# Population Fragmentation and Inter-Ecosystem Movements of Grizzly Bears in Western Canada and the Northern United States

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**ABSTRACT** Population fragmentation compromises population viability, reduces a species ability to respond to climate change, and ultimately may reduce biodiversity. We studied the current state and potential causes of fragmentation in grizzly bears over approximately 1,000,000 km² of western Canada, the northern United States (US), and southeast Alaska. We compiled much of our data from projects undertaken with a variety of research objectives including population estimation and trend, landscape fragmentation, habitat selection, vital rates, and response to human development. Our primary analytical techniques stemmed from genetic analysis of 3,134 bears, supplemented with radiotelemetry data from 792 bears. We used 15 locus microsatellite data coupled with measures of genetic distance, isolation-by-distance (IBD) analysis, analysis of covariance (ANCOVA), linear multiple regression, multi-factorial correspondence analysis (to identify population divisions or fractures with no a priori assumption of group membership), and population-assignment methods to detect individual migrants between immediately adjacent areas. These data corroborated observations of inter-area movements from our telemetry database. In northern areas, we found a spatial genetic pattern of IBD, although there was evidence of natural fragmentation from the rugged heavily glaciated coast mountains of British Columbia (BC) and the Yukon. These results contrasted with the spatial pattern of fragmentation in more southern parts of their distribution. Near the Canada–US border area, we found extensive fragmentation that corresponded to settled mountain valleys and major highways. Genetic distances across developed valleys were elevated relative to those across undeveloped valleys in central and northern BC. In disturbed areas, most inter-area movements detected were made by male bears, with few female migrants identified. North–south movements within mountain ranges (Mts) and across BC Highway 3 were more common than east–west movements across settled mountain valleys separating Mts. Our results suggest that relatively distinct subpopulations exist in this region, including the Cabinet, Selkirk South, and the decades-isolated Yellowstone populations. Current movement rates do not appear sufficient to consider the subpopulations we identify along the Canada–US border as 1 inter-breeding unit. Although we detected enough male movement to mediate gene flow, the current low rate of female movement detected among areas is insufficient to provide a demographic rescue effect between areas in the immediate future (0–15 yr). In Alberta, we found fragmentation corresponded to major east–west highways (Highways 3, 11, 16, and 43) and most inter-area movements were made by males. Gene flow and movement rates between Alberta and BC were highest across the Continental Divide

south of Highway 1 and north of Highway 16. In the central region between Highways 1 and 11, we found evidence of natural fragmentation associated with the extensive glaciers and icefields along the Continental Divide. The discontinuities that we identified would form appropriate boundaries for management units. We related sex-specific movement rates between adjacent areas to several metrics of human use (highway traffic, settlement, and human-caused mortality) to understand the causes of fragmentation. This analysis used data from 1,508 bears sampled over a 161,500-km$^2$ area in southeastern BC, western Alberta, northern Idaho, and northern Montana during 1979–2007. This area was bisected by numerous human transportation and settlement corridors of varying intensity and complexity. We used multiple linear regression and ANCOVA to document the responses of female and male bears to disturbance. Males and females both demonstrated reduced movement rates with increasing settlement and traffic. However, females reduced their movement rates dramatically when settlement increased to >20% of the fracture zone. At this same threshold, male movement declined more gradually, in response to increased traffic and further settlement. In highly settled areas (>50%), both sexes had a similar reduction in movements in response to traffic, settlement, and mortality. We documented several small bear populations with male-only immigration, highlighting the importance of investigating sex-specific movements. Without female connectivity, small populations are not viable over the long term. The persistence of this regional female fragmented metapopulation likely will require strategic connectivity management. We therefore recommend enhancing female connectivity among fractured areas by securing linkage-zone habitat appropriate for female dispersal, and ensuring current large source subpopulations remain intact. The fragmentation we documented may also affect other species with similar ecological characteristics: sparse densities, slow reproduction, short male-biased dispersal, and a susceptibility to human-caused mortality and habitat degradation. Therefore, regional inter-jurisdictional efforts to manage broad landscapes for inter-area movement will likely benefit a broad spectrum of species and natural processes, particularly in light of climate change. © 2011 The Wildlife Society.

# Fragmentación de Poblaciones y Movimientos Entre Ecosistemas de Osos Grizzli en el Oeste de Canadá y el Norte de Estados Unidos

**RESUMEN** La fragmentación de la población compromete su viabilidad, reduce la capacidad de una especie a responder a los cambios climáticos y a la larga, puede llegar a reducir la biodiversidad. Hemos estudiado el estado actual de la fragmentación de los osos Grizzli y sus causas posibles en un territorio de 1.000.000 km$_2$ que abarca el oeste de Canadá, el norte de los EE. UU. y el sureste de Alaska. Hemos compilado la mayor parte de la información a partir de proyectos emprendidos con varios fines incluyendo la estimación de las poblaciones y sus tendencias, la fragmentación de los paisajes, la selección del hábitat, los índices vitales y la respuesta al desarrollo humano. Nuestras técnicas primarias de análisis provienen de los análisis genéticos de 3134 osos, complementadas con datos de radio-telemetría de 792 osos. Utilizamos datos de marcadores de microsatélite en el locus 15 apareados con medidas de distancia genética, análisis de aislamiento por distancia, análisis de la covarianza (ANCOVA), regresión lineal múltiple, análisis de correspondencia multifactorial (para identificar divisiones en las poblaciones ó fragmentos sin asumir afiliación a un grupo) y métodos de asignación a fin de detectar los individuos migrantes entre áreas inmediatamente adyacentes. Estos datos corroboran observaciones de movimientos inter-áreas en nuestra base de datos de telemetría. En las áreas del norte se nota un patrón genético espacial de aislamiento por distancia aunque hay prueba de fragmentación natural por las montañas costeras escabrosas y los glaciares de Columbia Británica (BC) y del Yukon. Estos resultados contrastan con el patrón espacial de fragmentación de las partes más al sur y de su distribución. Cerca de la zona fronteriza Canadá-Estados Unidos, vemos una fragmentación extensiva que corresponde a los valles habitados y a las grandes autopistas. Se observaron distancias genéticas más elevadas en los valles desarrollados que en los valles naturales del centro y del norte de BC. En las áreas perturbadas, la mayoría de los movimientos inter-áreas los realizan los osos machos y se detectaron pocas hembras migrantes. Los movimientos norte-sur en las sierras y a través de la autopista 3 de BC fueron más comunes que los movimientos este-oeste en los valles habitados entre las sierras. Nuestros resultados sugieren la existencia de subpoblaciones relativamente distintas en esta región, incluyendo el Cabinet, Selkirk Sur y las poblaciones aisladas desde hace décadas de Yellowstone. Las tasas de movimiento actuales no parecen suficientes para considerar las subpoblaciones que identificamos a lo largo de la frontera Canadá-Estados Unidos como 1 unidad de entrecruzamiento. Aunque hemos detectado suficientes movimientos de machos para intervenir en el flujo de genes, la tasa actual de

movimientos de hembras es insuficiente para proveer un efecto de rescate demográfico entre las áreas en el futuro inmediato (0-15 años). En Alberta, hemos encontrado una fragmentación que corresponde a las principales autopistas este-oeste (3, 11, 16 y 43) y la mayoría de los movimientos inter-áreas fueron realizados por machos. El flujo de genes y las tasas de movimientos entre BC y Alberta son más importantes en la línea divisoria continental al sur de la autopista 1 y al norte de la 16. En la región central entre las autopistas 1 y 11, hemos encontrado pruebas de fragmentación natural asociada con los glaciares y campos de nieve extensivos a lo largo de la línea divisoria continental. Las discontinuidades identificadas formarían límites apropiados para las unidades de gestión. Se han relacionado tasas de movimientos especificas a cada sexo entre áreas adyacentes con varias medidas de uso humano (tráfico en autopistas, poblados y mortalidad causada por humanos) para entender las causas de fragmentación. Este análisis contiene datos de 1508 osos cuyas pruebas fueron recopiladas en un área de 161.500 km$_2$ que abarca el sureste de BC, el oeste de Alberta, el norte de Idaho y el norte de Montana del 1979 al 2007. En esta área se encuentran numerosos corredores de transporte y poblados humanos de intensidad y complejidad varias. Usamos la regresión lineal múltiple y ANCOVA para documentar las respuestas de hembras y machos a las perturbaciones. En ambos grupos se produjo una reducción de la tasa de movimientos ante el aumento de tráfico y poblados. Sin embargo, la tasa de movimiento de las hembras se vio reducida dramáticamente ante un aumento de poblado de más del 20% de la zona fragmentada. En este mismo punto la tasa de movimiento de los machos se redujo más gradualmente. En las zonas altamente pobladas (más del 50%) ambos sexos mostraron respuestas similares ante el tráfico, los poblados y la mortalidad. Se documentaron varias pequeñas poblaciones de osos con inmigración de machos solamente, lo que pone de manifiesto la importancia de examinar los movimientos específicos de cada sexo. Sin la conectividad de la hembra, las pequeñas poblaciones no son viables a largo plazo. La persistencia de esta meta-población fragmentada regional de hembras probablemente necesitará una gestión de conectividad estratégica. Por lo tanto, recomendamos acentuar la conectividad de hembras entre zonas fragmentadas para asegurar las conexiones entre zonas de hábitat apropiadas a la dispersión de hembras y asegurar la sobrevivencia de las grandes subpoblaciones originales actuales. La fragmentación aquí descrita puede también afectar otras especies de características similares: escasa densidad, reproducción lenta, la tendencia a la dispersión de los machos, susceptibilidad a mortalidad causada por humanos y degradación del hábitat. En consecuencia, un amplio espectro de especies y procesos naturales podrán beneficiar de los esfuerzos regionales interjurisdiccionales de gestión de paisajes de gran extensión para movimientos inter-áreas, particularmente ante los cambios climáticos.

# Fragmentation de la Population et Mouvements Inter-Ecosystèmes des Ours Grizzlis dans L'ouest du Canada et le Nord des États-Unis

**RÉSUMÉ** La fragmentation des populations compromet la viabilité des populations, réduit la capacité des espèces à s'adapter au changement climatique, pouvant ainsi réduire la biodiversité. Nous avons étudié l'état actuel et les causes potentielles de fragmentation chez les grizzlis sur environ 1 000 000 km$^2$ incluant l'ouest du Canada, le nord des Etats-Unis, et le sud-est de l'Alaska. La majorité de nos données provient de projets conduits avec différents objectifs de recherche, incluant l'estimation de la taille et de l'évolution démographique des populations, la fragmentation du paysage, la sélection d'habitat, les taux vitaux, et les réponses au développement urbain. Nos principales techniques d'analyse étaient basées sur l'analyse génétique de 3 134 grizzlys, et complétées par des données radio télémétriques provenant de 792 ours. Nous avons utilisé des données provenant de 15 locus microsatellites, combinées avec des mesures de distance génétique, d'isolement par la distance, d'analyse de covariance (ANCOVA), de régression linéaire multiple, d'analyse multifactorielle par correspondance (pour identifier les divisions de populations sans supposition préalable sur l'appartenance de chaque individu à un groupe), et avec des méthodes déterminant l'appartenance à une population pour détecter les individus migrant entre zones directement adjacentes. Ces données ont corroboré des observations de mouvements d'ours entre zones provenant de notre base de données télémétriques. Dans les zones du nord, nous avons trouvé un effet spatial d'isolement génétique par la distance, bien qu'il y avait des signes de fragmentation naturelle due aux chaînes côtières englacées de Colombie Britannique (BC) et du Yukon. Ces résultats contrastent avec les effets de fragmentation observés dans les zones plus au sud. Près de la frontière Canada-Etats-Unis, nous avons trouvé une fragmentation élevée correspondant aux vallées montagneuses développées et aux autoroutes principales. Les distances génétiques entre vallées développées étaient élevées en comparaison avec celles observées entre vallées non-développées dans le centre et le nord de la Colombie Britannique. Entre les zones perturbées, la majorité des mouvements étaient effectués par les ours mâles, tandis que peu de femelles en dispersion étaient identifiées. Les mouvements nord-sud au sein des chaînes de montagnes et traversant l'autoroute 3 de Colombie Britannique étaient plus fréquents que les mouvements est-ouest effectués entre les vallées développées séparant ces zones

montagneuses. Nos résultats suggèrent que des sous-populations plutôt distinctes existent dans cette région, incluant le Cabinet, Selkirk South, et les populations du Yellowstone isolées depuis plusieurs décennies. Les taux de mouvements actuels ne semblent pas suffisants pour considérer les sous-populations identifiées le long de la frontière Canada-Etats-Unis comme une unité de reproduction. Malgré le fait que nous avons détecté assez de mouvements de la part des mâles pour favoriser le flux de gènes, le faible taux de mouvements effectué par les femelles est insuffisant pour fournir un effet de renforcement démographique entre zones dans un futur immédiat (0-15 ans). En Alberta, nous avons trouvé que la fragmentation correspondait aux autoroutes est/ouest principales (autoroutes 3, 11, 16, et 43) et que la plupart des mouvements entre zones étaient réalisés par les mâles. Les taux de flux génétique et de mouvements entre l'Alberta et la Colombie Britannique étaient les plus élevés à travers la ligne de partage des eaux continentales (Continental Divide) au sud de l'autoroute 1 et au nord de l'autoroute 16. Dans la région centrale entre les autoroutes 1 et 11, nous avons détecté des signes de fragmentation naturelle associés aux larges glaciers et aux champs de glace situés le long du Continental Divide. Les discontinuités que nous avons identifiées forment des limites appropriées pour la création d'unités de gestion. Nous avons lié les taux de mouvements de chaque sexe entre zones adjacentes à plusieurs mesures d'activité humaine (trafic autoroutier, développement, mortalité due à l'homme) pour comprendre les causes de la fragmentation. Cette analyse a utilisé des données de 1508 ours obtenues sur une surface de 161 500 km$^2$ incluant le sud-est de la Colombie Britannique, l'ouest de l'Alberta, le nord de l'Idaho, et le nord du Montana entre 1979 et 2007. Cette surface était segmentée par de nombreuses infrastructures de transport, et par des corridors de développement d'intensité et de complexité variées. Nous avons utilisé des régressions linéaires multiples et des ANCOVA pour documenter les réponses des ours femelles et mâles aux perturbations. Les mâles ainsi que les femelles ont montré une réduction du taux de mouvements avec l'augmentation du développement et du trafic. Cependant, les femelles réduisait leurs mouvements très fortement quand le taux de développement était supérieur à 20% autour la zone autoroutière. A ce même seuil, les mouvements des mâles déclinaient de manière plus graduelle en réponse à l'augmentation du trafic routier et du développement. Dans les zones les plus développées (>50%), les 2 sexes avaient une diminution similaire du taux de mouvements en réponse au trafic, au développement, et à la mortalité. Nous avons documenté plusieurs petites populations d'ours avec une immigration faite uniquement par les mâles, soulignant l'importance de l'étude des mouvements de chaque sexe. Sans connectivité entre les femelles, les petites populations ne sont pas viables à long terme. La maintenance de cette métapopulation régionale fragmentée, due à l'absence de mouvements des femelles, va sûrement demander une gestion stratégique de la connectivité. Nous recommandons donc d'améliorer la connectivité des femelles en sécurisant des surfaces d'habitat "lien" appropriées pour faciliter leur dispersion entre les zones fragmentées, et d'assurer que les grandes sous-populations sources restent intactes. La fragmentation que nous avons documentée peut aussi affecter d'autres espèces ayant des caractéristiques écologiques similaires: faibles densités, reproduction lente, dispersion des mâles sur de courtes distances, et sensibilité à la mortalité due à l'homme ainsi qu'à la dégradation de l'habitat. Donc, des efforts régionaux entre juridictions pour gérer de larges paysages pour faciliter les mouvements entre zones vont probablement bénéficier un large spectre d'espèces et de processus naturels, en particulier en vue du changement climatique.

## Contents

# INTRODUCTION

Movement is an important process in population ecology (Hanski and Gilpin 1997, Clobert et al. 2001), chiefly allowing species to meet their ecological needs, but also helping them persist during dramatic ecological changes such as those brought on by human development and changing climates (Nathan et al. 2008). The interruption of movement by fragmentation is a major force underlying the recent extinction crisis (Wilcox and Murphy 1985, Zavaleta et al. 2009). Understanding fragmentation processes will improve our ability to manage landscapes to facilitate movement. Nonetheless, inter-population movements have been largely ignored in most population studies because of a lack of reliable data (MacDonald and Johnson 2001). The rise in prominence of the metapopulation paradigm has increased interest in obtaining inter-population movement data and incorporating them into population investigations (Young and Clarke 2000).

Dispersal is most often done by juveniles, and in mammals, males usually disperse farther than females (Greenwood 1980). Dispersal plays a role at multiple levels of biological organization. It can minimize inbreeding of individuals (Pusey 1987, Johnson and Gaines 1990, Pusey and Wolf 1996, Perrin and Goudet 2001), reduce competition for mates and resources among relatives (Greenwood 1980, Dobson 1982, Waser 1985), or both (Dobson and Jones 1985, Gandon and Michalakis 2001). At the population level, dispersal facilitates gene flow decreasing population structure (Slatkin 1987, Chesser et al. 1993) while maintaining or increasing genetic diversity (Hedrick 1995, Bushar et al. 1998, Paetkau et al. 1998b). It can facilitate source–sink dynamics (Pulliam 1988, Dias 1996), and drive colonization and recolonization of unoccupied habitats (Hanski and Gilpin 1997). Dispersal influences abundance and distribution at a species level (MacArthur and Wilson 1967, Dieckmann et al. 1999), facilitates range expansion (Lubina and Levin 1988, Swenson et al. 1998), and resists range contraction (Channell and Lomolino 2000a, Mattson and Merrill 2002).

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). At broad temporal and spatial scales, smaller population fragments have a higher likelihood of succumbing to unfavorable demographic forces (Lande 1988, Woodroffe and Ginsberg 1998, Parks and Harcourt 2002). Because demographic processes are the proximate cause of population extirpations, efforts to understand and resist range contractions require a means to measure movement at the level of specific individuals on a particular landscape. However, measuring natal dispersal and inter-population movements is challenging (Clobert et al. 2001), particularly for wide-ranging, long-lived species that occur at low densities. Studying movement is particularly difficult in multi-population systems (Koenig et al. 1996), yet is often required to understand population fragmentation.

Radiotelemetry has been used to measure movements, particularly by large mammals that can carry transmitters (Koenig et al. 1996, McLellan and Hovey 2001, Waser et al. 2001), but has been more successful at small (500–5,000 km$^2$) than large (10,000–50,000 km$^2$) spatial and temporal scales (Palsboll 1999). New telemetry systems using satellites to locate and record locations (Global Positioning Systems [GPS] telemetry) allow movement to be followed over large areas with increased location frequency, but limitations remain to the degree that collars are seldom worn during natal dispersal.

Another method for studying movement is with genetic assignment of origins, which can be compared to capture locations to infer movements since birth by specific individuals (Waser and Strobeck 1998, Pritchard et al. 2000, Paetkau et al. 2004). This ability to identify individual migrants forms the basis for sex-specific analyses that allow an understanding of demographic processes. Empirical studies using these techniques are now emerging (Manel et al. 2003, Proctor et al. 2005, Dixon et al. 2006, Manel et al. 2007). These methods have been tested on systems with known individual histories (Maudet et al. 2002), but few studies have applied them to large-scale systems. This approach is limited to population systems in which historic levels of gene flow have been low enough to permit genetic differentiation of populations, which is generally the case in population systems of greatest interest to conservation (Paetkau et al. 2009).

These methods are different from population genetics methods in which models are used to derive indirect estimates of long-term migration rates, most famously relating Wright's (1965) $F_{ST}$ statistic to inter-population migration rates (Slatkin 1985, Neigel 1997). Such traditional approaches do not provide inference about the movement of individual animals, rendering them inappropriate for assessing current patterns of movement, particularly in dynamic population systems (Ims and Yoccoz 1997, Steinberg and Jordan 1997, Whitlock and McCauley 1999, Rousset 2001, Neigel 2002). Using these methods on species with male-biased dispersal may detect male-mediated gene flow but potentially overlook fragmentation of females with demographic consequences (e.g., Schwartz et al. 2002b, Cegelski et al. 2003, Banks et al. 2005, Campbell and Strobeck 2006).

The North American range of grizzly bears (Ursus arctos) has contracted in the past century and a half because of human-caused mortality, habitat loss, and population fragmentation (Servheen 1999, Mattson and Merrill 2002). In the conterminous United States (US), 98% of their range has been lost (Mattson and Merrill 2002), with regions of extirpation extending north to include the non-mountainous regions of Alberta and portions of southern British Columbia (BC; Fig. 1; Benn 1998, McLellan 1998, Ross 2002, Nielsen et al. 2004). Grizzly bears in the Yellowstone region have been isolated from northern populations for close to a century (Merriam 1922, Mattson and Merrill 2002). At present, the region spanning the Canada–US border represents the southern limit of the contiguous North American range, making this area the active front for future changes in range. This region is currently affected by fragmentation (U.S. Fish and Wildlife Service [USFWS] 1993, McLellan 1998, Proctor et al. 2005, Apps et al. 2009), making it particularly important to understanding the factors that influence movement between fragments.

Fragmentation can create small isolates of grizzly bears in patches that cover thousands of square kilometers because the species occurs at low densities (i.e., 5–60 bears/1,000 km$^2$) in the interior of western North America where there are no or limited numbers of salmon (McLellan 1989a, Boulanger et al. 2005a, b, Mowat et al. 2005, Alberta Grizzly Bear Inventory Team 2007,
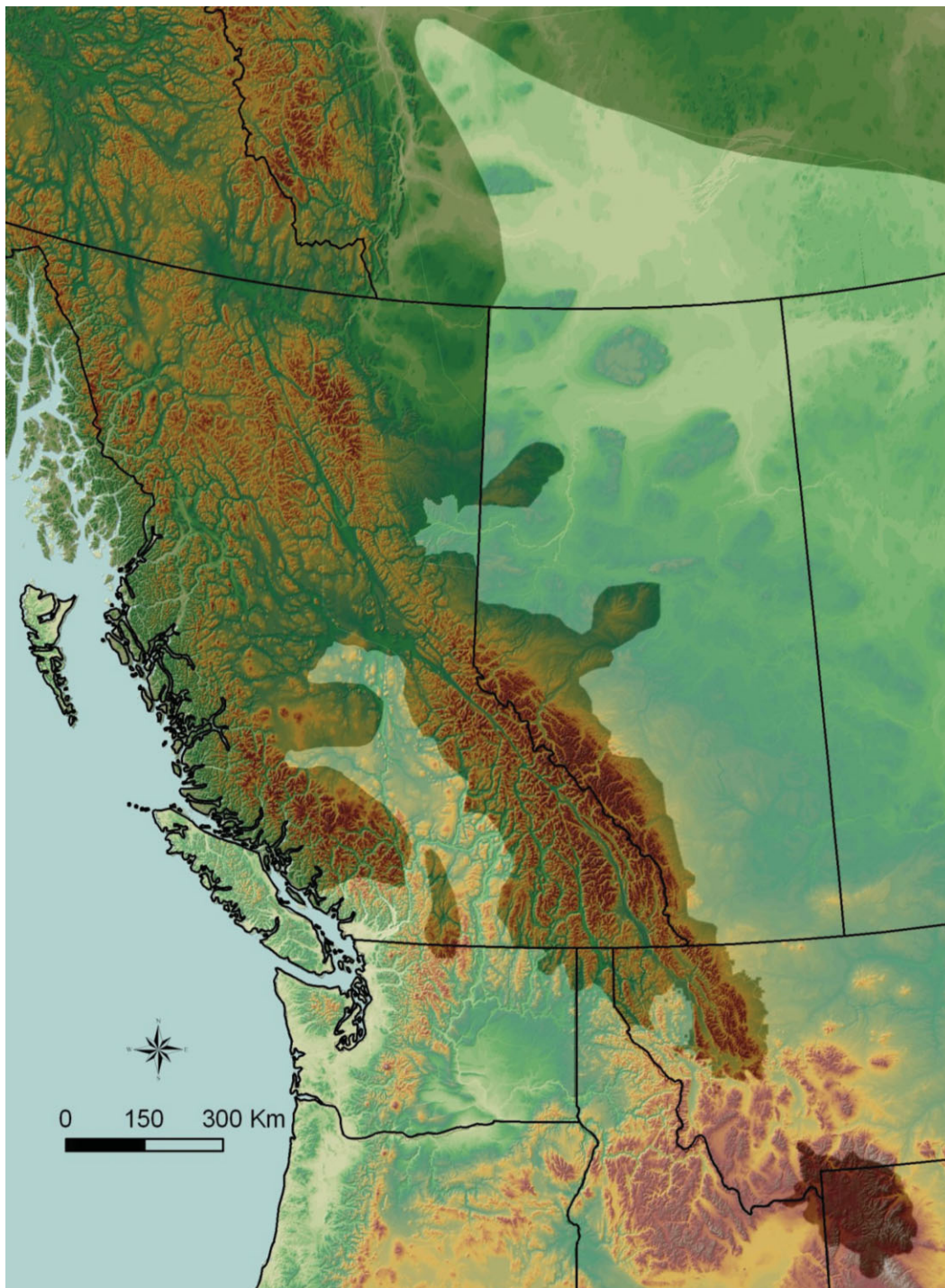
**Figure 1.** Topographic relief of study area. Shaded area is the current grizzly bear distribution in western North America.

Grizzly Bear Inventory Team 2008). Because of their reputation as dangerous carnivores, grizzly bears often experience higher rates of anthropogenic mortality in human-dominated landscapes than can be sustained by their low reproductive rate (McLellan 1989*b*, Miller 1990, Garshelis et al. 2005). Landscape fragmentation exacerbates concerns about population viability. When linear human developments separate regions of occupied habitat, they create extended areas of interface between bears and humans, exacerbating the problem of excessive mortality (Woodroffe and Ginsberg 1998).

Great effort has gone into grizzly bear conservation in the conterminous US in the past 2 decades (USFWS 1993, Wakkinen and Kasworm 1997, Mace and Waller 1998, Schwartz et al. 2002*a*, Boyce and Waller 2003, Mace 2004, Pyare et al. 2004, Wakkinen and Kasworm 2004, Mace et al. 2012). Management effort in the Yellowstone ecosystem resulted in increased population size and expanded distribution, resulting in the recommendation that this population be removed from the threatened species list of the Endangered Species Act (Schwartz et al. 2006*a*, *b*; USFWS 2007). Recently, assessments of

population size (Kendall et al. 2008, 2009) and trend (Mace et al. 2012) have been undertaken in the Northern US Rocky Mountains. Across the border in southern Canada, studies of abundance and fragmentation have identified population fragments requiring conservation effort to remain viable (Proctor et al. 2004b, 2005).

Movements of radiocollared bears in the Rocky mountain ranges (Mts) over the past 30 yr suggested east–west population fragmentation between Canada–US trans-border populations (Rockies, Cabinets, Purcell South Yaak, Selkirk South; USFWS 1993, McLellan 1998). To align conservation efforts with biologically based population units in this region, it is necessary to quantify the extent to which bears inhabiting adjacent Mts are demographically connected, particularly for the female segment of the population. Small population units may require immigration of females to ensure demographic viability, even if males are providing genetic connectivity (Proctor et al. 2004b).

We studied current rates of inter-population movement by grizzly bears in North America with a full suite of genetic (e.g., genetic distance measures, individual-based genetic analyses) and telemetry techniques that allowed us to identify sex-specific population fragmentation, explore its causes, and thus react appropriately with conservation management in an increasingly human-dominated landscape. Proctor et al. (2005) used genetic analyses to investigate sex-specific fragmentation in southeastern BC. The present work expands on Proctor et al. (2005) by providing a more comprehensive view over a broader spatial area. Our overall goal was to explore the gene flow and movements of grizzly bears across a range of human-influenced disturbance regimes at the southern limit of the contiguous North American grizzly bear range in northern US and southern Canada, and to compare these with gene flow and movements in relatively undisturbed regions in central and northern Canada. Our analyses were across multiple scales, examining gene flow patterns between broad regions and movements of individual bears between adjacent areas. Our study objectives were to determine where bear populations were fragmented naturally, identify sex-specific fragmentation, describe biologically based management units (MU) based on patterns of inter-breeding individuals and bear movement patterns, delineate isolated populations that may carry an elevated conservation risk, identify the spatial relationship of regional subpopulations, and perhaps most importantly, determine the presence and possible causes of anthropogenic fragmentation for male and female bears.

## STUDY AREA

Grizzly bears exist primarily in the mountainous regions of western North America (Fig. 1). Our genetic samples comprised 3,134 grizzly bears from approximately 1,000,000 km$^2$ of the grizzly bear distribution in the northern conterminous US (northwestern Montana, northwestern Wyoming, northern Idaho), most of BC and Alberta, and 3 small areas in the southern Northwest Territories (NWT), Yukon, and southeastern Alaska (Fig. 2). Our radiotelemetry sample of 792 individuals came from a subset of this area in northern Montana, southeastern BC, and western Alberta (Fig. 3).

The predominantly north–south Mts influence climate patterns across our study area. Precipitation (6 cm/yr to >200 cm/yr) and elevation (0 m to approx. 4,000 m) vary widely, producing ecological conditions ranging from dry grasslands and temperate and boreal forests to boreal and alpine tundra. Grizzly bear densities vary accordingly, with the more productive areas on the coast and the interior supporting approximately 80–90 bears/1,000 km$^2$ (McLellan 1989a, MacHutchon et al. 1993) and the drier systems harboring as few as 5–8 bears/1,000 km$^2$ (Boulanger et al. 2005b, Proctor et al. 2007).

The quality and type of bear diets vary across our study area with climate, topography, and location. In coastal and several interior areas, abundant precipitation, mostly falling as snow during winter, creates productive ecosystems (Meidinger and Pojar, 1991). Snow on steep mountain slopes results in avalanche paths that can provide abundant forage for grizzly bears in the spring and throughout the foraging season. Moist and productive riparian habitats scattered across the study area also provide excellent foraging habitat. In the summer, sub-alpine and alpine environments produce plentiful vegetative foods for grizzly bears. Inland, drier summer weather is associated with more frequent wildfire. Old burns (30–70 yr) from forest fires often yield berry crops that form an important part of bear diets (Hamer and Herrero 1987; McLellan and Hovey 1995; Hamer 1996, 1999). Other areas that have less rugged mountains and less precipitation because of a rain shadow effect have fewer avalanche chutes and less alpine habitats, adding to the variability across our study area. Higher densities of ungulates and the availability of fish in some areas allow some bears to include a large portion of meat in their diets. In areas near the Pacific coast, grizzly bears feed on salmon extensively (Mowat and Heard 2006). Most interior bears subsist on a vegetarian-dominated diet, although fluctuations in berry crops or the absence of *Vaccinium* spp. in some areas make the quality of these vegetarian diets variable (McLellan and Hovey 1995). The lower-quality habitats (e.g., foothills of Alberta) support lower densities of bears (5–15 bears/1,000 km$^2$; Boulanger et al. 2005a, b).

Indigenous people lived in the study area for millennia and had a significant effect on grizzly bear distribution (Mattson and Merrill 2002). Following fur traders of the 1700s and early 1800s, and gold miners of the mid-1800s, European and Asian immigrants as well as Metis began settling the area in the mid-1800s and ranching later in the century. The Canadian Pacific Railway crossed the continent in 1885 and the Great Northern Railroad crossed the US in 1893; both greatly increased settlement of the western portion of the continent. By the end of the 1800s, every major valley in the southeastern portion of the study area had been settled by people of European and Asian descent. If there was gold or silver found, there were sometimes far more people living there a century ago than there are today. Early settlers were notoriously intolerant of bears, extirpating grizzly bears in some areas and reducing their numbers in wilderness areas (Wright 1909, Storer and Tevis 1955).

Today, human development within grizzly bear range consists mainly of scattered rural settlements and concentrations of people in towns of <20,000. Forestry is the dominant industry in BC, Montana, and northern Idaho. Other resource-extraction activities, such as mining and oil and gas exploration and development,
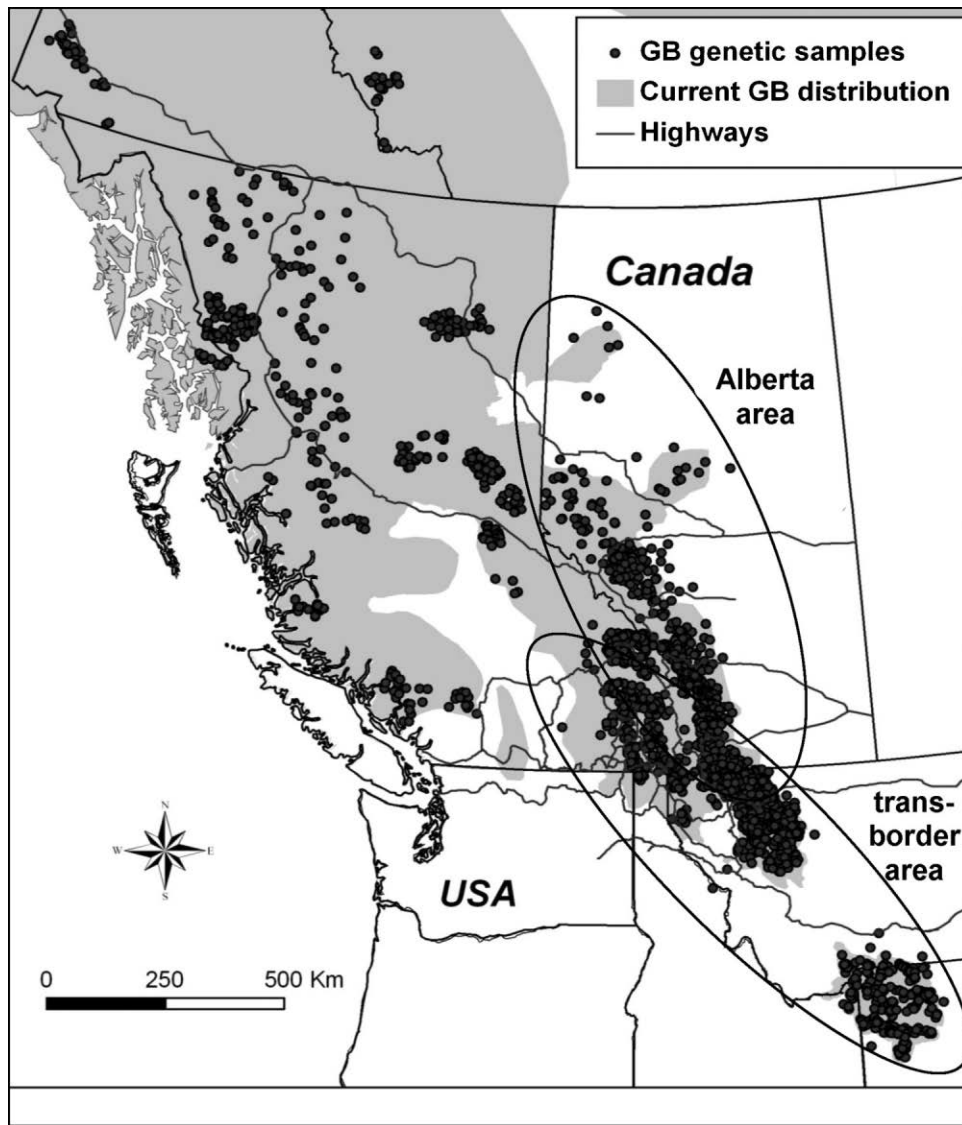
**Figure 2.** The spatial extent of the genetic sample base ($n = 3,134$) of grizzly bears (GB) over approximately 1,000,000 km² of the northern conterminous United States, western Canada, and southeast Alaska. Samples were collected between 1983 and 2007 and genotyped at 15 microsatellite loci. Labeled ovals depict our trans-border and Alberta sub-study regions.

are common in Montana, Alberta, and parts of BC. Major hydroelectric facilities have flooded several major valleys in each jurisdiction. Agriculture occurs in portions of grizzly bear range, particularly in portions of Alberta and Montana, and outdoor recreation including hunting is widespread in southern Canada and the conterminous US. Human influence also varies greatly across our study area, with a concentration of human disturbance in Montana, Wyoming, Idaho, and southern Canada in the form of major highways, settled valleys, and a higher density of towns and cities.

We divided our study area into northwestern and southeastern regions based on 2 factors. First, Paetkau et al. (1997) determined that isolation-by-distance (IBD) was the prevalent pattern for genetic relationships in undisturbed northern regions of North America. Second, we considered previous work by Proctor et al. (2005), which suggested highways and settled valleys are fragmenting bear populations. We chose the region around Highway 16 near the BC–Alberta border as our divider because human density, and therefore disturbance, decreased dramatically to the

north and west, and both are more pronounced to the south (Fig. 4).

For jurisdictional convenience, we divided the southeastern study area into 2 sub-areas, trans-border and Alberta (Fig. 2). There is overlap at the boundary between these jurisdictional designations in our analyses. The trans-border area extends over the Canada–US border across southern BC and south to the Yellowstone Ecosystem. Within Canada, it includes the Selkirk, Purcell, and Rocky Mountains from the Canada–US border to just north of BC Highway 3. The Alberta area includes all of Alberta's grizzly bear distribution, which parallels the Continental Divide from southern Alberta north, and west slightly into BC.

## METHODS

### Study Design

This study extends previous work that examined gene flow, movements, and fragmentation of grizzly bears within southeast
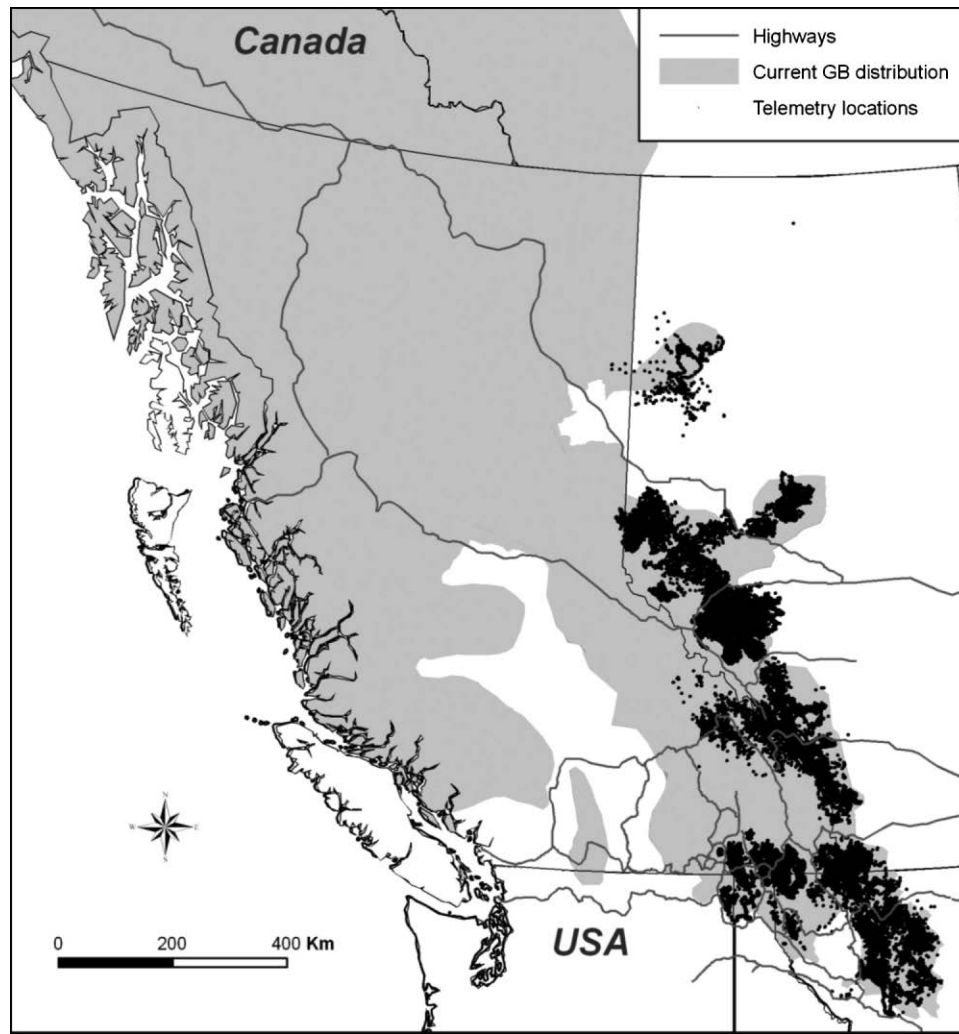
**Figure 3.** The spatial extent of our telemetry sample base ($n = 792$) grizzly bears (GB) spanning approximately 200,000 km² across our southeastern study area in the northern United States, southern British Columbia, and western Alberta. Telemetry data were obtained using very high frequency (VHF) and Global Positioning System (GPS) telemetry from 1979 to 2007.

BC, southwest Alberta, and adjacent portions of the US (Proctor et al. 2002, 2005) and detected fragmentation of grizzly bears in these human-influenced landscapes. In more northwestern areas of the grizzly bear distribution where there is less human influence, bear genotypes follow an IBD pattern where allele frequencies vary with geographic distance (Paetkau et al. 1997, 1998b). We used data from northern and southern grizzly bears to explore patterns in IBD, natural fragmentation, and anthropogenic fragmentation in greater detail. Our approach was a 4-staged hierarchical analysis that we briefly outline, accompanied by specific hypotheses tested with each analysis.

Our first analysis (isolation-by-distance) was to examine IBD and natural fragmentation. We hypothesized that bears in our northwestern study area were predominantly influenced by an IBD genetic structure (hypothesis A1), and that grizzly bears in our southeastern study area were predominantly influenced by factors other than IBD (hypothesis A2), such as anthropogenic fragmentation. This analysis was carried out in 2 steps using genetic samples collected from across our entire study area. Initially, we identified genetic discontinuities through a genetic clustering method without a priori assumptions of group

membership. Where IBD explained most of the variation (our northwestern study area), we explored possible sources of natural fragmentation, such as glaciated Mts. In areas where IBD explained a relatively minor amount of the variation (our southeastern study area), we explored hypotheses that anthropogenic fragmentation contributed to movement and gene flow patterns.

The southeastern study area was the focus of analytical stages 2–4. In the second analysis (genetic clustering), we hypothesized that genetic discontinuities within our southeastern study area corresponded to mountain valleys with human settlement and major highways (hypothesis B). This hypothesis was explored using the same clustering method mentioned above. In our third stage of analysis (migrant determination), we estimated sex-specific movement rates between adjacent areas to determine the extent and intensity of fragmentation. This analysis used genetically derived, sex-specific movement rates and telemetry data collected over several decades. These results, when combined with the cluster analysis, were used to delineate subpopulations. Besides providing additional testing of hypothesis B, Analysis 3 developed the dataset (sex-specific movement rates) that was used to test hypotheses within Analysis 4. Finally, in our fourth
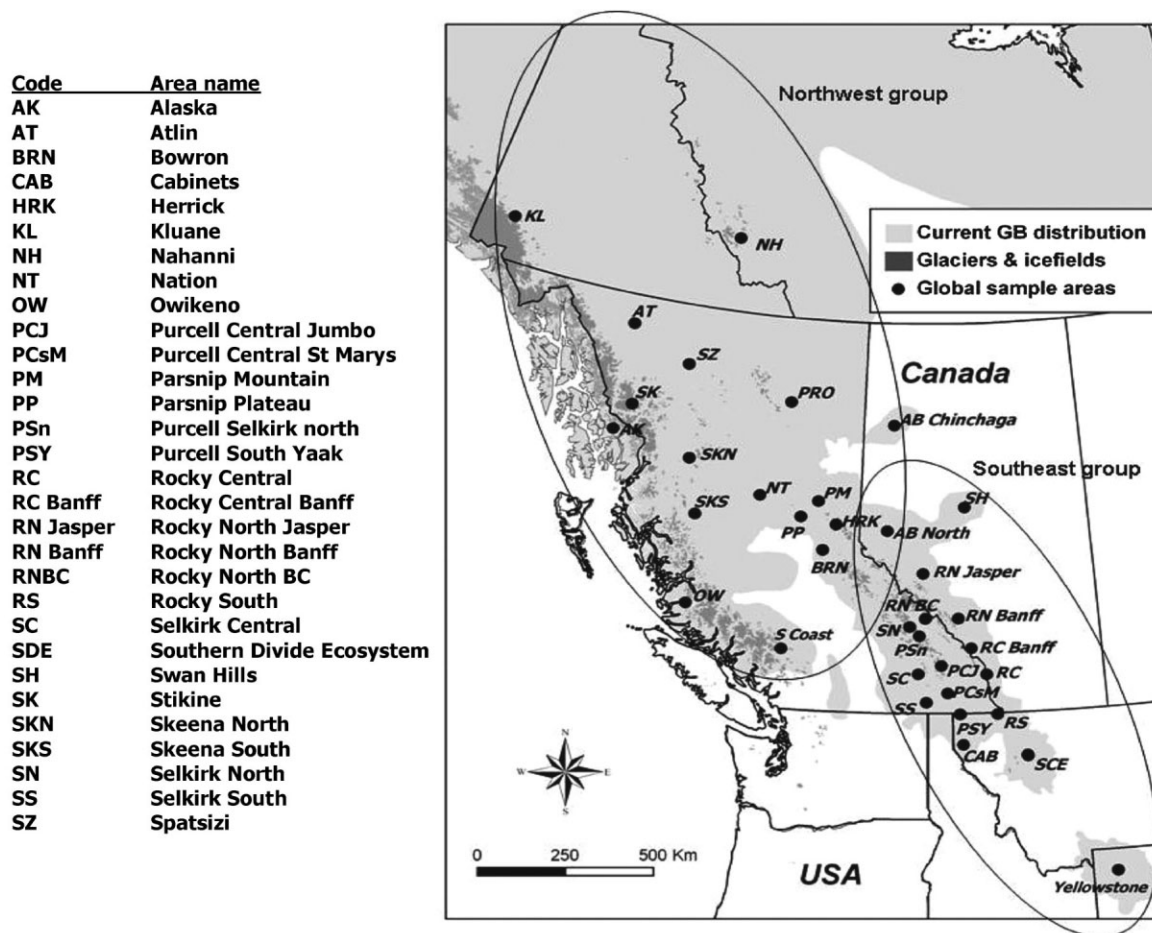
| Code | Area name |
|------|-----------|
| AK | Alaska |
| AT | Atlin |
| BRN | Bowron |
| CAB | Cabinets |
| HRK | Herrick |
| KL | Kluane |
| NH | Nahanni |
| NT | Nation |
| OW | Owikeno |
| PCJ | Purcell Central Jumbo |
| PCsM | Purcell Central St Marys |
| PM | Parsnip Mountain |
| PP | Parsnip Plateau |
| PSn | Purcell Selkirk north |
| PSY | Purcell South Yaak |
| RC | Rocky Central |
| RC Banff | Rocky Central Banff |
| RN Jasper | Rocky North Jasper |
| RN Banff | Rocky North Banff |
| RNBC | Rocky North BC |
| RS | Rocky South |
| SC | Selkirk Central |
| SDE | Southern Divide Ecosystem |
| SH | Swan Hills |
| SK | Stikine |
| SKN | Skeena North |
| SKS | Skeena South |
| SN | Selkirk North |
| SS | Selkirk South |
| SZ | Spatsizi |

**Figure 4.** Study area map with ovals delineating southeastern and northwestern sample regions. Genetic samples were collected between 1983 and 2007 and telemetry data were collected between 1979 and 2007. Solid circles represent geographic centers of grizzly bear (GB) sample areas over our entire study area. Overlap of ovals represents the fact that the Alberta North area was used in analyses of both northwestern and southeastern areas.

analysis (causes of fragmentation), we used individual-based movement rates derived from the migrant analysis to investigate the potential causes of fragmentation. We hypothesized that grizzly bear inter-area movement rates are influenced by human disturbance variables (i.e., traffic, settlement, and mortality; hypothesis C1), and that females and males respond differently to human influence variables in their inter-area movement rates (hypothesis C2).

### Field Techniques

We used genetic sampling and radiotelemetry for our data collection. A portion of our genetic and telemetry samples were collected specifically for fragmentation analysis, but most came from DNA sampling used to estimate population abundance and telemetry projects with other research goals.

*DNA sampling.*—Genetic samples were obtained from bears live-captured for research or management, from bears killed by hunters, or from DNA-based population surveys designed for estimation of population size or fragmentation (Table 1). Samples came from the entire remnant distribution in the conterminous 48 states and Alberta, much of southeastern BC, a portion of southwestern BC, part of central and northern BC, southern Yukon, Northwest Territories, and southeastern Alaska (Fig. 2).

Most hair sampling designed to estimate population abundance was distributed systematically using a grid, with hair samples collected approximately every 2 weeks in spring and early summer (Woods et al. 1999, Mowat and Strobeck 2000). We collected other genetic samples during visits to natural bear rubs (trees, sign and fence posts, power poles, and fence lines) fitted with barbed-wire hair collectors (Grizzly Bear Inventory Team 2008; Kendall et al. 2008, 2009). We stored hair samples at room temperature in paper envelopes. Tissue samples from dead bears (hunter kills or other causes) and ear tissue or blood from live captures were either frozen or placed in lysis buffer prior to analysis. After extracting DNA from snagged hair follicles and tissues, we used microsatellite analysis to identify individuals (Woods et al. 1999, Paetkau 2003). Samples obtained through DNA surveys (the vast majority of samples) were georeferenced with a GPS unit. Hunter-killed samples in BC were located with the accuracy of a watershed drainage (approx. 100 km²), whereas hunter-killed samples in Alberta were located by MU (approx. 1,000 km²).

*Radiotelemetry.*—The cumulative telemetry effort was carried out over several decades in some areas, and over a few years in others (Table 2). Our telemetry sample was limited to the southeastern region, which included Alberta, extreme southeastern BC, and northern Montana and Idaho (Fig. 3, Table 1). The

**Table 1.** Sources for genetic samples, previously analyzed genotypes, and telemetry data for grizzly bears collected between 1979 and 2007 across western North America. Mts abbreviates Mountains.

| Sample type | Ecosystem | Agency | Investigators |
|---|---|---|---|
| Genetic | Rocky Mts | US Geological Survey, | K. Kendall, C. Schwartz |
| Telemetry | Rocky Mts | Montana Fish Wildlife and Parks | R. Mace, J. Waller |
| Genetic and telemetry | Rocky Mts | BC Ministry of Forests, Lands, and Natural Resource Operations | B. McLellan |
| Genetic | Rocky Mts | BC Ministry of Forests, Lands, and Natural Resource Operations | G. Mowat |
| Genetic and telemetry | Rocky Mts | Foothill Research Institute | G. Stenhouse |
| Genetic | Rocky Mts | Alberta Sustainable Resource Development | B. McClymont |
| Genetic and telemetry | Rocky Mts | Birchdale Ecological Ltd. | M. Proctor |
| Genetic and telemetry | Rocky Mts | Parks Canada | M. Gibeau |
| Genetic and telemetry | Purcell Mts | US Fish & Wildlife Service | W. Kasworm |
| Genetic and telemetry | Purcell Mts | Birchdale Ecological | M. Proctor |
| Genetic | Cabinet Mts | US Fish & Wildlife Service | W. Kasworm |
| Genetic and telemetry | Selkirk Mts | Idaho Fish & Game | W. Wakkinen |
| Genetic and telemetry | Selkirk Mts | Birchdale Ecological Ltd. | M. Proctor |
| Genetic | Selkirk Mts | BC Ministry of Forests, Lands, and Natural Resource Operations | G. Mowat |
| Genetic and telemetry | Selkirk Mts | Parks Canada | J. Woods |
| Genetic | South Coast Mts | Aspen Wildlife Research Inc | C. Apps |
| Genetic | Central & North BC | BC Ministry of Forests, Lands, and Natural Resource Operations | G. Mowat, H. Schwantze D. Heard, L. Ciarmiello |
| Genetic | SE Alaska | Alaska Fish & Game | R. Flynn |
| Genetic | NWT[a] | Parks Canada, | D. Tate, J. Weaver |
| Genetic | Yukon | Yukon Department of Environment | R. Maraj |

[a] NWT, Northwest Territories.

areas over which telemetry data were examined for inter-area movements were similar to the genetic sampling area except that no telemetry effort occurred in the Selkirk Central and Rocky Central areas. Also, only a portion of the Purcell Central and Rocky South BC areas had collared bears.

Bears were captured for radiocollaring by a variety of techniques including Aldrich leg-hold snares, culvert traps, and helicopter darting. In Canada, animal care guidelines of the Canada Council on Animal Care Standards and of Cattet et al. (2003) were based on earlier practitioners of our methods, which were in turn followed by later practitioners. In the US, methods were similar to those described by Jonkel (1993) and the University of Montana Institutional Animal Care and Use Committee (protocol identification number is 007-06CSFWB-040106).

We used radiocollars from various companies (Telonics, Mesa, AZ; Lotek, Newmarket, ON; Televilt, Lindesberg, Sweden; Advanced Telemetry Systems, Isanti, MN). During 1974–1999, we used very high frequency (VHF) collars that were located every 4–14 days through the non-denning season, primarily with fixed-wing aircraft. During 1999–2007, we used GPS collars. The GPS collars were a combination of store-on-boards, spread-spectrum collars allowing periodic remote data downloads, and Argos collars allowing frequent remote downloads via satellite. We also used data from ear-tag returns of bears marked in 1 area and caught or found dead in another region. Movement data were examined by displaying location data derived from radiocollars or from ear-tag returns on maps within a Geographic Information System (GIS).

## Laboratory Techniques

We extracted DNA using the Chelex protocol before 1998 (Walsh et al. 1991), and DNeasy columns (Qiagen Inc., Mississauga, Ontario, Canada) after 1998. We initially identified individuals with 6 or 7 microsatellite loci (Paetkau et al. 1998a, Woods et al. 1999) and genotyped all individuals to 15 loci to increase analytical power. To eliminate genotypes created through genotyping error (Gagneux et al. 1997, Goossens et al. 1998, Taberlet et al. 1999, Paetkau 2003), we further scrutinized 15 locus genotypes for close mismatches. We reran all pairs of samples that matched at 1, 2, or 3 loci to confirm the genotype or resolve errors (Paetkau 2003). We used the following markers: G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10U, G10X, MU50, MU59, CXX20, and CXX110 (Ostrander et al. 1993, Taberlet et al. 1997, Paetkau et al. 1998a, Proctor et al. 2002). We determined genotypes on Applied Biosystems 377 and 3100 automated sequencers, and scored genotypes with the help of Genotyper software (Applied Biosystems, Foster City, CA). We distinguished grizzly bear from black bear samples using a species-specific microsatellite marker (G10J; Paetkau 2003) and determined sex according to protocols detailed by Taberlet et al. (1993) before 1998, and by Ennis and Gallagher (1994) after 1998.

## Analysis

We evaluated all 15 loci in all sampling areas for conformance to Hardy–Weinberg assumptions of random mating by testing for a deficit of heterozygotes (Rousset and Raymond 1995) and linkage disequilibrium (Garnier-Gere and Dillman 1992). We adjusted critical values for the experiment-wise error rate using the Dunn-Sidak method (Sokal and Rohlf 1995). We performed these tests within GENEPOP 3.1 (http://genepop.curtin.edu.au, accessed 10 Nov 2007; Raymond and Rousset 1995). We calculated unbiased estimates of mean expected heterozygosity ($H_E$) as an index of relative genetic variability (Nei and Roychoudhury, 1974). Further analyses consisted of 4 primary multi-staged analyses (see Study Design section).

*Analysis 1: Isolation-by-distance and natural fragmentation.*—We used a multi-stage analysis to provide insight into patterns in gene flow across our entire study area. First, we tested if IBD could explain the spatial variation in allele frequencies present

**Table 2.** Sample sizes for grizzly bear (GB) genetic analyses, years of collection, and expected ($H_E$) and observed ($H_O$) heterozygosities in our western North America study area. Indented text represents areas that were subdivisions for analytical purposes. Numerical superscripts indicate analyses in which samples were used.

| Sample area | Area (km²) | Genetic sampling | | | | Telemetry | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | Genotypes | Years | $H_E$ | $H_O$ | Years | No. GB collared | Type[a] |
| Trans-border | | | | | | | | |
|   Southern Divide Ecosystem[1,2,3,4] | 22,576 | 400 | 2004 | 0.68 | 0.67 | 1985–2004 | 172 | VHF, GPS |
|   Yellowstone[2,3] | 37,258 | 424 | 1983–2007 | 0.57 | 0.57 | | | |
|   Cabinets[1,2,3] | 5,148 | 14 | 1985–2005 | 0.62 | 0.64 | 1985–2007 | 12 | VHF |
|   Selkirk South[1,2,3,4] | 9,546 | 79 | 1999–2005 | 0.54 | 0.54 | 1985–2007 | 25 | VHF, GPS |
|   Selkirk Central[1,2,3,4] | 9,866 | 99 | 1996 | 0.68 | 0.68 | | | |
|     Selkirk Kokanee[2,3,4] | 2,530 | 15 | 1996 | 0.60 | 0.67 | | | |
|     Selkirk Goat[2,3,4] | 4,640 | 67 | 1996 | 0.68 | 0.67 | | | |
|     Selkirk Valhalla[2,3,4] | 2,695 | 17 | 1996 | 0.61 | 0.66 | | | |
|   Purcell Selkirk North[1,2,3,4] | 2,700 | 33 | 1996–1997 | 0.65 | 0.68 | | | |
|   Selkirk North[1,2,3,4] | 1,495 | 34 | 1996–1997 | 0.60 | 0.62 | | | |
|   Purcell Central St Mary[1,2,3,4] | 3,310 | 59 | 1998–2005 | 0.65 | 0.65 | 2004–2007 | 5 | GPS |
|   Purcell Central Jumbo[1,2,3,4] | 1,650 | 71 | 1998–2002 | 0.65 | 0.65 | | | |
|   Purcell South Yaak[1,2,3,4] | 5,870 | 51 | 1985–2005 | 0.62 | 0.63 | 1985–2007 | 32 | VHF, GPS |
|   Rocky South[1,2,3,4] | 17,652 | 404 | 1990–2004 | 0.68 | 0.68 | | | |
|     Rocky South US[2,3,4] | 11,232 | 276 | 1998–2004 | 0.68 | 0.68 | 1985–2007 | 199 | VHF, GPS |
|     Rocky South AB[2,3,4] | 3,688 | 45 | 1990–2004 | 0.64 | 0.67 | 2002–2006 | 6 | GPS |
|     Rocky South BC[2,3,4] | 2,732 | 83 | 1985–2000 | 0.66 | 0.67 | 1979–2006 | 123 | VHF, GPS |
|     RS Flathead east[2,3,4] | 1,500 | 35 | 1985–2000 | 0.65 | 0.67 | | | |
|     RS Flathead west[2,3,4] | 1,580 | 36 | 1985–2000 | 0.66 | 0.67 | | | |
|   Rockies Central[1,2,3,4] | 8,810 | 179 | 1996–1999 | 0.66 | 0.66 | | | |
|     Rocky Central AB[2,3] | 3,996 | 59 | 1998–2005 | 0.64 | 0.65 | 2002–2006 | 12 | GPS |
|     Rocky Central BC[2,3] | 4,814 | 120 | 1985–2005 | 0.66 | 0.66 | | | |
| Alberta | | | | | | | | |
|   Rocky Central Banff[1,2,3,4] | 5,122 | 109 | 1994–2005 | 0.62 | 0.62 | 1994–2006 | 51 | VHF, GPS |
|     Rocky central Banff east[3,4] | 4,040 | 20 | 1994–2005 | 0.60 | 0.61 | | | |
|     Rocky central Banff west[3,4] | 1,082 | 23 | 1994–2005 | 0.59 | 0.61 | | | |
|   Rocky North Banff[1,2,3,4] | 13,542 | 78 | 1994–2005 | 0.64 | 0.62 | 1994–2006 | 44 | VHF, GPS |
|   Rocky North BC[1,2,3,4] | 2,376 | 64 | 1996–1998 | 0.61 | 0.63 | 1995–1999 | 24 | VFH |
|   Rocky North Jasper[1,2,3,4] | 12,711 | 124 | 1999–2004 | 0.68 | 0.69 | 1994–2006 | 45 | GPS |
|   Alberta North[1,2,3,4] | 35,386 | 124 | 1999–2005 | 0.69 | 0.68 | 2002–2006 | 35 | GPS |
|   Alberta North Chinchaga[1,2,3] | 11,428 | 16 | 2002–2006 | 0.65 | 0.69 | | | |
|   Swan Hills[1,2,3] | 12,193 | 25 | 1990–2004 | 0.63 | 0.67 | 2002–2006 | 7 | GPS |
| Northern | | | | | | | | |
|   BC Northeast[1,2] | 17,979 | 231 | 1998–2004 | 0.69 | 0.68 | | | |
|     Prophet[1,2] | 8,527 | 36 | 1998 | 0.71 | 0.72 | | | |
|     ParsnipMt[1,2] | 6,168 | 170 | 2000 | 0.67 | 0.68 | | | |
|     Herrick[1,2] | 3,284 | 25 | 2000 | 0.65 | 0.68 | | | |
|   Nation[1] | 7,031 | 29 | 2003 | 0.67 | 0.65 | | | |
|   Parsnip Plateau[1] | 3,318 | 45 | 2000 | 0.67 | 0.67 | | | |
|   Kluane[1] | 11,824 | 56 | 2004 | 0.79 | 0.80 | | | |
|   Nahanni[1] | 10,085 | 29 | 2002–2004 | 0.75 | 0.76 | | | |
|   Atlin[1] | 30,462 | 28 | 1976–2002 | 0.76 | 0.74 | | | |
|   Spatsizi[1] | 36,897 | 29 | 1976–2002 | 0.74 | 0.75 | | | |
|   Stikine[1] | 10,119 | 105 | 1976–2002 | 0.73 | 0.73 | | | |
|   SE Alaska[1] | 1,700 | 27 | 2005 | 0.66 | 0.67 | | | |
|   Skeena N[1] | 23,889 | 28 | 1976–2002 | 0.70 | 0.72 | | | |
|   Skeena S[1] | 20,616 | 27 | 1976–2002 | 0.69 | 0.74 | | | |
|   Bowron[1] | 2,494 | 29 | 2001 | 0.63 | 0.62 | | | |
|   Owikeno[1] | 2,500 | 33 | 1998–2002 | 0.59 | 0.60 | | | |
|   South Coast Mts[1] | 10,000 | 51 | 2004 | 0.62 | 0.55 | | | |
| Total | 410,633 | 3,134 | | | | | 792 | |

[a] VHF, very high frequency transmitter; GPS, Global Positioning System transmitter.

[1] Used in isolation-by-distance (IBD) analysis across entire study area.

[2] Used in the cluster analysis.

[3] Used in the migrant analysis.

[4] Used in the regression analysis.

across broad regions within our study area. We used 2,710 15 locus microsatellite genotypes in multidimensional Factorial Correspondence Analysis (FCA; Benzecri 1973, She et al. 1987) within the program GENETIX (Belkhir 1999). Factorial correspondence analysis is a special case of principal components analysis that provides an objective exploration into groupings of similar genotypes with no a priori assumptions of group membership. Using individual genotype data, GENETIX develops a multidimensional hyperspace, with 1 dimension (axis) per allele for all loci. Values measured are the sharing of alleles, with 3 states for every allele: absent, 1 copy (heterozygous), or 2 copies (homozygous). The more alleles shared by multiple

individuals, the more they will cluster. The multidimensional hyperspace is ultimately reduced to the principal dimensions that capture the main axes of differences in clusters. An algorithm seeks the direction of a dimension to maximize the distance between clusters. At the large scale of Analysis 1, coarse patterns may be discernible.

We tested grizzly bears in the northwestern and southeastern study areas for IBD by comparing genetic distances ($D_{LR}$) and geographic distances between sample areas using Mantel tests. Program FSTAT (Goudet 2001) was used for Mantel tests and accounted for spatial autocorrelation through use of correlation matrices (Mantel 1967). Significance was based on 10,000 permutations and output yielded a coefficient of determination of genetic distance by geographic distance. We used a partial Mantel test that controlled for geographic distance to explore potential natural fragmentation by heavily glaciated mountains (Glaciers) and intervening Mts in the northwestern sampling area. We compared the strength (correlation), effect (slope), statistical significance, and explanatory power ($r^2$) of the correlations between areas. In areas where the IBD analysis did not explain the variation in genetic distance sufficiently, and where we had an adequate sample base, we further explored the extent and potential causes of fragmentation (Analyses 2–4).

*Analysis 2: Genetic clustering.*—We applied a genetic clustering analysis to the southeastern study area (Fig. 4) to cluster bears into groups or ultimately, subpopulations with limited or no inter-breeding with adjacent bears. We used a hierarchical analysis to consider population structure, fragmentation, and distinctness of grizzly bears in this area (Fig. 5). First, we used the FCA methods (as in Analysis 1) to identify genetic discontinuities and clusters of individuals that may form local subpopulations. We then used genetic distance, $D_{LR}$ (Paetkau et al. 1997), $D_S$ (Nei 1972), and $F_{ST}$ (Weir and Cockerham 1984), to compare levels of genetic separation between clusters. $D_{LR}$ is the mean of the ratio of the log likelihoods of individuals' genotypes occurring in their own population to the likelihood of it occurring in the compared population. $F_{ST}$ is the proportion of the variation in allele frequencies that is attributable to differences in populations. $D_S$ compares homozygosity between populations to estimate genetic distance by comparing the sum of squares of allele frequencies within populations and the sum of products of the frequencies of individual alleles in the 2 populations being compared. We calculated $D_{LR}$, $D_S$, and $F_{ST}$, and significance values for $F_{ST}$ in the assignment calculator at www2.biology.ualberta.ca/jbrzusto/Doh.php, FSTAT (Goudet 2001), and GENEPOP 3.1 (Raymond and Rousset 1995), respectively. Because genetic distance of grizzly bears in North America is known to be correlated with geographic distance (Paetkau et al. 1997), we standardized the genetic distance by dividing it by the geographic distance between mean capture locations of population pairs. We also compared genetic distances between adjacent sampling areas that were separated by human developments such as highways and settled valleys (2 clusters) to genetic distances between adjacent unsettled sampling areas without highways (that formed 1 cluster). To provide contrast, we present genetic distances (unadjusted), standardized genetic distances (adjusted for geographic distance), and $F_{ST}$ measures of adjacent sampling areas from our relatively undisturbed northwestern group.

*Analysis 3: Migrant detection.*—We defined a migrant as an individual bear that moved across an inter-mountain valley, Continental Divide, or potential fracture zone (an inter-mountain valley with roads and associated human development) and occupied an adjacent territory >1 km from the border of the source population. It was our intent to not include bears that moved across a major highway for a single brief event, evidenced by 1 or 2 locations very close to a highway. Age cannot be determined from genetic samples; therefore, we could not restrict our definition of migrants to potentially breeding adults (i.e., sub-adults may move into an adjacent area and be detected as migrants). We were therefore detecting bears that moved between areas regardless of breeding age or success.

Because genetic signals develop slowly (Hartl and Clark 1997), genetic distance and $F_{ST}$ measure past patterns of gene flow. Comparing values can identify areas where human influences have reduced movement in recent historic times (<100 yr; Hartl and Clark 1997, Steinberg and Jordan 1997, Whitlock and McCauley 1999, Proctor et al. 2005). For our analysis, we were most interested in calculating current movement rates to understand more recent fragmentation. Current migrants were identified through genetic assignments, captures of individuals (identical genotypes) on both sides of a potential fracture, or by use of telemetry documenting inter-area movements of individuals. The temporal span of our telemetry dataset varied among areas from 4 yr to 27 yr.

Using the genetic clustering results within the southeastern study area, we paired 24 adjacent areas across features with human disturbance such as major highways (500–15,000 vehicles/day) and settled valleys (20–98% settled) and across features with minimal human disturbance such as the Continental Divide and unsettled valleys (<500 vehicles/day, <20% settled). We then determined sex-specific movement rates between these pairs by identifying individual bears that moved between areas. These movement rates provide the data that underpins Analysis 4.

We used 2 assignment methods to estimate the amount of sex-specific movement between adjacent areas. First, we used area-specific allele frequencies in a likelihood-based assignment test (Paetkau et al. 1995) that calculates the probability of each individual's assignment to an area as the cumulative product of each allele's frequency of occurrence in all areas being examined. Each individual is assigned to the area with the highest probability of occurrence. Because the areas we compared shared recent ancestry, genotypes between adjacent areas may be similar. It is possible that cross-assigned individuals (assigned to an area other than that of their capture) were not real migrants, but appeared as such because of remnant similar genotypes. To examine our power to distinguish true from statistical migrants, we generated significance levels for individuals that cross-assigned to a neighboring area using the simulation routine within GENECLASS 2.0 software (Paetkau et al. 2004, Piry et al. 2004). We determined significance levels by comparing individual genotypes of cross-assigned individuals to a simulated set of 10,000 genotypes that were generated using area-specific allele frequencies. Although several other assignment methods determine migrant significance based on simulations, we chose the routine developed by Paetkau et al. (2004)
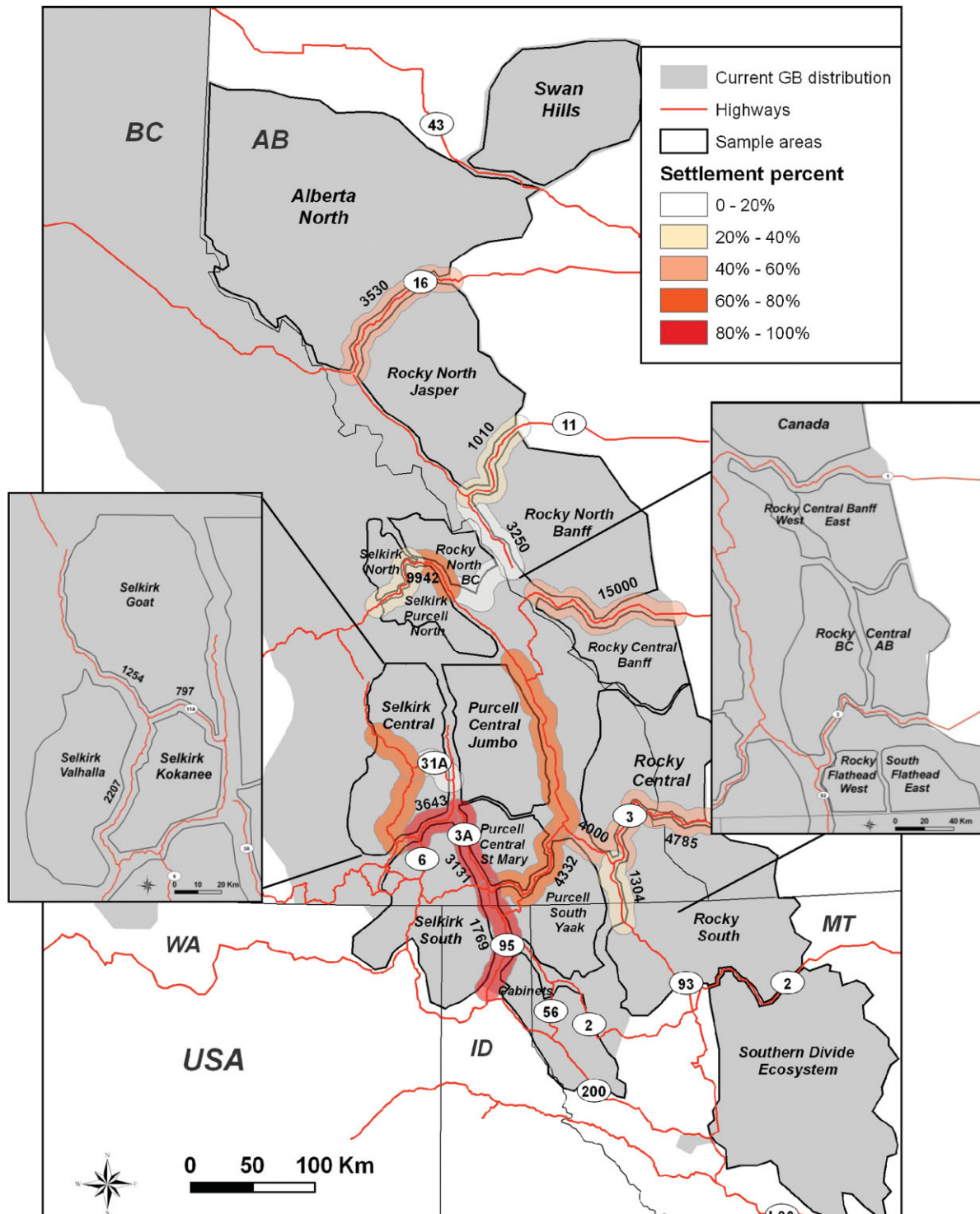
**Figure 5.** Sample areas within the southeastern grizzly bear (GB) study area. Genetic samples were collected between 1983 and 2007 and telemetry data were collected between 1979 and 2007. The areas on this map were involved in 3 separate analyses: clustering, migrant, and regression. Some areas were sub-divided for analytical purposes. For instance, the Selkirk Central area is included in the trans-border cluster and migrant analysis (Analyses 2 and 3) but is subdivided into 3 sub-areas (Selkirk Goat, Selkirk Kokanee, and Selkirk Valhalla) for the regression analysis (Analysis 4, see inset). The Rocky South and Rocky Central areas are similarly subdivided for the regression analysis (see inset). The degree of settlement is depicted for fracture zones used in the regression analysis. Numbers along highways are average daily summer traffic volumes.

because it produces accurate Type I error rates because of an improved simulation process. It mimics natural population processes by generating individuals through uniting gametes. For our candidate migrants, we identified individuals in the distribution tails beyond the $\alpha_{0.01}$ or $\alpha_{0.05}$ thresholds depending on sample sizes (i.e., when the sample is 50, alpha of 0.01 is less revealing). This pool contained putative migrants that could be explained by chance (Type I error rate). Individuals in excess of this number of chance migrants were likely to be true migrants.

Second, we independently tested for migrants in a model-based clustering method using a Monte Carlo Markov Chain (MCMC) algorithm (STRUCTURE; Pritchard et al. 2000). STRUCTURE clusters individuals into groups through iterative assignments and develops probabilities of area origin for each individual through the cumulative results of those assignments. Individuals that repeatedly assign to a group other than that of their capture are considered putative migrants from their source area. The strength of their migrant status is reflected in the resulting probability of their cross-assignment. We assumed adjacent areas had correlated allele frequencies because bears were recently 1 continuous population. We used a presumed migration rate (necessary for program input) of 0.01 between areas as this value conforms to our hypotheses that movements are limited because of fragmentation (Proctor et al. 2005). Because we used the results of our previous analyses (GENETIX) to identify subpopulations, and were testing for migration between 2 adjacent areas, we assumed 2 groups ($k = 2$), ran 100,000 burn-in iterations, and collected results from the subsequent 100,000 runs. We considered individuals migrants when both methods (GENECLASS and STRUCTURE) agreed on the number of individuals in excess of the Type I error rates determined by GENECLASS. In the rare event that these methods disagreed, migrant status was not applied. These assignment tests assume all loci in each area are in Hardy–Weinberg and linkage equilibria, which we verified using GENEPOP 3.1 (Raymond and Rousset 1995).

Where possible, we compared the ability of genetic and telemetry methods to detect migrants for 2 reasons. First, we wanted to corroborate the newer deductive genetic methods with direct telemetry observations. Second, we used results from both methods in an analysis exploring causes of fragmentation, and the validity of using both methods is justified with the comparison. Detecting inter-area movements can be influenced by the spatial extent and orientation of the capture effort. Capture efforts that occur near borders between areas are more likely to detect migrants. However, in both our genetic assignment and telemetry efforts, we assumed the sample sizes (for rate determination) to extend equally across the whole of each area to allow for long-distance migrants and to maximize our area of inference. We expressed migrant movement rates as the numbers of migrants detected by either genetic or telemetry methods relative to the number of individuals sampled. This standardization also compensated for the differing time periods of effort within and between each method.

*Analysis 4: Causes of fragmentation.*—To test hypotheses about the influence of various factors on bear movements, we modeled sex-specific movement rates across 24 potential fractures. Use of sex-specific movement rates resulted in 48 entries (24 male and 24 female). These potential fractures varied as to the intensity of various human-caused and natural features (Fig. 5). We used the number of migrants detected (Analysis 3) divided by the associated sample sizes to quantify movement rates (migrants/number of bears sampled in both areas = $m/n$) of each sex between each pair of adjacent areas.

We used multiple linear regression and analysis of covariance (ANCOVA) to estimate the effect of human influence on male and female grizzly bear movement rates between areas. We used linear regression to explore the relationship of these variables to movement rates of both sexes through various models. To determine if the sexes were responding differentially to our set of variables, we used ANCOVA to compare models that included sex as a categorical covariate.

We first tested for collinearity among potential factors and selected 4 uncorrelated (Pearson's correlation coefficients <0.7) variables to create univariate and multivariate candidate models derived from our knowledge of bear ecology. We created a variable termed *nonsettle* by placing a 500-m disturbance radius around all buildings determined from 1:50,000 topographic maps (following Mace et al. 1999) and then measured the proportion of the common boundary between adjacent areas that was not within these disturbance areas. *Traffic* was the average summer daily traffic volumes on the major roadway in the common boundary (Alberta Ministry of Transportation 2010, BC Ministry of Transportation 2010). Because boundary length, bear densities, and hunting regulations varied across our study area, we estimated relative mortality (*mort*) as all known non-hunting human-caused mortalities over the past 25 yr (T. Hamilton, BC Ministry of Environment, personal communication; G. Stenhouse, Foothills Research Institute, personal communication) within 18 km (average radius of a male home range) of the common boundary divided by the average number of bears found in the boundary area estimated from recent population surveys (Wielgus et al. 1994; Woods et al. 1999; Gibeau 2000; Mowat and Strobeck 2000; Boulanger 2001; Boulanger et al. 2002, 2004, 2005a, b; Mowat et al. 2005; Kasworm et al. 2007a; Proctor et al. 2007). We used the geographic distance (*geodist*) between sampling-area centers calculated from the geometric mean of the individual bear locations within each sampling area.

We developed a suite of models that we believe reflect ecological relationships between the 4 independent variables described above and bear movement rates between adjacent areas. Our suite of models reflected pure linear relationships, models with quadratic or cubic elements, and piecewise linear regression models (Montgomery et al. 2001). Piecewise regression models reflect situations where abrupt responses occur at thresholds resulting in a marked change in slope of a regression line. We used observations from previous work (Proctor 2003, Proctor et al. 2005) to develop 2 piecewise models. We hypothesized that in areas with <20% settlement, male and female bears would have a minimal response to human presence. We also hypothesized that females and males would respond differently in areas with 20–50% settlement and that in areas with high settlement (>50%), both sexes would respond with diminished movement rates. Candidate models with significance levels <0.1 that contained variables with significance levels <0.1 were evaluated using small sample-corrected Akaike Information Criteria (AIC$_c$; Burnham and Anderson 1998). The model representing each partition within piecewise models were also selected using AIC$_c$ methods. As recommended by Burnham and Anderson (1998), all models with a $\Delta$AIC$_c$ score $\leq 2.0$ were considered competing models. Multiple regressions and ANCOVA were performed in STATA 10.0 (StataCorp, College Station, TX). We graphed the predicted values of individual variables from multivariate models while accounting for covariates to gain insight into whether

relationships were negative (i.e., traffic increased and movement rates decreased) or positive (i.e., movement rates increased and mortality increased).

To further explore the influence of our suite of variables on genetic differentiation, we used the genetic-distance calculations from Analysis 2 for $D_{LR}$ (Paetkau et al. 1997), $F_{ST}$ (GENEPOP 3.1; Raymond and Rousset 1995), and $D_{S}$ (Nei 1972), to quantify genetic separation between subpopulations. Using the multiple (partial) Mantel test in FSTAT 2.9.3.2 (Goudet 2001) on the 24 paired samples used above, we evaluated partial correlations among 5 explanatory variables with these 3 measures of genetic differentiation; we included the effects of bear density (calculated as the average of both sample area densities), geographic distance, and the 3 human disturbance variables (*nonsettle*, *mort*, *traffic*). The partial Mantel test uses multiple regression and correlation of matrices of the residuals for all variable combinations, allowing the correlation between genetic distance and an explanatory variable to be known while holding other explanatory variables constant. We based significance values on 10,000 randomizations and arcsine or square-root transformed non-normal data as appropriate.

## RESULTS

We genotyped 3,134 grizzly bears (Table 2, Fig. 2) over our entire study area and collected locations from 792 radiocollared bears in the southeast area (Table 2, Fig. 3). Both types of data were collected over a period up to 27 yr (Table 2). There was no linkage disequilibrium, and loci in all areas were in Hardy–Weinberg equilibrium except 1, and that locus did not have a heterozygote deficit. Average expected heterozygosity in the overall study area was 0.63 and observed heterozygosity was 0.65 (Table 2). We found a trend for heterozygosities to decrease with latitude (Fig. 6, Table 2). Heterozygosities were highest in the northern Atlin (0.76) and Kluane (0.79) areas and lowest in the southern Yellowstone (0.57) and the Selkirk South (0.54) areas. Several notable sample areas had values that were below the trend line (Fig. 6). Those areas were located on the periphery of the main core area occupied by grizzly bears in western North America. Areas with lower than expected heterozygosities on the west side of the distribution were Southeast Alaska (0.66) and Owikeno (0.59), and on the east side of the distribution was Alberta's Swan Hills (0.63).
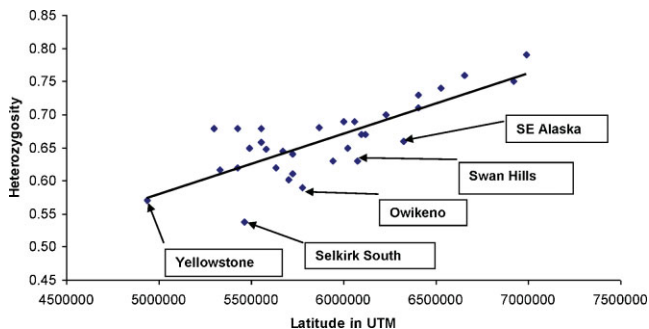


**Figure 6.** Expected heterozygosity of grizzly bears in sample areas (1983–2007) across western North America in relation to latitude as measured in Universal Transverse Mercator (UTM) units. Study areas well below the expected line are highlighted.

## Analysis 1: Isolation-by-Distance and Natural Fragmentation

The multidimensional FCA analyses across the entire study area found 2 primary patterns. First, there was a continuous chain of genetic clusters corresponding to a north–south gradient in the samples (Fig. 7). The GENETIX plot showed this clustering had a concordance with geography, with the cluster at the top of the graph representing bears at the northern extreme of the sample areas, and genotypes along the bottom of the plot were bears in the southern sites of the study area. This pattern corresponded to an IBD model (Wright 1943). The second pattern was the noncontinuous widening towards the bottom of the plot, where bears in the southeastern portion of the study area did not cluster with geographic concordance, suggesting deviation from an IBD model in this region (Fig. 7).

Using Mantel tests, we found that more of the variation on genetic distance was explained by the influence of geographic distance in the northwestern study area (Table 3, Fig. 8a; $r^2 = 0.38$, $P = 0.001$) than the southeastern study
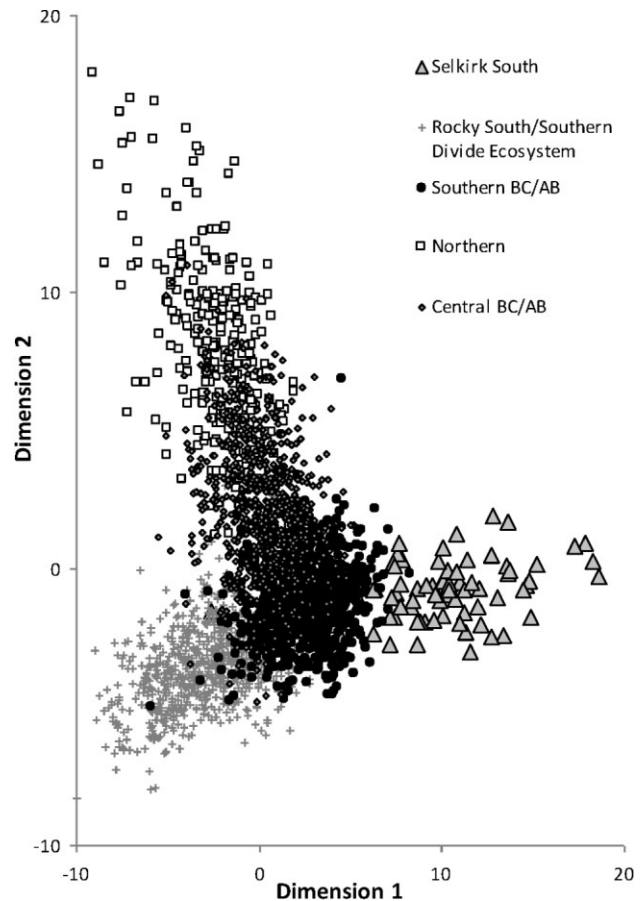


**Figure 7.** Clusters of 2,710 grizzly bear genotypes sampled between 1983 and 2007 in western North America from a factorial correspondence analysis (using GENETIX). The vertical "tower" is a south–north continuum of genotypes (north at top). The lower bulge represents bears in southeastern British Columbia (BC), northern United States, and southern Alberta (AB): Rocky South/Southern Divide Ecosystem also includes the Cabinets; Southern BC/AB includes Rocky Central, Rocky Central Banff, Rocky North Banff, Rocky North BC, Purcell Central St. Mary, Purcell South Yaak, Purcell Central Jumbo, Purcell Central St. Mary, Selkirk Purcell north, Selkirk Central, and Selkirk North; Central BC/AB includes Rocky North Jasper, Alberta North, Swan Hills, Bowron, Nation, Owikeno, Herrick, Parsnip Mountain, Parsnip Plateau, Prophet, South Coast, Skeena South, Skeena North; and Northern includes Spatsizi, Southeast Alaska, Stikine, Kluane, and Nahanni.

**Table 3.** Results of Mantel correlations (Mantel tests) testing for the relationship between grizzly bear geographic distance (GeoDist) and genetic distance ($D_{LR}$) among grizzly bear populations. $D_{LR}$ is the mean of the ratio of the log likelihoods of individuals' genotypes occurring in their own population to the likelihood of it occurring in the compared population. In the test of all northern British Columbia (NBC) populations, we controlled for coastal glaciers (CoastGlaciers) and interior mountains (Interior Mts). The partial Mantel test uses multiple regression and correlation of matrices of the residuals for all variable combinations, allowing the correlation between genetic distance and an explanatory variable to be known while holding other explanatory variables constant.

| Dataset | Mantel variable | Regression coeff. | Correlation coeff. | P-value | $R^2$ |
|---|---|---|---|---|---|
| NBC all populations | GeoDist | 0.007 | 0.62 | 0.001 | 0.38 |
| Southeast BC, AB | GeoDist | 0.007 | 0.32 | 0.005 | 0.10 |
| NBC all populations | GeoDist | 0.006 | 0.54 | 0.001 | 0.61 |
| | CoastGlaciers | 4.385 | 0.54 | 0.001 | |
| | Interior Mts | −0.452 | −0.20 | 0.620 | |
| NBC no coast populations | GeoDist | 0.007 | 0.74 | <0.001 | 0.55 |

area (Table 3, Fig. 8b; $r^2 = 0.10$, $P = 0.005$). When geographic distance was accounted for in the northwestern region, we found heavily glaciated mountains had a significant ($P = 0.001$) effect on genetic distance, increasing the explanatory power from 38% to 61% (Table 3). The effect of mountains that were not heavily glaciated was not significant ($P = 0.62$). When we removed the coastal sampling sites that were separated by heavily glaciated terrain (Alaska, Owikeno) from our northwestern dataset, the $r^2$ increased to 0.55, in contrast to 0.38 when all northwestern data were included (Table 3, Fig. 8c). Other patterns suggested that the genetic distances between the 2 Skeena areas and the areas to the east were greater than that explained by IBD alone (Fig. 8c). Similarly, bears in the Stikine region had a greater genetic distance from other populations than could be accounted for by geographic distance alone (Fig. 8c).

## Analysis 2: Genetic Clustering

*Cluster analysis—trans-border region.*—Factorial correspondence analysis revealed varying levels of genetic structure between adjacent areas across our study area (Fig. 9a–l). It essentially separated bears into clusters corresponding to Mts in an east–west dimension, and across BC Highway 3 in a north–south dimension (with the exception of Cabinet–Rocky South clustering) in the trans-border region. When trans-border and BC South Coast bears were pooled, the Selkirk South and BC South Coast bears formed the most discrete clusters (Fig. 9a). In the east–west dimension, the Rocky South and Purcell South Yaak clusters were not clear at this large geographic scale, but were relatively distinct at a finer-scale (Fig. 9b). Bears from the Cabinet Mts clustered closely with the Rocky South bears (Fig. 9b). We found separate clusters north and south of BC Highway 3 and 3A in the Rocky, Purcell, and Selkirk Mts, respectively (Fig. 9c–e). In the subdivided Central Selkirk area, we found separate clusters among the Goat, Valhalla, and Kokanee areas (Fig. 9f) separated by Highways 6 and 31A. Highway 1 in the Selkirk North area (Fig. 9g) had clusters to its north and south. We found some overlap in clustering between samples in the Rocky South and Southern Divide Ecosystem areas (Fig. 9h; Kendall et al. 2009). The bears of Yellowstone formed a distinct group from those to the north in
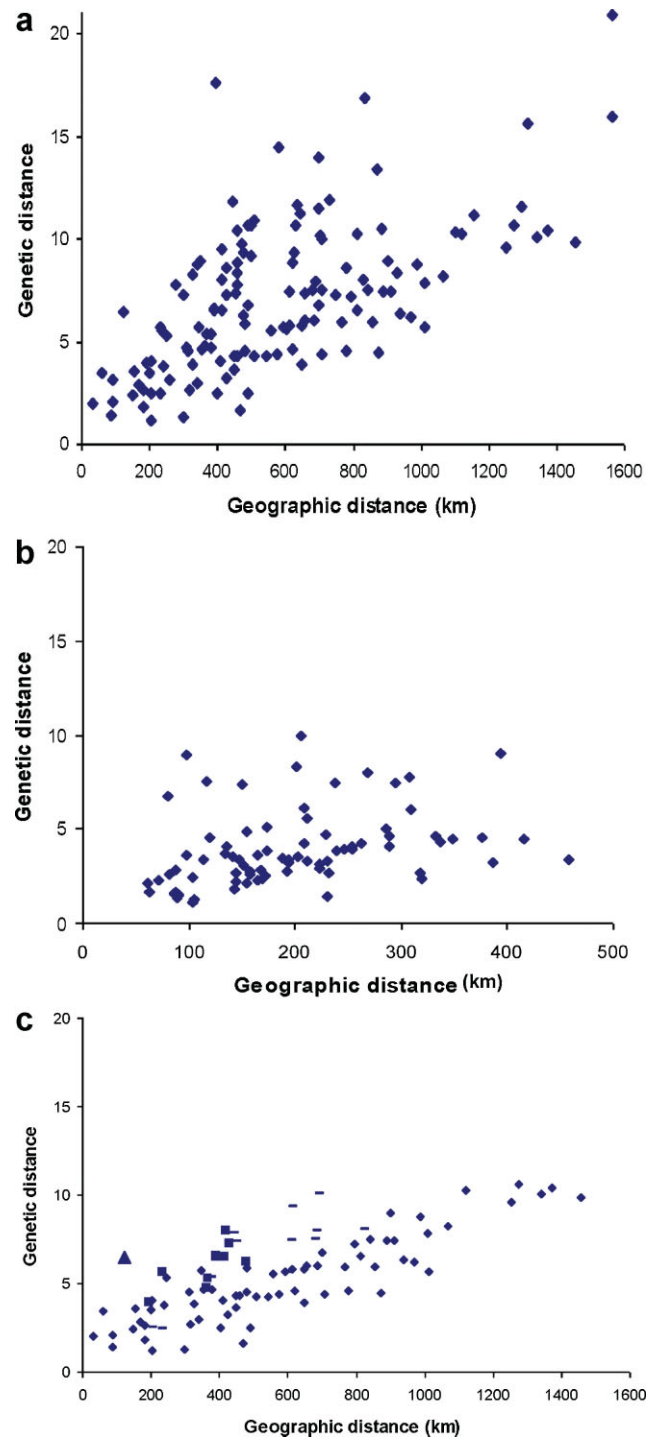


**Figure 8.** Scatterplot genetic distance as a function of geographic distance for grizzly bear in (a) northwestern study area, (b) southeastern study area, and (c) northwestern study area excluding the coast sampling sites (Alaska, Owikeno) where heavily glaciated mountains acted as natural barriers to gene flow. The triangle (▲) is the genetic distance across Highway 16 between the Bowron and Parsnip Plateau areas, dashes (—) represent genetic distances from the Stikine area to other areas, squares (■) represent genetic distances across the plateau that separates the Skeena North and South areas from the Nation, Parsnip, Herrick, and Bowron areas. Note the different x-axis scale for (c).

the Southern Divide Ecosystem (Fig. 9i; Haroldson et al. 2010). In contrast to these fragmented subpopulations, the animals across the Continental Divide in the Canadian Rocky South (Rocky South BC vs. Rocky South AB; Fig. 9j), Rocky Central
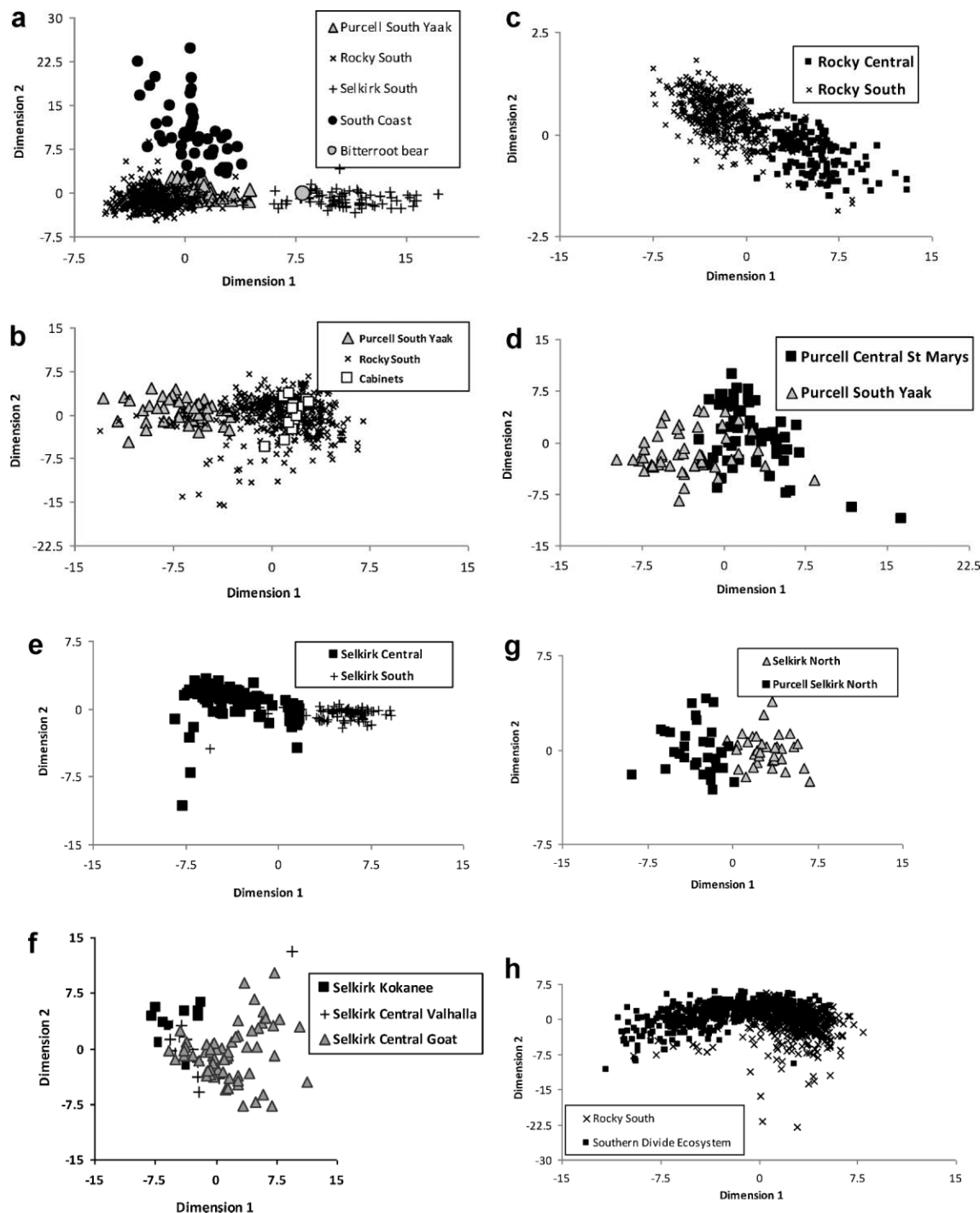
**Figure 9.** Multi-dimensional factorial correspondence analysis (FCA; GENETIX) plots for grizzly bears in the trans-border region: (a) south of British Columbia (BC) Highway 3 along the Canada–United States border; (b) from the Cabinets, Purcell South Yaak, and Rocky South across the Kootenay River, Koocanusa Reservoir, and Highways 2 and 97; (c) in the Rocky Central and Rocky South areas north and south of BC Highway 3; (d) Purcell Central St. Marys and Purcell South Yaak areas north and south of BC Highway 3 in the Purcell Mountains; (e) Selkirk Central and Selkirk South areas north and south of BC Highway 3A in Selkirk Mountains; (f) Selkirk Central Goat and Selkirk Central Valhalla areas north and south of BC Highways 6 and Selkirk Central Kokanee area south of Highway 31A in the sub-divided Central Selkirk area; (g) Selkirk North and Purcell Selkirk North areas north and south of Highway 1 in BC; (h) Rocky South and the Southern Continental Divide areas north and south of U.S. Highway 2; (i) Yellowstone versus Southern Divide Ecosystem (adapted from Haroldson et al. 2010); east and west of the Continental Divide in the Canadian Rockies south (j) and north (k) of Highway 3; and (l) east and west of Northfork Flathead River in southern BC.

area (Rocky Central BC vs. Rocky Central AB; Fig. 9k) and in the North Fork of the Flathead River, a wide but unsettled valley with no paved roads (Rocky South Flathead East vs. West; Fig. 9l), did not cluster separately.

*Cluster analysis–Alberta region.*—Factorial correspondence analysis in the Alberta region suggested that in the southern and northern portions of Alberta there is more population structure across major highways than exists across the Continental Divide.
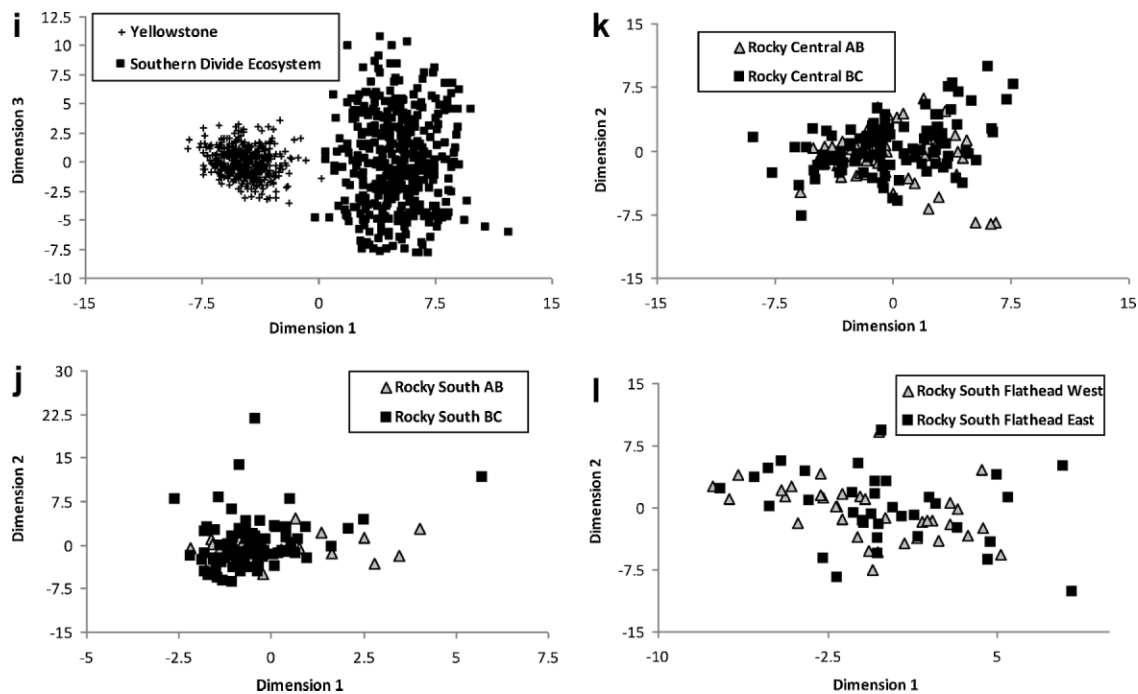
**Figure 9.** (*Continued*)

Results of cluster analyses in central Alberta were suggestive of this pattern but less conclusive. Bears in Alberta North (2 areas sampled) clustered with those in BC North (3 areas sampled) more than with bears just to the south within Alberta (Fig. 10a). Bears formed overlapping clusters across major east–west Highways 16 and 11 (Fig. 10a). In contrast to the separation evident across Highway 1 in BC (Fig. 9g), bears on either side of Highway 1 in Alberta were not in distinct clusters (Fig. 10b). Similarly, there was non-clustering of bears in adjacent areas across the Continental Divide north of Highway 1 (Fig. 10c), and across the Continental Divide both north and south of Highway 3 (Fig. 9j and k), suggesting that bears inter-breed freely across
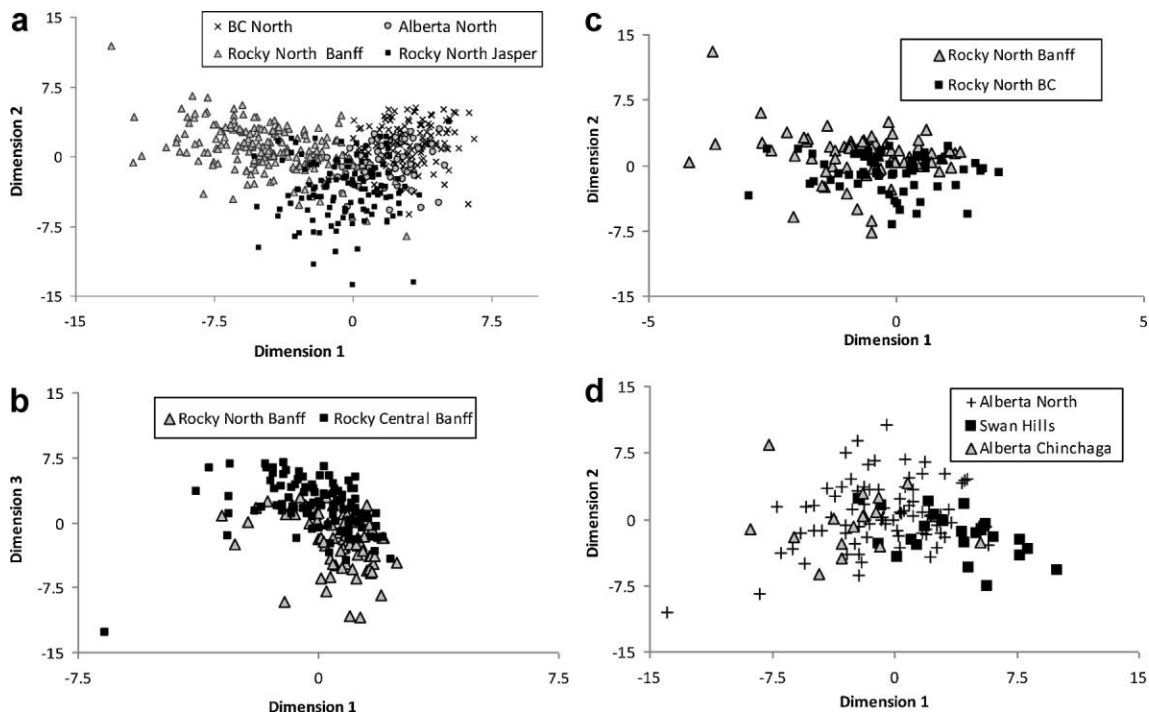


**Figure 10.** Multi-dimensional factorial correspondence analysis (FCA, GENETIX) plots for grizzly bears along the Alberta (AB)–British Columbia (BC) Continental Divide: (a) Alberta North, BC North, and Rocky North areas within Alberta (AB); (b) Rocky North Banff and Rocky Central Banff areas north and south of AB Highway 1; (c) Rocky North Banff and Rocky North BC areas east and west of the Alberta BC Continental Divide north of Highway 1; and (d) Alberta North, the Swan Hills, and Alberta Chinchaga areas north of Highway 16 within AB.

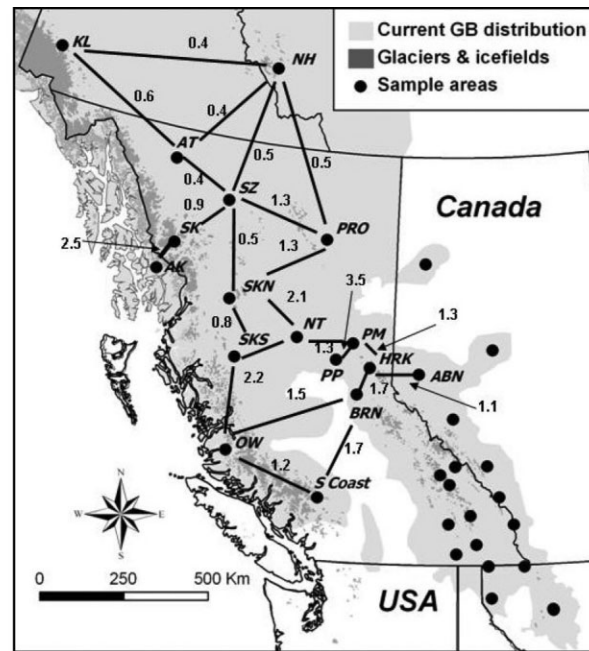| Code | Area name |
|------|-----------|
| ABN | Alberta North |
| AK | Alaska |
| AT | Atlin |
| BRN | Bowron |
| HRK | Herrick |
| KL | Kluane |
| NH | Nahanni |
| NT | Nation |
| OW | Owikeno |
| PM | Parsnip Mountain |
| PP | Parsnip Plateau |
| SK | Stikine |
| SKN | Skeena North |
| SKS | Skeena South |
| SZ | Spatsizi |

**Figure 11.** Grizzly bear (GB) genetic distance ($D_{LR}$; Paetkau et al. 1997) adjusted for geographic distance ($D_{LR}$/100 km), between GB sample areas in the northwestern portion of the study area. See Appendix for a comparison of raw (unadjusted) and adjusted genetic distances.

the Continental Divide between Alberta and BC. We found evidence of weak clustering of bears in the Swan Hills from those in Alberta North and the AB Chinchaga areas (Figs. 4 and 10d).

*Genetic distance–all areas.*—We present the genetic distance (both unadjusted and standardized for geographic distance [$D_{LR}$/100 km$^2$]) results sorted by potential fracture category (natural or human) for convenience (Appendix). Mean adjusted genetic distance differed ($t_{55} = -3.74$, $P < 0.001$) between the 2 types of fractures, natural ($D_{LR} = 1.2$) and human ($D_{LR} = 3.9$). The adjusted genetic distance between sampling areas were lowest (<1.0) in the northern undisturbed mountainous areas of our study area (Appendix, Fig. 11). Areas in central BC or associated with icefields and Continental Divides were generally between 1.0 and 2.0 (Appendix). One notable exception was the adjusted distance (3.45) between the Parsnip Mountain and the Parsnip Plateau areas, which was high relative to all other natural areas. Of areas separated by potential human features, bear populations across highways in Alberta have the lowest adjusted genetic distances (Appendix, Fig. 12), low enough to be consistent with other natural areas. The areas within the trans-border region with human influence had the highest values of genetic distance, culminating in the genetic distances between the Selkirk South area and other adjacent areas (Appendix, Fig. 13). Several pairs of areas (e.g., Rocky Central Banff East–Rocky Central Banff West, Rocky South Flathead East–Rocky South Flathead West) within the southeast region in the natural category had adjusted genetic distance values <1.0, similar to the far north undisturbed areas (Appendix). We did not provide genetic distances for the Cabinet area as sample sizes were too low for meaningful results, and 6 of 16 samples were from descendents of a translocated female from the Rocky South area (Kasworm et al. 2007b).

**Analysis 3: Migrant Detection**

Our effort (genetic and telemetry) to identify individual migrants was carried out in the southeastern region (Fig. 4) within each of the trans-border (Fig. 14) and Alberta sub-regions (Fig. 15). We identified 2,906 individual bears in 24 geographic areas by genetic assignment or physical capture and telemetry (Table 4). We sampled more than 50% of the estimated populations, as derived with DNA-based mark–recapture methods, in most cases in the southeastern study area. Totals of 131 male and 59 female bears moved between adjacent sampling areas (Table 4). Two individual bears were deemed not to be migrants because only 1 of the methods STRUCTURE and GENECLASS detected them (1% of migrants or 0.07% of tested individuals). The number of male migrants across potential fractures ranged from 25 crossing the uninhabited Flathead Valley (Rocky South Flathead East–Rocky South Flathead West) to 0 crossing various highways and human-settled areas (Table 4). Female migrants ranged from 17 across the Flathead Valley to 0 crossing various highways and human-settled areas (Table 4). We found little evidence of female movement across valleys with major highways and settlements in all 3 Mts (Figs. 16–18). Mean movement rates (migrants/sample size) across the entire southeastern region (trans-border and Alberta areas) did not differ between genetic assignment and telemetry (Table 4; assignment = 0.023, telemetry = 0.031, paired sample t-test, $t_7 = -0.38$, $P = 0.72$).

*Migrants trans-border region.*—Using genetic assignment methods, we found 25 male and 8 female migrants to move between adjacent areas in the trans-border region (Table 4). Of those that crossed major highways, 19 were male and 5 were female. Twenty-four of the migrants moved north–south within Mts; only 9 moved east–west between ranges. We found 1 female migrant that moved into the Selkirk South area (Table 4). There were 1 female and 4 male migrants across Highway 3 in the
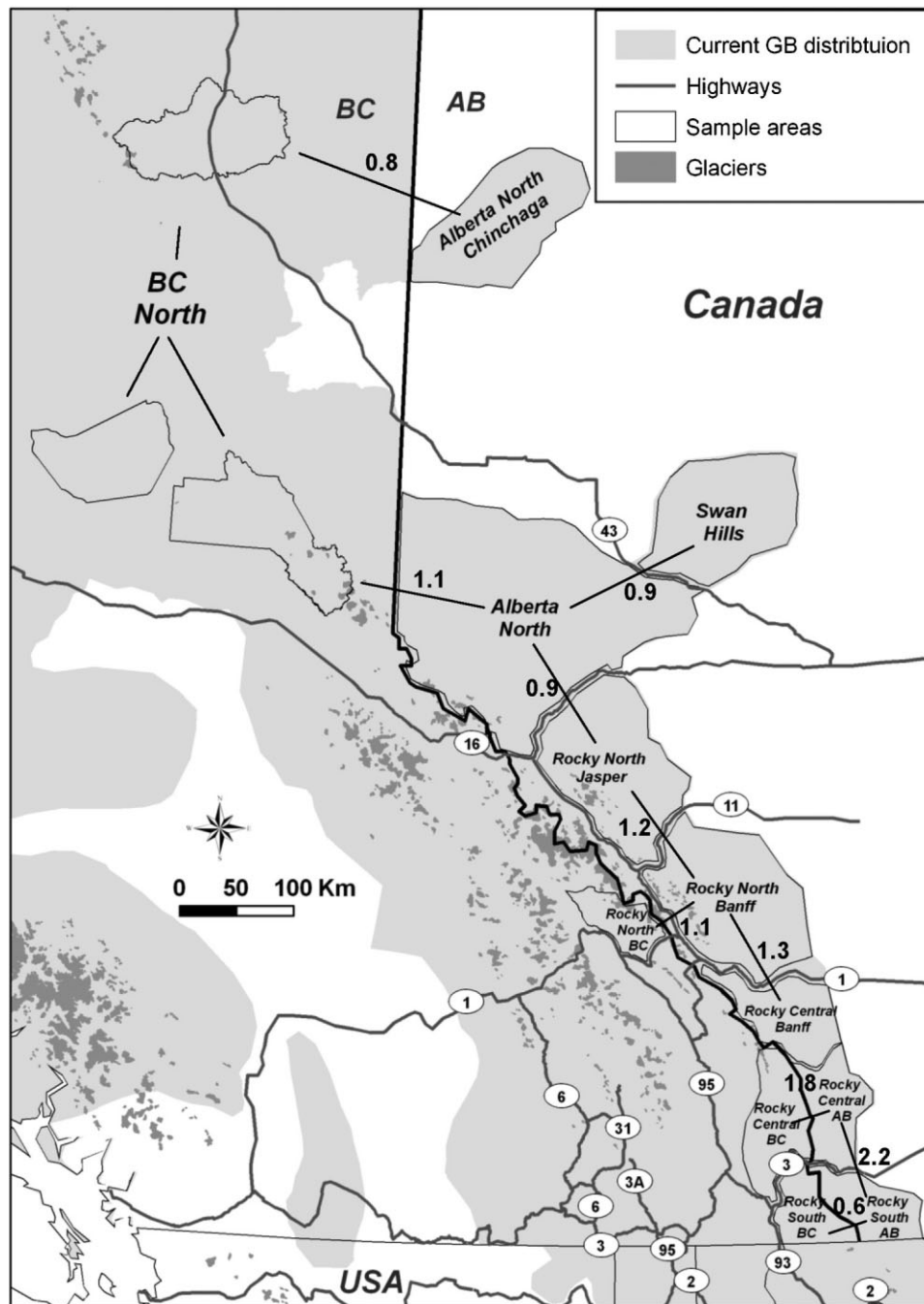
**Figure 12.** Grizzly bear (GB) genetic distance ($D_{LR}$; Paetkau et al. 1997) adjusted for geographic distance ($D_{LR}/100$ km), for GB sample areas in the Alberta region. See Appendix for a comparison of raw (unadjusted) and adjusted genetic distances.

Purcell Mountains. In the Rocky Mountains, Highway 3 had 1 female and 10 male migrants (including Alberta samples, see below).

We had telemetry locations for 580 bears from all trans-border sampling areas except the Rocky Central BC and Selkirk Central areas (Table 2, Fig. 3). In 4 of 6 areas, our telemetry sample spanned >20 yr (Table 2). As with the genetic assignment results, the telemetry data revealed more male than female migrants. A single radiocollared female moved between sampling areas separated by a settled valley with a major highway, and 4 radiocollared males moved across Highway 3 in the Purcells (between Purcell South Yaak and Purcell Central St. Marys)

during a 20-yr period. We also documented 1 sub-adult male that moved from the Purcell South Yaak area into the Selkirk South area (Fig. 16). We detected 19 male and 12 female migrants across US Highway 2 (Fig. 16). We do not present any telemetry data from the Yellowstone ecosystem, but after >33 yr and >576 individual bears radiocollared, there was no documented evidence of animals moving from the Yellowstone area into an adjacent subpopulation (Haroldson et al. 2010). We also detected other types of direct migrants from ear-tag returns or direct genetic matches from dead bears (Table 4).

*Migrants Alberta region.*—In the Alberta region, genetic assignment methods detected 11 male and 1 female (another was
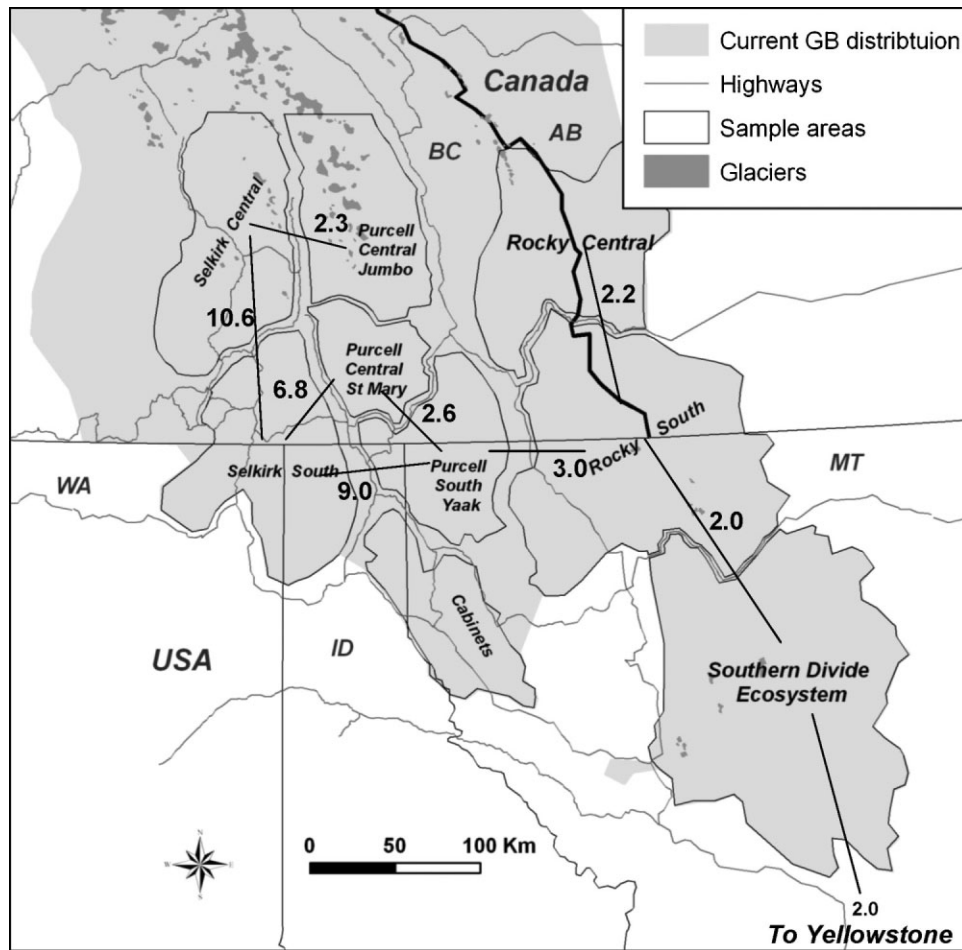
**Figure 13.** Grizzly bear (GB) genetic distance ($D_{LR}$; Paetkau et al. 1997) adjusted for geographic distance ($D_{LR}/100$ km), for GB sample areas in the trans-border area. See Appendix for a comparison of raw (unadjusted) and adjusted genetic distances.

moved by wildlife managers) likely migrants that crossed major east–west highways transecting Alberta's grizzly bear distribution (Table 4). Because of genetic similarity of bears on both sides of Highway 1, no putative migrants were detected in that area (Fig. 10b), but we found many moving across Highway 3. Seven of the 8 migrants that moved across Highway 3 within Alberta were from south to north, which may reflect bears in wildlife conflicts being moved by managers, not dispersing individuals. We detected 2 migrants originating from areas where wildlife managers captured them and subsequently moved them to areas where we sampled them. Overall, few migrants were detected through assignment methods throughout Alberta (12 of 519 genotyped bears). As was the case along Highway 1, genetic separation of adjacent areas across the Continental Divide was too low for migrant detection using genetic assignments. However, we captured 4 females and 3 males on both sides of the Continental Divide in 2 separate DNA surveys in the Rocky Central Alberta and the Rocky Central BC areas north of Highway 3 (not presented in Table 4). We also DNA-captured 1 female and 7 males on both sides of the Divide south of Highway 3 in the Rocky South AB and Rocky South BC areas. There were no recaptures of bears across the Divide north of Highway 1 between Rocky North Banff and Rocky North BC.

We captured and radiocollared bears across most of the grizzly bear distribution in Alberta (Fig. 3), including 114 bears (GPS collars) from the Foothills Model Forest Grizzly Bear Research Program Alberta-wide effort, 85 bears from the East Slope Grizzly Bear Project (78 VHF and 7 GPS), and 123 bears (116 VHF and 7 GPS) from the BC Flathead project (Flathead bears were only used to identify migrants across the Continental Divide, not Highway 3). Of these, 322 radiocollared bears in the Alberta study region, 6 males and 2 females, moved across one of the major highways (Table 4). Four males and 2 females moved across Highway 1 in Banff National Park (Table 4, Fig. 17). Two males moved across Highway 16 (Table 4, Fig. 17).

Trapping effort along the Continental Divide was not consistent north to south across grizzly bear range (Fig. 15). Effort was extensive in BC south of Highway 3 (Rocky South AB–Rocky South BC) because of long-term research by the Flathead Project where 123 bears were collared over 27 yr. Five females and 7 males used habitat across the Continental Divide in this area. Extensive sampling effort adjacent to the Divide also was undertaken by East Slope Grizzly Bear Project in the Banff National Park area (Rocky Central Banff–Rocky Central BC), where 5 males and 3 females used habitat across the Divide south of Highway 1. North of Highway 1 (Rocky North Banff–Rocky
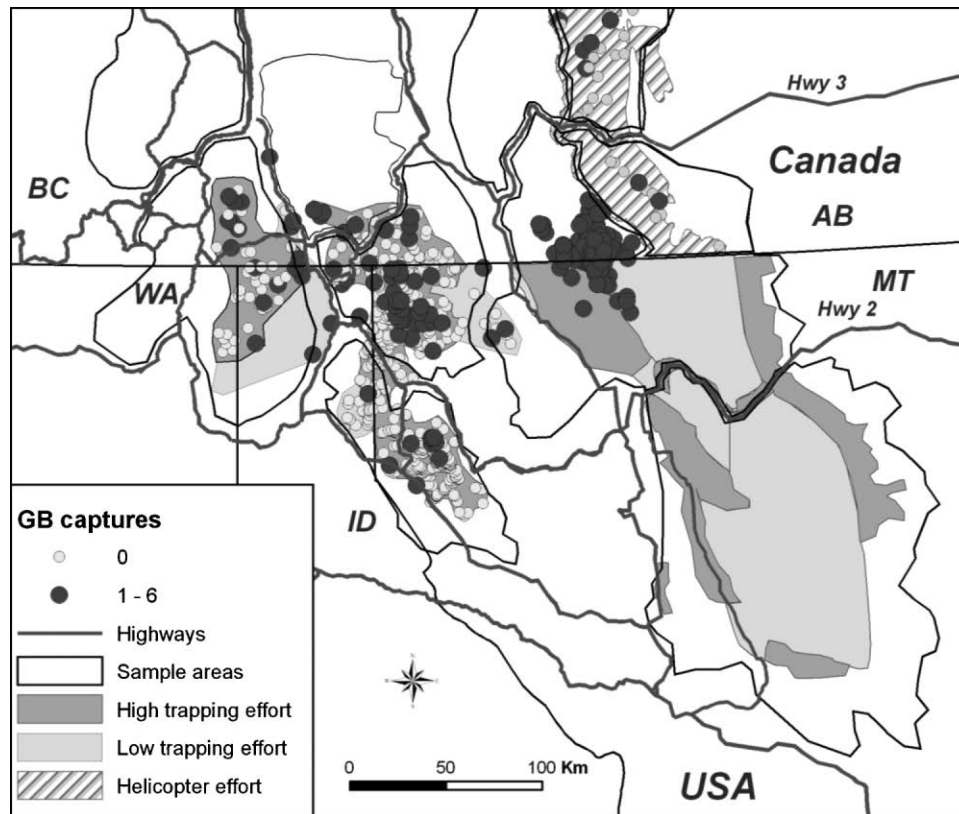
**Figure 14.** Capture effort for radiotelemetry of grizzly bears (GB) in the trans-border region. Shaded polygons represent trapping effort that took place between 1976 and 2006. Comprehensive site-specific trap effort was not available for the United States portion of the Rocky South and Southern Divide Ecosystem areas. Small light circles are trap sites that did not capture a GB, larger darker circles are sites that captured a GB.

North BC), 1 male and 1 female crossed the Divide. Because there was minimal genetic separation across the Divide and Highway 1, we were unable to look for assignment migrants, however.

In summary, using both genetic and telemetry methods, we found that males and females moved across areas with minimal settlement and highway traffic. In areas with major highways and settlement, males moved more than females (Fig. 18).

### Analysis 4: Causes of Fragmentation

The best approximating model from our suite of models compared using $AIC_c$ was the 3-partition piecewise model (Tables 5 and 6). The first partition was the undisturbed portion of the settlement continuum where less than 20% of the fracture length was settled. Within this partition, movement rates were not different between males and females (male $\bar{x} = 0.153$; female $\bar{x} = 0.120$), although male movement rates were approximately 27% higher than females. Male and female movement rates correlated similarly to traffic and mortality, with negative and positive relationships, respectively. The second partition (moderately settled areas of 20–50%) was delineated by a sharp decline in female movement rates as the percentage of human-settled area increased; at this same inflection point, the male movement rate decline was less abrupt, resulting in higher male movement rates than females. Movement rates of both sexes decreased with increasing traffic and settlement, but males and females responded differently to traffic with male movement rates ($\bar{x} = 0.017$) declining at a greater rate than female movement

rates ($\bar{x} = 0.001$), which were already low at the start of the partition because of a lower response threshold. In the most disturbed partition (>50% settlement of potential fracture), females had lower movement rates than males (males $\bar{x} = 0.020$; females $\bar{x} = 0.006$), yet the sexes responded to traffic, settlement, and non-hunt mortality with a similar negative relationship. In these highly settled areas, there was a trend for non-hunt mortality to be negatively correlated with movement.

The partial Mantel test showed *nonsettle* to correlate significantly (partial correlation 0.52 with $D_{LR}$) with all measures of genetic differentiation ($D_{LR}$, $F_{ST}$, and $D_S$; Table 7) across the study area. Mortality and traffic did not have significant correlations with the measures of genetic distance. This test controlled for the effect of geographic distance, although this variable had no influence on genetic distance ($P = 0.99$).

## DISCUSSION

Our large-scale genetic and telemetry sampling across the North American grizzly bear range has provided a comprehensive understanding of large-scale movement patterns of grizzly bears. In more remote areas (i.e., northwestern study area) of their distribution, bear movement, dispersal, and gene flow were influenced by distance and natural topographic features (extensive icefields). In contrast, in the southeastern part of their distribution, anthropogenic influence has disrupted these natural processes, with different fracturing thresholds for males and females. Our results suggest that diminishing demographic connectivity in our southeastern study area has transformed a once inter-connected grizzly
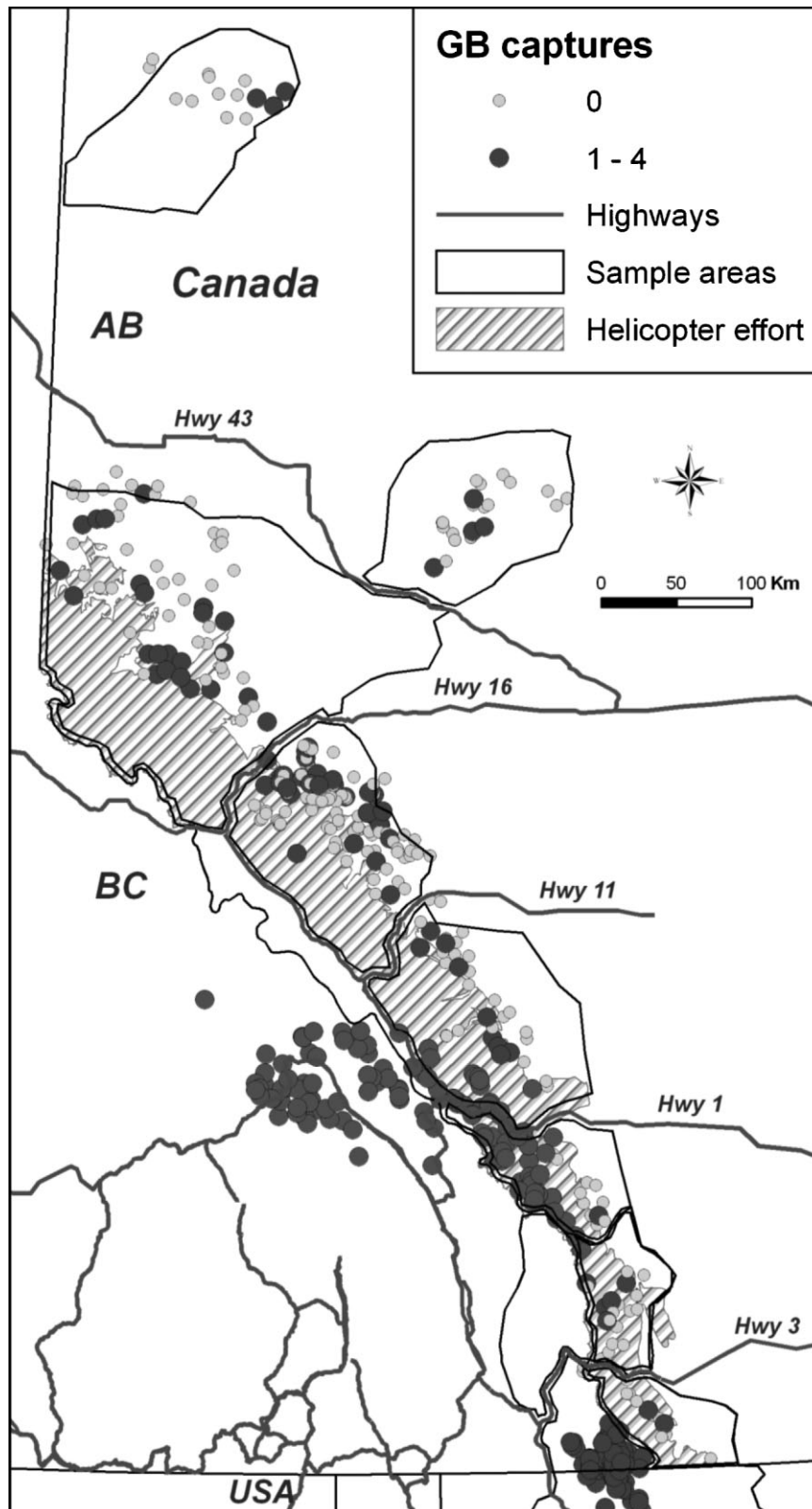
**Figure 15.** Capture effort for radiotelemetry of grizzly bears (GB) in the Alberta region between 1976 and 2006. Small light circles are trap sites that did not capture a GB, larger darker circles are sites that captured a GB. Effort was concentrated around Highway 1 within Banff National Park by the East Slope Grizzly Bear Project and south of Highway 16 by the Foothill Model Forest Project. Along the Alberta–British Columbia Continental Divide, trapping effort was only close enough to the Continental Divide to detect inter-provincial migrants in the extreme north and south of the study area.

**Table 4.** Summary of genetic and direct evidence of migrant grizzly bears between adjacent areas in the trans-border and Alberta study areas. Number of male (M) and female (F) migrants are listed for paired areas across each potential fracture. Genetic migrants were determined through assignment methods, direct migrants were determined either through radiotelemetry or through ear tag identification of captured animals. Some bears were used in multiple comparisons, and genetic samples and number of collared bears ($n$) are listed for each set of adjacent areas. Movement rates are expressed in terms of sample size (migrants/sample size, $m/n$). Movement rate entries indicated with a dagger (†) were used in the calculation of mean rates (labeled and presented in last row) to compare genetic and telemetry movement rates. In areas where there was minimal genetic structure, we present only migrants identified through telemetry.

| Areas | | Assignment migrants | | | | Direct migrants | | |
|---|---|---|---|---|---|---|---|---|
| | $n$ | M | F | Movement rate | $n$ | M | F | Movement rate |
| Trans-border | | | | | | | | |
| Selkirk South–Purcell South Yaak | 130 | 1 | 0 | 0.008† | 75 | 1 | 0 | 0.013† |
| Selkirk South–Purcell Central St Marys | 138 | 0 | 1 | 0.007 | 30 | 3[a] | 0 | 0.1 |
| Purcell South Yaak–Rocky South | 455 | 0 | 0 | 0† | 249 | 1 | 0 | 0.004† |
| Purcell South Yaak–Rocky Central | 230 | 0 | 0 | 0 | | | | |
| Purcell Central St Marys–Rocky Central | 238 | 1 | 0 | 0.004 | | | | |
| Purcell South St Marys–Selkirk Central | 148 | 1 | 1 | 0.014 | | | | |
| Selkirk South–Selkirk Kokanee | 168 | 0 | 0 | 0 | | | | |
| Purcell South Yaak–Purcell Central St Marys | 110 | 4 | 1 | 0.045† | 55 | 4 | 0 | 0.073† |
| Rocky South–Rocky Central | 583 | 10 | 1 | 0.0193 | | | | |
| Southern Divide Ecosystem–Yellowstone | 824 | 0 | 0 | 0 | | 0 | 0 | |
| Purcell Central St Marys–Purcell Central Jumbo | 126 | 4 | 2 | 0.048 | | | | |
| Selkirk Goat–Selkirk Valhalla | 76 | 1 | 1 | 0.026 | | | | |
| Selkirk North–Selkirk Purcell North | 66 | 0 | 0 | 0† | 27 | 2 | 1 | 0.111† |
| Purcell Central Jumbo–Selkirk Goat | 131 | 1 | 1 | 0.015 | | | | |
| Rocky North BC–Selkirk North | 97 | 1 | 0 | 0.01 | | | | |
| Rocky North BC–Selkirk Purcell North | 95 | 1 | 0 | 0.011† | | 1 | 0 | 0.025† |
| Selkirk Goat–Selkirk Kokanee | 74 | 0 | 0 | 0 | | | | |
| Selkirk Kokanee–Selkirk Valhalla | 26 | 0 | 0 | 0 | | | | |
| Rocky South Flathead East–West | | | | | 123 | 25 | 17 | 0.341 |
| Rocky South–Southern Divide Ecosystem | | | | | 242 | 19 | 12 | 0.128 |
| Alberta | | | | | | | | |
| Alberta North–Rocky North Jasper | 248 | 2 | 0 | 0.01† | 90 | 2 | 0 | 0.02† |
| Rocky North Jasper–Rocky North Banff | 202 | 2 | 1[b] | 0.01† | 89 | 0 | 0 | 0† |
| Rocky North Banff–Rocky Central Banff | 187 | | | 0[c] | 167 | 4 | 2 | 0.036 |
| Rocky South Alberta–Rocky Central Alberta | 84 | 7 | 1 | 0.1[d]† | 6 | 0 | 0 | 0† |
| Rocky Central Banff East–West | | | | | 42 | 11 | 7 | 0.429 |
| Rocky North Banff–Rocky North BC | | | | | 68 | 1 | 1 | 0.03 |
| Rocky Central BC–Rocky Central Banff | | | | | 51 | 5 | 3 | 0.16 |
| Rocky Central AB–Rocky Central BC | | | | | 12 | 2 | 1 | 0.25 |
| Rocky South AB–Rocky South BC | | | | | 135 | 7 | 5 | 0.09 |
| Total | | 36 | 10 | Mean rate = 0.023† | | 95 | 49 | Mean rate = 0.031† |

[a] Tag return migrants not identified through telemetry.

[b] Highway 11 female genetic migrant was translocated across highway.

[c] There is insufficient genetic separation across Highway 1 to detect migrants, similar to the Continental Divide areas, therefore we do not compare the assignment and telemetry migrants in this area.

[d] The assignment movement rates for Highway 3 areas in Alberta are likely artificially high because of the high number of problem bears that were translocated south to north across Highway 3 (83 between 1974 and 2006).

bear population into a human-induced, predominately female-fragmented metapopulation (Craighead and Vyse 1996, McLellan 1998, Proctor 2003).

To depict this metapopulation, we synthesized our results into a fragmentation map of the southeastern study area, showing the spatial relationship and population sizes of the resulting subpopulations (Fig. 19). To develop this map, we categorized fragmentation into 2 classes: no fragmentation and fragmentation. Fragmentation was not present between adjacent areas where there was no evidence of genetic clustering in the correspondence analysis and evidence of both sexes moving between areas. Fragmentation existed when 2 adjacent areas showed evidence of clustering in the correspondence analysis plus no female migrants or no migrants of either sex. We realize there are gray areas between our classification of fragmentation or no fragmentation. For example, within Alberta, we found essentially no genetic clustering between bears north and south of Highway

1 and evidence of female movements across Highway 1. However, because few females using habitat on each side of the highway survive in the long-term (M. Gibeau, Parks Canada, unpublished data), we have represented this area on our subpopulation map (Fig. 19) by a lighter dotted line indicating there are signs of female movement but with an associated mortality problem. We also present database population estimates where available, for the resulting subpopulations (Fig. 19, Table 8).

This unusual type of metapopulation is likely in a non-equilibrium state (McCullough 1996), where natural augmentation or recolonization may be inhibited for anthropogenic reasons, rather than the classic equilibrium paradigm where regionally extinct areas are recolonized over time (Hanski and Gilpin 1997). Currently, female interchange is limited in the subpopulations of our southeastern study area to the extent that natural demographic rescue of small threatened subpopulations is likely
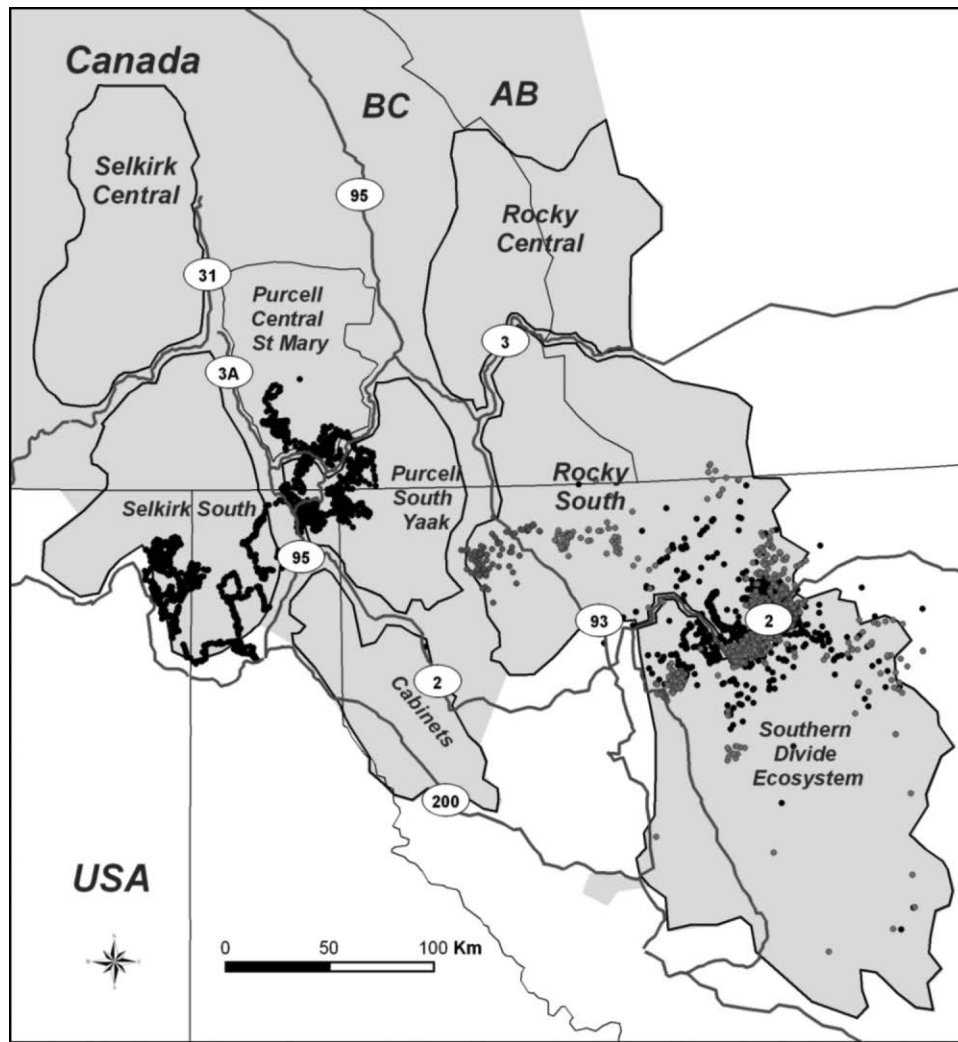
**Figure 16.** Telemetry locations for male and female migrant grizzly bears across highways and between subpopulations in the trans-border area from a sample of 580 bears between 1979 and 2007. Telemetry locations (dots) around Highways 3 and 95 represent 3 male inter-area migrants. Telemetry locations (dots) around US Highway 2 represent 12 female (gray) and 19 male (black) inter-area migrants between the Rocky South and Southern Divide Ecosystem.

not possible (or very limited at best). Whether this system will evolve to small isolated subunits that will eventually become extirpated, or evolve into a functioning metapopulation with inter-unit movement of both sexes will ultimately depend on successful habitat and population management in the coming years.

Human persecution in the last century was primarily responsible for the North American range contraction and extirpation of grizzly bears across 98% of the lower 48 states within the US (Mattson and Merrill 2002, Laliberte and Ripple 2004). Our results suggest a potential mechanism for future range contraction and regional extirpation of grizzly bears, as well as other species susceptible to anthropogenic fragmentation. The mechanism consists of fragmentation that will result in small and vulnerable isolated subpopulations (i.e., the small-population paradigm; Caughley 1994) with elevated extinction risk (Fagan et al. 2002) due to excessive human-caused mortality related to human-bear conflicts (McLellan et al. 1999). Multiple patterns of range contraction and extinction risk likely exist, including core extinction-peripheral persistence systems (Channell and Lomolino 2000a) and responses resulting from

factors unrelated to fragmentation and small isolates (Turvey et al. 2010). However, Channell and Lomolino (2000b) suggest that patterns of range contraction likely begin where the extirpating forces are greatest and move to those areas where they are lesser. These forces can often be anthropogenic (Channell and Lomolino 2000b), as our grizzly bear data suggest, and we agree with their conclusion that the most appropriate conservation strategy is to resist the range contraction process early in its evolution before a species is left with the drastic situation of small, isolated, threatened subpopulations, as are occurring on the southern periphery of the grizzly bear metapopulation. Furthermore, interactive forces such as habitat degradation and/or climate change which may lower productivity coupled with fragmentation that bring bears into conflict in human environments can exacerbate simpler historical forces (e.g., persecution). This synergistic interaction of multiple forces could push local subpopulations to extirpation (Brooks et al. 2008).

A sufficient number of females in a population is critical to decrease the risk of population extirpation in small fragmented populations because female grizzly bears do not mate every year
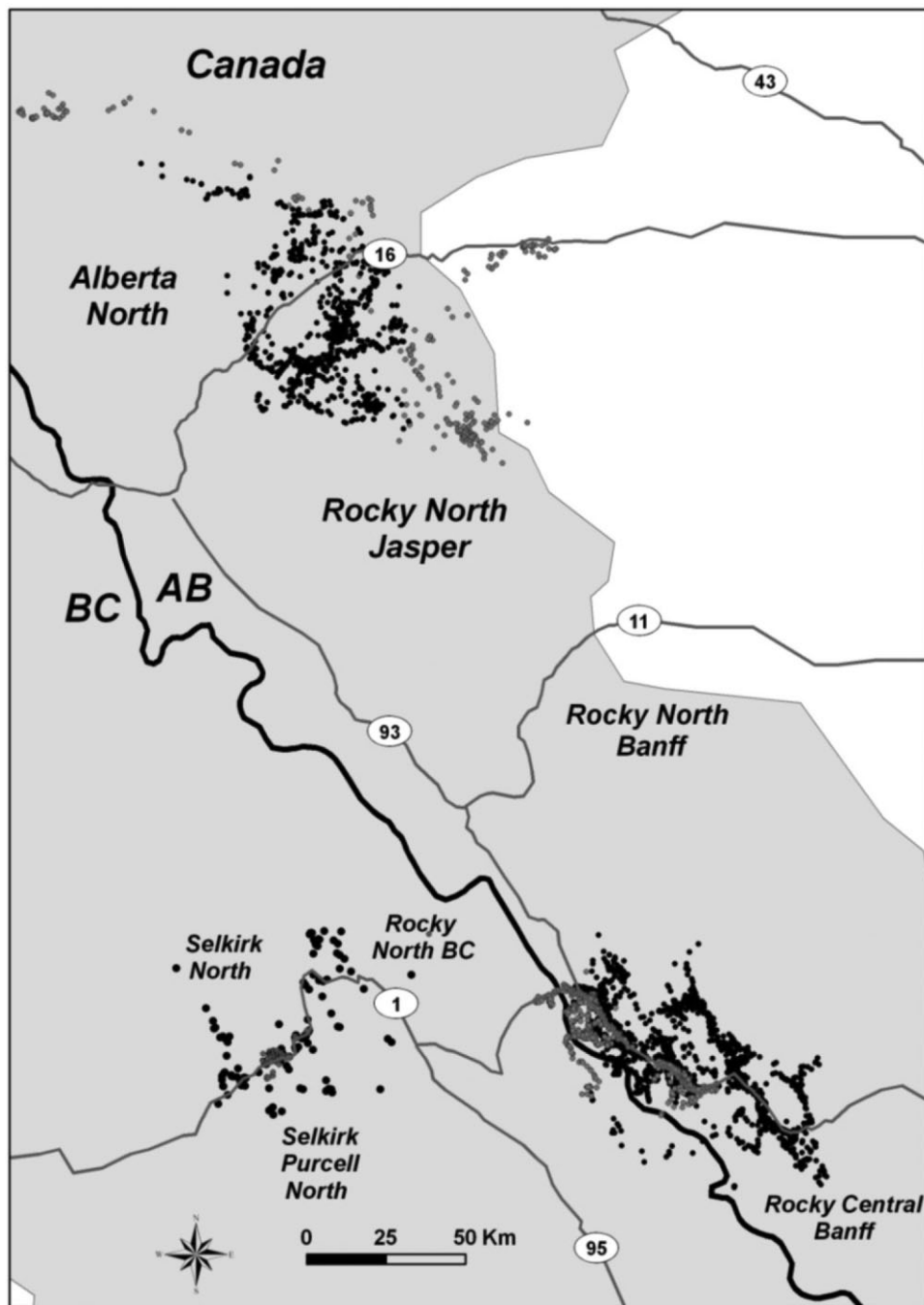
**Figure 17.** Telemetry points for male and female migrant grizzly bears between subpopulations across Alberta and along Highway 1 in British Columbia (BC) from a sample of 335 bears. Telemetry locations (dots) around Highways 16 represent 2 male (gray dots are 1 male, black dots a second male) inter-area migrants between the Alberta (AB) North and Rocky North Jasper areas. Telemetry locations (dots) around AB Highway 1 represent 2 female (gray) and 4 male (black) inter-area migrants between the Rocky North Banff and Rocky Central Banff areas. Telemetry locations (dots) around BC Highway 1 represent 1 female (gray) and 2 male (black) inter-area migrants between the Selkirk Purcell North and the Selkirk North–Rocky North BC areas.

and 1 male is capable of impregnating several females. Females provide population viability, and female immigration is needed to augment a dwindling population or recolonize one that has been extirpated. Small declining populations, such as the one south of Highway 3 in the Purcell Mts (Purcell South Yaak population <50 bears, declining at 3.9% annually; Figs. 5 and 19, Tables 8 and 9), are unlikely to be viable over the long-term without female immigration (Proctor et al. 2004*b*, Wakkinen and Kasworm 2004). Although genetic isolation is also a concern

with small populations (Frankham 1998), male immigration may be enough to resist loss of genetic diversity (Paetkau et al. 1998*a*). Genetic isolation is not as great nor as immediate a threat as interruption of demographic processes (Lande 1988, Caughley 1994), particularly for grizzly bears in this region where strong anthropogenic processes influence population vital rates (e.g., human-caused mortality; McLellan et al. 1999), habitat quality, population densities (Nielsen et al. 2006), and fragmentation that has resulted in small subpopulations. If management attains
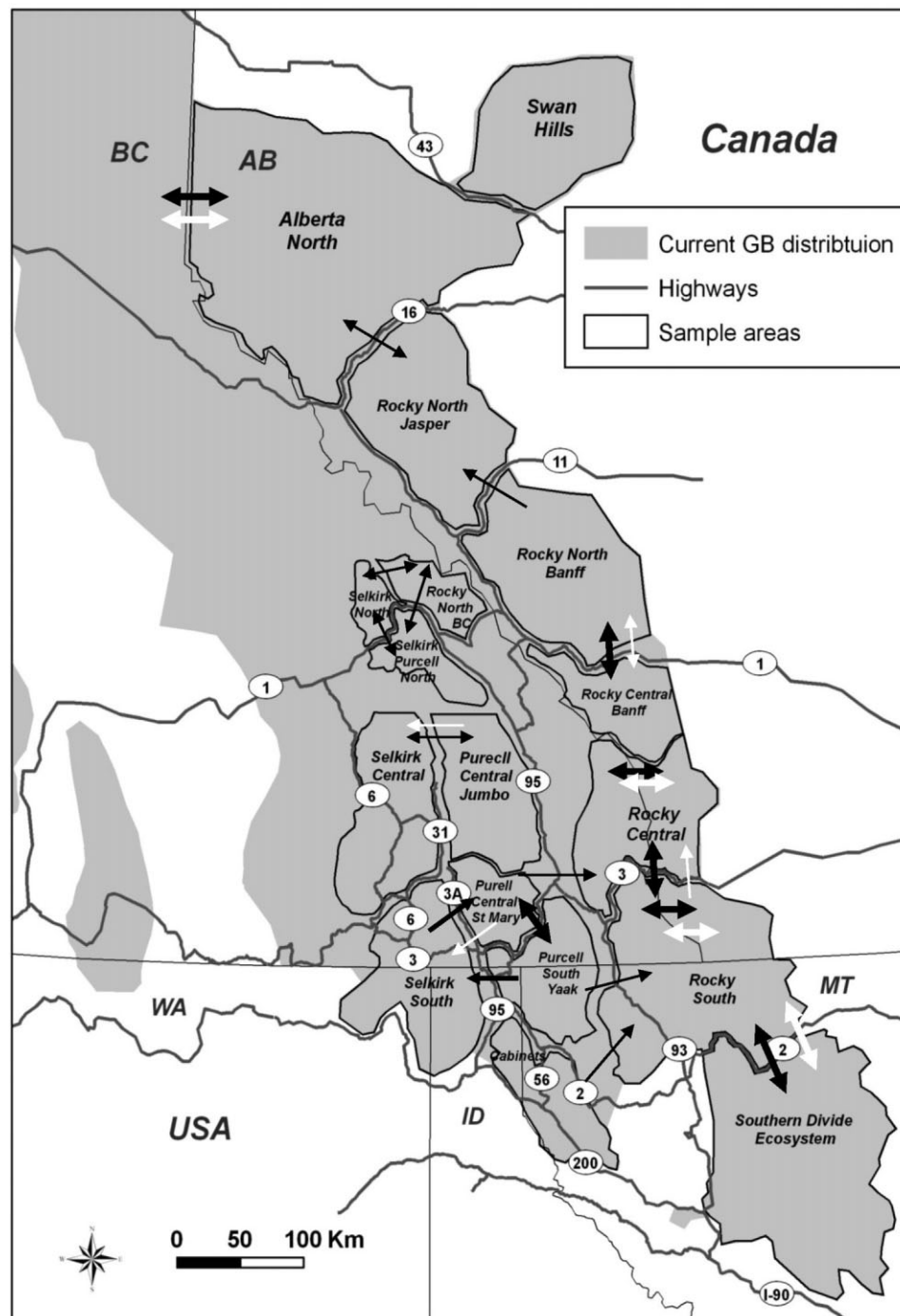
**Figure 18.** Summary of migrant grizzly bears (GB) as determined by genetic assignment and direct means between adjacent areas in the Canada–United States transborder and Alberta regions. Black arrows indicate male movements and white indicate female movements. Arrows indicate direction and thickness illustrates the rate of movements (i.e., thicker lines indicate more movements, each thin white arrow represents 1 female GB movement). There were no movements associated with the Yellowstone area (not on map).

demographic connectivity with both sexes dispersing across potential fractures, then genetic connectivity is ensured. Genetic connectivity, however, does not ensure demographic connectivity.

All lines of evidence presented here support the anthropogenic fragmentation hypotheses in our southeastern study region. The significantly higher geographic distance-adjusted genetic distances in the southeastern region relative to those in the northwestern region (Appendix), the relative paucity of explanatory power

of IBD to account for genetic structure (IBD analysis), the patterns of clustering on separate sides of settled valleys with highways (Figs. 9 and 10), the sex-specific migrant analysis (Table 4), and our regression analysis revealing sex-specific influences of fragmentation support the supposition that human settlement patterns and transportation corridors are inhibiting grizzly bear movements. Below, we discuss our results in relation to specific hypotheses associated with each of our 4 major analyses.

**Table 5.** Model ranking for linear regression candidate models examining grizzly bear movement rates in the trans-border and Alberta areas as functions of geographic distance (geodist), and 3 human disturbance variables: traffic, human settlement patterns (nonsettle), and human-caused non-hunting mortality (mort). Column headings: residual sum of squares (RSS), number of model parameters ($K$), small sample adjusted Akaike Information Criteria (AIC$_c$), difference in AIC$_c$ scores of each model relative to the "best" model ($\Delta$AIC$_c$), and relative likelihood of the model given the data ($w_i$). The best model had a "piecewise" structure reflecting situations where abrupt responses occur at thresholds resulting in a marked change in slope of the regression line.

| Models | RSS | $K$ | AIC$_c$ | $\Delta$AIC$_c$ | $w_i$ |
|---|---|---|---|---|---|
| Unsettled <20% (traffic mort), Modsettled 20–50% (sex traffic nonsettle sex × traffic), Highly settled >50% (sex traffic nonsettle mort traffic × nonsettle) | 0.778 | 12 | −166.4 | 0 | 0.732 |
| Sex traffic nonsettle mort nonsettle[2] traffic × nonsettle[3] nonsettle × mort sex × nonsettle[3] | 1.055 | 9 | −160.5 | 4.45 | 0.079 |
| Sex traffic nonsettle mort traffic × nonsettle nonsettle × mort | 1.213 | 7 | 159.8 | 5.15 | 0.055 |
| Traffic nonsettle mort traffic × nonsettle nonsettle × mort | 1.342 | 6 | −157.6 | 7.35 | 0.019 |
| Sex traffic nonsettle mort geodist | 1.473 | 6 | −153.2 | 11.75 | 0.002 |
| Traffic nonsettle mort geodist | 1.581 | 5 | −152.4 | 12.55 | 0.001 |
| Sex traffic nonsettle sex × traffic × nonsettle | 1.609 | 5 | −151.6 | 13.35 | 0.001 |
| Sex traffic nonsettle traffic × nonsettle | 1.616 | 5 | −151.3 | 13.65 | 0.001 |
| Traffic nonsettle traffic × nonsettle | 1.783 | 4 | −149.1 | 15.85 | 0.0003 |
| Sex nonsettle | 1.872 | 3 | −149.2 | 15.75 | 0.0003 |
| Nonsettle | 2.039 | 2 | −147.4 | 17.55 | 0.0001 |
| Sex nonsettle sex × nonsettle[a] | 1.867 | 4 | −146.9 | 18.05 | 0.0001 |
| Settled <0.5 (traffic mort) settled >0.5 (sex traffic nonsettle mort traffic × settle) | 1.415 | 9 | −146.4 | 18.55 | 6.9E−05 |
| Sex traffic | 2.037 | 3 | −145.1 | 19.85 | 3.6E−05 |
| Traffic | 2.204 | 2 | −143.6 | 21.35 | 1.7E−05 |
| Sex traffic sex × traffic[a] | 2.027 | 4 | −143.0 | 21.95 | 1.2E−05 |
| Sex geodist | 2.330 | 3 | −138.7 | 26.25 | 1.4E−06 |
| Geodist | 2.497 | 2 | −137.6 | 27.35 | 8.6E−07 |

[a] Models whose interaction terms were not significant.

## Analysis 1: Isolation-by-Distance and Natural Fragmentation

We found general evidence of more bear movement in the northwestern, less-disturbed study area compared with our southeastern study area. Genetic structure of bears in the northwestern study area follows an IBD pattern supporting hypothesis A1. Although most of the northwestern data suggested widespread gene flow, some natural fragmentation was documented due to extensive icefields and glaciers. Additionally, the region separating the Skeena North and South areas (Fig. 4) from the Nation, Parsnip, and Herrick areas is part of a large plateau that is dominated by sub-boreal conifer forests, rolling hills and low mountains, and numerous lakes and wetlands in the sub-boreal ecoprovince (Demarchi et al. 1990, Mowat et al. 2005). This plateau is a distinct interruption of an otherwise continuous mountainous landscape in our northwestern sample region (Fig. 1) and may be inhibiting bear movements between the mountainous areas adjacent to it. For example, within the Parsnip sampling area (Parsnip Mountain–Parsnip Plateau; Fig. 11), fine-scale genetic and telemetry evidence (Ciarniello 2006) suggested limited mountain-plateau gene flow (Appendix) and partially explained the increased genetic distances across this large plateau. Poole et al. (2001) reported a similar effect in the Prophet study area in northeastern BC, which straddles another mountain–plateau interface zone where no genetic recaptures could be found between these ecotypes. We concur with

**Table 6.** Parameter coefficients for the best multiple-regression model of grizzly bear movement rates selected through small-sample-adjusted Akaike Information Criteria (AIC$_c$) scores for predicting factors associated with grizzly bear movement rates. We present the relationships for each of the 3 partitions within the piecewise best model. The 3 human disturbance variables: traffic, human settlement patterns (nonsettle), and human-caused non-hunting mortality (mortality) were all supported in the best model.

| Partition | Variable | Coefficient | Probability | $R^2$ |
|---|---|---|---|---|
| Undisturbed | | | 0.009 | 0.513 |
| | Traffic | −0.010 | 0.016 | |
| | Mortality | 5.778 | 0.005 | |
| | Constant | 0.303 | 0.005 | |
| Moderately Disturbed | | | 0.001 | 0.910 |
| | Sex | 0.439 | 0.001 | |
| | Traffic | −0.002 | 0.009 | |
| | Nonsettle | −0.982 | 0.004 | |
| | Sex × traffic | −0.005 | 0.029 | |
| | Constant | 0.744 | 0.006 | |
| Disturbed | | | 0.081 | 0.471 |
| | Sex | 0.149 | 0.048 | |
| | Traffic | 0.008 | 0.440 | |
| | Nonsettle | −2.483 | 0.120 | |
| | Mortality | −2.534 | 0.071 | |
| | Traffic × nonsettle | 0.055 | 0.081 | |
| | Constant | 0.456 | 0.253 | |

**Table 7.** Partial Mantel's test of multiple predictor variables on grizzly bear genetic differentiation of trans-border and Alberta grizzly bear sampling areas. Models based on $D_{LR}$ (Paetkau et al. 1997), Nei's $D_S$ (Nei 1972), and $F_{ST}$ values (Weir and Cockerham 1984) all showed the same significance patterns: only $D_{LR}$ is presented. $D_{LR}$ is the mean of the ratio of the log likelihoods of individuals' genotypes occurring in their own population to the likelihood of it occurring in the compared population. $F_{ST}$ is the proportion of the variation in allele frequencies that is attributable to differences in populations. $D_S$ compares homozygosity between populations to estimate genetic distance by comparing the sum of squares of allele frequencies within populations and the sum of products of the frequencies of individual alleles in the 2 populations being compared. Regression coefficients, correlation coefficients, and probabilities are presented for each variable, with the overall amount of variation explained by the model ($R^2$) being 0.41 and the error sum of squares was 0.08.

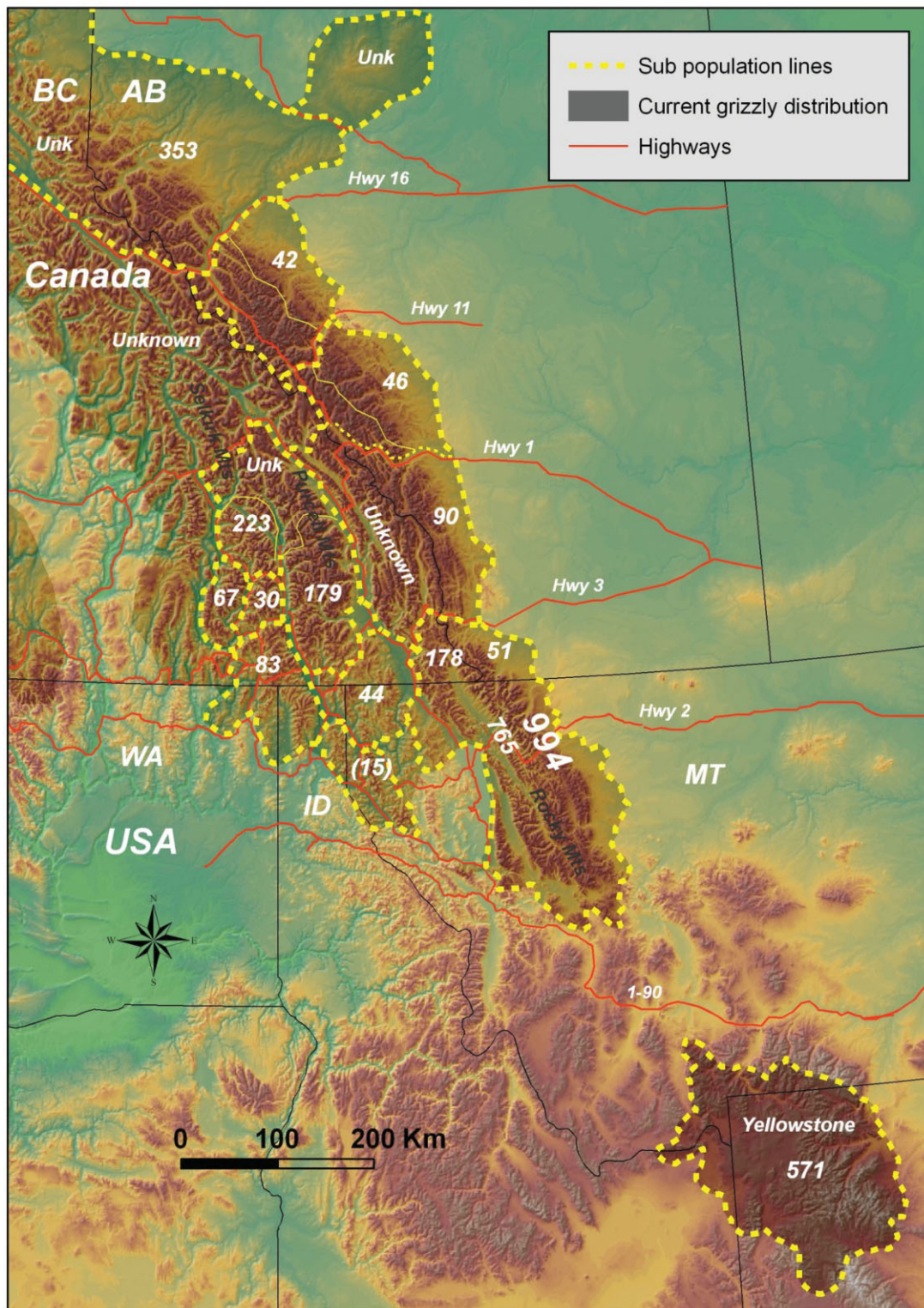| $D_{LR}$ partial Mantel | Coeff. | Correlation | P-value |
|---|---|---|---|
| Density | −0.0153 | −0.210 | 0.88 |
| Geodist | 0.0002 | 0.092 | 0.99 |
| Mort | −0.8856 | −0.267 | 0.98 |
| Nonsettle | 5.9500 | −0.523 | 0.01* |
| Traffic | −0.0453 | −0.103 | 0.19 |

* Significant variables.

**Figure 19.** Map of subpopulations of grizzly bears in the trans-border area and Alberta derived from the fragmentation synthesis. Subpopulations are enclosed within dotted polygons. Numerical values represent survey-based subpopulation estimates (see Table 8 for data sources and 95% confidence intervals). Where multiple numbers are within a subpopulation (dotted polygon), estimates are for separate jurisdictions delineated by a light solid line (i.e., provincial, international boundaries, or the limit of a survey effort). For example, there are 994 bears in the southern Rocky Mountains subpopulation, which includes 51 bears within the Alberta portion of that subpopulation, 178 in the British Columbia portion, and 765 in the United States portion. Unknown (unk) reflects no data. The lighter dotted line along Highway 1 in Alberta signifies only minimal fragmentation of females that may be disappearing.

**Table 8.** Reference table for map of grizzly bear subpopulations (Fig. 19). Data sources and confidence intervals for survey-derived subpopulation estimates in the trans-border and Alberta areas that are delineated in Figure 5. Estimates were derived from DNA survey-based estimates. Estimates in parentheses are researcher estimates where no formal survey has been carried out.

| Location | Population estimate | 95% CI | Refs. |
|---|---|---|---|
| Trans-border | | | |
| Selkirk South | 83 | | |
| Canada | 58 | 50–70 | Proctor et al. (2007) |
| USA | 25 | na | W. Wakkinen, Idaho Fish and Game, unpublished data |
| Purcell South Yaak | 44 | | |
| Canada | 24 | 20–28 | Proctor et al. (2007) |
| USA | 20 | na | Kasworm et al. (2007b) |
| Purcell/Selkirk Central | | | |
| Purcells | 179 | 139–234 | Proctor et al. (2007) |
| Selkirk Goat | 223 | 138–416 | Mowat et al. (2005) |
| Selkirk Valhalla | 67 | 43–133 | Mowat et al. (2005), M. Proctor, Birchdale Ecological, unpublished data |
| Selkirk Kokanee | 30 | 19–59 | Mowat et al. (2005), M. Proctor, unpublished data |
| Rockies South | 994 | 878–1189 | |
| Alberta | 51 | 34–87 | Grizzly Bear Inventory Team (2008) |
| BC | 178 | 129–271 | Grizzly Bear Inventory Team (2008) |
| USA | 765 | 715–831 | Kendall et al. (2008) |
| Cabinets | 15 | na | Kasworm et al. (2007b) |
| Yellowstone | 571 | 513–629 | Haroldson (2009) |
| Alberta | | | |
| US border–Hwy 3 | 51 | 34–87 | Grizzly Bear Inventory Team (2008) |
| Hwy 3–Hwy 1 | 90 | 71–116 | Alberta Grizzly Bear Inventory Team (2007) |
| Hwy 1–Hwy 11 | 46 | 41–52 | Boulanger et al. (2005a) |
| Hwy 11–Hwy 16 | 42 | 36–55 | Boulanger et al. (2005b) |
| Hwy 16–north | 353 | 288–516 | Alberta Grizzly Bear Inventory Research Team (2009) |

Mowat et al. (2005), who suggested this apparent fracture type may reflect different life-history strategies specific to dominant food supplies. This result is not dissimilar to several examples of carnivore genetic structure and dispersal relating to habitat or ecotype boundaries (coyotes [*Canis latrans*], Sacks et al. 2004; wolves [*Canis lupus*], Geffen et al. 2004). Historic mortality from early explorers and settlers throughout the 1800s and early 1900s may have additionally contributed to this fragmentation.

In contrast to the IBD and natural fragmentation present in the northeastern study area, the variation in the genetic distances explained by geographic distance in our southeastern region was much less, suggesting the involvement of other fragmenting forces and in support of hypothesis A2. Some evidence was found for natural fragmentation in our southeastern study area along the heavily glaciated sections of the Continental Divide, but fragmentation associated with roads and human settlements was predominant.

## Analyses 2–3: Genetic Clustering and Migrant Detection in the Southeastern Study Area

The cumulative clustering results support our hypothesis (B) that genetic discontinuities correspond to valleys with settlement and highways. Before carrying out our migrant analysis, it was important to first use the cluster analysis that assumed no a priori group membership. This method allowed us to identify genetic discontinuities in an unbiased manner. Furthermore, the clustering results provided the logical basis for testing migrants across human-settled valleys. We also added unsettled valleys and potential fractures to the migrant analysis as controls to strengthen the comparison. Results of the migrant analyses further supported the settlement-highway fracture hypothesis (B). The combined cluster and migrant detection Analyses (2 and 3) informed our synthesis of the regional female-fragmented

metapopulation and allowed us to determine spatially explicit subpopulation boundaries (Fig. 19).

*Trans-border region.*—The subpopulations within the trans-border region of our southeastern study area ranged from relatively secure units with >500 bears to several small units of <100 bears. Population size is one of the most powerful predictors of persistence and populations fewer than 50–100 adults are at higher risk of extirpation (Berger 1990, Shaffer et al. 2000, Reed et al. 2003). Several small populations (Purcell South Yaak, Selkirk South, Cabinet Mts, Selkirk Kokanee, and Selkirk Valhalla) throughout the trans-border area (Fig. 19, Table 8) have immediate conservation concern (Table 9). These fragmented units are immediately adjacent to a more secure unit in the central Purcell–Selkirk area (>500; Fig. 19, Table 8; Proctor et al. 2007) that represents a regional core or source population. Long-term persistence of the small populations is likely reliant upon their reconnection to this larger Purcell-Selkirk Central unit through appropriate management. Apps et al. (2009) recently documented a similar pattern of grizzly bear fragmentation in the South Coast Mountains of southern BC, with several isolated populations <30 bears.

The east–west fragmentation across the valley separating the Rocky South and the Purcell South Yaak areas (Appendix, Table 4, Fig. 19) might be in part due to the Koocanusa Reservoir, which has separated these areas since the early 1970s. Based on telemetry work in the Rocky South area, we determined that females especially were likely to treat a large water reservoir as a movement barrier (e.g., Hungry Horse; R. Mace, Montana Fish Wildlife and Parks, personal communication). Therefore, we might not expect to find females moving between these subpopulations. However, the dearth of male movements across the Koocanusa reservoir suggests that other factors beyond the effect of the reservoir may be at play. Historic

**Table 9.** Selected ecological, demographic, and conservation characteristics of the delineated subpopulations of grizzly bears within the southeastern study region including the Canada–US trans-border and Alberta regions. This summary may simplify some important spatial or temporal variation of reproduction, mortality rates, and trend, therefore consult references for more detail about individual subpopulations. Unk abbreviates unknown.

| Sub population | Reproduction | Mortality | Population trend | Population size | Fragmentation | Threats | Protected status | Management needs | Conservation status |
|---|---|---|---|---|---|---|---|---|---|
| Rocky South | Medium+[a] | Canada-medium[a], US-low[b] | Canada-increasing[a], US-increasing[b] | Large[c,d] (>500) | Medium[e,f] | Mortality | High | Stability | Good |
| Southern Divide Ecosystem | Medium+[b] | Low[b] | Increasing[b] | Large[e] (>400) | Low[e] | Mortality habitat security | High | Stability | Good |
| Yellowstone | High[g] | Low[g] | Increasing[g] | Large[g] (>500) | High[h] | Mortality | High | Stability | Good |
| Rocky Central | North low[i] south unk | North medium[i] south unk | North unk south unk | Large[d] (>300) | Medium[f] | Mortality | Medium | Stability | Cautious |
| Rocky North Banff | Low[j] | Low[j] | Increasing[j] | Small[j] (<100) | Medium | Mortality fragmentation habitat security | Medium | Habitat security mortality linkage | Poor |
| Rocky North Jasper | Low[k] | Medium[k] | Unk | Small[l] (<100) | Medium | Mortality fragmentation habitat security | Medium | habitat security mortality linkage | Poor |
| Alberta North | Unk | Unk | Unk | Large[m] (>300) | Medium | Mortality fragmentation habitat security | Medium | Habitat security mortality linkage | Good |
| Cabinets | Unk | Unk | Unk | Small[n] (<25) | High | Mortality fragmentation habitat security | Medium | Intensive habitat security mortality linkage augmentation | Poor |
| Purcell South Yaak | Medium[o] | High[o] | Decreasing[o] | Small[n,p] (<50) | High[f], female isolated | Mortality fragmentation habitat security | Low | Intensive habitat security mortality linkage augmentation | Poor |
| Selkirk South | Medium[o] | Medium[o] | Slightly increasing[o] | Small[p,q] (<100) | High[f] | Mortality fragmentation habitat security | Medium | Habitat security mortality linkage | Cautious |
| Purcell Selkirk Central | Unk | Unk | Unk | Large[p,r] (~500) | Medium[f] | Mortality fragmentation habitat security | Medium | Habitat security mortality linkage | Cautious |
| Selkirk Valhalla | Unk | Unk | Unk | Small[r] (<100) | High | Mortality fragmentation habitat security | Medium | Habitat security mortality linkage | Poor |
| Selkirk Kokanee | Unk | Unk | Unk | Small[r] (<50) | High | Mortality fragmentation habitat security | Medium | Habitat security mortality linkage | Poor |
| North Cascades | Unk | Unk | Unk | Small[s] (<25) | High[s] | Mortality fragmentation habitat security | High | Intensive habitat security mortality linkage augmentation | Poor |

[a] McLellan (1989a).
[b] Mace et al. (2012).
[c] Kendall et al. (2008).
[d] Grizzly Bear Inventory Team (2008).
[e] Kendall et al. (2009).
[f] Proctor et al. (2005).
[g] Schwartz et al. (2006b).
[h] Haroldson et al. (2010).
[i] Garshelis et al. (2005).
[j] Boulanger et al. (2005a).
[k] Boulanger and Stenhouse (2010).
[l] Boulanger et al. (2005b).
[m] Alberta Grizzly Bear Inventory Research Team (2009).
[n] Kasworm et al. (2007a).
[o] Wakkinen and Kasworm (2004).
[p] Proctor et al. (2007).
[q] W. Wakkinen, unpublished data.
[r] Mowat and Strobeck (2000).
[s] Almack et al. (1993).

mortality is suspected of severely reducing numbers of grizzly bears in the areas separating these subpopulations, minimizing the potential for inter-area movements.

The Cabinet sample ($n = 16$) contains 5 bears that are descendents of a bear transplanted into the Cabinet Mts from the Rocky South area in the early 1990s (Servheen et al. 1995, Kasworm et al. 2007b), thus precluding biologically relevant comparisons of genetic distance and genetic migrant analyses. In the FCA, close clustering of the Cabinet Mt. and Rocky South bears is noteworthy (Fig. 9c). The augmentation descendents would be expected to cluster tightly with the Rocky South area's bears. However, the bears that pre-date the 1990s augmentation and represent original (not introduced or translocated into) Cabinet bear genotypes, also cluster tightly with Rocky South bears (Fig. 9c), suggesting an historic close link between bears in the Cabinet and Rocky South areas. Three scenarios could have given rise to this clustering pattern. First, the Cabinet bears may have always remained connected with Rocky South bears at a level undetected through telemetry or tag returns. Second, the bears of the Cabinets were extirpated historically and recolonized from bears out of the Rocky South area (through metapopulation function). Third, perceived isolation of the Cabinet bears has occurred recently enough that no genetic signal is yet apparent. Although which scenario is correct is unknown, we have found no evidence of natural movement into the Cabinet area, and 3 bears that pre-date the 1990s augmentation effort were a family group of which the male and female parents were born in the 1950s.

Prolonged isolation and associated genetic drift in the Selkirk South and Yellowstone areas have led to genotypes in those areas clustering separately from other bears in their regions. The bears within the Yellowstone ecosystem have been isolated for many decades (Merriam 1922, Mattson and Merrill 2002, Miller and Waits 2003, Schwartz et al. 2006a). Haroldson et al. (2010) report no recent evidence of movements or genetic exchange between bears in the US Southern Divide Ecosystem and Yellowstone ecosystem. The Yellowstone bears are separated by approximately 150 km of human-settled valleys with extensive agriculture, 2 major US Interstate highways, and National Forest lands. Bears have been extirpated in this gap area through various mechanisms, largely by excessive human-caused mortality during settlement of the western US (Servheen 1999, Mattson and Merrill 2002). The range in raw genetic distances between Yellowstone and the Southern Divide Ecosystem, across Highway 2 between the Southern Divide Ecosystem and Rocky South areas, and across BC Highway 3 separating Rocky South and Rocky Central (Appendix) reflect the variation in individual movements we detected. However, adjusted genetic distances (genetic distance/geographic distance) were remarkably similar (Fig. 13). These patterns corroborate the result from Analysis 1 that found geographic distance played a small role in explaining genetic distances in our southeastern study area and suggest that researchers should be cautious drawing conclusions about levels of fragmentation in species where the relationship between genetic and geographic distances is complex or unknown. The genetic drift experienced by the isolated and small Selkirk South subpopulation was extreme enough to register clearly in the raw and adjusted genetic distance values, in contrast to the Yellowstone, which has been known to be isolated for

many decades. The difference in intensity of genetic drift between these 2 subpopulations was likely influenced by the difference in effective population sizes of those populations.

Yellowstone and Selkirk South bears set the fragmentation endpoint of this analysis (Figs. 9 and 10). The discrete clustering and low $H_E$ of the Selkirk South subpopulation when compared to the Yellowstone subpopulation, with its isolation history (Tables 2 and 4, Fig. 9i), suggest the Selkirk South subpopulation has essentially been genetically (and demographically) isolated for at least several generations. Proctor et al. (2005) found no evidence of any inter-population migrants in 43 bears identified before 1999. Our more recent detection of migrants in the Selkirk South area could reflect either greater sampling effort (our 2005 DNA population estimate survey captured 90% of the Canadian Selkirk South population; Proctor et al. 2007), or that migrants are a relatively new phenomenon and connectivity is increasing. However, movement between ecosystems does not necessarily imply that migrant males successfully bred before dying or returning. If inter-area movements are resulting in gene flow, then concern over inbreeding is reduced. In contrast to the Yellowstone fragmentation (decades of separation across approx. 150 km), the Selkirk South area is only separated from adjacent occupied habitat by a narrow settled valley (approx. 2 km). The Selkirk South subpopulation has experienced a 20% reduction in heterozygosity (and potentially genetic variation) relative to immediately adjacent areas <2 km away. Although we consider demographic threats to smaller grizzly bear subpopulations to be more urgent than reduced genetic variation, the lower heterozygosity in the Selkirk South subpopulation likely occurred over a relatively short time period (<100 yr). This short time frame may have minimized the purging of deleterious alleles that is typically a slow evolutionary and advantageous process (Frankham et al. 2002). Although $H_E$ is also low in Yellowstone, this low variability may be less severe than the Selkirk situation when compared to historic values (Miller and Waits 2003). Miller and Waits (2003) hypothesized that Yellowstone gene flow from the north has been historically low, and therefore the current reduced genetic diversity may not be due to recent fragmentation.

Subpopulation reconnection appears to be taking place in the eastern and southern portions of the Southern Divide Ecosystem population as determined by Kendall et al. (2009). We found a high number of migrants (Table 4) and weak clustering (Fig. 9h) between the Rocky South and Southern Divide Ecosystem areas (separated by US Highway 2), reflecting minor fragmentation of historic and unknown origin (possibly mortality patterns). Waller and Servheen (2005) documented similar movements in their study of collared bears across US Highway 2. Using techniques comparable to ours, Kendall et al. (2009) found evidence of clustering on either side of the more settled western portion of US Highway 2 but not across the minimally settled eastern section. Our telemetry data revealed similar patterns. The distribution of Highway 2 crossing events was heavily skewed to the eastern section (Fig. 16), in contrast to the western section where settlement and traffic were 3 times greater than the east (K. Kendall, US Geological Survey, unpublished data).

The number and density of bears in each of the Rocky Mts subpopulations spanning BC Highway 3 are relatively high (Fig. 19, Table 8; McLellan 1989a, Grizzly Bear Inventory

Team 2008, Kendall et al. 2008), resulting in slow genetic drift. Therefore, development of a genetic signal sufficient for detecting individual migrants and genetic clustering suggests strong historic limitations on movement and likely much lower densities due to high mortality pressures on bears in the region during the late 1880s and earlier 1900s (Mattson and Merrill 2002).

It is difficult to interpret what detection of inter-population migrants means relative to functional population connectivity (inter-area breeding). Intense study in the trans-border region has produced evidence of male bears crossing between areas with obvious genetic fragmentation. It is clear that the genetic structure in the trans-border region signifies reduced gene flow in past generations. It is less clear, however, to what extent inter-breeding is currently occurring between areas in the region. Future work will need to focus on understanding what, if any, genetic contribution is made by migrants to their new ecosystem in the genetically fractured trans-border region (Kasworm et al. 2007*b*). For now, we conclude that some migrants, mainly males, are being detected between areas but that genetic structure is evident among areas because of limited gene flow over past generations (Table 4, Fig. 9a–h). Because wildlife managers have moved problem bears between ecosystems (to remote areas), including female bears, natural movements would be less than what we report.

*Alberta region.*—The genetic fractures we found across most of Alberta's major east–west highways (3, 11, 16, and 43) are not sharp, but rather represent detectable discontinuities in genetic mixing across a region that overlay the constant of geographic distance's influence on genetic distance. In contrast, we detected higher rates of gene flow across the Continental Divide. Overall, the mean movement rate of bears (derived from telemetry) across the full length of the Continental Divide in our study area was approximately 4 times higher than across the major highways in Alberta. This pattern was weakest in the northern Rocky Mts area, where gene flow across the Continental Divide is just as limited as it is across the nearest major highway (Highway 11). The Continental Divide north of Highway 1 (Rocky North Banff–Rocky North BC) is the most rugged of the Continental Divide areas investigated, with several large icefields (Fig. 12) that may act as a partial barrier to gene flow between provinces. Furthermore, the Banff-Jasper Highway (Highway 93) closely parallels the Continental Divide and experiences an average of 3,250 vehicles per day in summer, which may further contribute to the lack of movements across the Divide. Bears in the Alberta North area clustered with bears directly west in BC more than they did with Alberta bears to the south across Highway 16 (Fig. 10a) suggesting that Highway 16 and associated developments have been acting as a partial barrier to bear movements. In southern Alberta, all lines of evidence suggest substantial gene flow across the Continental Divide north and south of Highway 3 but interrupted gene flow across Highway 3.

The number of bears moved by managers in Alberta suggests that natural movement is likely less than suggested by our results. The population estimate of bears in Alberta south of Highway 3 is 51 (95% CI: 34–87, Grizzly Bear Inventory Team 2008), although well connected to the >900 bears in Rocky South BC and Rocky South US. At least 83 grizzly bears were moved out of this area between 1979 and 2006 because of human-bear conflict management (G. Stenhouse, unpublished data), usually being released north of Highway 3. These translocated bears may explain why 7 of the 10 migrants we detected to have moved from the Rocky South to the Rocky Central area were bears found in Alberta.

As in the trans-border region, few migrants (mostly males) crossed the major Alberta highways except for Highway 1 within Banff National Park. Although collared females were documented crossing Highway 1 in Banff National Park, female mortality rate associated with having the highway within their home ranges is high, and few females survive long term (Benn and Herrero 2002, Nielsen et al. 2004). Recently (1996), wildlife crossing structures accompanied by extensive wildlife-resistant fencing were installed along Highway 1 in Banff National Park and male and female grizzly bears use of these structures has increased each year (Ford et al. 2009). Of the approximately 80 crossing events by grizzly bears in 2005 (Ford et al. 2009), DNA testing identified at least 3 different females and 2 males. Considering that we found traffic to inhibit bear movements, these crossing structures may be mitigating the otherwise fragmenting effect of this busy highway. Interestingly, the same highway in BC shows clear clustering (Fig. 9g) of bears immediately to the north and south and we speculate that differences related to habitat quality and spatial orientation relative to the highway are responsible for this difference. However, we cannot rule out that the crossing structures may be partly responsible for more migration events in the Banff area.

The fragmentation we document in Alberta is similar to other trends in the conservation status of grizzly bears in Alberta. Population sizes have recently been estimated through survey-based research methods across much of Alberta's grizzly bear distribution and those from south of Highway 16 are lower than previous provincial estimates (Kansas 2002, Boulanger et al. 2005*a*, *b*, Alberta Grizzly Bear Inventory 2007, Grizzly Bear Inventory Team 2008). Following these population surveys and a status review, the Alberta government declared grizzly bears in the province as "threatened" (Alberta Sustainable Resource Development 2010). Another cause of concern is the lower than expected extent of occupied habitat (Kansas 2002) realized from multiple DNA surveys and province-wide GPS telemetry data.

The Alberta population fragments, many of which contain <100 bears (Fig. 19, Table 8), are not as biologically small as they might otherwise be because of open gene flow with BC bears. The current low numbers of Alberta's grizzly bears are likely not caused by the fragmentation we have documented, but because of excessive human-caused mortality (Benn 1998, Nielsen et al. 2004). However, the fragmentation we document has partitioned the Alberta distribution into subpopulations. Theoretically, the connectivity between bear subpopulations in Alberta and BC would allow for demographic rescue across the Continental Divide. If rescue were to become necessary because of local extirpation within Alberta, whatever forces caused the extirpation would need to be remedied for this option to be viable. The DNA surveys also detected a ubiquitous pattern of higher abundance along the western boundary of provincial lands, declining rapidly to the east, raising the possibility that a west–east source–sink dynamic is already operating (Nielsen et al. 2004, 2006).

We found relatively consistent variation in heterozygosities among subpopulations of Alberta's bears, suggesting that no long-standing (several generations) isolated populations exist within this study area (Table 2). From a continental perspective, bears in Alberta represent the southeastern periphery of the remnant distribution and a decrease in $H_E$ would be expected due to regional inbreeding, as found in the peninsular Swan Hills subpopulation (Fig. 6; Frankham 1998).

## Analysis 4: Causes of Fragmentation

Long-term persistence (resisting range contraction) of bears in some parts of our southeastern study area is likely reliant upon appropriate management designed for re-establishing connectivity. Such a management effort requires understanding of the causal forces of fragmentation. Our regression analysis, which examined factors associated with sex-specific fragmentation, offers insight into the mechanisms (highway traffic, settlement, and historic mortality related to settlement) that helped shape the resulting anthropogenic distribution of bear subpopulations.

Human settlement has been fragmenting populations of grizzly bears from the mid-1800s through the 1970s, when there was persecution and little human tolerance of grizzly bears (Mattson and Merrill 2002). Our data show that greater settlement is associated with higher genetic distances, suggesting a cumulative historic cause of fragmentation. Because genetic differentiation reflects cumulative years of limited gene flow, it is not surprising that genetic distances correlate more with settlement patterns than with more recent phenomenon such as recorded bear mortalities and recent measures of traffic volumes. Our genetic differentiation and regression results combine to support the hypothesis that mortality associated with settlement has been and likely continues to be a primary fragmenting force.

Using more current movement rates, our regression and ANCOVA results support hypothesis C1, that inter-population movement by female and male grizzly bears correlate with various forms of human disturbance (traffic, settlement, and non-hunt human-caused mortality) in southeastern BC, southwestern Alberta, and northern Idaho and Montana. Traffic and settlement reduce movements of male and female bears (Table 6). Although each sex seems to be affected by the same fracturing forces, their thresholds differ. In unsettled areas, male and female movement rates were not different, suggesting that although females have shorter dispersal distances (Blanchard and Knight 1991, McLellan and Hovey 2001, Proctor et al. 2004a), females move through geographic areas where disturbance is minimal. In sharp contrast, and in support of hypothesis C2, when settlement increased to greater than 20%, female movement rates declined precipitously. This result suggests target human densities within future linkage zones that may be required to enhance inter-area movements of females and thus metapopulation function. Also, because female movement decreased sharply as traffic volume increased in settled areas between 20% and 50%, crossing structures may be necessary to overcome the effect of high traffic volumes.

The relationship between movement rates and non-hunt mortality was subtle. In areas with minimal settlement, our results suggest that increased inter-area movements were associated with increased mortality and this is not an unusual finding (Belichon et al. 1996; martens [*Martes americana*], Johnson et al. 2009). But in areas with higher levels of human settlement, increased, mortality was associated with a decrease in inter-area movements suggesting mortality has played a role in the fracturing of bear populations. Mortality-related fragmentation has been demonstrated in other species (Fahrig 2007).

Females moved less than males across the whole settlement spectrum, suggesting they likely naturally move less than males and may therefore be more susceptible to fragmentation. Furthermore, female movement rates were significantly lower than male rates in settled areas (moderate and high), adding further support for hypothesis C2 that males and females have different tolerances or thresholds for disturbance. This pattern was expected for 2 reasons: grizzly bears have male-biased dispersal and males have larger home ranges than females (McLellan and Hovey 2001, Proctor et al. 2004a). Natal dispersal of females takes place over a relatively short distance (10 km, McLellan and Hovey 2001; 14 km, Proctor et al. 2004a), compared with males (30 km, McLellan and Hovey 2001; 42 km, Proctor et al. 2004a). Female grizzly bear dispersal is also gradual, taking several years (McLellan and Hovey 2001) and this characteristic makes females more susceptible to fragmentation (Proctor 2003, Proctor et al. 2005) as they try to move through a human-dominated environment, increasing their risk of human-caused mortality.

Vehicle traffic, a by-product of large-scale patterns of settlement across southern Canada, was negatively associated with inter-area movement across the entire continuum of settlement. Other researchers have found that grizzly bears, particularly females, are reluctant to cross high-speed, high-traffic volume highways (Gibeau et al. 2002, Chruszcz et al. 2003). Waller and Servheen (2005) found that as traffic volume increased, movement rates decreased and that the majority of movements across a medium traffic volume highway were made by subadult bears. Consistent with our findings, it has previously been reported that grizzly bears avoid areas of high human influence (Mattson et al. 1987) and generally avoid use of habitat around busy highways, even in areas where human settlement is low (McLellan and Shackleton 1988, Munro 1999, Waller and Servheen 2005). Mace et al. (1996) documented lower survival rates for grizzly bears occupying rural roaded areas relative to areas with lower road densities. Mortality associated with high traffic volumes, although not high, likely also plays a role in fragmenting bear populations. Where monitored, traffic-related mortality data for grizzly bears exists (Canadian Highway 1, Chruszcz et al. 2003; Highway 3, G. Mowat, BC Ministry of Forests, Lands, and Natural Resource Operations, unpublished data; US Highway 2, Waller and Servheen 2005). Mortalities associated with trains also contribute to fragmentation where railroads parallel highways (Waller and Servheen 2005, Gibeau and Bertch 2009).

## Broad Issues

Management efforts to minimize or reverse fragmentation will offer benefits to the ability of grizzly bears and other wildlife to respond to climate change (Intergovernmental Panel of Climate Change [IPCC] 2007a). It is predicted that ecosystems will be altered significantly by climate change (Lovejoy and Hannah 2005, IPCC 2007b), producing biological responses and range

shifts (Parmesan 2006). The north–south orientation of the major Mts in western North America provide natural movement areas where bears and other species can respond to climate change effects on preferred habitats and foods. However, grizzly bears are not a range-restricted species as are polar bears (*Ursus maritimus*), and therefore may be more adaptable to climate change (Parmesan 2006, Paterson et al. 2008, Wiig et al. 2008). Because grizzly bears already inhabit much of the territory from their current southern extent in northern US and along the Canada border to the Arctic Ocean, movement in response to range shifts (Parmesan and Yohe 2003) may not be that critical. Also, because historic range for the species extended south to northern Mexico, and continues to include a range of habitats that includes hot, dry regions in Eurasia (Servheen 1999), climate and habitat change alone may not be a threat to grizzly bears along the Canada–US border unless their major foods do not adapt and shift in a timely manner.

Climate change is predicted to exacerbate fragmentation (Fleishman and MacNalley 2007) and as such, the importance of movement by grizzly bears in the context of regional meta-population dynamics may be heightened in the presence of habitat change reflecting shifts in the location of important seasonal food sources (e.g., fire-mediated berry patches or white-bark pine [*Pinus albicalis*] distribution and survival). Perhaps the biggest threat of climate change may be indirect, if it encourages human migration to the mountain valleys in our southeastern study region. It is difficult to predict any species' response to climate change (Araujo and Rahbek 2006, Pimm 2007), therefore it is prudent to manage for population and metapopulation resilience, thereby facilitating adaptation to change within and between geographic regions if possible (Andersen et al. 2009). This management would best be accomplished by re-connecting smaller population units and maintaining larger, more resilient units.

The ecological characteristics of grizzly bears that make them susceptible to anthropogenic population fragmentation are their low population density, slow reproductive rate, short dispersal, male-biased dispersal, and sensitivity to anthropogenic mortality and habitat degradation. These characteristics in other species, or combinations of several of these variables, may predispose their susceptibility to landscape level population fragmentation where they overlap with human societies. Indeed, other large mammals in the northern Rockies exhibit similar patterns of fragmentation. For example, fragmentation in the southern distribution of the western North American wolverine (*Gulo gulo*) has been inferred (Kyle and Strobeck 2001; Cegelski et al. 2003, 2006), whereas northern populations appear non-fragmented (Kyle and Strobeck 2001). In the western North American lynx (*Lynx canadensis*), Schwartz et al. (2002*b*) found no genetic structure and recommended maintenance of connectivity. At a finer scale, Campbell and Strobeck (2006) found genetic structure in lynx across a major highway in Alberta, suggesting that human disturbance may be influencing connectivity. Mountain caribou (*Rangifer tarandus*) in southern and central BC exist in a series of anthro-pogenically isolated populations (Apps and McLellan 2006). Although structurally appearing as a metapopulation, Van Oort et al. (2010) found no evidence of inter-population movements or breeding. They concluded the system was likely not

functioning as a metapopulation as much as a series of isolated populations heading toward regional extirpation one population at a time.

It is not clear whether the fragmented grizzly bear population is evolving towards a system similar to the caribou situation, or whether through appropriate management, inter-area movements can be reestablished to increase the probability of long-term persistence. Spatial patterns of grizzly bears throughout North America provide insight into spatio-temporal patterns of range contraction and extinction. In the north, bears within adjacent areas constitute a continuous distribution. In the southern extent of their distribution, they form a structured metapopulation, but inter-population connectivity decreases with southern latitude. This pattern is similar to that reported by Segelbacher et al. (2003) who found evidence in capercaillie (*Tetrao urogallus*) of an anthropogenic fragmentation pattern consisting of a gradient of spatial structure from continuous range, to an inter-connected anthropogenic metapopulation, to a series of isolated populations across northern, central, and eastern Europe. They suggested that the different stages represented a continuum of human disturbance over time, supporting the idea that anthropogenic metapopulations may be a stage in the progression from connectivity to increasingly vulnerable isolated populations.

Our results suggest that sex-specific fragmentation investigations also may be informative for anthropogenically fragmented American black bear (*Ursus americanus*) systems. Black bears were fragmented by a century of human development within the southeastern US (Dixon et al. 2006, 2007). Now, remnant corridors are allowing metapopulation function between at least 2 fragmented subunits within Florida (Dixon et al. 2006). Females from one population have moved into an intervening previously unoccupied habitat (corridor) and males from a relatively distant population have dispersed to and bred with these females (Dixon et al. 2006). Dixon et al. (2007) recommended that black bears in Florida be managed as a metapopulation to facilitate and enhance movements between units.

### Strengths and Limitations of Methods

Our results highlight the value of using individual-based telemetry and genetics to resolve questions regarding fragmentation. Where we could compare the 2 techniques in a given area, we found movement rates measured by telemetry and genetics to be similar on average (Table 4). Our methods allowed bear movement to be understood on an individual basis, rather than making assumptions about migration rates based on population-level analyses (e.g., genetic distance). Genetic migrants across fractured areas are not always detectable when genetic differentiation is insufficient to differentiate populations. Temporal and spatial scales, and sizes of populations (influencing speed of genetic drift), all influence the degree of genetic structuring resulting from limited gene flow. Only through an individual-based approach were we able to resolve sex-specific fractures in the grizzly bear population.

The inferential power of combined use of individual-based genetic and telemetry methods relative to inferential genetic distance methods can be illustrated by the example of Alberta's Highway 16, where low genetic distances suggested

a higher rate of movement than were detected with direct measures of movement. Presumably the slow pace of genetic drift in large populations accounts for this insensitivity. However, although a lack of genetic subdivision cannot be taken as a demonstration of connectivity, particularly when population sizes are large, higher genetic distances can only be explained by a lack of gene flow in recent generations. This scenario is exemplified in the Selkirk South, where high genetic distances with all neighbors (suggesting complete isolation over several generations) are inconsistent with our observation of recent migrants. Therefore, we concluded that the migrants we detected were likely evidence of a recent increase in successful movements into this population.

The use of genetics also has dramatically increased our ability to detect long-range movements. Reference samples from a suite of populations allowed us to determine natal origins through assignment methods (Waser and Strobeck 1998). For example, genetic assignment allowed for a grizzly bear shot in the extirpated Bitterroot Mountains in 2008 (last reported live grizzly bear here was in the 1940s; Moore 1984) to be identified as originating from the Selkirk South (Fig. 9a). Similarly, a grizzly shot halfway between the US Southern Divide Ecosystem and the Yellowstone area was shown using genetic assignment to be emigrating from the Southern Divide Ecosystem. Additionally, hair samples now allow genetic identification of long-distance migrants between genetically fragmented areas.

The potentially different temporal scales reflected in these 2 methods (i.e., telemetry and genetics) require acknowledgment. The time period of inference from genetic assignment analysis is from the bear's birth until it was sampled, which could be as many as 25 yr. The genetic analysis is powerful in that 1 sampling effort can provide inference over decades, making finer spatial and temporal resolution difficult. Telemetry only follows bears while collars are on and only extended efforts, such as those carried out in the Flathead Valley where 123 bears were collared over 27 yr, can yield inference over similar time periods as genetic data. Most of our telemetry data sample a smaller portion of a bear's life than genetic sampling. The telemetry has a temporal limit to its inference but offers finer resolution on timing and movement paths than genetic data.

The spatial extent and focus of our sampling effort ultimately affected our probability of detecting migrants (e.g., more effort near boundaries may increase migrant detection probabilities). We therefore tried to equalize our comparison of migrant detection rates by genetics or by telemetry where possible. For example, when comparing migrant detection rates across Highway 3, we did not include the Flathead telemetry because it was carried out relatively distant from the Highway 3 area. Instead, we used only bears captured in the Foothills Model Forest Grizzly Bear Program, where there was similar effort across the areas north and south of Highway 3 in Alberta and similar effort as went into the genetic sampling. In that regard, generally we extended our search effort across ecosystems to detect medium-range migrants.

A variable not included in our analysis but likely to account for unexplained variation in our models is habitat quality and alterations. Too little was known about area-specific habitat quality for these large omnivores to quantify it equitably across the broad area of our analyses. For instance, it is enlightening to examine the nature of habitat changes that have occurred within fracture zones. In many parts of the southeastern study area, habitat changes leading to reductions in food resources have accompanied human settlement. For example, hydroelectric development on the Columbia River has eliminated the anadromous salmon runs that once reached the study area (Ashley et al. 1997), eliminating a high-quality food resource found in valley bottoms. Furthermore, riparian habitats of several valleys have been usurped for human use, and fire-mediated berry patches have been reduced from fire suppression (McLellan 1998). Historically, these narrow valley bottoms had abundant resources attractive to bears and thus facilitate inter-population exchange (McLellan 1998). The width of fracture zones we tested varied from 0.5 km to 12 km. The human settlement along highways is generally <1 km wide, and for a grizzly bear, these distances are often less than their average daily movement distances (2.4 km in Flathead; B. McLellan, BC Ministry of Forests, Lands, and Natural Resource Operations, unpublished data).

We used data from 2 types of radiocollars. VHF collars only detect movements in areas that were searched, whereas newer GPS collars permit the accumulation of more detailed data that can be used to monitor long-range movements into unexpected areas. Some of our results suggest that movements between Mts and ecosystems in our southeast study area may be increasing, however, it may partially be an artifact of increased detection capability. Traditionally, inter-ecosystem movements have been detected through tracking a VHF-collared bear, or through recapture or mortality of a previously marked bear. Fragmentation, however, was not the focus of earlier research and capture effort was not focused close to suspected fracture areas. These were limitations of the available technology at the time the research was conducted. The 2 areas where we used VHF, across the Continental Divide in the Rocky South area and across Highway 1 in Banff National Park, had high migrant detection rates, indicating that researchers were searching appropriate areas.

It is difficult to determine if movement rates and fragmentation are increasing or decreasing. There are processes operating simultaneously that are responsible for improving the state of fragmentation and others that are responsible for intensifying it. The same persecution and intolerance for grizzly bears that was responsible for much of the extirpation of grizzly bears in the lower 48 states in the past century, is suspected of being a primary force of population decline and fragmentation in human-settled valleys in many areas of our southeastern study area. Alternatively, increased tolerance for grizzly bears and improved hunting regulations in recent decades have likely allowed population increases and offered potential for increased inter-area movements, particularly from density-dependent dispersal. Successful management of mortality in many areas, such as Yellowstone, the Southern Divide Ecosystem, and the Selkirk South, have been responsible for increased numbers of bears in these ecosystems (McLellan 1989b, Pyare et al. 2004, Wakkinen and Kasworm 2004, Schwartz et al. 2006a, Proctor et al. 2007, Kendall et al. 2008). This management may have played a role in increasing intra-area connectivity (Kendall et al. 2008, see Selkirk South discussion above). In contrast, the Purcell South Yaak area is declining in numbers (Wakkinen and Kasworm 2004), yet there is evidence that bears are immigrating into and emigrating

from this population, suggesting that density dependence is not the only mechanism driving inter-area dispersal. Forces working to intensify fragmentation are also operating. We show a connection between levels of fragmentation and mortality, settlement, and highway traffic volume. These processes are largely occurring outside of (but not entirely) large protected areas. Human development and highway traffic volume in the region is increasing (BC Ministry of Transportation 2010, Montana Department of Transportation 2010) and these factors likely will act to reduce inter-area connectivity.

The long-term persistence of this large carnivore in landscapes that overlap significant human densities will require extraordinary management beyond that normally applied to most ungulates and/or black bears (Schwartz et al. 2006b). This philosophy will likely be necessary in the trans-border region and Alberta where subpopulations are peripheral within the diminished North American distribution. Vast expanses of central and northern BC may retain healthy populations with less intense management and conservative hunt quotas, but as human densities and resource extraction pressures increase in these regions, management strategies may benefit from experience in the trans-border region.

## MANAGEMENT IMPLICATIONS

It is clear that fragmentation in the interior mountains is affecting other species as well as grizzly bears; therefore, management oriented to improve regional connectivity might benefit from a multi-species approach. Management strategies at local and regional scales designed to reconnect fragmented units, particularly of the smaller subpopulations, or to resist local extirpations that make connectivity very challenging to restore, may reduce the possibility of further range contraction in the region. Less obvious, but likely more important, is to maintain the larger subpopulations by resisting policies that would contribute to their fragmentation. Those larger units with the highest probability of long-term persistence can act as source areas for adjacent, threatened small subpopulations with appropriate management. For example, long-term persistence of Purcell South Yaak and Selkirk South areas, which are small isolated subpopulations, likely depends on connectivity to the adjacent larger Central Purcell Mountains immediately to the north and northeast (Fig. 19). To allow fragmentation of the larger Purcell-Central/Selkirk-Central subpopulation could inhibit the long-term sustainability of bears across the region.

Securing habitat for bears to safely disperse between adjacent areas in human-dominated landscapes encourages long-term connectivity among the network of subpopulations that have been created through the human-induced fragmentation process. Understanding the sex-specific forces of fragmentation and inter-population movements in natural and human-dominated environments facilitates the design of appropriate mitigation strategies (Banks et al. 2005). The fact that females are more susceptible to fragmentation calls for a unique sex-specific approach to managing connectivity for bears in human-dominated landscapes.

Maintenance or enhancement of habitat to ensure female dispersal is a current land management challenge. Linkage areas need to be identified (Apps et al. 2007, Proctor et al. 2008a,

Chetkiewicz and Boyce, 2009) and established wide enough to allow females to live and reproduce within them during their slow dispersal. Managers also need to maintain areas with low human densities (and/or improve human behavior) to reduce human-bear conflicts and thus bear mortalities during movements through fracture zones (e.g., across major settled transportation corridors; Proctor et al. 2008a). A broad array of management actions can be deployed to enhance inter-area connectivity. Public education and management actions can reduce bear attractants and conflict-related mortalities within linkage zones.

Strategic land purchase or easements, highway infrastructure planning to facilitate highway permeability to wildlife, and appropriate forest management strategies in linkage areas (Proctor et al. 2004b, 2008b) may improve usage of and survival in linkage zones. Other strategies include black bear hunter education to minimize killing of grizzly bears due to mistaken identity, minimization of hydroelectric development in key areas, periodic augmentation of small populations with females (Kasworm et al. 2007b), and in the trans-border area, improved inter-jurisdictional cooperation on population management.

Increasing habitat security through access management in linkage zones and adjacent backcountry habitats enhances core areas that require connecting. Managing human access to improve habitat security and minimize displacement, particularly for females, is one of the cornerstones of grizzly bear management in recovery zones within the conterminous US (Mace 2004, Summerfield et al. 2004), and may be necessary within the fragmented landscape of southern BC and Alberta (Proctor et al. 2008b, Roever et al. 2008, Schwartz et al. 2010). Linkage zones and habitat security will only be effective in combination with reduced female mortality.

Threats to grizzly bears from human settlement and highway traffic appear minimal at this time in the relatively undeveloped northern region of BC, which has experienced a (human) population decline in the past 12 yr (Bogh 2010). If settlement increases as a result of climate change or other influences, grizzly bear management might benefit from lessons learned in our southeastern study area by taking a proactive approach to maximizing connectivity and minimizing fragmentation. Management to mitigate future anthropogenic fragmentation would benefit by considering existing patterns of natural fragmentation and planning around sources of anthropogenic fragmentation suggested by this study.

Our findings suggest fragmentation of grizzly bears in several areas within the trans-border region. Deciding how to partition conservation effort within the trans-border region requires an understanding of population size and major limiting factors of individual population units. Designating conservation status below the species level is challenging (Gärdenfors et al. 2001) but should lead to population-specific action required for recovery (Green 2005). Thiemann et al. (2008) demonstrated a comprehensive approach similar to that suggested by Green (2005) on Canadian polar bears using genetics, movements, ecology, demographics, population size, and abundance trends to determine conservation status of subpopulation units. They recommended that their subpopulations be considered legally distinct subpopulations within Canada and were based on naturally formed

genetic discontinuities (Paetkau et al. 1999) significantly less intense than we found in the trans-border area.

Management plans tailored to the specific requirements of each grizzly bear subpopulation in the Canada–US trans-border region will be necessary to effectively and efficiently stabilize or recover these fragmented populations. We compiled ecological, demographic, and conservation characteristics for each of the trans-border subpopulations (Table 9) to evaluate their conservation and management needs similar to Thiemann et al. (2008) for polar bears. Using data published previously (or in reports), we illustrated that the Cabinet, Purcell South Yaak, and Selkirk South subpopulations (Table 9) are small, relatively isolated, and include a low percentage of protected land (Fig. 19). By contrast, the Rocky South-Southern Divide Ecosystem is a relatively large, stable population with relatively good conservation status, and it requires a management regime with the goal of long-term stability. The Cabinet and Purcell South Yaak areas have the poorest conservation status because of their smaller sizes and decreasing population trends, and require more intense management effort, including augmentation, if they are to be maintained. The Selkirk South population is currently stable and possibly increasing (Wakkinen and Kasworm 2004) and requires special conservation management at a level less urgent and intense than the Purcell South Yaak and Cabinet subpopulations (Proctor et al. 2004b, Kasworm et al. 2007a). We recommend that the entire regional metapopulation be considered, that multiple jurisdictions work together on a larger strategy to manage the system for inter-area connectivity, particularly of females, and that larger core subpopulations be managed as potential sources of bears for adjacent smaller threatened subpopulations.

We suggest that management strategies to enhance movement of grizzly bears across major highways of Alberta and maintain movements across the Continental Divide with BC would be prudent to ensure future persistence of grizzly bears in Alberta. We recommend appropriate connectivity-oriented research and management (Schwab 2003; Proctor et al. 2004b, 2005, 2007; Clevenger and Waltho 2005; Apps et al. 2007; Chetkiewicz and Boyce, 2009; Ford et al. 2009) where specific linkage zones might be identified and established. Spatially explicit information on where bears move across major highways and through human-dominated environments can be used to guide management efforts to allow safe movement of bears between areas (Ford et al. 2009). Also, to foster density-dependent dispersal, it would be beneficial to build population numbers in the fragments south of Highway 16 by managing for habitat quality and security through access management in areas of identified high-quality habitat. This management could reduce mortality risk in what otherwise might become attractive sinks (Nielsen et al. 2006).

Alberta's bears form the southeastern periphery of the Canadian grizzly bear distribution. They are essentially bounded by human settlement to the east, and will likely require monitoring through time to ensure persistence, particularly east of the protected areas that are almost continuous along the Continental Divide. In addition to the important need to distribute hunting impacts throughout a region, it has been suggested that MUs be based on areas where birth and death rates are more important to population dynamics than immigration and emigration (Moritz et al.

1995). Therefore, the genetic discontinuities we document could appropriately form the boundaries of biologically based MUs; in fact, such spatial partitioning has already been incorporated within the Alberta Recovery Plan. Each area is responding to internal demographics more than immigration and emigration, therefore region-specific mortality, habitat, and physiological stress issues can be addressed within each MU. The influence of source areas should not be expected to extend across the discontinuities created by the major east–west highways we identified, unless management restores movement rates across the highways.

## SUMMARY

- Spatial genetic structure of grizzly bears in the relatively undisturbed northwest BC generally conformed to an isolation-by-distance paradigm but extensive glaciers and icefields contribute a measure of natural fragmentation.
- In southeastern BC, western Alberta, and the northern US, grizzly bears were fragmented into an anthropogenically female-fragmented metapopulation by human settlement patterns, highway traffic, and mortality patterns.
- The subpopulations in the trans-border area of the Canada–US border were limited in their female interchange and therefore were demographically fragmented to the extent that natural demographic rescue of small threatened subpopulations likely is not currently possible.
- Within Alberta, males were mediating gene flow but female inter-area movements were rare, mainly because of major highways. Within subpopulations, Alberta bears were connected to BC bears across the Continental Divide.
- Females responded more negatively than males to traffic volumes, settlement, and mortality, especially in moderately disturbed areas.
- Male inter-area movements were reduced, contributing to regional fragmentation, but their response differed from that of females by having a more gradual reduction of movement as traffic and settlement increased.
- Several subpopulations within the regional metapopulation were small (<100 bears) and therefore carried a high conservation risk. Conversely, several large subpopulations (>500 bears) may provide regional meta-population stability (through being a source of bears to adjacent small subpopulations) if management improves the potential for female inter-area movements, which are currently limited.
- We recommend an inter-jurisdictional strategy that includes management to maintain or enhance inter-area movements, particularly of females, and that maintains the stability of large core subpopulations, which may act as sources to adjacent threatened small subpopulations.

## ACKNOWLEDGMENTS

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**Appendix.** Genetic distances as measured by $D_{LR}$ (Paetkau et al. 1997), Nei's $D_S$ (Nei 1972), and $F_{ST}$ values (Weir and Cockerham 1984) and geographic distance for adjacent grizzly bear subpopulations in western North America. $F_{ST}$ values marked by an asterisk (*) were not significantly different than zero. Those without an * were different (P < 0.05) than zero. $D_{LR}$/100 km values are the genetic distances standardized (adjusted) for geographic distance (geo dist). See Figures 11–13 for genetic distances on maps. We categorized the areas separating sampling areas into 2 categories; natural, where no highway or very limited settlement exists, and human, where a major highway with associated settlement exists. Numerical superscripts indicate analyses in which samples were used.

| Areas | $D_{LR}$ | $F_{ST}$ | Nei's $D_S$ | Geo Dist | $D_{LR}$/100 km | Potential fracture | Fracture type |
|---|---|---|---|---|---|---|---|
| Rocky Central Banff East–West[3,4] | 0.0 | 0.003* | 0.030 | 31 | 0.00 | Spray Valley | Natural |
| Atlin–Spatsizi[1] | 0.8 | 0.007* | 0.077 | 202 | 0.42 | None | Natural |
| Kluane–Nahanni[1] | 2.9 | 0.033 | 0.168 | 647 | 0.45 | None | Natural |
| Spatsizi–Skeena North[1] | 1.4 | 0.017* | 0.094 | 297 | 0.45 | None | Natural |
| Nahanni–Atlin[1] | 1.9 | 0.017 | 0.113 | 401 | 0.48 | None | Natural |
| Nahanni–Spatsizi[1] | 2.2 | 0.021 | 0.120 | 425 | 0.52 | None | Natural |
| Nahanni–Prophet[1] | 2.9 | 0.032 | 0.140 | 542 | 0.54 | None | Natural |
| Kluane–Altin[1] | 3.0 | 0.033 | 0.177 | 481 | 0.63 | None | Natural |
| Rocky South Flathead East–West[3,4] | 0.3 | 0.001* | 0.030 | 43 | 0.67 | Flathead River | Natural |
| AB North Chinchaga–Prophet[1] | 2.4 | 0.040 | 0.149 | 314 | 0.75 | CD[a] | Natural |
| Atlin–Stikine[1] | 2.0 | 0.024 | 0.107 | 257 | 0.79 | Icefields | Natural |
| Prophet–Parsnip Mt[1] | 2.8 | 0.036 | 0.105 | 327 | 0.84 | None | Natural |
| Spatsizi–Stikine[1] | 1.9 | 0.024 | 0.101 | 205 | 0.93 | Icefields | Natural |
| Prophet–Nation[1] | 3.3 | 0.040 | 0.135 | 313 | 1.05 | None | Natural |
| Alberta North–BC North[3] | 2.1 | 0.027 | 0.089 | 198 | 1.07 | CD | Natural |
| Rocky North Banff–Rocky North BC[3] | 1.1 | 0.014 | 0.037 | 90 | 1.22 | CD | Natural |
| Owikeno–South Coast[1] | 3.8 | 0.090 | 0.190 | 308 | 1.22 | Icefields | Natural |
| Skeena North–Prophet[1] | 4.5 | 0.050 | 0.184 | 345 | 1.29 | None | Natural |
| Parsnip Mt–Herrick[1] | 1.1 | 0.011 | 0.046 | 86 | 1.30 | None | Natural |
| Spatsizi–Prophet[1] | 2.1 | 0.025 | 0.114 | 163 | 1.31 | None | Natural |
| Nation–Parsnip Mt[1] | 2.2 | 0.029 | 0.085 | 168 | 1.33 | None | Natural |
| Rocky South Alberta–Rocky South BC[3] | 0.6 | 0.000 | 0.025 | 43 | 1.40 | CD | Natural |
| Herrick–Alberta North[1] | 2.1 | 0.029 | 0.089 | 148 | 1.43 | CD | Natural |
| Rocky Central Alberta–Rocky Central BC[3] | 0.5 | 0.006 | 0.023 | 30 | 1.76 | CD | Natural |
| Purcell Central Jumbo–Purcell Central St Marys[3,4] | 1.6 | 0.018 | 0.050 | 86 | 1.81 | St. Mary's River | Natural |
| Skeena North–Nation[1] | 4.8 | 0.065 | 0.212 | 230 | 2.08 | Plateau | Natural |
| Skeena South–Owikeno[1] | 6.0 | 0.098 | 0.239 | 278 | 2.17 | Icefields | Natural |
| Stikine–Alaska SE[1] | 2.2 | 0.027 | 0.089 | 90 | 2.47 | Icefields | Natural |
| Parsnip Mt–Parsnip Plateau[1] | 1.4 | 0.018 | 0.055 | 40 | 3.45 | Ecosystem border | Natural |
| Skeena North Skeena South[1] | 1.5 | 0.022 | 0.097 | 183 | 0.84 | Hwy[b] 16 | Human |
| Alberta North–Rocky North Jasper[1,2,3,4] | 1.5 | 0.014 | 0.042 | 167 | 0.89 | Hwy 16 | Human |
| Alberta North–Swan Hills[1,2,3] | 2.0 | 0.030 | 0.088 | 217 | 0.92 | Hwy 43 | Human |
| Rocky North Jasper–Rocky North Banff[1,2,3,4] | 2.2 | 0.026 | 0.062 | 179 | 1.23 | Hwy 11 | Human |
| Rocky North Banff–Rocky Central Banff[1,2,3,4] | 1.3 | 0.013 | 0.032 | 95 | 1.41 | Hwy 1 | Human |
| Owikeno–Bowron[1] | 6.3 | 0.100 | 0.223 | 425 | 1.48 | Icefields/Plateau | Human |
| Skeena South–Nation[1] | 3.0 | 0.043 | 0.143 | 192 | 1.58 | Hwy 16/Plateau | Human |
| Purcell Central St Marys–Rocky Central[1,2,3,4] | 2.3 | 0.023 | 0.059 | 145 | 1.62 | Hwy 95 | Human |
| Rocky Central–Purcell South Yaak[1,2,3,4] | 2.4 | 0.037 | 0.077 | 147 | 1.66 | Hwy 3 | Human |

(continued)

**Appendix.** (*continued*)

| Areas | $D_{LR}$ | $F_{ST}$ | Nei's $D_S$ | Geo Dist | $D_{LR}$/100 km | Potential fracture | Fracture type |
|---|---|---|---|---|---|---|---|
| Bowron–South Coast[1] | 5.6 | 0.080 | 0.187 | 325 | 1.71 | Plateau | Human |
| Herrick–Bowron[1] | 1.6 | 0.019 | 0.072 | 89 | 1.74 | Hwy 16 | Human |
| Rocky South–Southern Divide Ecosystem[1,2,3] | 2.3 | 0.023 | 0.053 | 117 | 1.95 | US Hwy 2 | Human |
| Yellowstone–Southern Divide Ecosystem[2,3] | 9.0 | 0.105 | 0.221 | 462 | 1.96 | US I-90, 150 km | Human |
| Rocky Central–Rocky South[1,2,3,4] | 3.4 | 0.036 | 0.084 | 153 | 2.20 | Hwy 3 | Human |
| Rocky North BC–Purcell Selkirk North[1,2,3,4] | 1.2 | 0.021 | 0.060 | 46 | 2.66 | Hwy 1 | Human |
| Purcell South Yaak–Rocky South[1,2,3,4] | 4.1 | 0.045 | 0.098 | 133 | 3.08 | Hwy 95 | Human |
| Purcell South Yaak–Purcell Central St Marys[1,2,3,4] | 2.6 | 0.045 | 0.097 | 76 | 3.43 | Hwy 3 | Human |
| Selkirk Central–Purcell Central Jumbo[1,2,3,4] | 2.3 | 0.037 | 0.092 | 64 | 3.59 | Hwy 31 | Human |
| Purcell Central Jumbo–Selkirk Central[3,4] | 2.3 | 0.004* | 0.090 | 63 | 3.64 | Lardeau River | Human |
| Rocky North BC–Selkirk North[1,3,4] | 2.1 | 0.024 | 0.060 | 55 | 3.78 | Columbia River | Human |
| Selkirk Goat–Selkirk Valhalla[3,4] | 2.1 | 0.031 | 0.100 | 53 | 3.88 | Hwy 6 | Human |
| Selkirk North–Selkirk Purcell North[3,4] | 1.6 | 0.018 | 0.060 | 32 | 5.05 | Hwy 1 | Human |
| Selkirk Goat–Selkirk Kokanee[3,4] | 3.8 | 0.057 | 0.160 | 70 | 5.48 | Hwy 31A | Human |
| Selkirk Central–Selkirk South[1,2,3,4] | 7.5 | 0.122 | 0.259 | 112 | 6.70 | Hwy 3A | Human |
| Selkirk Kokanee–Selkirk Valhalla[3,4] | 3.2 | 0.031 | 0.160 | 41 | 7.78 | Hwy 6 | Human |
| Purcell South Yaak–Selkirk South[1,2,3,4] | 9.0 | 0.146 | 0.287 | 95 | 9.44 | Hwy 21 Creston Valley | Human |
| Purcell Central St Marys–Selkirk South[1,2,3,4] | 6.8 | 0.042 | 0.230 | 54 | 12.50 | Hwy 21 Creston Valley | Human |
| Selkirk Kokanee–Selkrik South[3,4] | 10.6 | 0.197 | 0.410 | 59 | 17.91 | Hwy 3A | Human |

[a] CD abbreviates Continental Divide.
[b] Hwy abbreviates Highway.
[1] Used in isolation-by-distance (IBD) analysis across entire study area.
[2] Used in the cluster analysis.
[3] Used in the migrant analysis.
[4] Used in the regression analysis.