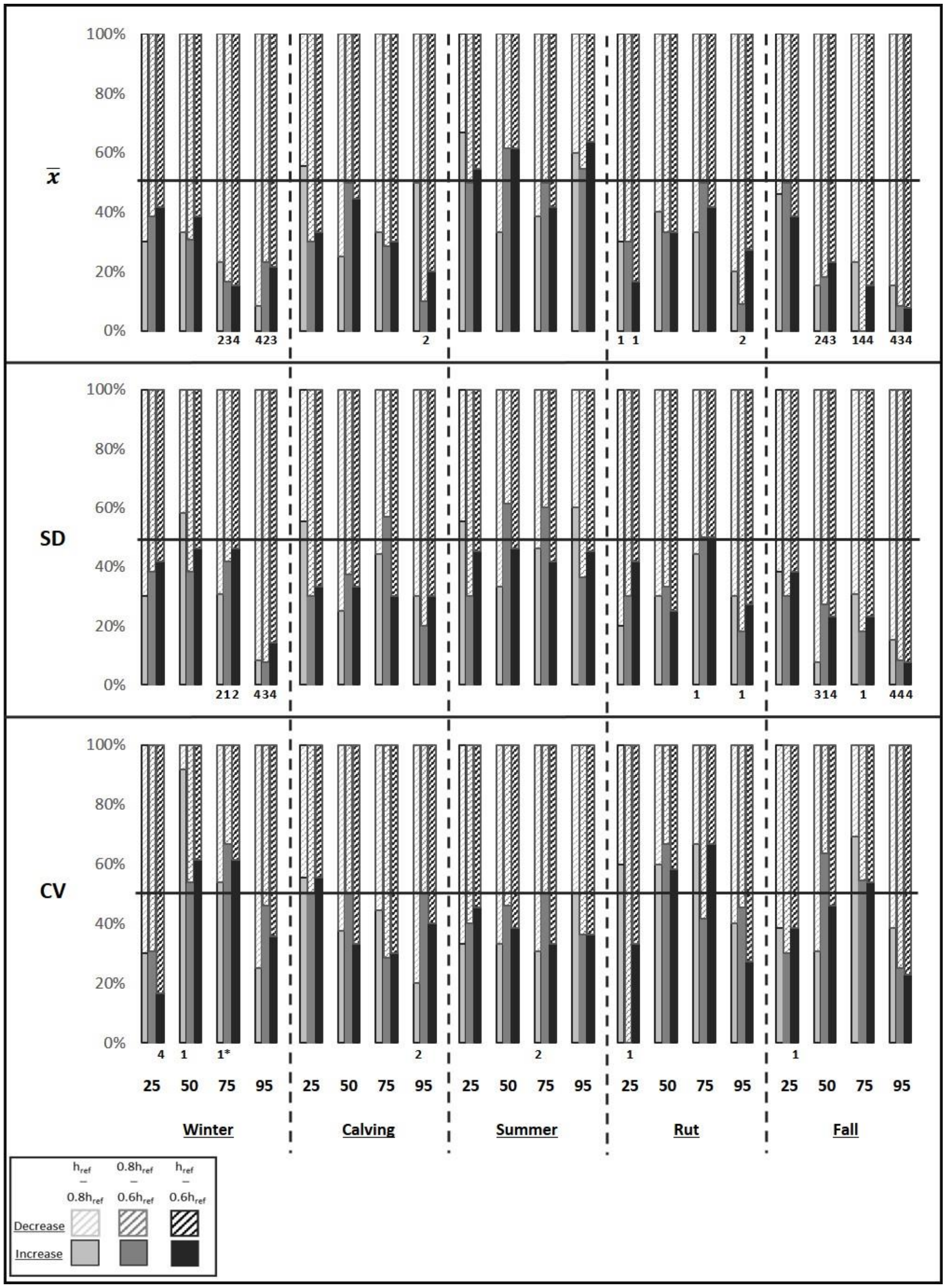

Figure 2.3 Proportion of increases vs. decreases in mean, SD and CV of slope (%) with each change in bandwidth in the four contours (25, 50, 75 and 95%) of the five seasonal home ranges (winter, calving, summer, rut and fall).

$^{1, 2, 3, 4}$ indicates the number of resolutions at which significant differences were found using the exact binomial test of proportions (p<0.05).

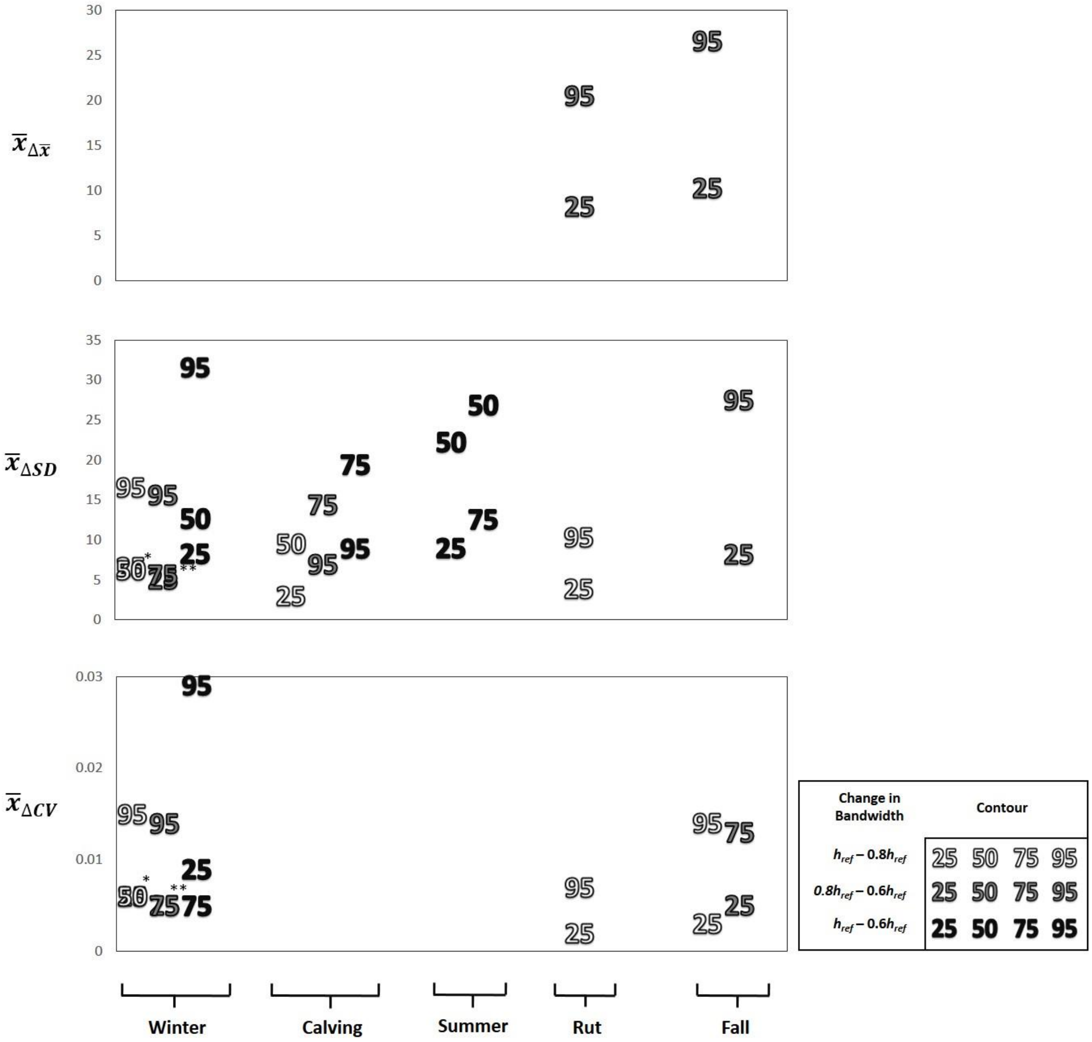

Figure 2.4 **Significant differences (p<0.05) in the descriptive metrics of elevation (m) between contours within each seasonal home range at each of the three changes in bandwidth (h_{ref} – 0.8h_{ref}, 0.8h_{ref} - 0.6h_{ref} and h_{ref} - 0.6h_{ref}).**

*** contours 25% and 50%**

**** contours 25% and 75%**

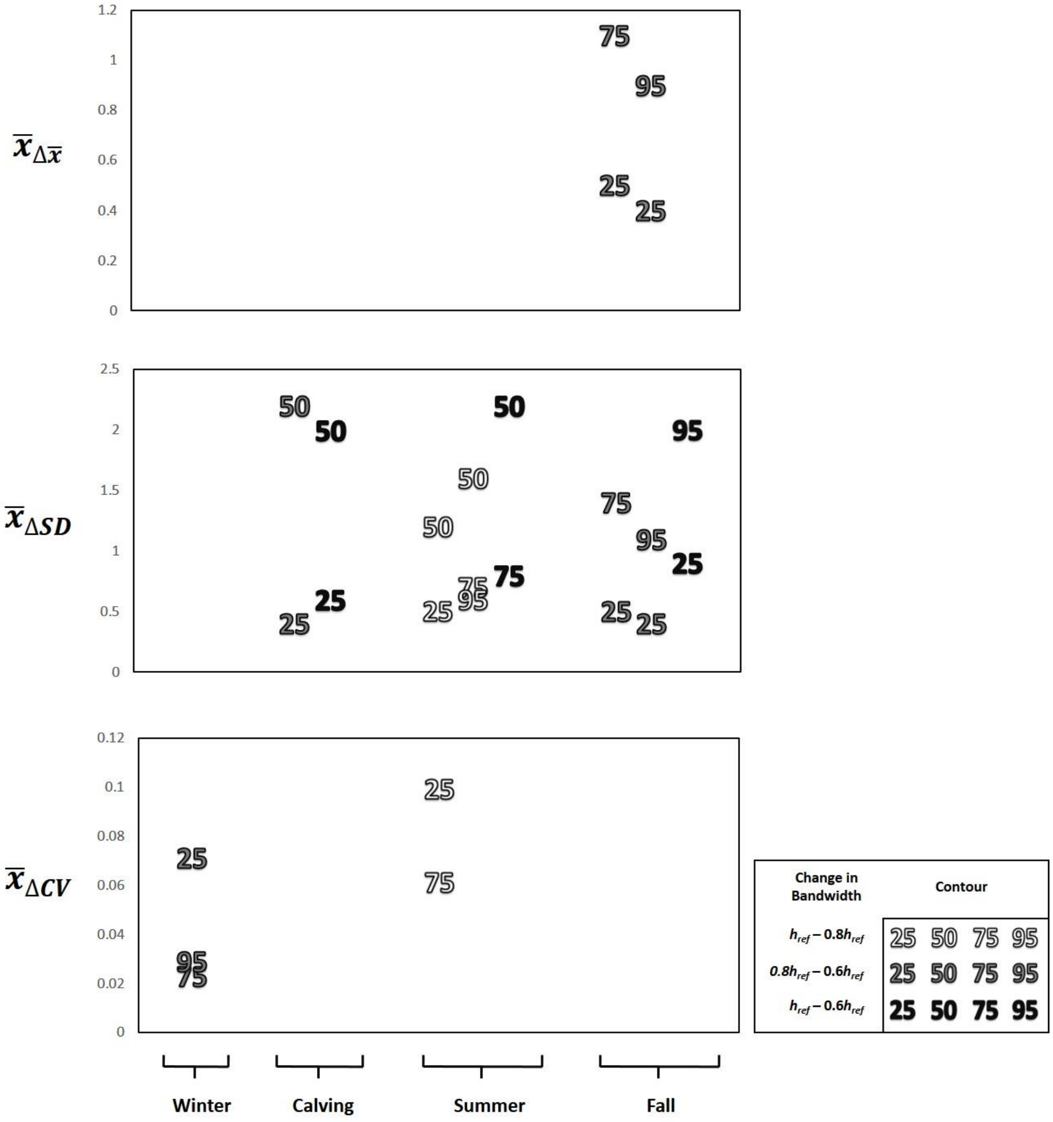

Figure 2.5 Significant differences ($p<0.05$) in the descriptive metrics of slope (%) between contours within each seasonal home range at each of the three changes in bandwidth (h_{ref} – 0.8h_{ref}, 0.8h_{ref} - 0.6h_{ref} and h_{ref} - 0.6h_{ref}).

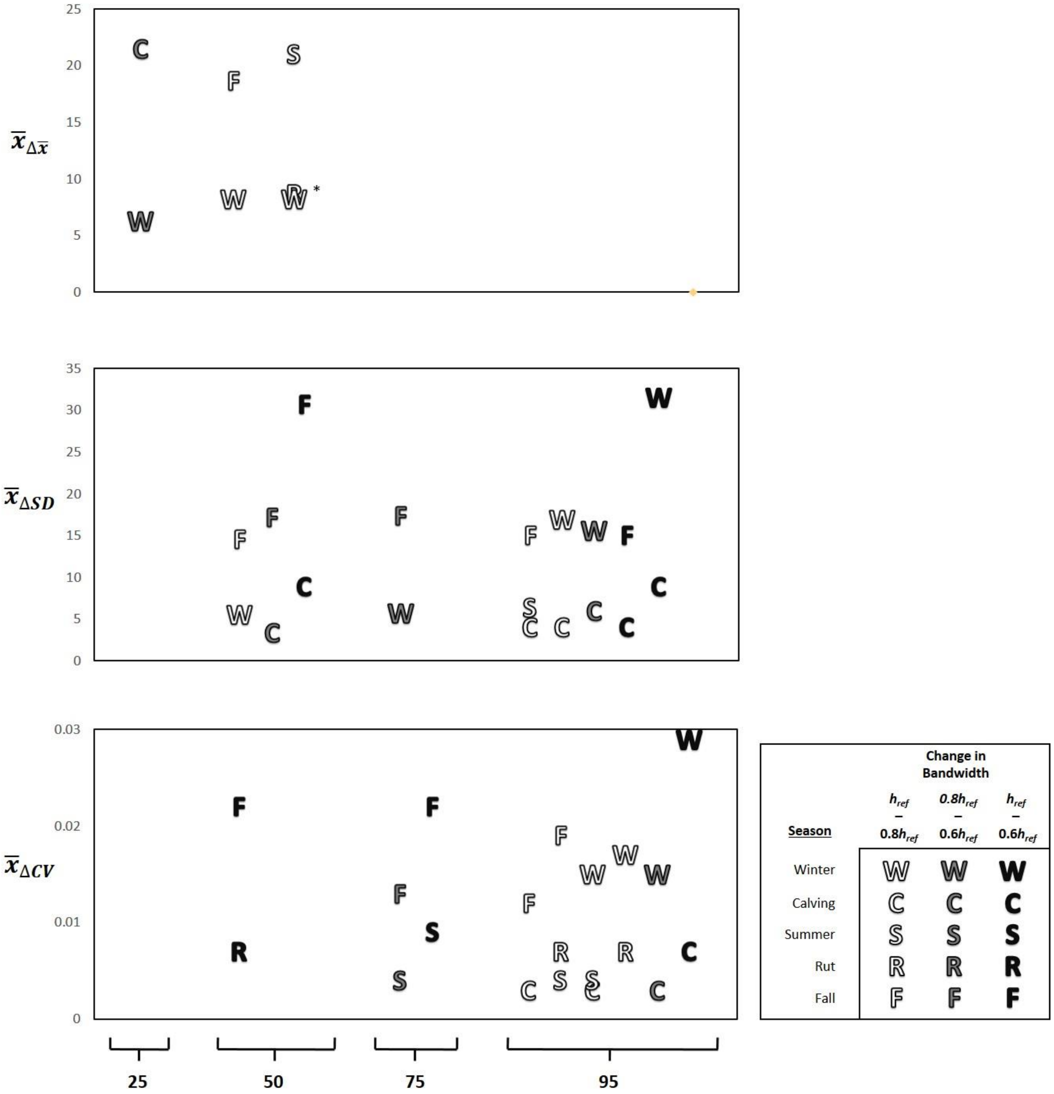

Figure 2.6 Significant differences ($p<0.05$) in the descriptive metrics of elevation (m) within contours of the same value between the five seasonal home ranges (winter, calving, summer, rut and fall) at each of the three changes in bandwidth (h_{ref} – 0.8h_{ref}, 0.8h_{ref} - 0.6h_{ref} and h_{ref} - 0.6h_{ref}).

*** Rut and winter**

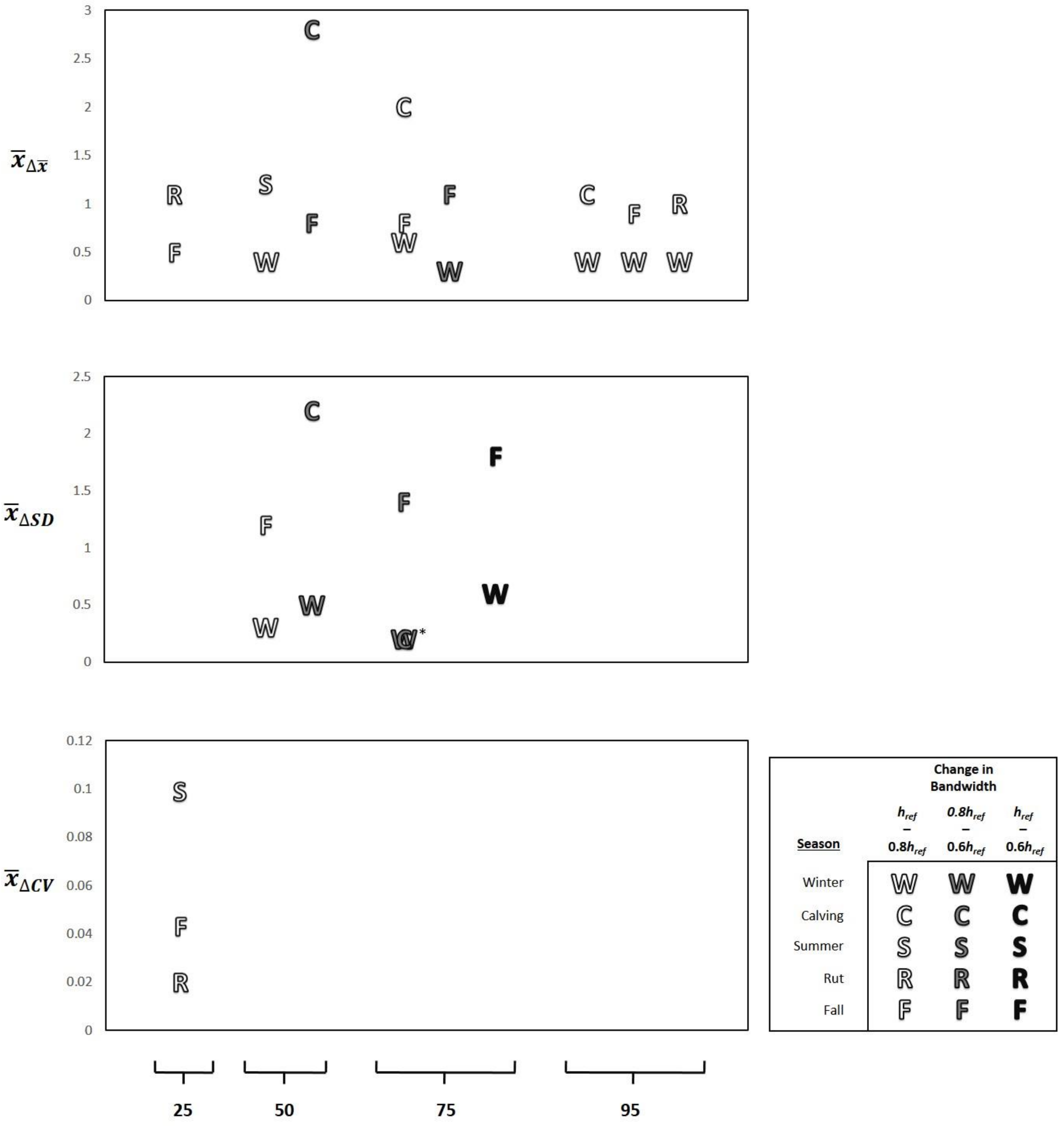

Figure 2.7 Significant differences ($p<0.05$) in the descriptive metrics of slope (%) within contours of the same value between the five seasonal home ranges (winter, calving, summer, rut and fall) at each of the three changes in bandwidth (h_{ref} – $0.8h_{ref}$, $0.8h_{ref}$ - $0.6h_{ref}$ and h_{ref} - $0.6h_{ref}$).

*** Calving and winter**

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3 The Modifiable Areal Unit Problem and caribou (*Rangifer tarandus*) home range delineation: effects of utilization distribution contour choice.

3.1 Abstract

The concept of an animal's home range in ecology is frequently used to provide insight into patterns of habitat use or selection. Kernel Density Estimation is a common method used to delineate home ranges base on an animal's utilization distribution (UD): A continuous surface that estimates the probability or intensity of use by an animal based on known locations. Volume contours of the UD are then used to delineate home range outer bounds (typically 95%) or areas within the home range with higher levels of use (typically 50%). An overlooked factor in selection of UD contours in home range analyses relates to the Modifiable Areal Unit Problem (MAUP). MAUP arises during the spatial analysis of aggregated data whereby the results of analyses change when different aggregation schemes are used. MAUP takes two forms: The scale effect and the zone effect. The scale effect refers to the changes in the data and, ultimately, the results, as a consequence of aggregating data to coarser spatial units of analysis. The zone effect refers to the number of ways spatial units of analysis can be delineated in space when holding scale constant. Home range analyses are also subject to MAUP as a result of the modifiable grain at which habitat variables can be assessed and, specifically, when the KDE method is used by virtue of having a modifiable bandwidth which will determine not only the size and shape of the animal's home range, but will also affect the values of the UD surface.

To investigate the potential implications of MAUP in home range analyses with respect to contour choice we used as a model population 13 northern woodland caribou from the Level Kawdy herd in British Columbia. Our purpose was to determine the degree to which topographic variables (elevation and slope) important in caribou seasonal habitat selection, varied between the contours of caribou home ranges. We also assessed how the choice of bandwidth in Kernel Density Estimation (KDE) and the resolution at which topographic values were measured changed the observed differences in elevation and slope values between contours. Using KDE, we created seasonal home ranges for each caribou with three different bandwidths (h_{ref}, 0.8h_{ref} and 0.6h_{ref}) and determined the difference in values (mean, standard deviation and coefficient of variation) of elevation and slope between four contours of the UD (25, 50, 75 and 95%) at four different resolutions (25, 75, 125 and 175m). Elevation and slope were significantly different between all contours of caribou seasonal home ranges. Certain seasons, such as winter and fall, showed an increasing trend in topographic values between the inner and outer contours. Differences in topographic values were higher between certain contours within a season (e.g. 25-95%) and between seasons (e.g., differences in slope were higher in summer relative to fall and winter). Changes in the values of elevation and slope as a result of contour choice could potentially alter the results of habitat use or selection analyses.

3.2 Introduction

An animal's home range is often defined as the "area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 194:351). A more quantitative definition is that an animal's home range is the smallest area associated with a 95% probability of finding a particular animal (White and Garrott 1990). This latter definition uses an animal's utilization distribution (UD) for its calculations, a continuous three-dimensional surface that estimates the intensity or probability of use by an animal based on known or recorded locations (e.g. using GPS telemetry data) (Van Winkle 1975, Worton 1989, Seaman and Powell 1996, Millspaugh et al. 2006). Regions of a home range with differing levels of use are delineated based on isopleths or volume contours of the UD representing different probabilities or rates of usage by individuals (Jenrich and Turner 1969, Fieberg and Kochanny, 2005, Millspaugh et al 2006). The areas within these volume contours are frequently used to investigate aspects of habitat selection (e.g., Belant and Follmann 2002, Metsaranta 2008), resource use (e.g., Terry et al. 2000, Marzluff et al. 2004, Millspaugh et al. 2006, Metsarenta and Mallon 2007) or home range overlap of individuals or populations (e.g., Fieberg and Kochanny 2005, Hoset et al. 2007, Thiebot et al. 2012).

The selection of a specific UD volume contour determines the spatial extent and, indirectly, the shape of the area characterizing an animal's home range. Importantly, the UD represents an areal unit composed of positional data that have been aggregated, thus rendering them susceptible to nonstationarity across a range of measures (e.g., mean and variance). This ability to modify the area analysed via choice of contour volume makes home range analyses based on UDs subject to the Modifiable Areal Unit Problem (MAUP; Gehlke and Biehl 1934, Openshaw 1984). When spatial data are aggregated, the results are conditional on both the scale at which data are collected, and the configuration of the areal units employed to represent given phenomena (e.g., Karl et al. 2000, Jackson et al. 2006). There are two main components to MAUP. The first component is the scale effect whereby the aggregation of data into larger spatial units can average out the fine scale detail and, as a result, change the observed values as well as spatial patterns (e.g., Turner et al. 1989). The second component of MAUP, the zoning effect, refers to the number of different ways in which spatial data can be delineated in space (when holding scale constant). For example, depending on the direction (i.e., orientation) in which a rectangular transect or sampling grid is placed on the landscape, it may capture or, conversely, fail to capture, the spatial patterns of a phenomenon due to the anisotropic nature of some landscapes (e.g., Leduc et al. 1994).

Accordingly, in home range analyses the potential for MAUP issues may arise because contour choice will determine the specific delineation of (i.e., zoning), as well as the geographical extent (i.e., aggregation) of, areas associated with differing levels of use. Landscapes are heterogeneous by definition (Forman and Godron 1981), but the level of heterogeneity increases with increasing extent (Wiens 1989, Dungan et al. 2002). It holds true, therefore, that within a given contour volume there will be areas that have more attributes that ultimately impact forage resources, fewer predators, high quality bedding sites, and more mating opportunities. In consequence, inferences concerning, say, habitat selection within the bounds of a home range, are scale-dependent, and in these cases will depend on the scale (volume) of the contours at which they are investigated (Börger et al 2006a, Hébert and Weladji 2013).

Home range bounds are typically delineated using the 95% contour of an animal's UD (e.g., Belant and Follman 2002, Brown et al. 2003, Berger and Gese 2007, Rayl et al. 2014), whereas areas of higher or more concentrated levels of use, typically called "core areas", are often delineated using the 50% contour of the UD (e.g., White et al 1996, Dickson and Beier 2002, Metsaranta and Mallory 2007, Webb et al. 2007). These delineations, while commonly used (Laver and Kelly 2008), have been criticized for their lack of biological significance (Vander Wal and Rodgers, 2012), as well as for their relatively arbitrary selection (Barg et al. 2005, Wilson et al. 2010). Although Laver and Kelly (2008) argued for the continued use of 95% and 50% for the sake of consistency and comparability, a number of authors have suggested alternative contour values. For example, Seaman et al. (1999) recommend using volume contours <80% whereas Börger et al. (2006b) found that the 90% contour produced unbiased estimates of home range size.

Home range analyses based on an animal's UD are increasingly more common given technological advances such as the production of relatively inexpensive radio-collars, the satellite-based receipt and transmission of signals to researchers in near real-time, and the enhanced computational abilities that couple GIS (e.g., ArcGIS; ESRI 2010) with analytical tools (e.g., Geospatial Modeling Environment, Beyer 2012; Home Range Tools, Rodgers et al. 2007). This widespread use of UD based studies demands a better understanding of the implications of changing volume contours for analyses.

We used the Kernel Density Estimation method (KDE, Worton 1989) to demonstrate the effects of MAUP, in terms of contour selection, on home range analyses. The KDE method is advantageous because it is non-parametric, has the ability to produce less biased estimates of HR size (Worton 1995) and is capable of identifying multiple centers of activity (Kernohan et al. 2001). The KDE method is one of the most commonly used methods in home range analyses (Laver and Kelly 2008). In addition, by using the KDE method we were able to explore how (one of) two other aspects of home range analyses that make it subject to MAUP interact with contour choice to affect the observed differences in values of elevation and slope, namely, 1) bandwidth choice in KDE and 2) the resolution of topographic variables.

The first additional aspect of home range analyses that we examined, (that is, bandwidth choice), is one of the most important parameters in KDE. The KDE method estimates an animal's UD by placing a kernel or probability density function over each location, which then calculates the density of observed locations within the kernel, the width of which (i.e., radius) is determined by the selection of an appropriate bandwidth (smoothing parameter). The use of fine-scale bandwidths (i.e., small bandwidths) may cause nearby locations to have a greater influence on the UD surface, potentially underestimating home range size (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001). Conversely, coarse scale bandwidths assign distant animal locations more influence and tend to over-smooth the data resulting in larger home ranges (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001). The bandwidth used in a KDE will, therefore, not only determine the size and shape of the area that depicts an animal's home range, but will also ultimately determine the level of smoothing applied to the data and influence the values of the UD (Seaman and Powell 1996, Seaman et al. 1999, Gitzen and Millspaugh 2003, Fieberg 2007).

The second additional aspect of home range analyses that we examined was the resolution (i.e., grain) at which habitat variables were aggregated. The aggregation of habitat data to coarser resolutions can alter the data in such a way that it leads to changes in the outcome of statistical analyses (Lawler et al. 2004, Lechner et al. 2012a). The effect that aggregation has on analytical results can be due to the loss of fine-scale detail

(Clark and Avery 1976, Turner et al. 1989) or changes in the observed distribution or spatial patterns in the data (Bowyer et al. 1996, Rahbek 2005).

The overall objective of this study was to determine the potential effect of MAUP on home range analyses in terms of the choice of UD volume contours. To demonstrate the complexities of the changing volume contours from a MAUP perspective, we used as a model system a population of northern woodland caribou (*Rangifer tarandus*) and specifically assessed how topographic values varied between different contours of a given caribou home range. Northern woodland caribou are one of three ecotypes of woodland caribou in British Columbia, the other two being mountain and boreal. Each ecotype is distinguished based on its geographic location, diet and seasonal movement patterns (Stevenson and Hatler 1985, Seip and Cichowski 1996). Northern caribou are located throughout north central and western BC, and utilize altitudinal migrations to subalpine and alpine habitats during calving and summer to avoid predation by wolves (Bergerud et al. 1984, Bergerud and Page 1987, Johnson et al. 2004a). They use low elevation pine forests in winter to forage on lichens by cratering, especially on south facing slopes (Bergerud et al. 1984, Bergerud and Page 1987). Thus seasonal home range selection is, in part, driven by slope and elevation (Poole et. al., 2000; Culling and Culling, 2005; Gustine et al., 2006; DeCesare et al., 2012). Furthermore, because the temporal scales of analyses may affect the habitat patterns of northern woodland caribou (Börger et al. 2006a, Basille et al. 2012, van Beest et al. 2013), our analyses included a seasonal component.

To determine how the values of topographic variables (specifically the $\bar{x}$, SD and CV of elevation and slope) measured within caribou home ranges varied depending on contour selection, we used high frequency GPS telemetry data from 13 female caribou of the Level Kawdy herd in northern British Columbia (Figure 3.1) to create seasonal home ranges for each caribou using KDE. Within each seasonal home range, we delineated contours based on four different levels of the UD and using a 25m Digital Elevation Model (DEM) calculated the mean, SD and CV of slope and elevation to determine:

1. How values of topographic variables varied between the four contours of each seasonal home range in terms of magnitude and direction.
2. How the choice of KDE bandwidth altered the observed differences in topographic values between contours.
3. How the DEM resolution at which values were calculated altered the observed differences in topographic values between contours.
4. How the differences in topographic values between contours varied depending on the specific season in which differences were assessed.

We hypothesized that values of elevation and slope would be different within each seasonal home range between all contours examined. However, we also expected that differences between certain contours or within certain seasons would likely be higher as a result of greater differences in size (i.e. area) between certain contour pairs or within seasonal home ranges with a greater amount of variability in terrain (in terms of topography). The former (influence of size) may contribute to greater differences in topographic values as a result of the increased probability of including a larger range of habitats simply as a result of increasing the geographic extent of analysis. We expected that the use of different bandwidths would change the observed differences in values of elevation and slope between contours. For example, that smaller bandwidths, by decreasing the total home range size, would decrease the differences observed between contours. Similarly, we expected that as a result of aggregation, topographic variables measured within each home range would be more homogeneous (Thieken et al. 1999, Wolock and McCabe 2000, Thompson et al. 2001), thus decreasing the observed differences in values between contours.

3.3 Methods

3.3.1 Caribou data

We used GPS telemetry data obtained from 13 northern woodland caribou of the Level Kawdy herd, British Columbia (58° N, 131° W) (Figure 2.1) equipped with ATS G2110E radio-collars (Advanced Telemetry Systems, ATS, Isanti, MN). Collars for these 13 caribou were deployed in October 2011 (eight caribou) and March 2012 (five caribou). The transmission rate of collars was one per day with the exception of a period between March 3rd-9th (2012) where transmission rate was five-six per day for eight of the caribou as identified in Table 3.1.

Telemetry data for the thirteen caribou was categorized into the following seasons: Winter, calving, summer, rut and fall. There are a variety of methods employed to separate caribou location data into seasons. For example, some investigators use pre-determined, somewhat arbitrary dates for each season (e.g., Poole et al. 2000, James et al. 2004, Said et al. 2005, Wittmer et al. 2007). However, these dates may vary between herds, between years within a particular herd and even between individuals within a herd (Hatler 1986, Culling et al. 2005, Jones et al. 2007).

We determined dates of each season for individual caribou based on distinct shifts in values of net displacement, elevation and slope. Net displacement is a measure of the distance of a particular recorded caribou location from a point of origin and has been used by some authors, for example, to aid in identifying seasons for wolves (Lesmerises et al. 2012), moose (Dettki and Ericsson, 2008) and caribou (Courbin et al. 2009). For our purposes, the point of origin used was the first recorded GPS location for each caribou. We plotted values of net displacement against time (Julian day) and overlaid the values of elevation and slope extracted at each caribou location from a 25m resolution Digital Elevation Model (DEM). We used these plots of net displacement and dates identified by other authors (e.g., Poole et al 2000, Culling et al. 2005, Jones et al. 2007) as guidelines to identify seasons for each caribou based on distinct shifts in location as coupled with distinct shifts in elevation and slope. Distinct shifts in location were identified as a sharp directional increase or decrease in values of net displacement. These distinct shifts were both preceded and followed by relatively stable values of net displacement and accompanied by a change in the range of elevations and/or slopes occupied by a caribou.

Selected season dates varied for each caribou (Table 3.1). We were not able to identify a distinct calving season for two of the caribou (D030457 and D030465), therefore only four seasons were subsequently analyzed for these two caribou. In addition, we identified two separate winter locations for caribou D030468. All other caribou migrated to a well-defined wintering area between Dec 4th and Jan 19th where they remained until the spring whereupon they travelled to calving areas. With that said, D030468 migrated to its winter area on Dec 20th, remained there until Jan 24th, then traveled approximately 87 km to a secondary wintering grounds where it remained until spring. We therefore analyzed these two sets of winter locations separately in all further analyses.

3.3.2 Kernel Density Estimation

3.3.2.1 Utilization distributions

Utilization distributions for each of the thirteen caribou were produced using fixed kernel density estimation (Worton 1989) in the ArcGIS 9.3 (ESRI 2008) extension Home Range Tools (HRT, Rodgers et al. 2007). A kernel (probability density function) is placed over each observation (e.g., radio-telemetry location) and a density estimate for that location is then determined based on the average of the calculated densities that overlap at that point. The estimated probability density function, $\widehat{f_h}(x)$ of an unknown UD is calculated using:

$$\widehat{f_h}(x) = \frac{1}{nh^2} \sum_{i=1}^{n} K \left[\frac{x - X_i}{h} \right]$$

where *n* is the number of locations, *K* is the kernel function used (e.g., bivariate normal/Guassian, Epanechnikov), *h* is the smoothing parameter or bandwidth of the kernel, *x* is the *x, y* location at which the estimate is calculated and *X* represents the *x, y* coordinates of the *n* locations in the dataset (Silverman, 1986; Worton, 1989; Seaman and Powell, 1996; Kernohan et al., 2001).

The number of locations used to estimate each UD ranged from 16 to 168 (Table 3.1). This number was occasionally lower (see Table 3.1) than recommended by Seaman et al. (1999) (minimum 30, > 50 preferred) and Girard et al. (2002) (30-100 for seasonal home ranges). This discrepancy was due to a collar transmission rate of one per day and the inherently short nature of some seasons (e.g., calving). Although not all caribou seasonal home ranges met the recommended minimum number of locations indicated above, they did meet the minimum of one location per day as recommended by Girard et al. (2002). In addition, the seasonal location data for each caribou was spatially autocorrelated as indicated by values of the Swihart and Slade index (Swihart and Slade 1985a) > 0.6, and Schoener index (Schoener 1981) >2.4 or <1.6 (Swihart and Slade, 1985b; Rogers and Kie, 2011). Some argue, though, that the benefit of obtaining a representative sample of animal locations outweighs the possible negative effects of autocorrelated data (De Solla et al., 1999; Blundell et al., 2001; Fieberg, 2007). Therefore, despite the spatial autocorrelation of caribou data, all recorded locations were used. The Rut home range produced for D030470 was approximately 3.3km^2, which was deemed too small relative to other home ranges and thus excluded from any further analysis.

3.3.2.2 Contour delineation

Conceptually, the KDE method produces a continuous probability surface. However, in practice, (i.e., in the computer algorithm), the KDE method produces a gridded raster surface where each cell contains a probability/density value which represents the estimation of an animal’s UD (Worton, 1987, Kernohan et al. 2001). To investigate the effect of contour selection on values of slope and elevation within northern woodland caribou home ranges we delineated the following four UD contours: 25, 50, 75 and 95%. The 50 and 95% contours were selected based on their common use in the home range literature (Laver and Kelly 2008), and the 25 and 75% contours were selected as approximate mid-points between the other two contours.

3.3.2.3 Bandwidth

To investigate the effect of bandwidth selection on differences in topographic variables between contours, we created the seasonal UDs for each caribou using three bandwidth sizes in KDE. Bandwidth size was varied by using three proportions (1.0, 0.8 and 0.6) of the reference bandwidth (h_{ref}). The reference method selects a bandwidth based on sample size and the standard deviation of each observed x,y location (Worton, 1989; Gitzen, 2006):

$$h_{ref} = n^{-1/6}\sqrt{\frac{s_x^2 + s_y^2}{2}}$$

where s_x^2 and s_y^2 are estimates of the variances of the point locations in the x and y direction respectively (Worton 1995). As a result, h_{ref} is appropriate if data are unimodal (i.e., have one center of activity) and are normally distributed in bivariate space (Worton 1989, 1995). However, animal location data are typically not normally distributed (Blundell et al. 2001, Downs and Horner 2008, Kie et al. 2010) and often have multiple modes (centers of activity) (Seaman and Powell 1996, Seaman et al. 1999, Börger et al. 2008). In these cases h_{ref} tends to produce a bandwidth value that is so large that it over-smoothes the data (Kie et al. 2010). Using a proportion of the reference bandwidth (scaled-h_{ref}) is sometimes recommended (Rodgers et al. 2011) as it can produce less biased estimates of home range size (Worton 1995). The proportions of h_{ref} used in this study were deemed representative of the range of scaled- h_{ref} values used in the literature (e.g., Bertrand et al. 1996, Kie et al, 2002, Berger and Gese 2007, Jaques et al. 2009). Differences in topographic values between contours were assessed at each of the three bandwidths used.

3.3.2.4 Topographic data

To assess how DEM resolution changed the observed differences in values of slope and elevation between contours, we used a 25m DEM that we aggregated to three additional resolutions (75, 125 and 175m). All subsequent analyses were performed at each of the four resolutions. The DEM was resampled using bilinear interpolation. This method assigns the new, coarser-resolution cell, a value based on the weighted average of the nearest four cells (Wu et al., 2005). This resampling method was selected over other methods such as nearest neighbour and cubic convolution as it is commonly used (e.g., Chaubey et al., 2005; Descleé et. al., 2006; Bader and Ruijten, 2008; Kerns et al., 2009) and because the method used (e.g., bilinear interpolation) has less impact than the act of resampling itself (Rees, 2000; Wu et al 2005; Wu et al., 2008). Slope (%) values were calculated at each resolution (i.e., they were not calculated at the original 25m DEM and then resampled to coarser resolutions) in the spatial analyst extension of ArcGIS 9.3 (ESRI 2008). We then calculated the summary statistics, namely mean ($\bar{x}$), standard deviation (SD), and coefficient of variation (CV) of slope and elevation within the mutually exclusive bounds of each of the four contours of a caribou's home range. For example, summary statistics for the 50% contour were calculated for the area between the 25% and 50% contour of a caribou's UD.

3.3.3 Data analysis

3.3.3.1 Difference between contours

All statistical analyses were performed in SPSS (IBM 2013). We used pairwise multiple comparisons to determine whether the $\bar{x}$ of elevation or slope was significantly different ($p<0.05$) between each of the following six contour pairs: 25-50, 25-75, 25-95, 50-75, 50-95, and 75-95. Pairwise comparisons were conducted using either the Games-Howell (Games and Howell 1976) or Tukey-Kramer (Tukey 1953, Kramer, 1956) methods and were performed in the context of each contour/season for individual caribou at each of the four resolutions. The Games-Howell method is recommended in unbalanced designs (i.e., unequal sample sizes between groups) when variances are unequal (Keselman and Rogan 1978, Jaccard et al. 1984, Rafter et al. 2002, Ruxton and Beauchamp 2008). However, in unbalanced designs when variances are equal, the Games-Howell method can inflate the Family-Wise Error Rate (Rafter et al. 2002) and be less powerful than the Tukey-Kramer method (Jaccard et al. 1984, Rafter et al. 2002), which is the recommended alternative in these cases (Dunnett 1980a, Hayter 1984, Rafter et al. 2002).

Values of elevation and slope within each contour were not normally distributed (Kolmogorov-Smirnov test $p<0.05$). However, transformations were not applied to the data for two reasons. Firstly, both pairwise comparison methods (Games-Howell and Tukey-Kramer) use the studentized range distribution and are robust to non-normal data (Petrinovich and Hardyck 1969, Ramseyer and Tcheng 1973, Jaccard et al. 1984). Secondly, if the mean-variance relationship is not maintained after a transformation is applied, this can inflate Type I error rate (McArdle and Anderson 2004). Variance homogeneity was assessed using the Brown-Forsythe (1974) modification of Levene's test ($\mathrm{Lev}_{\mathrm{med}}$), which uses the median instead of the mean of the data and is more robust when data are non-normal (Conover et al. 1981, Day and Quinn 1989). When results of $\mathrm{Lev}_{\mathrm{med}}$ indicated variances were homogeneous, the Tukey-Kramer pairwise comparison method was used, otherwise the Games-Howell procedure was used.

Of all of the results of the above pairwise comparisons, it was those that indicated a significant difference (*p*<0.05) in $\bar{x}$ elevation or slope between contour pairs that were then used to calculate the mean difference in $\bar{x}$ ($\bar{x}_{\Delta\bar{x}}$), SD ($\bar{x}_{\Delta SD}$), and CV ($\bar{x}_{\Delta CV}$) between contour pairs for each combination of season, bandwidth and resolution. The $\bar{x}$ difference in values of elevation and slope for each scenario were then used (as detailed in the following section) to assess the differences between seasons, as well as the interactive effect of bandwidth or resolution on differences in topographic values between contours.

To assess whether values of elevation and slope were, within a season, consistently higher or lower in one contour relative to another, we used the Exact Binomial Test of Proportions. This test is recommended for use specifically in the analysis of 2 x 1 contingency tables with small (<100) sample sizes (Richardson 1994). Also, because sample sizes were small ($n \leq 14$), we used the Exact form of this test, whereby p values are not estimated asymptotically, but are instead calculated based on the exact distribution of the test statistic (Mehta and Patel 2011). All further analyses (see below) were performed on the absolute and/or directional values of $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$. However, directional $\bar{x}_{\Delta}$ values for a particular contour-pair/season were only further assessed if the binomial test of proportions indicated a significantly higher proportion of differences in one direction (*p*<0.05).

3.3.3.2 Pairwise comparisons of descriptive metrics.

The $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ (hereafter referred to as the ‘descriptive metrics’ when discussing all three) of each contour pair for each combination of season, bandwidth and resolution were used to further explore the effects :

1. *KDE bandwidth:* We compared the descriptive metrics of elevation and slope for each season/resolution between each of the three bandwidths used (h_{ref}, 0.8h_{ref} and 0.6h_{ref})
2. *DEM resolution*: For each season/bandwidth we compared the descriptive metrics of slope and elevation between each of the four resolutions examined (25, 75, 125, 175m).
3. *Specific contour pair*: We compared the descriptive metrics of slope and elevation between contour pairs of each season/bandwidth/resolution.
4. *Season*: We compared the descriptive metrics of slope and elevation for each contour pair/bandwidth/resolution between the five seasons (winter, calving, summer, rut and fall).

Comparisons of $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ were performed using either the Tukey-Kramer, Games-Howell or T3 procedures for pairwise multiple comparisons. All three parameters ($\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$) were tested using the Shapiro-Wilk test for normality (Shapiro and Wilk 1965). Homogeneity of variances was tested using either the Levene's (Lev_{mean}; Levene 1960) or the Brown-Forsythe (1974) modification of Levene's test (Lev_{med}). The Lev_{med} method is appropriate for samples with non-normal distributions, although, and especially for small sample sizes, it has reduced power (higher Type II error rates) if distributions are in fact normal (O'Brien 1978, Games et al. 1979). In these instances where the distribution of both samples was in fact normal (Shapiro-Wilk, $p<0.05$), the Lev_{mean} method of testing variance homogeneity was used. If the results of the Lev_{mean} or Lev_{med} tests indicated variances were homogeneous then the Tukey-

Kramer pairwise comparison method was used, otherwise the Games-Howell method was used. Where variance homogeneity could not be assessed due to small sample sizes or differences in the distribution of each sample (i.e., one normally distributed and the other not) Dunnett’s (1980b) modification (T3) of Tamhane’s (1979) pairwise comparison procedure was used. Similar to the GH method, the T3 method is used when variances are not homogeneous, although it has less power than the GH method (Rafter et al. 2002). The T3 method while having less power does not have the same inflated Type I error rate in cases where variances are homogeneous (Jaccard et al. 1984, Rafter et al. 2002).

3.4 Results

When we tested the effect of bandwidth and resolution on the observed differences between contours, we found that the descriptive metrics did not differ significantly for any contour pair/season between each of the bandwidths or DEM resolutions examined (p>0.05). For example, there was not a significant difference in the $\bar{x}_{\Delta\bar{x}25-50\%}$of the calving season when compared between home ranges delineated using $h_{ref,,}$ 0.8h_{ref} or 0.6h_{ref}. Although DEM resolution did not affect the overall mean of differences between a certain season/contour pair (e.g., $\bar{x}_{\Delta\bar{x}25-50\%}$ in summer), the number of significant differences between contours did decrease at coarser resolutions (Tables C.1 and C.2, Appendix C). In addition, results of other comparisons (e.g., between seasons) were not consistent (i.e., significant) at each bandwidth or resolution examined. To illustrate our findings we report the results at the largest bandwidth and finest resolution for which significant differences were found. Further details including, for example, the 95% confidence intervals of pairwise comparisons, as well as the resolutions and bandwidths at which significant differences were found, are reported in Tables C.3-C.6 (Appendix C).

3.4.1 Range and proportion of differences between contours

Significant differences in elevation and slope were found between all contours of each season ($p<0.05$) (Tables 3.2 and 3.3). For each the contour pair of each season pair (e.g., summer 25-50%), values of elevation and slope were both higher and lower within the larger contour of the comparison depending on the specific caribou examined. Consistent change in a particular direction (i.e., an increase or decrease in topographic values from the inner to outer contours) was only significant (as measured by the binomial test of proportions, p) for certain contour pairs/seasons ($p<0.05$) (Figures 3.2 and 3.3).

Mean elevation was higher in the 95% contour of winter ranges relative to all other contours ($p<0.05$) (p = 0.86-0.93). For a significant proportion of caribou home ranges in the fall (p = 0.83-0.93) and winter (p = 0.85-1.0), the SD and CV of elevation was higher in the outer contour of all comparisons ($p<0.05$). This was also the case for home ranges in the calving (p = 0.89-1.0) and rut (p = 0.83-1.0) seasons with the exception of comparisons between the 50 and 75% contours ($p<0.05$). With some exceptions (e.g., 50-75% contours in winter), all values of slope were lower in the smaller contour of a comparison for a significant proportion of caribou home ranges in the fall (p = 0.83-1.0) and winter (p = 0.83-1.0) (Figure 3.3). The mean and SD of slope were lower within the 25% contour of rut ranges relative to all other contours and in the 50% contour relative to the 95% contour (p = 0.83-1.0).

All values of both slope and elevation were frequently lower (p<0.05) within the smaller contours of a comparison in the fall and winter home ranges with the exception of mean elevation. In addition, significant differences (p<0.05) in proportions for these two seasons were also were typically found at all three (or at least two) of the bandwidths examined (with the exception of CV slope in winter). Contours within the summer ranges showed the fewest number of significant differences in proportions for variables of both slope and elevation (i.e., mean, SD and CV of slope were not often consistently higher or lower within the smaller or larger contour of a comparison).

3.4.2 Differences between contour pairs

Within each season, there was a greater difference in the $\bar{x}$, SD and/or CV of elevation and slope between certain contours compared to others (Tukey-Kramer, Games-Howell orT3 pairwise comparison, p<0.05) (Figure 3.4).

Elevation

Significantly larger differences (p<0.05) between some contour pairs were observed for $\bar{x}$ elevation (34-82m) in the summer, rut and fall home ranges, for SD of elevation (27-75m) in all seasons except for the rut, and for CV (0.01-0.07) in all seasons except summer (values in brackets indicate the range of differences found between two contour pairs). Differences in elevation were frequently highest between the 25 and 95% contours (70% of all differences), and to a lesser extent, between the 25-75% and 50-95% contour pairs (14 and 16% of all differences respectively). When compared to differences between adjacent contours (e.g. 25-50%), descriptive metrics between the 25 and 95% contours were significantly larger (p<0.05) at all bandwidths, whereas the descriptive metrics between the 25-75 or 50-95% contour pairs were larger at the two smallest bandwidths (0.8h_{ref} and/or 0.6h_{ref}).

Slope

Significantly larger differences ($p<0.05$) between certain contour pairs were observed for $\bar{x}$ slope (1.6-5.3%) in the fall, summer and winter home ranges for SD of slope (1.8-4.9%) in all seasons except for the summer, and for CV (0.12-0.19) in all seasons except winter (Figure 3.4) (values in brackets indicate the range of differences found between two contour pairs). Relative to differences between adjacent contours (e.g., 25 and 50%), descriptive metrics were frequently higher between the 25-75% or 25-95% contour pairs. Compared to the 75-95% contour pair, descriptive metrics were higher at all bandwidths between the 25-95% contours of the fall and the 25-75% contours of the rut ($\bar{x}_{\Delta CV}$ only). Otherwise, higher differences between certain contour pairs were typically only statistically significant at one or both of the largest bandwidths ($p<0.05$).

3.4.3 Differences between seasons

The difference in the $\bar{x}$, SD and/or CV of elevation and slope between certain contour pairs were significantly higher in some seasons relative to others. ($p<0.05$) (Figures 3.5 and 3.6).

Elevation

Depending on the specific contour pair, descriptive metrics were typically higher in the summer, fall and winter ranges (27%, 24% and 39% of all differences respectively). At bandwidths of 0.8h_{ref} and 0.6h_{ref}, the $\bar{x}_{\Delta\bar{x}}$ between most contours of the rut and/or winter ranges was lower than in summer ($p<0.05$). By contrast, for winter ranges there was a greater difference in $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ between the 95% contour and the inner contours relative to the calving, rut and summer ranges. Similarly, the $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ of elevation between the 25% contour of the fall home ranges and one or both of the outer contours was higher relative to the rut, summer and winter ($\bar{x}_{\Delta SD}$ only) ranges.

Slope

Differences in $\bar{x}$ slope between contours was higher in summer ranges relative to fall, rut and/or winter ($p<0.05$). The $\bar{x}_{\Delta SD}$ between the 75% contour and the two inner contours was higher in the calving season relative to winter and in the summer ranges relative to fall, winter and rut (50-75% only) ($p<0.05$). In the winter ranges, $\bar{x}_{\Delta CV\ 25-50\%}$ was lower compared to summer, and $\bar{x}_{\Delta CV\ 25-75\%}$ was lower compared to summer, rut and fall ($p<0.05$).

3.5 Discussion

Animals do not roam aimlessly across landscapes in a random fashion but rather the spatial distribution of individuals (i.e. animals) within a population is determined by their interactions with the environment (Lima and Zollner1996). The use of finite space by individuals within a population is often described in terms of having a home range (Burt 1943). Burt’s (1943:351) definition describes home ranges as the “area traversed by the individual in its normal activities of food gathering, mating and caring for young.” Early analyses used known locations to construct an animal’s utilization distribution (UD), a three-dimensional surface representing the probability or density of use by an animal that is created based on known or recorded locations (Van Winkle 1975, Seaman and Powell 1996). Worton (1987, 1989) first proposed the Kernel technique for estimating a UD, which is a three-dimensional probability density map that shows which areas of the home range have more concentrated use.

Researchers must select a specific volume contour to delineate the bounds of a home range (typically 95%) or areas with more concentrated use, often characterized as “core areas”, and often specified as 50% (Laver and Kelly 2008). However, whatever the choice of contour it will ultimately determine the size and shape of the home range. It is within the home range that additional analyses on habitat structure are often made (Harris et al. 1990, Laver and Kelly 2008). Therefore, how the home range is delineated has consequences in terms of determining habitat-animal interactions. By virtue of aggregating individual location data for a specific animal renders the construction of the UD vulnerable to the Modifiable Areal Unit Problem (MAUP) Gehlke and Biehl 1934, Openshaw 1984). Simply stated, MAUP arises when the spatial units of an investigation are modifiable in terms of their size and shape, and the scale at which they are analysed can alter the outcome of statistical results and inferences thereof. There are two components to MAUP. The first component is the scale effect whereby the aggregation of data to larger spatial units can potentially alter the outcome of analyses. The second component is the scale effect whereby different delineations of spatial units (e.g., 1km^2 gridded vs. 1km^2 hexagonal data) can also affect statistical results.

In the last 15 years or so ecologists have increasingly recognized MAUP as a serious issue (Jelinski and Wu 1996, Hay et al. 2001, Hui et al. 2010, Lechner et al. 2012b, Wu 2013). Notwithstanding the emerging appreciation of MAUP in ecological analyses, we believe that MAUP has not yet received an acceptable amount of critical attention in home range analyses despite its potential effect to many studies of wildlife habitat (see Kie et al 2010). We examined the variable role of contour choice on woodland caribou home range analyses, focusing on slope and elevation as habitat variables. We used these two variables because they are important in habitat selection of northern woodland caribou (Poole et al. 2000, Culling et al. 2005, Gustine et al. 2006, Jones et al. 2007). Our specific objectives were to assess, (1) how the values of elevation and slope varied between contours of northern caribou seasonal home ranges and, (2) how the observed differences varied depending on the bandwidth used in KDE, as well as the resolution of the DEM from which topographic values were derived

3.5.1 Home range delineation

The 95% contour of an animal’s UD is widely used to delineate home range outer bounds (e.g., Wilson et al. 2012, Rayl et al. 2014, Kochanny et al. 2009, Quinn et al. 2013, Anich et al. 2009, Persson et al. 2010, Steyaert et al. 2011). However, use of this contour is somewhat of a contentious issue (Seaman et al. 1999, Powell and Mitchell 2012). Specifically, the 95% contour has been criticised for its arbitrary choice and lack of biological significance (Seaman et al. 1999, Powell 2000, Dickson and Beier 2002, Powell and Mitchell 2012). Seaman et al. (1999) and Börger et al. (2006b) found that relative to other contours, home ranges created using the 95% contour had a higher degree of bias (i.e., over-estimated home range size) and recommend using contours at 90% (Börger et al. 2006b) or <80% (Seaman et al. 1999) of the UD. The use of the 95% contour and the potential over-estimation of home range size can alter the outcome of statistical results. For example, Börger et al. (2006a) found that climatic variables best explained the variation in roe deer home range size when the 90% contour was used compared to smaller contours of 70 and 50%. Despite the potential to overestimate home range size and influence subsequent results, a recent review by Laver and Kelly (2008) found that of those studies using UD based methods 82% still used the 95% contour to delineate the outer bounds of an animal's home range.

Within the seasonal home ranges of the Level Kawdy caribou, slope and elevation were significantly different in the 95% contour relative to all other contours. The differences in topographic summary statistics between the 95% and other contours has implications in terms of Johnson's (1980) 2nd or 3rd order selection analyses. Johnson (1980) recognized the hierarchical nature of habitat use whereby a selection process will be of higher order than another if it is conditional upon the latter. He described four ordered selection processes. Second order analyses attempt to identify what habitat or resources an animal selects from the greater landscape (available) to establish a home range (used), while 3rd order selection assesses the differential selection of habitats or resources within an animal's home range (e.g., areas used for foraging).

Changes in the values and observed heterogeneity of variables as a result of different delineations (i.e., size and shape) of habitat that is available (3rd order) or used (2nd order) can change the apparent selection for certain resources (Boyce et al. 2003). Using different definitions of availability (i.e., the size of area defined as available) can change the direction of seeming apparent selection, as well as the relative importance of certain variables in models of habitat selection. For example, Apps and Kinley (2000) found that mountain caribou selected for steep slopes and rugged terrain at coarse scales of availability, whereas they selected against these features when availability was defined at a finer scale. Gustine et al. (2006) assessed the relative importance of predation risk (i.e., likelihood of encountering predators based on wolf habitat preferences) to woodland caribou within the framework of Johnson's (1980) 3rd order selection. They used two different definitions of availability: Seasonal movement (an individual's potential for movement in each season) and seasonal home range (100% Minimum Convex Polygon; Mohr 1947). They found that the relative importance of predator avoidance was high at the seasonal home range scale and low when measured at the scale of seasonal movement (Gustine et al. 2006).

The effect that the selection of the 95% contour had on the summary statistics for slope and elevation was more pronounced within certain seasons. For example, differences in topographic values between the 95% contour and inner contours were higher in the winter (SD and CV of elevation) and summer ($\bar{x}$ of slope and elevation). In their winter range, northern caribou are typically found in low elevation contiguous tracts of forest (Wood 1996, Jones et al. 2007, Culling et al. 2005). Thus, in winter, the increased variability in elevation (within the 95% contour) values could potentially increase the seemingly apparent selection for low elevations within the home range, whereas it could alternatively decrease apparent selection for low elevation within the larger landscape. In addition, the impact on selection analyses when the 95% contour is used may be greater in seasons such as the fall winter and rut. In these seasons, the differences between the 25% and 95% contour were significantly higher than between other contour pairs. The increase in topographic variability when the 95% contour is used in these seasons could, in terms of 2nd order selection analyses, indicate that there is not a high degree of selection for specific elevations when in fact there is one.

3.5.2 Habitats of greater use

Analyses of those areas of habitat characterized by more concentrated use are often designated as “core areas” (Samuel et al.1985, Seaman and Powell 1990). Core areas are frequently delineated using the 50% contour of the UD (e.g., Webb et al. 2007, Shuter and Rodgers 2012, Bastille-Rousseau et al. 2013). While used extensively (Laver and Kelly 2008), the 50% contour has also been criticized for its arbitrary selection and lack of biological rationale (Vander Wal and Rodgers 2012). Thus “true” core habitat may not always coincide with the 50% contour (e.g., central place foragers vs. wanderers; Powell 2000). In addition, core areas can vary between individuals of the same species (Wilson et al 2010), between seasons (Burdett et al. 2007) and the specific research objectives (Harris et al. 1990). For example, Burdett et al. (2007) found the UD contour delineating the core area of female Lynx (*Lynx Canadensis*) varied seasonally and ranged from 56% (±1%) in summer-fall to 78% (±6%) during the denning season. Similarly, Wilson et al. (2011) found the UD contours delineating coyote (*Canis latrans*) core areas ranged from 10.-70.0% depending on the individual. Consequently, the delineation of supposed core area using the 50% could potentially alter conclusions of animal use of core habitat if the habitat variables are significantly different than those within an animal’s actual core of, say, 30%.

Our findings indicate that the summary statistics for elevation and slope vary between all four contours of the Level Kawdy caribou home ranges. Therefore, habitat use in terms of these variables within core habitat appear dependent on the contour at which analyses are performed, even highly so in some cases. As indicated by our findings, the degree to which contour choice will affect habitat analyses will vary depending on the season, as well as potentially between individuals within a season. For example, there was a greater difference in mean elevation and all values of slope between contours of the summer ranges relative to winter, rut and fall. By comparison, summer and calving ranges of northern caribou are characterized by the use of higher elevation areas with steeper slopes (Wood 1996, Poole et al. 2000, Culling et al. 2005). The summer ranges of the Level Kawdy caribou had significantly higher values of slope (mean and SD) relative to other seasons (Table A.3, Appendix A). Greater variability in slope within these ranges and conversely the use of areas of lower elevation and gentler slopes in winter (Culling et al. 2005) may have contributed to the larger differences (in summer) between contours.

Changes in the extent of area analysed can have a greater impact on variable values and subsequent analyses in areas that are more heterogeneous. For example, Schaeffer and Messier (1995) found little change in habitat selection of muskoxen (*Ovibos moschatus*) when analysed at different scales (i.e., extents). They attribute this lack of variation in selection between scale to the relatively homogeneous environment of the arctic and the range of scales analysed (i.e., from feeding crater to a minimum area polygon around all feeding sites in the study area). In other words, the scales analysed by Schaeffer and Messier (1995) were likely all within the scale domain of the variables measured (i.e., an area where patterns/values of a variable remain relatively consistent) and did not pass a scale threshold (the point at which there is a significant change in the values and spatial patterns of a variable) (Turner et al. 1989, Wiens 1989, Wu and Loucks 1995). Conversely, in a more heterogeneous environment such as Yellowstone National park, the scale at which elk (*Cervus canadensis*) habitat selection was measured (four scales ranging from home range to study area) had a significant impact on analysis results (Boyce et al. 2003).

Seasonal home ranges located in areas of greater topographic variability may have more variation between contours in terms of elevation and slope. Further confounding this is the seasonal variation in the scale of caribou habitat selection (e.g., Johnson et al 2002, Leblond et al. 2011). For example, Leblond et al. (2011) found that the extent at which models best explained resource selection of caribou varied seasonally. They found that measures of terrain ruggedness (the CV of either slope or elevation) explained more variation in caribou habitat selection at buffer scales of a 2km radius in the rut, 4km radius in summer and 8km in all other seasons (2011). These differences in the scale of selection between seasons could be the result of seasonal differences in patchiness of resources (e.g. forage), as well as the physical requirements (e.g., diet) of caribou (Johnson et al 2002, Leblond et al. 2011).

Summer ranges had some of the largest differences in values between contours, although the direction of change in values was less consistent than in other seasons. In other words, topographic values were higher in outer contours of summer ranges for approximately half of the Level Kawdy caribou, and, conversely, lower in the outer contours for the other half of the caribou. This lack of consistency (in terms of direction of change in values) could also be the result of habitat use of northern caribou in summer relative to other seasons.

In the summer months caribou habitat use may not be limited to the same degree as in other seasons such as, for example, winter and calving. For example, winter's snow conditions, (which are often associated with topography and aspect), affect forage abundance and accessibility (Wood 1996, Apps et al. 2001, Johnson et al. 2004b). Similarly, topography is important during the calving season when caribou select high elevation areas with steep slopes as a predator avoidance tactic (Bergerud et al 1984, Bergerud and Paige 1987). While caribou may still use higher elevations and slopes in summer as a predator avoidance tactic, they have been found to use a wider variety of habitats in terms of vegetation and topography (Cichowski 1993, Johnson et al. 2002, Gustine and Parker 2008). In addition, habitat selection by caribou is in part an attempt to spatially separate themselves from predators as well as alternate prey (e.g., moose) (Seip 1990, James et al 2004). However, some herds have been found to occupy the same areas/habitats as predators and alternative prey during the summer season (Seip 1990, Gustine and Parker 2008). The fewer limiting factors in terms of habitat use (topography, forage, snow, predation), may have contributed to the lack of a consistent pattern in terms of the relative magnitude of topographic values between contours of the summer range.

Conversely, seasons such as fall and winter showed a consistent trend of increasing values of elevation and slope in outer contours. In addition, differences in the SD and CV of elevation were frequently higher between contours of the fall and winter home ranges relative to other seasons. The trends observed in the fall and winter could be related to the size of these home ranges and the relative sizes of contours within these seasons. Caribou home ranges in the fall and winter were significantly larger than in other seasons, and although outer contour(s) (95% and occasionally 75%) were larger than inner contours (25 and 50%) in all seasons, the differences in size were greater within the fall and winter (Table A.2, Appendix A). Increasing the size/extent of the area can increase the probability of including habitats not found in smaller extents (Wiens 1989, Lechner et al. 2012a). Therefore the use of larger contours for analysing higher levels of habitat use within a home range may increase the variability of values measured simply as a result of increasing the areal extent.

3.5.3 Bandwidth and resolution

Differences in elevation and slope between contours were assessed within caribou home ranges created using three different bandwidths (h_{ref}, $0.8h_{ref}$, and $0.6h_{ref}$), as well as at four different DEM resolutions (25, 75, 125 and 175m). We then compared the summary statistics of topographic values for each seasonal contour pair between bandwidths (holding resolution constant) and between DEM resolutions (holding bandwidth constant) and no significant differences were found. However, when other comparisons were made (e.g. comparing observed difference between the 25 and 95% contours across seasons), these results were not always consistent (i.e. significant) at all bandwidths or resolutions. For example, the difference in mean elevation between contours in winter ranges was only higher than other seasons at the largest bandwidth (h_{ref}) examined, whereas differences in mean elevation between contours in the summer were typically higher relative to other seasons at the two smaller bandwidths ($0.8h_{ref}$ and $0.6h_{ref}$). Therefore, bandwidth used in KDE could alter the differences that may occur between seasons in resource selection studies as a result of contour choice. In other words, the contour choice may have more of an impact within the analyses of specific season only when certain bandwidths are used in KDE.

3.6 Conclusions

We have demonstrated that elevation and slope vary between the UD contours of northern caribou seasonal home ranges. The use of specific UD contour values to delineate the outer bounds of a home range (e.g. 95%) or areas with higher levels of use (e.g., 50%) will therefore determine the values of topographic variables measured within each of these areas and could potentially alter the results of habitat use or selection studies. We agree with Laver and Kelly (2008) that the continued use of the 95% contour is important for consistency between studies. However, researchers should consider using a second/additional contour such as the 90% suggested by Seaman et al. (1999) or <80% recommended by Börger et al. (2006b) to assess whether different delineations of a home range significantly affect their results.

Investigations into higher levels of use within the home range should consider additional contours or the use of more objective methods to delineate core areas (e.g. Samuel et al. 1985, Seaman and Powell 1990, Kenward et al. 2001, Wilson et al. 2010, Vander Wal and Rodgers 2012). Empirical use of these methods has produced core ranges at UD values smaller as well as larger than 50% (e.g., 85% Florkiewicz et al. 2007; 18.7 – 71.5%, Wilson et al. 2010; 40%, Barg et al. 2005; and 56-78%, Burdett et al. 2007). Use of one of these methods would still, as a consequence of imposing a hard boundary, determine/impact the habitat values within each core area and, hence, also impact statistical results and inferences about habitat use or selection. However, because of the increased objectivity, they have the potential to more accurately depict an animal's "true" core area and thus produce more reliable results. In addition, the method suggested by Wilson et al. (2010) allows for the identification of multiple core areas since the internal structure of an animal's home range may be the result of more than one behavioural processes.

Further investigations should be conducted to determine specifically how the variation observed in this study in topographic values between contours of northern caribou seasonal home ranges will affect analyses of habitat use or selection. In addition, our results indicated that differences between contours varied between seasons, with some showing a larger difference in certain values between contours, while other seasons had a more consistent pattern in terms of the change in values from inner to outer contours. As indicated previously, these variations between seasons could be the result of the topography within each seasonal home range or differences in home range/contour size. If this is the case, the patterns observed in this study may apply to other caribou herds that exhibit similar trends in seasonal habitat use or home range size such as, for example, Metsaranta and Mallory (2007) who found that fall and winter home ranges were larger than other seasons. However, both Ferguson and Elkie (2004) and Cichowski (1993) reported that summer home ranges of were larger relative to other seasons. Further investigations would therefore benefit from analysing additional herds, as well as over multiple years as habitat use can vary within a herd depending on the year.

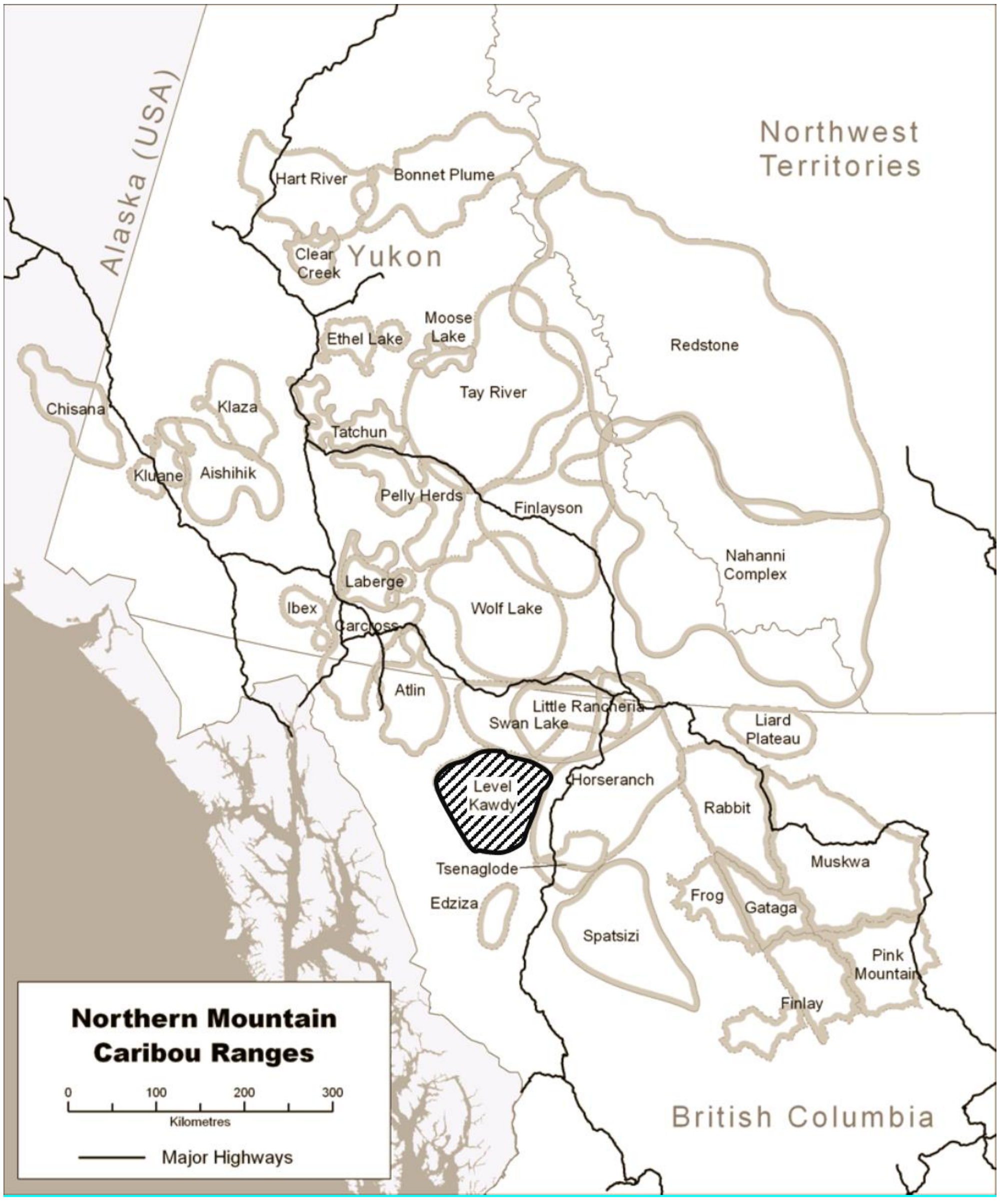

Figure 3.1 Ranges of Northern woodland caribou herds (*Rangifer tarandus caribou*) in western Canada. (reproduced from: Environment Canada, 2012)

Table 3.1 Selected season dates for each caribou and sample sizes used to create seasonal home ranges

	Season														
	Winter			**Calving**			**Summer**			**Rut**			**Fall**		
Caribou	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**
D030452	Dec 27	May 4	119	May 23	Jun 15	23	Jul 5	Sep 11	69	Sep 12	Oct 24	41	Oct 25	Dec12	49
D030453	Dec 13	Apr 30	168	May 24	Jul 11	46	Jul 12	Sep 9	59	Sep 11	Oct 10	29	Oct 21	Dec25	66
D030457	Dec 23	Apr 10	142	n/a	n/a	n/a	May 22	Sep 6	104	Sep 14	Oct 20	37	Oct 21	Dec 12	53
D030460	Dec 27	Apr 16	90	May 24	July 1	39	Jul 2	Aug 22	52	Sep 12	Oct 22	41	Oct 23	Dec3	42
D030461	Jan 11	Apr 18	131	May 27	Jun 24	26	Jun 26	Sep 5	72	Sep 6	Oct 20	44	Oct 22	Dec7	47
D030462	Jan 17	Apr 24	130	May 22	Jul 6	46	Jul 17	Aug 26	39	Aug 27	Oct 19	53	Oct 21	Dec 5	44
D030464	Dec 20	Apr 28	164	May 27	Jul 11	46	Jul 22	Sep 11	52	Sep 12	Oct 22	38	Oct 23	Dec20	59
D030465	Jan 12	Apr 27	133	n/a	n/a	n/a	May 30	Sep 11	103	Sep 15	Oct 11	27	Oct 12	Dec7	57
D030466	Dec 28	May 10	130	May 30	Jun 25	27	Jun 26	Sep 13	77	Sep 14	Oct 16	33	Oct 17	Dec 10	53
D030468	Dec 21	Jan 24	36	May 13	Jun 16	35	Jun 18	Aug 25	69	Sep 7	Oct 17	39	Oct 18	Dec 13	55
	Feb 3	Apr 21	75												
D030470	Jan 19	Apr 28	101	May 24	Jun 8	16	Jun 10	Aug 11	61	Aug 12	Oct 25	70	Oct 26	Nov 27	33
D030471	Dec 23	Apr 16	148	May 22	Jul 9	35	Jul 13	Aug 29	31	Sep 7	Oct 22	32	Nov 10	Dec 6	26
D030490	Dec 4	May 5	148	May 21	Jun 17	28	Jul 3	Sep 10	67	Sep 15	Oct 20	36	Oct 21	Nov 24	35

Table 3.2 The range of descriptive metrics and maximum observed difference in values of elevation (m) between contours of all seasonal home ranges.

		Absolute difference						**Small contour < Large contour**						**Small contour > Large contour**					
Elevation Variable	**Contour Pair**	$\bar{x}_{\Delta low}$	**(±SD)**	**-**	$\bar{x}_{\Delta high}$	**(±SD)**	**Max**	$\bar{x}_{\Delta low}$	**(±SD)**	**-**	$\bar{x}_{\Delta high}$	**(±SD)**	**Max**	$\bar{x}_{\Delta low}$	**(±SD)**	**-**	$\bar{x}_{\Delta high}$	**(±SD)**	**Max**
Mean	**25-50**	19.1	19.1	-	77.9	59.3	151.6	15.1	18.5	-	63.6	44.5	151.6	9.0	10.2	-	101.0	59.7	149.0
	25-75	36.3	22.6	-	111.1	74.0	260.2	26.3	19.4	-	115.5	95.4	260.2	17.1	15.3	-	132.9	84.8	192.8
	25-95	46.1	34.8	-	139.3	71.9	347.0	28.5	29.7	-	201.9	72.7	278.5	13.4	6.5	-	162.6	122.6	347.0
	50-75	22.7	19.4	-	70.8	48.4	190.6	15.5	13.7	-	105.9	49.7	190.6	21.5	19.3	-	82.2	52.6	125.3
	50-95	35.0	31.4	-	109.8	62.0	269.8	13.1	4.9	-	159.2	82.5	263.4	20.5	12.4	-	126.5	117.6	269.8
	75-95	24.8	18.6	-	71.8	49.4	177.2	10.7	10.4	-	69.5	13.7	99.7	25.7	19.0	-	89.1	46.2	177.3
SD	**25-50**	23.7	11.6	-	71.3	64.9	192.5	24.9	21.0	-	80.2	65.4	192.5	3.3	3.4	-	44.4	28.4	76.8
	25-75	38.9	29.7	-	75.1	46.0	192.3	32.5	20.4	-	89.9	50.2	192.8	13.7	8.5	-	49.2	24.2	83.1
	25-95	43.2	20.3	-	101.6	55.3	203.5	45.9	22.2	-	108.6	51.4	203.7	5.8	6.6	-	28.3	16.7	53.0
	50-75	12.5	15.7	-	44.7	40.5	156.1	11.0	17.9	-	58.0	51.8	156.8	2.0	2.3	-	39.2	1.6	49.1
	50-95	23.5	18.6	-	70.1	37.0	164.4	25.9	18.9	-	73.5	48.4	164.8	14.3	17.6	-	57.0	66.5	105.1
	75-95	13.5	14.2	-	50.6	39.1	112.1	12.1	9.4	-	54.4	37.9	112.3	2.0	2.4	-	27.5	35.4	70.3
CV	**25-50**	0.02	0.001	-	0.05	0.05	0.14	0.02	0.01	-	0.06	0.05	0.14	0.004	0.003	-	0.03	0.02	0.05
	25-75	0.02	0.01	-	0.05	0.02	0.13	0.02	0.01	-	0.06	0.03	0.13	0.01	0.01	-	0.03	0.02	0.05
	25-95	0.03	0.14	-	0.09	0.05	0.17	0.03	0.01	-	0.09	0.05	0.17	0.01	0.004	-	0.03	0.01	0.03
	50-75	0.01	0.01	-	0.03	0.03	0.10	0.01	0.01	-	0.04	0.04	0.10	0.003	0.003	-	0.02	0.02	0.04
	50-95	0.02	0.01	-	0.07	0.04	0.14	0.02	0.01	-	0.07	0.04	0.14	0.01	0.01	-	0.04	0.05	0.08
	75-95	0.01	0.01	-	0.05	0.04	0.12	0.01	0.01	-	0.05	0.04	0.12	0.004	0.01	-	0.02	0.03	0.04

Table 3.3 Range of descriptive metrics and maximum observed difference in values of slope (%) between contours of all seasonal home ranges.

		Absolute difference						Small contour < Large contour						Small contour > Large contour					
Elevation Variable	Contour Pair	$\bar{x}_{\Delta low}$	(±SD)	-	$\bar{x}_{\Delta high}$	(±SD)	Max	$\bar{x}_{\Delta low}$	(±SD)	-	$\bar{x}_{\Delta high}$	(±SD)	Max	$\bar{x}_{\Delta low}$	(±SD)	-	$\bar{x}_{\Delta high}$	(±SD)	Max
Mean	**25-50**	1.4	(0.8)	-	5.7	(3.1)	15.2	1.4	(0.6)	-	4.2	(2.8)	8.5	0.8	(0.7)	-	9.3	(1.5)	15.2
	25-75	1.5	(1.1)	-	8.6	(5.4)	20.0	4.5	(1.2)	-	8.0	(6.9)	20.0	0.7	(0.8)	-	12.1	(5.0)	17.0
	25-95	2.1	(1.4)	-	9.2	(7.2)	24.2	2.2	(1.4)	-	9.5	(8.1)	24.2	0.3	(0.1)	-	9.1	(6.1)	19.2
	50-75	0.7	(0.5)	-	4.9	(3.5)	13.4	0.6	(0.3)	-	6.1	(4.0)	13.4	0.6	(0.4)	-	4.7	(1.5)	10.0
	50-95	1.2	(0.9)	-	6.4	(5.7)	18.4	1.2	(0.9)	-	6.8	(6.0)	18.4	0.7	(0.5)	-	9.4	(2.2)	17.6
	75-95	1.3	(1.1)	-	3.6	(2.9)	10.4	1.4	(0.7)	-	3.8	(2.3)	6.8	0.5	(0.3)	-	4.8	(2.9)	10.4
SD	**25-50**	1.5	(1.1)	-	4.3	(3.5)	11.0	1.5	(0.8)	-	4.3	(4.1)	11.0	0.5	(0.6)	-	5.9	(3.4)	10.4
	25-75	1.2	(1.6)	-	8.0	(5.0)	18.5	1.3	(1.0)	-	7.5	(5.3)	18.5	0.3	(0.3)	-	9.3	(4.4)	13.6
	25-95	2.4	(2.0)	-	7.0	(5.2)	17.6	2.4	(1.6)	-	8.3	(6.0)	17.6	<0.1	(<0.1)	-	6.1	(0.8)	10.1
	50-75	0.6	(0.6)	-	4.8	(3.0)	11.7	0.3	(0.1)	-	5.5	(2.2)	11.7	0.8	(0.1)	-	4.8	(0.1)	5.8
	50-95	1.4	(1.4)	-	4.6	(3.5)	11.0	1.7	(1.5)	-	5.4	(4.3)	11.0	<0.1	(<0.1)	-	4.3	3.1	8.8
	75-95	0.7	(0.6)	-	2.8	(2.0)	7.2	0.4	(0.2)	-	3.1	(2.1)	6.5	0.21	(0.2)	-	3.7	(2.0)	7.2
CV	**25-50**	0.09	(0.08)	-	0.31	(0.20)	0.77	0.05	(0.04)	-	0.33	(0.21)	0.77	0.02	(0.01)	-	0.19	(0.16)	0.33
	25-75	0.09	(0.06)	-	0.35	(0.23)	0.76	0.07	(0.06)	-	0.37	(0.23)	0.76	0.02	(0.01)	-	0.30	(0.16)	0.42
	25-95	0.12	(0.09)	-	0.36	(0.21)	0.78	0.14	(0.01)	-	0.44	(0.21)	0.78	0.01	(0.01)	-	0.37	(0.08)	0.60
	50-75	0.05	(0.04)	-	0.22	(0.15)	0.54	0.03	(0.04)	-	0.26	(0.09)	0.55	0.03	(0..02)	-	0.33	(0.13)	0.47
	50-95	0.11	(0.06)	-	0.21	(0.13)	0.73	0.09	(0.01)	-	0.29	(0.27	0.73	0.06	(0.05)	-	0.32	(0.21)	0.53
	75-95	0.06	(0.05)	-	0.19	(0.18)	0.70	0.05	(0.03)	-	0.22	(0.19)	0.70	0.01	(0.02)	-	0.14	(0.10)	0.34

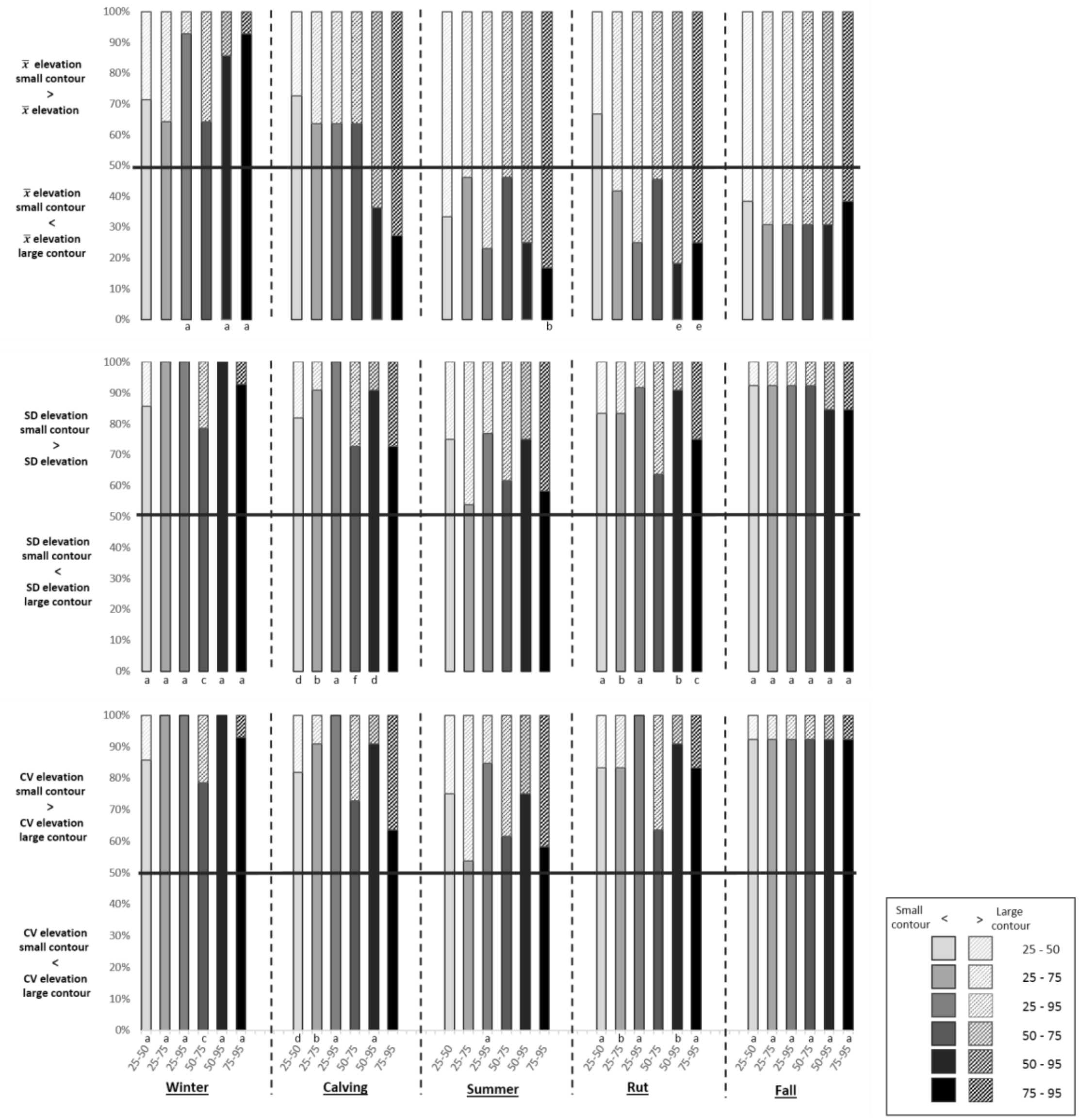

Figure 3.2 Proportion of instances where mean (top), SD (middle) and CV (bottom) of elevation (m) was higher and lower within the smaller contour of a comparison in each of the five seasonal home ranges (winter, calving, summer, rut and fall). Each letter identifies the bandwidth(s) at which differences in proportions were significant.

Bandwidths:
a = all
b = h_{ref} and 0.8h_{ref}
c = 0.8h_{ref} and 0.6h_{ref}
d = h_{ref}
e = 0.8h_{ref}
f = 0.6h_{ref}

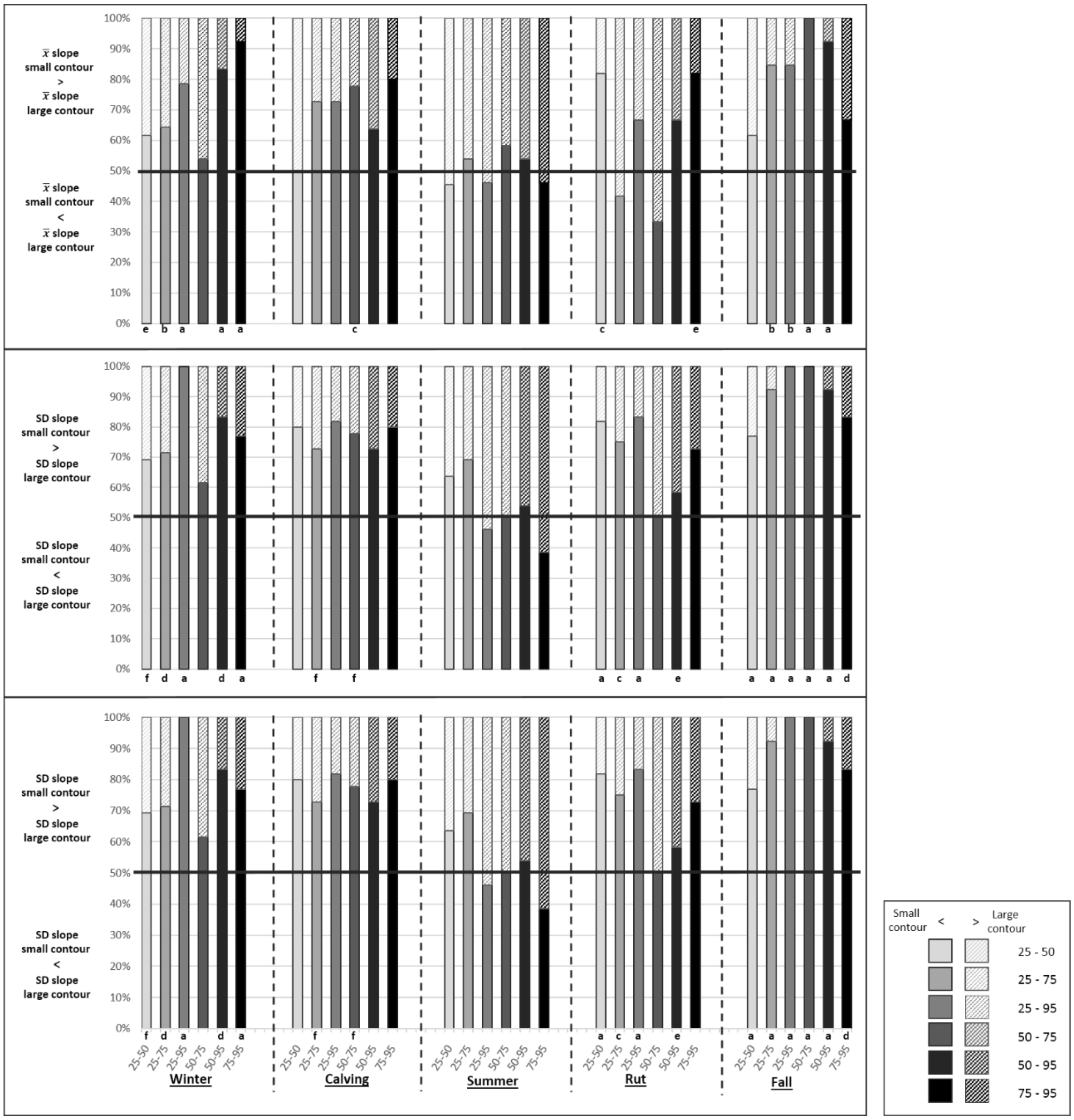

Figure 3.3 Proportion of instances where mean (top), SD (middle) and CV (bottom) of slope (%) was higher and lower within the smaller contour of a comparison in each of the five seasonal home ranges (winter, calving, summer, rut and fall). Each letter identifies the bandwidth(s) at which differences in proportions were significant.

Bandwidths:
a = all
b = h_{ref} and 0.8h_{ref}
c = 0.8h_{ref} and 0.6h_{ref}
d = h_{ref}
e = 0.8h_{ref}
f = 0.6h_{ref}

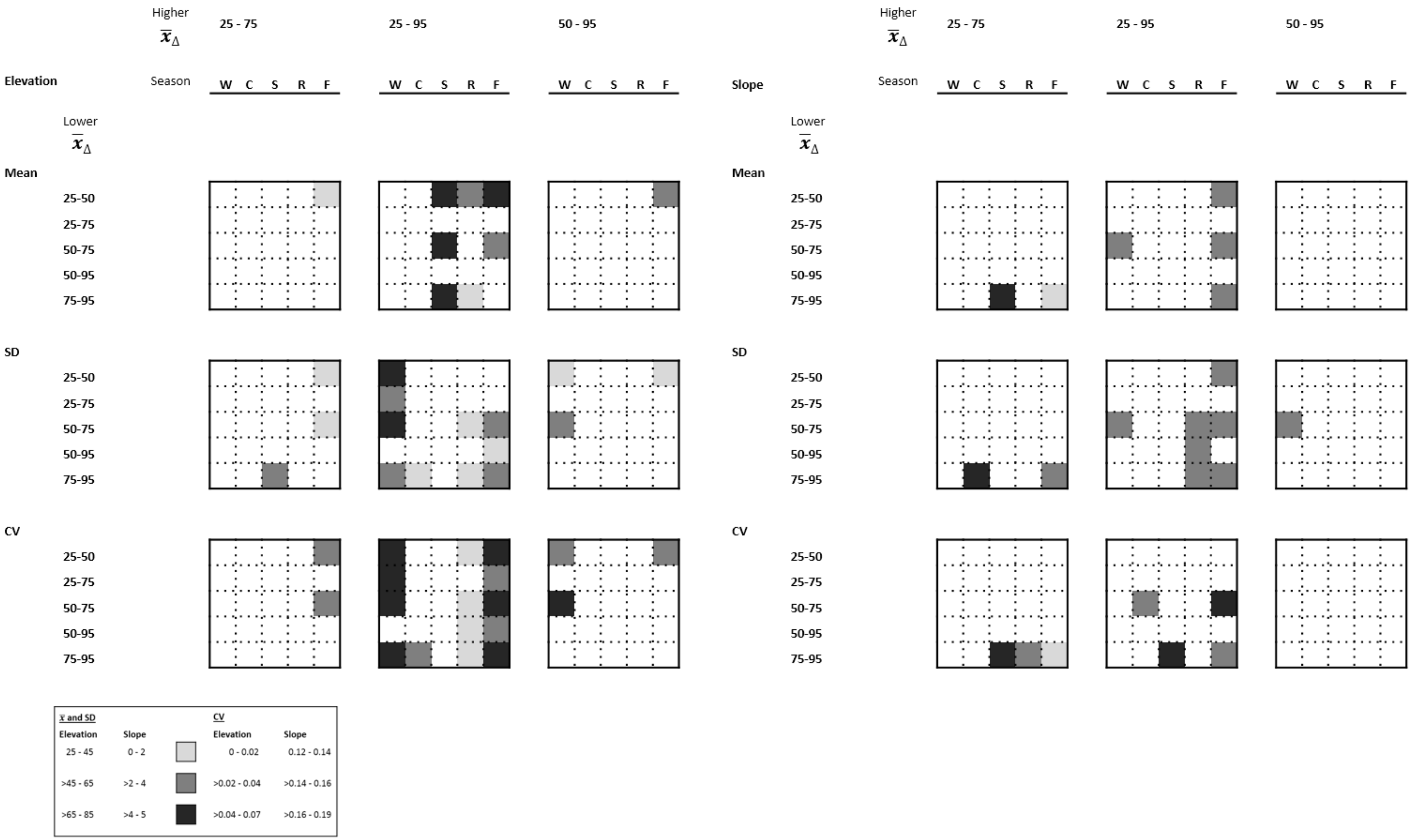

Figure 3.4 Significant pairwise differences ($p<0.05$) in the descriptive metrics of elevation (m) (right) and slope (%) (left) between contour pairs within each seasonal home range (winter, calving, summer, rut and fall)

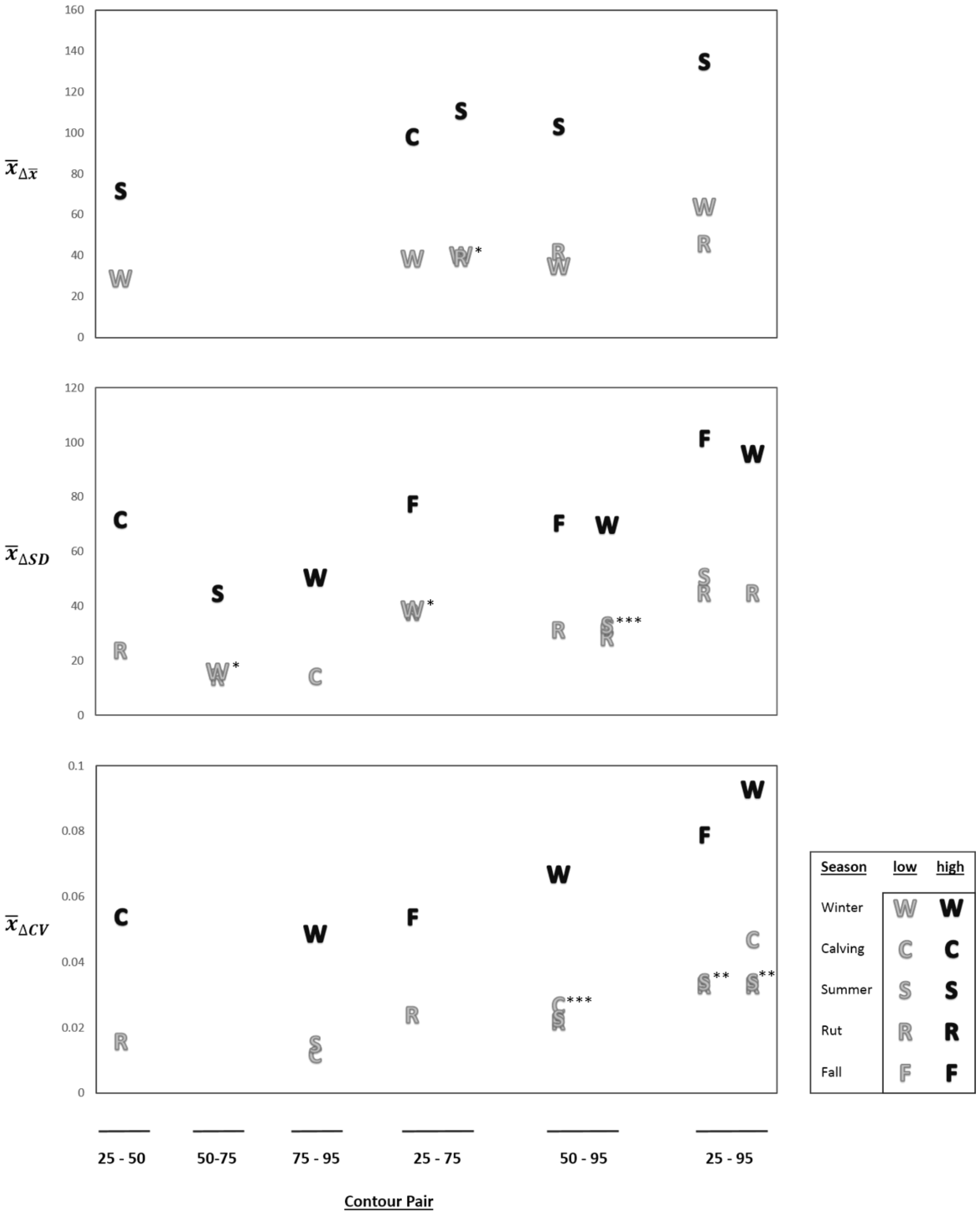

Figure 3.5 **Significant pairwise differences between seasons (winter, calving, summer, rut and fall) (p<0.05) in the descriptive metrics of elevation (m) between contours.**

*** winter and rut**
**** summer and rut**
***** summer, calving and rut**

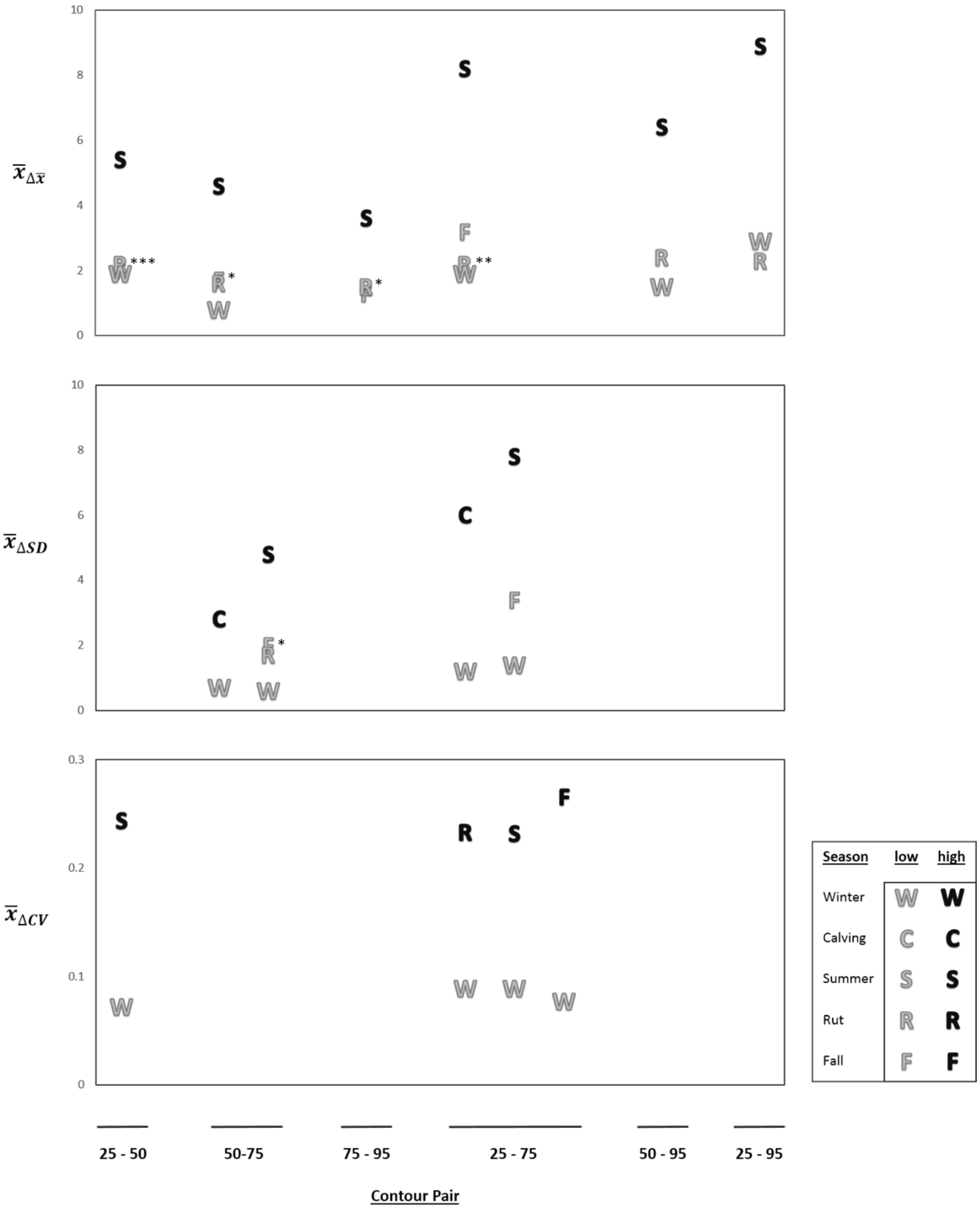

Figure 3.6 Significant pairwise differences between seasons (winter, calving, summer, rut and fall) ($p<0.05$) in the descriptive metrics of slope (%) between contours.

*** rut and fall**
**** winter and rut**
***** winter, rut and fall**

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4 The Modifiable Areal Unit Problem and caribou (*Rangifer tarandus*) home range delineation: effects of aggregating slope and elevation

4.1 Abstract

Home range analyses often attempt to assess use or selection by animal for certain habitat characteristics (e.g., vegetation cover or topography). Although somewhat common practice, the aggregation of this habitat data to larger spatial units of analysis can potentially alter the nature of the data was well as statistical results or inferences regarding wildlife-habitat associations. This is one component (i.e., scale effect) of what is known as the Modifiable Areal Unit Problem. MAUP refers specifically to the effect that changes to the scale at which spatial data are assessed can potentially lead to spurious results as well as ecological inferences. The two components of MAUP pertain to the size (scale effect) and shape (zone effect) at which areal units are analysed. The scale effect (as previously discussed) refers to the change in analysis results due to the aggregation of data to coarser spatial units which, can average out the fine-scale detail present in the data. The second component, the zone effect, refers specifically to (regardless of size) how areal units are delineated in space and the resulting variation in measured values of habitat variables assessed within, for example 1km^2 grids vs. 1km^2 hexagonal units. Thus, home range analyses that aggregate spatial habitat data are potentially subject to the MAUP.

In addition, home range analyses that specifically use methods such as Kernel Density Estimation Method (KDE) that are based on an animal's UD (a surface representing an estimation of the intensity of use of an area by an animal) may also be subject to MAUP for two reasons. First, in the KDE method the size and shape of an

animal's home range will in part be determined by the specific choice of bandwidth which determines the level of smoothing applied to animal location data. Small bandwidths will capture the fine-scale detail in animal space use and produce smaller home ranges than larger bandwidths which will provide a more general (or coarse-scale) depiction of animal space use. The second reason why home range analyses using the KDE method may be subject to MAUP is by virtue of being able to select a particular volume contour of an animal's UD (i.e. an area representing a specific level or intensity of use). Both the size and shape of the areas used in home range analysis as determined by KDE bandwidth and UD contour will determine the habitat variables measured there-within.

The objective of this study was to determine the effect of MAUP in home range analyses in terms of the aggregation of habitat variables. In addition, we assessed how the effect of aggregation on habitat values varied when assessed within different delineations of home range outer bounds (by varying KDE bandwidth) or areas of higher levels of use (by varying UD contour). To demonstrate the issue of MAUP in home range analyses we used a model population of 13 northern woodland caribou (*Rangifer tarandus*). We created seasonal home ranges for each caribou using three KDE bandwidths and delineated areas of differing levels of use within each home range based on four levels of the UD. Within each seasonal contour we assessed values of elevation and slope (mean, standard deviation and CV), as both these variables are important in caribou habitat selection. We assessed the magnitude and direction of change in elevation and slope that occurred when aggregated to coarser resolutions (25, 75, 125 and 175m). We found no significant differences in elevation at coarser resolutions.

Conversely, we found a significant decrease in both the mean and SD of slope in all home ranges. The magnitude of change in slope values was, in general greater in the outer contours of caribou home ranges as well as in the summer and calving seasons. Thus, while the aggregation of topographic data could potentially alter the outcome of woodland caribou home range analyses the particular effect may be more pronounced within certain seasons or when specific UD contours are analysed.

4.2 Introduction

A wide range of ecological studies assess wildlife-habitat associations with respect to, for example, species distributions (Guisan and Thuiller 2005, Araújo and Guisan 2006, Elith and Leathwick 2009), biodiversity (Hansen et al. 2001, Fahrig 2003, Goetz et al. 2007), habitat use (Osborne et al. 2001, Lindenmayer et al. 2003, Mackenzie 2006) or resource selection (Gilles et al. 2006, Millspaugh et al. 2006, McLoughlin et al. 2010). For this research, ecologists make extensive use of data relating to habitat composition (e.g., Dickson and Beir 2002, Hebblewhite and Merril 2008) and habitat configuration (e.g., Ewers and Didham 2006, Vallecillo et al. 2008). As a result of the long recognized importance of scale in ecology (Turner et al. 1989, Wiens 1989, Jelinski and Wu 1996), there are numerous studies investigating the effect that aggregating thematic land cover or vegetation data to coarser scales (e.g., grains or resolutions) has on wildlife-habitat analyses (e.g., Karl et al. 2000, Betts et al. 2006, Li et al. 2006, Guisan et al. 2007, Stickler and Southworth 2008, Carter et al. 2010, Gottschalk et al. 2011, Song et al. 2013).

The aggregation of spatial ecological data to coarser grains is common for a number of reasons. For example, this may be necessary to match the resolution of other variables used (e.g., Kie et al., 2002, Hamada et al. 2007, Roger et al., 2007, Enwright et al. 2011) or due to limitations in analysis and/or storage capabilities (Gao 1999; e.g., Twiss et al. 2001, Erdey-Heydorn 2008, Kimmerer et al. 2009, Semeniuk 2012). Although it is somewhat common practice, the aggregation of spatial data can change the outcome of statistical analyses and ultimately impact ecological inferences (Van Rensburg et al. 2002, Lawler et al. 2004, Lechner et al. 2012). Analytical results may be affected by the aggregation of data due to the loss of fine-scale detail (Clark and Avery 1976, Turner et al. 1989), or changes in the observed distribution or spatial pattern of phenomena (Bowyer et al. 1996, Rahbek 2005).

This potential impact of aggregation on data and the results of subsequent analysis is one component of the Modifiable Areal Unit Problem (MAUP, Gehlke and Biehl, 1934, Openshaw, 1984). MAUP refers to the consequences of modifying the spatial units of areal data (e.g., size or configuration of units) on statistical analyses and inferences thereof. There are two main components to MAUP. The first components is the scale effect whereby the aggregation of data into increasingly larger spatial units may average out fine-scale detail thus changing data values such as variance (Jelinski and Wu 1996). The second component of MAUP is the zoning effect, which refers to the multitude of ways that spatial units can be delineated in space when holding scale constant. For example, Fortin (1999) found that the orientation of rectangular sampling quadrats (10m x 20m vs. 20m x 10m) changed the magnitude of spatial autocorrelation in woody plant species abundance. Both aspects of MAUP (scale and zoning) have the potential to alter results of statistical analyses using ecological data and more importantly the ultimate conclusions (Jelinski and Wu, 1996; Dark and Bram, 2007).

The importance of topography in habitat use and selection has been demonstrated for many species such as bighorn sheep (*Ovis canadensis*) (Turner et al. 2004, Bangs et al 2005), mule deer (*Odocoileus hemionus*) (Long et al. 2009), wolves (*Canis lupus*) (Wittington et al. 2005), grizzly bears (*Ursus arctos*) (Mace et al. 1999, Apps et al. 2004) and cougars (Dickson et al.2005) and is frequently included in models assessing these relationships (e.g., Rupp and Rupp 2010, Apps and McLellan 2006, Jones et al. 2007, Chetkiewicz and Boyce 2009). Despite the role of topographic variability in habitat use of many species, this abiotic feature has been largely overlooked (although not completely) in terms of the effect of data aggregation on the results of habitat analyses. Studies that have in fact assessed the change in analytical results as a consequence of aggregating topographic data have found both a decreased performance in models of habitat suitability (Li et al. 2006, Song et al. 2013), as well as species distribution (Guisan et al. 2007).

The effect that aggregating data to coarser resolutions has on the values of a particular variable can vary across different landscapes. This variation can be a result of differences between landscapes in the heterogeneity, spatial patterns and spatial autocorrelation of the variable in question (Turner et al. 1989, Karl et al. 2000, Fisher and Tate 2006, Lin et al. 2008). In particular, when topographic data are aggregated to coarser resolutions, the magnitude of change in values (e.g. mean) of, for example, slope, has been shown to vary depending on the geographical area. There is typically a greater decrease in slope values at coarser resolutions in areas characterized by steeper or more rugged terrain compared to less rugged areas (Wolock and Price 1994, Zhang and Montgomery 1994, Gao 1997). Therefore, the observed impact of resolution in analyses of wildlife-habitat associations may vary depending on the area (i.e., geographic location or extent) in which the change is assessed. The specific geographic location will be dependent on the location of the animal(s) in question. However, the extent of area analysed may vary depending on the analytical methods or method parameters chosen by the researcher. For example, investigations into habitat selection sometimes comprise of measuring habitat characteristics within buffers centered around each animal location (e.g., Rettie and Messier 2000, Apps et al. 2001) and the extent (e.g., km^2) of each buffer will depend on the chosen buffer radius.

Wildlife-habitat associations are commonly investigated within the context of an animal’s home range (e.g., Long et al. 2008, Carter et al. 2010, van Beest et al. 2010). There are a number of methods by which an animal’s home range can be delineated including the Jenrich-Turner estimator (Jenrich and Turner 1969), the harmonic mean method (Dixon and Chapman 1980) or the minimum convex polygon (Mohr 1947).The use of another method, Kernel Density Estimation (KDE, Worton 1989), is advantageous because it is non-parametric, has the ability to produce less biased estimates of home range size (Worton 1995) and is capable of identifying multiple centers of activity (Kernohan et al. 2001). Due to the recognized benefits of KDE as well as its inclusion in numerous GIS analytical packages (e.g., Geospatial Modelling Environment, Beyer 2012; Home Range Tools, Rodgers et al. 2007), it is one of the most commonly used methods in home range analyses (Laver and Kelly 2008).

Within KDE, the size and shape of a home range is dependent, in part, on the bandwidth selected. The KDE method places a kernel over each recorded animal location (e.g., GPS location) and calculates the density of locations within each kernel, the radius of which is determined by the chosen bandwidth. The average density of all overlapping kernels is then determined at each point on the estimation surface. This produces a Utilization Distribution (UD); a continuous three-dimensional surface that estimates the intensity or probability of use by an animal (Van Winkle 1975, Seaman and Powell 1996, Millspaugh et al. 2006). The outer bounds of a home range is then delineated based on a fixed percentage or volume contour of the UD, typically 95% (Laver and Kelly 2008). Researchers often make use of a variety of UD contours to either assess different delineations of a home range (e.g. Börger et al. 2006b) or those areas within the home range associated with higher levels of use (e.g., 50% core area; Webb et al. 2007, Hébert and Weladji 2013).

The bandwidth used in a KDE will determine the level of smoothing applied to the data which, in consequence, specifies the size and shape of an animal's home range or contours assessed within the home range (Seaman and Powell 1996, Seaman et al. 1999, Gitzen and Millspaugh 2003, Fieberg 2007). Fine-scale bandwidths (i.e., small bandwidths) cause nearby animal locations to have a stronger influence on the resulting KDE surface and can underestimate home range size (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001). Conversely, coarse-scale bandwidths (i.e., large bandwidths) assign a greater influence to distant animal locations. The net result is a smoothing of "peaks" and "valleys" of the distribution, thus providing a more general representation of an animal's UD (Worton 1989, Seaman and Powell 1996, Kernohan et al 2001). Thus MAUP may arise in home range analyses that use KDE because the choice of bandwidth and contour will both determine the specific delineation (i.e. zoning) of and size (i.e. geographical extent) of the areas analysed and, as a result, determine the values of measured habitat features within these areas (Boyce et al. 2003, Borger et al. 2006a). In addition, since the effect of aggregating topographic habitat variables such as, for example, slope, can vary depending on the extent or geographic location of analyses (e.g., Wolock and Price 1994, Zhang and Montgomery 1994, Gao 1997), the choice of bandwidth or UD contour in KDE could potentially alter the effect of aggregation on variable values. In other words, the change that occurs in the values of habitat variables at coarser resolutions may vary when assessed within home ranges created using different bandwidths or UD contours.

The overall objective of this study was to determine the potential effect of MAUP on home range analyses in terms of the resolution at which variables are assessed and how the observed change in values varies with different delineations of home range outer bounds (i.e., bandwidths) and areas of higher use (i.e., contours). To meet this objective we used as a model system a population of northern woodland caribou (*Rangifer tarandus*) and assessed the changes in topographic summary statistics measured within each caribou's home range at different resolutions. Northern caribou are located throughout north central and western BC and utilize altitudinal migrations to subalpine and alpine habitats during calving and summer to avoid predation by wolves (Bergerud et al. 1984, Bergerud and Page 1987, Johnson et al. 2004). They use low elevation pine forests in winter to forage on lichens by cratering, especially on south facing slopes (Bergerud et al. 1984, Bergerud and Page 1987). Thus seasonal home range selection of northern caribou is, in part, driven by slope and elevation (Poole et. al. 2000, Culling et al. 2005, Gustine et al. 2006, DeCesare et al. 2012). Furthermore, because the temporal scale at which habitat analyses are conducted can affect the observed habitat use patterns of caribou (Börger et al. 2006a, Basille et al. 2012, van Beest et al. 2013), our analyses also includes a seasonal component.

For our research we used high frequency GPS telemetry data from 13 northern woodland caribou of the Level Kawdy herd, BC to create seasonal home ranges coupled with topographic data from a Digital Elevation Model (DEM) to address the following specific questions:

1. How do the values of topographic variables measured within the contours of each seasonal home range change at coarser resolutions (in terms of magnitude and direction) and is there more change at certain levels of aggregation?
2. How do the observed changes in topographic values at coarser resolutions vary between the contours of each seasonal home range and between seasonal home ranges?
3. How do the observed changes in topographic values with increasing resolution vary when different bandwidths are used to create seasonal home ranges?

We hypothesized that the aggregation of topographic data within the home ranges of northern caribou would result in the homogenization of both elevation and slope values (i.e. a decrease in variance), as well as a decrease in the mean of slope. We also hypothesized that due to changes in the size, shape and geographical area in which they are analysed, the degree to which values of elevation and slope change at coarser resolutions would vary depending on the bandwidth used to create each home range, as well as the contour or season in which they were assessed.

4.3 Methods

4.3.1 Caribou data

We used GPS telemetry data obtained from 13 northern woodland caribou of the Level Kawdy herd, British Columbia (58° N, 131° W) (Figure 4.1) equipped with ATS G2110E radio-collars (Advanced Telemetry Systems, ATS, Isanti, MN). The collars for these 13 caribou were deployed in October 2011 (eight caribou) and March 2012 (five caribou). The transmission rate of collars was one per day with the exception of a period between March 3rd-9th (2012) where transmission rate was five-six per day for eight of the caribou as identified in Table 4.1.

Caribou telemetry data were categorized into the following seasons: Winter, calving, summer, rut and fall. There are a variety of methods employed to separate caribou location data into seasons. For example, some investigators use pre-determined, somewhat arbitrary dates for each season (e.g., Poole et al. 2000, James et al. 2004, Said et al. 2005, Wittmer et al. 2007). However, these dates may vary between herds, between years within a particular herd and even between individuals within a herd (Hatler 1986, Culling et al. 2005, Jones et al. 2006). Therefore, delineation of seasons based on the data (e.g., individual movement, habitat use) is important when investigating animal space use, as incorrect or inappropriate division of temporal scale may affect observed patterns or inferences (Börger et al. 2006a. Basille et al. 2012, van Beest et al. 2013).

The dates of each season for individual caribou were determined based on distinct shifts in values of net displacement, elevation and slope. Net displacement is a measure of the distance of a particular recorded caribou location from a point of origin and has been used, for example, by some authors to aid in identifying seasons for wolves (Lesmerises et al. 2012), moose (Dettki and Ericsson 2008) and caribou (Courbin et al.

2009). The point of origin was the first recorded GPS location for each caribou. We plotted values of net displacement against time (Julian day) and overlaid the values of elevation and slope extracted at each caribou location from a 25m resolution Digital Elevation Model (DEM). Using these plots of net displacement and dates identified by other authors (e.g., Poole et al 2000, Culling et al. 2005, Jones et al. 2007) as guidelines we identified seasons for each caribou based on distinct shifts in location as coupled with distinct shifts in elevation and slope. Distinct shifts in location were identified as a sharp directional increase or decrease in values of net displacement. These distinct shifts were both preceded and followed by relatively stable values of net displacement and accompanied by a change in the range of elevations and/or slopes occupied by a caribou.

Selected season dates varied for each caribou (Table 4.1). We were not able to discern a calving season for two of the caribou (D030457 and D030465). Therefore, only four seasons were subsequently analyzed for these two caribou. In addition, we identified two separate winter locations for caribou D030468. All other caribou migrated to a well-defined wintering area between Dec 4th and Jan 19th where they remained until the spring whereupon they travelled to calving areas. However, D030468 migrated to its winter area on Dec 20th, remained there until Jan 24th, then traveled approximately 87 km to a secondary wintering grounds where it remained until spring. Therefore these two sets of winter locations for D030468 were analysed separately in all further analyses.

4.3.2 Kernel Density Estimation

4.3.2.1 Home range delineation

Utilization distributions and home ranges for each of the thirteen Level Kawdy caribou were produced using fixed kernel density estimation (Worton 1989) in the

ArcGIS 9.3 (ESRI 2008) extension Home Range Tools (HRT, Rodgers et al. 2007). KDE is a non-parametric probability density function used to estimate an animal's home range or UD based on known locations of that animal. A kernel (probability density function) is placed over each observation (e.g., radio-telemetry location) and a density estimate for that location is then determined based on the average of the calculated densities that overlap at that point. The estimated probability density function, $\widehat{f_h}(x)$ of an unknown UD is calculated using:

$$\widehat{f_h}(x) = \frac{1}{nh^2} \sum_{i=1}^{n} K \left[\frac{x - X_i}{h} \right]$$

where *n* is the number of locations, *K* is the kernel function used (e.g., bivariate normal/Guassian, Epanechnikov), *h* is the smoothing parameter or bandwidth of the kernel, *x* is the *x, y* location at which the estimate is calculated and *X* represents the *x, y* coordinates of the *n* locations in the dataset (Silverman 1986, Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001).

To investigate the possible effect of home range size and shape on the impact of aggregating topographic data, we created three home ranges per caribou for each season using different proportions (1.0, 0.8, and 0.6) of the reference bandwidth (h_{ref}). We selected these as representative of the range of proportions of h_{ref} used in the literature (e.g., Bertrand et al. 1996, Kie et al. 2002, Berger and Gese 2007, Jaques et al. 2009). The reference method selects a bandwidth based on sample size and the standard deviation of each observed x,y location (Worton 1989, Gitzen 2006):

$$h_{ref} = n^{-1/6} \sqrt{\frac{s_x^2 + s_y^2}{2}}$$

where s_x^2 and s_y^2 are estimates of the variances of the point locations in the x and y direction respectively (Worton 1995). As a result, h_{ref} is appropriate if data are unimodal (i.e., have one center of activity) and are normally distributed in bivariate space (Worton 1989, 1995). However, animal location data are typically not normally distributed (Blundell et al. 2001, Downs and Horner 2008, Kie et al. 2010) and often have multiple modes (centers of activity) (Seaman and Powell 1996, Seaman et al. 1999, Börger et al. 2008). In these cases, h_{ref} tends to produce a bandwidth value that is too large and over-smoothes the data (Kie et al. 2010), in which case using a proportion of the reference bandwidth (scaled-h_{ref}) will sometimes be recommended (Rodgers et al. 2011) as it can produce less biased estimates of home range size (Worton 1995).

The number of locations used to create each seasonal home range ranged from 16 to 168 (Table 4.1). This number was occasionally lower (see Table 4.1) than that recommended by Seaman et al. (1999) (minimum 30, > 50 preferred) and Girard et al. (2002) (30-100 for seasonal home ranges). This discrepancy was due to a collar transmission rate of one per day and the inherently short nature of certain seasons (e.g., calving). Although not all caribou seasonal home ranges met the recommended minimum number of locations indicated above, they did meet the minimum of one location per day as recommended by Girard et al. (2002). In addition, despite the presence of spatial autocorrelation in the seasonal subsets of location data for our caribou, as indicated by values of the Swihart and Slade index (Swihart and Slade 1985a) > 0.6, and Schoener index (Schoener 1981) >2.4 or <1.6 (Swihart and Slade 1985b, Rogers and Kie 2011), all recorded locations were used as recommended by De Solla et al. (1999), Blundell et al. (2001) and Fieberg (2007). The Rut home range produced for D030470 using h_{ref} was approximately 3.3km^2 and was deemed too small to assess the impact of changing resolution and thus was not included in any further analyses

4.3.2.2 Contour delineation

To investigate the effect of contour selection on changes in values of slope and elevation with increasing resolution, four contours were delineated within each home range: The 25, 50, 75 and 95% volume contours of the UD. The 50 and 95% contours were selected based on their common use in the home range literature (as discussed previously), and the 25 and 75% contours were selected as (roughly) logical mid-points between the other two contours. All subsequent values and change in values of slope and elevation were calculated within the context of each of the four contours of a home range.

4.3.3 Topographic data

To assess the effect of resolution on measured values of slope and elevation within each seasonal contour we used a 25m Digital Elevation Model (DEM) and aggregated it to three additional resolutions (75, 125, and 175m) using bilinear interpolation. This method assigns the new, coarser-resolution cell, a value based on the weighted average of the nearest four cells (Wu et al. 2005). This resampling method was selected over other methods, such as nearest neighbour and cubic convolution, as it is commonly used (e.g., Chaubey et al. 2005, Descleé et. al. 2006, Bader and Ruijten 2008, Kerns et al. 2009) and because the specific method used has less impact than the act of resampling itself (Rees 2000, Wu et al. 2005, 2008). Slope (%) values were calculated at each resolution (i.e., they were not calculated at the original 25m DEM and then resampled to coarser resolutions) in the spatial analyst extension of ArcGIS 9.3 (ESRI 2008). We then calculated the summary statistics, namely the mean ($\bar{x}$), standard deviation (SD), and coefficient of variation (CV) of slope and elevation, within each of the four contours of all home ranges at each DEM resolution.

4.3.4 Data analysis

4.3.4.1 Magnitude and direction of change

All statistical analyses were performed in SPSS (IBM 2013). We used pairwise multiple comparisons to determine whether the $\bar{x}$ of elevation or slope within each seasonal contour was significantly different ($p<0.05$) at each successive increase in DEM resolution (25-75m, 75-125m and 125-175m). Pairwise comparisons were conducted using either the Games-Howell (Games and Howell 1976) or Tukey-Kramer (Tukey 1953, Kramer 1956). The Games-Howell method is recommended in unbalanced designs (i.e., unequal sample sizes between groups) when variances are unequal (Keselman and Rogan 1978, Jaccard et al. 1984, Rafter et al. 2002, Ruxton and Beauchamp 2008). However, in unbalanced designs when variances are equal, the Games-Howell method can inflate the Family-Wise Error Rate (Rafter et al. 2002) and be less powerful than the Tukey-Kramer method (Jaccard et al. 1984, Rafter et al. 2002), which is the recommended alternative in these cases (Dunnett 1980a, Hayter 1984, Rafter et al. 2002).

Values of elevation and slope within each contour were not normally distributed (Kolmogorov-Smirnov test $p<0.05$). However, transformations were not applied to the data for two reasons. Firstly, both pairwise comparison methods (Games-Howell and Tukey-Kramer) use the studentized range distribution and are robust to non-normal data (Petrinovich and Hardyck 1969, Ramseyer and Tcheng 1973, Jaccard et al. 1984). Secondly, if the mean-variance relationship is not maintained after a transformation is applied, this can inflate type I error rate (McArdle and Anderson 2004). Variance homogeneity was assessed using the Brown-Forsythe (1974) modification of Levene's test (Lev_{med}), which uses the median instead of the mean of the data and is more robust when data are non-normal (Conover et al. 1981, Day and Quinn 1989). When results of Lev_{med} indicated variances were homogeneous, the Tukey-Kramer pairwise comparison method was used, otherwise the Games-Howell procedure was used.

Of all of the results of the above pairwise comparisons, it was those that indicated a significant difference ($p<0.05$) in $\bar{x}$ elevation or slope between resolutions that were then used to calculate the mean change in $\bar{x}$ ($\bar{x}_{\Delta\bar{x}}$), SD ($\bar{x}_{\Delta SD}$), and CV ($\bar{x}_{\Delta CV}$) for each combination of season, bandwidth and contour. In other words, we determined for each seasonal contour, the $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ of elevation and slope at the three increases in resolution at each of the three bandwidths. The $\bar{x}$ change in values of elevation and slope for each scenario were then used (as detailed in the following section) to assess how the change in elevation and slope values differed between seasons, contours, KDE bandwidths and at each increase in resolution.

To assess whether values of elevation and slope were consistently higher or lower within a particular contour/season at each increase in resolution (i.e., direction of change) we used the Exact Binomial Test of Proportions. This test is recommended for use specifically in the analysis of 2 x 1 contingency tables with small (<100) sample sizes (Richardson 1994). Also, because sample sizes were small (in our case ≤14) we used the exact form of this test, whereby p values are not estimated asymptotically but are instead calculated based on the exact distribution of the test statistic (Mehta and Patel 2011). All further analyses (see below) were performed on the absolute and/or directional values of $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$. However, directional $\bar{x}_{\Delta}$ values for a particular contour/season were only assessed in further analyses if the binomial test of proportions indicated a significantly higher proportion of change in one direction ($p<0.05$).

4.3.4.2 Pairwise comparisons of descriptive metrics

The $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ (hereafter referred to as the descriptive metrics when discussing all three) of each combination of contour, season and bandwidth at each increase in resolution were used to further explore the effects of:

4. *Contour choice*: We compared the descriptive metrics of elevation and slope between the contours within each season.
5. *KDE bandwidth*: We compared the descriptive metrics of slope and elevation within each contour/season between each of the three bandwidths used to create home ranges.
6. *Specific change in resolution*: We compared the descriptive metrics of slope and elevation within a contour/season/bandwidth between each successive increase in resolution.
7. *Season*: We compared the descriptive metrics of slope and elevation within each contour/bandwidth/change in resolution between each of the five seasons (winter, calving, summer, rut and fall).

All comparisons of $\bar{x}_{\Delta\bar{x}}$, $\bar{x}_{\Delta SD}$ and $\bar{x}_{\Delta CV}$ were performed using either the Tukey-Kramer, Games-Howell or T3 procedures for pairwise multiple comparisons. Normality of the descriptive metrics was tested using the Shapiro-Wilk test for normality (Shapiro and Wilk 1965). Homogeneity of variances was tested using either the Levene's ($\mathrm{Lev}_{\mathrm{mean}}$; Levene 1960) or the Brown-Forsythe (1974) modification of Levene's test ($\mathrm{Lev}_{\mathrm{med}}$). The $\mathrm{Lev}_{\mathrm{med}}$ method is appropriate for samples with non-normal distributions, although it has a reduced power (higher Type II error rates) if distributions are in fact normal (O'Brien 1978, Games et al. 1979). This exception is especially notable with smaller sample sizes. In the instances where the distribution of both samples were in fact normal (Shapiro-Wilk, $p<0.05$), the Lev_{mean} method of testing variance homogeneity was used. If the results of the Lev_{mean} or Lev_{med} tests indicated variances were homogeneous, the Tukey-Kramer pairwise comparison method was used, otherwise the Games-Howell method was used. In cases where variance homogeneity could not be accurately assessed due to small sample sizes or differences in the distribution of each sample (i.e., one normally distributed and the other not), Dunnett's (1980b) modification (T3) of Tamhane's (1979) pairwise comparison procedure was used. Similar to the GH method, the T3 method can be used when variances are not homogeneous, but is typically considered to be less powerful than the GH method (Rafter et al. 2002). Although it is less powerful than the GH method, the T3 method has not been found to have the same inflated Type I error rate in cases where variances are in fact homogeneous (Jaccard et al. 1984, Rafter et al. 2002).

4.4 Results

At each increase in resolution, the changes in topographic values within a contour/season were assessed at each of the three bandwidths used in KDE. Results (i.e., the change in values) obtained at each bandwidth were compared and no significant differences were found ($p>0.05$). For example, as resolution increased from 25 to 75m, the $\bar{x}_{\Delta\bar{x}}$ of elevation in the 50% contour of summer was not significantly different when home ranges were created using h_{ref}, $0.8h_{ref}$ or $0.6h_{ref}$. However, the results of other comparisons (e.g., comparisons of the descriptive metrics between contours of a season) were not consistent at each of the three bandwidths used. Therefore, to illustrate our findings in this section, we are reporting the results for the largest bandwidth at which significant results were found. More detailed numerical results of pairwise comparisons are presented in Tables D.1-D.4 (Appendix D). These tables include, for example, the 95% confidence intervals of pairwise comparisons, as well as the bandwidths at which significant results were found.

4.4.1 Range and direction of change in topographic variables

As resolution increased, there was little change in values of elevation and no significant differences were found ($p>0.05$), whereas conversely, slope changed significantly ($p<0.05$). Within each contour/season, both the $\bar{x}$ and SD of slope were lower at coarser resolutions, whereas CV of slope both increased and decreased (Table 3.2). The descriptive metrics of slope varied by contour and season, as well as by the specific change in resolution (as detailed below) of up to a maximum of 6.1%, 4.7% and 0.28 for the $\bar{x}$, SD and CV respectively (Table 4.2). There was also a significant difference in the proportion (p) of caribou's home ranges that showed a decrease/increase in CV. For some seasonal contours there was a higher proportion of home ranges that experienced a decrease in CV at coarser resolutions ($p<0.05$, figure 4.2). This occurred, for example, for all contours of the rut (p = 0.85-1.0) and summer (p = 0.85-1.0), the 25, 50 and 75% contours of the calving (p = 0.90-1.0) and winter (p = 0.85-1.0) ranges, and the outer two contours of the fall (p = 0.85-1.0). The trend in decreasing values of CV within a particular contour/season was not always consistent at each bandwidth (h_{ref}, 0.8 h_{ref}, 0.6 h_{ref}) or specific change in resolution (25-75m, 75-125m and 125-175m) (Figure 3.2).

4.4.2 Difference between changes in resolution

To determine whether there was a greater amount of change in values of slope at a particular resolution we compared the descriptive metrics of slope within the contours of each season between each successive change in resolution (i.e., 25-75m vs. 75-125m and 75-125m vs. 125-175m). The $\bar{x}_{\Delta CV}$ of slope did not differ significantly between successive changes in resolution for any contour/season ($p>0.05$). However, the $\bar{x}_{\Delta\,\bar{x}}$ and $\bar{x}_{\Delta SD}$ were both significantly different between each successive change in resolution within the fall, winter and rut ($\bar{x}$ only) ranges (Figures 3.3 and 3.4) ($p<0.05$).

4.4.3 Difference between contours

The effect of increasing resolution on the $\bar{x}$, SD and CV of slope was significantly different between contours of the fall and rut home ranges ($p<0.05$) when resolution increased from 75-125m and 125m-175m (figure 3.5). In the fall ranges, $\bar{x}_{\Delta\,\bar{x}}$ and $\bar{x}_{\Delta SD}$ were higher in the 95 and/or 75% contours relative to one or both of the two inner contours (depending on the bandwidth and specific change in resolution). In the 25% contour of the rut home ranges, $\bar{x}_{\Delta\,\bar{x}}$ was lower relative to the 95% contour and $\bar{x}_{\Delta SD}$ was lower relative to both the 75 and 95% contours. The $\bar{x}_{\Delta CV}$ of slope was higher in the 25% contour relative to the 75% contour in the fall home ranges at h_{ref} only.

4.4.4 Difference between seasons

As resolution increased, the descriptive metrics of slope were greater within certain seasons relative to others ($p<0.05$) (Figure 3.6). However, this varied depending on the specific contour, change in resolution and bandwidth. The $\bar{x}_{\Delta\,\bar{x}}$ of slope was higher in the contours of the calving and summer home ranges relative to other seasons. Differences in $\bar{x}_{\Delta\,\bar{x}}$ between seasons typically occurred at the initial increase in resolution (from 25 to 75m). In other words, the magnitude of change in slope was, in general, not significantly different between seasons past the initial change in resolution. The exception to this was the $\bar{x}_{\Delta\,\bar{x}}$ in the 95% contour of the calving season, which was higher relative to winter, at the second increase in resolution (75-125m).

Differences in $\bar{x}_{\Delta SD}$ between seasons were found at each increase in resolution (25-75m, 75-125m and 125-175m), and, similar to changes in $\bar{x}$ slope, were frequently higher in contours of the calving and summer home ranges (77% of all differences between seasons) ($p<0.05$). The $\bar{x}_{\Delta SD}$ was lower in the 95% contour of the winter ranges relative to all other seasons, at one or more increase in resolution.

Significant differences in $\bar{x}_{\Delta,CV}$ between seasons occurred at the initial (25-75m) and last (125-175m) increases in resolution and were more varied (in terms of which seasons had higher $\bar{x}_{\Delta CV}$) compared to $\bar{x}_{\Delta\,\bar{x}}$ and $\bar{x}_{\Delta SD}$. For example, in the 25% contour of the winter ranges, $\bar{x}_{\Delta,CV}$ was higher relative to summer at the initial increase in resolution, (0.8 h_{ref} and 0.6 h_{ref}) but lower than fall at the last increase in resolution (h_{ref}). In addition, the $\bar{x}_{\Delta,CV}$ in the winter ranges was higher compared to the 75% contour of the calving ranges (0.8 h_{ref}) but lower than the fall and rut ranges in the 25% (h_{ref}) and 95% (h_{ref}) contours respectively.

Differences in the descriptive metrics between seasons varied depending on bandwidth. For example, significant differences in $\bar{x}_{\Delta\,\bar{x}}$ between seasons were frequently found at all bandwidths in the 95% contour, at the smallest bandwidth (0.6 h_{ref}) within the 25% contour, and had no consistent pattern within the 75% contour, whereas differences in $\bar{x}_{\Delta CV}$ between seasons were found only at h_{ref} within the 95% contour and 0.8h_{ref} within the 75% contour.

4.5 Discussion

Studies of wildlife habitat use or habitat selection often use home range analyses (e.g. Dickson and Beier 2002, Ciarniello et al. 2007, Wittmer et al. 2007). The aggregation of habitat data used in these analyses (e.g., to coarser resolutions) can potentially alter the outcome of statistical analyses and thus ecological (Boyce 2006, Meyer and Thuiller 2006). A major issue of scale in many studies where there is aggregation of spatial data has been described as the Modifiable areal Unit Problem (Gehlke and Biehl 1934, Openshaw 1984). In the last 15 years or so, the role of MAUP has been investigated in studies of wildlife habitat interactions especially in terms of using thematic land cover data to determine the effect of resolution on model performance (e.g., Karl et al. 2000, Betts et al. 2006, Li et al. 2006, Guisan et al. 2007, Stickler and Southworth 2008, Carter et al. 2010, Gottschalk et al. 2011, Song et al. 2013). However, the potential for the resolution of topographic data in studies of habitat use or selection has received little attention despite its relative importance for certain species. For example, Bowyer et al. (1998) found that neonate black-tailed deer (*Odocoileus hemionus columbianus*) avoided areas with a high degree of terrain ruggedness (a combined measure of SD of slope and aspect). Similarly, Dickson et al. (2005) found that cougar (*Puma concolor*) movement paths were generally along areas with gentler slopes relative to what was available in the landscape.

We examined the issue of aggregating slope and elevation habitat data in the construction of woodland caribou home ranges (Poole et al. 2000, Culling et al. 2005, Gustine et al. 2006, Jones et al. 2007). Our specific objectives were to determine how aggregating topographic data to coarser resolutions changed the summary statistics of elevation and slope within the home ranges of 13 northern woodland caribou and how these observed changes varied with the use of different bandwidths and UD contours. Home ranges were created using the commonly employed Kernel Density Estimation (Laver and Kelly 2008). The degree to which aggregation changes the values or spatial pattern of a variable is, in part, dependent on the characteristics of the landscape in which changes are assessed (Fisher and Tate 2006, Lin et al. 2008). In KDE, the choice of bandwidth and volume contour determines the size and shape of the home range and thus determines the habitat characteristics found within each analysis unit (i.e. home range). What follows is the discussion of our major findings in terms of the magnitude and direction of change in slope and elevation values, and how the observed changes differed between each increase in resolution and the four contours within and between each season.

4.5.1 Change in slope and elevation

Understanding the degree to which aggregating data to coarser resolutions affects the observed values and spatial patterns of said data is critical to understanding the potential impact on subsequent analyses. For example, land cover/thematic data are often aggregated and, consequently, rare or small habitat classes are often “lost” (Turner et al. 1989, Gottschalk et al. 2011). Researchers may therefore fail to detect associations between a particular species and the use of those rare habitat types (Gottschalk et al. 2011). Within our study, the mean and SD of slope both decreased at coarser resolutions for all contours/seasons. This indicates homogenization of slope within the home ranges of northern woodland caribou and thus suggesting caribou are occupying areas with lower slope values. This observed homogenization of slope summary statistics within the contours of caribou home ranges has the potential to alter the results of habitat analyses by decreasing the relative importance of, and/or apparent selection for, steeper slopes or more variable terrain (e.g., Boyce et al. 2003).

We did not find significant changes in elevation within the contours of northern caribou seasonal home ranges with increasing resolution. By comparison, Usery et al. (2004) resampled a DEM to seven resolutions ranging from 30m to 1920m and tested the correlation between the coarser resolution data and the original 30m data. They found a continual decrease in the correlation between the elevation values at 30m and coarser resolutions (2004). Other studies that have included elevation as a variable of interest in models of, for example, habitat suitability or species distribution, found changes in model performance (Li et al. 2006, Song et al. 2013) and the relative importance of elevation at coarser resolutions (Li et al. 2006).

4.5.2 Differences in observed change with increasing resolution

Changes in variable values when data are aggregated to coarser resolution may not follow a consistent linear pattern with each level of aggregation. Depending on the specific variable and the landscape, the observed difference in values and hence spatial pattern may be more pronounced when data are aggregated within a certain range of resolutions (Wu et al. 2008, Lin et al. 2008, Wiens 1989). This has been observed in a number of studies investigating the effect of aggregation of, for example, topographic variables (e.g., Wu et al. 2005, 2008, Deng et al. 2007), metrics of landscape structure (e.g., Wu et al. 2002, Shen et al. 2004, Wu 2004), and measures of spatial autocorrelation (e.g., Qi and Wu 1996). These studies found that most of the change in variable values occurred within a limited range of the resolutions examined (e.g., typically at the first few aggregation levels). Our findings are in agreement with those of, for example, Wu et al.

(2005) and Deng et al. (2007), in that there was less change in slope values with each successive increase in resolution. However, statistically significant differences in the amount of change between each increase in resolution were only found for the mean and SD of slope in contours of the fall, rut and winter ranges.

The change that occurs, or the variability observed, in values at a particular scale is dependent on how the scale of observation (e.g., resolution) matches the spatial pattern of the phenomena being measured (Wiens 1989, Atkinson and Curran 1997). The resolutions at which a large or conversely little degree of change occurs can vary depending on the variable of interest, as well as landscape in which it is measured (e.g., Marceau et al. 1994, Gao 1997, Marceau and Hay 1999, Lin et al. 2008). The fall, rut and especially winter home ranges of northern caribou are characterized by lower elevations and slopes relative to summer and calving (Culling et al. 2005), as was the case, in terms of the $\bar{x}$ and SD of slope, in the home ranges of the Level Kawdy caribou (Table A.3, Appendix A). The initial increase in resolution (25-75m) in these seasons (fall, winter and rut) may have averaged out most of the variability in slope and as a result subsequent increases in resolution resulted in significantly less change in slope values. The detection of selection for these areas within the greater landscape (e.g., 2nd order selection *sensu* Johnson 1980) is partially dependent on differences in the variability between areas considered to be used (the home range) and available (the greater landscape) to the animal (Boyce 2003, Ciarniello et al. 2007). The homogenization of slope values within these ranges (thus a reduction in slope variability) could potentially increase apparent selection (2nd order) for lower slopes during these seasons. In addition, because a significantly higher amount of variability was lost at the initial increase in resolution (25 – 75m), this indicates that the effect of aggregating data on selection analyses may be most pronounced when DEM resolution is aggregated, for example, from 25 to 75m. Thus a further aggregation of data (i.e., to resolutions coarser than 75 or 125m) may see little change in the degree of selection by caribou for lower slopes in the fall, winter and rut seasons.

4.5.3 Differences in observed change between contours and seasons

The effect of changing resolution is known to vary between landscapes as a result of inherent heterogeneity (Theobald 1989, Karl et al.2000, Fisher and Tate 2006, Lin et al. 2008, Guo et al. 2010). The aggregation of DEM resolution on values of slope in particular has been shown to vary depending on the variability in topography. For example, a number of studies have found that when aggregating DEMs to coarser resolutions there is typically a greater amount of change in slope values in areas characterized by steeper or more variable slopes (e.g., Deng et al. 2007, Wu et al. 2008). In the home ranges of the Level Kawdy caribou, the change in mean and SD of slope was typically higher in contours of calving and summer seasons (74% of all differences between seasons) and lower in the winter and rut home ranges (68% of all differences between seasons). The greater amount of change in slope in certain seasons may be the result of differences in the variability of slope within each of these regions.

In the winter, northern mountain caribou select regions characterized by contiguous tracts of mature forest located in low elevation areas with only moderate-to-gentle slopes (Wood 1996, Jones et al. 2007, Culling et al. 2005). Conversely, in the calving and summer seasons, northern caribou make use of areas with higher elevations and steeper slopes (Wood 1996, Bergerud et al. 1984, Gustine et al. 2006, Culling et al.

2005). The mean and SD of slope in the winter home ranges caribou in this study were significantly lower compared to slope values in the contours of the calving and summer (Table A.3, Appendix A). Thus, differences in the topographic variability between seasonal home ranges potentially led to the differences observed in the change in slope values with increasing resolution.

The variation between seasons (in terms of changes in slope at coarser resolutions) could result in seasonal differences in the effect of aggregation on habitat selection analyses. As discussed previously, identifying selection for certain habitat features is dependent on the relative variability of those areas considered used and available to an animal (Boyce 2003, Ciarniello et al. 2007). Therefore, the effect of aggregating DEM resolution on the outcome of habitat selection analyses of woodland caribou may be greater (i.e., result in more change in the degree of apparent selection) within those seasons where the change in slope values was higher (e.g., calving and summer). Furthermore, compounding this effect could be the higher importance of, or selection for, certain slopes in specific seasons. For example, in the calving season, higher elevations and steeper slopes are used as a predator avoidance tactic (Bergerud and Paige 1987, Gustine et al. 2006) or, in winter, when snow pack and forage availability are inextricably linked to the use of different elevations and slopes (Wood 1996, Jones et al. 2007). Other studies assessing the impact of resolution in resource selection analyses have found a greater impact in terms of changes in model performance for individuals that exhibit a higher degree of selectivity or have more specific habitat requirements (Carter et al. 2010, Gottschalk et al. 2011). For example, Gottschalk et al. (2011) found that while increasing habitat variable resolution led to a decrease in bird species-habitat model performance, and even more so for birds classified as specialist species.

4.5.4 Effect of bandwidth

The effect of aggregating the resolution of data can vary depending on the extent (i.e., area) at which analyses are performed. For example, Cai and Wang (2006) found that the change in the spatial autocorrelation of a topographic index (a measure of flow accumulation) with increasing DEM resolution varied depending on the spatial extent examined. Furthermore, Bar-Massada et al. (2012) found a complex interaction between avian species richness and landscape pattern metrics when they altered both the grain and extent of analysis. As a result of using different bandwidths in KDE, we expected that the change in home range size (and, hence, also contour size) would change the observed impact of aggregating resolution in the contours of each season. However, this was not the case as the observed changes in slope values within the contours of each season were not significantly different between each of the three bandwidths. Despite this, other comparisons of the change in slope values with increasing resolution, for example, between seasons or between contours, did vary depending on the specific bandwidth at which they were examined. Therefore, while the bandwidth used (e.g., h_{ref}) did not significantly change the effect of resolution within each combination of contour and season, it did have enough of an impact to alter the relative difference in observed change between different areas (seasons or contours). For example, relative to other seasons, the decrease in mean and SD of slope was significantly higher in the contours of the calving season but generally only at 0.8 and/or $0.6h_{ref}$. Therefore, when smaller bandwidths are examined, the calving ranges may see more of an impact when habitat selection analyses are done using coarser resolutions, whereas when larger bandwidths are used, the effect of aggregating topographic data on selection analyses may be more consistent for each season.

4.6 Conclusions

We sought to determine how aggregating the resolution of a DEM changed the values of slope and elevation measured within the seasonal home ranges of northern woodland caribou. The values of slope changed significantly when the original 25m DEM was aggregated to coarser resolutions. Conversely, no differences were found in the values of elevation at coarser resolutions, although this may have been the result of the methods used to detect change (e.g., pairwise comparisons of mean elevation). Further analyses should be conducted not only to identify how resolution affects the values of slope and elevation in other ways (i.e., not solely the mean, SD and CV), but also to identify if and how the change in values, variance and spatial distribution patterns of slope and elevation within caribou home ranges ultimately affect analyses of habitat use. A decrease in variability of habitat values can change the outcome of resource selection analyses (Boyce et al. 2003, Gottschalk et al. 2011), thus the homogenization of slope values in the home ranges of northern caribou has the potential to reduce the apparent selection of an animal for that variable. Further investigations should also be able to assess whether the level of homogenization of slope values observed in the northern caribou home ranges in this study is enough to significantly affect analyses of habitat use.

The differences found between seasons, as well as within seasons between different contours, are likely due to variations in topography between areas (in terms of variance, slope gradients, heterogeneity etc…). This seasonal variation in topography within home ranges of caribou can vary between different herds and even within a herd between individuals or years (Hatler 1986, Culling et al. 2005, Jones et al. 2006). Assessing the effect of resolution on topography in the home ranges of northern caribou would therefore benefit from the inclusion of data from other herds, as well as analysis over multiple years.

Figure 4.1 Ranges of northern woodland caribou herds (*Rangifer tarandus caribou*) in western Canada. (reproduced from: Environment Canada, 2012)

Table 4.1 Selected season dates for each caribou and sample sizes used to create seasonal home ranges.

	Season														
	Winter			**Calving**			**Summer**			**Rut**			**Fall**		
Caribou	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**	**Start**	**End**	**n**
D030452	Dec 27	May 4	119	May 23	Jun 15	23	Jul 5	Sep 11	69	Sep 12	Oct 24	41	Oct 25	Dec12	49
D030453	Dec 13	Apr 30	168	May 24	Jul 11	46	Jul 12	Sep 9	59	Sep 11	Oct 10	29	Oct 21	Dec25	66
D030457	Dec 23	Apr 10	142	n/a	n/a	n/a	May 22	Sep 6	104	Sep 14	Oct 20	37	Oct 21	Dec 12	53
D030460	Dec 27	Apr 16	90	May 24	July 1	39	Jul 2	Aug 22	52	Sep 12	Oct 22	41	Oct 23	Dec3	42
D030461	Jan 11	Apr 18	131	May 27	Jun 24	26	Jun 26	Sep 5	72	Sep 6	Oct 20	44	Oct 22	Dec7	47
D030462	Jan 17	Apr 24	130	May 22	Jul 6	46	Jul 17	Aug 26	39	Aug 27	Oct 19	53	Oct 21	Dec 5	44
D030464	Dec 20	Apr 28	164	May 27	Jul 11	46	Jul 22	Sep 11	52	Sep 12	Oct 22	38	Oct 23	Dec20	59
D030465	Jan 12	Apr 27	133	n/a	n/a	n/a	May 30	Sep 11	103	Sep 15	Oct 11	27	Oct 12	Dec7	57
D030466	Dec 28	May 10	130	May 30	Jun 25	27	Jun 26	Sep 13	77	Sep 14	Oct 16	33	Oct 17	Dec 10	53
D030468	Dec 21	Jan 24	36	May 13	Jun 16	35	Jun 18	Aug 25	69	Sep 7	Oct 17	39	Oct 18	Dec 13	55
	Feb 3	Apr 21	75												
D030470	Jan 19	Apr 28	101	May 24	Jun 8	16	Jun 10	Aug 11	61	Aug 12	Oct 25	70	Oct 26	Nov 27	33
D030471	Dec 23	Apr 16	148	May 22	Jul 9	35	Jul 13	Aug 29	31	Sep 7	Oct 22	32	Nov 10	Dec 6	26
D030490	Dec 4	May 5	148	May 21	Jun 17	28	Jul 3	Sep 10	67	Sep 15	Oct 20	36	Oct 21	Nov 24	35

Table 4.2 Range of descriptive metrics and maximum observed change in values of slope with increasing resolution (25-75m, 75-125m and 125-175m). Absolute as well as directional changes in CV of slope are provided, as CV is the only variable which both increased and decreased at coarser resolutions.

		Increase in Resolution																	
		25 - 75m						**75 – 125m**						**125 – 175m**					
Slope Variable	**Direction of Change**	$\bar{x}_{\Delta low}$	**(±SD)**	**-**	$\bar{x}_{\Delta high}$	**(±SD)**	**max**	$\bar{x}_{\Delta low}$	**(±SD)**	**-**	$\bar{x}_{\Delta high}$	**(±SD)**	**max**	$\bar{x}_{\Delta low}$	**(±SD)**	**-**	$\bar{x}_{\Delta high}$	**(±SD)**	**max**
Mean	**Decrease**	1.1	(0.4)	-	2.4	(0.4)	5.1	0.5	(0.3)	-	1.5	(1.8)	6.1	0.2	(0.03)	-	1.4	(1.0)	2.2
SD	**Decrease**	1.1	(0.5)	-	2.1	(0.6)	4.7	0.6	(0.4)	-	1.8	(1.2)	4.0	0.2	(0.1)	-	1.2	(0.9)	4.2
CV	**Absolute**	0.02	(0.02)	-	0.09	(0.08)	0.22	0.02	(0.01)	-	0.06	(0.10)	0.28	0.01	(0.01)	-	0.08	(0.03)	0.15
	Decrease	0.02	(0.01)	-	0.10	(0.08)	0.22	0.02	(0.01)	-	0.06	(0.10)	0.28	0.01	(0.01)	-	0.08	(0.03)	0.11
	Increase	0.01	(0.01)	-	0.07	(0.02)	0.14	0.01	(<0.01)	-	0.04	(0.04)	0.08	<0.01	(<0.01)	-	0.04	(0.07)	0.15

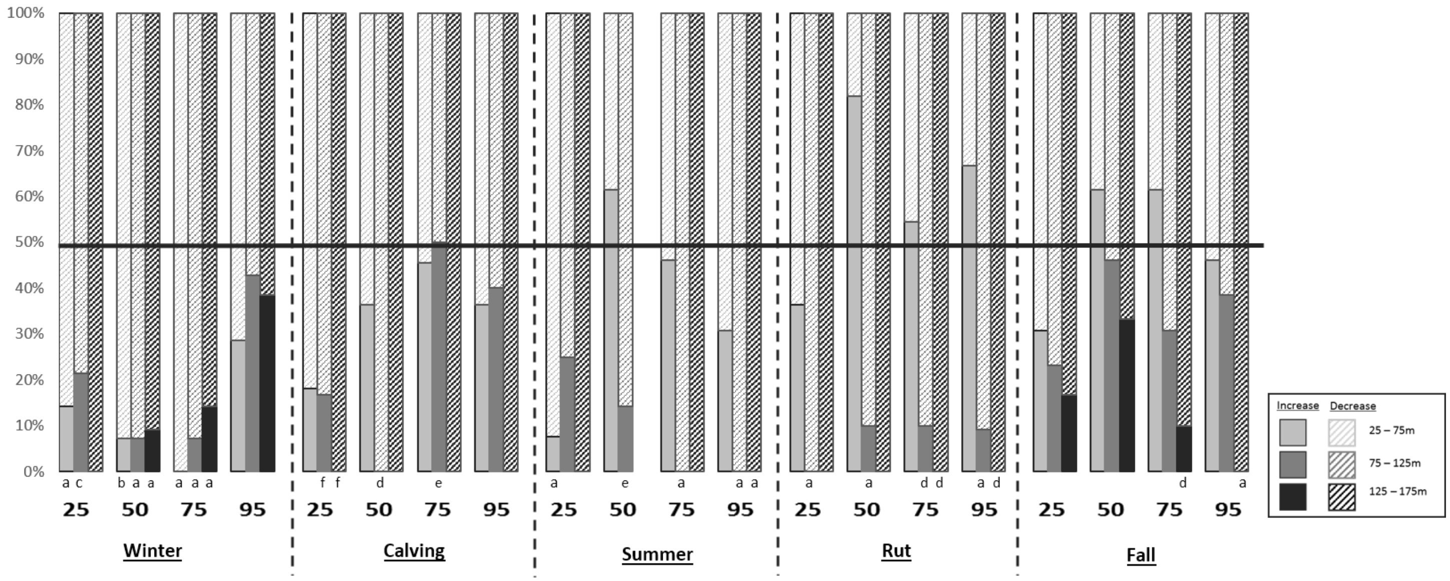

Figure 4.2 Proportion of increases vs. decreases in CV of slope with each change in resolution (25-75m, 75-125m and 125-175m) in the four contours (25, 50, 75 and 95) of the five seasonal home ranges (winter, calving, summer, rut and fall). Letters (a-f) indicate significant difference in proportions (exact binomial test of proportions, $p<0.05$) at one or more of the bandwidths examined (h_{ref}, $0.8h_{ref}$, and/or $0.6h_{ref}$).

Proportions significantly different at:
a = all bandwidths.
b = h_{ref} and 0.6 h_{ref}
c = 0.8 h_{ref} and 0.6 h_{ref}
d = h_{ref}
e = 0.8 h_{ref}
f = 0.6 h_{ref}

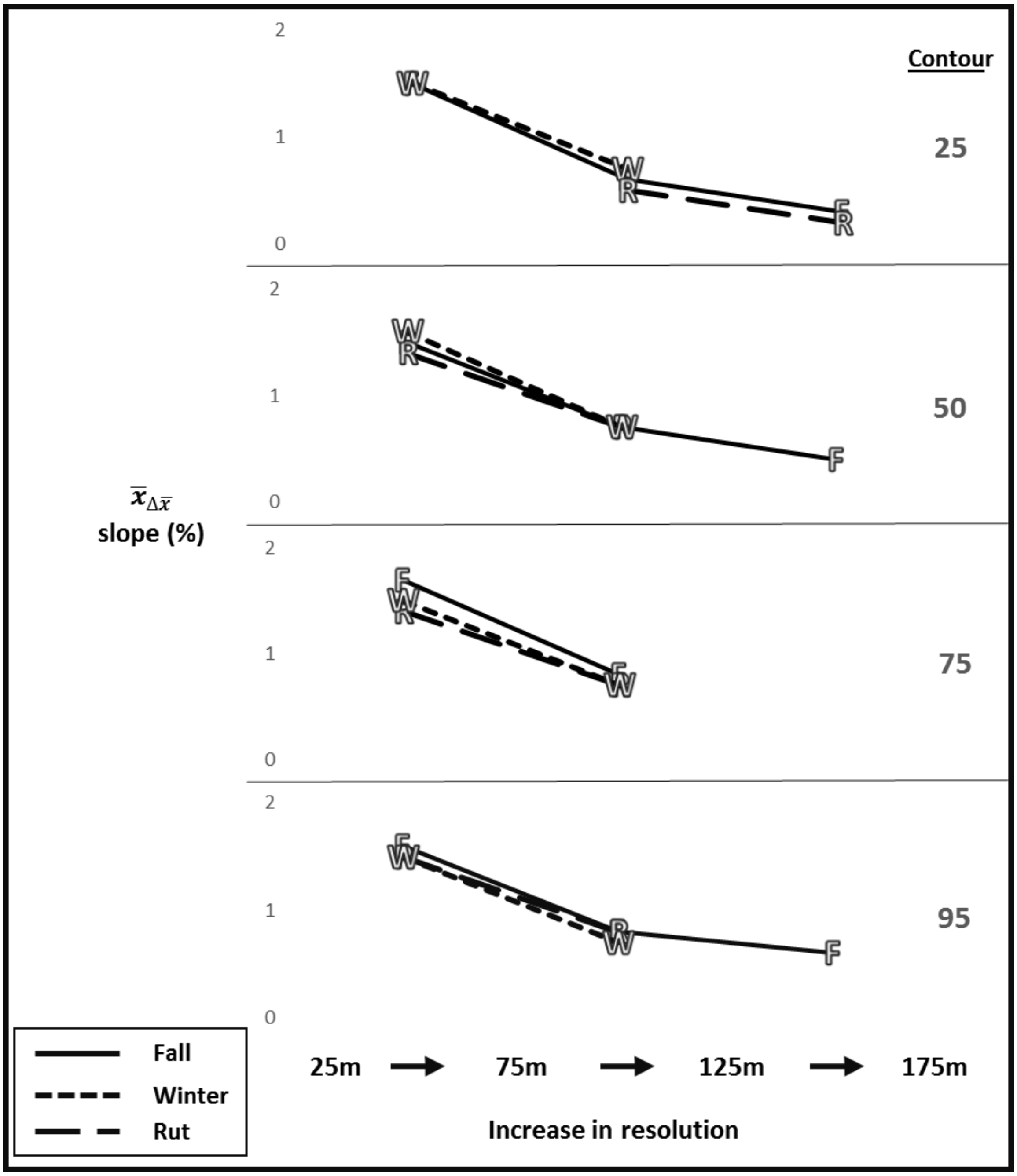

Figure 4.3 Statistically significant pairwise differences (p<0.05) in $\overline{x}_{\Delta\overline{x}}$ of slope with increasing resolution (25-75m vs. 75-125m, and 75-125m vs. 125-175m) within each contour (25, 50, 75 and 95) and seasonal home range (winter, calving, summer, rut and fall).

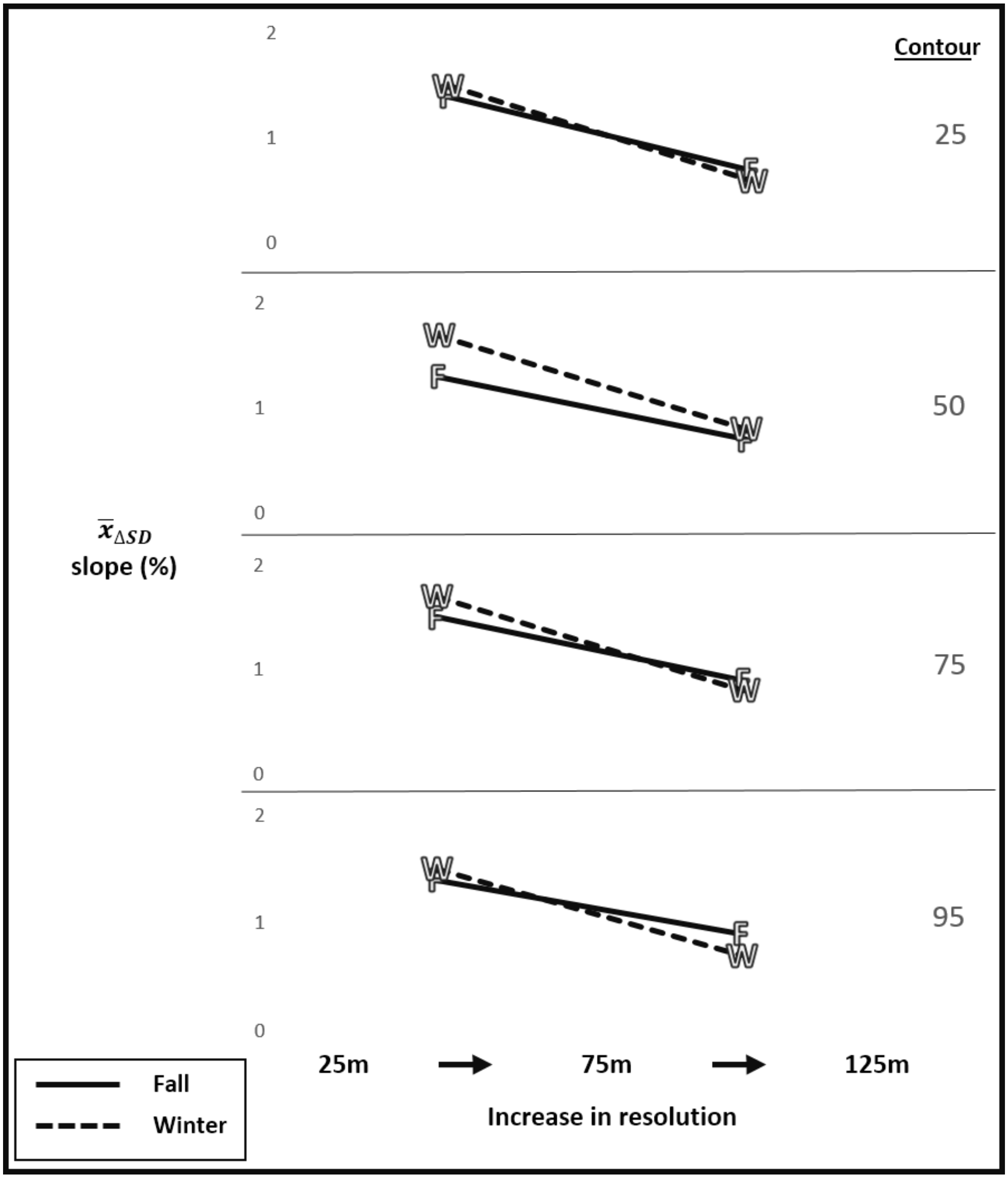

Figure 4.4 Statistically significant pairwise differences (p<0.05) $\bar{x}_{\Delta SD}$ of slope with increasing resolution (25-75m vs. 75-125m, and 75-125m vs. 125-175m) within each contour (25, 50, 75 and 95) and seasonal home range (winter, calving, summer, rut and fall).

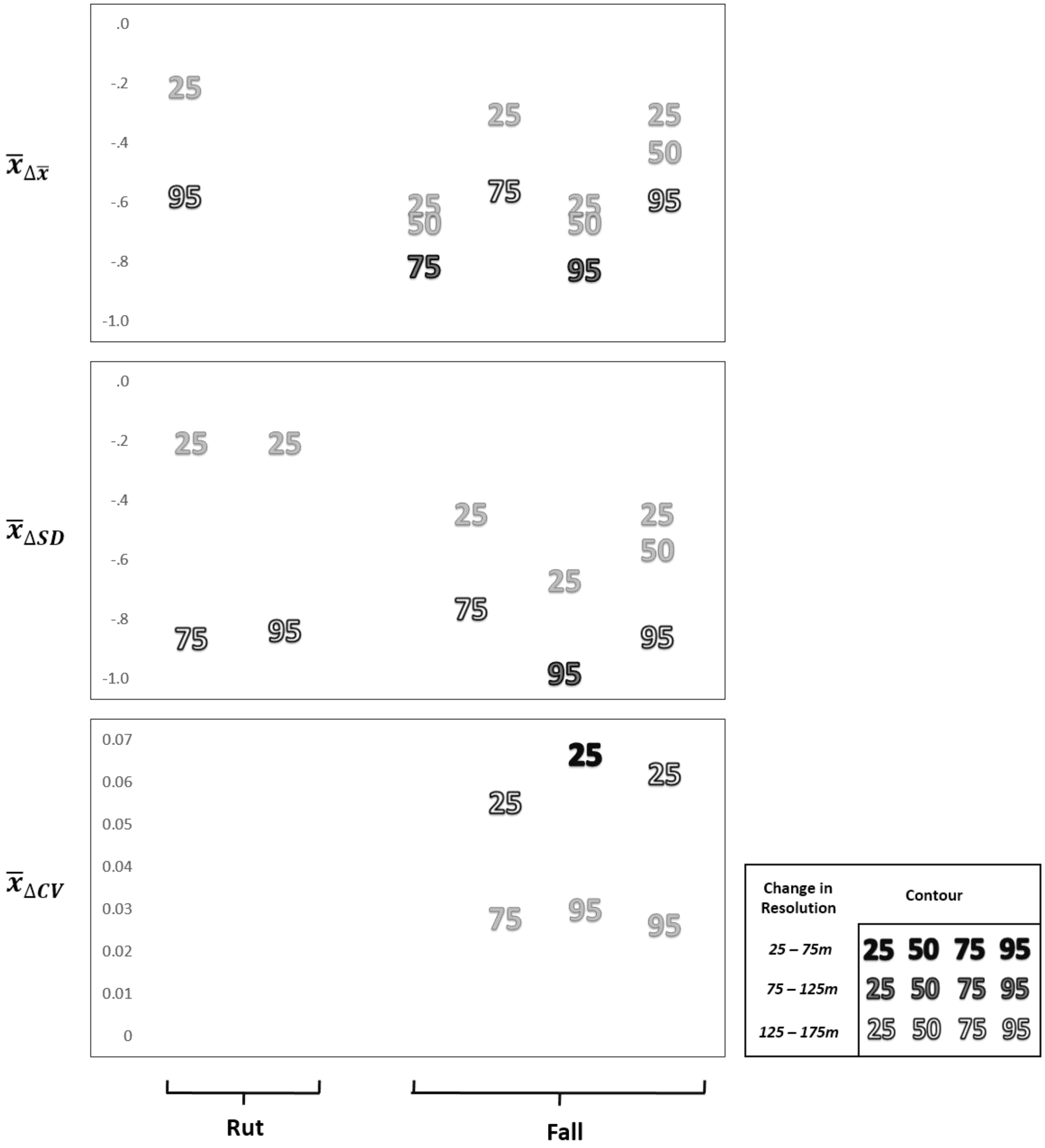

Figure 4.5 Significant pairwise differences ($p<0.05$) in the descriptive metrics of slope (%) between the four contours (25, 50, 75 and 95) of each seasonal home range (winter, calving, summer, rut and fall) at each increase in resolution (25-75m, 75-125m and 125-175m). Lightest grey represents the contours in which descriptive metrics of slope were lowest. Note, $\bar{x}_{\Delta CV}$ are the absolute values of differences.

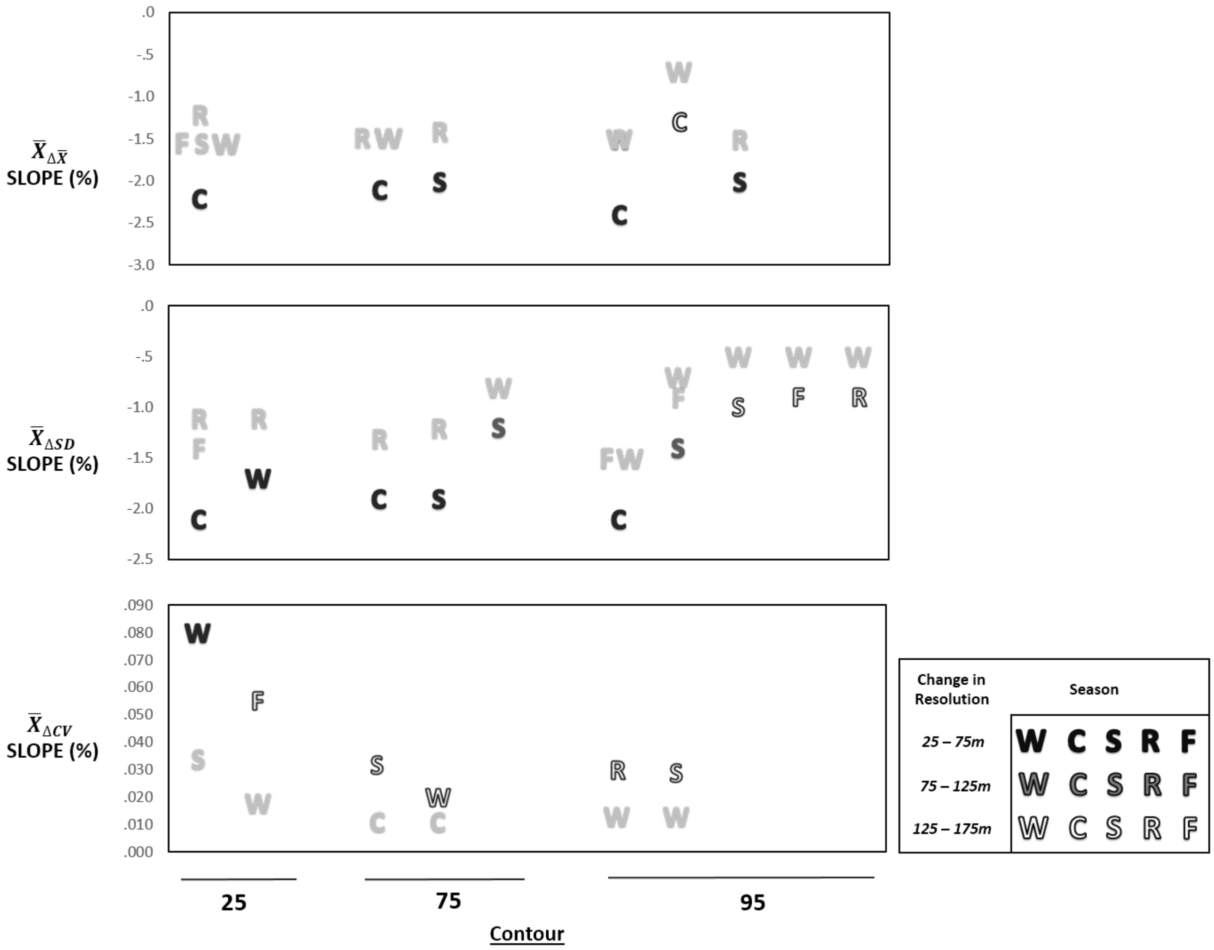

Figure 4.6 Significant differences (p<0.05) in the descriptive metrics of slope within each of the four contours (25, 50, 75 and 95) between each of the five seasonal home ranges (winter, calving, summer, rut and fall). Lightest grey represents the contours in which descriptive metrics of slope were lowest. Note, $\bar{x}_{\Delta CV}$ are the absolute values of differences.

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5 Conclusion

5.1 Discussion and Conclusion

The importance of the scale at which analyses are performed has long been recognized in ecological studies (e.g., Urban et al. 1987, Turner et al. 1989, Wiens 1989, Cooper et al. 1998). Jelinski and Wu (1996) introduced ecologists to a specific issue of scale known as the Modifiable Areal Unit Problem (MAUP; Gehlke and Biehl 1934, Openshaw 1984). MAUP refers to the issue when using spatial data, whereby changes to the size and shape of the areal units used can alter the outcome of statistical analyses and potentially ecological inferences. Since the introduction by Jelinski and Wu (1996), the potential impact of MAUP on the outcome of results has not only been recognized in a myriad of ecological studies (e.g., He and Gaston 2000, Koper and Schmiegelow 2006, Duchamp and Swihart 2008), but has also been the specific focus in a number of ecological investigations (e.g., He et al. 2007, Lechner et al. 2012). One specific area of ecological analyses in which the issue of MAUP has been largely overlooked is that of home range analyses.

Researchers often use the bounds of an animal's home range to assess the use or selection for certain habitat variables or resources (e.g., Gibeau 1998, Dickson and Beier 2002, McLoughlin et al. 2005). One technique in particular, the Kernel Density Estimation (KDE; Worton 1989), is frequently employed to delineate animal home ranges. The KDE method is based on an animal's utilization distribution (UD): An estimation surface representing the probability or intensity of use (Van Winkle 1975, Worton 1989). In KDE, the size and shape of an area analysed as an animal's home range or areas within the home range of higher levels of use are dependent on both the choice of 1) the bandwidth which determines the level of smoothing applied to location data, and

2) the contour based on different volumes of the UD. Thus, home range analyses that use the KDE method are subject to MAUP as a result of the effect that choice of bandwidth or UD contour will have on the size and shape of areas included in analyses and the potential changes to the habitat data that is assessed (Börger et al. 2006, Gitzen et al. 2006). In addition, the grain at which habitat variables area assessed (e.g., resolution) can also change data values and potentially alter the outcome of home range analyses.

In this study we assessed how each parameter of scale that renders home range analyses subject to the MAUP changed the values of associated habitat variables. Specifically, we looked at how 1) KDE bandwidth (chapter 2), 2) UD contour (chapter 3) and 3) resolution (chapter 4) each individually changed the values of habitat variables measured within home ranges. In each chapter we also examined how the effects of changes to one scale parameter (e.g., bandwidth) varied when we varied the scale of the two other parameters (e.g., contour and resolution). We examined the issue of MAUP in home range analyses using as a model population 13 northern woodland caribou of the Level Kawdy herd, BC. Seasonal habitat selection of woodland caribou is, in part, driven by selection for specific topographic features, such as, for example, high elevations and steep slopes in the calving season (Bergerud and Page 1987, Wood 1996). Thus, we used summary statistics (mean ($\bar{x}$), Standard Deviation (SD) and Coefficient of Variation (CV)) of slope and elevation to assess the potential impact of MAUP in home range analyses of northern woodland caribou.

We found that all three scale parameters assessed led to significant changes in the values of elevation and slope within the home ranges of northern woodland caribou. One exception to this is that no significant change occurred in measured values of elevation when the data was aggregated to coarser resolutions. We also found interactive effects of all three scale parameters, although the interaction of each of these parameters was less direct than initially anticipated. For example, we expected that as a result of the homogenization of topographic variables at coarser resolutions (Wolock and Price 1994, Thieken et al. 1999, Thompson et al. 2001), there would be less difference in values of elevation and slope when compared between contours (chapter 3) or at each decrease in KDE bandwidth (chapter 2). However, comparisons between contours as well as between bandwidths did not change significantly when assessed at each DEM resolution. Conversely, the specific UD contour of home ranges had a significant effect on the change that occurred in topographic values as a result of decreasing bandwidth or increasing resolution. The individual effect of contour choice on topographic values (as demonstrated in chapter 3), as well as the interactive effect with other changes in scale, highlights the importance and possible implications of contour choice within home range analyses. Although the 95% and 50% contours area frequently used in home range analyses (Laver and Kelly 2008), researchers should consider conducting analyses multiple UD contours (e.g., Börger et al. 2006) in order to assess how contour choice might affect their results.

Our results demonstrated that choice of contour, bandwidth and resolution in home range analyses significantly change topographic variables measured within caribou home ranges. One confounding issue in studies of scale in ecology is distinguishing between the effect of scale on analyses that result from MAUP and those that result from the intrinsic scales at which animal’s perceive and interact with their environments (Lechner et al. 2012). In addition, it may also be difficult to extend our results to other herds or ecotypes of woodland caribou due to the variation in seasonal habitat selection found between caribou of different regions (e.g. Culling et al. 2005, Jones et al. 2007), as well as the difficulty in generalizing the effects of scale on species-habitat analyses due the variations in heterogeneity or spatial patterns of different landscapes in which these analyses area conducted (Boyce 2006). Therefore, while our results indicate that, for example, there was a greater decrease in topographic variability in certain seasons at coarser resolutions, this pattern may not hold true in other investigations. Thus, researchers investigating habitat selection of woodland caribou should consider using multiple scales of analysis.

5.2 Research Contributions

This research contributes to the ever growing body of ecological literature that assesses the impact of scale on wildlife habitat analyses (e.g., Stephens 2004, Rahbek 2005, Schaefer and Mayor 2007, Bar-Massada et al. 2012). Our approach was somewhat unique in that we examined not only the individual effects of altering one aspect of scale in home range analyses (e.g., bandwidth), but also the interactive effects of changes in other scales (e.g. contour and resolution). Our results highlighted the potential interplay between different aspects of scale not only in home range analyses of caribou but potentially in home range analyses of other species for which topography is important such as black bears (*Ursus americanus*) (Carter et al. 2010), cougars (*Puma concolor*) (Dickson and Beier 2002), or mule deer (*Odocoileus hemionus*) (Long et al. 2009).

Often multi-scale studies examine the effects of changing only one scale of analysis such as grain (e.g., Van Rensburg et al. 2002, Li et al. 2006) or extent (e.g., Antonio et al. 2003, Thrush et al. 2005). Those studies that do examine more than one type of scale (e.g., both grain and extent) often do so by holding one scale constant while varying the other (e.g., Song et al. 2013). While individual scale effects are important to understand, as demonstrated here, different parameters of scale may in fact interact. For example, Bar-Massada et al (2012) found an interaction between the grain and extent at which landscape pattern predicted avian species richness. Specifically, they found that at a 10m grain size, the predictive power of patch and edge density decreased within increasing extent, whereas, conversely, at a 30m grain size, these same variables increased in predictive power with increasing extent (2012). Ecological studies are rarely limited to making choices with regards to only one parameter of scale. Researchers must invariably make choices with regards to a multitude of scales such the grain of variables, the radius of analysis buffers or the geographical extent of the study area. Our research has highlighted the fact that different scale choices may interact and thus alter the effect on analysis results that changes in one scale will have.

Our results also identify the importance and potential impact of varying the scale of analysis specifically in home range studies of northern woodland caribou. There are a multitude of studies investigating woodland caribou habitat use and selection (e.g., Johnson et al. 2004, Culling et al. 2005, Gustine et al. 2006, Jones et al. 2007). While our study assessed the effect of changes in scale on topographic variables, other biotic (e.g., lichen biomass, Johnson et al. 2004; predators, Gustine et al. 2006; vegetation cover, Jones et al. 2007) and abiotic (e.g., climatic conditions, Culling et al. 2005) habitat features important to caribou might also be impacted by the use of different KDE bandwidths, contours or resolutions. Northern woodland caribou are considered a species of special concern as assessed by the Committee on Status of Endangered

Wildlife in Canada (COSEWIC) in 2002 and listed under the *Species at Risk Act* in 2005 (Environment Canada 2012). As such, understanding the habitat use or selection preferences of woodland caribou can help in the effective management and conservation of this species (e.g., Jones et al. 2010, Ryder et al. 2010), which, as our study has demonstrated, may be dependent on the scale(s) of analyses.

5.3 Research opportunities

This research has demonstrated that choice of KDE bandwidth, UD contour and DEM resolution significantly change the values of elevation and slope within northern woodland caribou home ranges. To further our understanding of the potential impact of MAUP in home range analyses of woodland caribou, this research should be extended in two directions. The first direction would be to assess specifically how other factors such as home range size, distribution patterns and topographic variability associated with each seasonal home range influence the observed change in topographic values when the scale of bandwidth, contour or resolution are varied. For example, while areas characterized by greater variability in slope may see a greater decrease in slope values at coarser resolutions (Zhang and Montgomery 1994, Gao 1997), the amount of variability present within each area may be dependent on home range size (Wiens 1989, Dungan et al. 2002). An understanding of the specific characteristics of caribou home ranges that may render them more, or less, susceptible to changes in scale and hence MAUP could benefit researchers.

The second direction this research should take is to assess the actual effect on caribou habitat selection analyses. Based on the findings of other studies (e.g., Apps and Kinley 2000, Boyce et al. 2003) we can hypothesize as to how the observed decrease or conversely increase in topographic variability within a home range could potentially alter the outcome of Johnson's (1980) 2nd or 3rd selection analyses. However, the actual impact could be significant or, conversely, negligent. Other studies examining the effect of, for example, resolution on wildlife-habitat associations have found mixed results. For example, some found that the performance of species-habitat models was higher at finer grains (e.g. Gottschalk et al. 2011) or, conversely, at coarser grains (e.g., Stickler and Southworth 2008), while others found little to no difference in model performance between resolutions (e.g., Betts et al. 2006). Therefore, while we found significant changes in topographic values, it is not clear what impact this will ultimately have on selection analyses. Thus, further investigations should be conducted in order to assess the actual effect of KDE bandwidth, UD contour and DEM resolution on the outcome of woodland caribou habitat analyses.

5.4 Implications

The results of this study found that changes in the scale of bandwidth, contour and resolution led to changes in the mean and variability of elevation and slope in northern caribou home ranges. This could potentially alter the outcome of topographic habitat analyses and as a consequence, our understanding of northern woodland caribou habitat use. Our results also have implications with respect to the comparability of home range analyses. By changing the results of topographic habitat analyses, the use of different bandwidths, UD contours or DEM resolutions in different studies might limit our ability to compare results of these studies. These differences could also affect our understanding of how herds, populations or even ecotypes vary in terms of the importance of, or their selection for certain topographic features.

The potential variation in habitat analysis results could also have implications with respect the management of caribou populations. For example, studies conducted on different herds using different scales could potentially come to the same conclusions with respect to the importance or use of certain topographic features. Thus more generalized management decisions might be applied to different herds when in fact management decisions more specific to each herd may be required.

The variation in values of elevation and slope at different scales of home range analyses might also alter our understanding of the relative importance of topography versus other habitat features in different seasons. For example, decreased variability of topographic values as a result of different scales could potentially increase the apparent selection for these topographic features at the level of the home range (2nd order selection, *sensu* Johnson 1980). This could mask the actual selection for (or importance of) other habitat features (e.g. forage). Thus again potentially affecting management decisions by changing the focus to topographic features when in fact other habitat features may be more important with respect to caribou habitat selection.

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Appendix A: Seasonal comparisons

A. 1 Significant differences (p<0.05) in contour size (km^2) between seasons.

		High				**Low**				**Pairwise comparison**			
												95% Confidence interval	
Contour	**Bandwidth**	**season**	**mean high**	**SD high**	**n high**	**season**	**mean low**	**SD low**	**n low**	**diff mean**	**SE**	**lower**	**upper**
25	h_{ref}	**Fall**	82.6	± 50.4	(13)	**Calving**	14.3	± 12.2	(11)	68.3	(14.5)	27.6	109.0
	$0.8h_{ref}$		63.3	± 38.0	(13)		10.8	± 9.8	(11)	52.6	(11.2)	21.2	84.0
	$0.6h_{ref}$		45.3	± 26.8	(13)		7.5	± 7.6	(11)	37.8	(8.1)	14.9	60.6
50	h_{ref}		120.5	± 77.8	(13)		22.3	± 18.1	(11)	98.2	(22.1)	35.9	160.5
	$0.8h_{ref}$		96.8	± 61.6	(13)		17.5	± 15.4	(11)	79.3	(17.9)	28.9	129.7
	$0.6h_{ref}$		73.9	± 46.8	(13)		13.1	± 13.0	(11)	60.8	(13.8)	21.9	99.7
75	h_{ref}		198.3	± 130.8	(13)		40.0	± 33.2	(11)	158.3	(35.3)	59.0	257.6
	$0.8h_{ref}$		162.0	± 104.2	(13)		32.4	± 27.9	(11)	129.6	(28.9)	48.1	211.0
	$0.6h_{ref}$		125.3	± 80.2	(13)		24.5	± 22.4	(11)	100.8	(22.6)	37.1	164.5
95	h_{ref}		394.2	± 254.3	(13)		85.4	± 73.5	(11)	308.8	(67.4)	119.3	498.3
	$0.8h_{ref}$		320.8	± 205.4	(13)		70.6	± 61.1	(11)	250.2	(55.1)	95.2	405.2
	$0.6h_{ref}$		246.2	± 157.0	(13)		53.0	± 45.9	(11)	193.2	(43.1)	72.0	314.4
25	h_{ref}	**Fall**	82.6	± 50.4	(13)	**Summer**	23.9	± 19.4	(13)	58.7	(14.5)	18.0	99.4
	$0.8h_{ref}$		63.3	± 38.0	(13)		19.1	± 15.8	(13)	44.3	(11.2)	12.8	75.7
	$0.6h_{ref}$		45.3	± 26.8	(13)		14.6	± 12.4	(13)	30.7	(8.1)	7.9	53.6
50	h_{ref}		120.5	± 77.8	(13)		37.9	± 28.9	(13)	82.6	(22.1)	20.3	144.9
	$0.8h_{ref}$		96.8	± 61.6	(13)		31.9	± 25.1	(13)	64.9	(17.9)	14.5	115.3
	$0.6h_{ref}$		73.9	± 46.8	(13)		25.5	± 20.7	(13)	48.3	(13.8)	9.5	87.2

75	h_{ref}		198.3 ± 130.8	(13)		67.1 ± 46.7	(13)	131.2	(35.3)	31.9	230.5
	$0.8h_{ref}$		162.0 ± 104.2	(13)		57.1 ± 40.2	(13)	104.9	(28.9)	23.5	186.3
	$0.6h_{ref}$		125.3 ± 80.2	(13)		46.7 ± 33.7	(13)	78.6	(22.6)	14.9	142.3
95	h_{ref}		394.2 ± 254.3	(13)		140.3 ± 95.6	(13)	253.9	(67.4)	64.5	443.4
	$0.8h_{ref}$		246.2 ± 157.0	(13)		95.6 ± 66.0	(13)	150.6	(43.1)	29.4	271.7
	$0.6h_{ref}$		320.8 ± 205.4	(13)		118.6 ± 81.2	(13)	202.3	(55.1)	47.3	357.2
50	$0.8h_{ref}$	**Winter**	43.9 ± 29.7	(14)	**Calving**	13.1 ± 13.0	(11)	30.9	(9)	58.4	3.4
	$0.6h_{ref}$		58.2 ± 42.8	(14)		17.5 ± 15.4	(11)	40.6	(12.6)	79.6	1.7
75	h_{ref}		130.5 ± 89.6	(14)		40.0 ± 33.2	(11)	90.5	(26.5)	172.2	8.9
	$0.8h_{ref}$		108.0 ± 71.6	(14)		32.4 ± 27.9	(11)	75.5	(21.3)	141.0	10.0
	$0.6h_{ref}$		84.3 ± 52.4	(14)		24.5 ± 22.4	(11)	59.8	(15.8)	108.1	11.4
95	h_{ref}		265.9 ± 177.3	(14)		85.4 ± 73.5	(11)	180.5	(53.2)	343.5	17.4
	$0.8h_{ref}$		219.5 ± 142.3	(14)		70.6 ± 61.1	(11)	148.9	(42.9)	280.2	17.6
	$0.6h_{ref}$		174.5 ± 111.0	(14)		53.0 ± 45.9	(11)	121.5	(43.1)	242.7	.3

A. 2 Significant differences ($p<0.05$) in contour size (km^2) within each season.

		High				Low				Pairwise comparison			
												95% Confidence interval	
Season	**Bandwidth**	**Contour**	$\bar{x}$	**± SD**	**n**	**Contour**	$\bar{x}$	**± SD**	**n**	**Mean Difference**	**(SE)**	**lower**	**upper**
Winter	h_{ref}	**75**	130.5	± 89.6	(14)	**25**	44.4	± 37.2	(14)	86.0	(26.9)	9.1	163
		95	265.9	± 177.3	(14)	**25**	44.4	± 37.2	(14)	221.5	(41.2)	111.9	331.1
						50	73.2	± 57.0	(14)	192.7	(41.2)	83.2	302.3
						75	130.5	± 89.6	(14)	135.4	(41.2)	25.8	245
	$0.8h_{ref}$	**75**	108.0	± 71.6	(14)	**25**	34.1	± 27.8	(14)	73.9	(21.3)	12.7	135
		95	219.5	± 142.3	(14)	**25**	34.1	± 27.8	(14)	185.4	(32.8)	98.1	272.7
						50	58.2	± 42.8	(14)	161.3	(32.8)	74	248.6
						75	108.0	± 71.6	(14)	111.5	(32.8)	24.2	198.9
	$0.6h_{ref}$	**75**	84.3	± 52.4	(14)	**25**	24.5	± 19.4	(14)	59.7	(15.5)	15.2	104.3
		95	174.5	± 111.0	(14)	**25**	24.5	± 19.4	(14)	150.0	(25.1)	83.3	216.7
						50	43.9	± 29.7	(14)	130.6	(25.1)	63.9	197.2
						75	84.3	± 52.4	(14)	90.2	(25.1)	23.6	156.9
Calving	h_{ref}	**95**	85.4	± 73.5	(11)	**25**	14.3	± 12.2	(11)	71.2	(16.4)	27.5	114.8
						50	22.3	± 18.1	(11)	63.2	(16.4)	19.5	106.8
						75	40.0	± 33.2	(11)	45.5	(16.4)	1.9	89.1

	$0.8h_{ref}$	**95**	70.6 ± 61.1	(11)	**25**	10.8 ± 9.8	(11)	59.8	(13.6)	23.5	96.1
					50	17.5 ± 15.4	(11)	53.1	(13.6)	16.7	89.4
					75	32.4 ± 27.9	(11)	38.2	(13.6)	1.9	74.5
	$0.6h_{ref}$	**95**	53.0 ± 45.9	(11)	**25**	7.5 ± 7.6	(11)	45.5	(10.4)	17.7	73.2
					50	13.1 ± 13.0	(11)	39.9	(10.4)	12.2	67.7
					75	24.5 ± 22.4	(11)	28.5	(10.4)	0.7	56.3
Summer	**h_{ref}**	**75**	67.1 ± 46.7	(13)	**25**	23.9 ± 19.4	(13)	43.2	(14)	3.1	83.3
		95	140.3 ± 95.6	(13)	**25**	23.9 ± 19.4	(13)	116.5	(22)	58	174.9
					50	37.9 ± 28.9	(13)	102.4	(22)	44	160.8
					75	67.1 ± 46.7	(13)	73.2	(22)	14.8	131.7
	$0.8h_{ref}$	**75**	57.1 ± 40.2	(13)	**25**	19.1 ± 15.8	(13)	38.0	(12)	3.6	72.3
		95	118.6 ± 81.2	(13)	**25**	19.1 ± 15.8	(13)	99.5	(18.7)	49.7	149.2
					50	31.9 ± 25.1	(13)	86.6	(18.7)	36.9	136.4
					75	57.1 ± 40.2	(13)	61.5	(18.7)	11.8	111.2
	$0.6h_{ref}$	**75**	46.7 ± 33.7	(13)	**25**	14.6 ± 12.4	(13)	32.1	(10)	3.4	60.8
		95	95.6 ± 66.0	(13)	**25**	14.6 ± 12.4	(13)	81.1	(15.3)	40.4	121.7
					50	25.5 ± 20.7	(13)	70.1	(15.3)	29.4	110.8
					75	46.7 ± 33.7	(13)	49.0	(15.3)	8.3	89.6

Rut	h_{ref}	**95**	216.7 ± 191.9	(12)	**25**	49.8 ± 48.7	(12)	166.9	(46.7)	42.6	291.3
					50	77.1 ± 74.0	(12)	139.6	(46.7)	15.3	264
	$0.8h_{ref}$	**95**	180.3 ± 161.0	(12)	**25**	39.5 ± 38.7	(12)	140.8	(39.3)	36.1	245.4
					50	64.8 ± 62.8	(12)	115.5	(39.3)	10.8	220.2
	$0.6h_{ref}$	**95**	145.7 ± 130.0	(12)	**25**	29.7 ± 29.1	(12)	116.0	(31.7)	31.6	200.3
					50	51.4 ± 50.4	(12)	94.3	(31.7)	9.9	178.7
Fall	h_{ref}	**75**	198.3 ± 130.8	(13)	**25**	82.6 ± 50.4	(13)	115.7	(38.9)	4	227.4
		95	394.2 ± 254.3	(13)	**25**	82.6 ± 50.4	(13)	311.7	(59)	154.8	468.6
					50	120.5 ± 77.8	(13)	273.7	(59)	116.8	430.6
					75	198.3 ± 130.8	(13)	196.0	(59)	39.1	352.9
	$0.8h_{ref}$	**95**	320.8 ± 205.4	(13)	**25**	63.3 ± 38.0	(13)	257.5	(47.3)	131.5	383.5
					50	96.8 ± 61.6	(13)	224.0	(47.3)	98	350
					75	162.0 ± 104.2	(13)	158.8	(47.3)	32.8	284.8
	$0.6h_{ref}$	**75**	125.3 ± 80.2	(13)	**25**	45.3 ± 26.8	(13)	80.0	(23.5)	12.2	147.8
					25	45.3 ± 26.8	(13)	98.6	(30.7)	10.1	187.2
		95	246.2 ± 157.0	(13)	**25**	45.3 ± 26.8	(13)	200.9	(36.2)	104.7	297.1
					50	73.9 ± 46.8	(13)	172.3	(36.2)	76.1	268.6
					75	125.3 ± 80.2	(13)	120.9	(36.2)	24.7	217.1

A. 3 Significant differences (p<0.0.5) in values of slope (%) between seasons.

	High					Low				Pairwise comparison				
												95% Confidence interval		
Slope Variable	**Season**	**Contour**	**$\bar{x}$**	**± SD**	**(n)**	**Season**	**$\bar{x}$**	**± SD**	**(n)**	**Mean Difference**	**(SE)**	**lower**	**upper**	**Bandwidths**
Mean	**Calving**	**25**	17.8	± 12.8	(11)	**Winter**	7.8	± 2.2	(14)	10.0	(3.5)	.1	19.9	all
		50	18.2	± 11.6	(11)	**Winter**	8.5	± 2.7	(14)	9.7	(3.3)	.3	19.1	0.6h_{ref}
		75	20.0	± 10.4	(11)	**Rut**	10.6	± 4.8	(12)	9.4	(3.3)	.1	18.7	All
						Winter	9.2	± 3.3	(14)	10.8	(3.2)	1.8	19.8	All
						Fall	10.3	± 2.0	(13)	10.0	(3.2)	.9	19.0	0.6h_{ref}
		95	20.5	± 9.8	(11)	**Fall**	12.2	± 1.7	(13)	8.3	(2.9)	.2	16.3	All
						Rut	12.0	± 4.8	(12)	8.5	(2.9)	.3	16.8	All
						Winter	10.4	± 3.3	(14)	10.1	(2.8)	2.2	18.0	All
Mean	**Summer**	**25**	20.6	± 13.4	(13)	**Fall**	9.0	± 3.1	(13)	-11.6	(3.4)	2.0	21.2	All
						Rut	9.9	± 6.1	(12)	-10.6	(3.5)	.8	20.4	All
						Winter	7.8	± 2.2	(14)	12.7	(3.3)	3.3	22.2	All
		50	19.2	± 13.3	(13)	**Fall**	10.0	± 2.3	(13)	-9.2	(3.2)	.0	18.3	All
						Winter	9.0	± 3.5	(14)	10.1	(3.2)	1.2	19.1	All
		75	21.0	± 13.2	(13)	**Fall**	11.9	± 2.9	(13)	-9.2	(3.1)	.4	17.9	All
						Rut	10.6	± 4.8	(12)	-10.4	(3.2)	1.4	19.3	All

					Winter	9.2 ± 3.3	(14)	11.8	(3.1)	3.2	20.4	All
		95	20.0 ± 11.0	(13)	**Fall**	12.2 ± 1.7	(13)	-7.8	(2.7)	.0	15.5	All
					Rut	12.0 ± 4.8	(12)	-8.0	(2.8)	.1	15.9	All
					Winter	10.4 ± 3.3	(14)	9.6	(2.7)	2.0	17.2	All
SD	**Calving**	**75**	15.1 ± 6.6	(11)	**Winter**	7.7 ± 2.6	(14)	7.3	(2.1)	1.6	13.1	All
		95	15.7 ± 6.5	(11)	**Winter**	9.5 ± 2.8	(14)	6.2	(1.9)	1.0	11.4	All
SD	**Fall**	**75**	11.5 ± 3.2	(13)	**Winter**	7.7 ± 2.6	(14)	3.8	(1.1)	.5	7.1	h_{ref}, $0.8h_{ref}$
		95	12.9 ± 2.4	(13)	**Winter**	9.5 ± 2.8	(14)	3.4	(1)	.4	6.3	h_{ref}, $0.8h_{ref}$
SD	**Summer**	**25**	14.0 ± 7.0	(13)	**Fall**	7.8 ± 2.4	(13)	-6.2	(2.1)	.3	12.1	All
					Winter	6.7 ± 2.3	(14)	7.3	(2.1)	1.5	13.1	all
		50	14.7 ± 6.8	(13)	**Winter**	7.7 ± 3.1	(14)	7.0	(2)	1.3	12.7	all
		50	14.6 ± 6.2	(13)	**Fall**	8.1 ± 1.9	(13)	-6.5	(1.9)	1.1	11.9	$0.8h_{ref}$, $0.6h_{ref}$
		75	16.7 ± 6.5	(13)	**Winter**	7.7 ± 2.6	(14)	9.0	(2)	3.5	14.5	all
		75	16.2 ± 7.0	(13)	**Fall**	9.9 ± 2.4	(13)	-6.3	(2)	.7	12.0	$0.6h_{ref}$
		95	16.1 ± 5.4	(13)	**Winter**	9.5 ± 2.8	(14)	6.6	(1.8)	1.6	11.6	all
CV	**Fall**	**25**	0.88 ± 0.14	(13)	**Calving**	0.69 ± 0.14	(11)	-.19	(0.06)	.03	.36	all

		75	0.97	± 0.10	(13)	**Calving**	0.79	± 0.13	(11)	-.18	(0.06)	.01	.36	all
						Winter	0.85	± 0.08	(14)	.12	(0.04)	.01	.23	h_{ref}, 0.8h_{ref}
		95	1.05	± 0.09	(13)	**Calving**	0.79	± 0.13	(11)	-.26	(0.06)	.08	.43	all
						Winter	0.92	± 0.11	(14)	.12	(0.04)	.01	.24	h_{ref}, 0.8h_{ref}
CV	**Rut**	**50**	1.01	± 0.24	(12)	**Calving**	0.78	± 0.15	(11)	-.23	(0.08)	.01	.44	h_{ref}, 0.8h_{ref}
		75	1.02	± 0.21	(12)	**Calving**	0.79	± 0.13	(11)	-.24	(0.06)	.06	.41	all
						Winter	0.85	± 0.08	(14)	.17	(0.06)	.00	.34	all
		75	1.05	± 0.23	(12)	**Summer**	0.86	± 0.20	(13)	.19	(0.07)	.01	.38	0.6h_{ref}
		95	1.04	± 0.17	(12)	**Calving**	0.79	± 0.13	(11)	-.25	(0.06)	.07	.42	all
CV	**Winter**	**25**	0.82	± 0.14	(14)	**Calving**	0.67	± 0.11	(11)	-.15	(0.05)	.00	.30	0.6h_{ref}

Appendix B: Supplementary Results for chapter 2

B. 1 Number of significant differences in $\bar{x}$ of elevation within each of the four UD contours (25, 50, 75 and 95%) between successive ($h_{ref} - 0.8h_{ref}$ and $0.8h_{ref} - 0.6h_{ref}$) and overall ($h_{ref} - 0.6h_{ref}$) changes in KDE bandwidth at each of the four DEM resolutions (25, 75, 125 and 175m).

		Contour (%):	**25**				**50**				**75**				**95**			
Season	**Change in bandwidth**	**Resolution (m):**	**25**	**75**	**125**	**175**	**25**	**75**	**125**	**175**	**25**	**75**	**125**	**175**	**25**	**75**	**125**	**175**
Winter	$h_{ref} - 0.8h_{ref}$		12	9	5	5	13	12	10	6	12	11	9	9	13	13	12	10
	$0.8h_{ref} - 0.6h_{ref}$		12	9	6	5	11	9	7	5	12	10	7	6	14	13	12	10
	$h_{ref} - 0.6h_{ref}$		13	11	10	7	11	10	9	8	14	13	12	10	14	14	14	13
Calving	$h_{ref} - 0.8h_{ref}$		11	9	2	2	11	5	5	4	11	9	5	5	11	10	10	10
	$0.8h_{ref} - 0.6h_{ref}$		10	5	3	2	10	7	3	1	11	9	7	4	11	11	9	8
	$h_{ref} - 0.6h_{ref}$		11	9	9	5	10	9	8	5	11	11	9	8	11	11	11	11
Summer	$h_{ref} - 0.8h_{ref}$		12	8	5	4	12	9	7	6	13	12	11	8	13	11	11	10
	$0.8h_{ref} - 0.6h_{ref}$		12	8	7	5	12	9	7	6	13	13	7	8	13	11	10	10
	$h_{ref} - 0.6h_{ref}$		12	11	8	8	12	10	8	9	13	12	12	11	13	13	12	11
Rut	$h_{ref} - 0.8h_{ref}$		10	10	6	3	10	9	7	4	11	9	8	8	11	10	9	9
	$0.8h_{ref} - 0.6h_{ref}$		10	8	6	5	10	8	5	5	10	8	8	8	11	11	10	10
	$h_{ref} - 0.6h_{ref}$		11	10	8	8	11	11	9	7	11	11	9	9	11	11	11	11
Fall	$h_{ref} - 0.8h_{ref}$		13	11	10	7	12	11	11	10	13	13	12	11	12	12	10	9

$0.8h_{ref} - 0.6h_{ref}$	13	10	8	7	11	11	9	7	12	11	10	10	12	10	9	8
$h_{ref} - 0.6h_{ref}$	12	11	10	10	12	12	11	10	13	12	12	10	12	10	10	10

B. 2 Number of significant differences in $\bar{x}$ slope within each of the four UD contours (25, 50, 75 and 95%) between successive (h_{ref} – $0.8h_{ref}$ and $0.8h_{ref}$ – $0.6h_{ref}$) and overall (h_{ref} - $0.6h_{ref}$) changes in KDE bandwidth at each of the four DEM resolutions (25, 75, 125 and 175m).

		Contour (%):	25				50				75				95			
Season	**Change in bandwidth**	**Resolution (m):**	**25**	**75**	**125**	**175**	**25**	**75**	**125**	**175**	**25**	**75**	**125**	**175**	**25**	**75**	**125**	**175**
Winter	$h_{ref} - 0.8h_{ref}$		10	4	4	4	12	8	6	3	13	8	7	7	12	12	9	8
	$0.8h_{ref} - 0.6h_{ref}$		13	5	4	4	13	9	5	4	12	9	8	5	13	13	8	6
	$h_{ref} - 0.6h_{ref}$		12	11	7	6	13	11	8	7	13	12	10	10	14	13	12	12
Calving	$h_{ref} - 0.8h_{ref}$		9	5	2	0	8	7	6	4	9	5	5	3	10	9	8	3
	$0.8h_{ref} - 0.6h_{ref}$		10	7	3	2	8	3	3	2	7	5	4	4	10	6	4	4
	$h_{ref} - 0.6h_{ref}$		9	8	7	5	9	7	7	5	10	8	7	6	10	10	8	5
Summer	$h_{ref} - 0.8h_{ref}$		9	6	3	3	12	7	5	5	13	9	9	8	10	10	6	6
	$0.8h_{ref} - 0.6h_{ref}$		10	7	6	4	13	8	5	3	10	7	3	3	11	8	6	3
	$h_{ref} - 0.6h_{ref}$		11	7	6	6	13	10	8	7	12	12	10	9	11	9	9	6
Rut	$h_{ref} - 0.8h_{ref}$		10	6	3	2	10	9	9	6	9	7	6	6	10	9	9	9
	$0.8h_{ref} - 0.6h_{ref}$		10	5	3	3	9	8	6	4	12	9	8	7	11	10	8	7
	$h_{ref} - 0.6h_{ref}$		12	8	7	4	12	9	9	9	12	10	9	8	11	11	10	10
Fall	$h_{ref} - 0.8h_{ref}$		13	12	10	9	13	12	12	9	13	12	12	9	13	12	11	10

$0.8h_{ref} - 0.6h_{ref}$	10	9	7	4	11	10	10	8	11	12	9	8	12	11	9	8
$h_{ref} - 0.6h_{ref}$	13	12	10	10	13	12	12	11	13	13	12	12	13	12	12	12

B. 3 Significant differences ($p<0.05$) between seasons (winter, calving, summer, rut and fall) in the decrease in contour size (km^2) with each decrease in KDE bandwidth ($h_{ref} – 0.8h_{ref}$, $0.8h_{ref} – 0.6h_{ref}$ and $h_{ref} - 0.6h_{ref}$).

		High					Low					Pairwise Comparison			
														95% Confidence interval	
Change in bandwidth	**Contour**	**Season**	**$\bar{x}$**		**SD**	**(n)**	**Season**	**$\bar{x}$**		**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**
$h_{ref} – 0.8h_{ref}$	**25**	**Fall**	-20.8	±	11.8	(13)	**Winter**	-10.3	±	9.8	(14)	10.5	(3.4)	0.9	20.1
							Calving	-3.8	±	2.6	(11)	17	(3.5)	7.3	26.8
							Summer	-5.2	±	3.7	(13)	15.7	(3.5)	5.9	25.4
	50	**Fall**	-25.7	±	16.0	(13)	**Calving**	-5.2	±	3.3	(11)	20.5	(4.6)	7.5	33.6
							Summer	-6.5	±	3.7	(13)	19.2	(4.6)	6.1	32.2
	75	**Fall**	-39.3	±	26.8	(13)	**Calving**	-8.2	±	6.2	(11)	31.2	(7.1)	11.2	51.1
							Summer	-10.9	±	6.4	(13)	28.4	(7.1)	8.5	48.4
							Rut	-18.7	±	16.0	(12)	20.6	(7.1)	0.7	40.6
	95	**Fall**	-79.5	±	46.8	(13)	**Calving**	-16.1	±	12.6	(11)	63.5	(12.8)	27.3	99.6
							Summer	-23.6	±	14.2	(13)	56	(12.8)	19.8	92.1
							Rut	-39.4	±	31.0	(12)	40.1	(12.8)	4	76.3
$0.8h_{ref} – 0.6h_{ref}$	**25**	**Fall**	-19.5	±	10.7	(13)	**Winter**	-9.6	±	8.5	(14)	10	(3.1)	1.2	18.7

												Pairwise Comparison			
		High					**Low**							**95% Confidence interval**	
Change in bandwidth	**Contour**	**Season**	$\bar{x}$		**SD**	**(n)**	**Season**	$\bar{x}$		**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**
							Calving	-3.5	±	2.4	(11)	16	(3.2)	7.1	25
							Summer	-4.9	±	3.5	(13)	14.7	(3.2)	5.7	23.6
	50	**Fall**	-24.8	±	14.2	(13)	**Calving**	-4.9	±	2.9	(11)	20	(4.4)	7.7	32.3
							Summer	-6.9	±	4.2	(13)	17.9	(4.4)	5.6	30.2
	75	**Fall**	-39.7	±	22.9	(13)	**Calving**	-8.6	±	6.0	(11)	31.1	(6.8)	12.1	50.2
							Summer	-11.2	±	6.4	(13)	28.5	(6.8)	9.5	47.5
	95	**Fall**	-80.8	±	47.0	(13)	**Winter**	-45.0	±	36.0	(14)	35.8	(12.6)	0.3	71.3
							Calving	-19.1	±	15.7	(11)	61.8	(12.8)	25.6	98
							Summer	-24.8	±	14.8	(13)	56	(12.8)	19.8	92.2
							Rut	-37.5	±	30.8	(12)	43.3	(12.8)	7.1	79.6
$h_{ref} - 0.6h_{ref}$	**25**	**Fall**	-40.4	±	22.4	(13)	**Winter**	-19.9	±	18.2	(14)	20.5	(6.5)	2.2	38.7
							Calving	-7.3	±	4.9	(11)	33.1	(6.6)	14.5	51.7
							Summer	-10.1	±	7.2	(13)	30.3	(6.6)	11.7	48.9
							Rut	-21.7	±	19.8	(12)	18.6	(6.6)	0	37.3
	50	**Fall**	-50.5	±	30.0	(13)	**Calving**	-10.0	±	6.2	(11)	40.5	(8.9)	15.3	65.7

												Pairwise Comparison			
		High					**Low**							**95% Confidence interval**	
Change in bandwidth	**Contour**	**Season**	$\bar{x}$		**SD**	**(n)**	**Season**	$\bar{x}$		**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**
							Summer	-13.4	±	8.0	(13)	37.1	(8.9)	11.9	62.3
	75	**Fall**	-79.0	±	49.4	(13)	**Calving**	-16.8	±	12.0	(11)	62.3	(13.7)	23.7	100.8
							Summer	-22.1	±	12.8	(13)	56.9	(13.7)	18.4	95.5
							Rut	-39.5	±	34.4	(12)	39.5	(13.7)	1	78.1
	95	**Fall**	-160.4	±	93.3	(13)	**Calving**	-35.2	±	27.9	(11)	125.2	(25.5)	53.3	197.1
							Summer	-48.4	±	28.9	(13)	112	(25.5)	40	183.9
							Rut	-76.9	±	61.1	(12)	83.5	(25.5)	11.5	155.4

B. 4 Significant differences ($p<0.05$) in the decrease in contour size (km^2) within each season (winter, calving, summer, rut and fall) between contours at each decrease in KDE bandwidth ($h_{ref} - 0.8h_{ref}$, $0.8h_{ref} - 0.6h_{ref}$ and $h_{ref} - 0.6h_{ref}$).

												Pairwise comparison			
		High					Low							95% Confidence interval	
Season	**Change in bandwidth**	**Contour**	$\overline{x}$		**SD**	**(n)**	**Contour**	$\overline{x}$		**SD**	**(n)**	**Mean difference**	**(SE)**	**lower**	**upper**
Winter	$h_{ref} - 0.8h_{ref}$	**95**	-46.4	±	37.3	(14)	**25**	-10.3	±	9.8	(14)	36.1	(10.7)	4.9	67.3
							50	-15.0	±	14.6	(14)	31.4	(9.1)	7.3	55.5
	$0.8h_{ref} - 0.6h_{ref}$	**95**	-45.0	±	36.0	(14)	**25**	-9.6	±	8.5	(14)	35.4	(10.3)	5.4	65.4
							50	-14.2	±	13.4	(14)	30.8	(8.7)	7.7	53.9
	$h_{ref} - 0.6h_{ref}$	**95**	-91.4	±	73.1	(14)	**25**	-19.9	±	18.2	(14)	71.5	(20.9)	10.5	132.5
							50	-29.2	±	27.8	(14)	62.2	(17.6)	15.3	109.1
Calving	$h_{ref} - 0.8h_{ref}$	**95**	-16.1	±	12.6	(11)	**25**	-3.8	±	2.6	(11)	12.3	(3.7)	1.3	23.3
	$0.8h_{ref} - 0.6h_{ref}$	**95**	-19.1	±	15.7	(11)	**25**	-3.5	±	2.4	(11)	15.6	(4.6)	1.9	29.2
							50	-4.9	±	2.9	(11)	14.2	(4.6)	.5	27.9
	$h_{ref} - 0.6h_{ref}$	**95**	-35.2	±	27.9	(11)	**25**	-7.3	±	4.9	(11)	27.9	(8.2)	3.5	52.2
							50	-10.0	±	6.2	(11)	25.1	(8.3)	.7	49.6

Summer	**$h_{ref} - 0.8h_{ref}$**	**95**	-23.6	±	14.2	(13)	**25**	-5.2	±	3.7	(13)	18.4	(4.2)	5.9	30.9
							50	-6.5	±	3.7	(13)	17.1	(4.2)	4.6	29.6
	$0.8h_{ref} - 0.6h_{ref}$	**95**	-24.8	±	14.8	(13)	**25**	-4.9	±	3.5	(13)	19.9	(4.4)	6.9	32.9
							50	-6.9	±	4.2	(13)	17.9	(4.4)	4.8	31.0
							75	-11.2	±	6.4	(13)	13.6	(4.7)	.2	27.0
	$h_{ref} - 0.6h_{ref}$	**95**	-48.4	±	28.9	(13)	**25**	-10.1	±	7.2	(13)	38.3	(8.6)	12.9	63.8
							50	-13.4	±	8.0	(13)	35.0	(8.7)	9.5	60.5
							75	-22.1	±	12.8	(13)	26.3	(9.1)	.0	52.6
Rut	**$h_{ref} - 0.8h_{ref}$**	**95**	-39.4	±	31.0	(12)	**25**	-11.1	±	10.1	(12)	28.3	(9.4)	.8	55.9
	$h_{ref} - 0.6h_{ref}$	**95**	-76.9	±	61.1	(12)	**25**	-21.7	±	19.8	(12)	55.2	(18.6)	.9	109.5
Fall	**$h_{ref} - 0.8h_{ref}$**	**95**	-79.5	±	46.8	(13)	**25**	-20.8	±	11.8	(13)	58.7	(13.9)	17.6	99.8
							50	-25.7	±	16.0	(13)	53.9	(14.3)	12.2	95.5
							75	-39.3	±	26.8	(13)	40.2	(11.7)	8.9	71.6
	$0.8h_{ref} - 0.6h_{ref}$	**95**	-80.8	±	47.0	(13)	**25**	-19.5	±	10.7	(13)	61.3	(13.9)	20.0	102.6
							50	-24.8	±	14.2	(13)	56.0	(14.2)	14.4	97.6
							75	-39.7	±	22.9	(13)	41.1	(11.3)	11.0	71.2

h_{ref} – 0.6h_{ref}	**95**	-160.4	±	93.3	(13)	**25**	-40.4	±	22.4	(13)	120.0	(27.7)	38.0	202.0
						50	-50.5	±	30.0	(13)	109.9	(28.3)	27.0	192.7
						75	-79.0	±	49.4	(13)	81.3	(22.9)	20.3	142.4

B. 5 Significant differences (p<0.05) in the descriptive metrics of elevation (m) between contours (25, 50, 75 and 95%) within each seasonal home range (winter, calving, summer, rut and fall) at each of the three changes in bandwidth (h_{ref}-$0.8h_{ref}$, $0.8h_{ref}$ – $0.6h_{ref}$ and h_{ref} – $0.6h_{ref}$). We indicate the resolutions (25, 75, 125 and 175m) at which differences between contours were significant.

			High					Low					Pairwise comparison		95% Confidence interval		
Elevation Variable	**Season**	**Change in bandwidth**	**Contour**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Contour**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolutions (m)**
Mean	**Rut**	**$0.8h_{ref}$-$0.6h_{ref}$**	***95***	20.6	±	13.9	(11)	***25***	8.3	±	8.4	(10)	12.3	(4.5)	0.3	24.4	25
	Fall	**$0.8h_{ref}$-$0.6h_{ref}$**	***95***	26.6	±	13.3	(8)	***25***	10.3	±	4.1	(7)	16.2	(5.5)	1.1	31.4	175
SD	**Winter**	**h_{ref}-$0.8h_{ref}$**	***95***	16.6	±	12.8	(13)	***25***	6.6	±	5.7	(9)	10.0	(3.7)	<0.1	20	75
			95	17.8	±	12.7	(12)	***50***	5.7	±	4.4	(10)	12.1	(3.9)	0.3	24.0	125
			95	-16.9	±	13.4	(13)	***50***	-6.2	±	5.2	(10)	10.7	(3.8)	0.5	20.9	25, 125
		$0.8h_{ref}$-$0.6h_{ref}$	***95***	15.6	±	10.9	(14)	***25***	5.1	±	5.2	(12)	-10.6	(3.3)	1.4	19.7	25, 75, 175
								75	5.7	±	4.9	(12)	-9.9	(3.2)	0.8	19	25, 75
		h_{ref}-$0.6h_{ref}$	***95***	31.6	±	23.5	(14)	***25***	8.3	±	9.6	(13)	-23.2	(6)	7.3	39.2	all
								50	12.8	±	13.6	(12)	-18.7	(6.3)	2	35.5	25, 75
	Calving	**h_{ref}-$0.8h_{ref}$**	***50***	9.5	±	2.5	(5)	***25***	3	±	0.4	(2)	-6.5	(1.1)	1.8	11.2	125
		$0.8h_{ref}$-$0.6h_{ref}$	***75***	14.5	±	5.1	(4)	***95***	7	±	3.1	(8)	7.5	(2.4)	1	13.9	175

			High					Low					Pairwise comparison				
															95% Confidence interval		
Elevation Variable	**Season**	**Change in bandwidth**	**Contour**	$\bar{x}_{\Delta}$	±	**SD**	**(n)**	**Contour**	$\bar{x}_{\Delta}$	±	**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolutions (m)**
		h_{ref}-$0.6h_{ref}$	***75***	19.5	±	10	(11)	***95***	8.9	±	5.1	(11)	10.5	(3.4)	0.8	20.3	25, 75, 175
	Summer	**h_{ref}-$0.6h_{ref}$**	***50***	22.3	±	15.9	(12)	***25***	9	±	7.2	(12)	-13.2	(4.7)	0.8	25.7	25, 125
			50	27.0	±	16.2	(8)	***75***	12.7	±	12.3	(12)	14.2	(5.1)	0.5	28	125
	Rut	**h_{ref}-$0.8h_{ref}$**	***95***	12.0	±	7.4	(10)	***25***	3.6	±	2.9	(10)	8.5	(2.8)	0.9	16.0	75, 175
			95	-10.3	±	4.6	(7)	***25***	-3.9	±	2.7	(9)	6.4	(2)	0.3	12.5	25, 75, 175
	Fall	**$0.8h_{ref}$-$0.6h_{ref}$**	***95***	-27.6	±	19.5	(8)	***25***	-8.2	±	7.2	(7)	19.4	(6.5)	1.6	37.1	125
CV	**Winter**	**h_{ref}-$0.8h_{ref}$**	***95***	0.015	±	0.011	(13)	***25***	0.006	±	0.005	(9)	0.009	(0.003)	<0.001	-0.018	75
								50	0.006	±	0.005	(10)	0.01	(0.003)	<0.001	0.019	75, 125, 175
			95	-0.15	±	0.012	(13)	***50***	-0.006	±	0.005	(10)	0.01	(0.041)	<0.001	0.019	25, 175
		$0.8h_{ref}$-$0.6h_{ref}$	***95***	0.014	±	0.01	(14)	***25***	0.005	±	0.006	(12)	0.009	(0.003)	<0.001	0.017	25
								75	0.005	±	0.005	(12)	0.009	(0.003)	<0.001	0.017	25
		h_{ref}-$0.6h_{ref}$	***95***	0.029	±	0.022	(14)	***25***	0.009	±	0.01	(13)	0.02	0.006	0.005	0.034	25, 75
								50	0.012	±	0.012	(11)	0.016	(0.006)	<0.001	0.032	25, 75
	Rut	**h_{ref}-$0.8h_{ref}$**	***95***	0.007	±	0.004	(11)	***25***	0.002	±	0.002	(10)	0.005	(0.001)	<0.001	0.01	all
			95	-0.008	±	0.003	(7)	***25***	-0.025	±	0.002	(9)	0.006	(0.001)	<0.001	0.01	all

			High					**Low**					**Pairwise comparison**				
															95% Confidence interval		
Elevation Variable	**Season**	**Change in bandwidth**	**Contour**	$\overline{x}_{\Delta}$	±	**SD**	**(n)**	**Contour**	$\overline{x}_{\Delta}$	±	**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolutions (m)**
	Fall	**h_{ref}-$0.8h_{ref}$**	***95***	0.014	±	0.01	(10)	***25***	0.003	±	0.005	(10)	0.011	(0.003)	0.001	0.021	125
			95	-0.019	±	0.007	(7)	***25***	-0.004	±	0.005	(8)	0.015	(0.005)	0.001	0.028	125
		$0.8h_{ref}$-$0.6h_{ref}$	***75***	0.013	±	0.008	(12)	***25***	0.005	±	0.004	(13)	0.008	(0.003)	<0.001	0.016	25

B. 6 Significant differences (p<0.05) in the descriptive metrics of slope (%) between contours (25, 50, 75 and 95%) within each seasonal home range (winter, calving, summer, rut and fall) at each of the three changes in bandwidth (h_{ref}-0.8h_{ref}, 0.8h_{ref} – 0.6h_{ref} and h_{ref} – 0.6h_{ref}). We indicate the resolutions (25, 75, 125 and 175m) at which differences between contours were significant.

			High					**Low**					**Pairwise comparison**				
															95% Confidence interval		
Slope Variable	**Season**	**Change in bandwidth**	**Contour**	$\bar{x}_\Delta$		**SD**	**(n)**	**Contour**	$\bar{x}_\Delta$		**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolution (m)**
Mean	**Fall**	**0.8h_{ref}-0.6h_{ref}**	**75**	1.1	±	0.6	(11)	**25**	0.5	±	0.2	(10)	0.6	(0.2)	0.1	1.2	ALL
			95	0.9	±	0.4	(8)	**25**	0.4	±	0.1	(4)	0.5	(0.2)	0	1.0	175
SD	**Calving**	**h_{ref}-0.6h_{ref}**	**50**	2	±	1.1	(9)	**25**	0.6	±	0.8	(9)	1.4	(0.5)	0.1	2.6	25
		0.8h_{ref}-0.6h_{ref}	**50**	2.2	±	0.5	(3)	**25**	0.4	±	0.4	(7)	1.7	(0.3)	0.2	3.3	75, 125
	Fall	**0.8h_{ref}-0.6h_{ref}**	**75**	1.4	±	0.9	(11)	**25**	0.5	±	0.3	(10)	0.9	(0.3)	0.1	1.8	25
			95	1.1	±	0.6	(9)	**25**	0.4	±	0.3	(7)	0.7	(0.2)	0	1.4	125
		h_{ref}-0.6h_{ref}	**95**	2	±	1	(13)	**25**	0.9	±	0.5	(13)	1.0	(0.3)	0.1	1.9	25, 75
	Summer	**h_{ref}-0.8h_{ref}**	**50**	1.2	±	0.7	(12)	**25**	0.5	±	0.3	(9)	0.7	(0.2)	0	1.3	25, 75
			50	1.6	±	0.7	(7)	**75**	0.7	±	0.7	(9)	0.9	(0.3)	0.1	1.6	75
								95	0.6	±	0.4	(10)	1	(0.3)	0.3	1.8	75
		h_{ref}-0.6h_{ref}	**50**	2.2	±	1.4	(8)	**75**	0.8	±	1	(10)	1.4	(0.5)	0.1	2.8	125, 175
CV																	
	Summer	**h_{ref}-0.8h_{ref}**	**25**	0.10	±	0.01	(3)	**75**	0.06	±	0.03	(9)	0.04	(0.01)	<0.01	0.08	125, 175

			High					**Low**					**Pairwise comparison**				
															95% Confidence interval		
Slope Variable	**Season**	**Change in bandwidth**	**Contour**	$\bar{x}_{\Delta}$		**SD**	**(n)**	**Contour**	$\bar{x}_{\Delta}$		**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolution (m)**
	Winter	**$0.8h_{ref}$-$0.6h_{ref}$**	**25**	0.07	±	0.03	(5)	**75**	0.02	±	0.02	(9)	0.05	(0.02)	0.01	0.09	75
				0.07	±	0.03	(5)	**75**	0.01	±	0.01	(4)	0.06	(0.02)	<0.01	0.12	75
		$0.8h_{ref}$-$0.6h_{ref}$	**25**	0.07	±	0.03	(5)	**95**	0.03	±	0.03	(13)	0.04	(0.02)	<0.01	0.08	75

B. 7 Significant differences (p<0.05) in the descriptive metrics of elevation (m) within contours of the same value between the five seasonal home ranges (winter, calving, summer, rut and fall) at each of the three changes in bandwidth (h_{ref}-0.8h_{ref}, 0.8h_{ref} – 0.6h_{ref} and h_{ref} – 0.6h_{ref}). We indicate the resolutions (25, 75, 125 and 175m) at which differences between contours were significant.

	High							Low					Pairwise Comparison				
															95% Confidence Interval		
Slope Variable	season	Contour	Change in bandwidth	$\overline{x}_{\Delta}$	±	SD	(n)	Season	$\overline{x}_{\Delta}$	±	SD	(n)	Mean Difference	(SE)	Lower	Upper	Significant resolutions (m)
Mean	**Calving**	**25**	**0.8h_{ref}-0.6h_{ref}**	21.5	±	8.1	(5)	**Winter**	6.3	±	4.2	(9)	15.2	(5)	0.8	29.7	75
	Summer	**50**	**h_{ref}-0.8h_{ref}**	21	±	10.7	(9)	**Winter**	8.2	±	6.2	(12)	12.8	(3.8)	1.9	23.6	75, 125
								Rut	8.7	±	5.9	(9)	12.3	(4.1)	0.7	23.9	75
	Fall	**50**	**h_{ref}-0.8h_{ref}**	18.7	±	8.9	(11)	**Winter**	8.2	±	6.2	(12)	10.5	(3.6)	0.2	20.8	75
SD	**Winter**	**95**	**h_{ref}-0.8h_{ref}**	16.9	±	13.4	(13)	**Calving**	4	±	4.4	(11)	12.8	(3.5)	3	22.7	all
			0.8h_{ref}-0.6h_{ref}	15.6	±	10.9	(14)	**Calving**	6	±	3.5	(11)	9.7	(3.1)	0.2	19.1	25, 75, 125
			h_{ref}-0.6h_{ref}	31.6	±	23.5	(14)	**Calving**	8.9	±	5.1	(11)	22.6	(6.5)	2.6	42.7	all
	Fall	**50**	**h_{ref}-0.8h_{ref}**	14.6	±	10.8	(12)	**Winter**	5.5	±	4.9	(13)	9.1	(3)	0.7	17.4	25
			0.8h_{ref}-0.6h_{ref}	17.2	±	4.2	(9)	**Calving**	3.4	±	3.5	(3)	13.8	(2.4)	2.2	25.5	125
			h_{ref}-0.6h_{ref}	30.7	±	13.5	(10)	**Calving**	8.9	±	7.4	(5)	21.8	(7.4)	0.6	43.1	175
		75	**0.8h_{ref}-0.6h_{ref}**	17.3	±	12	(12)	**Winter**	5.7	±	4.9	(12)	11.6	(3.7)	0	23.2	25

	High							**Low**					**Pairwise Comparison**				
															95% Confidence Interval		
Slope Variable	**season**	**Contour**	**Change in bandwidth**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Season**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolutions (m)**
		95	**h_{ref}-0.8h_{ref}**	15.1	±	8.8	(12)	**Calving**	4	±	4.4	(11)	11	(2.9)	2.3	19.8	all
				15.1	±	8.8	(12)	**Summer**	6.4	±	3.9	(13)	8.7	(2.8)	0.2	17.3	all
			h_{ref}-0.6h_{ref}	38.8	±	26.7	(10)	**Calving**	9.1	±	5.3	(11)	29.7	(8.6)	1.3	58.1	75, 125, 175
CV	**Winter**	**95**	**h_{ref}-0.8h_{ref}**	0.015	±	0.012	(13)	**Calving**	0.003	±	0.004	(11)	0.012	(0.003)	0.004	0.021	all
				-0.015	±	0.012	(13)	**Calving**	-0.003	±	0.004	(10)	0.012	(0.003)	0.003	0.021	All
				-0.017	±	0.011	(10)	**Rut**	-0.007	±	0.005	(7)	0.01	(0.003)	0	0.02	175
				0.015	±	0.011	(13)	**Summer**	0.004	±	0.005	(11)	0.011	(0.003)	0.002	0.02	75, 125, 175
				-0.015	±	0.011	(13)	**Summer**	-0.004	±	0.005	(9)	0.010	(0.003)	0.003	0.020	75, 125, 175
			0.8h_{ref}-0.6h_{ref}	0.015	±	0.011	(13)	**Calving**	0.003	±	0.005	(11)	0.013	(0.003)	0.002	0.023	75, 125
			h_{ref}-0.6h_{ref}	0.029	±	0.021	(14)	**Calving**	0.007	±	0.006	(11)	0.022	(0.007)	0.004	0.04	all
				-0.029	±	0.021	(14)	**Calving**	-0.008	±	0.007	(8)	0.021	(0.006)	0.002	0.040	75, 125, 175
	Fall	**50**	**h_{ref}-0.6h_{ref}**	0.022	±	0.01	(12)	**Rut**	0.007	±	0.009	(11)	0.014	(0.005)	0.001	0.028	75
		75	**0.8h_{ref}-0.6h_{ref}**	0.013	±	0.009	(11)	**Summer**	0.004	±	0.005	(13)	0.009	(0.003)	0.001	0.017	75
		75	**h_{ref}-0.6h_{ref}**	0.022	±	0.017	(13)	**Summer**	0.009	±	0.01	(13)	0.013	(0.004)	0.001	0.026	25
		95	**h_{ref}-0.8h_{ref}**	0.012	±	0.009	(12)	**Calving**	0.003	±	0.004	(11)	0.01	(0.003)	0.001	0.018	25, 125

	High							Low					Pairwise Comparison				
															95% Confidence Interval		
Slope Variable	**season**	**Contour**	**Change in bandwidth**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Season**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolutions (m)**
				-0.015	±	0.008	(9)	**Calving**	-0.003	±	0.004	(10)	0.012	(0.003)	0.002	0.22	25, 125, 175
				-0.019	±	0.007	(7)	**Rut**	-0.007	±	0.005	(7)	0.011	(0.004)	0.001	0.022	125, 175
				-0.019	±	0.007	(7)	**Summer**	-0.004	±	0.005	(9)	0.014	(0.003)	0.004	0.024	125, 175

B. 8 Significant differences (p<0.05) in the descriptive metrics of slope (%) within contours of the same value between the five seasonal home ranges (winter, calving, summer, rut and fall) at each of the three changes in bandwidth (h_{ref}-$0.8h_{ref}$, $0.8h_{ref} – 0.6h_{ref}$ and $h_{ref} – 0.6h_{ref}$). We indicate the resolutions (25, 75, 125 and 175m) at which differences between contours were significant.

	High					Low			Pairwise Comparison				
											95% Confidence interval		
Slope Variable	**season**	**Contour**	**Change in bandwidth**	$\bar{x}_\Delta$ ± **SD**	**(n)**	**Season**	$\bar{x}_\Delta$ ± **SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolutions (m)**
Mean	**Calving**	**50**	**$0.8h_{ref}$-$0.6h_{ref}$**	2.8 ± 0.3	(2)	**Fall**	0.8 ± 0.6	(8)	2	(0.3)	0.4	3.6	175
		75	**h_{ref}-$0.8h_{ref}$**	2.0 ± 0.8	(5)	**Fall**	0.8 ± 0.7	(12)	1.3	(0.4)	0.1	2.4	125
				2.0 ± 0.8	(5)	**Winter**	0.6 ± 0.5	(7)	1.4	(0.4)	0.1	2.7	125
		95	**h_{ref}-$0.8h_{ref}$**	1.1 ± 0.4	(9)	**Winter**	0.4 ± 0.3	(12)	0.7	(0.2)	0.1	1.3	75
				-1.1 ± 0.4	(4)	**Winter**	-0.4 ± 0.3	(11)	0.6	(0.2)	<0.1	1.3	75
	Fall	**75**	**$0.8h_{ref}$-$0.6h_{ref}$**	1.1 ± 0.6	(11)	**Winter**	0.3 ± 0.2	(12)	0.8	(0.2)	0.2	1.4	25, 75
		75		-1.1 ± 0.6	(11)	**Winter**	-0.4 ± 0.6	(10)	0.8	(0.2)	0.1	1.4	25, 75
		95	**h_{ref}-$0.8h_{ref}$**	0.9 ± 0.5	(12)	**Winter**	0.4 ± 0.3	(12)	0.5	(0.2)	<0.1	1	75
	Rut	**25**	**h_{ref}-$0.8h_{ref}$**	1.1 ± 0.3	(2)	**Fall**	0.5 ± 0.3	(9)	0.7	(0.1)	0.3	1.2	175
		95	**h_{ref}-$0.8h_{ref}$**	1.0 ± 0.5	(9)	**Winter**	0.4 ± 0.3	(12)	0.6	(0.2)	<0.1	1.2	75
	Summer	**50**	**h_{ref}-$0.8h_{ref}$**	1.2 ± 0.8	(12)	**Winter**	0.4 ± 0.3	(12)	0.9	(0.3)	<0.1	1.7	25

	High							**Low**					**Pairwise Comparison**				
															95% Confidence interval		
Slope Variable	**season**	**Contour**	**Change in bandwidth**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Season**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Significant resolutions (m)**
SD	**Calving**	**50**	**$0.8h_{ref}$-$0.6h_{ref}$**	2.2	±	0.5	(3)	**Winter**	0.5	±	0.8	(9)	1.7	(0.4)	0.1	3.2	75
	Fall	**25**	**h_{ref}-$0.8h_{ref}$**	0.6	±	0.4	(9)	**Summer**	0.5	±	0.6	(3)	0.1	(0)	0.1	0.1	175
		50	**h_{ref}-$0.8h_{ref}$**	1.2	±	0.7	(12)	**Winter**	0.3	±	0.5	(12)	0.9	(0.3)	0.1	1.6	25, 75
		75	**$0.8h_{ref}$-$0.6h_{ref}$**	1.3	±	0.9	(9)	**Calving**	0.2	±	0.1	(4)	1.1	(0.3)	<0.1	2.2	125
				1.4	±	0.9	(11)	**Winter**	0.2	±	0.2	(12)	1.2	(0.3)	0.3	2.1	25, 75
				-1.7	±	0.8	(9)		-0.2	±	0.2	(7)	1.4	(0.3)	0.5	2.4	all
			h_{ref}-$0.6h_{ref}$	1.8	±	1.3	(13)	**Winter**	0.6	±	0.5	(13)	1.2	(0.4)	<0.1	2.4	25, 75
				-2.4	±	0.8	(9)		-0.8	±	0.6	(8)	1.6	(0.5)	0.2	3.0	75, 125, 175
CV	**Summer**	**25**	**h_{ref}-$0.8h_{ref}$**	0.099	±	0.009	(3)	**Fall**	0.043	±	0.04	(10)	-0.056	(0.014)	-0.009	-0.103	125
								Rut	0.02	±	0.019	(3)	-0.079	(0.012)	-0.004	-0.154	125

Appendix C: Supplementary Results for chapter 3

C. 1 Number of significant differences in in $\overline{x}$ of elevation between each contour pair of a season (winter, calving, summer, rut and fall) at each KDE bandwidth (h_{ref}, $0.8h_{ref}$ and $0.6h_{ref}$) and DEM resolution (25, 75, 125 and 175m).

		Bandwidth:	***h_{ref}***				***$0.8h_{ref}$***				***$0.6h_{ref}$***			
Season	**Contour Pair**	**Resolution (m):**	**25**	**75**	**125**	**175**	**25**	**75**	**125**	**175**	**25**	**75**	**125**	**175**
Winter	**25 - 50**		14	13	11	11	14	13	13	11	14	12	10	9
	25 - 75		14	13	13	12	14	14	13	13	14	14	14	13
	25 - 95		14	14	14	14	13	13	13	13	14	14	13	13
	50 - 75		14	14	14	14	14	13	13	13	14	13	12	11
	50 - 95		14	14	14	14	14	14	14	14	14	14	14	13
	75 - 95		14	14	14	14	14	14	14	13	13	13	13	13
Calving	**25 - 50**		11	10	9	8	11	9	8	6	11	10	9	7
	25 - 75		11	10	10	9	11	11	11	9	11	11	11	10
	25 - 95		11	11	11	11	11	11	11	10	11	11	11	11
	50 - 75		11	8	7	6	10	10	10	8	11	10	9	7
	50 - 95		11	10	8	8	11	9	9	9	11	10	10	10
	75 - 95		11	10	10	8	11	9	9	8	11	8	8	8
Summer	**25 - 50**		12	10	10	10	12	11	10	9	11	7	7	6
	25 - 75		13	13	13	13	13	13	13	13	13	13	11	11
	25 - 95		13	13	13	13	13	13	13	13	13	12	12	12
	50 - 75		13	13	12	12	13	13	13	11	13	12	11	11
	50 - 95		12	12	12	12	13	13	13	13	13	13	13	12
	75 - 95		12	12	12	12	13	12	12	12	13	13	13	13
Rut	**25 - 50**		12	11	11	9	12	10	9	9	11	10	10	10

	25 - 75	12	11	11	11	12	12	10	10	11	11	10	9
	25 - 95	12	11	11	11	12	11	11	11	12	10	9	9
	50 - 75	11	9	9	9	10	9	9	8	12	10	10	9
	50 - 95	11	11	11	11	12	11	10	10	12	11	10	10
	75 - 95	12	11	10	10	11	10	10	9	12	11	11	10
Fall	**25 - 50**	13	13	12	12	13	13	13	12	13	11	10	9
	25 - 75	13	13	13	13	13	12	12	12	13	12	12	12
	25 - 95	13	13	13	13	13	13	13	13	13	13	13	13
	50 - 75	13	13	13	13	13	12	12	11	13	13	11	10
	50 - 95	13	13	13	13	13	13	12	12	13	13	13	12
	75 - 95	13	12	12	12	13	12	11	8	13	12	12	11

C. 2 Number of significant differences in in $\overline{x}$ slope between each contour pair of a season (winter, calving, summer, rut and fall) at each KDE bandwidth (h_{ref}, $0.8h_{ref}$ and $0.6h_{ref}$) and DEM resolution (25, 75, 125 and 175m).

Season	Contour Pair	Bandwidth:	h_{ref}				$0.8h_{ref}$				$0.6h_{ref}$			
		Resolution (m):	25	75	125	175	25	75	125	175	25	75	125	175
Winter	25 - 50		13	12	9	9	13	11	9	9	12	11	11	10
	25 - 75		14	12	11	11	14	12	13	12	14	13	11	11
	25 - 95		14	12	12	11	14	11	11	11	14	11	12	12
	50 - 75		13	11	10	8	13	10	9	6	13	11	7	6
	50 - 95		12	12	13	13	14	12	13	12	14	14	13	14
	75 - 95		13	13	12	11	13	11	11	11	11	11	10	10
Calving	25 - 50		10	8	7	6	9	8	8	7	11	10	9	8
	25 - 75		11	9	8	7	11	10	8	7	9	8	7	7
	25 - 95		11	11	11	11	10	10	10	9	10	10	9	8
	50 - 75		9	8	9	8	10	10	9	7	9	10	9	8
	50 - 95		11	9	9	8	10	10	10	9	10	9	9	6
	75 - 95		10	7	7	6	9	7	6	5	8	8	8	7
Summer	25 - 50		11	10	8	8	11	10	9	8	12	12	11	8
	25 - 75		13	13	11	11	13	12	10	9	11	10	10	10
	25 - 95		13	12	11	9	13	12	12	10	12	12	11	11
	50 - 75		12	11	11	10	13	11	10	9	11	11	10	9
	50 - 95		13	12	11	11	13	12	11	11	13	11	11	11
	75 - 95		13	12	9	9	13	13	12	11	12	12	11	11
Rut	25 - 50		11	11	11	10	12	12	10	10	10	10	9	8

	25 - 75	12	11	10	10	12	11	10	10	10	10	10	9
	25 - 95	12	10	10	9	11	9	8	8	11	11	9	9
	50 - 75	12	12	11	11	11	11	10	10	12	11	10	9
	50 - 95	12	11	10	10	12	12	11	11	12	11	11	10
	75 - 95	11	11	10	10	11	10	9	8	10	9	9	8
Fall	**25 - 50**	13	12	11	11	12	12	12	11	12	9	8	7
	25 - 75	13	13	13	12	13	12	12	12	12	12	12	11
	25 - 95	13	12	10	10	13	13	12	12	13	13	13	13
	50 - 75	12	11	11	11	13	13	11	11	13	10	10	10
	50 - 95	13	12	12	12	13	13	13	12	13	13	13	13
	75 - 95	12	12	13	13	13	13	12	9	12	12	11	11

C. 3 Significant differences ($p<0.05$) in the descriptive metrics of elevation (m) between contour pairs within each seasonal home range (winter, calving, summer, rut and fall). We indicate the KDE bandwidths (h_{ref}-0.8h_{ref}, 0.8h_{ref} – 0.6h_{ref} and h_{ref} – 0.6h_{ref}) as well as DEM resolutions (25, 75, 125 and 175m) at which significant differences were found.

		High			Low			Pairwise comparison				Significant resolutions (m)		
										95% Confidence interval		Bandwidth:		
Elevation Variable	Season	Contour Pair	$\bar{x}_{\Delta}$ ± SD	(n)	Contour Pair	$\bar{x}_{\Delta}$ ± SD	(n)	Mean Difference	(SE)	Lower	Upper	h_{ref}	$0.8h_{ref}$	$0.6h_{ref}$
Mean	**Fall**	**25-75**	66.0 ± 35.5	(12)	**25-50**	27.7 ± 22.8	(13)	38.3	(12.04)	0.1	76.5		75, 125	
		25-95	94.4 ± 55.6	(13)	**25-50**	27.6 ± 22.8	(13)	66.7	(16.67)	13.0	120.4		all	25, 75, 125
		25-95	94.4 ± 55.6	(13)	**50-75**	38.2 ± 30.0	(13)	56.2	(17.53)	0.6	111.7		25	25, 75
		50-95	82.5 ± 53.5	(12)	**25-50**	27.7 ± 22.8	(13)	54.8	(16.7)	0.4	109.2		125	25
	Rut	**25-95**	90.1 ± 60.0	(11)	**25-50**	28.3 ± 24.0	(11)	61.8	(18.21)	8.2	115.5	75, 125, 175		
		25-95	60.7 ± 26.7	(9)	**75-95**	26.6 ± 18.5	(11)	34.1	(11.05)	1.5	66.8		all	125, 175
	Summer	**25-95**	139.2 ± 69.4	(13)	**25-50**	60.2 ± 47.8	(12)	79.0	(22.43)	13.2	144.7	25	25, 75, 125	25
		25-95	139.2 ± 69.4	(13)	**50-75**	57.5 ± 48.2	(13)	81.7	(21.98)	17.3	146.1	all	25, 75, 125	75
		25-95	139.2 ± 69.4	(13)	**75-95**	59.4 ± 33.0	(12)	79.7	(22.43)	14.0	145.5	all	all	75, 125, 175
SD	**Calving**	**25-95**	58.9 ± 39.3	(11)	**75-95**	14.4 ± 10.1	(11)	44.5	(12.24)	3.0	86.0	all		
	Fall	**25-75**	61.3 ± 18.6	(13)	**25-50**	29.7 ± 21.6	(13)	31.6	(7.9)	7.2	56.1			25, 75, 125
			61.3 ± 18.6	(13)	**50-75**	31.6 ± 16.8	(13)	29.7	(9.94)	0.6	58.8			25, 75
		25-95	101.6 ± 55.2	(13)	**25-50**	46.4 ± 23.1	(13)	55.3	(16.59)	1.8	108.7	all	all	all
			101.6 ± 55.2	(13)	**50-75**	34.6 ± 22.1	(13)	67.1	(16.48)	13.9	120.3	all	all	all

		High			Low			Pairwise comparison				Significant resolutions (m)		
										95% Confidence interval		Bandwidth:		
Elevation Variable	**Season**	**Contour Pair**	$\bar{x}_\Delta$ ± SD	**(n)**	**Contour Pair**	$\bar{x}_\Delta$ ± SD	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	***h**_{ref}*	***0.8h**_{ref}*	***0.6h**_{ref}*
			86.7 ± 23.3	(13)	**50-95**	57.4 ± 37.9	(13)	29.3	(9.94)	0.2	58.4			25, 75, 175
			101.6 ± 55.2	(13)	**75-95**	39.0 ± 29.0	(13)	62.6	(14.31)	20.7	104.5	all	all	all
		50-95	62.1 ± 35.3	(12)	**25-50**	27.6 ± 21.2	(12)	34.5	(10.09)	4.9	64.1			25, 75, 125
	Rut	**25-95**	43.8 ± 22.5	(12)	**50-75**	12.5 ± 15.7	(12)	31.2	(7.43)	9.4	53.1			all
		25-95	47.7 ± 25.4	(12)	**75-95**	19.8 ± 13.5	(11)	27.8	(8.38)	1.1	54.6		25, 75, 125	all
	Summer	**25-75**	74.9 ± 45.7	(11)	**75-95**	20.4 ± 11.3	(13)	54.6	(14.12)	6.4	102.7			125, 175
	Winter	**25-95**	96.1 ± 48.7	(14)	**25-50**	27.3 ± 25.8	(14)	68.8	(14.74)	22.4	115.2	all	all	all
		25-95	96.1 ± 48.7	(14)	**25-75**	45.7 ± 38.3	(14)	50.4	(13.51)	10.9	89.9	all	all	
		25-95	96.1 ± 48.7	(14)	**50-75**	20.7 ± 16.1	(14)	75.4	(13.72)	31.2	119.7	all	all	all
		25-95	96.1 ± 48.7	(14)	**75-95**	50.6 ± 39.1	(14)	45.5	(13.51)	6.0	85.0	all		25, 125, 175
		50-95	70.1 ± 37.0	(14)	**25-50**	27.3 ± 25.8	(14)	42.8	(13.51)	3.3	82.3	all		
		50-95	70.1 ± 37.0	(14)	**50-75**	20.7 ± 16.1	(14)	49.4	(10.8)	15.1	83.8	all	all	125, 175
CV	**Calving**	**25-95**	.0470 ± .0240	(11)	**75-95**	.0120 ± .0100	(11)	0.034	(0.008)	0.009	0.060	25, 75, 125	25, 175	
	Fall	**25-75**	.0440 ± .0130	(13)	**25-50**	.0200 ± .0140	(13)	0.023	(0.005)	0.007	0.040			all
		25-75	.0450 ± .0120	(12)	**50-75**	.0240 ± .0110	(13)	0.022	(0.007)	0.000	0.043			75
		25-95	.0790 ± .0440	(13)	**25-50**	.0330 ± .0170	(13)	0.046	(0.013)	0.004	0.089	all	all	all
		25-95	.0670 ± .0150	(12)	**25-75**	.0440 ± .0140	(12)	0.024	(0.007)	0.002	0.046			25
		25-95	.0790 ± .0440	(13)	**50-75**	.0250 ± .0170	(13)	0.054	(0.013)	0.012	0.097	all	all	all

		High			Low			Pairwise comparison				Significant resolutions (m)		
										95% Confidence interval		Bandwidth:		
Elevation Variable	**Season**	**Contour Pair**	$\bar{x}_\Delta$ ± **SD**	**(n)**	**Contour Pair**	$\bar{x}_\Delta$ ± **SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	h_{ref}	$0.8h_{ref}$	$0.6h_{ref}$
		25-95	.0800 ± .0300	(12)	**50-95**	.0510 ± .0350	(13)	0.029	(0.01)	0.000	0.057		25	25, 75, 125
		25-95	.0790 ± .0440	(13)	**75-95**	.0310 ± .0260	(13)	0.047	(0.012)	0.013	0.082	all	all	all
		50-95	.0440 ± .0270	(13)	**25-50**	.0200 ± .0140	(13)	0.024	(0.007)	0.003	0.045			25, 125
	Rut	**25-95**	.0330 ± .0170	(12)	**25-50**	.0180 ± .0080	(12)	0.015	(0.005)	0.000	0.030	25, 75, 125	all	
		25-95	.0330 ± .0170	(12)	**50-75**	.0160 ± .0100	(11)	0.017	(0.005)	0.002	0.033	all	all	all
		25-95	.0300 ± .0140	(12)	**50-95**	.0160 ± .0130	(12)	0.014	(0.005)	0.000	0.028			25, 75
		25-95	.0330 ± .0170	(12)	**75-95**	.0170 ± .0110	(12)	0.016	(0.005)	0.001	0.030	25, 75, 125	all	all
	Winter	**25-95**	.0930 ± .0450	(14)	**25-50**	.0270 ± .0230	(14)	0.066	(0.014)	0.024	0.109	all	all	all
		25-95	.0930 ± .0450	(14)	**25-75**	.0450 ± .0330	(14)	0.048	(0.015)	0.002	0.095	all	all	
		25-95	.0930 ± .0450	(14)	**50-75**	.0210 ± .0150	(14)	0.073	(0.013)	0.032	0.114	all	all	all
		25-95	.0930 ± .0450	(14)	**75-95**	.0490 ± .0380	(14)	0.044	(0.013)	0.007	0.081	all	all	all
		50-95	.0670 ± .0370	(14)	**25-50**	.0270 ± .0230	(14)	0.040	(0.013)	0.003	0.078	all		
		50-95	.0670 ± .0370	(14)	**50-75**	.0210 ± .0150	(14)	0.047	(0.011)	0.012	0.081	all	all	

C. 4 Significant differences ($p<0.05$) in the descriptive metrics of slope (%) between contour pairs within each seasonal home range (winter, calving, summer, rut and fall). We indicate the KDE bandwidths (h_{ref}-$0.8h_{ref}$, $0.8h_{ref}$ – $0.6h_{ref}$ and h_{ref} – $0.6h_{ref}$) as well as DEM resolutions (25, 75, 125 and 175m) at which significant differences were found.

										Pairwise comparison				**Significant resolutions (m)**		
		High				**Low**						**95% Confidence interval**		**Bandwidth:**		
Elevation Variable	**Season**	**Contour Pair**	$\bar{x}_\Delta$	**± SD**	**(n)**	**Contour Pair**	$\bar{x}_\Delta$	**± SD**	**(n)**	**Mean difference**	**(SE)**	**Lower**	**Upper**	***h**$_{ref}$*	***0.8h**$_{ref}$*	***0.6h**$_{ref}$*
Mean	**Fall**	**25-75**	2.9	± 1.4	(12)	**75-95**	1.3	± 1.1	(12)	1.6	(0.5)	0.1	3.1		125	
		25-95	4.4	± 1.4	(10)	**25-50**	2.0	± 1.0	(11)	2.4	(0.7)	0.5	4.3	125, 175	125	
		25-95	4.4	± 1.4	(10)	**50-75**	1.8	± 1.2	(11)	2.6	(0.7)	0.7	4.5	125, 175		
		25-95	4.4	± 1.4	(10)	**75-95**	1.9	± 1.4	(13)	2.5	(0.6)	0.7	4.4	125, 175	75, 125, 175	25, 75, 125
	Summer	**25-75**	8.2	± 5.1	(13)	**75-95**	2.9	± 2.2	(13)	5.3	(1.5)	0.4	10.3	25		
	Winter	**25-95**	3.0	± 1.9	(11)	**50-75**	0.8	± 0.6	(11)	2.2	(0.6)	0.1	4.2		75, 125, 175	75, 175
SD	**Calving**	**25-75**	6.0	± 3.2	(7)	**75-95**	1.1	± 1.1	(6)	4.9	(1.3)	0.2	9.6	175		
	Fall	**25-75**	4.0	± 2.6	(13)	**75-95**	1.6	± 1.4	(13)	2.4	(0.8)	0	4.8		25, 75, 125	
		25-95	5.5	± 2.4	(10)	**25-50**	2.4	± 1.9	(11)	3.1	(0.9)	0.5	5.6	125, 175		25, 75, 125
		25-95	5.1	± 2.9	(13)	**50-75**	1.9	± 1.4	(12)	3.2	(0.9)	0.3	6.1	all		
		25-95	5.5	± 2.4	(10)	**75-95**	2.2	± 1.2	(13)	3.3	(0.8)	0.8	5.7	125, 175	25, 75, 125	75, 125
	Rut	**25-95**	4.4	± 2.5	(11)	**50-75**	1.7	± 1.0	(12)	2.7	(0.9)	0.2	5.3			25

		25-95	4.4 ± 2.5	(11)	**50-95**	1.9 ± 1.7	(12)	2.5	(0.9)	<0.1	5.0			25
		25-95	4.4 ± 2.5	(11)	**75-95**	1.5 ± 1.1	(10)	2.9	(0.9)	0.3	5.5			25, 75
	Winter	**25-95**	3.0 ± 1.9	(11)	**50-75**	0.6 ± 0.6	(11)	2.4	(0.6)	0.4	4.5		75, 125	75, 125
		50-95	2.9 ± 1.7	(12)	**50-75**	1.1 ± 0.8	(13)	1.8	(0.5)	0.1	3.6	25		
CV	**Calving**	**25-95**	0.20 ± 0.11	(11)	**50-75**	0.05 ± 0.04	(9)	0.15	(0.04)	0.02	0.27	125, 175		
	Fall	**25-75**	0.18 ± 0.13	(13)	**75-95**	0.06 ± 0.05	(13)	0.12	(0.04)	<0.01	0.24		25, 125, 175	
		25-95	0.28 ± 0.17	(12)	**50-75**	0.12 ± 0.08	(11)	0.16	(0.05)	<0.01	0.31		175	
		25-95	0.25 ± 0.16	(10)	**75-95**	0.10 ± 0.09	(13)	0.15	(0.05)	0.01	0.29	125, 175	125, 175	175
	Rut	**25-75**	0.23 ± 0.13	(12)	**75-95**	0.09 ± 0.07	(11)	0.15	(0.05)	0.01	0.28	25	175	all
	Summer	**25-75**	0.23 ± 0.14	(13)	**75-95**	0.08 ± 0.07	(13)	0.16	(0.04)	0.02	0.29	25, 75		
		25-95	0.32 ± 0.19	(11)	**75-95**	0.13 ± 0.10	(11)	0.19	(0.06)	<0.01	0.38			175

C. 5 Significant pairwise differences between seasons ($p<0.05$) in the descriptive metrics of elevation (m) between contours between each season (winter, calving, summer, rut and fall). We indicate the KDE bandwidths (h_{ref}-$0.8h_{ref}$, $0.8h_{ref} – 0.6h_{ref}$ and $h_{ref} – 0.6h_{ref}$) as well as DEM resolutions (25, 75, 125 and 175m) at which significant differences were found.

										Pairwise Comparison				Bandwidth/Resolution (m)		
												95% Confidence Interval				
Elevation Variable	**High Season**	**Contour Pair**	$\bar{x}_\Delta$	**± SD**	**(n)**	**Low Season**	$\bar{x}_\Delta$	**± SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	h_{ref}	0.8 h_{ref}	0.6 h_{ref}
Mean	**Calving**	**25-75**	98.1	± 81.6	(10)	**Winter**	38.7	± 21.7	(13)	59.4	(26.5)	27.8	146.7			175
	Summer	**25-50**	71.7	± 44.1	(10)	**Winter**	29	± 29.2	(11)	42.7	(14.7)	1	84.4	175		
		25-75	107.7	± 65.1	(13)	**Rut**	39.1	± 23.2	(12)	68.6	(19.2)	9.3	128		all	all
		25-75	110.8	± 74.3	(13)	**Winter**	40.3	± 36.1	(14)	70.5	(22.8)	1.3	139.7	25	all	all
		25-95	127.9	± 78.5	(13)	**Rut**	46.1	± 34.8	(12)	81.8	(24)	8.7	154.9			all
		25-95	134.8	± 78.1	(13)	**Winter**	64.1	± 44.2	(13)	70.7	(25)	0.2	141.2		175	all
		50-95	103.2	± 65.5	(13)	**Rut**	42.1	± 33.3	(12)	61.1	(20.8)	2.6	119.5			25
		50-95	103.2	± 65.5	(13)	**Winter**	35	± 31.4	(14)	68.2	(20)	7.2	129.1			all
SD	**Calving**	**25-50**	71.7	± 62.1	(6)	**Rut**	23.9	± 11.5	(9)	47.8	(25.6)	53.3	148.9		175	
	Fall	**25-75**	77.4	± 23.2	(12)	**Rut**	37.9	± 23.9	(9)	39.5	(13.8)	0.3	78.7	175		
		25-75	77.5	± 23	(12)	**Winter**	38.9	± 29.7	(13)	38.7	(13)	1.7	75.6	75,125		
		25-95	101.6	± 55.2	(13)	**Rut**	44.9	± 27	(12)	56.8	(17.2)	4.7	108.8	all	25	
		25-95	101.6	± 55.2	(13)	**Summer**	50.9	± 41	(13)	50.7	(17.2)	2.4	99	all	all	

Elevation Variable	High Season	Contour Pair	$\bar{x}_\Delta$	± SD	(n)	Low Season	$\bar{x}_\Delta$	± SD	(n)	Pairwise Comparison				Bandwidth/Resolution (m)		
												95% Confidence Interval				
										Mean Difference	(SE)	Lower	Upper	h_{ref}	0.8 h_{ref}	0.6 h_{ref}
		50-95	70.5	± 42.6	(12)	**Rut**	31.3	± 23.1	(10)	39.2	(13.3)	1.6	76.8		25	
	Summer	**50-75**	44.7	± 40.5	(11)	**Rut**	14.2	± 16.9	(10)	30.6	(10.1)	1.8	59.3			125
		50-75	44.7	± 40.5	(11)	**Winter**	16.1	± 14.2	(12)	28.6	(9.7)	1.1	56.1			125
	Winter	**25-95**	96.1	± 48.7	(14)	**Rut**	44.9	± 27	(12)	51.2	(15.2)	4.2	98.3	all		
		50-95	70.1	± 37	(14)	**Calving**	32.5	± 24.1	(11)	37.6	(13.2)	0.3	74.9	all		
		50-95	70.1	± 37	(14)	**Rut**	28.7	± 17.3	(11)	41.4	(11.2)	7.9	75	all		
		50-95	70.1	± 37	(14)	**Summer**	33.2	± 19.2	(12)	36.9	(11.4)	3	70.9	all		
		75-95	50.6	± 39.1	(14)	**Calving**	14.4	± 10.1	(11)	36.2	(10.9)	2.6	69.7	all		
CV	**Calving**	**25-50**	0.05	± 0.05	(6)	**Rut**	0.02	± 0.01	(9)	0.04	(0.02)	0.04	0.11		175	
	Fall	**25-75**	0.05	± 0.02	(13)	**Rut**	0.02	± 0.01	(12)	0.03	(0.01)	<0.01	0.06	all		
		25-95	0.08	± 0.04	(13)	**Rut**	0.03	± 0.02	(12)	0.05	(0.01)	0.01	0.09	all	all	25
		25-95	0.08	± 0.04	(13)	**Summer**	0.03	± 0.03	(13)	0.04	(0.01)	0.01	0.08	75, 125, 175	all	
	Winter	**25-95**	0.09	± 0.05	(14)	**Calving**	0.05	± 0.02	(11)	0.05	(0.01)	0.01	0.09	all	25, 75, 125	
		25-95	0.09	± 0.05	(14)	**Rut**	0.03	± 0.02	(12)	0.06	(0.01)	0.02	0.10	all	all	all
		25-95	0.09	± 0.05	(14)	**Summer**	0.03	± 0.03	(13)	0.06	(0.01)	0.02	0.10	all	all	all
		50-95	0.07	± 0.04	(14)	**Calving**	0.03	± 0.02	(11)	0.04	(0.01)	0.01	0.07	all		

										Pairwise Comparison						
												95% Confidence Interval		Bandwidth/Resolution (m)		
Elevation Variable	**High Season**	**Contour Pair**	$\overline{x}_{\Delta}$	**± SD**	**(n)**	**Low Season**	$\overline{x}_{\Delta}$	**± SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	h_{ref}	**0.8** h_{ref}	**0.6** h_{ref}
		50-95	0.07	± 0.04	(14)	**Rut**	0.02	± 0.01	(11)	0.05	(0.01)	0.01	0.08	all	all	25, 75
		50-95	0.07	± 0.04	(14)	**Summer**	0.02	± 0.01	(12)	0.04	(0.01)	0.01	0.08	all	all	175
		75-95	0.05	± 0.04	(14)	**Calving**	0.01	± 0.01	(11)	0.04	(0.01)	0.01	0.07	all		
		75-95	0.05	± 0.04	(14)	**Summer**	0.02	± 0.01	(12)	0.03	(0.01)	<0.01	0.07	all		

C. 6 Significant pairwise differences between seasons ($p<0.05$) in the descriptive metrics of slope (%) between contours between each season (winter, calving, summer, rut and fall). We indicate the KDE bandwidths (h_{ref}-$0.8h_{ref}$, $0.8h_{ref}$ – $0.6h_{ref}$ and h_{ref} – $0.6h_{ref}$) as well as DEM resolutions (25, 75, 125 and 175m) at which significant differences were found.

										Pairwise comparison				Significant resolutions (m)		
												95% Confidence interval		Bandwidth:		
Slope Variable	**High Season**	**Contour Pair**	$\overline{x}_\Delta$	**± SD**	**(n)**	**Low Season**	$\overline{x}_\Delta$	**± SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	h_{ref}	$0.8h_{ref}$	$0.6h_{ref}$
Mean	**Summer**	**25-50**	5.4	± 3.3	(11)	**Fall**	2.0	± 1.2	(13)	3.4	(1.0)	0.1	6.8	25, 75, 125	75, 175	175
			5.6	± 2.8	(10)	**Rut**	2.2	± 1.8	(11)	3.4	(0.9)	0.8	5.9	75, 125, 175	175	
			5.6	± 2.8	(10)	**Winter**	1.9	± 2.2	(12)	3.7	(0.9)	1.2	6.2	75, 125, 175	75, 125, 175	
		25-75	8.2	± 5.1	(13)	**Fall**	3.2	± 2.5	(13)	5.0	(1.6)	<0.1	10.0	25, 125, 175	125	75, 125, 175
			8.2	± 5.1	(13)	**Rut**	2.2	± 2.4	(12)	6.0	(1.6)	1.2	10.8	all	all	75, 125, 175
			8.2	± 5.1	(13)	**Winter**	1.9	± 1.7	(14)	6.3	(1.5)	1.7	11.0	all	all	all
		25-95	8.9	± 6.7	(12)	**Rut**	2.3	± 2.1	(11)	6.6	(2.0)	0.2	13.0			75
			7.3	± 5.5	(11)	**Winter**	2.9	± 1.9	(12)	4.4	(1.5)	0.1	8.6	125		175
		50-75	4.6	± 3.1	(11)	**Fall**	1.7	± 1.3	(10)	2.9	(1.0)	0.1	5.6			75,125, 175
			4.9	± 3.5	(11)	**Rut**	1.6	± 1.6	(12)	3.3	(1.0)	0.6	6.0			all
			4.9	± 3.5	(11)	**Winter**	0.8	± 0.6	(13)	4.1	(0.9)	1.4	6.7		all	all
		50-95	6.4	± 5.7	(11)	**Rut**	2.4	± 1.8	(11)	4.1	(1.4)	0.1	8.0			75, 125
			5.5	± 5.6	(13)	**Winter**	1.5	± 1.4	(14)	4.1	(1.3)	0.4	7.7		25	

										Pairwise comparison				Significant resolutions (m)		
												95% Confidence interval		Bandwidth:		
Slope Variable	**High Season**	**Contour Pair**	$\overline{x}_\Delta$	**± SD**	**(n)**	**Low Season**	$\overline{x}_\Delta$	**± SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	h_{ref}	$0.8h_{ref}$	$0.6h_{ref}$
		75-95	3.6	± 2.1	(13)	**Fall**	1.3	± 1.2	(13)	2.3	(0.7)	0.2	4.4		25, 75	
			3.6	± 2.1	(13)	**Rut**	1.5	± 1.0	(11)	2.0	(0.6)	0.1	4.0		25, 75	
SD	**Calving**	**25-75**	6.0	± 3.2	(7)	**Winter**	1.2	± 1.0	(11)	4.8	(1.2)	0.3	9.3	175		
		50-75	2.8	± 1.5	(8)	**Winter**	0.7	± 0.5	(6)	2.1	(0.6)	0.2	3.9			175
	Summer	**25-75**	7.8	± 4.7	(10)	**Fall**	3.4	± 2.4	(12)	4.4	(1.5)	0.2	8.6			75
			6.4	± 5.3	(13)	**Winter**	1.4	± 1.3	(14)	5.0	(1.5)	0.3	9.7	all	all	all
		50-75	4.8	± 3.0	(11)	**Fall**	2.0	± 2.1	(13)	2.8	(0.9)	0.3	5.3			25
			4.8	± 3.0	(11)	**Rut**	1.7	± 1.0	(12)	3.1	(1.0)	0.1	6.2		175	25, 125, 175
			4.8	± 3.0	(11)	**Winter**	0.6	± 0.7	(13)	4.2	(0.8)	1.7	6.7		all	all
CV	**Rut**	**25-75**	0.23	± 0.13	(12)	**Winter**	0.09	± 0.10	(14)	0.14	(0.05)	0.01	0.28	25	all	25, 75
			0.28	± 0.11	(8)	**Winter**	0.08	± 0.08	(7)	0.20	(0.07)	0.002	0.39	25		25, 75, 175
	Summer	**25-75**	0.27	± 0.19	(13)	**Winter**	0.10	± 0.06	(14)	0.21	(0.05)	0.03	0.38		75	
	Fall	**25-75**	0.27	± 0.16	(9)	**Winter**	0.08	± 0.04	(11)	0.19	(0.05)	0.01	0.37			75

										Pairwise comparison				**Significant resolutions (m)**		
												95% Confidence interval		**Bandwidth:**		
Slope Variable	**High Season**	**Contour Pair**	$\overline{x}_{\Delta}$	**± SD**	**(n)**	**Low Season**	$\overline{x}_{\Delta}$	**± SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	***h_{ref}***	***$0.8h_{ref}$***	***$0.6h_{ref}$***
	Summer	**25-50**	0.24	± 0.10	(6)	**Winter**	0.07	± 0.06	(9)	0.17	(0.06)	0.004	0.34	25, 125		
		25-75	0.27	± 0.20	(8)	**Winter**	0.10	± 0.06	(9)	0.21	(0.05)	0.03	0.38		75	

Appendix D: Supplementary Results for chapter 4

D. 1 Number of significant differences in $\overline{x}$ of slope between each increase in resolution (25-75m, 75-125m and 125-175m) within each of the four UD contours (25, 50, 75 and 95%) in each season (winter, calving, summer, rut and fall) at each KDE bandwidth (h_{ref}, $0.8h_{ref}$ and $0.6h_{ref}$).

		Contour:	**25**			**50**			**75**			**95**		
Season2	**Increase in resolution (m)**	***Bandwidth:***	h_{ref}	$0.8h_{ref}$	$0.6h_{ref}$	h_{ref}	$0.8h_{ref}$	$0.6h_{ref}$	h_{ref}	$0.8h_{ref}$	$0.6h_{ref}$	h_{ref}	$0.8h_{ref}$	$0.6h_{ref}$
Winter	**25 – 75**		14	14	14	14	14	14	14	13	14	14	14	14
	75 – 125		14	14	12	14	13	13	14	14	14	14	14	14
	125 - 175		5	3	1	11	10	6	14	10	11	13	13	12
Calving	**25 – 75**		11	11	10	11	11	11	11	11	11	11	11	11
	75 – 125		6	6	6	7	5	4	8	6	7	10	10	9
	125 - 175		2	1	1	2	1	1	2	2	1	5	4	3
Summer	**25 – 75**		13	12	11	13	12	13	13	13	13	13	13	13
	75 – 125		4	4	3	7	7	5	10	9	7	11	11	11
	125 - 175		1				1		3	2	1	9	8	7
Rut	**25 – 75**		11	11	11	11	11	11	11	11	11	12	12	12
	75 – 125		10	10	8	10	10	10	10	10	10	11	10	10
	125 - 175		2	2	2	2	1	1	6	5	2	9	8	7
Fall	**25 – 75**		13	13	13	13	13	13	13	13	13	13	13	13
	75 – 125		13	11	11	13	12	12	13	13	13	13	13	13
	125 - 175		6	5	2	6	3	4	10	7	5	11	12	11

D. 2 Significant pairwise differences ($p<0.05$) in $\overline{x}_{\Delta\overline{x}}$ and $\overline{x}_{\Delta SD}$ of slope (%) between each successive increase in resolution (25-75m vs. 75-125m, and 75-125m vs. 125-175m) within each contour (25, 50, 75 and 95) and seasonal home range (winter, calving, summer, rut and fall). Significant differences between each increase in resolution were not found for $\overline{x}_{\Delta CV}$. We indicate the bandwidths (h_{ref}, $0.8h_{ref}$ and $0.6h_{ref}$) at which differences between resolutions were significant.

			High				Low				Pairwise Comparison				
													95% Confidence interval		
Slope Variable	**Season**	**Contour**	**Increase in resolution (m)**	$\overline{x}_{\Delta}$	**± SD**	**(n)**	**Increase in resolution (m)**	$\overline{x}_{\Delta}$	**± SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Bandwidths**
Mean	**Fall**		**25 - 75**				**75 - 125**								
		25		-1.5	± 0.30	(13)		-0.6	± 0.13	(13)	0.9	(0.09)	0.6	1.2	all
		50		-1.5	± 0.31	(13)		-0.7	± 0.10	(13)	0.9	(0.09)	0.6	1.1	all
		75		-1.7	± 0.21	(13)		-0.8	± 0.10	(13)	0.8	(0.06)	0.6	1.0	all
		95		-1.6	± 0.14	(13)		-0.8	± 0.12	(13)	0.8	(0.08)	0.6	1.0	all
			75 - 125				**125 - 175**								
		25		-0.6	± 0.13	(13)		-0.3	± 0.03	(6)	0.3	(0.04)	0.2	0.4	all
		50		-0.7	± 0.10	(13)		-0.4	± 0.04	(6)	0.2	(0.03)	0.1	0.3	h_{ref}, 0.8 h_{ref}
		95		-0.8	± 0.10	(13)		-0.6	± 0.09	(12)	0.2	(0.08)	0.0	0.5	0.8 h_{ref}
	Rut		**25 - 75**				**75 - 125**								
		50		-1.4	± 0.40	(11)		-0.7	± 0.23	(10)	0.8	(0.14)	0.3	1.2	h_{ref}
		75		-1.4	± 0.34	(11)		-0.7	± 0.25	(10)	0.7	(0.23)	0.1	1.4	all
		95		-1.5	± 0.38	(12)		-0.8	± 0.24	(11)	0.7	(0.22)	0.1	1.3	all

			High				Low				Pairwise Comparison		95% Confidence interval		
Slope Variable	Season	Contour	Increase in resolution (m)	$\bar{x}_{\Delta}$	± SD	(n)	Increase in resolution (m)	$\bar{x}_{\Delta}$	± SD	(n)	Mean Difference	(SE)	Lower	Upper	Bandwidths
			75 - 125				**125 - 175**								
		25		-0.5	± 0.25	(10)		-0.2	± 0.06	(2)	0.3	(0.09)	0.0	0.7	h_{ref}, 0.8 h_{ref}
	Winter		**25 - 75**				**75 - 125**								
		25		-1.5	± 0.26	(14)		-0.7	± 0.12	(14)	0.8	(0.1)	0.5	1.1	all
		50		-1.6	± 0.33	(14)		-0.7	± 0.21	(14)	0.8	(0.16)	0.4	1.3	all
		75		-1.5	± 0.19	(14)		-0.7	± 0.17	(14)	0.8	(0.11)	0.5	1.1	h_{ref}, 0.8 h_{ref}
		95		-1.5	± 0.26	(14)		-0.7	± 0.18	(14)	0.8	(0.13)	0.4	1.2	h_{ref}, 0.8 h_{ref}
SD	**Fall**		**25 - 75**				**75 - 125**								
		25		-1.4	± 0.25	(13)		-0.7	± 0.23	(13)	0.7	(0.14)	0.3	1.1	all
		50		-1.3	± 0.35	(13)		-0.7	± 0.24	(13)	0.6	(0.18)	0.1	1.1	all
		75		-1.5	± 0.23	(13)		-0.9	± 0.26	(13)	0.6	(0.16)	0.1	1.0	all
		95		-1.4	± 0.29	(13)		-0.9	± 0.22	(13)	0.5	(0.15)	0.1	0.9	0.6 h_{ref}
	Winter		**25 - 75**				**75 - 125**								
		25		-1.5	± 0.41	(14)		-0.6	± 0.19	(14)	0.9	(0.12)	0.5	1.3	all
		50		-1.7	± 0.76	(14)		-0.8	± 0.32	(14)	1.0	(0.3)	0.1	1.8	h_{ref}

											Pairwise Comparison				
			High				**Low**						**95% Confidence interval**		
Slope Variable	**Season**	**Contour**	**Increase in resolution (m)**	$\overline{x}_{\Delta}$	**± SD**	**(n)**	**Increase in resolution (m)**	$\overline{x}_{\Delta}$	**± SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Bandwidths**
		75		-1.7	± 0.39	(14)		-0.8	± 0.25	(14)	0.9	(0.18)	0.4	1.4	h_{ref}, 0.8 h_{ref}
		95		-1.5	± 0.38	(14)		-0.7	± 0.22	(14)	0.8	(0.12)	0.4	1.2	all

D. 3 Significant pairwise differences (p<0.05) in the descriptive metrics of slope (%) between the four contours (25, 50, 75 and 95) of each seasonal home range (winter, calving, summer, rut and fall) at each increase in resolution (25-75m, 75-125m and 125-175m). We indicate the bandwidths (h_{ref}, $0.8h_{ref}$ and $0.6h_{ref}$) at which differences between resolutions were significant.

			High			Low			Pairwise Comparison		95% Confidence interval		
Slope variable	**Season**	**Increase in Resolution (m)**	**Contour**	**$\overline{x}_\Delta$ ± SD**	**(n)**	**Contour**	**$\overline{x}_\Delta$ ± SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Bandwidths**
Mean	**Fall**	**75 – 125**	**25**	-0.6 ± 0.13	(13)	**75**	-0.8 ± 0.1	(13)	0.2	(0)	0.1	0.3	h_{ref}
		125 – 175		-0.3 ± 0.03	(6)		-0.6 ± 0.14	(7)	0.2	(0)	0.1	0.4	h_{ref}, 0.8 h_{ref}
		75 – 125	**25**	-0.6 ± 0.13	(13)	**95**	-0.8 ± 0.12	(13)	0.2	(0)	0.1	0.3	all
		125 – 175		-0.3 ± 0.03	(6)		-0.6 ± 0.09	(11)	0.2	(0)	0.2	0.4	h_{ref}, 0.8 h_{ref}
		75 – 125	**50**	-0.7 ± 0.1	(13)	**75**	-0.8 ± 0.1	(13)	0.1	(0)	0	0.3	h_{ref}
		75 – 125	**50**	-0.7 ± 0.1	(13)	**95**	-0.8 ± 0.12	(13)	0.1	(0)	0	0.3	all
		125 – 175		-0.4 ± 0.04	(6)		-0.6 ± 0.09	(11)	0.1	(0)	0	0.3	all
	Rut	**125 – 175**	**25**	-0.2 ± 0.06	(2)	**95**	-0.6 ± 0.17	(9)	0.3	(0.1)	0.1	0.6	all
SD	**Fall**	**125 – 175**	**25**	-0.4 ± 0.13	(6)	**75**	-0.8 ± 0.2	(7)	0.3	(0.1)	0.1	0.6	h_{ref}

		75 – 125	**25**	-0.7 ± 0.23	(13)	**95**	-1.0 ± 0.32	(13)	0.3	(0.1)	0	0.6	h_{ref}, 0.8 h_{ref}
		125 – 175		-0.4 ± 0.13	(6)		-0.9 ± 0.17	(11)	0.4	(0.1)	0.2	0.6	h_{ref}, 0.8 h_{ref}
		125 – 175	**50**	-0.6 ± 0.17	(6)	**95**	-0.9 ± 0.17	(11)	0.2	(0.1)	0.1	0.5	h_{ref}, 0.6 h_{ref}
	Rut	**125 – 175**	**25**	-0.2 ± 0.08	(2)	**75**	-0.9 ± 0.33	(5)	0.6	(0.2)	0.1	1.2	0.8 h_{ref}
		125 – 175	**25**	-0.2 ± 0.08	(2)	**95**	-0.8 ± 0.22	(8)	0.6	(0.1)	0.3	0.9	0.8h_{ref}, 0.6h_{ref}
CV	**Fall**	**125 – 175**	**25**	0.055 ± 0.023	(6)	**75**	0.028 ± 0.014	(7)	0.027	(0.009)	0.002	0.052	h_{ref}

D. 4 Significant differences (p<0.05) in the descriptive metrics of slope (%) within each of the four contours (25, 50, 75 and 95) between each of the five seasonal home ranges (winter, calving, summer, rut and fall). We indicate the bandwidths (h_{ref}, $0.8h_{ref}$ and $0.6h_{ref}$) at which differences between resolutions were significant.

			High					Low					Pairwise Comparison				
															95% Confidence interval		
Slope variable	**Contour**	**Increase in resolution (m)**	**Season**	$\bar{x}_\Delta$	**±**	**SD**	**(n)**	**Season**	$\bar{x}_\Delta$	**±**	**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Bandwidths**
Mean	**25**	**25 - 75**	**Calving**	-2.2	±	.6	(10)	**Fall**	-1.5	±	.3	(13)	0.7	(0.2)	0.1	1.4	$0.6h_{ref}$
				-2.0	±	.7	(11)	**Rut**	-1.2	±	.4	(11)	0.8	(0.3)	0.2	1.6	all
				-2.2	±	.6	(10)	**Summer**	-1.6	±	.7	(11)	0.6	(0.2)	0.1	1.2	$0.6h_{ref}$
				-2.2	±	.6	(10)	**Winter**	-1.6	±	.2	(14)	0.6	(0.2)	0.1	1.3	$0.6h_{ref}$
	75	**25 - 75**	**Calving**	-2.1	±	.5	(11)	**Rut**	-1.4	±	.3	(11)	0.6	(0.2)	0.1	1.3	all
				-2.1	±	.5	(11)	**Winter**	-1.5	±	.2	(14)	0.6	(0.2)	0.1	1.1	h_{ref}, $0.8h_{ref}$
			Summer	-2.0	±	.8	(13)	**Rut**	-1.4	±	.3	(11)	0.5	(0.2)	0.0	1.1	h_{ref}
	95	**25 - 75**	**Calving**	-2.4	±	.4	(11)	**Fall**	-1.6	±	.1	(13)	0.7	(0.1)	0.4	1.2	all
				-2.4	±	.4	(11)	**Rut**	-1.5	±	.4	(12)	0.9	(0.2)	0.5	1.4	all
				-2.4	±	.4	(11)	**Winter**	-1.5	±	.3	(14)	0.9	(0.2)	0.5	1.3	all
			Summer	-2.0	±	.6	(13)	**Rut**	-1.5	±	.4	(12)	0.5	(0.2)	0.1	0.9	all
		75 - 125	**Calving**	-1.3	±	.5	(10)	**Winter**	-.7	±	.2	(14)	0.5	(0.2)	0.0	1.1	h_{ref}

													Pairwise Comparison				
			High					Low							95% Confidence interval		
Slope variable	Contour	Increase in resolution (m)	Season	$\overline{x}_{\Delta}$	±	SD	(n)	Season	$\overline{x}_{\Delta}$	±	SD	(n)	Mean Difference	(SE)	Lower	Upper	Bandwidths
<u>SD</u>	**25**	**25 - 75**	**Calving**	-2.1	±	.6	(10)	**Fall**	-1.4	±	.3	(13)	0.7	(0.2)	0.1	1.4	0.6 h_{ref}
				-1.9	±	.7	(11)	**Rut**	-1.1	±	.4	(11)	0.7	(0.3)	0.0	1.5	$0.8h_{ref}$, $0.6h_{ref}$
			Winter	-1.7	±	.4	(14)	**Rut**	-1.1	±	.5	(11)	0.6	(0.2)	0.0	1.2	$0.6h_{ref}$
	75	**25 - 75**	**Calving**	-1.9	±	.5	(11)	**Rut**	-1.3	±	.3	(11)	0.6	(0.2)	0.1	1.2	$0.8h_{ref}$, $0.6h_{ref}$
		25 - 75	**Summer**	-1.9	±	1.0	(13)		-1.2	±	.3	(11)	0.7	(0.2)	0.0	1.4	$0.6h_{ref}$
		75 - 125		-1.2	±	.4	(10)	**Winter**	-.8	±	.3	(14)	0.4	(0.1)	0.1	0.8	h_{ref}
	95	**25 - 75**	**Calving**	-2.1	±	.5	(11)	**Fall**	-1.5	±	.4	(13)	0.6	(0.2)	0.1	1.1	all
				-2.1	±	.5	(11)	**Rut**	-1.5	±	.4	(12)	0.6	(0.2)	0.1	1.2	all
				-2.1	±	.5	(11)	**Winter**	-1.5	±	.4	(14)	0.5	(0.2)	0.0	1.1	h_{ref}, 0.8 h_{ref}
		75 - 125	**Summer**	-1.3	±	.5	(11)	**Fall**	-.9	±	.2	(13)	0.4	(0.2)	0.0	0.9	$0.6h_{ref}$
				-1.4	±	.4	(11)	**Winter**	-.7	±	.2	(14)	0.6	(0.2)	0.2	1.1	h_{ref}, $0.6h_{ref}$
		125 - 175		-1.0	±	.3	(9)	**Winter**	-.5	±	.2	(13)	0.5	(0.1)	0.1	0.9	h_{ref}, $0.8h_{ref}$
		125 - 175	**Fall**	-.9	±	.2	(11)	**Winter**	-.5	±	.2	(13)	0.3	(0.1)	0.0	0.7	h_{ref}

			High					**Low**					**Pairwise Comparison**				
															95% Confidence interval		
Slope variable	**Contour**	**Increase in resolution (m)**	**Season**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Season**	$\bar{x}_{\Delta}$	**±**	**SD**	**(n)**	**Mean Difference**	**(SE)**	**Lower**	**Upper**	**Bandwidths**
		125 - 175	**Rut**	-.9	±	.2	(9)	**Winter**	-.5	±	.2	(13)	0.3	(0.1)	0.0	0.7	h_{ref}
CV	**25**	**25 - 75**	**Winter**	.080	±	.045	(14)		.034	±	.014	(11)	0.05	(0.013)	0.01	0.09	$0.6h_{ref}$
		125 - 175	**Fall**	.055	±	.023	(6)	**Winter**	.018	±	.008	(5)	0.04	(0.011)	0.01	0.07	h_{ref}
	75	**125 - 175**	**Summer**	.032	±	.003	(2)	**Calving**	.011	±	.004	(2)	0.02	(<0.001)	0.02	0.02	$0.8h_{ref}$
			Winter	.020	±	.008	(10)	**Calving**	.011	±	.004	(2)	0.01	(0.003)	<0.01	0.02	$0.8h_{ref}$
	95	**125 - 175**	**Rut**	.030	±	.010	(9)	**Winter**	.013	±	.014	(13)	0.02	(0.005)	<0.01	0.03	h_{ref}
			Summer	.029	±	.011	(9)	**Winter**	.013	±	.014	(13)	0.02	(0.005)	<0.01	0.03	h_{ref}