THE UNIVERSITY OF CALGARY

Genetic analysis of movement, dispersal and population fragmentation of grizzly bears in southwestern Canada.

by

Michael F. Proctor

A DISSERTATION SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA, CANADA

MAY 2003

THE UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a dissertation entitled "Genetic analysis of movement, dispersal and population fragmentation of grizzly bears in southwestern Canada" submitted by Michael F. Proctor in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

R.M.R. Barclay, Biological Sciences, Supervisor

B.N. McLellan, British Columbian Ministry of Forests

C. Strobeck, University of Alberta, Biological Sciences

R. Owen, Biological Sciences, Adjunct

C. Gates, Environmental Design

C. Servheen, United States Fish and Wildlife Service,
External Examiner

ABSTRACT

I studied dispersal and inter-population movement of grizzly bears near the southern extent of their North American range in southwestern Canada and northwestern U.S.A. This area represents the interior portion of the southern edge of grizzly bear distribution following 100 years of range contraction. Fragmentation, as a result of the increasing human presence, is influencing ecosystems around the globe. I address whether anthropogenic fragmentation has affected grizzly bear populations in this vulnerable area. Human attitudes toward grizzly bears, and large carnivores in general, have experienced a paradigm shift from active persecution towards tolerance and respect. However, major forces underpinning range contraction including human-caused mortality and fragmentation, may be still operating, albeit, more subtly and less intentionally. Checking further range contraction requires specific knowledge of the processes at work. Improvements have been made in managing and monitoring human-caused mortality, however, besides the obviously isolated populations (e.g. Yellowstone National Park), the status of fragmentation in this region was largely unknown. My goals were to use genetic analyses to explore bear movement and dispersal within and between the relictually occupied mountain ranges in southwestern Canada. I genetically sampled and generated 15-locus microsatellite genotypes for 835 bears across approximately 100,000 km^2 in immediately adjacent geographic areas. I used population assignment techniques, parentage analysis, cluster analysis, multiple linear regression and several matrices of population genetics. I present evidence of natural and human-caused fragmentation, identify fragmenting forces, establish population and sub-population boundaries in the region, identify small vulnerable sub-populations, describe dispersal behaviour, and discuss factors that make bears susceptible to fragmentation. Female movement was restricted by human transportation and settlement corridors, and male movement appeared to be reduced in some areas. Fragmentation by north/south oriented major human-settled valleys and the major east/west transportation corridors have left much of the area a partially fragmented set of local sub-populations varying in size and intensity of fragmentation. I found one small isolated population ($n < 100$) in the southern Selkirk Mountains, several small sub-populations ($n < 100$), including several "female demographic islands" and several population sub-units that were relatively large ($n > 300$). Through multiple linear regression, I implicate human settlement patterns, human-caused mortality, and traffic volumes as inhibiting rates of inter-population movement. I also measured dispersal distances of grizzly bears and found that males, on average, dispersed approximately 46 km and females 14 km, a result similar to previous radiotelemetery findings for the region. Because several fragmented sub-units are small, maintaining regional connectivity may be necessary to ensure persistence. Despite grizzly bear vagility, their conservative dispersal behaviour and difficulty in living close to humans, make maintenance of regional connectivity challenging.

ACKNOWLEDGEMENTS

I would like to gratefully acknowledge my supervisor, Dr. Robert Barclay. His ecological insight, organizational skills, enthusiasm, and patient grace were necessary and welcome in helping me complete this project and thesis. Bruce McLellan provided practical and ecological advice throughout this entire process and I appreciate his enthusiasm right to the finish. Curtis Strobeck's interest and theoretical and practical perspectives were essential to the completion of this work. Also, David Paetkau's sage advice cleared many cloudy subjects along the way. I am indebted to Cory Davis for patiently guiding a field ecologist through the world of molecular genetics. I would like to give special thanks to Cori Lausen for her piercing feedback and unerring editing skills. And I would like to thank John Woods for getting me started in bear research and providing me with inspiring opportunities within the West Slopes Bear Research Project.

A project of this size has many people to acknowledge. Not only has it taken 6 years, but my study area was over 100,000 km^2, and overlapped several other collaborative bear research projects, all of which provided me with genetic samples to complement my own field work. I thank Garth Mowat, Wayne Kasworm (US Fish and Wildlife Service), Wayne Wakkinen (Idaho Fish and Game), John Woods (West Slopes Bear Research Project), Mike Gibeau and Steve Herrero (East Slope Grizzly Bear Project), Gordon Stenhouse (Foothills Model Forest), the British Columbia Ministry of Water Lands and Air Protection, and the Alberta Department of Natural Resources.

Funding from the following generous institutions made this project possible and successful: Parks Canada, B.C. Water Lands and Air Protection, B.C. Ministry of Forests, Wilburforce Y2Y Science Grants, and Slocan Forest Products. Personal funding from the following organizations was also greatly appreciated: Killam Trusts, National Science and Engineering Research Council, iCORE Graduate Student Fellowships, Nesbitt Burns Inc., Province of Alberta, and the University of Calgary.

And last but not least, were the many individuals that made this project possible: Jen Bonneville, Leni Neumeier, Kelly Stalker John Bergenske, Tom Duchastel, Gillian Saunders, Tim McAllister, and Karen Barren.

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CHAPTER 1: GENERAL INTRODUCTION

Natal dispersal of individuals and inter-population movement are two important ecological processes in population and metapopulation ecology (Clobert et al. 2001; Hanski and Gilpin 1997). The interruption of these processes (i.e. habitat and population fragmentation) is considered to be a major force underpinning the recent extinction crisis (Wilcox and Murphy 1985). Yet in the vast majority of population dynamic studies these two processes have been ignored or modeled, primarily because reliable data for most species do not exist (MacDonald and Johnson 2001). The rise in prominence of the metapopulation paradigm has dramatically increased interest in obtaining inter-population movement data (immigration and emigration) and incorporating them into more realistic population dynamic studies (Young and Clarke 2000). The ability to obtain accurate inter-population movement data will profoundly improve our understanding of, and ability to manage, systems containing multiple populations, particularly metapopulations created by the increasing human influence. However, as is often the case, interest and theory have preceded our ability to measure dispersal and inter-population movement in real ecological systems (MacDonald and Johnson 2001). This situation is changing rapidly as a result of an increase of innovative ecological tools in recent years (Waser and Strobeck 1998; Goldstein and Schlotterer 1999; Luikart and England 1999; Clobert et al. 2001; Gittleman et al. 2001; Frankham et al. 2002). Central to my thesis is measuring inter-population movement and dispersal, and understanding the effects that interruption of these processes have on a large vagile carnivore at scales from the individual to the metapopulation.

Natal dispersal, or the movement of offspring from their natal home range to their own breeding area, is an important ecological and evolutionary process. At the individual level, dispersal is hypothesized to be a mechanism to minimize inbreeding (Pusey 1987; Johnson and Gaines 1990; Pusey and Wolf 1996; Perrin and Goudet 2001), reduce competition for resources among related individuals, (Greenwood 1980; Waser 1985), reduce competition for mates among related individuals (Greenwood 1980; Dobson 1982), or a combination of the above (Dobson and Jones 1985; Gandon and Michalakis 2001). At the population level, dispersal may be inter-population geneflow (Slatkin 1987) influencing population structure (Chessier et al. 1993), genetic diversity (Hedrick 1995; Wayne and Koepfli 1996; Bushar et al. 1998; Paetkau et al. 1998a), inter-population source-sink dynamics (Pulliam 1988; Dias 1996), and population colonization and recolonization (Hanski and Gilpin 1997). At a species level, dispersal mediates abundance and distribution (MacArthur and Wilson 1967; Dieckmann et al. 1999), facilitates range expansion (Lubina and Levin 1988; Swenson et al. 1998), and operates, often ineffectively, to resist range contraction (Channell and Lomolino 2000; Mattson and Merrill 2002). At the ecosystem level, dispersal plays a role in community structure across a landscape and therefore community function (Mouquet et al. 2001). For example, interruption of dispersal may result in isolation and eventual extirpation of a species, the eventual loss of which may significantly alter community structure and function (e.g. Berger 1999). More recently, the distinction between condition-dependent and condition-independent dispersal has been made, reflecting an ecological plasticity to dispersal (Waser 1996; Ims and Hjermann 2001).

Population fragmentation has played a role in the range contraction of large carnivores (Woodroffe and Ginsberg 1998), thus altering the structure and function of many ecosystems (Berger 1999). It is therefore important to understand the mechanisms driving these changes. At a broad temporal and spatial scale, fragmentation may isolate a population that has a higher likelihood of succumbing to demographic forces such as excessive mortality (Lande 1988; Woodroffe and Ginsberg 1998; Parks and Harcourt 2001). The contribution of population fragmentation and negative demographic trends is particularly dangerous in the "small" and "declining" population paradigm (Darwin 1859; Caughley 1994; Young and Clarke 2000). It is precisely because demographic processes may be the proximate cause of population extirpations, that efforts to understand and resist range contractions require a measure of "demographic fragmentation", that is, the interruption of inter-population movement for each gender.

Measuring natal dispersal is challenging (Clobert et al. 2001), particularly in species with long life spans, as following individuals over time becomes impractical. Species whose individuals range over large spatial scales are especially difficult to follow in multi-population systems (Koenig et al. 1996), yet this is often the information required to understand the processes mediating population fragmentation. Two methods have attempted to measure dispersal and inter-population movement by large mammals: radiotelemetry and indirect population genetic measures of geneflow. Often such studies obtain unsatisfactory results. Radiotelemetry, while an improvement over mark-recapture efforts, has been relatively successful at small spatial scales (Koenig et al. 1996; Waser et al. 2001), but at large spatial and temporal scales it is impractical (Palsboll 1999). Estimates of inter-population geneflow are often estimated indirectly using the theoretical relationship between genetic population differentiation as measured by Wright's (1965) F_{ST} statistic, and inter-population migration rates (Slatkin 1985; Neigel 1997). Population differentiation is mediated by several factors including random genetic drift, mutation, natural selection, and migration (Slatkin 1985; Hartl and Clark 1997). The degree of differentiation is further influenced by effective population size (the number of individuals contributing genes to subsequent generations; Futuyma 1986) and the time since separation or fragmentation. A problem arises from the theoretical assumptions about the relationship between the populations being studied. The theoretical relationship between F_{ST} and Nm (number of migrants per generation where N is the effective population size and m is the migration rate per generation) requires that populations be in equilibrium with respect to the above forces (Slatkin 1985, Niegal 1997). These assumptions are rarely met (Whitlock and McCauley 1999), particularly in recently disturbed systems (Steinberg and Jordan 1999), and therefore estimates of inter-population migration rates are unreliable (Ims and Yoccox 1997; Whitlock and McCauley 1999; Rousett 2001).

When I began my graduate research in 1997, the idea of using genetic analysis to measure individual-based inter-population movement was just forming within the scientific community. There was a revolution beginning in the interdisciplinary union of ecology and molecular techniques. Paetkau et al. (1995) had just developed a genetic-based population assignment test, used primarily to detect population genetic structure, with the vision of using it for individual migrant detection. Individual-based assignment methods are based on the cumulative genotypes of many individuals, a mathematical improvement over using allele frequency averages (Waser and Strobeck 1998; Neigel

2002). In subsequent years, statistical advancements have been used in genetically measuring individual-based inter-population movement (Waser and Strobeck 1998; Davies et al. 1999; Luikart and England 1999). Several reviews (Palsboll 1999; Rousett 2001; Taberlet et al. 2001; Waser et al. 2001; Frankham et al. 2002) describe the possibility, and more techniques have been developed (Rannala and Mountain 1997; Corunet et al. 1999; Pritchard et al. 2000; Wilson and Rannala *in press*), but empirical studies are just emerging to validate these promises (Manel et al. 2003). These methods have been tested on systems with known individual histories (e.g. Maudet et al. 2002), but few studies have applied them to large-scale systems.

The goal of my research was to explore individual-based inter-population movement in the classic, yet challenging, conservation problem of a recently disturbed (fragmented) large-scale system, investigating immediately adjacent local populations at a regional scale.

WHY GRIZZLY BEARS?

I chose grizzly bears (*Ursus arctos*) as a study species for several reasons, including conservation concern, theoretical compatibility with my research questions, and the availability of an efficient, broad-scale, non-invasive genetic sampling technique (Woods et al. 1999).

Conservation need

Grizzly bears in North America have undergone an extensive range contraction in the past century as a result of many forces summarized within the categories of human-caused mortality, habitat loss, and population fragmentation (Servheen et al. 1999; Mattson and Merrill 2002). The current conservation status of grizzly bears is "Special Concern" in Canada (COSEWIC) and "Threatened" in the conterminous U.S.A. (Servheen et al. 1999). There has been a paradigm shift in human attitudes towards grizzly bears, and large carnivores in general, from that of competitive pests to a desired member of the ecological community. Recent mortality-management within the conterminous U.S.A. has been successful in reducing human-caused mortality (Mattson and Merrill 2002). Despite the improved image, the question remains, whether forces of fragmentation and human-caused mortality are still operating and contributing to further, albeit slower range contraction? Because grizzly bear population numbers change slowly (Bunnell and Tait 1981; Miller 1990) detection of changes in grizzly bear abundance, distribution, and inter-population movement may be difficult to detect in the short term.

Theoretical compatibility

Detection of individual inter-population movement using genetic analysis requires populations that have a certain degree of population genetic structure. Bears in adjacent geographic areas that share many migrants will have little genetic structure (Slatkin 1985), and detection of individual migrants will be difficult. Likewise, a recently fragmented population will develop sufficient genetic structuring as genetic drift outpaces the mitigating inter-population migration. The degree and speed that genetic structure develops is related to the effective population size (N_E) and the amount of time since disturbance. Grizzly bears are desirable in this context because they live at sparse densities (Bunnell and Tait 1981; Miller 1990) and therefore in relatively small populations over relatively large spatial scales. A recently fragmented grizzly bear population will develop genetic structure relatively quickly, over several generations. If sufficient, the resulting structure will allow detection of individual migrants.

To fully understand inter-population movement in a conservation context (i.e. fragmentation), it is necessary to consider behavioural, physiological, and ecological mechanisms. Driven by conservation management needs, many fine-scale ecological studies provide a reasonably developed picture of these requisite characteristics. Based on previous grizzly bear research, there are several characteristics that lead me to hypothesize that grizzly bears are susceptible to human-caused fragmentation even in the absence of purposeful excessive mortality (Mattson and Merrill 2002).

One primary reason for the above hypothesis is the relationship between grizzly bears and humans. The Ursidae (Carnivora), began its evolutionary split from the Canidae twenty-five to thirty million years ago (McLellan and Riener 1994). The early ancestors to both the dog and bear families were obligate carnivores (Stirling and Derocher 1990; McLellan and Reiner 1994) that ultimately evolved along different paths. Bears expanded to an omnivorous diet (Stirling and Derocher 1990; McLellan and Reiner 1994) culminating in eight extant species of bears (Nowak 1999), six of which retain the proclivity for both plant and animal-derived energy resources (Stirling and Derocher 1990). However, the evolutionary change from carnivory to omnivory was accompanied by minimal changes in digestion, resulting in a system less efficient at digesting the more abundant plants than the less abundant animal prey (Bunnell and Hamilton 1983; Stirling and Derocher 1990). Despite their digestive limitation and the seasonal limitation in obtaining energy, omnivory served ursids well until humans, another omnivorous species with a generalist foraging strategy, began dominating ecosystems around the globe. As the range of humans expanded into and usurped bear habitats, sympatric existence brought humans and bears together in conflict over the less abundant protein food resources (Servheen et al. 1999). The modern context of this story involves grizzly bears that are often attracted to human food resources where conflict arises (Mace and Waller 1998; McLellan et al. 1999).

It is also hypothesized that grizzly bears evolved a relatively aggressive nature in response to selection for open habitats (Herrero 1985). Due to the formidable size, strength, and weaponry of bears (Herrero 1985; Stirling and Derocher 1990), a real and/or perceived threat to human security and property have resulted in bear mortality (McLellan et al. 1999). Consequently in North America, the 20th century found grizzly bears relegated to remote mountainous regions. The increasing human population has moved into many valleys within these occupied mountains resulting in linear human settlements that offer the potential to fragment relict grizzly bear populations in the mountains (McLellan 1998).

Exacerbating the tendency for grizzly bears to be attracted to human food is the fact that they hibernate. Successful reproduction necessitates sufficient energy storage during the season leading up to hibernation. Delayed implantation of the fertilized zygote until late fall is hypothesized to be a physiological decision based on sufficient storage of energy resources (Bunnell and Tait 1981).

What little we know about grizzly bear dispersal (see below, Blanchard and Knight 1991; McLellan and Hovey 2001a) suggests that, like most mammals, dispersal is sex-biased, with males dispersing further than females (Greenwood 1980; Pusey 1987;

Johnson and Gaines 1990). Furthermore, in mountainous southwestern Canada, male and female dispersal is a gradual process taking several years (McLellan and Hovey 2001a). This gradual process makes surviving dispersal through human settled areas potentially difficult.

Genetic considerations

The final reason I chose grizzly bears for my research was that an efficient system for non-invasively obtaining genetic samples existed, and genetic markers had been developed. I was part of a research team that developed a hair-grabbing technique from wild free-roaming bears (Proctor 1996; Woods et al. 1999). This technique has been adopted throughout North America and the world as a population survey method for bears. Several grizzly bear surveys have been conducted in my study area, providing a base of genetic samples to underpin my work. I carried out several of these formal population surveys myself and to fulfill my study design criteria, I used the hair-grab technique to fill unsampled portions in my study area, eventually sampling most of the occupied regions across much of the southern interior distribution of grizzly bears in North America.

In addition to the field sampling technique, sufficient genetic markers have been developed for use in grizzly bears (Paetkau et al. 1998a). Microsatellite markers (Tautz et al. 1986; Bruford and Wayne 1993) have quickly become the marker of choice for individual and population studies (Forbes and Boyd 1997; Paetkau et al. 1998a; Waser and Strobeck 1998; Carmichael et al. 2001). Microsatellites are inherited in a Mendelian fashion and thus are useful in determining parentage as well as for population assignments (Queller et al. 1993; Blouin et al. 1996; Marshall et al. 1998; Waser et al. 2001). Microsatellites consist of tandem repeat nucleotide sequences between protein-coding genes throughout the genome (Bruford and Wayne 1993; Goldstein and Schlotterer 1999). Their short length (100-300 base pairs including flanking regions with primers) allows for relatively easy and accurate detection of allelic variants at multiple loci. Such is the accuracy of analyzing microsatellites that these markers are routinely used in human forensics (Goldstein and Schlotterer 1999).

DISPERSAL AND INTER-POPULATION MOVEMENT

Grizzly bears have a promiscuous mating system (Craighead et al. 1995) and both sexes live in undefended overlapping home ranges (Mace and Waller 1997). Their reproductive lives begin when females are 5-7 years old (LeFranc et al. 1987; Craighead et al. 1995) and while males display mating behaviour at the same age, evidence suggests they may not successfully reproduce until they are approximately nine years old (Craighead et al. 1995). The inter-birth interval is 3-4 years (LeFranc et al. 1987; Hovey and McLellan 1996), and their reproductive lives extend to approximately 20-25 years old. Home ranges for grizzly bears vary dramatically across North America (LeFranc et al. 1987). In the southern Canadian Rocky Mountains, within my study area, McLellan's (1989a) long-term study found that female home ranges averaged 176 km^2 and males averaged 437 km^2 (95% fixed kernel, F. Hovey pers. comm.). Further north in the Rocky Mountain's Banff National Park area, females average 293 km^2 and males 835 km^2 (Gibeau and Herrero 1998). In the Columbia Mountains of British Columbia, females average 90 km^2 and males 250 km^2 (J. Woods pers. comm.).

Because grizzly bears are highly vagile and long-lived, reliable estimates of sex-specific dispersal distances have proven difficult to obtain although anecdotal (unquantified) reports are common. In a review, LeFranc et al. (1987) suggest that Alaskan and arctic male grizzly bears disperse "long distances" out of their natal home range and females are relatively philopatric (e.g. Glenn and Miller 1980). Supporting this supposition are indirect inferences from population genetic measures. At a larger scale, grizzly bears, appear to fit the isolation-by-distance model across much of their northern North American distribution (Paetkau et al. 1997). F_{ST} values of 0.04 correspond to a geographical distance of 1000 km. This suggests that either grizzly bears in northern North America are long distance dispersers or they are connected by uninterrupted stepping-stone dispersal events (Kimura and Weiss 1964). From the data coming out of the north, it is reasonable to hypothesize that grizzly bears are long distance dispersers.

Contradicting the above hypothesis are data from several studies of grizzly bears from the southern interior mountainous region of their North American distribution. Like most mammals, grizzly bear dispersal was found to be sex-biased with males dispersing further than females (Blanchard and Knight 1991; Mace and Waller 1998; McLellan and Hovey 2001a). The only study with sufficient sample sizes found that on average, females dispersed 10 km and males 30 km from their maternal range (McLellan and Hovey 2001a), not "long" distances as hypothesized in studies from northern bears. Another important finding was the gradual process of dispersal, taking several years to complete (McLellan and Hovey 2001a). Dispersal in grizzly bears may in fact be condition-dependent (Ims and Hjermann 2001) allowing for different dispersal behaviour in different regions of North America as ecological conditions change significantly (Clegg et al. 1998).

Paetkau et al. (1998a) studied population structure and geneflow in southeast Alaska and found that a 2 km oceanic distance deters female but not male movement, while a distance of 7 km of water appears to limit movement of both sexes. The 40 km of ocean separating Kodiak Island from the Alaska mainland is a barrier to male and female movement (Paetkau et al. 1998a). Several North American studies based on mitochondrial DNA provide indirect evidence that female dispersal may be limited in grizzly bears (Waits et al. 1998a and b), but they provide no estimates of dispersal distances. While most reports on North American grizzly bears suggest that females are philopatric, several European studies report range expansion and dispersal of males and females into "new" recolonized habitat (Pulliainen 1983; Chestin et al. 1992; Ademic 1996; Swenson et al. 1998).

THESIS OBJECTIVES

The goal of my thesis is to explore the relationships among dispersal, inter-population movement, and fragmentation in a large-scale, recently disturbed system of adjacent local populations. Specifically I set out to measure gender-specific inter-population movement in grizzly bears occupying three mountain ranges encompassing approximately 100,000 km^2 in southwestern Canada and northwestern U.S.A. (Chapters 2 and 3). Further, I wanted to determine if the human environment has fragmented grizzly populations and, to the extent possible, determine the causes of the population structure and bear movement rates I detect (Chapter 3). I also wanted to determine what sub-population boundaries might be under natural conditions compared to those as a result of fragmentation (Chapter 4). Lastly, I wanted to quantify the mean and range of dispersal distances for each sex (Chapter 5).

HYPOTHESES AND PREDICTIONS

What is known about grizzly bear ecology, behaviour, physiology and evolutionary history (discussed above) and life history traits (discussed below) led me to make several hypotheses. First, because grizzly bears appear to have male-biased dispersal, and because of their non-territorial overlapping home range and promiscuous mating behaviour, inbreeding is minimized (McLellan and Hovey 2001a). Therefore, I predicted that male-biased dispersal would hold true in my study area. Second, I developed a set of competing hypotheses concerning dispersal distance and susceptibility to fragmentation. One hypothesis is derived from the patterns of life history traits and their relationship with dispersal. Large body size is associated with large home ranges (McNab 1963) and both of these traits are associated with long-range dispersal (Wolff 1999). Further, asocial and non-territorial generalist species also tend to have longer dispersal (Wolff 1999). Because grizzly bears have all of these characteristics, one hypothesis is that males should be "long distance" dispersers leaving their maternal home range. This hypothesis is supported by the relatively long dispersal distances of the ecologically and evolutionarily similar black bear (*Ursus americanus*; Rogers 1987). A contrasting hypothesis is built on the idea that increased habitat complexity and heterogeneity may inhibit long dispersal (Clegg et al. 1998). This supposition is supported by McLellan and Hovey (2001a) suggesting that female dispersal in SW

Canada results in home ranges that overlap the maternal home range and males disperse on average, one male home range diameter from the center of their maternal range. As for susceptibility to fragmentation, the attraction to human food and aggressive disposition, in combination with wide-ranging foraging habits (discussed above), led me to hypothesize that grizzly bears are susceptible to human-caused fragmentation. Because females tend to be more philopatric, I also predicted that they will be more susceptible to fragmentation than males.

In this thesis, I test several specific predictions. I predicted that major human transportation and settlement corridors within the mountainous regions of southwestern Canada and the northwestern U.S.A. inhibit bear movements; the greater the human disturbance, the less the movement. This would be detectable as high genetic distances across short physical distances (fracture areas) and low numbers of detectable inter-population migrants across these corridors, relative to undisturbed areas. Further, I predicted that female movement rates across human-dominated landscapes would be less than male movement rates. Another prediction is that human-caused fragmentation has resulted in a form of "metapopulation," with sub-population borders varying in intensity of bear movements.

Any effort to detect inter-population movement and fragmentation requires a system with components (i.e. population pairs) of sufficient genetic structure, a sufficient number of informative markers to determine individual migrants, and variability in the system to ensure the power to detect a difference between disturbed and undisturbed components. Chapter 2 describes sex-specific population fragmentation across a human transportation and settlement corridor as it transverses three mountain ranges, encompassing much of the southern interior distribution of grizzly bears in the trans-boundary region near the Canada-U.S.A. border. At the lower reaches of this relictual area, grizzly-bear distribution is hypothesized to be in peninsular habitats, corresponding to the north/south mountain ranges (Craighead and Vyse 1996; McLellan 1998). East/west fragmentation has the potential to isolate relatively small, and therefore vulnerable, populations that extend into the northwest U.S.A. U.S. grizzly bear researchers and managers suggest that the viability of several of these populations requires connection to Canadian populations (U.S.F.W.S. 1993; Servheen et al. 1999). Clearly this is an important geographic area to explore human-caused population fragmentation. This region is one of the areas where further North American range contraction is probable. Because I predict varying levels of inter-population movement and fragmentation, it is important to test the power of the markers and statistical techniques. Most appropriate statistical treatments of migrant detection appear to perform well with strong genetic structuring (Cornuet et al. 1999), but as genetic structure diminishes, so does the power to detect migrants (Maudet et al. 2002). Furthermore, if I detect low levels of bear movement across a potential fracture, can I determine what historical "pre-disturbance" movement rates might have been? To test this question, I used a control area of similar ecology and topographic structure, but with a lack of human disturbance (i.e. large river valley with no major highway or human settlement) in my analysis.

Chapter 3 uses my entire study area to examine causal relationships between sex-specific inter-population movement rates. I used 23 adjacent local population pairs to examine the role that human disturbance plays in fragmentation. Practical applications may allow land use managers to incorporate reliable data while increasing our understanding of the characteristics of bears that contribute to their susceptibility to fragmentation. In Chapter 3, I arbitrarily defined "populations" for the purposes of analysis and as such adopted the use of the term "local" population (used throughout thesis) to refer to assemblages of bears within one geographic area that are not necessarily biological populations. In the following chapter (Ch. 4) I determine and define biologically-based population boundaries for my study area and refer to them as "populations" and "sub-populations" depending on their discreteness. Evolutionary biologist, D. Futuyma (1986) defines a population as a group of conspecific organisms that occupy a "more or less" well defined geographic region, with spatial and temporal reproductive continuity that breed more within their group than between groups. I therefore use the term "population" to refer to relatively discrete groups of inter-breeding bears with little-to-no inter-population movement. I use the term "sub-population" to refer to less discrete groups characterized by limited inter-population movement.

Fragmentation is a reality in the modern ecological landscape and reversing the process is challenging. It may be more practical to minimize further encroachments and monitor existing sub-population units for abundance trends and regional connectivity. Therefore it is useful, from a conservation perspective, to have the ability to detect biologically-based sub-population boundaries. Knowing the intensity of the boundary (quantifying inter-population movement) is essential if one is to monitor changes in connectivity over time. This topic is the objective of Chapter 4. Measuring real yet subtle population boundaries across a landscape is a challenging task. Population genetic analyses are relegated to making *a priori* assumptions about population boundaries.

Recent development of a clustering algorithm to group individuals with no prior location data (Pritchard et al. 2000) has enabled the detection of population structure based on geneflow among groups of bears. This methodology also allows a distinction between older natural movement barriers and more recent anthropogenic barriers.

In chapter 5, I explore the nature of sex-specific dispersal in grizzly bears. Previous work measuring differences in dispersal distances between males and females is based on radiotelemetry studies following 30, nine, and seven sub-adults (Blanchard and Knight 1991; Mace and Waller 1998; McLellan and Hovey 2001a). The paucity of dispersal studies and low sample sizes reflect the practical difficulties of following large vagile mammals over large geographic areas for many years. In contrast to radiotelemetry methods, genetic analysis allows better detection of long-term and long-range dispersal (Koenig et al. 1996). I used the spatial configuration of parent-offspring relationships detected through genetic analysis to measure male-biased dispersal and calculate sex-specific dispersal distances.

By tackling dispersal and demographic population fragmentation at a large scale, it is my hope to simultaneously provide valuable conservation-related data for a difficult species, and advance our ability to measure and understand inter-population movement and its impact on ecosystems. My ultimate goal is to inspire a deeper explanation of ecosystem fragmentation, investigated through the long-term study of multiple species representing several guilds.

CHAPTER 2: DNA REVEALS DEMOGRAPHIC FRAGMENTATION

INTRODUCTION

Habitat fragmentation is a serious threat to biological diversity and at the root of the present extinction crisis (Wilcox and Murphy 1985; Wilcove 1987; Young and Clarke 2000). Fragmented systems yielding small isolated populations suffer increased extirpation or extinction probabilities primarily from the faster-acting demographic and stochastic/catastrophic processes (Lande 1988; Caughley 1994; Woodroffe and Ginsberg 1998), and secondarily from more gradual genetic processes (Soule 1987; Frankham et al. 2002). In fragmented ecosystems, inter-population dispersal, or connectivity, of both sexes may be important for population augmentation, rescue, or in extreme cases, re-colonization within natural (Hanski and Gilpin 1997) and human-caused (McCullough 1996) metapopulations. In species with sex-biased dispersal, the movement of one sex, often males in mammals (Greenwood 1980; Pusey 1987), may mediate genetic connectivity while females are required to inject demographic functionality in a recipient population. Furthermore, species that display sex-biased dispersal may experience gender-specific fragmentation and in some cases, one sex may be an obligate disperser and the other density dependent (Aars and Ims 2000). Therefore, to be useful, any connectivity measure (or study) should have the ability to distinguish between gender-specific inter-population movement.

Several large carnivores such as grizzly bear, wolf (*Canis lupus*), and lynx (*Lynx canadensis*) are threatened in the conterminous U.S.A. (Novak et al. 1987). Viability of these carnivores may require immigration from Canada. For example, human persecution led to the extirpation of wolves from the western U.S.A. in the last century. Tolerant attitudes toward carnivores, however, allowed natural re-colonization of the wolf into the U.S.A. from source populations in southern Canada (Mech 1995; Forbes and Boyd 1996).

Continental range contraction of grizzly bears over the past two centuries has resulted in four sub-populations within the conterminous U.S.A. All four are isolated from one another, but three of these are assumed to be connected to Canadian populations (Servheen et al. 1999; Mattson and Merrill 2002). To resist further range contraction and reduce the risk of eventual extirpation from the U.S.A., maintaining the connections to the Canadian populations is thought essential (U.S.F.W.S. 1993). However, factors that caused historic declines of grizzly bears in the U.S.A. also were active in southern Canada and in particular there is a major East-West transportation corridor that bisects the entire range of grizzly bears just north of the Canada-U.S.A border. Grizzly bear connectivity across this corridor is an important but untested assumption in grizzly bear conservation (McLellan 1998). My objective was to quantify the extent to which grizzly bears in the U.S.A. and Canada are genetically and demographically connected. I also set out to test the hypothesis that it is the transportation corridor and associated human settlement, and not simply major valleys that has caused any reduction in connectivity. To meet my objective, traditional methods of measuring animal movement such as radiotelemetry were impractical because following the fates of many individuals over a regional scale and over generations of time would have been required (Palsboll 1999). Similarly, traditional genetic methods provide unreliable estimates of inter-population migration in recently disturbed systems (Steinberg and Jordan 1997; Whitlock and McCauley 1999). Extrapolations of migration from measurements of genetic differentiation (F_{ST} and Nm) require equilibrium between the long-term forces driving genetic differentiation and are therefore difficult to base in contemporary time scales (Slatkin and Barton 1989, Neigel 1997; Palsboll 1999; Whitlock and McCauley 1999) while they also do not provide gender-specific estimates of inter-population movement.

To quantify sex-specific connectivity of grizzly bears, I used regional-scale, non-invasive sampling (Woods et al. 1999) in three mountain ranges across the trans-border area that included both sides of the human transportation and settlement corridor that is a potential fracture for bears (Fig. 2.1). I also sampled both sides of a wide, but uninhabited valley that did not contain a transportation corridor. The broad-based sampling was followed by 15-locus microsatellite genotyping (Tautz et al. 1986) linked with analyses that measured inter-population movements of individuals (Waser and Strobeck 1998; Corunet et al. 1999; Davies et al. 1999).

METHODS

I genetically sampled wild, free-roaming grizzly bears on both sides of Canadian Highway 3 as it traverses the Rocky, Purcell, and Selkirk mountain ranges in southern British Columbia (B.C.) and Alberta just north of the Canada-U.S.A. border (Fig. 2.1). This human transportation/settlement corridor is an historic route through the mountains. The highway was paved in the 1960's and vehicular traffic has increased tenfold during the past 20 years (British Columbia Ministry of Transportation and Highways). Average traffic volume is 7000 vehicles/day during summer in the Rockies and 4000 vehicles/day in the Purcells and Selkirks. In the Selkirk Mountains I sampled on both sides of an alternative route, B.C. Highway 3A, and associated human settlements. A railway with 8 - 16 trains/day parallels Highways 3 and 3A for their entire length. Communities along

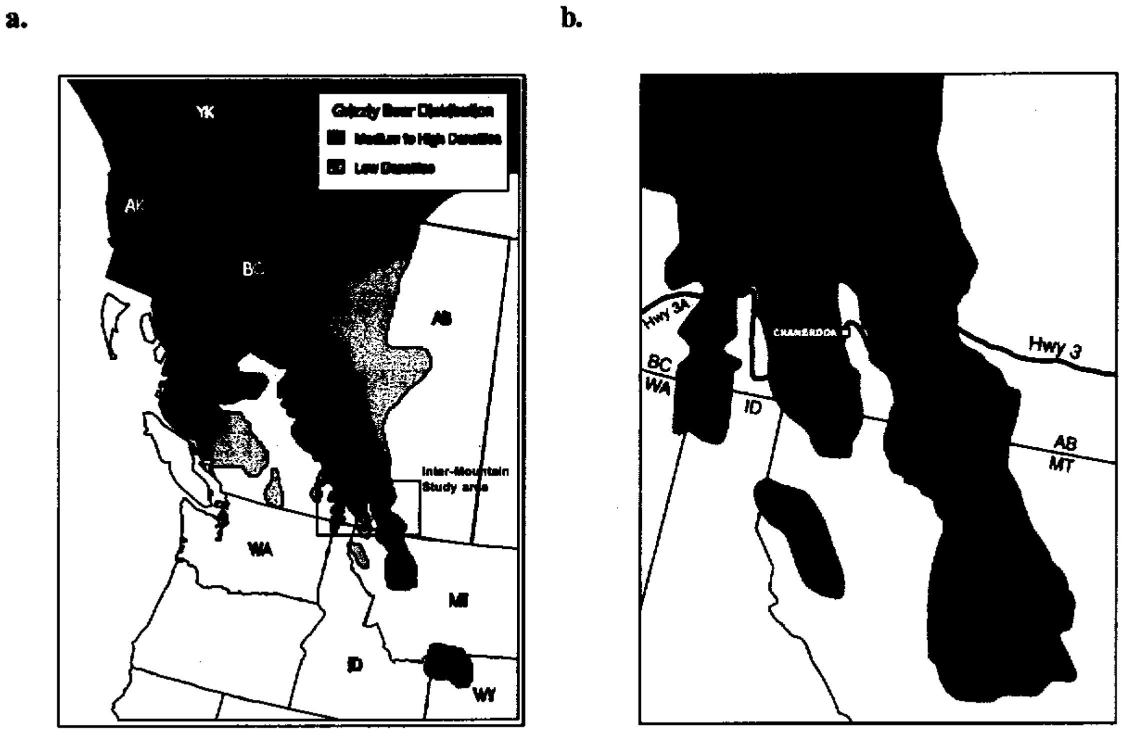


Figure 2.1 a. Grizzly bear distribution and inter-mountain study area in western North America. b. Southern Rocky, Purcell, and Selkirk Mountain study area. Dotted lines outline geographic areas where bears were genetically sampled on both sides of Highway 3 and 3A. CS is the Central Selkirks, SS is the Southern Selkirks, SPN and SPS are the Southern Purcells North and South of Hwy 3 and SRS and SRN are the Southern Rockies North and South of Hwy 3. FHW and FHE are sampled areas west and east of the Flathead River and constitute the "control" area ecologically within and similar to the southern Rocky system. Map 2.1a. adapted from McLellan (1998).

Highway 3 range from 500 to 10,000 inhabitants. The Rocky and Purcell Mountain routes have a discontinuous set of rural enclaves between towns while the Selkirk Highway 3A route has a narrow yet continuous human settlement separating the southern and central Selkirk Mountain local grizzly populations. For a control, I also quantified connectivity across the large North Fork of the Flathead River Valley in the Rocky Mountains, which does not have a major transportation corridor or settlements.

In my 32,000 km^2 study area, between 1996 and 2000, I sampled bears using hair-traps that consisted of a single strand, barbed-wire corral surrounding a scent lure (Woods et al. 1999) and biopsy samples from hunter kills and bears captured for research or management. A portion of my samples was obtained from DNA-based population surveys (Boulanger 2001, Mowat and Strobeck 2000). Total cell DNA was extracted using Qiagen (Qiagen Inc., Mississauga, Ontario, Canada) from 5-10 hair follicles or a tissue biopsy, and six-locus microsatellite genotypes (Paetkau et al. 1998a) were determined for all samples. Individuality was determined by unique genotypes with the probability of detecting a matching sibling of < 0.05 (Woods et al. 1999). One sample from each individual was sexed (Ennis and Gallagher 1994) and genotyped to 15 loci (Paetkau et al. 1998a). Close genotypes were reviewed or rerun to minimize human and PCR (polymerase chain reaction) amplification errors (Taberlet et al 1999; Woods et al. 1999).

The challenge in determining individual migrants is distinguishing true migrants from statistical migrants, or those who only appear as migrants by chance. I used three methods to test for individual migrants between populations. First, I used population-specific allele frequencies in a likelihood-based assignment test (Paetkau et al. 1995) that calculates the probability of each individual's assignment to a particular population as the cumulative products of each allele's frequency of occurrence in any of several populations being examined. The individual is assigned to the population with the highest probability of occurrence as a result of, in this instance, considering 30 alleles (15 loci, 2 alleles/loci). Any individual that was cross-assigned to an area other than the area of its capture with a Likelihood Ratio (LR) greater than 2.0 (corresponding to a 100x probability) was considered a putative migrant. This test assumes all loci in each population are in Hardy-Weinberg equilibrium and linkage equilibrium, which I verified using GENEPOP 3.1.

Second, I used a model-based clustering method and a Monte Carlo Markov Chain (MCMC) simulation routine to distinguish real migrants from "statistical" migrants (STRUCTURE, Pritchard et al. 2000). The goal was to use population allele frequencies and individual genotypes to probabilistically assign individuals to populations and determine migrant status (Program STRUCTURE).

To corroborate population assignment-based migrant decisions I looked for the presence of parent-offspring relationships between "migrants" and an individual in the source population using a likelihood-based parentage analysis (CERVUS; Marshall et al. 1998; Slate et al. 2000). CERVUS compares the likelihood of potential parentage calculated from allele frequencies within the population based on Mendelian inheritance principles. For all potential offspring it compares the two most likely parentage candidates (maternal and paternal done separately) by log ratio. It then simulates parents and offspring developing a distribution of relative log ratios to determine a significance level for any given potential parent-offspring relationship. The simulation routine incorporates estimates of the rate of genotyping error, the number and proportion of potential parents sampled, and the proportion of genotyping success.

I also used the genetic distance (D_{LR}; Paetkau et al. 1997) and F_{ST} (Hartl and Clark 1997) to compare genetic connectivity between systems. To control for geographic distance as a variable influencing genetic distance, I measured all genetic distances using samples for each local population such that the cumulative individual locations separating each pair were equal to the geographic distance (80 km) separating my control populations. Unbiased estimates of mean expected heterozygosity (H_e) were calculated as an index of relative genetic variability (Nei and Roychoudury 1974).

RESULTS

I identified 437 individual grizzly bears in the study (Table 2.1) and found no evidence of female movement across the entire southern distribution of grizzly bears just north of the U.S.-Canada border. Furthermore, I found one isolated small population in the southern Selkirk Mountains.

In the Rocky Mountains, three putative male migrants had moved north to south across the transportation corridor (Figs.2.2a) but no natural female movements were detected. I found one female "migrant" that was translocated by wildlife managers and detected by my analysis (Fig. 2.2a). Both assignment methods used to identify migrants selected the same three individuals and two males were captured on both sides of the highway. Two of the three migrants had presumed parent-offspring relationships across the corridor (Fig. 2.2). In total, I found zero of 94 females, and five of 112 males (4.4%) had moved across the highway corridor in the Rocky MountainsIn the Purcell Mountains, I found evidence of male movement from north to south but no evidence of female movement. Two males were cross-assigned by the assignment test with a LR > 2.0 (2.2b), one was DNA-captured on both sides of the highway and a fourth was known to cross from radiotelemetry (Kasworm et al. 2000). Both cross-assigned males were significant according to STRUCTURE and each had a parent-offspring relationship across Highway 3. One additional male had a parent-offspring relationship with individuals across the highway but was cross-assigned with a LR < 2.0 and was not significant according to STRUCTURE.

The Selkirk Mountain population had the greatest degree of isolation. I found no evidence of movement for either gender between the Southern Selkirk populations and those to the north (Central Selkirk Mountains) or east (Purcell Mountains). Assignment plots (Fig. 2.2c) suggest that all bears were captured in their population of birth. The strong segregation of individuals corresponding to each geographic area clearly separates the bears from the two areas based on their differing cumulative allele frequencies. Furthermore, the discrete separate clusters of individuals imply excellent resolving power to detect migrants.

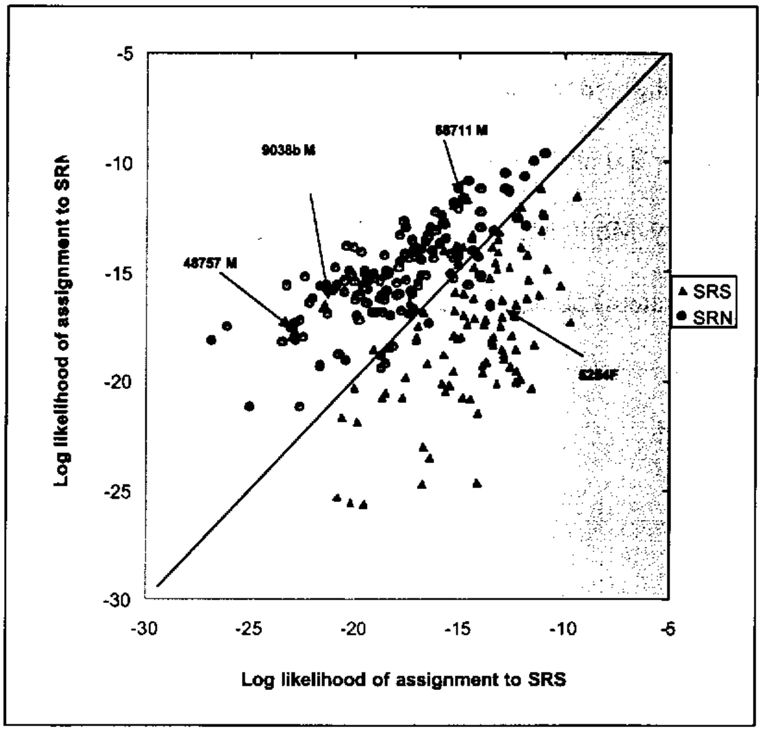
The results along the Highway 3 corridor in all three mountain ranges contrast sharply with the control populations in the Flathead River system. Comparing 42 grizzly bears found on the east side of the undeveloped valley with 38 on the west side, I found the populations were genetically similar, suggesting that individuals mix freely across the river valley (Fig. 2.2d). The genetic distance (D_{LR}) between the populations in the control set was 0.15 ($F_{ST} = 0.001$), while the test sets were, 2.97 ($F_{ST} = 0.035$), 2.04 ($F_{ST} = 0.024$) and 14.4 ($F_{ST} = 0.23$) for the Rocky, Purcell, and Selkirk Mountains respectively.

Table 2.1 Grizzly bear sample and study area sizes for three mountain ranges north and south of B.C. Highway 3 in SW Canada and the NW U.S.A. H_E is average expected heterozygosity.

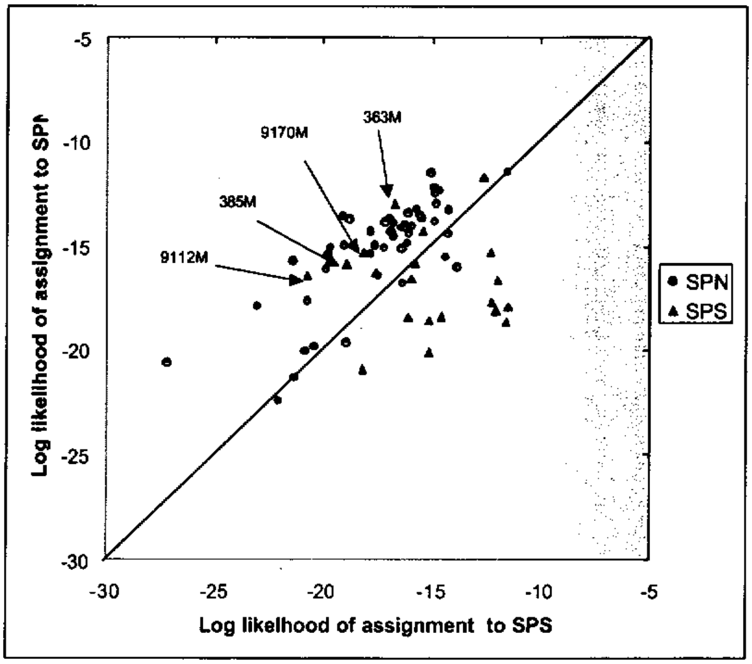
Population	N	Females	Males	Unknown	Area (km^2)	H_E
S Rockies South	99	37	54	8	4695	0.67
S Rockies North	122	57	58	7	6268	0.66
S Purcell South	21	10	11	0	4693	0.64
S Purcell North	48	23	23	2	3117	0.66
S Selkirk	43	20	20	3	5500	0.54
Central Selkirk	104	45	40	19	9582	0.68

Figure 2.2. Population assignments of grizzly bears in SW Canada and NW United States across B.C./Alberta Highway 3 in three mountain ranges and one control system. Individuals highlighted by an arrow are putative migrants across Highway 3 with a likelihood ratio > 2.0 and are significant according to STRUCTURE. M = Male and F = Female. a. Rocky Mountain, b. Purcell Mountain, c. Selkirk Mountain, and d. Flathead River (control system) population assignments.

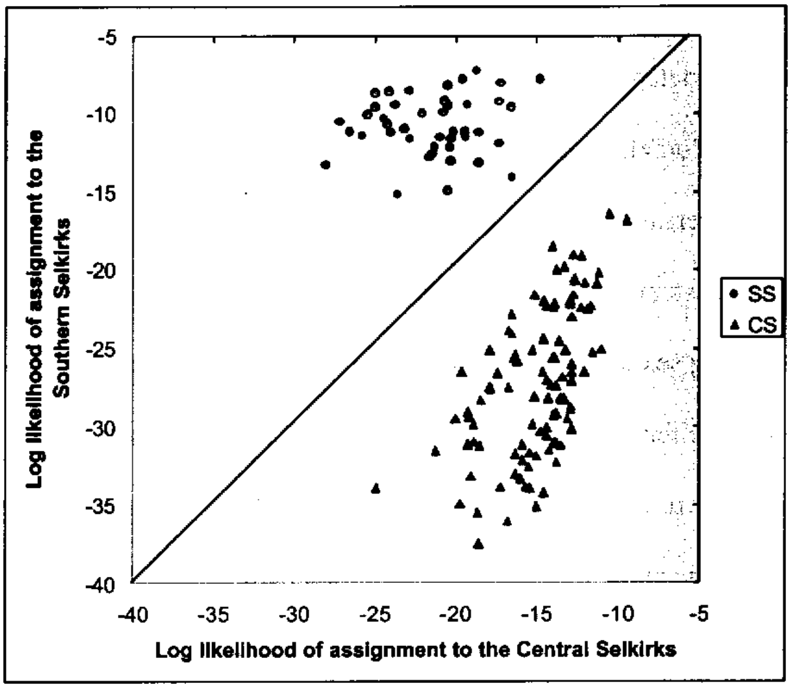
a.


-5
-10
-15
-20
-25
-30
-30
-25
-20
-15
-10
-5
Log likelihood of assignment to SR
Log likelihood of assignment to SRS
68711 M
9038b M
48757 M
8284F
▲ SRS
● SRN

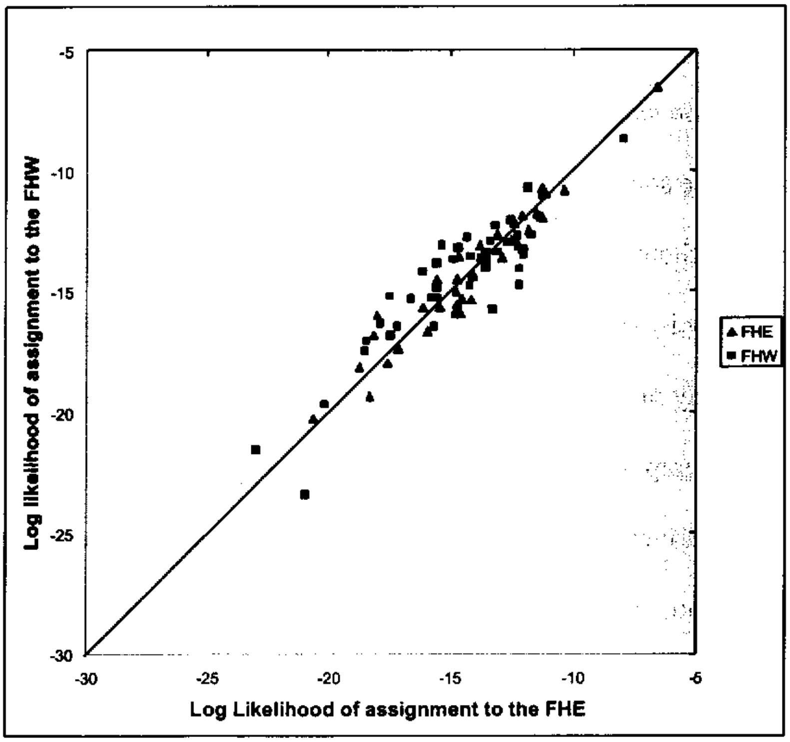
b.


-5
-10
-15
-20
-25
-30
-30
-25
-20
-15
-10
-5
Log likelihood of assignment to SP
Log likelhood of assignment to SPS
363M
9170M
385M
9112M
● SPN
▲ SPS

c.


Log likelihood of assignment to the Southern Selkirks
Log likelihood of assignment to the Central Selkirks
-5
-10
-15
-20
-25
-30
-35
-40
-40
-35
-30
-25
-20
-15
-10
-5
● SS
▲ CS

d.


Log likelihood of assignment to the FHW
Log Likelihood of assignment to the FHE
-5
-10
-15
-20
-25
-30
-30
-25
-20
-15
-10
-5
▲ FHE
■ FHW

DISCUSSION

The Highway 3 transportation corridor that crosses southwestern Canada is fragmenting U.S. grizzly bear populations from those to the north. Female movement is particularly restricted while some males are moving north and south across Highway 3 in the Rocky and Purcell Mountains, and as such, continue to mediate genetic connectivity. Sex-biased dispersal is widespread in mammals (Greenwood 1980; Pusey 1987) and my results are consistent with the hypothesis that in a species with sex-biased dispersal, the lesser dispersing sex may be more affected by human influence. Furthermore, the disruption of the female dispersal process diminishes the possibility of natural population augmentation or re-colonization (Lande 1988) and may have serious implications for the small populations along the Canada-U.S. border. The lack of functional demographic connectivity in this fragmented human-induced "metapopulation" threatens the Purcell/Yaak population, with an estimated 40-50 bears (Kasworm et al. 2000; M Proctor, unpub. data) and the Selkirks with approximately 70-100 animals (Wielgus et al. 1994).

The bear movement from north to south in the Purcells suggests that the grizzly persistence to the south of Highway 3 into the U.S.A. may be dependent on connectivity to the north. Without demographic connectivity, persistence in these small demographically isolated populations is vulnerable to stochastic events and reliant on positive fecundity rates, a challenge where the threat of local extirpation is primarily driven by demographic forces in the form of human-induced mortality (McLellan et al. 1999). Locally-driven strategies for increasing habitat security and minimizing the ubiquitous human-caused mortalities are important tools for conserving grizzly bears in these populations, however my results suggest that internationally inspired connectivity management may be required for the Purcell and Selkirk populations. Loss of these two border populations would leave only one U.S. border population tenuously linked to Canadian populations.

Had my analysis been limited to traditional population genetic techniques (genetic distance and F_{ST}) and not individual-based analyses, I would have found evidence of population structure and fragmentation, or reduced animal movements between populations. What would have been missed was the evidence of gender-specific fragmentation. In other words, ecologically, I would have missed a major factor affecting grizzly bear conservation - the almost complete lack of female movement (i.e. demographic connectivity) across the highway corridor. These methods demonstrate the ability and value of genetic data to provide insight into the gender-specific demographic processes of immigration and emigration in recently disturbed systems, traditionally an intractable yet increasingly important ecological question worldwide.

The genetic distances across the highway corridor in all three mountain ranges are much larger than in the control system, indicating that although some movement of males has occurred across the highway, movement rates are sufficiently low allowing genetic drift to mediate genetic structure. While there are no historical data on the connectivity rates across Highway 3 and 3A, my comparison with the control valley suggests that the number of migrants has been greatly reduced and the reduction is a result of human influence.

The mechanism leading to limited movement across the transportation and settlement corridor is likely a combination of some bears avoiding human activity centers

(Mattson et al. 1987) plus increased grizzly bear mortality in these areas which is often related to bear attractants such as garbage and human foods (Mace and Waller 1998; McLellan et al. 1999). Dispersal of male and female grizzly bears in the southern Rocky Mountains requires several years with resulting newly established home ranges often overlapping or adjacent to the maternal home range (Blanchard and Knight 1991; McLellan and Hovey 2001a). When this gradual dispersal process requires moving through human dominated landscapes, successful dispersal is diminished as bears spend extended periods in proximity to human dominated landscapes. Grizzly bears are attracted to human food sources and killed as a result of a perceived threat to human safety and property. All three migrant males in the Rocky Mountains were killed either by hunters or because they were too close to human habitation. During the past 10 years, 60 grizzly bears were removed from the study area by conservation officers because of conflicts with people, and over the past 25 years an additional 500 were harvested legally (B.C. Ministry of Water, Land, and Air Protection files). These mortalities also may affect movement across the corridor if dispersal rates are density dependent (Swenson et al. 1998; McLellan and Hovey 2001a).

The totally isolated southern Selkirk population has a 20% lower average expected heterozygosity (Table 2.1) relative to neighbouring areas. Demographic processes appear to be the dominant influence over grizzly bear persistence (McLellan et al. 1999) within North America. Excessive mortality and isolation played a primary role in the extirpation of approximately 31 small isolated populations between 1922 and 1970 within the conterminous U.S.A. (Mattson and Merrill 2002). There is evidence that genetic processes such as the deleterious effects of reduced genetic variation are minimal in grizzly bears. Paetkau et al. (1998a) report that the 10,000 year isolated Kodiak Island grizzly bear has 33% of the genetic variation of its nearest mainland counterpart yet the Kodiak Island bears have been thriving for centuries by any standard of measure. These findings suggest that demographic processes should be the most threatening to the small populations along the Canada-U.S. border I describe. However, the Kodiak Island bear population is large (3000; L. Van Daele pers. comm.) relative to the isolated southern Selkirk 70-100 bears and the effects of inbreeding depression tend to be more detrimental for small populations (Frankham et al. 2002).

The power of my results is enhanced by the relatively high percentage (~50%) of sampled bears in all the populations surveyed. Four of the six areas were sampled during surveys to estimate population size (Central Selkirks, Mowat and Strobeck 2000; Rocky Mountains, Boulanger 2001; N. Purcell Mountains, M. Proctor unpub. data), and two areas were part of radio telemetry studies that estimated population size (S. Selkirk Mountains, Wielgus et al. 1994; S. Purcell Mountains, W. Kasworm unpub. data)

My results contrast with those of Paetkau et al. (1998b) who found genetic structure of grizzly bears in northern North America to vary as a function of geographic distance. For example, the genetic differences I found across Highway 3 in the Rocky Mountains are equivalent to an 800 km separation in the undisturbed northern Canada populations. It should be noted that habitat is much less complex and grizzly bear home ranges are larger in many areas of northern North America (see review in LeFranc et al. 1987). Schwartz et al. (2002) found little genetic structure in lynx populations in western North America and concluded that maintenance of connectivity was therefore an important management and conservation concern. However Schwartz et al. (2002) used an F_{ST} /Nm based analysis (not an individual-based analysis) and may therefore not have measured recent fragmentation. At a finer scale, Campbell (2002) found genetic structure in lynx across a major highway in Alberta, Canada, suggesting that human disturbance may be influencing connectivity. Kyle and Strobeck (2002) found increased genetic structure in southern peripheral populations relative to northern core populations in the North American wolverine (*Gulo gulo*) although they did not measure immediately adjacent populations within the dispersal distance of a wolverine. Cegelski et al. (*in press*) also found wolverines to be fragmented in the southern periphery of their western North America distribution.

Identification of individual inter-population migrants and gender-specific fragmentation through genetic data is a valuable and recent ecological tool for studying increasingly fragmented landscapes. However, several challenges have been discussed in the literature. One problem is identifying the true source population for an animal that has recently migrated when that population may not have been sampled (Corunet et al. 1999). In this instance, assignment tests may specify the population that is most genetically similar to the true source population. My study was fortunate in this regard as I sampled the entire east-west distribution of grizzly bears in the interior trans-boundary region and most of those to the north of the study area (unpub. data not included in this analysis). In the Selkirk and Purcell Mountains there are no significant numbers of bears living to the south of my study area. In the Rocky Mountains, the bears are known to regularly cross the border into what I assume is one continuous population.

Another challenge is setting thresholds for migrant status that may be somewhat arbitrary. For instance, what Log Ratio is the appropriate cut off for distinguishing migrants from those who are cross-assigned by chance. Lowering the cross-assigned Log Ratio > 2.0 to LR > 1.5 added one male and one female putative migrants in the Rocky Mountains and no migrants in the Purcell or Selkirk Mountains.

CONCLUSION

I demonstrated gender-specific population fragmentation of a carnivore in a recently disturbed system of immediately adjacent geographic areas at the regional scale in western North America. This work highlights the importance of measuring gender-specific inter-population movement (dispersal) particularly in species where demographic processes may operate faster than negative genetic processes on small populations. The lack of evidence for female inter-population movement suggests several small populations may have lost demographic connectivity and thus have an elevated risk of local extirpation from the negative processes at work on grizzly bears historically (Mattson and Merrill 2002) and in the present (McLellan et al. 1999).

My results alter the magnitude, scope, and jurisdiction of efforts required to ensure grizzly bear persistence in the region of the Canada-U.S. border and underscore the need for internationally motivated connectivity management. Methods such as those used in this study may be a prerequisite for understanding dispersal, spatial population ecology, and demographic management needs for maintenance or enhancement of carnivores in North America and a wide variety of species worldwide. My methods offer promise towards understanding large-scale, inter-population processes in time scales relevant to modern conservation problems, a paradigm view that is required for long-term human/carnivore coexistence.

CHAPTER 3: HUMAN DISTURBANCE AND GENDER-SPECIFIC POPULATION FRAGMENTATION

INTRODUCTION

Dispersal movement between populations is a challenging population parameter to measure, yet it is becoming increasingly important as humans alter ecosystems and landscapes (MacDonald and Johnson 2001). Population ecology is shaped by the equation that population change is equal to births minus deaths, plus immigration minus emigration (Ricklefs 1990). Most work has centered on the birth/death part of the equation as immigration and emigration are traditionally difficult to measure and assumed to be relatively minor. For instance, viability analyses of endangered species usually resort to modeling immigration and emigration due to lack of adequate inter-population dispersal data (Clobert et al. 2001). The interruption of inter-population dispersal, or population fragmentation, is thought to be a major factor influencing the present worldwide biodiversity crisis (Wilcox and Murphy 1985). Fragmentation may convert a panmictic population into a non-equilibrium metapopulation (McCullough 1996) or completely isolate segments of a population. Fragmentation events that result in small isolated populations are the largest conservation concern due to an elevated risk of extirpation (Gilpin 1987; Berger 1990) contributing to local extinction events and range contractions (Woodroffe and Ginsberg 1998).

Fragmentation and its antithesis, connectivity, have two types of consequences: genetic and demographic. Genetic isolation can lead to reductions in genetic diversity, increasing the risk of extirpation, particularly in small populations (Frankham et al.

2002). However, genetic connectivity can be mediated by one gender. Therefore, when managing for genetic connectivity, the movement of one gender may be sufficient to resist losses of genetic diversity (Paetkau et al. 1998a). For a small population to remain viable over the long-term, it must maintain genetic diversity. But more importantly, in the short-term it must be able to resist population declines from stochastic variation of birth and death rates, or catastrophic events. Therefore, interruption of demographic processes due to fragmentation are of more urgent concern than genetic isolation (Lande 1988; Caughley 1994). Lack of demographic connectivity may result in the loss of several inter-population processes including population augmentation or recolonization, resulting in the loss of metapopulation function (McCullough 1996; Hanski and Gilpin 1997). Demographic connectivity requires the movement of both sexes and is thus a more difficult to maintain. However, if one manages for and attains demographic connectivity, genetic connectivity is ensured. On the other hand, if one manages only for genetic connectivity, demographic connectivity is not necessarily attained.

It is important to measure gender-specific inter-population movement in fragmented systems to understand conservation status. When studying large mammals over large spatial and temporal scales, radio telemetry techniques are impractical (Koenig et al. 1996; Palsboll 1999). Furthermore, traditional population genetic techniques (F_{ST} and Nm, or genetic distance) that measure population structure and estimate migration rates as an index of fragmentation, do not measure recent movement, sex-specific movement, or demographic connectivity (Slatkin 1985; Steinberg and Jordan 1997; Whitlock and McCauley 1999). Individual-based genetic analyses, particularly when coupled with an efficient sampling technique, offer the possibility of examining gender-specific inter-population movements (Waser and Strobeck 1998; Davies et al. 1999).

To explore the extent and causes of population fragmentation in a large vagile carnivore, I used individual-based genetic analyses (Waser and Strobeck 1998; Davies et al. 1999; Luikart and England 1999) to measure sex-specific movement rates of grizzly bears in southwestern Canada and the northwest conterminous U.S.A. The study area is well suited as it is located at the southern extent of the contracted North American distribution of grizzly bears and is partially fragmented. Grizzly bears are an appropriate study animal because I hypothesize that they are sensitive to fragmentation. They exhibit limited sex-biased dispersal (Blanchard and Knight 1991; McLellan and Hovey 2001a) increasing their susceptibility to demographic fragmentation. They are highly vagile due to their large body size and large home range (Bunnell and Tait 1981; Wolff 1999), and their generalist foraging habits allow them to exploit a variety of dispersed food resources (McLellan and Hovey 1995). Large movements put them at greater risk of death as they overlap human dominated environments (Woodroffe and Ginsberg 1998). Grizzly bears also have low reproductive rates and therefore are susceptible to excessive mortality (Miller 1990; Caughley and Sinclair 1994; Kokko et al. 2001). Mortality provides a mechanism for human-induced fragmentation on several fronts. Grizzlies may compete with humans for ungulate or fish resources and are often killed when attracted to food resources in human dominated landscapes (McLellan et al. 1999), and they may be killed when they threaten human security by their aggressive nature (Herrero 1985). Furthermore, grizzly bears are killed by humans as legal game. These factors also put the grizzly bear at greater risk of local population extinction (Woodroffe and Ginsberg 1998; Purvis et al. 2000; Woodroffe 2001).

I asked the following research questions: how do bears move between geographic areas in a mountainous landscape at a regional scale? is there a difference in male and female movements? does the human environment affect bear movements? I discuss the implications of the answers to these questions for grizzly bears at the southern extent of their contracting North American distribution and the principles of human induced population fragmentation as they may apply to other species and ecosystems.

METHODS

Study area

I sampled wild free-roaming bears across 100,000 km^2 in SW Canada and the NW U.S.A. (Fig. 3.1) in three mountain ranges, the Rockies, Purcells, and Selkirks. In the Rocky Mountains I sampled from the Canada-U.S. border through Banff National Park (latitude 49-52°). In the Purcell and Selkirk Mountains I sampled bears from the southern extent of their distribution in the U.S.A. north to almost the 52nd parallel. This area included the entire Purcell range and all but the northern tip of the Selkirk range. These forested mountain ranges are separated by human-settled valleys that range in width from 0.5 to 12 km. A variety of highways cross my study area including two major east-west transportation corridors, Canadian Highways 1 and 3 (Fig. 3.2). Average summer traffic volumes for these highways range from several hundred to over 15,000 vehicles per day in the Rocky Mountain's Highway 1. Human settlement is primarily in the valleys adjacent to the highways and varies from relatively unsettled wilderness in several

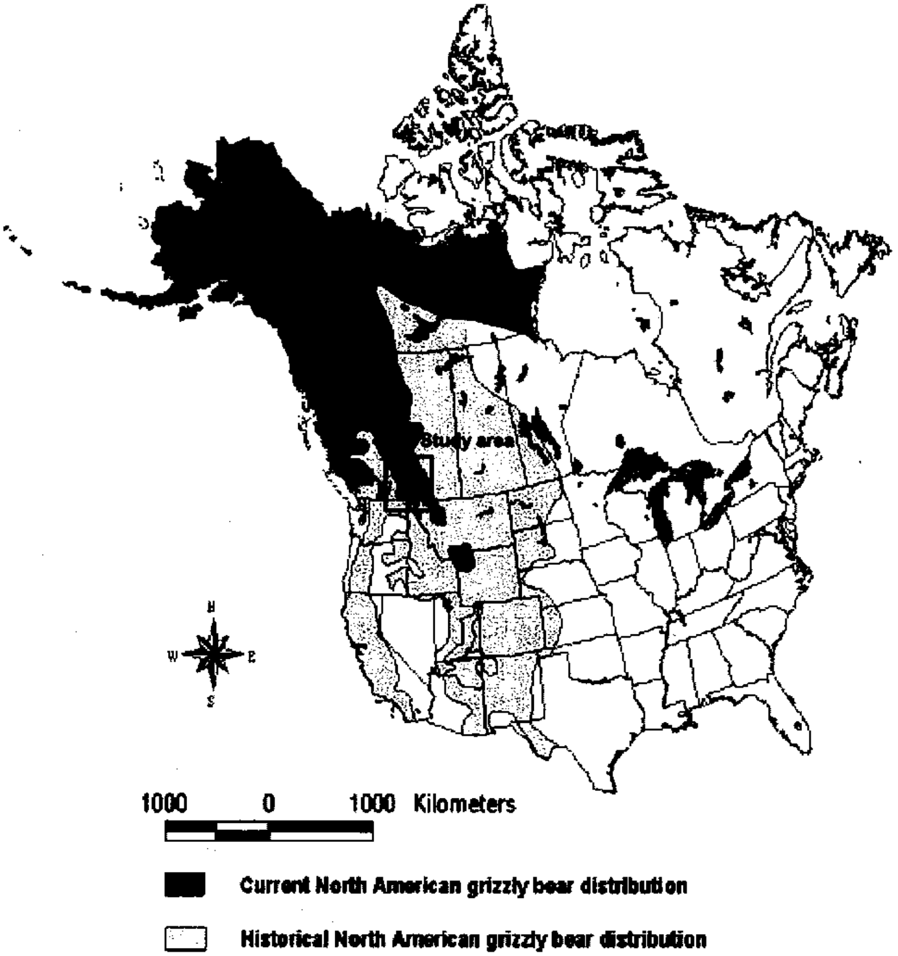


Figure 3.1 Map of study area within current and historical North American grizzly bear distribution.

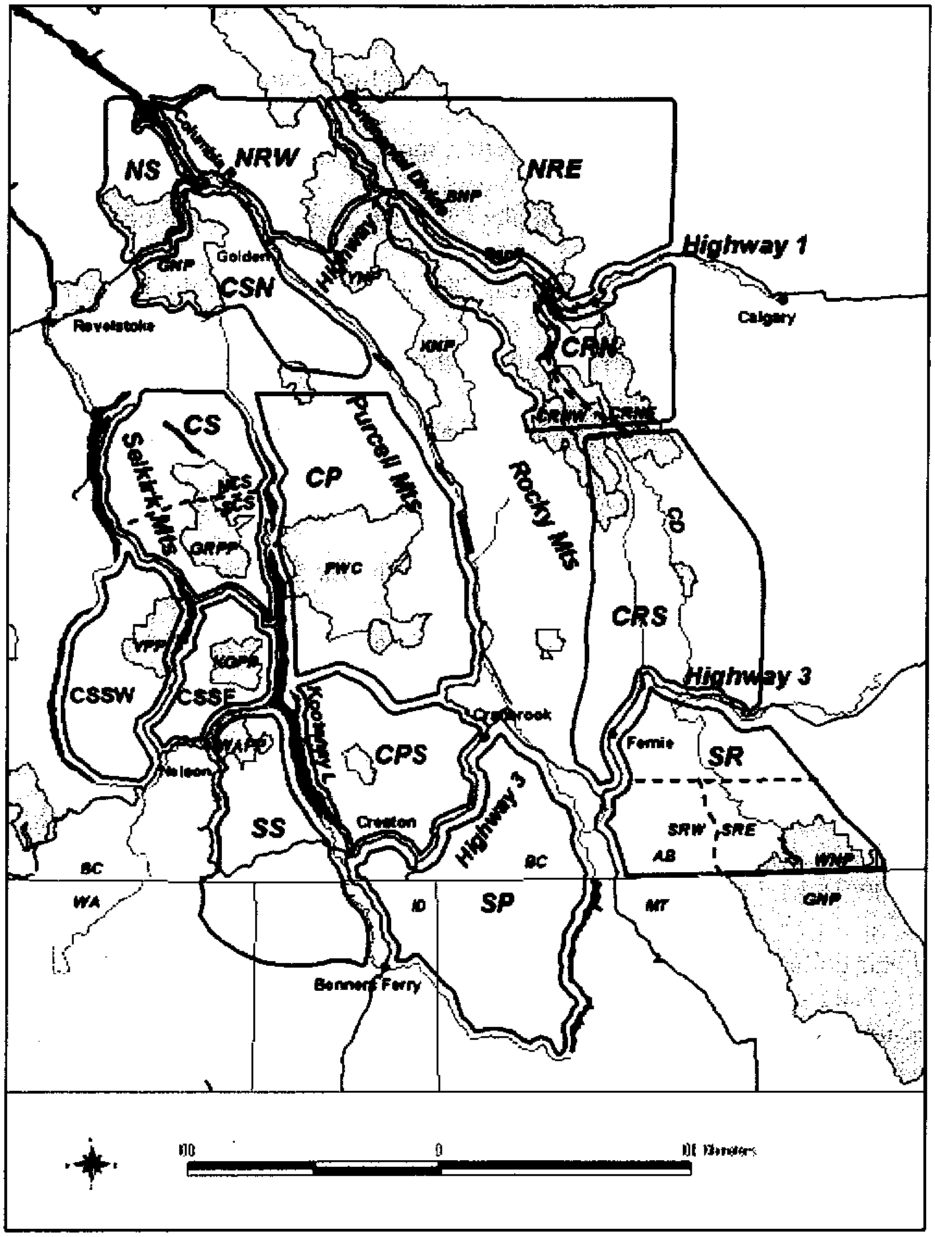


Figure 3.2. Arbitrary local populations of grizzly bears in the Rocky, Purcell, and Selkirk Mountains of SW Canada and NW U.S.A. Internal dotted lines are "control" areas. Protected areas are in gray, and map labels BNF. YNP, KNP, WNP, GNP are Banff, Yoho, Kootenay, Waterton, and Glacier National Park respectively. Provincial park labels PWC, GRPP, VPP, KGPP, and WAPP are Purcell Wilderness Conservancy, Goat Range, Valhalla, Kokanee, and West Arm Provincial Park Provincial Park respectively. See text for subdivision criteria and Table 3.1 for local population names and details.

National Parks to essentially continuous linear settlement along Highway 3A in the Selkirk Mountains. The Selkirk Mountains and the western slopes of the Purcell and Rocky Mountain ranges tend to be wetter, more productive ecosystems as Pacific air masses yield their moisture to high elevation orographic precipitation stimulating an interior wet belt in much of these areas. The eastern slopes of the Purcell and Rocky Mountains fall within a "rain shadow" yielding a drier ecosystem. The study area has a diverse suite of land uses and jurisdictional landscapes including towns, farming communities, industrial timber harvest (provincial and private), mining, eight provincial parks, and six national parks. The majority of the mountainous land is controlled by Canadian provincial governments or the U.S. Forest Service.

Genetic analysis

Samples consisted of biopsy samples of handled bears (Gibeau 2000; Kasworm et al. 2000; B. McLellan, B.C. Ministry of Forests, and W. Wakkinen Idaho Fish & Game) and hair collected using hair-traps that consisted of a single strand, barbed-wire corral surrounding a scent lure (Woods et al. 1999) between 1996 and 2001. Some samples came from previous DNA-based population surveys (Gibeau and Herrero 1997; Woods et al. 1999, Mowat and Strobeck 2000; Boulanger 2001; Boulanger et al. *in press*).

I extracted DNA from hair roots using the Chelex protocol (Walsh et al. 1991) before 1998 and DNeasy columns (Qiagen Inc., Mississauga, Ontario, Canada) after 1998, and used it to identify individuals with six microsatellite loci (Paetkau et al. 1998a; Woods et al. 1999). All samples from identified individuals were re-extracted using DNeasy from 10 guard hairs when available. I switched to DNeasy to improve the quantity and quality of extracted DNA based on the results of a small test trial (unpub.

data). I discarded samples with fewer than five hairs to reduce genotyping errors such as allelic dropout and non-specific bands associated with using samples with low quantities of DNA (Gagneux et al. 1997; Goossens et al. 1998; Taberlet et al. 1999). I expanded the six-locus microsatellite genotypes to 15 loci for all individual bears previously identified during the population surveys. All 15 loci were used for newly captured bears in 1999-2001. Markers used were those previously developed by Ostrander et al. (1993), Taberlet et al. (1997), and Paetkau et al. (1998a). Specifically, I used G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10U, G10X, MU50, MU59, CXX20, CXX110. Two of Ostrander's markers, CXX 20 and CXX110, were designed for canids and worked poorly on ursid hair-derived DNA. Therefore, I redesigned them by sequencing them in grizzly bear DNA, and moving the primers into bear sequence (Proctor et al. 2002). Genotypes were determined on an Applied Biosystems 377 automated sequencer and scored with the help of Genotyper software (Applied Biosystems, Foster City, California, U.S.A.). I visually double checked all genotypes on the original electrophoresis gels. All genotype pairs with a single mis-match at the original six loci were scrutinised for potential errors and rerun for verification, as were any genotypes represented by only one sample of hairs (I sampled most bears multiple times). I also ran all 15-locus genotypes through the software program Relatedness (Queller and Goodnight 1989) to look for close genotypes that were erroneously considered to be two individuals, and CERVUS (Marshall et al. 1998; Slate et al. 2000), to look for potential parent-offspring pairs that did not share an allele at each locus through genotyping error. I reanalysed all similar genotypes such that I had no pairs of genotypes with less than three mismatching loci in the final data set. I distinguished grizzly bear from black bear hair samples using a consistent deletion in grizzly bear mtDNA (Woods et al. 1999). I determined sex in one of two ways. On individuals identified before 1997, I used the SRY-ZFX/ZFY system (Taberlet et al. 1993; Woods et al. 1999). Due to an extra band in occasional female samples using the SRY-ZFX/ZFY system (unpub. data), I switched in 1997 to the observation of alleles at the Amelogenin locus (Ennis and Gallagher 1994) which I ran with a positive and negative control to detect contamination. I identified individuals statistically using six loci and a P_{SIB} statistic (Woods et al. 1999). My threshold for acceptance of a new individual was a P_{SIB} value of 0.05, differentiating one individual from the genotype of a potential full sibling.

I tested all 15 loci in all local populations for conformance to Hardy-Weinberg assumptions of random mating using the probability test for a deficit of heterozygotes (Rousset and Raymond 1995). All loci in all local populations were tested for linkage disequilibrium using a probability test (Garnier-Gere and Dillman 1992). Critical values for these tests were adjusted for the experiment-wise error rate using the Dunn-Sidak method (Sokal and Rohlf 1995). These tests were performed within GENEPOP 3.1 (Raymond and Rousset 1995). To establish that two local populations of bears were not one homogeneous unit, I tested the allele frequencies for heterogeneity using the log likelihood G test (Sokal and Rohlf 1995). Unbiased estimates of mean expected heterozygosity (H_e) were calculated as an index of relative genetic variability (Nei and Roychoudury 1974).

My goal was to test for the fragmentation effects of the highway/settlement corridors and natural fractures within the study area. I compared bears inhabiting immediately adjacent geographic areas to explore anthropogenic population fragmentation. I arbitrarily divided the study area into "local" populations to span a range of levels of human disturbance. First, I divided the area using the valleys separating the three main mountain ranges. Some of these valleys contained human settlement with a major highway, others had only minor roads or potential natural fractures (i.e. large lakes). Each of these was further divided into sub-units by the east/west human transportation/settlement corridors, including Highway 1 and 3 and several smaller corridors and by areas that potentially are natural fractures. I then paired local populations if they had a common boundary and limited the pairings to those immediately adjacent local population pairs within the probable dispersal distance of female grizzly bears in the region (McLellan and Hovey 2001a). I acknowledge that some adjacent pairs may in fact be well connected. Chapter 4 will explore the existence of biologically-based population boundaries. These common boundaries were tested for bear movements to measure levels of connectivity. In an effort to insure I included areas of minimal human disturbance, I sub-divided several of the resulting local population units across a natural boundary that was similar to the human dominated boundaries but that lack disturbance. I chose ecologically similar areas in each of the three mountain ranges. Criteria for these groups were that I had sufficient samples on each side of a dividing line. These dividing lines had to be ecologically and topographically similar to the areas that separated the local population pairs, that is, they contained a river valley and mountain pass but had no settlement or highway. I found four such control systems in the three mountain ranges: 1. East and west of the Flathead River valley in the Rocky Mountains, 2. East and west of the Spray Lake/Dorian Highway corridor in the Rocky Mountains, 3. North and south of the Redding Creek/St. Mary's River corridor through the Purcell Mountains, and, 4. North and south of the Poplar Creek/Bremner Creek corridor in the Selkirk Mountains (Table 3.1, Fig 3.1). In total I compared 23 local population-pairs with common boundaries.

I used three types of information to document movement of bears across the potential fracture boundary areas separating local population pairs. First, I used genetic data for population assignment analyses in which I detected individuals that I inferred to be migrants from their source population (where their genotypes were more likely), across one of the boundary areas into the area of their capture. Second, I used genetic data to directly identify individual bears that were captured in two local populations on both sides of a boundary area. Third, I used radiotelemetry location of bears in two systems to detect movement between local populations. These methods are discussed in detail below.

I used genetic-based assignment methods to test for individual migrants between local populations and parentage analysis to corroborate these results. First, I used population-specific allele frequencies in a likelihood-based assignment test (Paetkau et al. 1995). This assignment test calculates the probability of each individual's assignment to a particular population as the cumulative product of each allele's frequency of occurrence in any of several populations being examined. The individual is assigned to the population with the highest probability of occurrence as a result of, in this instance, considering 30 alleles (15 loci, 2 alleles/loci). This test assumes that all loci in each population are in Hardy-Weinberg equilibrium and that there is linkage equilibrium. The power of this test is increased as the proportion of individuals sampled and number of loci used increases, and as the connectivity between the study populations decreases.

Using assignment methods, "true" migrants must be distinguished from those that cross-assign by chance. I chose a threshold for putative migrant status as those bears with a likelihood ratio for cross-assignment of 2.0, corresponding to a 100 times probability of being cross-assigned. To test and corroborate this threshold of being a "true" migrant, I used the distribution of gender-specific log-ratios (of cross-assignment to capture population). As grizzly bears are hypothesized to have sex-biased dispersal (McLellan and Hovey 2001a), I tested the hypothesis that the log-ratio distributions for males and females would diverge at the "true" migrant log-ratio threshold. The logic is that the male and female distributions should be similar up until the point where the more vagile males had log-ratios reflecting their cross-assignment (Favre et al. 1997)

To corroborate my conclusions based on the frequency-based assignment test of Paetkau et al. (1995), I used model-based clustering and a Bayesian approach to develop probability distributions built from Monte Carlo Markov Chain (MCMC) simulations. The goal was to use population allele frequencies, individual genotypes, and population-specific capture information to probabilistically assign individuals to populations and determine migrant status (STRUCTURE, Pritchard et al. 2000).

To corroborate assignment-based migrant decisions, I identified parent-offspring relationships between putative migrants and an individual in the source population using a likelihood-based parentage analysis (CERVUS; Marshall et al. 1998; Slate et al. 2000). CERVUS compares the likelihood of potential parentage calculated from allele frequencies within the population based on Mendelian inheritance principles. For all potential offspring, it compares the two most likely parental candidates (maternal and paternal done separately) by log ratio. It then simulates parents and offspring developing a distribution of relative log ratios to determine a significance for any given potential parent-offspring relationship. The simulation routine incorporates estimates of the rate of genotyping error, the number and proportion of potential parents sampled, and the proportion of genotyping success. I also used Paetkau et al.'s (1997) genetic distance (D_{LR}), related to the above frequency-based assignment test, and F_{ST} (Wright 1965; Weir and Cockerham 1984; Slatkin 1985; Hartl and Clark 1997) to quantify genetic separation between populations.

I used multiple linear regression to explore the association of several aspects of the human environment, human settlement, traffic volume, and human-caused mortality, with bear movements between population pairs. I believe that other habitat-based variables likely influence bear movements, but they were omitted in this analysis because I had no reliable measurement of these potential variables at the scale of this work (see Discussion). Regression models were developed as hypotheses based on several combinations of four variables, geographic distance between local population pairs, traffic volume, human settlement patterns and human-caused mortality as measured within the boundary areas separating local population pairs. The complexity of models was limited by the number of comparable adjacent population pairs.

I represented patterns of human settlement by measuring the amount of a transportation/settlement corridor that was free of human settlement. On 1:50,000 topographic maps, I drew a 500m radius around all buildings and calculated the percent of the linear boundary between the local population pair that had no buildings. Settlement input data were Arcsine transformed as is recommended for relative percent data (Krebs 1995). I used average summer traffic volumes between human settlements within the local population pair common boundary (B.C. Ministry of Transportation, Alberta Transportation). Traffic data regression inputs were square root-transformed due to distribution skewness. Because boundary length and bear densities varied across my study area, I estimated "Relative Mortality" by tabulating all human-caused mortality over the past 25 years (B.C. Ministry of Land, Water, and Air Protection files) within 18 km of the common boundary, and divided this total by the average number of bears found in the boundary area. I estimated the number of bears in the boundary area using average densities for the surrounding area based on the results of previous DNA population surveys (Weilgus et al. 1994; Strom et al. 1999; Woods et al. 1999; Gibeau 2000; Kasworm et al. 2000; Mowat & Strobeck 2000; Boulanger 2001; Boulanger et al. 2002; Boulanger et al. *in press* ; Mowat et al. *in press*). I used the average densities because this represents the pool of bears in and adjacent to the boundary area that would be potential inter-population dispersers. Finally, I used the geographic distance between local populations calculated from the geometric mean of the cumulative individual bear locations sampled within each local population.

To optimize the trade-off in model fitting and the number of variables in any particular model, I used Akaike Information Criteria (AIC) to choose models that were best supported by the data (Burnham and Anderson 1998). Specifically, I used the small sample corrected AICc (when $N < 40$, Anderson and Burnham 2002) represented by the equation:

$$\text{AICc} = N(\text{Ln}(\text{RSS}/N) + 2K + \text{CF (correction factor)}$$

$$CF = 2K(K+1) / N-K-1$$

Where RSS is the residual sum of squares, N is the number of populations considered in each model, and K is the number of parameters in each model + 2. To compare differences in AICc scores, I report delta AICc (ΔAICc) which is the difference in each model relative to the "best" fit model with the lowest AICc score. As a rule of thumb, all models with a ΔAICc score less than 2.0 should be considered plausible models (Burnham and Anderson 1998; Anderson and Burnham 2002).

The dependent variable, bear movement rate, was determined in one of two ways. The genetically-derived number of "migrants" between local population pairs was divided by the total number of individuals sampled in the two local populations being considered. In two systems where the genetic distance was very low, resulting in very little power to detect migrants using assignment methods, I used the number of bears moving between local population pairs detected by radiotelemetry. I divided the total number of bears with at least 15% of their locations on each side of the valley by the total number of bears followed by telemetry methods. These radio telemetry data were provided by B. McLellan for the Flathead River Valley system and M. Gibeau for the Central Rockies East and West system. Admittedly, there is an asymmetry of search effort between radio telemetry and DNA methods. In a radio telemetry study, using VHF equipment with weekly searches over six months (typical season), the average effort was 45 searches per radio-collared bear. The search effort with DNA is typically 4-5 searches per year. I limited the radio telemetry data I used to five years of effort in the two areas where I used radio data. DNA data are derived from population assignments and therefore detect movement that may have occurred over a longer time span – up to 20 years for a 25 year old bear that dispersed across a boundary area at approximately age five. Because an accurate comparison of effort is difficult, I report regression results with the two telemetry migrant systems included and with them omitted. The advantage of their inclusion is a 10% increase in sample size (23 comparisons vs. 21) which may be useful when considering 4 to 8 regressor variables.

RESULTS

Tests for equilibrium

I identified 706 (339 males, 291 females, 76 unknown – 10% sex test failure rate) grizzly bears at 15 microsatellite loci in 14 geographic areas (Table 3.1). Loci in all areas were in Hardy Weinberg equilibrium except one, and that locus did not have a heterozygote deficit. Sixteen of 1470 (1.1%) comparisons were rejected by the linkage disequilibrium test, yet there was no discernible pattern between loci and populations, suggesting that this linkage disequilibrium signal may have causes other than chromosomal linkage. These occurred in areas that are open to bear movements with adjacent geographic areas and I suggest that immigration may be responsible for this weak signal (Proctor et al. 2002; Hartl and Clark 1997). Otherwise, I assume loci are operating independently. All groups of bears in each geographic area were genetically heterogeneous, suggesting that each was an independent breeding unit sufficient for comparison except for the population pairs where I used radiotelemetry data for bear movements. Average expected heterozygosity in the study area was 0.64 and observed heterozygosity was 0.65 (Table 3.1).

Table 3.1. Sample sizes of arbitrary local grizzly bear populations in SW Canada and the NW U.S.A. organized by mountain range and south to north: sample size (*N*), male (*M*), female (*F*), unknown sex (*Unk*), average expected heterozygosity (H_E), observed heterozygosity (H_O). See text for the sub-division criteria and Figure 3.2.

	Local Populations	**Code**	**N**	**M**	**F**	**Unk**	$\mathbf{H_E}$	$\mathbf{H_O}$
Selkirk Mts.								
	Southern Selkirks	SS	43	19	21	3	0.54	0.57
	Central Selkirks SE	CSSE	15	6	6	3	0.62	0.67
	Central Selkirks SW	CSSW	18	5	10	3	0.62	0.67
	Central Selkirks	CS*	71	29	29	13	0.68	0.66
	Central Selkirks North	CSN	34	23	8	3	0.61	0.62
	North Selkirks	NS	35	21	10	4	0.66	0.64
Purcell Mts.								
	Southern Purcells	SP	21	12	9	0	0.64	0.68
	Central Pucells S	CPS	48	23	23	2	0.66	0.68
	Central Purcells	CP	45	17	26	2	0.66	0.66
Rocky Mts.								
	Southern Rockies	SR	111	59	37	15	0.67	0.66
	Central Rockies S	SRS	110	58	37	15	0.66	0.66
	Central Rockies N	CRN	50	21	25	4	0.61	0.61
	North Rockies E	NRE	40	15	19	6	0.64	0.64
	North Rockies W	NRW	65	31	31	3	0.61	0.62
	Total		706	339	291	76	0.64	0.65
Control populations*								
	North CS*	NCS	25	10	11	4	0.63	0.62
	South CS*	SCS	30	12	12	6	0.64	0.62
	C Rockies N East*	CRNE	22	10	11	1	0.58	0.57
	C Rockies N West*	CRNW	22	9	12	1	0.60	0.61
	S Rockies East*	SRE	38	19	13	6	0.64	0.65
	S Rockies West*	SRW	38	19	15	4	0.63	0.62

*** Control populations are arbitrarily sub-divided local populations (see text).**

Population assignments

I found evidence of female movement between local populations, with female inter-change occurring in seven of 23 local population pairs (Table 3.2). In total, 16 females of 307 were presumed to have moved between local populations (Table 3.3). Of the population pairs with putative female migrants, two moved across a major highway, Highway 6, through porous human settlement (one between CSSW and CS and one between CSSW and CSSE, Fig. 3.2). The remaining 14 females that moved between areas, moved through areas with no major road or human settlement. I found no evidence of female movement across B.C. Highway 1 or 3 in all three mountain ranges.

Forty-four of 339 males moved in 16 adjacent local population pairs (Table 3.3). The environments that these males moved through included most of the major highways and human settled areas in the study area. One population had no male or female inter-population movement, the southern Selkirk Mountain population (Fig. 3.2) which appears to be isolated, corroborated by the fact that the genetic distance is 4-10x greater than that of the other pairs and the heterozygosity is 20% lower (Table 3.1 and 3.3).
Another local population, the Central Selkirk Southeast area (CSSE, Fig. 3.2), had evidence of only one individual (female) inter-population movement. Also, the genetic distance between the CSSE and its three neighboring local populations was elevated from that of pairs with movement (Table 3.2). When I compared the distribution of sex-specific log ratios, the male and female curves diverged near LR = 2.0 (Fig. 3.3). Figure 3.4 is a summary representation of detected sex-specific movements between geographic areas in my study area.

Table 3.2. Summary of gender specific movements and genetic distances between adjacent arbitrary local grizzly bear populations in SW Canada and the NW U.S.A.: Sample size (*N*), log ratio genetic distance (D_{LR}; Paetkau et al. 1997), genetic differentiation measure (F_{ST}; Weir and Cockerham 1984), male movement between local populations (*M Mvt*), male movement rate between local populations (*M rate*), female movement between local populations (*F Mvt*), female movement rate between local populations (*F rate*), total movement between local populations (*MF Mvt*), total movement rate between local populations (*MF rate*).

Pop pairs	2 Pop N	D_{LR}	F_{ST}	M Mvt	M rate	F Mvt	F rate	MF Mvt	MF rate
NRW-NS	101	1.64	0.032	2	0.038	0	0.000	2	0.020
NRW-CSN	100	1.16	0.004	2	0.036	0	0.000	2	0.020
NS-CSN	69	1.03	0.024	2	0.044	0	0.000	2	0.030
CP-CS	118	2.35	0.047	1	0.022	0	0.000	1	0.008
CP-CSSE	62	6.47	0.030	0	0.000	0	0.000	0	0.000
NRE-NRW	95	2.19	0.012	2	0.048	0	0.000	2	0.021
NRE-CRN	74	1.64	0.013	2	0.069	0	0.000	2	0.027
CRN-CRS	167	2.09	0.028	4	0.052	1	0.013	5	0.030
CS-CSSE	86	5.27	0.019	0	0.000	0	0.000	0	0.000
CS-CSSW	89	2.14	0.059	1	0.029	1	0.026	2	0.022
CSSE-CSSW	33	3.72	0.077	0	0.000	1	0.063	1	0.030
CSSE-SS	58	14.44	0.228	0	0.000	0	0.000	0	0.000
CPS-SP	69	2.04	0.024	4	0.118	0	0.000	4	0.058
CPS-CRS	170	3.83	0.021	3	0.037	0	0.000	3	0.018
CPS-SS	91	12.08	0.127	0	0.000	0	0.000	0	0.000
SP-CRS	142	3.26	0.049	2	0.026	0	0.000	2	0.014
SP-SR	42	3.62	0.025	0	0.000	0	0.000	0	0.000
SP-SS	64	12.96	0.173	0	0.000	0	0.000	0	0.000
CRS-SR	143	2.97	0.035	3	0.043	0	0.000	3	0.021
CP-CPS	95	1.47	0.022	4	0.100	2	0.039	6	0.063
NCS-SCS	56	1.00	0.016	1	0.035	2	0.069	3	0.054
CRNE-CRNW*	52	-0.26	0.003	4	0.182	4	0.133	8	0.154
SRE-SRW*	80	0.15	0.001	7	0.182	5	0.125	12	0.150
Total				43		16		59	
Average		3.794			0.043		0.024		0.032

* Genetic distance is too low (D_{LR}<1.0) to determine migrants so I used radiotelemetry data

Table 3.3. Summary of data for the human environment variables used in the multiple linear regression associated with movement rates between adjacent arbitrary local grizzly bear populations in SW Canada and the NW U.S.A. *Traffic volume* is the summer average (vehicles/day), *% no settlement* is the relative distance of the common boundary between local population pairs with no human settlement, *mortality* is the human-caused bear mortality 18 km out from the center of the common boundary divided by the average density in boundary area, and geographic distance (*G. distance*) is between local population pairs measured using the mean location of all sampled individuals within each population location.

Pop pairs	Boundary (km)	Traffic Volume	% No Settlement	Mortality	G. Distance (km)
CP-CS	140	184	69	0.50	59
CP-CSSE	43	2310	21	1.36	82
CS-CSSE	50	797	88	0.76	69
CS-CSSW	47	2207	36	0.32	51
CSSE-CSSW	80	1254	20	0.31	41
CSSE-SS	43	3643	1	0.42	63
NRE-CRN	80	15,000	56	1.94	67
NRE-NRW	50	3240	80	0.88	92
CRN-CRS	45	1	100	0.72	93
CPS-SP	110	4332	24	2.06	81
CPS-CRS	50	4129	30	1.11	115
CPS-SS	80	3131	10	0.81	50
SP-CRS	55	4000	29	1.89	134
SP-SR	36	1304	75	0.59	90
SP-SS	20	1769	8	0.19	87
CRS-SR	157	4785	34	1.85	93
NRW-NS	50	200	75	0.45	42
NRW-CSN	45	9942	20	0.42	45
NS-CSN	126	9942	68	0.81	44
CP-CPS	80	35	75	1.53	89
NCS-SCS	60	20	100	0.34	45
CRNE-CSNW	65	500	90	1.43	35
SRE-SRW	47	100	98	1.04	40

Of the local population pairs with a major highway, those across Canadian Highway 1 had the smallest genetic distances yet Highway 1 has the highest traffic volume (Table 3.3, Fig. 3.2). This was measured in two systems, one in the Rocky Mountains and the other in the Selkirk Mountains. Generally, as genetic distance increased, movement rates decreased. Total male and female movement was associated with genetic distance (D_{LR}) in a univariate linear regression ($p = 0.005$, $R^2 = 0.32$). When the genetic distance exceeded 4.0, there was no evidence of individual animal movement.

The two population assignment methods had 85% consistency in selecting migrants. Of those 40 DNA-captured individuals with a cross assignment log ratio greater than 2.0, the cluster-based test (STRUCTURE) selected 34 of the same individuals. Additionally, the STRUCTURE algorithm detected two individuals as migrants that had a cross-assignment ratio less than 2.0. Forty-five percent (18 of 40) of the DNA-based migrants had a putative parent-offspring relationship in their source population.

Regression

In the regression that explored male and female movement rates together, six models had ΔAICc scores less than 2.0 (Table 3.4) and therefore should be considered plausible models (Burnham and Anderson 1998). All six models contained human-caused mortality, five of six contained human settlement patterns and geographic distance and three contained traffic as significant variables. All four variables are contained in two models. All four variables appear to be associated with fragmentation of grizzly bears in my study area. A similar pattern was evident for the male movement models with five models having ΔAICc scores less than 2.0 (Table 3.4) suggesting similar model viability

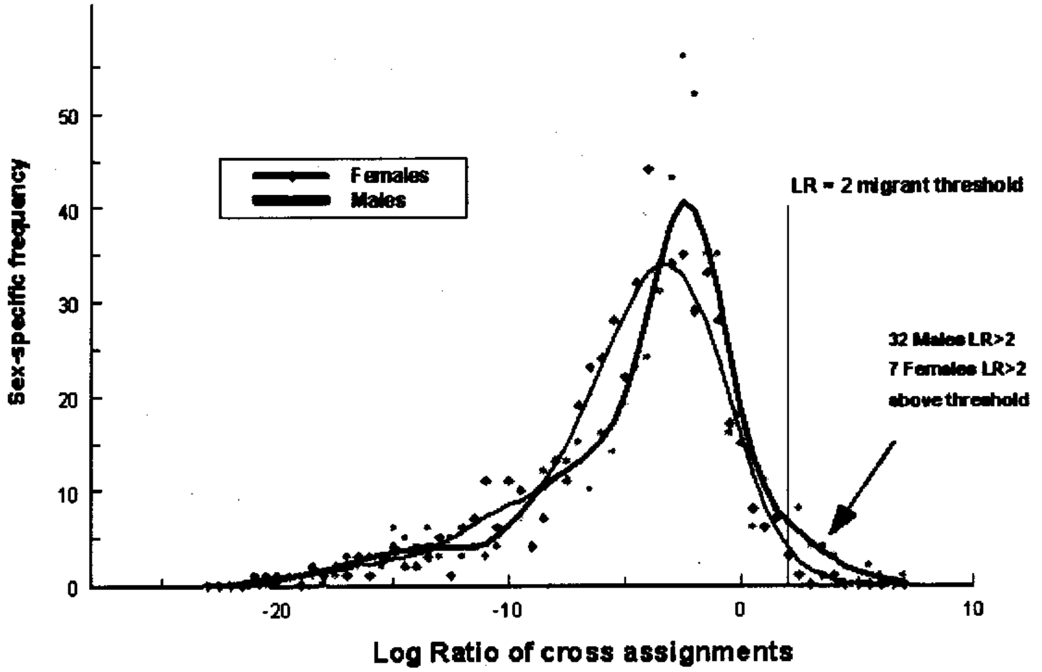
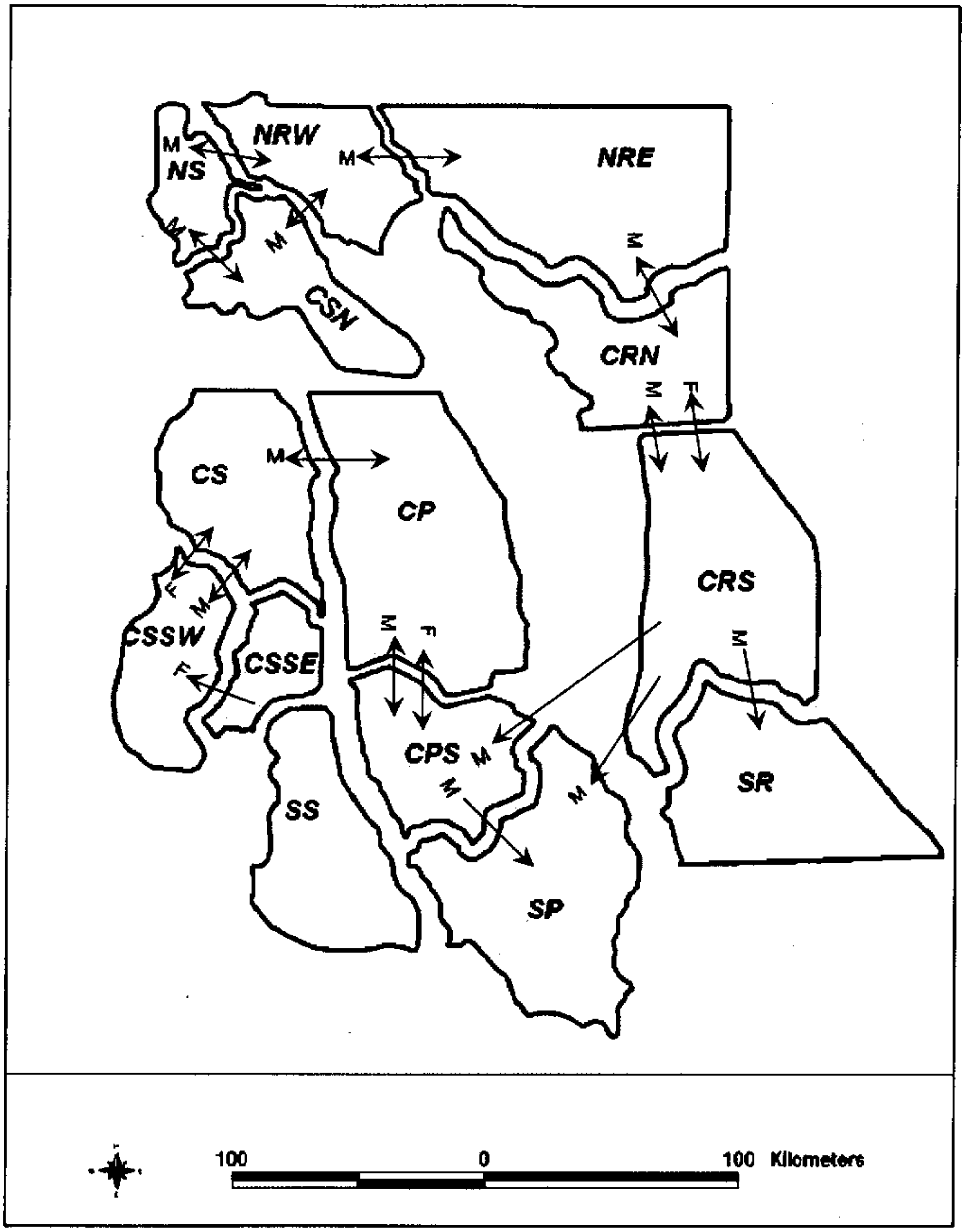


Figure 3.3. Distribution curves for male and female grizzly bear cross-assignments between adjacent local populations in SW Canada and NW U.S.A. Note divergence of male and female curves at LR = 2.0, putative migrant threshold.



3.4. Summary map of sex-specific movement rates of grizzly bears between arbitrary local populations in SW Canada and NW U.S.A. See Table 3.1 for population names and specific movement rates. See Figure 3.2 for map details. Arrows ←-→ indicate genetic evidence for sex-specific movement, M is male and F is female. The absence of a arrow indicates no movement detected. Only immediately adjacent local population pairs were compared. See Table 3.1 and Figure 3.2 for population name codes.

implicating all four variables. Comparing the models exploring female movement, the one containing geographic distance, human-caused mortality, and traffic was the only one with a ΔAICc less than 2.0 suggesting that besides geographic distance and morality, traffic may be more influential than human settlement patterns for female movement Table 3.4). The most parsimonious model variables, p values, and R^2 values are shown in Table 3.5. Models that were built solely on genetic data (no telemetry migrants) yielded similar results, although the relationships were weaker (Table 3.5).

DISCUSSION

My results demonstrate that inter-population movement by female and male grizzly bears correlates negatively with human disturbance. The difference in movement rates between males and females between geographic areas with more human disturbance may be related to the fact that grizzly bears display male-biased dispersal (McLellan and Hovey 2001a). That is, the inhibitory effect of human disturbance may operate equally on males and females but because females naturally move less, it may be easier for them to be fragmented. Female grizzly bears disperse and move across valley bottoms in the absence of human disturbance, as approximately 70% of all detected female inter-population movements were through relatively undisturbed areas, with almost no traffic or human settlement. This is supported by several radiotelemetry studies in my study area. Female grizzly bears have home ranges spanning large undisturbed river valleys, while little movement is reported across the high traffic-volume Highway 1 corridor (Gibeau 2000, J. Woods pers. comm. West Slopes Bear Project). Also, female bears

Table 3.4. AICc (Akaike Information Criteria adjusted for small sample sizes) scores for multiple linear regression models examining sex-specific grizzly bear movement rates and geographic distance (*geo*), traffic, human settlement (*settle*) patterns and human-caused mortality (*mort*). Column headings: residual sum of squares (*RSS*), number of population pairs in regression (*N*), number of model parameters + 2 (*K*), small sample adjusted Akaike Information Criteria (*AICc*), difference in AICc scores of each model relative to the "best" model (*ΔAICc*). An * indicates an interaction term.

a. Models for male and female movement rates

Model	RSS	N	K	AICc	ΔAICc
geo traffic mort	0.02919	23	5	-139.87	0.000
geo settle mort	0.02981	23	5	-139.38	0.483
geo traffic mort settle*mort	0.02547	23	6	-139.28	0.585
geo settle mort settle*mort	0.02602	23	6	-138.79	1.076
settle mort	0.03576	23	4	-138.51	1.362
geo settle mort traffic*mort	0.02647	23	6	-138.40	1.471
geo settle traffic mort	0.02870	23	6	-136.54	3.331
geo settle traffic	0.03693	23	5	-134.46	5.410

b. Models for male movement rates

Model	RSS	N	K	AICc	ΔAICc
geo settle mort	0.03577	23	5	-135.19	0.000
settle mort	0.04140	23	4	-135.14	0.055
geo settle mort settle*mort	0.03127	23	6	-134.56	0.628
geo traffic mort	0.03691	23	5	-134.47	0.722
geo traffic mort settle*mort	0.03162	23	6	-134.31	0.884
geo settle mort traffic*mort	0.03364	23	6	-132.88	2.309
geo settle traffic mort	0.03585	23	6	-131.42	3.772
geo settle traffic	0.04973	23	5	-127.61	7.578

c. Models for female movement rates

Model	RSS	N	K	AICc	ΔAICc
geo traffic mort	0.02826	23	5	-140.61	0.000
geo traffic mort settle*mort	0.02674	23	6	-138.16	2.449
settle mort	0.03633	23	4	-138.14	2.470
geo settle mort	0.03154	23	5	-138.09	2.526
geo settle traffic	0.03179	23	5	-137.90	2.707
geo settle mort traffic*mort	0.02789	23	6	-137.19	3.417
geo settle mort settle*mort	0.02861	23	6	-136.61	4.004
geo settle traffic mort	0.02872	23	6	-136.52	4.092

Table 3.5. Summary of the significance of model variables in multiple linear regressions. The models describe both sexes (*MF*), male only (*M*), and female only (*F*) inter-population grizzly bear movement rates as functions of geographic distance, and three human disturbance variables: traffic, mortality and settlement. Two regressions for movement of both sexes (*MF*) are shown because both models had very close AICc scores (ΔAICc = 0.4) demonstrating that both traffic and settlement variables influence movement rates. Models in Table (a) include two population pairs using radio telemetry data (see text). Table (b) models have those telemetry systems omitted.

a.

Model	**P values**					**R^2**	**F**
	geo	**mort**	**settle**	**traffic**	**model**		
MF = geo traffic mort	0.0010	0.0007		0.0067	0.0007	0.585	$F_{3,19}$ = 8.91
MF = geo settle mort	0.0055	0.0048	0.0103		0.0010	0.567	$F_{3,19}$ = 8.29
M = geo settle mort	0.0120	0.0004	0.0146		0.0005	0.598	$F_{3,19}$ = 9.14
F = geo traffic mort	0.000	0.018		0.003	0.001	0.565	$F_{3,19}$ = 8.24

b.

Model	**P values**					**R^2**	**F**
	geo	**mort**	**settle**	**traffic**	**model**		
MF = geo mort settle	0.1204	0.0299	0.0504		0.0595	0.346	$F_{3,17}$ = 3.00
M = mort settle		0.004	0.121		0.009	0.408	$F_{2,18}$ = 6.21
F = geo traffic	0.1025			0.0304	0.031	0.320	$F_{2,18}$ = 4.24

move and disperse across the large unsettled Flathead Valley (McLellan and Hovey 2001b).

Are female bears avoiding human dominated environments or are they having trouble surviving as they attempt to move through them? There is evidence that both forces are operating. Grizzly bears avoid areas of high human influence (Mattson et al. 1987) and males and females avoid use of habitat around busy highways, even in areas where human settlement is low (McLellan and Shackleton 1988; Munro 1999). Three radiotelemetry studies found minimal female movement across busy highways in remote unsettled areas in my study area (Canada Highway 1 in the Banff NP area, Gibeau 2000, and Selkirk Mountains, J. Woods pers. comm., B.C. Highway 3 in the southern Selkirk Mountains, W. Wakkinen, pers. comm.) supporting the hypothesis that avoidance plays a role in fragmentation. Indeed, my regression results suggest traffic volume may be more inhibitive to females than males.

The lack of female grizzly bear movement is also associated with mortality. The mechanism for bear mortality in the boundary areas can be partially explained by the dispersal process of grizzly bears. Natal dispersal of male and female grizzly bears in the southern Rocky Mountains is a gradual process, requiring several years with resulting newly established home ranges often overlapping or adjacent to the maternal home range (McLellan and Hovey 2001a). During this gradual dispersal process, successful dispersal is diminished as bears spend extended periods in proximity to human dominated landscapes. Grizzly bears are attracted to human food sources and killed as a result of a perceived threat to human safety and property (Mace and Waller 1998; McLellan et al. 1999). For instance, in the southern Rocky Mountains, 60 grizzly bears were removed from the ecosystem, being translocated or killed by wildlife managers, between 1990 and 2000 near Highway 3, a major transportation and settlement corridor (B.C. Ministry of Air Water and Lands files).

As the human environment interrupts the dispersal process for female grizzly bears, population dynamic processes will be affected on several levels. My data provide evidence that diminishing demographic connectivity is turning the likely historically inter-connected regional grizzly bear population into a human-induced (fragmented) metapopulation at the southern extent of their North American distribution, as has been anecdotally hypothesized by several authors (Craighead and Vyse 1996; McLellan 1998). The potential for the region to operate as a "metapopulation" is dependent on the demographic connectivity (male and female movement) between the local population components. Female inter-population movements are required to facilitate population augmentation, rescue, or recolonization. Diminished female movement decreases the viability of several of the smaller population sub-units in my study area. The paucity of female movement leaves female-isolated sub-units with only two parameters of the population dynamic equation, births and deaths, to remain functionally self-sustaining. Smaller populations will experience increased chances for local extirpations over the long-term (Gilpin 1987; Lande 1988; Caughley 1994).

In species with sex-biased dispersal, as is the case for most mammals (Greenwood 1980; Pusey 1987), one gender may mediate a large portion of the genetic connectivity. In grizzly bears, male movements may mediate nuclear-based genetic connectivity and heavily influence genetic distances. This appears to be the case in my study area. Average expected heterozygosties were consistent throughout most of the study area, suggesting that genetic connectivity has been maintained primarily through male inter-population movements. However, male connectivity can be fractured. The southern Selkirk population appears totally isolated, demographically and genetically (Chapter 2 and 3) corroborated by a 20% lower average expected heterozygosity and extremely high genetic distance. Less obvious, is the case of the Central Selkirk Southeast (CSSE) area just to the north of B.C. Highway 3A. I detected no male and only one female movement in or out of this area, suggesting that inter-population movements are limited. While the genetic distances between the CSSE and neighboring areas are elevated relative to most other systems in my study, heterozygosity values are not depressed. Exacerbating the high genetic distance measures is also the relatively small sample size for this population. This is not a consequence of less sampling effort or a lower ratio of sampled individuals to true population size (see below), but likely reflects a truly smaller population, bounded by human environments on three sides. Simulation work (Paetkau et al. unpub. data) suggests that in small populations one should expect a positive bias in migrant detection above the expected Type I error rate. That is, one tends to report more migrants than there may really be. In my case, this translates to the fact that there may be less migration than I report in the three systems with less than 50 individuals.

While I have no historical data concerning bear movements in my study area, the contrast between systems at the extremes of human influence suggests that historical movement rates were higher than I found, and that the human environment has played a role in inhibiting that movement. In today's human-dominated environments, grizzly bears are often relegated to remote mountain habitats (McLellan 1998) when human activity dominates the valleys. In relatively undisturbed valleys, without human settlement or a major highway, bears use and cross major valley bottoms throughout the spring and summer if food resources are present (McLellan and Hovey 2001b).

It is enlightening to examine the nature of many of the fractured habitats and the habitat changes that have occurred within some boundary areas. The width of all the fracture zones I tested is between 0.5 and 12 km. Often the human environment is less than a kilometer wide. For the grizzly bear, a large wide-ranging carnivore, these distances are often less than their average daily movement distances (2.4 km linear daily movement in Flathead; B. McLellan unpub. data). In many parts of my study area, habitat changes leading to reductions in the availability of food resources have accompanied human settlement. Extensive hydroelectric development (dam building) on the Columbia River has eliminated the historic oceanic salmon runs that reached many inland systems in my study area. This reduction in high quality food resources has likely influenced the seasonal movement and distribution patterns of bears, potentially resulting in a reduction of valley bottom use and population interchange. An example of the cumulative effect of habitat changes and human settlement patterns occurs in the west arm of Kootenay Lake paralleling Hwy 3A (the area mediating the isolation of the southern Selkirks) which has historically had a landlocked salmon (*Onchorynchus nerki*) spawning run in many of the lake's tributaries. This seasonally abundant high quality bear food has been reduced to a few protected spawning channels as a result of human influence (Ashley et al. 1997). Furthermore, the valley's riparian habitat has been usurped for human use, adding to the reduction in bear food from the loss of early seral habitats (fire-mediated berry patches) due to fire suppression to protect human settlements. Historically, this narrow valley had abundant resources to attract bears to the valley bottom.

Connectivity is an important parameter in population viability analyses of threatened and endangered species and enhances the probability of persistence of a population from genetic and demographic perspectives (Gilpin 1987; Hanski and Gilpin 1997; Frankham et al. 2002). My results suggest that how you measure connectivity is important. Had I measured it strictly using measures of genetic differentiation (F_{ST} and Nm) or genetic distance as a surrogate for relative amounts of geneflow, I would have missed a major factor affecting grizzly bear ecology and conservation - the almost complete lack of female movement (i.e., demographic connectivity) across the settled and busy highway corridors. These methods demonstrate the ability and value of genetic data to provide insight into the gender-specific demographic processes of immigration and emigration in recently disturbed systems, traditionally an intractable yet increasingly important ecological question worldwide.

It is also important to note that when looking for individual migrants using population assignment tests, results will always yield a "most likely" population of origin. However, if the true population of origin is not within the study area, then some assignments may not really point to the true population. To guard against this potential bias, my study area encompassed almost the entire area of occupied grizzly bear habitat in the southern reaches of the greater Rocky Mountain habitat peninsula in southern Canada. Furthermore, within my sampling area I sampled immediately adjacent geographic areas looking for inter-population movements well within the dispersal distances for my study species.

The power to detect inter-population movements is positively correlated to the degree of genetic structure between populations. Therefore, many of the movement estimates reported in this study should be considered conservative. To consider what effect lowering the migrant threshold of the frequency-based assignment test would have on my conclusions, I looked at additional putative migrants identified when the threshold was lowered to LR = 1.5. Eight males were found to cross-assign with a LR > 1.5 in five population pairs as were 7 females in five populations pairs. Eleven of these 15 additional putative migrants were in systems that already had detected migrants of each sex. Three females were cross-assigned across Highway 1 in the Selkirk Mountains as was 1 female in the southern Rocky Mountains across Highway 3. Considering these putative migrants as a result of lowering my threshold, there is minimal change in my ecological conclusions.

Determination of individual migrants based on genetic data is relatively new. In recently disturbed systems it is particularly challenging, as genetic signals lag behind fragmentation events. Also, the theoretical literature is just developing; all published methods for detecting migrants have only appeared in recent years. Therefore, I feel it was prudent to base my results on a combination of methodologies. In this work I used the frequency-based assignment (Paetkau et al. 1995) to assign putative migrants and the cluster-based method (Pritchard et al. 2000) to corroborate my results. The methods yielded similar results. The strengths of my ecological conclusions are bolstered by the fact that even though there was some disagreement between assignment techniques in selecting individual migrants, the ecological implications did not change - female migration is limited in human-dominated systems, while males are still moving between populations. The differences in "migrants" between the two assignment methods resulted in only 1-2 individuals for 10 of the 23 local population pairs. One limitation of the

STRUCTURE method (Pritchard et al. 2000) is that to build a Bayesian posterior probability of being a migrant, prior information on inter-population migration rates is required. This parameter may be difficult to estimate.

My regression is based on Information-Theoretic (IT) methods that rely on a quantitative approach comparing several hypotheses represented by different models, rather than testing a hypothesis against an often simplistic null hypothesis based on an arbitrary threshold of acceptance (p value). Rather than reaching a discrete conclusion about one hypothesis being "probable" or not, several hypotheses are compared and therefore several models may be relatively equally supported by the data (Burnham and Anderson 1998; Anderson and Burnham 2002). While it appears that geographic distance, human-caused mortality, settlement patterns, and traffic volume influence bear movements, there may be several explanations as to why the two best models (one with geo-mort-settle and the other with geo-mort-traffic, Table 3.4) do not perform better when in a global model containing all four variables. First, is that the settlement and traffic variables may be correlated; this is not the case, however, as all variables were not correlated, according to Spearman's rank correlation test. Second, and more plausible, is that the model's ranked third and forth are identical to the top two models with the addition of the interaction term of mortality and settlement, supplying more support for this interaction than when these variables are considered alone within the global model. Sample size limitations likely constrain the plausibility of a model with too many variables. In a post-analysis exploratory exercise, the model with all four solo variables and the interaction term, mortality x settlement, yields a regression with an R^2 of 0.72 and all variables with p values < 0.05, but has a ΔAIC score of 6.1. This exercise yields two insights. First, it demonstrates the effect of the Information-Theoretic analysis trade-off between the number of variables and improved model fit. Second, this model is likely over-parameterized in relation to the number of data points building the model. In essence, the small sample size in the regression limits the complexity of a model's ability to score well with the AICc system. However, the fact that several models all have ΔAICc scores under 2.0 including a combination of all four variables, suggests that all variables play a role in fragmentation of grizzly bears in my study area.

In some of the population pairs, genetic distances and F_{ST} values were low, and in a few cases essentially zero. In these instances I had little power to detect inter-population movements. However, in the areas where this was the case, I had access to radiotelemetry data that measured movements across the boundaries. Although genetics and radiotelemetry do not necessarily measure the same movements, there is justification for combining information from both techniques. My goal was to measure bear movements across various "boundary areas" separating two geographic areas. Some of these movements were related to dispersal events and others were movements within a home range that spanned the boundary. In practice, however, there may not be much difference. McLellan and Hovey (2001a), working in one of my control areas for over 20 years, determined that dispersal is a gradual process, taking several years. In the context of my study, a bear dispersing across the boundary areas could appear for a time as having a home range that spans the boundary area.

As with radiotelemetry, DNA techniques detect bears living on each side of the boundaries, although likely with less efficiency, and detects bears that move across the boundary and set up a home range (more likely captured with DNA methods). Some of these detections will be a bear that has completely moved across and some will be bears in the process of moving. The main difference in the two techniques is that assignment methods allow detection of events that have occurred over a longer time span, whereas radiotelemetry may detect more movements over a shorter time period. In essence, to not use the combined genetic and radiotelemetry data would bias my estimates of movement rates because of the reduced power to detect movements in areas that are not fractured (i.e. are genetically similar). Using the two additional systems (population pairs) where I only had telemetry data allowed me to improve my analytical power by increasing the sample size for the regression analysis and include systems where there was little human disturbance. The patterns in the ecological conclusions did not change substantially just the clarity of the result.

Other factors that likely influence bear movements and fragmentation were not included in this analysis but include: natural barriers, habitat quality, habitat changes, habitat saturation (density vs. carrying capacity), and social forces within bear communities. There is evidence that dispersal in bears (Swenson et al. 1998; McLellan and Hovey 2001a) and mammals in general (McPeet and Holt 1992; Doncaster et al. 1997), is density dependent yet this variable is too complex for me to measure over the scale of my study area.

I found that peripheral mortality is contributing to the insularity of local populations. This process may be part of a larger continuum. Mortality at the periphery of insular protected areas plays a dominant role in local extinction events within reserves (Woodroffe and Ginsberg 1998; Parks and Harcourt 2002). Large home ranges were the most significant factor in this phenomenon, as large vagile mammals move into human landscapes and suffer high mortality rates. I hypothesize that if peripheral mortality contributes to the fragmentation of populations, then a continuation of excessive human-caused peripheral mortality may operate on the sub-units increasing the risk of local extirpation. This process was likely the mechanism for continental range contraction of grizzly bears over the past century (Woodroffe and Ginsberg 1998; Mattson and Merrill 2002). Human motives behind grizzly bear mortality have shifted from that of minimizing a competitive pest in the century prior to 1970 (Mattson and Merrill 2002), to more tolerance with managed mortality. The future of grizzly bears at the southern edge of their present North American distribution may depend on the ability to effectively manage mortality.

My results suggest that the cost of dispersal may be elevated for grizzly bears in my study area due to human influences. While my regression analysis suggests that mortality certainly influences successful dispersal, my data do not satisfactorily distinguish how mortality affects dispersal of bears. Does mortality remove potential dispersers, or open previously filled habitat in nearby areas removing the incentive to disperse? The hypothesis that mortality may increase dispersal by opening up distant niches is not supported by my results.

My evidence suggests that grizzly bears are susceptible to population fragmentation at a fine scale of distances less than 10 kilometers. My results contrast with those of Paetkau et al. (1997), who found genetic structure of grizzly bears in northern North America fits an isolation-by-distance model. The genetic distance I found across Highway 3 in the Rocky Mountains, for instance, is equivalent to an 800 km separation in undisturbed northern Canadian populations. It should be noted that habitat is much less complex and grizzly bear home ranges are larger in many areas of northern North America (see review in LeFranc et al. 1987).

It is interesting to view genetic distance with a specific biological interpretation. Is there a measurable link between genetic distance and level of migration between two populations? I found that there may be a threshold genetic distance above which there is no movement. When D_{LR} was 3.5 – 4.0 or higher, inter-population movement no longer was detected. Paetkau et al. (1999) found that above a D_{LR} value of 3.5 there was no inter-population movement in polar bears (*Ursus maritimus*), as measured with radiotelemetry. Paetkau et al. (1999) used the same microsatellite loci used in this study and their system was likely at equilibrium between the forces driving genetic differentiation. This contrasts with systems in this study which are most likely not in equilibrium. In other words, as inter-population movement decreases through time, genetic distance will continue to increase. This relationship reduces my ability to determine an exact genetic distance threshold for predicting inter-population migration.

The lower genetic distances I found across Highway 1 may be confounded by the larger population sizes involved. Genetic differentiation is driven by several factors, including natural selection, mutation, migration, and genetic drift (Hartl and Clark 1997). The differentiation signal (genetic distance) I report is most likely driven by genetic drift and as such, is heavily influenced by effective population size, migration rates, and time since disturbance. Small populations drift faster, driving up genetic distances (Hartl and Clark 1997). In recently disturbed systems with large populations, the genetic distance signal will lag behind the disturbance. Effective population sizes north and south of Highway 1 are likely larger than in many of the smaller local population units in the southern Purcell and Selkirk ranges, and genetic distances are likely changing relative to my "snapshot" measurement. While I found a significant inverse relationship between total inter-population movements and genetic distance, measures of genetic differentiation are not perfect measures of recently fragmented systems, and individual movements provide better resolution (Neigel 2002).

What life history characteristics underpin fragmentation susceptibility? My results suggest that grizzly bears are easy to fragment because they have gradual sex-biased dispersal, are vagile with large home ranges, reproduce slowly, compete with humans, threaten human safety, and are exploited by humans. Several of these characteristics suggest that other large mammals, particularly carnivores, may have a similar fragmentation susceptibility to that of grizzly bears. However, it is difficult to compare and therefore extrapolate my results to other carnivore fragmentation studies because they did not use similar individual-based analysis techniques. For example, wolverines (*Gulo gulo*) were found to have increased population structure at the southern periphery of their North American distribution (Kyle and Strobeck 2002) using circumstantial evidence from populations beyond the individual dispersal distances. Lynx (*Lynx canadensis*) populations in western North America were found to have little genetic structure using an F_{ST} /Nm based analysis and may therefore not have measured recent fragmentation (Schwartz et al. 2002). At a finer scale, Campbell (2002) found genetic structure in lynx across a major highway in Alberta, Canada, suggesting that human disturbance may be influencing connectivity.

I do not know to what extent the remaining components of the Canadian mountain ecosystem are being fragmented by human influence. Other large mammals, such as mountain caribou (*Rangifer tarandus caribou)* have had their southern distribution severely fragmented, resulting in several highly threatened, small isolated populations (Hatter 2002). I recommend that further regional-scale fragmentation studies be done on a suite of species in an effort to discover whether other species are being affected and ecosystem-level fragmentation is occurring.

The future of fragmentation in my study area may be dependent on the behaviour and abundance of the human population. Growth is predicted in the southern interior of British Columbia and Alberta (B.C. Statistics) and if settlement follows past patterns, linear human development in valley bottoms will continue. Connectivity management should include strategies to leave human transportation and settlement corridors porous, that is, resist "continuous human settlement". Fortunately, most of the human corridors in my study area are not continuously settled and the possibility exists to limit development in strategic linkage areas through local zoning or land acquisition. Increased education regarding co-existence with bears (i.e. bear attractant management) should occur in human-settled linkage zones. Increased traffic volumes are predicted to accompany the increases in the human population (B.C. Ministry of Transportation) continuing past trends. For instance, the Trans-Canada Highway 1 traffic has grown an average of 1-2% since it's construction 40 years ago (B.C. Ministry of Transportation). Wildlife crossing structures may be necessary to overcome a bear's inhibitions to heavy traffic volumes (Munro 1999; Gibeau 2000).

One variable implicated in fragmentation of bear populations that has some potential for mitigative management is human-caused mortality. I hypothesize that mortality's effect on fragmentation is twofold. First, human-caused mortality can be an immediate limit to dispersal by eliminating migrants. Dispersing bears are in unfamiliar terrain, move extensively, likely share movement corridors with hunters, or become attracted to human food sources, and thereby increase their chances of a lethal human encounter. Second, if grizzly bear dispersal is density dependent, as some evidence suggests for bears (Swenson et al. 1998; McLellan and Hovey 2001a) and other mammals (McPeet and Holt 1992; Doncaster et al. 1997), higher survival rates should increase bear densities and increase socially mediated "dispersal pressure". Many jurisdictions in southern Canada have a legal grizzly bear hunt. Reducing this harvest in areas where management of connectivity is warranted may decrease fragmentation. Reductions in human-caused mortality have resulted in the expansion of the Yellowstone Ecosystem grizzly bear (C. Servheen pers. comm.) and the Scandinavian bear (Swensen et al. 1998).

My work is based on relatively large sample sizes with the exception of three local populations. Many samples were collected during population surveys and in most of these areas I sampled greater than 50% of the estimated population in the local area. This relatively high ratio of sampled-to-total population is also the case for the three areas where are sample sizes are below 40 individuals. This does not represent a higher divergence in sampled versus total population, but the reality of a small population. This success is primarily due to the efficiency of non-invasive genetic sampling methods for bears (Woods et al. 1999). I believe that the methods used in my study are useful for investigating the effects of recent fragmentation at a demographic level, an important step forward in the use of genetic analysis as a tool in conservation biology.

CHAPTER 4 – DELINEATION OF POPULATION AND SUB-POPULATION BOUNDARIES

INTRODUCTION

While grouping organisms into populations is fundamental to organizing living systems, the process of delineation is not well defined or easily carried out. In some cases distinct population boundaries are obvious, such as oceanic islands (Grant 1987; Frankham 1998), in others, boundaries are unexpected and therefore cryptic (Buerkle 1999; Castella et al. 2000). In most cases however, population boundaries are not distinct and species distributions cannot be divided into discrete units. In many cases populations are distributed continuously such that no biological basis for population definitions exist, even though widely separated populations may be ecologically and genetically distinct. Adjacent populations often exchange migrants at some low level creating populations within a metapopulation (Ricklefs 1990; Hanski and Gilpin 1997).

In a matrix of populations, the permeability of boundaries reflects the ecological conditions under which they were created. Migration across boundaries varies spatially and temporally with relative migration resulting in differential boundary intensities (i.e. different inter-populations movement rates). A population should have varying boundary intensities on all sides to all adjacent neighbor populations and, because inter-population migration is a continuous variable, criteria used to define populations across the landscape becomes complicated. What level of migrant exchange results in groups of organisms being separate populations or sub-populations? Does gender-specific migration alter this threshold? The answer to these questions may vary with different species and ecological situations. For instance, in systems where high vagility of one gender homogenizes genetic variability between geographic areas, no evidence of a genetic boundary may be detectable. However, this lack of genetic evidence for separation could co-exist with little or no movement of one gender which could have important demographic consequences. In this chapter, I explored biological boundaries in grizzly bears within a regional system experiencing gender-biased anthropogenic fragmentation in southwestern Canada.

Detection of biological population boundaries is necessary for testing hypotheses about evolutionary processes (Ciofi et al. 2002), understanding historical biogeographical events (Small et al. 2003), identifying units relevant for conservation (Moritz 1994; Mortiz et al. 1995; Crandell et al. 2000), and assessing metapopulation structure and function (McCullough 1996; Hanski and Gilpin 1997). Ecological studies investigating abundance or vital rates could also benefit from knowing population boundaries (McLellan 1989b) particularly when managing a population's trend over time. Application of management strategies will differ depending on whether animals in adjacent areas constitute one population or two. Finally, understanding ecological systems at the landscape or regional scale requires an understanding of population units and their spatial limits (Barrett and Peles 1999).

Two common methods have been used to try to delineate population boundaries in mammals: radiotelemetry and population genetics. Extensive radiotelemetry work may detect population boundaries by the cumulative individual home range boundaries (Bethke et al. 1996; Taylor et al. 2001; McLoughlin et al. 2002). However, practical considerations may spatially limit results. Some long-term efforts have yielded useful multiple population data (Bethke et al. 1996; Taylor et al. 2001) but the effort required is extensive, often taking decades for large mammals and requires random or systematic capture throughout the entire area. Population genetic studies often appear to be analyzing multiple population data but most analytical tools require *a priori* assumptions of population units often based on clustered sampling locations or phenotypic-based clustering. Sample partitioning, determined by trial and error comparisons of suspected groupings, may yield clues to population boundaries through comparisons of various "hypothetical" boundaries (Goudet et al. 1994). However, recent development of several techniques to cluster groups with no *a priori* assumption of membership have been introduced (Pritchard et al. 2000; Dawson and Belkhir 2001; Vazquez-Dominguez et al. 2001; Gaggiotti et al. 2002; Schaefer and Wilson 2002; Corander et al. 2003). These techniques have been used in a wide range of contexts including investigation of historical phylogeographic relationships and delineation of hybridization zones between subspecies of American marten (*Martes americana*; Small et al. 2003), hybridization of introduced of wild boar (*Sus scrofa*; Vernesi et al. 2003), grey seal (*Halichoerus grypus*) colonization (Gaggiotti et al. 2002), population structure of crocodiles (*Crocodylus moreletti*; Dever et al. 2002), genetic divergence of island-based tortoises (*Geochelone elephantopus*; Coifi et al. 2002), and integration of domestic stocked trout (*Salmo trutta*) with wild populations (Hansen 2002).

Here I use a Bayesian model-based clustering technique to delineate groups of individuals that may be the basis for population (or sub-population) units in a conservation context (Pritchard et al. 2000). The method uses no *a priori* assumptions of population boundaries. Grizzly bears at the southern extent of their North American distribution are fragmented by the human ecological footprint at various levels depending on the intensity of human disturbance. In Chapter 3, I reported a difference in gender-specific fragmentation while looking at multiple potential fractures to grizzly bear movements. I left unresolved what structured population sub-units result from the documented fragmentation. In other words, are the grizzly bears in SW Canada and NW U.S.A. divided into biologically-based sub-population units? And if so, what are the "boundary intensities" for the adjacent pairs of population units? I used the Pritchard et al. (2000) algorithm on microsatellite genotypes of 813 grizzly bears sampled from approximately 100,000 km^2 in southwest Canada and northwest U.S.A. I combined the cluster analysis results with the gender-specific movement results from Chapter 3 in a synthesis resulting in biologically-based sub-populations relevant for management units.

Determining population or management units for grizzly bears in this region is useful for several reasons. First, grizzly bears in this region are where further range contraction will likely occur. Efforts to ensure future occupation of this territory would benefit from knowing population and sub-population units thereby allowing population-specific management strategies and monitoring. If some form of metapopulation structure exists, monitoring trends in abundance, distribution, and connectivity of any small and therefore vulnerable units will allow adaptive management as necessary.

METHODS

Refer to Chapter 3 for the details of field methods and microsatellite genotyping.

Cluster analysis

I used a model-based Bayesian clustering method to determine the clusters or "populations" of bears independent of their capture location (STRUCTURE, Pritchard et al. 2000). That is, the groupings were made with no *a priori* assumptions of spatially-derived group membership. Populations were determined by "best fit" of the data to one of several models each assuming a different number of populations. Within each run, a Monte Carlo Markov Chain (MCMC) algorithm iteratively calculates the group allele frequency and the likelihood of individual assignment to the groups. Individuals are moved among groups as group allele frequency and therefore individual population assignment changes with each iteration in the Markov chain. Ideally, the most likely group members and allele frequencies stabilize, reflecting groups of similar genotypes in Hardy Weinberg equilibrium. Ultimately, the probability of the genotypes given the population memberships and allele frequencies, $P\,(X \mid K)$, was used to estimate the number of populations based on the genotypes, $P\,(K \mid X)$, where X represents the individual genotypes and K represents the number of populations. I ran this algorithm using as series of values for K, in this case one through 20. I then calculated the Bayesian posterior probability for each of the values of K using the equation,

$$P\,(K_i \mid X) = P\,(X \mid K_i) / \sum_{i=1}^{\infty} P\,(X \mid K_i)$$

where i varies from one to infinity to include the total theoretical probability space. In practice however, K varies from one to the maximum number of population groupings tested as the probability becomes exceedingly small as K approaches infinity. Here the sum in the right hand denominator ranges from 1 to maximum 20. The most probable model, or the "best fit" number of population groups is the highest $P\,(Ki \mid X)$ value. The "burn in" period was 10,000 iterations (MCMC iterating but no data collected) and the number of repetitions where I collected data was 100,000. Because the Monte Carlo process begins from a random start position, I used the stabilized mean after 10 runs for each value of K (Rosenberg et al. 2001).

Sub-population delineation

My ultimate goal was to delineate biologically relevant population and sub-population units within my study area. Pritchard et al. (2000) suggests that the interpretation of STRUCTURE-based cluster analysis should be done cautiously, including other biological information when relevant and available. For instance, STRUCTURE may create two clusters from two sample sets separated by space that are genetically separate but fit the isolation-by-distance model. Therefore, they may or may not deserve separate sub-population status. Further, STRUCTURE has difficulty identifying a cluster that is represented by a low number of samples (Pritchard et al. 2000). More importantly, STRUCTURE does not have the ability to detect genetic structure as a result of differential geneflow between the sexes. Because grizzly bears in my study area are primarily regulated by demographic forces (e.g. human-caused mortality; McLellan et al. 1999), the absence of female connectivity is relevant from an ecological and conservation perspective. Therefore, to understand the complexity of population structure within my study area from a genetic and demographic perspective, I used a synthesis of the results from the genetic-based data presented in this chapter and the gender-specific movement results (Chapter 3). I used this synthesis to delineate spatially explicit biological sub-population boundaries within my study area. The first criterion for a sub-unit is that STRUCTURE recognized a cluster. The second criterion is whether or not I detected no movement, male movement only, or both sexes moving between clusters (Chapter 3). If I detected a cluster and no movement of either sex with adjacent units, then I called that cluster a separate population. If I detected a cluster with male movement only, I called it a female limited sub-population. If I detected both sexes moving, I combined the clusters into one sub-population if the combined group was in Hardy-Weinberg equilibrium.

The "intensity" or genetic distinctness of the original STRUCTURE-derived clusters and the resulting population sub-units was measured as follows. First, the strength of the clusters was determined by examining the proportion of individuals in each sampling area that were assigned to each of the clusters identified from the "best fit" model. Second I associated each cluster with a geographic area delineating the cluster boundaries using a fixed kernel home range algorithm (Animal Movement extension within ArcView, Geographic Information System software). I then calculated pairwise F_{ST} values (Wright 1965; Weir and Cockerham 1984) for sub-population units that result from the synthesis of cluster and gender-specific movement analyses described above.

RESULTS

I found that the number of clusters with the highest likelihoods were from 9 to13, with 12 clusters having low likelihood (Table 4.1). I show the set of 10 clusters (Fig. 4.1) which had the highest posterior probability, or likelihood, of 0.79 (Table 4.1). The Rocky, Purcell and Selkirk Mountain populations are rather discrete, particularly in the southern portion of the study area. Within the Selkirk Mountains, the southern Selkirk population south of B.C. Highway 3A is the most discrete, having no overlap with adjacent clusters of bears. To the north, the central Selkirks appear as one cluster with a few overlapping bears from the central Purcells to the east. Also the central Selkirk cluster has several members in the northern Selkirk Mountain cluster near Highway 1. The sampling hiatus between the central Selkirks and the northern Selkirk Mountain cluster merely reflects an area that was not sampled. At the north end of Kootenay Lake there is a some mixing of the Selkirk and Purcell clusters.

Within the Purcell Mountains, the area south of Highway 3 has no dominant genetic similarity to one cluster. However, this is likely an artifact of the low number of sampled bears in the area relative to the power of the STRUCTURE clustering algorithm. The central Purcell bears appear to be a cluster despite the sampling gap in the Purcell Wilderness Conservancy (PWC). There are several bears that cluster with the Rocky Mountain bears (see Discussion).

There are four overlapping clusters of bears in the Rocky Mountains south of Highway 1 (Fig.4.1). Southern-most are the bears south of Highway 3, which show a definite cluster, yet with considerable overlap with the bears to the north of the highway. The three clusters of bears between Highways 3 and 1 have the most overlap of anywhere in the study area. The northern-most cluster, just south of Highway 1, and the adjacent cluster to the south, appear to overlap across the continental divide that holds a large and relatively low mountain pass (Elk Pass). This cluster south of the continental divide also overlaps heavily with the cluster that is just north of Highway 3. To provide a sense of the strength of clustering assignments, I calculated the average assignment of all individuals within each sampling area to each of the 10 clusters from the "best fit" model (Table 4.2)

Interesting patterns of spatial structure emerge as one observes the patterns of subdivision sequentially starting with two predefined clusters (i.e. 2 clusters, 3 clusters

Table 4.1. Bayesian-derived log likelihoods and posterior probabilities of various models representing a different number of population clusters of grizzly bears in SW Canada and the NW U.S.A. K is the number of populations assumed in each model. P (X | K) is the estimated probability of the data given K number of populations. P (K | X) is the estimated posterior probability of the particular K number of populations.

K	Ln Pr(X | K)	Pr(K | X)
1	-37333	~0
2	-36635	~0
3	-36040	~0
4	-35517	~0
5	-35174	~0
6	-34879	~0
7	-34731	~0
8	-34603	~0
9	-34522	0.000005
10	-34510	0.79
11	-34512	0.107
12	-34566	~0
13	-34512	0.107
14	-34546	~0
15	-34850	~0
16	-35315	~0
17	-35151	~0
18	-35587	~0
19	-36486	~0
20	-36193	~0

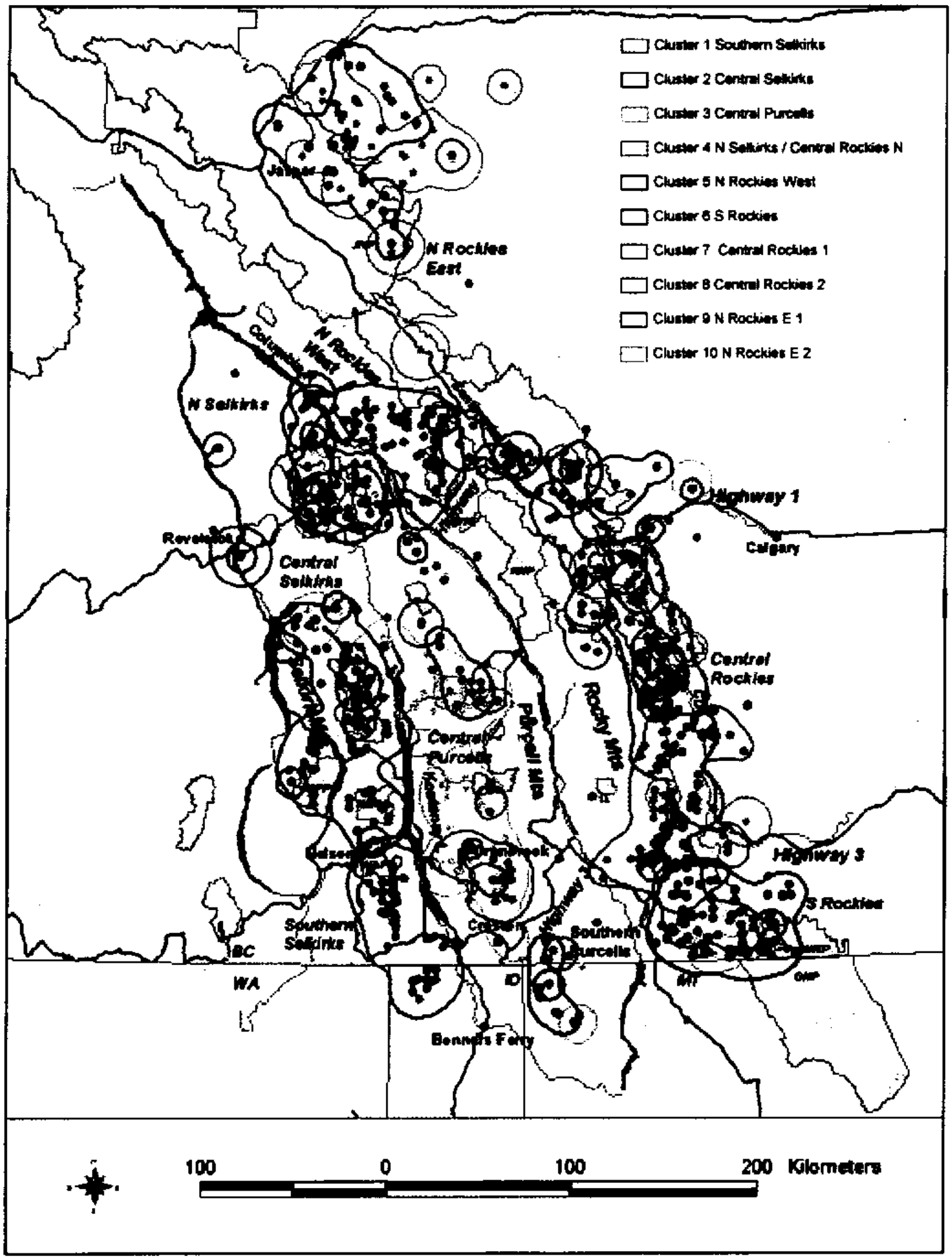


Figure 4.1. Putative population boundaries resulting from the STRUCTURE algorithm (Pritchard et al. 2000) with no *a priori* assumptions of group membership of grizzly bears in SW Canada and NW U.S.A. JNP, BNP, KNP, GNP, WNP are Jasper, Banff, Kootenay, Glacier, Waterton National Parks respectively. GRPP, KGPP, VPP, WAPP, are Goat Range, Kokanee Glacier, Valhalla, and West Arm Provincial Parks respectively. PWC is the Purcell Wilderness Conservancy. Roads are red bold. Colored dots are bear locations within similarly colored clusters.

Table 4.2. Average values of assignment to each of 10 clusters for all individual grizzly bears within each geographic sampling area as depicted in Fig. 3.2, Table 3.1 (NRE North is the northern portion of NRE in Fig. 4.2). The ten-cluster model (K = 10) was found to be the "best fit" to account for observed genotypes in a model-based cluster algorithm (STRUCTURE, Pritchard et al. 2000). Bold values are the higher proportion of assignments for each sampling area.

	Cluster									
Area	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
CP	0.042	0.172	0.019	0.016	**0.435**	0.029	0.059	0.032	0.019	0.177
CPS	0.026	**0.266**	0.022	0.015	**0.502**	0.028	0.041	0.054	0.017	0.028
CRN	**0.377**	0.143	0.051	0.018	0.029	0.016	0.066	**0.256**	0.011	0.033
CRS	0.057	**0.332**	0.034	0.023	0.040	0.053	0.054	**0.374**	0.011	0.023
CS	0.076	0.036	0.021	0.043	0.131	0.029	0.068	0.024	0.018	**0.554**
CSN	0.187	0.060	0.035	0.026	0.075	0.046	0.214	0.046	0.047	**0.263**
CSSE	0.021	0.025	0.018	0.051	0.018	0.014	0.017	0.016	0.020	**0.800**
CSSW	0.010	0.012	0.034	0.053	0.060	0.010	0.011	0.008	0.011	**0.790**
NRE	0.186	0.064	0.082	0.056	0.058	0.025	**0.302**	0.177	0.022	0.028
NRE North	0.033	0.025	**0.387**	**0.346**	0.019	0.035	0.045	0.044	0.010	0.055
NRW	0.059	0.023	0.044	0.024	0.036	0.039	**0.648**	0.074	0.013	0.039
NS	0.143	0.050	0.024	0.038	0.075	0.026	**0.501**	0.101	0.013	0.027
SP	0.040	**0.324**	0.027	0.024	0.184	**0.273**	0.036	0.060	0.010	0.022
SR	0.074	0.145	0.030	0.028	0.036	**0.550**	0.033	0.053	0.031	0.019
SS	0.009	0.010	0.007	0.005	0.010	0.006	0.012	0.009	**0.922**	0.008

etc., Pritchard et al. 2000; Rosenberg et al. 2002). For example, assuming two populations (K = 2), the southern Rocky and Purcell Mountains separate from the Selkirk Mountains and central Purcells. At K = 3, the same cluster pattern is apparent except that the Rocky Mountains show the beginnings of structure across the Continental Divide (Elk Pass). At K = 4, the southern Selkirk Mountains separate into a discrete cluster. The splits that appeared when K was set to 9 and 10 occurred in the northern Rocky Mountains (NRE North within Table 4.2, Fig 4.1).

Population boundary synthesis

My population and sub-population boundaries (Fig 4.2) result from the synthesis of the STRUCTURE-based clustering (Fig 4.1) and sex-specific movement rates from Chapter 3. In the Selkirk Mountains, I found the discrete southern Selkirk cluster to warrant separate population status supported by the lack of male or female movement with adjacent areas as shown by the sex-specific analysis. The separate clusters in the Selkirk and Purcell Mountains suggest sub-population status as I also found no evidence of female, and limited evidence of male movement between them. The Central Selkirk cluster overlaps the Glacier National Park (GNP) cluster at the north end of the Central Selkirks (Fig. 4.1) despite the area between the two clusters that was not sampled. There is, however, some ambiguity in interpreting sub-population status where the Purcell Mountains end just south of Highway 1. At the north end of the Purcell cluster there is some overlap with the Central Selkirk cluster. While GNP bears south of Highway 1 appear connected to the Central Selkirk cluster (even across the area not sampled), the amount of connectivity between the GNP and the Central Purcell bears is not clear. I classified the Central Selkirk Southeast (CSSE) area as a sub-population; while three sides of the area were found to have no inter-population movement from either sex, the fourth side had evidence of one emigrating female and no male movement.

There is overlap in the clusters across the Columbia River in the Highway 1 area of the Columbia Mountains (N. Rockies West and N. Selkirks, Fig 4.1). However, I found no evidence of female and limited male movement and this is corroborated with telemetry data (J. Woods pers. comm.), suggesting sub-population status between these areas. North of this area I did no genetic sampling within B.C. Bears west of the Columbia River across Highway 1 in the Glacier National Park area clustered together with some overlapping across the Columbia River and with the central Selkirk cluster. I found no genetic evidence of female movement across Highway 1 and radio telemetry work found limited female movement across the highway.

In the Rocky Mountains south of Highway 1, the set of 3 overlapping clusters was grouped into two sub-populations. I grouped the two clusters north of Highway 3 into a single sub-population due to the extensive spatial overlap of the clusters (Central Rockies 1 and 2, Fig. 4.1 and 4.2), the sex-specific analysis showed male and female movement across the continental divide and the resulting grouped sub-population did not deviate significantly from Hardy-Weinberg equilibrium. I found evidence of one female putative migrant across the continental divide, an individual that was also identified through radio telemetry (M. Gibeau unpub. data). I also found evidence of four male putative migrants not identified through telemetry work. Radio telemetry also identified two females with home ranges that spanned the divide in an area where I did no genetic sampling. The cluster south of Highway 3 (S. Rockies, Fig. 4.1) was given sub-population status based

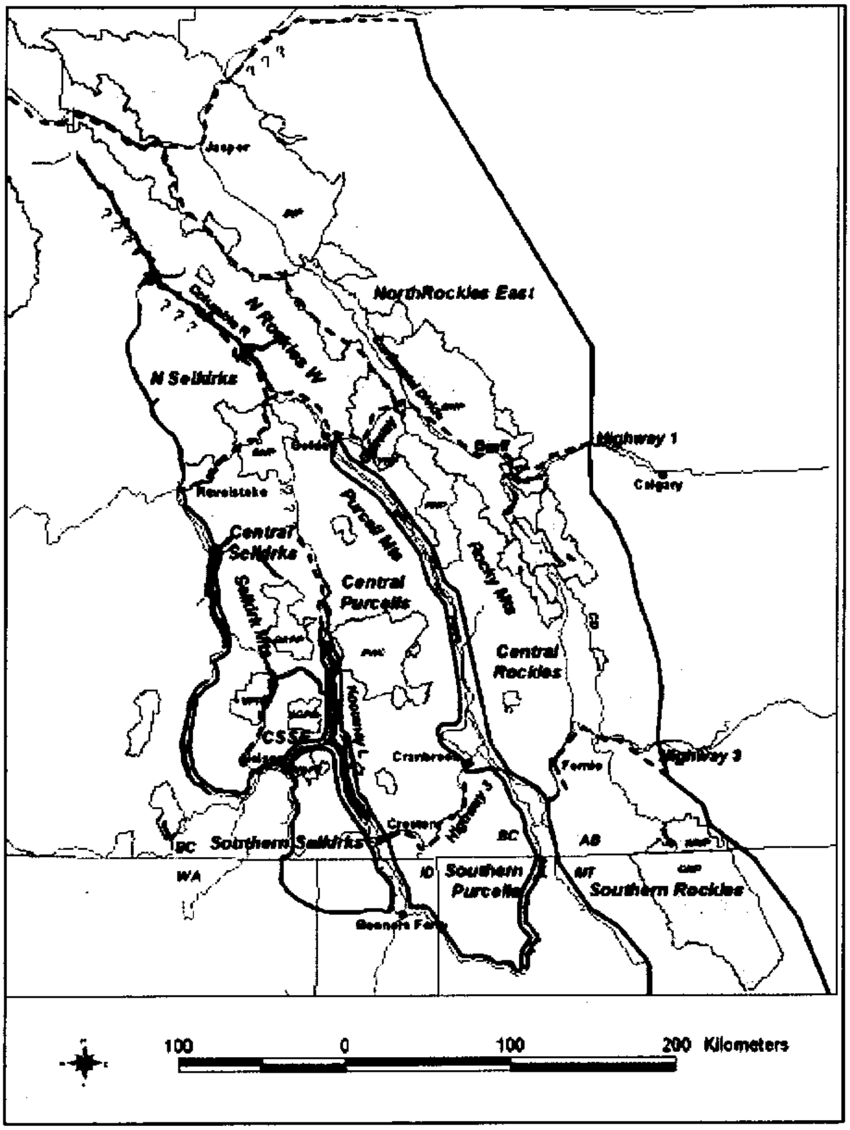


Figure 4.2. Grizzly bear population and sub-population boundaries derived from a synthesis of the STRUCTURE clustering algorithm and sex-specific movement rates (Chapter 3) in SW Canada and NW U.S.A. Internal solid lines represent barriers to male and female bear movement. Dotted lines represent limited female movement. Exterior solid lines represent study area boundary. JNP, BNP, KNP, GNP, WNP are Jasper, Banff, Kootenay, Glacier, Waterton National Parks respectively. GRPP, KGPP, VPP, WAPP, are Goat Range, Kokanee Glacier, Valhalla, and West Arm Provincial Parks respectively. PWC is the Purcell Wilderness Conservancy. CD is Continental Divide.

on the clustering and the fact that I found no evidence of female movement across the highway. I grouped clusters north of Highway 1 and east of the continental divide in the Rocky Mountains (N. Rockies East, Fig. 4.1) into one sub-population because the clusters are separated by a significant un-sampled area and likely represent isolation-by-distance. There is no particular natural or anthropogenic fracture between the clusters, and this may be a common result of the STRUCTURE algorithm (Pritchard et al. 2000). The genetic distinctness of the sub-populations is characterized by the F_{ST} values between adjacent sub-population pairs (Table 4.3).

DISCUSSION

Evolutionary biologist, D. Futuyma (1986) defines a population as a group of conspecific organisms that occupy a "more or less" well defined geographic region, with spatial and temporal reproductive continuity that breed more within their group than between groups. There needs to be an inherent degree of flexibility in defining a population to reflect the complex nature of living systems. Likewise there is no clear distinction between a population and a sub-population as these categories are based on relative amounts of individual movement or geneflow.

My results support the supposition that populations have borders that differ in intensity in different directions and that boundaries are not always discrete (Schaefer and Wilson 2002). In essence, a sub-population's discreteness may be a continuous variable as are likely the populations within a metapopulation. In my study area, the intensity of the population boundaries varies across the region, reflecting complexity that more

Table 4.3. F_{ST} values for grizzly bear sub-populations in SW Canada and NW U.S.A. as depicted in Figure 4.2. Central Selkirks Southeast (CSSE) is abbreviated. Immediately adjacent sub-populations pairs are bolded.

Sub-populations	**CP**	**SP**	**SS**	**CSSE**	**CS**	**NS**	**NRW**	**NRE**	**CR**
S Purcels (SP)	**0.032**								
S Selkirks (SS)	**0.131**	**0.156**							
CSSE	**0.071**	0.096	**0.203**						
C Selkirks (CS)	**0.028**	0.048	**0.126**	**0.052**					
N Selkirks (NS)	0.038	0.052	0.131	0.101	**0.032**				
N Rockies West (NRW)	**0.051**	0.055	0.161	0.106	0.042	**0.020**			
N Rockies East (NRE)	0.041	0.045	0.136	0.073	0.030	0.022	**0.023**		
C Rockies (CR)	**0.025**	**0.027**	0.137	0.082	0.038	0.031	0.036	**0.025**	
S Rockies (SR)	0.041	**0.035**	0.136	0.101	0.048	0.036	0.046	0.036	**0.030**

realistically reflects populations in terrestrial habitats, particularly for populations that have limited dispersal characteristics or are susceptible to human-caused population fragmentation. Most metapopulation models simplify population complexity or heterogeneity. While this can provide useful systemic information (Hanski and Gilpin 1997), the increase in anthropogenic metapopulations (McCullough 1996) may be on the increase and spatially explicit models may be required to understand specific systems and tailor management or conservation strategies (McCullough 1996; Smith and Gilpin 1997).

Most population definitions have several concepts in common, including groups of interbreeding individuals that share a common area (Colinvax 1986; Futuyma 1986; Ricklefs 1990). Several definitions include the idea that the group shares a commonality of population dynamic processes in which fecundity and mortality over-shadow immigration and emigration (Moritz et al. 1995). In the field, the discrete categories I use may be blurred by biological complexity. This should not present a problem as long as we keep in mind the duality of theory and reality. For instance, several of the cluster pairs resulting from this analysis have overlapping boundaries and this is not an unreasonable result (McLoughlin et al. 2002; Schaefer and Wilson 2002). How one interprets overlapping boundaries is an important consideration. Are overlapping boundaries showing separate breeding groups that share space, or less distinct breeding groups that share migrants? For instance, distinct breeding groups of killer whales (*Orca orcinus*) are sympatric yet are divided by diet preference, one group feeding on marine mammals and the other feeding primarily on salmon (Hoelzel 1998).

In some instances, there may be sufficient geneflow between overlapping clusters to warrant considering the two clusters one sub-population. In other instances, the overlapping clusters should be considered separate sub-populations. My approach, using sex-specific movement rates between geographic areas as a criterion for interpreting overlapping boundaries, is based on population dynamic and conservation considerations. Is a barrier to one sex's movement sufficient to declare a "biological boundary"? If that gender-specific boundary has an ecological or conservation significance, the answer is yes. Avise (1995) argues from a theoretical perspective that because demographic processes dominate population dynamics, and many mammalian species have sex-biased (male dominated) dispersal, female connectivity is entirely relevant. Avise (1995) continued to argue that studies of geneflow that make no attempt to discriminate between the genders may miss this valuable biological information, e.g female boundaries.

One perspective in exploring the significance of biological boundaries is to examine the potential existence of Evolutionarily Significant Units (ESUs; Moritz 1994) and Management Units (Moritz et al. 1995). Are any of the identified populations or sub-populations I identified ESUs? Moritz (1994) suggested that separate ESUs be isolated long enough to have distinct genetic paths potentially measured by mtDNA-based reciprocally monophyletic status, that is, mtDNA lineages within each group are more related than lineages are between groups. Paetkau (1999) argues that this criterion may be too stringent in many situations (where parent populations are large this measure lags behind actual divergence) but offers no universal replacement. Crandell et al. (2000) argues that multiple characteristics including adaptive and molecular genetic data, be considered for evolutionarily significant unit determination. While the southern Selkirk bear population does not appear to be exchanging genes with adjacent populations, there is some evidence of bears moving out of that population and being killed (W. Wakkinen pers.comm.). I have no mtDNA data, nor is there any evidence of adaptive uniqueness for this population and suggest that while isolated, there is no evidence to proclaim this population an ESU.

The criterion suggested for management unit (MU) or conservation unit status may be more relevant in this system. It has been suggested that management units may exist where birth and death dominate population dynamics over immigration and emigration and divergent allele frequencies may be a tool to measure this (Moritz et al. 1995). Paetkau (1999) argues that more information is required than divergent allele frequencies, suggesting that some indication of actual movement rates would be more realistic. In my study area, the southern Selkirk population would easily qualify as a management unit by any standard, allele frequencies are extremely divergent, and it appears as there is minimal-to-no movement between adjacent populations (Chapter 3).

What about the other less obviously divergent sub-populations within the study area? Most units have evidence of male movement mediating geneflow, but very little-to-no female movement. Does the limitation of female movement warrant management unit or sub-population status? Because grizzly bears are so vulnerable to excess human-caused mortality (Mace and Waller 1998; McLellan et al. 1999), it may be prudent to consider geographic areas that have lost their female connectivity as separate management units and therefore sub-populations. These “female limited islands” must rely on the present cohort of females to drive any changes in their birth rates.

While both types of sub-population units found in my study (female limited and both-sex isolated) should be put in the management unit category, further distinction would be useful. I suggest that there should be several levels of descriptive sub-population or management unit categories reflective of their demographic and genetic situations. For the purposes of grizzly bear management in western North America it would be useful to have three categories of potential management units, 1) limited but measurable movement of both sexes, 2) restricted female movement or "female islands", and 3) isolated populations with restricted movement of both sexes.

Little work has dealt with delineating spatially explicit population units. In the Canadian arctic, grizzly bears have overlapping cluster-based "populations" (as determined from radio telemetry), based on 70% fixed-kernel contours of cumulative individual home ranges. While discrete clusters were "identified", movement rates of up to 13 and 35% for females and males, respectively, led researchers to conclude the area should be considered a continuous population (McLoughlin et al. 2002).

Underlying genetic relationships with clustered groups of individuals has been detected with varying degrees of connectivity as I did. Dever et al. (2002) found significantly overlapping clusters using the STRUCTURE algorithm and concluded that crocodiles in Belize were moving extensively between sub-populations according to a "mainland/island" model of geneflow, homogenizing genetic diversity among several smaller peripheral sub-population units. Small et al. (2002) found varying degrees of population boundaries and therefore a set of discrete populations and less discrete sub-populations, the creation of which were attributed to historical phylogeographic processes (e.g. natural fragmentation).

The STRUCTURE algorithm may be able to detect deeper divisions between clusters, or putative population or sub-population boundaries, when information reflecting discontinuities related to Hardy-Weinberg equilibrium is available. This is illustrated in the results from the sequential K analysis (Pritchard et al. 2000; Rosenberg et al. 2002). The ability to distinguish historic divisions from more recent, but perhaps more intense divisions, is not well understood. Therefore, it is only through an understanding of the specific study area that interpretation is possible, and it should therefore be done with caution (Pritchard et al. 2000; Rosenberg et al. 2002). For instance, when documenting fragmentation across any area that has substantial human disturbance, it is useful to distinguish what natural fragmentation may have existed in the past. The split that occurred when two populations were assumed (K = 2), separated the southern Rocky and Purcell Mountains from the Selkirk and central Purcell Mountains. At K = 3,. the split was across the Continental Divide (Elk Pass) suggesting that this natural fracture may be historically important. These two scenarios also suggest that the genetic link between the southern Rocky and Purcell Mountains was more significant than that between the southern Purcells and Selkirks, supporting the hypothesis that Kootenay Lake is a natural partial barrier to bear movement. At K = 4, the southern Selkirk Mountains separate into a discrete cluster. The southern Selkirk cluster is the most intense (i.e. no inter-population movement, large F_{ST} and genetic distance; Chapter 3) yet it appeared as the third split, reflecting the relationship between the degree of clustering and smaller sample sizes within the STRUCTURE algorithm (Rosenberg et al. 2001, N. Rosenberg pers. comm.).

While the Rocky, Purcell, and Selkirk Mountain bears are rather discrete (particularly in the southern part of the study area) there are several exceptions to this pattern. First, is a set of bears in the Purcell Mountains that appear to be genetically similar to a cluster of bears in the Rocky Mountains (Fig. 4.1). This signal is likely the result of the fact that problem bears from the southern Rocky Mountains were regularly translocated into the Purcell Mountains (B.C. Ministry of Water, Land and Air Protection files). Second, the area within the Rocky Mountains just north of Highway 1 near Banff National Park appears to be less discrete, with no clear genetic affiliations with any one cluster of bears. As many of the individuals captured in this population cluster with bears from the North Selkirk bears, it is likely that these bears also reflect the fact that many problem grizzlies were translocated from the north Selkirk Mountain area into the Rocky Mountains in the past (Proctor and Neumeier 1996). A third anomaly occurs in the Northern-most area around Jasper National Park (Fig. 4.1). The model with the highest posterior probability (10 clusters) subdivided this cluster into two sub-clusters with no particular spatial pattern. I have no satisfactory explanation for this result. Finally, there also are a few individuals within several areas that co-assign between clusters, contributing to the overlapping nature of those boundaries. For instance, five bears were co-assigned to the Central Selkirks and Central Purcells. These co-assignments have one of several interpretations. They may have common alleles between the two clusters and therefore assign to the two merely by chance. Alternatively, they may be offspring of inter-cluster matings. This imperfect clustering aspect is one reason why the individual-based gender-specific analysis was integrated into the population delineation. While inter-population mating is likely occurring providing geneflow, it is difficult to precisely measure these events; F_{ST} and genetic distance values provide a general measure of their influence.

The mechanisms resulting in the regional population and sub-population units described in this chapter are likely a combination of natural and anthropogenic barriers or filters to bear movement. I have implicated human settlement patterns, human-caused mortality, and traffic volume as forces affecting levels of bear movement in this system (Chapter 3). Natural habitat heterogeneity is a common driving force in structuring populations (Slatkin 1987; Clegg et al. 1998; Paetkau et al. 1999). One would assume therefore that a certain amount of induced genetic structure should not threaten the system. However, smaller population units may be vulnerable to demographic and genetic risks. Of particular concern, is that many of the population sub-units in this system appear to share very few females. This lack of demographic connectivity may threaten the persistence of smaller populations of which there are several.

While there are no absolute thresholds for a population number below which a population should be considered at risk, bears exhibit several life history characteristics that suggest several of the smaller populations in this study should be considered at elevated conservation risk. First, grizzly bears have low reproductive rates (Bunnell and Tait 1980) and therefore lower resilience to negative population dynamic processes (Miller 1990; Weaver et al. 1996). Vagility associated with large home ranges tends to bring bears into contact with humans and, as is the case for many large carnivores, often results in excessive mortality (Mace and Waller 1998; Woodroffe and Ginsberg 1998; McLellan et al. 1999). Smaller populations tend to have higher human-interface areas at the population perimeter, usually where increased human-caused mortality has a disproportionate influence on population dynamics (Aune and Kasworm 1989) that can result in localized extinction (Woodroffe and Ginsberg 1998; Parks and Harcourt 2002).

Sub-population units defined within my study area that are not small involve no immediate conservation risk. However, there are several long-term concerns that should be considered. First, to the extent that these larger units are adjacent to smaller units, the lack of movement of individuals from the large to the small units may be problematic. Second, future human-caused fragmentation may break these larger units into smaller units (e.g. see Strom et al. 1999), or mortality and habitat alienation may slowly decrease the overall number of the larger units or their future fragments (Mattson and Merrill 2002).

Genetic connectivity is often mediated by males within my study area, except in the instance of the southern Selkirk population where genetic connectivity is severed. This population has 20% lower genetic variability (microsatellite heterozygosity) than other sub-populations within my study area, and with the relatively small population (< 100), reduced genetic variability should be considered a variable in its viability (Frankham et al. 2002; Chapter 2 and 3). The Kodiak island population of grizzly bears in Alaska has 33% lower heterozygosity than neighboring mainland populations, yet appears to be thriving (Paetkau et al. 1998a). However, the Kodiak Island bear population is large (approx. 3000, L. Van Daele pers. comm.) relative to the isolated southern Selkirk population (70-100 bears; Weilgus et al. 1994) and the effects of inbreeding depression tend to be more detrimental for small populations (Frankham et al. 2002). Further, the Kodiak Island population has been isolated for approximately 10,000 years (Paetkau et al. 1998a), and the loss of genetic diversity has been a slow process, allowing selection to purge deleterious alleles. The southern Selkirk population has only been fragmented gradually over the past 50 - 100 years.

Abundance estimates

It is useful from both theoretical and practical perspectives to associate abundance estimates with the population sub-units resulting from this work. In my study area several population surveys for grizzly bears have been completed, and I used these results to derive population estimates for the sub-units, where appropriate (Table 4.4, Fig. 4.2). Because several areas do not have reliable data to build a population estimate, I also report geographic areas for the sub-populations to put them in some context. Continuous grizzly bear habitat north of Canada Highway 1 within British Columbia extend significantly beyond my study area and no reliable population estimates exist for this extended area. Therefore, I have not presented abundance estimates for these areas. The goal of this exercise was not to put precise abundance or density estimates to my population sub-units, but to give the results some relative context in terms of population sizes of specific units. For instance, an isolated population of 50-75 animals that might be considered at conservation risk, deserves separate consideration than one of 500-750 animals. I found one isolated population unit and two sub-population units, defined by having limited female exchange, each with under 100 animals that should be considered conservation risks.

CONCLUSION

What do my results mean for the future of grizzly bears and ecosystems at the southern edge of their North American distribution? The answer may depend on the ability of grizzly bears to function in some form of metapopulation. In the absence of effective regional connectivity planning, fragmentation is inevitable, and a permanent component of our modern human-dominated landscape. As smaller sub-populations are created through fragmentation, there will likely be additional threats to population viability through human-caused mortality. As the perimeter/core ratio of any sub-unit increases, the bear-human encounter rate and bear mortality increases (Aune and Kasworm 1989; Woodroffe and Ginsberg 1998; Mattson and Merrill 2002). Through metapopulation function, that is inter-population demographic connectivity, a matrix of core, growing grizzly populations can potentially augment and "rescue" more disturbed areas suffering from the low points of stochastic variability of vital rates and population abundance over time (Begon et al. 1996). The alternative scenario, in which isolated fragments are not demographically connected and experience a slow undetectable population decline, may result in smaller sub-populations disappearing and a continuation of the North American range contraction. Historically, the North American range contraction was primarily mediated by fragmentation and human-caused mortality when attitudes towards grizzly bears and large carnivores in general were relatively hostile (Mattson and Merrill 2002). While there is an improved attitude and tolerance toward bears and other carnivores, the processes of fragmentation and human-caused mortality still persist. Can we learn enough about the mechanics of these processes to halt them in the face of an increasing human population? Only through concerted effort. Considering the level of fragmentation described in this study, it would be prudent to minimize human-caused mortality (including legal harvest) within and adjacent to the smaller sub-population units (N < 100; Table 4.4).

Potentially more important than any one species, is the role this grizzly bear system plays as an indicator of ecosystem fragmentation. Grizzly bears are likely more sensitive to human-caused fragmentation than many other species and they generally occur only in remote, less disturbed areas. While it is unrealistic to retain wild, fully intact ecosystems across much of North America, large areas remain close to this condition particularly in north and western areas. The study of grizzly bear fragmentation may be a tool for monitoring the beginnings of ecosystem fragmentation at the continental and local scale. Given this logic, my results suggest that it may be prudent to investigate the state of fragmentation in a wider variety of species in southwestern Canada.

Table 4.4. Approximate abundance estimates for grizzly bear population and sub-population units in SW Canada and NW U.S.A. Estimates were determined using published density estimates for several of the areas based on DNA population surveys in some portion of the total sub-population area. The goal of this exercise is not to put precise abundance or density estimates to these sub-population units but to give the results some relative context in terms of population sizes of the specific units. Populations marked with an asterisk (*) are extrapolated from population estimates derived from a small proportion of the estimate area and therefore should be considered with caution.

Sub-population unit	**Area**	**Pop Est**	**Source**
North Rockies East*	38180	191-382	Gibeau 2000, Mowat et al. 2003
North Rockies West*	9576	192-393	Boulanger et al. *in press*
Central Rockies	13663	251-427	Mowat & Strobeck 1999; Boulanger 2001; Gibeau 2000
Southern Rockies	13695	330-720	Boulanger et al. 2002
Southern Purcells	4693	23-47	Kasworm et al 2000; Proctor unpub. data
Central Purcell*	14240	271-527	Strom et al. 1999; Proctor unpub. data
Central Selkirks	6966	190-334	Mowat & Strobeck 1999; Boulnager et al. 2003
Central Selkirk SW	3252	39-120	Mowat et al. 2003
Central Selkirk SE	1666	20-62	Mowat et al. 2003
Southern Selkirks	2857	48-95	Weilgus et al. 1994

CHAPTER 5: GENDER-BIASED DISPERSAL DISTANCE

INTRODUCTION

Natal dispersal, or the movement of offspring from their natal home range to their adult breeding area, is an important ecological and evolutionary process. At the individual level, dispersal is hypothesized to be a mechanism to minimize inbreeding (Pusey 1987; Johnson and Gaines 1990; Pusey and Wolf 1996; Perrin and Goudet 2001), reduce competition of resources among related individuals (Greenwood 1980; Waser 1985), reduce competition for mates among related individuals (Greenwood 1980; Dobson 1982), or a combination of the above (Dobson and Jones 1985; Gandon and Michalakis 2001). At the population level, dispersal may become inter-population geneflow (Slatkin 1987), influencing population structure (Chessier et al. 1993), genetic diversity (Hedrick 1995; Wayne and Koepfli 1996; Bushar et al. 1998; Paetkau et al. 1998a) inter-population source-sink dynamics (Pulliam 1988; Dias 1996), and population colonization and recolonization (Hanski and Gilpin 1997). At a species level, social organization and breeding system are linked to dispersal behaviour (Greenwood 1980; Waser and Jones 1983; Pusey 1987; Waser 1996; McLellan and Hovey 2001a). As well, dispersal mediates abundance and distribution (MacArthur and Wilson 1967; Dieckmann et al. 1999), facilitates range expansion (Lubina and Levin 1988; Swenson et al. 1998), and operates to resist range contraction (Channell and Lomolino 2000; Mattson and Merrill 2002). At the ecosystem level, dispersal plays a role in community structure (across a landscape) and therefore community function (Mouquet et al. 2001). For example, interruption of dispersal may result in isolation and eventual extirpation of a species with an important ecological role, the eventual loss of which may significantly alter community structure and function (e.g. Berger 1999).

While dispersal plays a central role in population viability and conservation of fragmented species (MacDonald and Johnson 2001), there is a perceived shortage of reliable dispersal data (Reed and Dobson 1993; Doak and Mills 1994; Caro 1999; MacDonald and Johnson 2001). This lack of dispersal information is directly related to the practical difficulty in its measurement. Traditional mark-recapture dispersal studies have a tendency to underestimate dispersal distance due to spatial limitations on the size of study areas (Koenig et al. 1996). Radio-telemetry offers an improvement, but may still be limiting for some long-distance dispersal events (Koenig et al. 1996). Genetic-based estimates of dispersal distance are often made using inferences from indirect measures of geneflow (F_{ST} and migration rate; Waser and Elliot 1991; Dobson 1994) with varying success. The presence of sex-biased dispersal (not dispersal distance) has been documented with microsatellite genotype-based data (Favre et al. 1997; Mossman and Waser 1999; Dallimer et al. 2002). Use of genetic tools to measure dispersal distance has been limited; Spong and Creel (2001) used genetic analysis based on sex-biased dispersal to estimate dispersal distances of male lions (*Panthera leo*).

The possibility of using family relationships to determine dispersal distance from genetic data has been discussed (Palsboll 1999) but to my knowledge has not been attempted. Here I use the spatial relationships from parent-offspring dyads, determined through genetic analysis, to estimate the dispersal distances of male and female grizzly bears. Measuring natal dispersal in grizzly bears is temporally and spatially challenging as they have relatively long generation times and live at low densities over large spatial scales.

Grizzly bears near the southern extent of their current North American distribution live in partially fragmented habitats and are potentially susceptible to further human-caused fragmentation (Chapters 2,3,4). As part of a larger fragmentation study I wanted to determine the dispersal behavior of male and female grizzly bears and ultimately relate dispersal behaviour to fragmentation susceptibility. In an anthropogenically fragmented landscape, where a once 'panmictic" population has been transformed into a set of sub-populations, how well will inter-population movement of grizzly bears be able to imitate a "metapopulation"? Can dispersal behavior or migration mediate population augmentation in light of the shifting stochastic demographic problems associated with small populations?

Patterns in mammalian dispersal derived from comparing life history traits suggest that grizzly bears should display long distance dispersal because of their large body size, non-territorial nature, asociality, and generalist foraging habits (Wolff 1999) although there are exceptions to many of these patterns (i.e. North American wolf). Food resources that are seasonal, ephemeral, or unpredictable should result in selection for individuals that are capable of foraging over large areas. These food conditions describe grizzly bear ecology in the interior regions of North America, where the generalist dietary habits reflect the range of food resources used across the continent (reviewed in LeFranc et al. 1987). Bears subsist on ephemeral sources: they prefer ungulates when available (LeFranc et al. 1987) and fire-mediated berry patches that create spatial and temporal habitat mosaics (McLellan and Hovey 1995). Furthermore, much of the sparse, anecdotal documentation of dispersal in grizzly bears suggests that males typically move long distances from their maternal range (Glenn and Miller 1980; Reynolds and Hechtel 1986; reviewed in LeFranc et al. 1987).

Grizzly bears in the southern interior of British Columbia have relatively short dispersal distances (McLellan and Hovey 2001a). McLellan and Hovey (2001a) found that male-biased dispersal is a gradual process, taking several years, and the resulting post-dispersal adult home ranges of females usually overlap and males are on average one male home range from the maternal range. McLellan and Hovey (2001a) concluded that because grizzly bears are non-territorial, have overlapping home ranges, and are promiscuous breeders, they do not need to disperse far to mitigate the effects of inbreeding and competition with close relatives for mates or resources. Because McLellan and Hovey's (2001a) result was unexpected considering the typical large carnivore trend discussed above, I wanted to test whether their result held true over a larger study area, where sample sizes are larger and detection of long distance dispersal is more likely. My analysis is based on genetic data. I use the spatial relationships from parent-offspring dyads, determined through microsatellite genotypes, to estimate dispersal distances of males and females. I also explore the additional factors that may contribute to the variation in dispersal distance intra- and inter-specifically, and the relationship of dispersal distance to fragmentation susceptibility.

METHODS

Refer to Chapter 3 for the details field methods and microsatellite genotyping.

Sex-biased dispersal

I first wanted to test a genetic method for determining sex-biased dispersal (Favre et al. 1997: Mossman and Waser 1999) that compares the inter-population assignment likelihood (ln P(Assignment)) between males and females. The sex that disperses the furthest, will have, on average, lower assignment likelihoods to the population of its capture. I determined population assignments for all individuals using an allele frequency-based assignment test (Paetkau et al. 1995). Because I used average assignment likelihoods between geographic areas I used my entire set of individuals divided into 15 different geographic areas as in Chapter 3 (Fig. 3.2). For this analysis, I was not concerned with population boundaries or inter-population movement rates. For each individual I calculated an index of the assignment likelihood (AIc) from the following equation:

$$AIc = \ln [P(A_{CAP})] - \ln [P(A_{AVE})]$$

Where $P(A_{CAP})$ is the probability of assignment to the population of capture, and $P(A_{AVE})$ is the average assignment probability to each population. Subtracting the population average assignment allows comparison between populations which have different allele frequencies and therefore different average assignment probabilities (Favre et al. 1997). In this way, relative assignments, not absolute assignments, are compared. The parameters of interest are the mean and variance of each sex's average AIc values. I tested equality of variances using the F-test and means using a t-test (Sokal and Rohlf 1995). A non-parametric t-test was used when the variances were unequal. A difference in means between the sexes implies inter-population sex-biased dispersal, while a difference in the variance reflects different dispersal behaviour.

I used a likelihood estimator of parent-offspring status among pairwise comparisons of individuals captured throughout my study area (CERVUS, Marshall et al. 1998; Slate et al. 2000). CERVUS compares the likelihood of potential parentage calculated from allele frequencies within the population based on Mendelian inheritance principles. For all potential offspring, it compares the two most likely parentage candidates (maternal and paternal done separately) by log ratio. It then simulates parents and offspring developing a distribution of relative log ratios to determine a probability for any given potential parent-offspring relationship. Some of the strengths in using this likelihood estimator are that the simulation routine incorporates estimates of the rate of genotyping error, the number and proportion of potential parents sampled, and the proportion of genotyping success. I have biologically reasonable estimates of these parameters. Because most of my samples were obtained from formal population surveys conducted to estimate abundance, I was able to estimate the proportion of potential parents sampled with some confidence. I also know the rate of genotyping success. The difficult parameter is the genotyping error rate. Because CERVUS incorporates a genotyping error rate, it allows parent-offspring pairs to mismatch at some low number of loci and still be considered related even though the individuals do not share an allele at all loci compared, as is the typical pattern for a parent and an offspring (assuming no mutations have occurred). I entered a relatively low error rate of 0.001 to ensure that parent-offspring dyads did not mismatch by more than one locus. This minimizes my Type I error rate but potentially reduced my sample size.

Sex-specific dispersal distance

Female dispersal distance

To estimate the dispersal distance of each gender, I used the average distance between capture locations of parent-offspring pairs, excluding any pairs thought to be a pre-dispersed offspring traveling with their mother (individuals that appear as parent offspring that were captured together twice). For the female dispersal distance, I compared female-female parent-offspring dyads. Because age cannot be determined from genetic data, an individual cannot be labeled as the "mother" or "daughter". To calculate the dispersal distance between two individuals, ideally I should know the centres of both of their post-dispersal home ranges and subtract them to get the "dispersal distance" (McLellan and Hovey 2001a). However, my capture locations were point locations within each of the two individuals' home ranges. Sometimes by chance, I captured the individuals when they were closer than the distance between the centres of their home ranges, and other times when they were further. Given sufficient sample sizes, the distances should average out and be a relatively unbiased estimate of the dispersal distance as defined as the distance between the centres of the post-dispersal home ranges.

Male dispersal distance

Estimating male dispersal distance is more complicated. I estimated the distance that males and females moved away from their maternal range to set up their own adult ranges. When I found a female-female parent-offspring relationship, it was safe to assume that one individual was the mother and the other the daughter. However, because

I do not have age information, I could not differentiate a mother-son relationship from a father-daughter. Therefore to estimate male dispersal I used only male-male relationships. The assumption required in doing so is that the father's location can be used to estimate the mother's location relative to the son. In essence, I used the distance between the father and son to estimate the distance between the mother and son and therefore needed to quantify the bias associated with this assumption.

To calculate the bias in using the father-son distance to estimate the mother-son distance, I used the biological information regarding grizzly bear mating patterns and spatial relationships of parent-offspring pairs. First, males have larger non-exclusive home ranges that overlap several non-exclusive female home ranges (reviewed in LeFranc et al. 1987; Gibeau and Herrero 1998). Because the male and female mated, some portion of their home ranges overlap. Also, because sons disperse from their mother's home range, the father-son distance should be, on average, farther than the mother-son distance.

I calculated the average bias between the father-son distance and the mother-son distance (Fig. 5.1) using a simulated re-sampling algorithm based on 10,000 repetitions using father, mother, and son locations in the following manner. I simulated the location of a potential father within a spatial distribution of locations based on average male home range size within my study area. I simulated father positions by using a random direction between 0-359 degrees and a random distance constrained to yield on average, the average adult male home range for my study area. Then, assuming that the mother's home range overlaps some portion of the father's home range, I simulated the location of a potential mother within a spatial distribution including and surrounding the father's home range distribution in a similar fashion. Assuming that the son disperses from its natal (maternal) home range, I located a potential son within a distribution including and surrounding the mother's distribution. I simulation a random direction between 0-359 degrees and random distance from the mother's position that was constrained to yield on average, the average male-male distance I measure in this study. Each repetition located a father, mother and son. With the locations in two-dimensional space, I calculated the difference between the father-son distance and the mother-son distance. I used the average of 10,000 repetitions to correct the father-son (male-male) calculation of dispersal distance by the "biased" amount thus estimating the mother-son dispersal distance. Simulation calculations were based on male and female home ranges of 579 km^2 and 186 km^2 respectively (mean values for three radio telemetry projects within my study area, J. Woods, unpub. data; F. Hovey pers. comm; Gibeau and Herrero 1998).

Home ranges were assumed to be circular in shape for the sake of computation. I also wanted to detect long distance dispersal. Because I have inter-population assignment information, I have a subset of individuals (i.e. putative migrants, Ch. 3) where I could measure dispersal distance by subtracting the distance between capture location and source population. As a conservative measurement I used the nearest boundary of the source population.

RESULTS

I genotyped 711 grizzly bears, 344 females and 367 males associated with specific location data from 15 geographic areas. I found reasonable genetic variability across 15 microsatellite loci within my area as measured by expected average ($H_E = 0.64$)

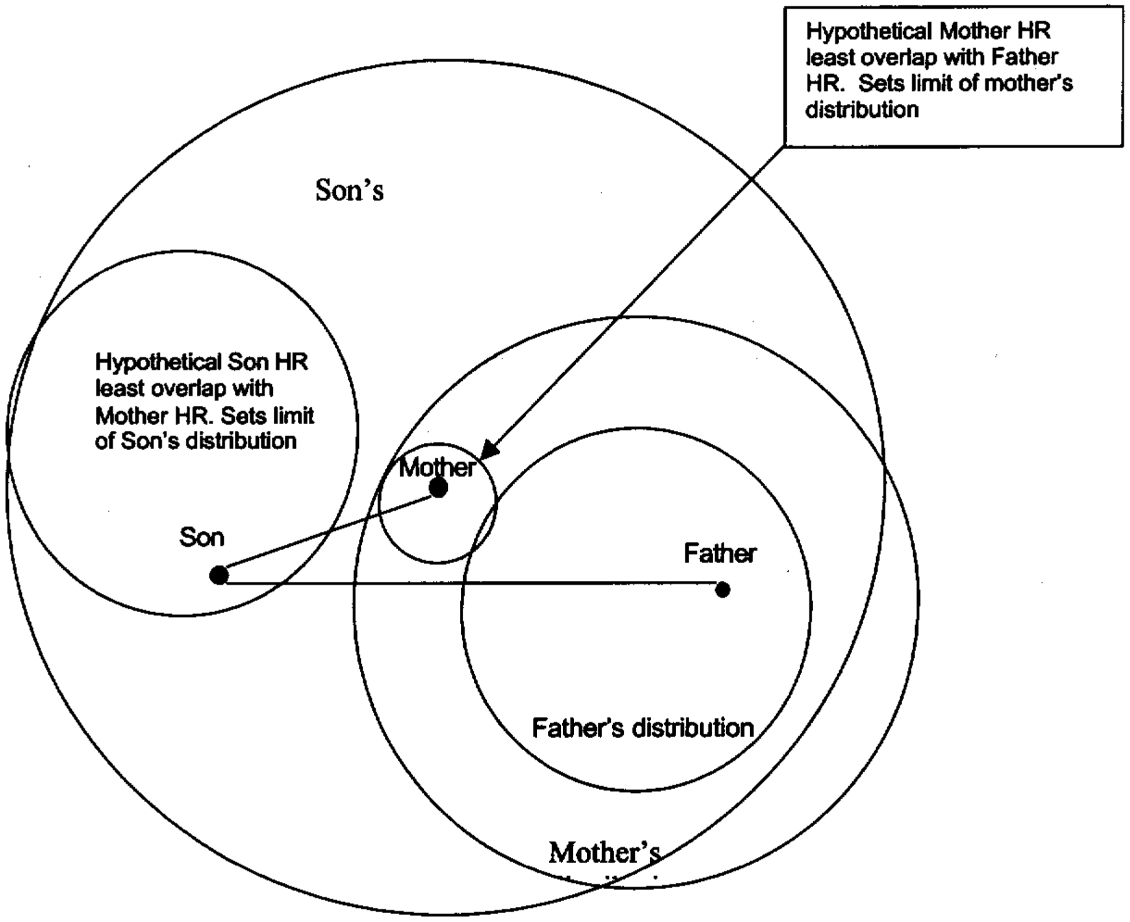


Figure 5.1. Diagram underpinning measurement of bias when measuring father-son distance as an estimate of mother-son distance. Calculation assumes the following: i. mother's home range (HR) overlaps the father's HR – they mated; ii. son's post-dispersal HR is on average the size of an adult male HR and the range of distance was constrained to yield the average male-male distance measured in this study. Procedural steps: i. Select random father point from within father distribution - constrained to yield average male HR radius, choose random direction between 0-359 and random distance between 0 and maximum distance; ii. select random mother point within mother distribution - constrained to yield average female HR radius plus male HR diameter - choose random direction between 0-359 at center of father distribution and random length between 0 and maximum distance; iii. select son point within son distribution (relative to mother's point) constrained to yield average male-male distance measured in this study - choose random direction between 0-360 and random length between 0 and maximum distance from mother's point; iv. calculate father-son distance minus mother-son distance; v. repeat 10,000 times.

and observed heterozygosity ($H_O = 0.65$). There was moderate population structure across all 15 geographic areas ($F_{ST} = 0.050$).

Sex-biased dispersal

As expected, the means and variances of the cross-assignment likelihood values were significantly different for male and female grizzly bears (two-tailed t-test, female mean = 0.225 and variance = 6.42, male mean = -0.219 and variance = 7.94, t = 2.13, d.f. = 688, P = 0.033; F-test, $F_{328,360} = 0.809$, P = 0.025).

Sex-specific dispersal distance

I found 98 dyads that met the criteria of parent-offspring relationship (54 mother-daughter and 44 father-son). Using the mother-daughter pairs I found the average dispersal distance for females was 14 km. When I added the inter-population dispersers detected using the assignment test, the mean rose to 15 km. Using the father-son pairs I found the average dispersal distance for males was 42 km and 49 km when the inter-population dispersers were included. I found the estimated bias associated with using father-son distances to estimate mother-son distances to be 3.2 km (SE = 0.12). Therefore the adjusted (unbiased) estimate of mother-son dispersal distance is 45.8 km (49-3.2; SE = 9.4 associated with mean of 49).

DISCUSSION

Patterns in mammalian dispersal derived from comparing life history and behavioural ecological traits suggest that grizzly bears should disperse long distances (Wolff 1999). Large body size is correlated with large home range size (McNab 1963) and long dispersal behavior (Wolff 1999). Species that evolved in patchy disturbance-driven unpredictable habitats may have evolved to move longer distances through unsuitable and/or naturally fragmented habitat. This contrasts with species that evolved in stable continuous habitats which select for conservative movement patterns through unsuitable habitat (Merriam 1995; Lima and Zollner 1996; Wolff 1999). Habitat generalists may respond better to fragmented landscapes as a result of having to meet their ecological needs from a variety of habitat types, whereas habitat specialists may view complex mosaics as barriers to movement (Laurence 1995; Wolff 1999). Non-territorial asocial species should be less influenced by social considerations and therefore be able to move freely through the landscape (reviewed in Wolff 1996) (see below). These characteristics support the hypothesis that grizzly bears should have "long" distance dispersal.

A brief review of dispersal distances of several North American large carnivores reveals that while the grizzly bear is one of the largest, the bears in my study area have some of the shortest reported average dispersal distances. Black bears have home ranges approximately one fifth the size of grizzly bears (Aune 1994), and also have male-biased dispersal. Males dispersed 61 km on average in Minnesota (Rogers 1987), 30 to 200 km in Massachusetts (Elowe and Dodge 1989), and 11 km in the Kenai Peninsula, Alaska (Schwartz and Franzmann 1992). Female black bears were philopatric in all studies. Male and female wolves in Minnesota dispersed 88 and 65 km, respectively, on average (Gese and Mech 1991). Maine coyotes (*Canis latrans*) of both sexes disperse similar distances, 98 km on average (Harrison 1992). In two studies in fragmented California habitat, cougars (*Puma concolor*) dispersed 63 km and 85 km (Beier 1995; Anderson et al. 1992). Male and female lynx in the Northwest Territories had no difference in average dispersal distance (163 km; Poole 1997). While methods for measuring average dispersal distance vary among studies, and most estimates were not put in context of home range diameters, there is a trend suggesting that grizzly bears disperse in my study area less than many large carnivores in North America.

McLellan and Hovey (2001a) offered an hypothesis for limited dispersal distance in grizzly bears - that their non-territorial overlapping home range behavior and promiscuous breeding system may have resulted in selection for shorter dispersal. They argue that long distance dispersal is not required to reduce potential inbreeding effects and competition for mates and resources with close relatives. My results support McLellan and Hovey's (2001a) hypothesis and suggest that grizzly bears do not disperse long distances from their maternal home range moving less than predicted from behavioral ecology and life history patterns among mammals (Wolff 1999).

Male grizzly bears appear to have a longer dispersal distance than females, likely partially explained by the fact that males have larger home ranges than females. The reigning hypothesis for the larger home range is that it is a part of a reproductive strategy to increase individual fitness by increasing mating opportunities. Females are hypothesized to tend towards philopatry to maximize offspring success through parental investment and habitat familiarity (Greenwood 1980).

The trophic level of an animal may influence the ecological plasticity of dispersal distance. Although they are in the carnivore family, grizzly bears are omnivorous and in interior regions of western North America most populations obtain the majority of their energy from plant matter (LeFranc et al. 1987; McLellan and Hovey 1995; Hilderbrand et al. 1999). Herbivores have consistently shorter dispersal distances than carnivores (Wolff 1999). Additionally, human-caused fragmentation in southern Canada may limit dispersal distance as any long distance dispersal may result in death from trying to cross human-dominated areas (B. McLellan unpub. data; Chapter 3). Fragmentation related human-caused mortality may affect bears more than North American canids and felids as bears are attracted to human food sources such as garbage and this often results in the bear's death (McLellan et al.1999).

There may be ecological plasticity to dispersal behaviour (Waser 1996). Increased population structure, or reduced regional connectivity and movement, have been associated with topographical and habitat complexity (Clegg et al. 1998). This may explain a portion of the variance in dispersal behaviour between the northern and southern Canadian bear populations. However, an alternative explanation is that "long" distance dispersal observed in northern areas may be an artifact of larger male home ranges that extend outside study area boundaries. This hypothesis is difficult to substantiate because reports of "long" distance dispersal from northern areas in Canada and Alaska are not derived from analysis of reliable post-dispersal data, but were inferred from male radio-collared bears often "leaving" the study area or being reported killed at some distance from their natal range. In the interior mountains of southwestern Canada, McLellan and Hovey (2001a) found that the average male dispersal was one male home range diameter. In Yellowstone National Park, male grizzly bears disperse on average 59 km or 0.85 home range diameters. Due to variation in movement and home range sizes in different regions, measuring home ranges in terms of home range diameters may be a more ecologically relevant comparative measure, however this will have to be tested through reliable dispersal studies in a range of ecological conditions.

As genetic-derived estimates of dispersal distances become prevalent, discrepancies with radiotelemetry estimates emerge (Koenig et al. 1996). Traditional mark-recapture estimates of dispersal distance have several limitations including the inability to detect long-distance dispersal events in spatially limited study areas (Koenig et al. 1996). Increasing study area size and using radiotelemetry to detect dispersal distances improve the probability of detecting long distance dispersal, but both solutions suffer from the fact that detection probability decreases as dispersal distance increases (Koenig et al. 1996). Genetic-based estimates of dispersal distance are often made using inferences from indirect measures of geneflow (F_{ST} and migration rate). Often when using these techniques, it is difficult to detect the exact mechanism responsible for the level of geneflow. Has geneflow resulted from a few long distance dispersal events or by more frequent levels of short, stepping-stone-like dispersal (Dobson 1994)? Or, is geneflow a result of dispersal events or temporary movements for breeding purposes (Waser and Elliot 1991)? These questions have been left unanswered using indirect genetic methods.

My work incorporates dispersal measurement improvements by using individual-based genetic techniques to estimate dispersal distances. My results for dispersal distances for each sex were similar to the only radiotelemetry-based dispersal study done on grizzly bears in my study area which found females dispersed on average 10 km from their maternal home range while males dispersed 30 km on average (McLellan and Hovey 2001a). My values are 40-50% higher, which may be a result of several factors.

My study area was much larger, increasing the chance of detecting long distance dispersal events, and I sampled in areas where the average home range is larger than those in the area where McLellan and Hovey (2001a) worked (Gibeau and Herrero 1998). When the average male dispersal distance is corrected for the bias associated with using the distance between a father and son to estimate the distance between a mother and son, the male/female dispersal ratio is similar to results found by McLellan and Hovey (2001a, 30/10 = 3; this study 46/14 = 3.3). Furthermore, my results could be an underestimate because I do not have age data. Some of the relationships that underpin my data may include animals that are in the process of dispersing and may be on average, closer than their "final" adult home range will be.

Use of genetic tools to estimate population parameters is a new and evolving methodology. Previous studies using genetic analysis to detect sex-biased dispersal through asymmetrical assignment probabilities have not corroborated their results by measuring dispersal distance of each sex. My results from the parent-offspring-derived dispersal distance support the use of assignment-based detection of sex-biased dispersal. One limitation in my methodology is the assumption that point locations for two individuals can estimate the "average" distance between them. This requires relatively large sample sizes, so that dispersal is "randomly" sampled. Half of the time, two individuals will be captured closer than average and the other half, they will be captured further than average. Given sufficient sample sizes, the resulting mean will be unbiased although the variance will be positively biased. There are also limitations in using a likelihood estimator for relationship analysis. There is a low rate of dyads, that CERVUS determined to be parent-offspring relationships, that are likely full siblings (Marshall et al. 1998). Siblings have a different pattern of allele sharing than do parent-offspring dyads and therefore should be excluded most of the time when using 15 locus genotypes. Parent-offspring share one allele at each locus while full siblings share one allele at half their loci, both alleles at one quarter of their loci, and neither allele at one quarter of their loci on average (Jacquard 1974).

While longstanding evolutionary forces likely explain observed dispersal behaviour, it is also important to consider the more recent selective forces imposed by humans. Large movements and therefore large home ranges superficially suggest that bears should be able to move easily between habitat patches across the landscape. However, in many regions these movements also bring bears into contact with humans, often resulting in bear mortality (Mace and Waller 1998; McLellan et al. 1999). In that context, human settlement is likely an index for past mortality associated with human-bear conflicts. In the past 10 years, in one linear transportation and settlement corridor in my study area (B.C. Highway 3 in the southern Rocky Mountains) 60 grizzly bears were killed or removed due to concerns for human property and safety. In essence, human activity in the boundary areas separating sub-populations has effectively increased the "distance" between the sub-populations from a bear dispersal perspective. Of particular importance, but not often considered, is the asymmetric susceptibility to fragmentation experienced by sexes that do not disperse equal distances. Because females naturally have relatively short dispersal distances and gradual dispersal, human-caused fragmentation will make it that much more difficult to retain the female component of demographic connectivity. In other words, males and females may respond equally to human disturbance, yet female inter-population connectivity may be reduced as a consequence of their tendency for short dispersal. This connection, of limited female dispersal and susceptibility to fragmentation, may partially explain the sex-biased fragmentation of grizzly bears in southern Canada described in Chapters 2 and 3.

In the long-term, fragmentation may alter the selection pressures on dispersal, particularly if increased mortality plays a role in mediating fragmentation (Hanski 2001), as is often the case with carnivores (Woodroffe and Ginsberg 1998; Chapter 3). One hypothesis suggests that mortality of dispersing individuals through fragmented habitat will inadvertently cause selection of individuals with shorter dispersal thereby decreasing dispersal distance. A second hypothesis suggests that increased fragmentation will lead to metapopulation persistence due to more sub-population creation and therefore more colonization. Increased metapopulation persistence results in selection for individual colonizers thereby increasing dispersal distance. Because grizzly bears in southern Canada may not be in a classical metapopulation that experiences some rate of extinction and recolonization, the former hypothesis may be more applicable.

CHAPTER 6: SYNTHESIS

Dispersal is the thread that links the chapters of this thesis as much as it links the sub-populations throughout my study area and the disciplines of behaviour, landscape ecology, and evolution. Historically, or in areas such as northern North America, grizzly bear habitat was, and remains more continuous than is the case currently for bears at the southern edge of the North American distribution in the region around the Canada-U.S.A. border. Historically, home range overlap and dispersal linked geographic areas, some of which had a degree of natural fragmentation. Today, in anthropogenically-fragmented habitats, the function of dispersal may have an elevated role; because some fragments hold small populations, the need for dispersal-driven connectivity may be an important link to larger more productive populations that may be less susceptible to stochastic variation in demographic or environmental forces. In this way, dispersal spatially equalizes the effects of pressures on an otherwise small population.

Ultimately, the subject of this thesis is ecosystem change. I have documented the anthropogenic alteration of movement patterns of grizzly bears. Ecosystem change is and has always been ubiquitous. The question is "can the system adjust to or withstand the change?" The answer to this question is difficult to obtain or predict and is often related to the rate of change as much as it is the intensity. The range contraction of grizzly bears in the U.S.A. south of the Canadian border occurred rapidly, within 100 years (Mattson and Merrill 2002). Metapopulation function may have had no chance to operate. Contraction of grizzly bear range in Europe has been operating for centuries, slowly and in one direction until recent efforts for range expansion and recolonization have been actively pursued (Swenson et al. 1995; Servheen et al. 1999). The lesson from the European situation is that in the absence of eradication efforts, bears can persist in isolated, slowly declining populations for a long time. Theory and history tell us that small isolated populations in conjunction with human disturbance may be difficult to sustain. For example, true oceanic island populations of various species have persisted for millennia, in spite of minimal genetic variability (Frankham et al. 2002), but when humans colonized these islands, viability of many species decreased. Twenty percent of the world's avian species were found on oceanic islands, but account for 80% of the avian extinctions worldwide (Frankham et al. 2002). The hope for long-term persistence of fragmented bear populations in regions where human presence is high and fragmentation is immutably present is inter-population movement mediating some form of "metapopulation", ultimately providing sufficient connectivity function. This is our challenge to ensure long-term grizzly bear persistence in southeastern Canada and northwestern U.S.A.

Another important question is "from a fragmentation perspective, has the change slowed or stopped?" In other words, at what point in the chronology from historically-connected grizzly bear habitat to population fragmentation are we at this point in time? I imagine that we are not at the end. Human populations are increasing in this region (reviewed in McLellan 1998) and so is the amount of our movement. Of course, we do have a modicum of influence over our behaviour, and work such as this thesis may influence how we react. However, if the forces that mediate fragmentation are increasing, it will be that much more challenging to halt and reverse these processes. Genetic analysis invariably reveals processes that have occurred in the past. I have made an effort to minimize this by measuring recent bear movement, but there are still two temporal scales to my results. Based on the life span of the individual bears within this study, measurement of individual migrants reflects events that have occurred within the past 20-25 years. For example, a female migrant may have dispersed across a highway 15 years ago, and I detected it this year. Genetic distances are driven primarily by genetic drift, which operates at variable rates in different populations due to effective population size differences, creating differential distances between population pairs. In other words, the time scale that genetic distances reflect is variable across the study area and is difficult to quantify, highlighting the advantage and importance of measuring individual migrants. This is especially important when recent events are being studied, such as monitoring changes in inter-population movement.

Detecting presence or absence of movement does not fully illustrate movement patterns. It is difficult to say with certainty what type of movement I measured; do the putative "migrants" I identified have current home ranges that span the boundary areas, or have these individuals permanently moved from one area to an adjacent area? As part of my sampling regime, I made an effort to genetically sample bears immediately adjacent to the human transportation and settlement corridors. However, I only sampled a portion of the bears living in my study area. As such, there are likely bears moving across these corridors that were not detected by my sampling. As I only sampled during one season (early summer) it was difficult to capture individuals that may move across my boundary areas outside of that season. Because my most powerful analytical tool was population assignment, I detected movement between sub-populations when I captured an animal in a local population other than the one it was born into. For this reason, my results are likely skewed towards dispersal events as opposed to the occasional animal that has a home range that spans a boundary area. That is, when I identified a migrant, it was more likely an individual that permanently moved between areas, rather than an individual whose home range currently spanned the boundary area. Detecting more migrants rather than animals whose home range spans an highway may result because I could capture any animals that may have dispersed sometime over the past 20-25 years. In contrast, the short seasonal sampling period of 2 months (the usual length of sampling) would minimize the chance of capturing an animal on both sides of a highway. Further, as the genetic distances decrease between two geographic areas, the power to detect movements using assignment methods decreases.

The implications of the above for my study are that there may be more migrants moving between areas with low genetic distances than I detected. To test this, I did an exploratory exercise to determine the effects on my conclusions of lowering the putative migrant threshold LR from 2.0 to 1.5 and found that there was very little change in the ecological conclusions. In other words, the patterns of sex-specific movement remained the same; limited female movement in human-disturbed systems. In spite of the uncertainty over the exact number of migrants moving between geographic areas, sex-biased fragmentation is apparent. Furthermore, the large genetic distances found across these relatively narrow boundary areas, suggests that there has been a reduction in the amount of bear movement and geneflow between the areas.

The major conclusions from this work are two-fold: First, there are relatively large genetic distances across the human-dominated transportation and settlement corridors, and second, naturally moderate female movement is limited due to human disturbance. Fragmentation will likely impact the ecological resilience of grizzly bear populations in my study region. As human activities change spatially and temporally across the landscape, grizzly bear populations in various areas will be less resilient in absorbing and rebounding to significant disturbance. Dispersal is a mechanism that spatially equalizes positive and negative (e.g. source to sink) events or processes. Fragmentation may limit this function. Stochastic and deterministic increases in mortality may be difficult to overcome, as will detrimental changes to habitat quality. Grizzly bears have relatively large home ranges and this vagility allows them to meet their ecological needs throughout their life. Many high quality energy sources are disturbance oriented (e.g. fire-mediated berry patches; McLellan and Hovey 1995). The reduction in access, through fragmentation, to this spatially changing supply of resources may have implications for some populations.

Fragmentation may increase the selective pressure on bears by increasing mortality around the ever increasing perimeters of populations. As fragmentation increases, the amount of human-bear interface areas around the perimeters increases. Bears that attempt to disperse through these areas will experience higher mortality, and this may have an effect on the evolution of life history traits of bears.

Possible consequences of fragmentation on North American grizzly bears may be similar to those found in European grizzly bears. Future selection may favour smaller animals that can survive and reproduce in smaller areas. Selection may favor younger age of first reproduction and shorter inter-birth intervals. Also, less bold animals will likely live longer and reproduce more. This selection process may result in the grizzly bear adapting to be closer in these life history traits to the American black bear.

The work encompassed by my thesis has been exploratory rather than experimental in nature. I did not design an experiment to manipulate variables nor test specific hypotheses based on the outcomes of experiments. My study design was purposeful, and organized around measuring an existing state, knowing that by measuring variation in that state, I would have the ability to detect correlative patterns, if they existed. Ultimately, I could describe a system and attempt to explain potential proximate causes. Through this exploratory process I have uncovered interesting and potentially important patterns in grizzly bear population fragmentation. However, several important factors were omitted in this analysis and should be considered subjects for further research.

Habitat quality in and adjacent to my boundary areas may prove to be an important variable in inter-population movement and was not considered for logistical reasons. Further, dispersal in grizzly bears may be density-dependent and this should be tested. Also, the fine-scale distribution of bears across the landscape may be an important variable in fragmentation. Bears are not uniformly distributed spatially (or temporally) and vacancies in distribution may influence inter-population movement. Why do some areas have low numbers of bears? Have recent habitat alterations or past mortality patterns caused some of this patchy distribution? More practically, where and in what types of habitat do bears successfully move through human environments? The answers to these questions may reveal specific mitigation strategies.

Because of the strong genetic structuring between many adjacent sub-populations in my study area, it would be possible to monitor future changes of inter-population movement and thus provide feedback on any connectivity management strategies carried out. For example, because human-caused mortality may be acting as a fragmentation force, the impact of reducing human-caused mortality (e.g. reducing legal harvest quotas) in several experimental areas could be measured over time. There is evidence that this type of approach may be useful for increasing inter-population connectivity. Scandinavia for example, has reduced human-caused mortality through management, resulting in an expanding grizzly bear population (Swensen et al. 1998); similar results have recently been reported in Yellowstone National Park (C. Servheen pers. comm.).

My research questions have been on the minds of researchers for many years. Fragmentation has been an important topic since the discipline of conservation biology emerged two decades ago. Grizzly bears are notoriously difficult to study at any scale. They are relatively dangerous to work with and live cryptic lives at low densities over large areas. The advent of radiotelemetry enabled many ecological studies that have provided insight into their ecology and interestingly, their ecological plasticity and variability. Genetic techniques have recently enabled new insights in wildlife research.

Two interesting perspectives underpin this thesis. First is the ability to link individuals to other individuals (i.e. parents to offspring) and to populations (migrant detection and genetic distance as an index to geneflow). The second is the ability and opportunity to study a species such as the grizzly bear at small and large scales simultaneously. Population genetic tools have explored questions at the multiple-population scale for decades. The approach has been from the theoretical perspective, based on idealized, naturally undisturbed systems that are not entirely relevant for modern conservation questions about recently disturbed systems. The recent shift into individual-based genetic analyses overcomes this limitation. Theoretical, simulation-based papers are becoming common, and with work such as this project, these newer techniques are being applied to real conservation problems. Detecting and measuring population fragmentation is probably in its infancy, and I hope work stemming from this thesis will further advance this field.

Potentially more important than fragmentation of grizzly bear populations themselves, is the role bear fragmentation plays as an indicator of ecosystem fragmentation. Grizzly bears are likely sensitive to human-caused fragmentation relative to many other species and generally occur only in remote less disturbed areas. While it is unrealistic to retain wild, fully intact ecosystems across much of North America, large areas remain close to this condition particularly in north and western regions. The study of grizzly bear fragmentation may be a tool for monitoring the beginnings of ecosystem fragmentation at the continental and local scales.

I do not know to what extent the remaining components of the Canadian mountain ecosystem are being fragmented by human influence. Other large mammals, such as mountain caribou have had their southern distribution severely fragmented, resulting in several highly threatened, small isolated populations (Hatter 2002). While susceptibility of carnivores to fragmentation is not universal, there is some evidence that other carnivore species may be experiencing anthropogenic fragmentation in western North America. For example, wolverines have increased population structure at the southern periphery of their North American distribution (Kyle and Strobeck 2002; Cegelski et al. *in press*). Lynx populations in western North America were found to have little genetic structure (Schwartz et al. 2002) although at a finer scale, and Campbell (2002) found genetic structure across a major highway, implying that human disturbance may be influencing connectivity. These results, together with my results, suggest that it may be prudent to investigate the state of fragmentation of a wider variety of species in southwestern Canada. I recommend that further regional-scale fragmentation studies be done on a suite of species in an effort to discover whether other species are being affected and ecosystem-level fragmentation is occurring.

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