POPULATION FRAGMENTATION OF GRIZZLY BEARS IN SOUTHEASTERN BRITISH COLUMBIA, CANADA

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Abstract: The distribution of grizzly bears (*Ursus arctos*) at the southern edge of their North American range includes 5 mountain peninsulas extending from the contiguous northern distribution. In several cases, these peninsulas cross into the conterminous United States. The long-term survival of these populations may depend on the retention of demographic links to the contiguous northern distribution. We investigated whether a major transportation corridor fragments the population of grizzly bears in the Central Rocky Mountain Ecosystem. Using non-invasively obtained hair samples collected in 1996–99, we generated 15-locus microsatellite genotypes for 220 bears, 120 to the north, 98 to the south, and 2 on both sides of the highway corridor. We used a population assignment test with a related genetic distance measure to determine the amount of gender-specific connectivity between areas directly north and south of the highway corridor. We found evidence of 1 female and 3 male grizzly bears moving across BC (British Columbia) Highway (Hwy) 3 using the population assignment test, and we DNA-captured 2 males on both sides of the highway. Our use of individually based genetic measures, coupled with a large sample of bears from 2 immediately adjacent populations, allowed us to efficiently examine the ecological questions of dispersal and fragmentation across a potential fracture. Our data suggests that female movement across the human transportation corridor has been negligible and male movement has been reduced from historic levels.

Habitat fragmentation and its extreme relative, population fragmentation, are serious threats to species conservation (Caughley and Gunn 1996). Maintaining population connectivity for large, wide ranging carnivores is particularly challenging in modern landscapes (Weaver et al. 1996). Several factors make grizzly bear conservation difficult from a fragmentation perspective. Grizzly bears require regional-sized areas to thrive at a population level, have limited dispersal ability (McLellan and Hovey 2001), and have a mutually intolerant relationship with humans (McLellan et al. 1999); their contracting distribution in North America has already resulted in an uneven distribution (McLellan 1998). The limited information on grizzly bear dispersal suggests that female and male adult home ranges often overlap that of their mothers' (Blanchard and Knight 1991, McLellan and Hovey 2001) and that the dispersal process often takes several years (McLellan and Hovey 2001). Grizzly bear dispersal across human-dominated landscapes is often associated with an elevated mortality risk because they are attracted to human-associated food sources (Mace and Waller 1998, McLellan et al. 1999). Further, the distribution of grizzly bears near the southern edge of their North American range is essentially a series of occupied peninsulas along mountain ranges (McLellan 1998). Relict island populations hang from the tips of peninsulas in the North Cascades of southern British Columbia (McLellan 1998) and the Cabinet Mountains of Idaho and Montana (Fig. 1; see also Kasworm et al. 2000). Less obvious is the fragmented island population in the southern Selkirk Mountains straddling the Canada–U.S. border (M. Proc-

tor, unpublished data). As the human population expands in southern Canada, vehicle traffic along transportation corridors is increasing and adjacent land is being developed and settled (Apps 1997). Whether highways and associated human settlements are fragmenting grizzly bear
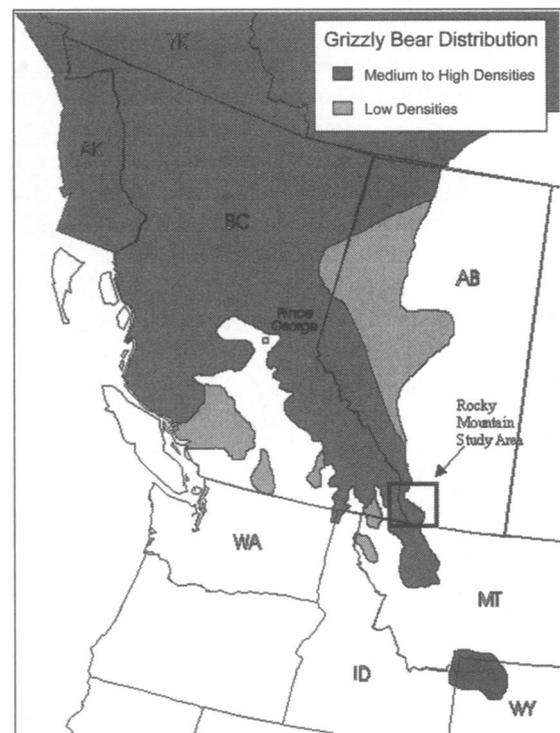

Fig. 1. Map of North American grizzly bear distribution and Rocky Mountain study area.

populations is an important question.

Quantifying fragmentation is difficult, especially at large spatial and temporal scales. Monitoring a large sample of bears using traditional radiotelemetry methods over the scales necessary to investigate dispersal and population fragmentation is impractical. However, molecular genetic techniques offer a solution because it is relatively easy to sample a large number of bears genetically (Woods et al. 1999, Mowat and Strobeck 2000) and because informative markers are being linked with new statistical techniques (Luikart and England 1999, Waser and Strobeck 1999) that use cumulative individual genotypes to increase power. In this paper we apply broad-based genetic sampling and molecular techniques to quantify population fragmentation of the central Rocky Mountain ecosystem in southeastern British Columbia and southwestern Alberta across the BC–Alberta Highway 3 corridor. We address the following questions: Is the Highway 3 corridor a barrier to both sexes, a barrier to a group of bears such as females, open to reduced movements of all groups of bears, or open to significant movements of both sexes?

STUDY AREA

Our study area was the width of the Rocky Mountains in southeastern British Columbia and southwestern Alberta from the Canada–U.S. border (49° N) north to the headwaters of the Elk River (50°30'N; Fig. 1, 2). The eastern boundary was the Rocky Mountain foothills in Alberta; the western boundary was the Rocky Mountain Trench and Bull River. The communities of Blairmore, Crowsnest Pass, Sparwood, and Fernie punctuate the Highway 3 corridor as it crosses the study area from east to west for approximately 100 km. Rural enclaves are found along this corridor, but they do not constitute continuous human development (Apps 1997). Highway 3 evolved slowly from the early 1900s and was paved in the 1960s. In the last 20 years vehicle use has increased 10-fold, with average summer traffic volumes on the highway during 1998 and 1999 reaching 7,000 cars/day (BC Ministry of Transportation, Cranbrook, BC, Canada).

Highway 3 is paralleled by the Crowsnest River to the east and the Elk River to the west of Sparwood. The study area is mountainous; Crowsnest Pass is at 1500 m and peaks rise to 2800 m. The western slopes of the Continental Divide capture abundant moisture, yielding a wet, productive ecosystem. Forests dominate the study area consisting of lodgepole pine (*Pinus contorta*), larch (*Larix occidentalis*), spruce (*Picea engelmannii* and *P. glauca*), sub-alpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*). Avalanche paths, alpine meadows, riparian areas, logging blocks, and old burns are common

throughout the area. The drier eastern slopes are forested with lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and sub-alpine fir. Prairies and extensive agriculture dominated by cattle ranching occur east of the foothills. Secondary roads are common throughout the area, except in Waterton National Park in extreme southwestern Alberta.

Grizzly bears have been hunted in the study area in both BC and Alberta prior to and since European settlement. Nonetheless, grizzly bear density in the Flathead River drainage south of Highway 3 is high (McLellan 1989*a*) and is increasing (McLellan 1989*b*, Hovey and McLellan 1996). A high density of bears is also suspected in the upper Elk River north of Highway 3 (B. Warkentin, BC Ministry of Environment, Cranbrook, BC, Canada, personal communication, 2001; Boulanger 2001). We define the portion of the study area north of Highway 3 to be Rockies North (RN) and the portion to the south Rockies South (RS).
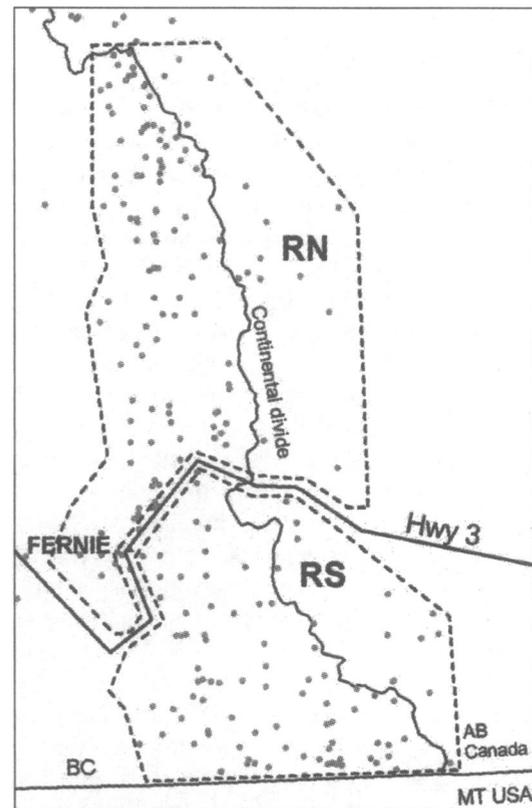

Fig. 2. Grizzly bear capture map in the adjacent populations north and south of BC–Alberta Highway 3 in the Rocky Mountains of southern Canada. RN indicates the Rockies North portion of the study area north of the Highway 3 corridor and RS indicates the Rockies South area south of the Highway 3 corridor. Gray dots are hair-capture locations.

METHODS

Genetic Samples

We obtained genetic samples of grizzly bears over several years. In 1996 and 1997, 3 DNA-based grizzly bear population surveys were conducted by the BC government and by Mowat and Strobeck (2000). We acquired samples from these projects as well as samples from bears captured for telemetry research in the Flathead River drainage. To obtain DNA from bears with a higher potential of crossing Highway 3, in 1999 we sampled what we judged was the best available bear habitat within 25 km north and south of Highway 3.

Field Data

DNA survey samples were collected using methods of Woods et al. (1999) and Mowat and Strobeck (2000). A sampling station consisted of 1 strand of barbed wire stapled to several trees about 50 cm above the ground with a lure of rotten meat scraps and fish oil hung out of a bear's reach in the center. As bears investigated scent lures, they left a hair sample on the barbed wire. Samples were collected using a combination of helicopter and vehicle access.

Laboratory Procedures

DNA from the grizzly bear population surveys was extracted from the hair samples using the Chelex protocol (Walsh et al. 1991) and was then used to identify individuals with 6 microsatellite loci. All samples from identified individuals were re-extracted using QIAamp columns (Qiagen, Mississauga, Ontario, Canada) from 10 guard hairs, when available. We switched to QIAamp to improve the quantity and quality of extracted DNA based on the results of a small test trial (unpublished data). We discarded samples with less than 5 hairs to reduce genotyping errors such as allelic dropout and non-specific bands associated with using samples with low quantities of DNA (Gagneux et al. 1997, Goossens et al. 1998, Taberlet et al. 1999). We expanded the original 6 locus microsatellite genotypes to 15 loci for all individual bears previously identified during the population surveys. All 15 loci were used for newly captured bears in 1999. Markers used were those previously developed by Ostrander et al. (1993), Taberlet et al. (1997), and Paetkau et al. (1998a). Specifically, we used G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10U, G10X, MU50, MU59, CXX20, and CXX110. Two of Ostrander et al.'s (1993) markers, CXX20 and CXX110, were designed for canids and worked poorly on ursid hair-derived DNA. Therefore, we redesigned them by sequencing them in grizzly bear DNA and moved them into bear sequence (Table 1).

Table 1. New primer sequences used for loci CXX20 and CXX110 for grizzly bear DNA for a study in Alberta and British Columbia, Canada, 1996–97.

Loci	Sequence
CXX20	
3′ primer	TGA ATA GTC CTC TGC GGT CA
5′ primer	CC CAT TTA CTG GAG TTC TTC CT FAM
	(dye attached to 5′ primer)
CXX110	
3′ primer	GCA TCC AAG TAA ATC AAG A
5′ primer	AAT CTA AGC CAA TAT TCT CC HEX
	(dye attached to 5′ primer)

Specific PCR conditions are available upon request from the senior author.

Genotypes were determined on an Applied Biosystems' 377 automated sequencer and scored with the help of Genotyper software (Applied Biosystems, Foster City, California, USA). All genotypes were visually double-checked on the original electrophoresis gels for authenticity. All genotypes with a single mismatch at the original 6 loci were scrutinized for potential errors and rerun for verification as were any genotypes represented by only one hair sample. Our ultimate single-mismatch rate was compared to 2 reference data sets built from 148 and 119 individuals (Paetkau et al. 1998b). We chose these reference data sets because the bears were captured and handled by field researchers and genotyped from tissue-derived DNA, and thus had a low amplification error rate (D. Paetkau, Wildlife Genetics International, Nelson B.C., personal communication, 2000).

We distinguished grizzly bear from black bear (*Ursus americanus*) hair samples using a consistent deletion in grizzly bear mitochondrial DNA (mtDNA), as described in Woods et al. (1999). Sex was determined in one of 2 ways. On individuals identified before 1997, we used the SRY–ZFX/ZFY system as described in Woods et al. (1999) and Taberlet et al. (1993). Due to an extra band in occasional female samples using the SRY–ZFX/ZFY system (unpublished data), in 1997 we switched to alleles at the amelogenin locus (Ennis and Gallagher 1994), which we analyzed with a positive and negative control to detect contamination. We identified individuals statistically using 6 loci and a P_{sib} statistic described in Woods et al. (1999). Our threshold for acceptance of a new individual was a $P_{sib} < 0.05$ differentiating one individual from the genotype of a potential full sibling.

Analysis

We tested all 15 loci for conformance to Hardy-Weinberg (H-W) assumptions of random mating using the probability test within GENEPOP 3.1d (Raymond and Rousset 1995). Any locus within each population that failed the H-W test was tested for a deficit of heterozy-

gotes using a global test (Rousset and Raymond 1995). All loci in both populations were tested for linkage disequilibrium using a probability test (Garnier-Gere and Dillman 1992). Critical values for these tests were adjusted for the experiment-wise error rate using the Dunn-Sidak method (Sokal and Rohlf 1995). These tests were performed within GENEPOP 3.1d (Raymond and Rousset 1995). To establish that these 2 local populations of bears were not one homogeneous unit, the allele frequencies were tested for heterogeneity using the log-likelihood *G*-test (Sokal and Rohlf 1995). Unbiased estimates of mean expected heterozygosity (H_E) were calculated as an index to relative genetic variability (Nei and Roychoudury 1974).

Population Assignment Test and Genetic Distance Measures

The population assignment test (Paetkau et al. 1995, Waser and Strobeck 1999) uses individual genotypes and allele frequencies from competing populations. The likelihood of assigning a bear to a population is the cumulative probability of occurrence of 30 alleles in this instance (15 loci/bear and 2 alleles/locus). Each bear is assigned to the population with the highest probability of assignment. To establish how many cross-assigned individuals were real migrants and how many were cross-assigned by chance (statistical migrants), we randomly generated 1,000 data sets using the observed allele frequencies of each local population. If >50 randomized data sets out of 1,000 (5%) resulted in more cross-assignments than we observed in the real data, we concluded that the observed cross-assignment rate could be explained by chance. Conversely, if we found fewer than 50 data sets resulted in more cross-assignments than we observed in our data, we concluded that the observed number of cross-assignments could not be explained by chance alone. In this situation we concluded that some of the cross-assignments were real migrants. We then used a threshold of a log-likelihood ratio (LR) value ≥3.0 to distinguish between individuals cross-assigned by chance and likely migrants. A likelihood ratio of 3.0 can be interpreted as an individual having a 1,000 times higher probability of being cross-assigned to one of the two competing populations, in this case, the population across Highway 3. Because choosing a threshold for migrant status is somewhat arbitrary, we also explored the consequences of using a lower threshold of a LR ≥ 2.0, or a 100 times probability of being cross assigned.

We used a genetic distance measure, D_{LR} (log ratio distance, Paetkau et al. 1997), to quantify the genetic separation between populations. We also report F_{st}, a measure of genetic differentiation (Weir and Cockerham 1984, Hartl and Clark 1997).

RESULTS

Tests for Equilibrium

Our sample consisted of 220 grizzly bears: 120 to the north (58 males, 57 females, and 5 unknown), 98 to the south (54 males, 37 females, and 7 unknown), and 2 males captured on both sides of the Highway 3 corridor (Fig. 2). All loci conformed to the assumption of random mating as tested by the Hardy-Weinberg heterozygote deficit probability test, also providing no evidence of null alleles. We found that 5 of the 210 tests for nonrandom association (linkage disequilibrium) had *P* values smaller than the Dunn-Sidak experiment-wise error correction (Sokal and Rohlf 1995), but none were found to have a significant result in both populations. Migration in and out of both sub-populations may explain the higher than expected linkage disequilibrium rejection rate (Hartl and Clark 1997). In this paper we demonstrate limited migration between the 2 sub-populations, and both geographic areas have extensive boundaries open to bear movements. In particular, the Rockies North has a long continuous open boundary with excellent grizzly bear habitat to the west. The Rockies South has an open boundary with bears to the south within the U.S. Paetkau et al. (1997) tested 8 of the loci used here for physical linkage using pedigree data and found no evidence for linkage. We suggest that migration may be causing our slight linkage signal, and we assume loci are otherwise operating independently.

When tested for genetic heterogeneity, the 2 local populations, Rockies South and Rockies North, had significantly different allele frequencies ($P < 0.0005$), supporting the hypothesis that these areas were acting as separate breeding units and were suitable for comparison. Mean expected heterozygosity was 66% for both the RN and RS, and observed heterozygosity was 66%. The genetic distance, D_{LR}, between RS and RN populations was 3.04 and the F_{st} was 0.034.

Population Assignment Test

Using the population assignment test, 16 individuals captured in RS were assigned to RN (across Highway 3) and 13 individuals captured in RN were assigned to RS (Fig. 3). From our randomization test, 0 of 1,000 results had an equal or greater number of cross-assignments in both directions, suggesting that chance alone could not explain our observed cross-assignment rate. Therefore, some fraction of the cross-assigned individuals probably were true migrants.

We found 4 cross-assignments (Table 2), 1 female and 3 males, which met the criterion of LR ≥3.0 (Fig. 3). All 3 of these males were killed, either by legal hunting or in
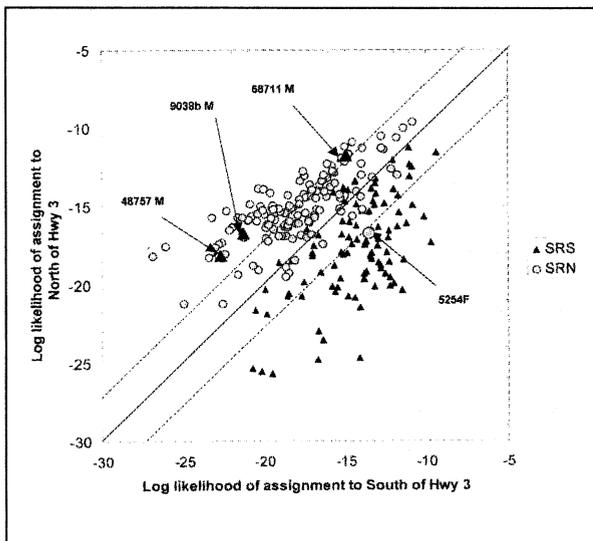
Fig. 3. Population assignment of grizzly bears in the Rocky Mountains north (RN) and south (RS) of British Columbia–Alberta Highway 3 in southern Canada based on cumulative probability of occurrence of 30 alleles. Cross-assignments across Highway 3 that have a likelihod ratio >3.0 (likely migrants) are labeled with ID number and sex. Dotted lines represent likelihood ratio = 3.0.

Table 2. Likely grizzly bear migrants across British Columbia–Alberta Highway 3 based on hair samples captured in 1996–97 (Captures across Highway 3) and based on cumulative probability of occurrence of 30 alleles (assignment test). Cross-ssigned bears had a likelihood ratio LR = 3.0.

	Total identified	Migrants	
	n	Female	Male
Captures across Highway 3	220	0	2
Assignment test	220	1	3

problem wildlife events. When we lowered the migrant threshold (LR) to 2.0, we found 1 extra male that could be considered a potential migrant.

DISCUSSION

Natural habitat fragmentation is common for some species (Buskirk and Ruggerio 1994, Paetkau et al. 1999, Castella et al. 2000). Demonstrating fragmentation is therefore accompanied by the need to differentiate between natural and anthropogenic fragmentation. This differentiation can be difficult to measure because historic levels of connectivity are typically unknown. In our study area, it is unknown what proportion of the identified fragmentation was caused by human presence along the Highway 3 corridor and what proportion was due to the Crowsnest and Elk rivers and wide valley in an otherwise continuous mountainous habitat.

However, comparisons with similar areas that lack the human use associated with the Highway 3 corridor may help differentiate the cause of the apparent fragmentation. The Flathead River drains a wide but unsettled drainage (McLellan 1989a), approximately 50 km south of the Highway 3 corridor. In the Flathead River drainage, the genetic distance (D_{LR}) between bears from opposite sides of the river is 0.15 $(F_{st} = 0.0019;$ Proctor and McLellan, unpublished data), much lower than the 3.04 $(F_{st}\ 0.034)$ found across the Highway 3 corridor. Because the Flathead system is ecologically similar to the Highway 3 corridor area, yet has no major road or human development, the comparison suggests that the level of fragmentation noted along Highway 3 is due to the historic and present human activity and not the geography of the area.

We found little evidence of female movement across the Highway 3 corridor. Unfortunately, age cannot be determined from DNA, so the age of the female migrant in our sample is unknown. Because bears can live >20 years, the female migrant could have crossed the highway anytime in the last 20–25 years. Although we do not know if the Highway 3 corridor is a complete fracture for females, the low level of female movement may be insufficient to functionally connect the two sides.

We found greater evidence of male movement across the Highway 3 corridor than we did for females. However, the relatively high genetic distance across such a short geographic distance suggests a reduction from historic levels of gene flow. Although genetic distance is related to migration and mutation rates, population sizes, genetic drift, and time (Hartl and Clark 1997), an exact relationship between genetic distance and movement rates has not been established. However, progress on this topic has been made. Paetkau et al. (1999) report from field observations and extensive radiotracking that population pairs with a $D_{LR} > 3.5$ $(F_{st} = 0.05)$ had no observed interpopulation migrants. This indicates that a threshold of genetic distance may exist above which migration is extremely limited or non-existent. The D_{LR} values in Paetkau et al.'s (1999) polar bear (*Ursus maritimus*) population pairs ranged from 0 to 7.8 $(F_{st} = 0.002–0.11)$. These polar bear populations might be approximately at equilibrium between mutation, migration, and genetic drift, and natural fractures are responsible for the observed population structure (Paetkau et al. 1999). In contrast, the southern Rocky Mountain system is unlikely in equilibrium, and the genetic distance of 3.04 is mediated by an anthropogenic population fracture. If migration between these 2 sub-populations is decreasing, then the measured D_{LR} should be increasing. Waits et al. (2000) found D_{LR} values of 5.5 and 5.8 $(F_{st} = 0.076$ and 0.074) between 2 pairs of adjacent sub-populations in Scandinavia that also had few male migrants. Swenson et al. (1995) reported that

these sub-populations experienced a bottleneck 65 years ago of approximately 35 individuals each, but they are now expanding in number and distribution (Swenson et al. 1998). Strong genetic drift during this bottleneck may explain the high D_{LR} values between these sub-population pairs that are now probably being reduced through increased migration.

In northern North America, the genetic distance of grizzly bear populations is correlated with geographic distance (Paetkau et al. 1997). Compared to northern, connected grizzly bear populations, the equivalent D_{LR} value measured across Highway 3 would represent an 800 km geographic separation, further suggesting that factors other than geographic distance are likely affecting the connectivity of bears in our study area.

The mechanism causing the Highway 3 corridor to disrupt bear movement is likely a combination of bears avoiding areas with high levels of human activity (Mattson et al. 1987) and high levels of mortality in the corridor (Mace and Waller 1999, McLellan et al. 1999). Fourteen percent of the sampled bears in this study were obtained from compulsory inspection of hunter kills or problem wildlife mortalities. However 50% of our migrants were hunter kill or problem wildlife mortalities. This suggests that dispersing bears may be at greater risk of mortality by humans and that human-caused mortality plays a role in connectivity. Fifty-five grizzlies were translocated out of the ecosystem or destroyed by conservation officers between 1990–2000 from the BC portion of the study area (B. Warkentin, personal communication, 2001). In addition, 120 bears have been legally harvested within the BC portion of our study area. This legal kill may also affect movement across the corridor if dispersal rates are density dependent (Swenson et al. 1998, McLellan and Hovey 2001).

Limitations

It is important to note several limitations in our methods and data. Determining exact individuals as migrants using the assignment test is challenging. The difficulty lies in distinguishing real migrants from those cross-assigned by chance. Although we offer our likelihood threshold of 3.0 as a reasonable approach, we hope to improve our ability to delineate individual migrants in the future. When the likelihood threshold is lowered to 2.0, one more potential male migrant is detected, which does not alter the ecological story.

Our methods have rarely been used to investigate population fragmentation with such a relatively high percentage of the population sampled (Cornuet et al. 1999, Waser and Strobeck 1999). We believe that these methods offer promise in investigating immigration between populations

in recently disturbed systems with minimal genetic differentiation at ecologically relevant time scales. Traditional population genetic measures of migration between populations have rarely used individually specific data, nor have they answered individually specific questions; therefore, they have been criticized by ecologists and conservation biologists (Ims and Yoccoz 1997, Steinberg and Jordan 1997, Whitlock and McCauley 1999). New molecular based statistics being developed offer hope of exploring what has traditionally been a vexing question (Cornuet et al. 1999, Luikart and England 1999, Waser and Strobeck 1999).

IMPLICATIONS

Fragmentation may be a significant issue when it results in the isolation of a small population (Soule 1987). We believe that population fragmentation coupled with excessive human related mortality and habitat degradation is a threat to grizzly bear populations at the southern edge of their North American distribution. The peninsular shape of their distribution makes population isolation a predictable result of fragmentation in our study area as well as other areas, such as the Selkirk Mountains of southern Canada with an isolated a population of approximately 100 bears (M. Proctor unpublished data).

At this time, there appears to be some fraction of historic levels of male bear movement and very little if any female movement across the Highway 3 corridor in the Rocky Mountains. Continued development may further decrease bear movements across this fracture. We recommend the establishment of linkage zones that connect the best available grizzly bear habitat at several locations across the corridor as suggested by Apps (1997). These zones would offer potential benefits to other species as well.

Fragmentation is a reality in our modern landscape and it is impossible to completely alleviate. Our goal should be to maintain female and male connectivity to a level where long-term persistence of populations is not threatened. Establishing the thresholds mediating fragmentation and influencing human development patterns is our challenge. It would be valuable to understand female dispersal and fragmentation sufficiently to predict what level and combination of human development, settlement, and vehicle traffic would cut off movement between adjacent areas. This information would be useful in guiding land-use policy to avoid increased fragmentation. At this time it is difficult to conclude what combination of human and natural factors precludes female dispersal. We hope to gain insight into this question in the future as our fragmentation analysis continues.

ACKNOWLEDGMENTS

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