Gender-specific dispersal distances of grizzly bears estimated by genetic analysis

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Abstract: Natal dispersal is difficult to quantify, and long-distance events are often undetected, leading to biased estimates. Following offspring from their natal home range to their postdispersal adult breeding home range is challenging, and gathering sufficient data for large mammals with long generation times is particularly difficult. Here we measure average sex-specific dispersal distances in grizzly bears (*Ursus arctos* L., 1758) using individual-based genetic analysis. We genetically sampled and generated 15-locus microsatellite genotypes for 711 grizzly bears over a range of 100 000 km² in southwestern Canada. Microsatellite markers are inherited in a Mendelian fashion, allowing us to use likelihood-based parentage analyses to estimate parent–offspring dyads. We used the distance between individually captured females of parent–offspring pairs (i.e., mother–daughter) to estimate female natal dispersal distances and found that, on average, females dispersed 14.3 km from the center of their natal home range. We used the distance between males of parent–offspring pairs (i.e., father–son) to estimate average male dispersal distances and found that males dispersed, on average, 41.9 km from their natal, or maternal, home range (mother–son dispersal distance). We used a simulation model to estimate the bias associated with measuring the father–son (male–male) distance as an estimate of the mother–son distance.

Résumé : La dispersion à la naissance est difficile à évaluer quantitativement et certains événements qui ont lieu sur de grandes distances peuvent souvent passer inaperçus, ce qui fausse les estimations. Suivre les petits depuis leur aire de naissance jusqu'à leur aire de reproduction à l'âge adulte après la dispersion présente un important défi, particulièrement chez les grands mammifères à durée de génération longue chez qui l'accumulation suffisante de données est particulièrement difficile. Nous avons mesuré la distance moyenne de la dispersion en fonction du sexe chez des grizzlis (*Ursus arctos* L., 1758) à l'aide d'une analyse génétique individuelle. Notre échantillonnage génétique a révélé l'existence de 15 génotypes reliés aux locus microsatellites chez 711 grizzlis sur un territoire de 100 000 km² dans le sud-ouest du Canada. La transmission des marqueurs microsatellites suit un pattern de type mendéléen, ce qui nous permet de faire des analyses d'ascendance vraisemblable pour estimer les couples parent–petit. La distance entre les couples parent–rejeton (mère–fille) de femelles capturées individuellement a servi à estimer la distance de dispersion natale des femelles, soit en moyenne 14,3 km du centre de leur aire natale. La distance entre les couples parent–rejeton (père–fils) de mâles a servi à estimer la distance de dispersion natale des mâles, soit en moyenne 41,9 km du centre de leur aire natale ou de l'aire maternelle (distance de dispersion mère–fils). Un modèle de simulation a permis d'estimer l'erreur associée à la mesure de la distance père–fils (mâle–mâle) comme estimation de la distance mère–fils.

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Introduction

Natal dispersal, or the movement of offspring from their natal home range to their adult breeding area, is an important ecological and evolutionary process. At the individual level, dispersal is hypothesized to be a mechanism to mini-

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Lomolino 2000; Mattson and Merrill 2002). At the ecosystem level, dispersal plays a role in community structure function (Mouquet et al. 2001).

While dispersal plays a central role in population viability and conservation of fragmented species (MacDonald and Johnson 2001), there is a perceived shortage of reliable dispersal data (Reed and Dobson 1993; Doak and Mills 1994; Caro 1999; MacDonald and Johnson 2001). This lack of dispersal information is related to the practical difficulty of its measurement. Traditional mark-recapture dispersal studies have a tendency to underestimate dispersal distance because of spatial limitations on the size of study areas (Koenig et al. 1996). Radiotelemetry offers an improvement but may still be limiting for some long-distance dispersal events (Koenig et al. 1996). Genetic-based estimates of dispersal distance are often made using inferences from indirect measures of gene flow (F_{ST} and migration rate; Waser and Elliot 1991; Dobson 1994; Vitalis 2002), with varying success. The presence of sex-biased dispersal (not dispersal distance) has been documented with microsatellite genotype-based data and asymmetric population assignment probabilities between males and females (Favre et al. 1997; Mossman and Waser 1999; Dallimer et al. 2002; Goudet et al. 2002; Prugnolle and de Meeus 2002). Spong and Creel (2001) used the genetic similarity of female lions as a function of distance (or number of prides apart) to estimate the average dispersal distance of male lions (Panthera leo L., 1758) based on the genetic similarity of males to females.

The possibility of using family relationships to determine dispersal distance from genetic data has been discussed (Palsboll 1999) but, to our knowledge, has not been attempted. Here we use the spatial relationships between members of parent–offspring dyads, determined through genetic analysis, to estimate the dispersal distances of male and female grizzly bears (*Ursus arctos* L., 1758). Measuring a large sample of dispersal events in a species with relatively long generation times that lives at low densities over a large spatial scale is challenging. We used the genetic samples obtained during population surveys and a large-scale population fragmentation study (Proctor 2003) in southwestern Canada for this analysis.

Grizzly bears near the southern extent of their current North American distribution live in fragmented habitats that are susceptible to further human-caused fragmentation. As part of a larger population fragmentation study (Proctor 2003), we wanted to relate dispersal behaviour of male and female grizzly bears to fragmentation susceptibility. In an anthropogenically fragmented landscape, where a once presumed panmictic population has been transformed into a set of subpopulations (Proctor 2003), it is important to determine whether dispersal and interpopulation movement allow this system to function as a metapopulation. Can dispersal or migration mediate population augmentation, given the stochastic demographic problems associated with small populations?

Patterns in mammalian dispersal derived from comparison of life history traits suggest that grizzly bears should display long-distance dispersal because of their large body, nonterritorial and asocial nature, and generalist foraging habits (Wolff 1999). Food resources that are seasonal, ephemeral, or unpredictable should result in selection for individuals that are capable of foraging over large areas. Such resources characterize the foraging conditions of grizzly bears in the interior of North America (reviewed in LeFranc et al. 1987). Bears subsist on ephemeral sources: they prefer ungulates, when available, (LeFranc et al. 1987) and fire-mediated berry patches that create spatial and temporal habitat mosaics (McLellan and Hovey 1995). Furthermore, much of the anecdotal documentation of dispersal of grizzly bears suggests that males typically move long distances from their maternal range (Glenn and Miller 1980; Reynolds and

Hechtel 1986; reviewed in LeFranc et al. 1987). In contrast, grizzly bears in the southern interior of British Columbia have relatively short dispersal distances (McLellan and Hovey 2001). Using radiotelemetry to follow dispersing subadults, McLellan and Hovey (2001) found that malebiased dispersal is a gradual process, taking several years, and the resulting postdispersal adult home ranges of females usually overlap and males are, on average, one male home range diameter from the maternal range. McLellan and Hovey (2001) concluded that because grizzly bears are nonterritorial, have overlapping home ranges, and are promiscuous breeders, they do not need to disperse far to mitigate the effects of inbreeding and competition with close relatives for mates or resources. Because McLellan and Hovey's (2001) result was unexpected, considering the typical large carnivore trend discussed above, we wanted to test whether their result held true over a larger study area, with larger sample sizes. Our analysis is based on genetic data. We use the spatial relationships between members of putative parent-offspring dyads, determined from microsatellite genotypes, to estimate dispersal distances of males and females. We also explore the relationship between dispersal distance and population fragmentation susceptibility.

Methods

Study area

We sampled wild, free-roaming bears over a range of 100 000 km² in southwestern Canada and the northwestern United States of America (Fig. 1) in three mountain ranges: the Rocky, Purcell, and Selkirk mountains. In the Rocky Mountains, we sampled from the Canada-USA border through Banff National Park (latitude 49°N-52°N). In the Purcell and Selkirk mountains, we sampled bears from the southern extent of their distribution in the USA north to almost the 52nd parallel. This area included the entire Purcell Mountain range and all but the northern tip of the Selkirk Mountain range. These forested mountain ranges are separated by human-settled valleys (Fig. 1b). The Selkirk Mountains and the western slopes of the Purcell and Rocky mountain ranges tend to be wetter, more productive ecosystems, as Pacific air masses yield their moisture to highelevation, orographic precipitation, stimulating an interior wet belt in much of these areas. The eastern slopes of the Purcell and Rocky mountains fall within a rain shadow that yields a drier ecosystem. The study area has a diverse suite of land uses and jurisdictions, including towns, farming communities, industrial timber harvest (provincial and private), mining, eight provincial parks, and six national parks. The majority of the mountainous land is controlled by Canadian provincial governments or the US Forest Service.

Fig. 1. (*a*) Map showing study area (black frame) and current and historical North American grizzly bear (*Ursus arctos*) distribution. (*b*) Arbitrary local populations of grizzly bears in the Rocky, Purcell, and Selkirk mountains of southwestern Canada and northwestern USA: SS, south Selkirk Mountains; CS, central Selkirk Mountains; CSSE, CS southeast; CSSW, CS southwest; CSN, CS north; NS, north Selkirk Mountains; SP, south Purcell Mountains; CP, central Purcell Mountains; CPS, CP south; SR, south Rocky Mountains; CRS, central Rocky Mountains south; CRN, central Rocky Mountains north; NRE, north Rocky Mountains east; NRW, north Rocky Mountains west; NNRE, northern north Rocky Mountains east. Protected areas are shown in gray, and map labels BNP, YNP, KNP, WNP, and GNP are Banff, Yoho, Kootenay, Waterton Lakes, and Glacier national parks, respectively. Labels PWC, GRPP, VPP, KGPP, and WAPP are Purcell Wilderness Conservancy, Goat Range, Valhalla, Kokanee Glacier, and West Arm provincial parks, respectively. See text for subdivision criteria.





Grizzly bears in this area have experienced population fragmentation induced primarily by linear human disturbance in the form of human-caused mortality and settlement along transportation corridors in most major valleys (Proctor 2003). Dispersal is likely limited through several of these human corridors.

Genetic analysis

Samples consisted of biopsy tissue of handled bears (Gibeau 2000; Kasworm et al. 2000; B. McLellan, British Columbia Ministry of Forests, and W. Wakkinen, Idaho Fish and Game) and hair collected using hair traps that consisted of a single-strand, barbed wire corral surrounding a scent lure (Woods et al. 1999) between 1996 and 2001. Some samples came from previous DNA-based population surveys (Gibeau and Herrero 1997; Woods et al. 1999; Mowat and Strobeck 2000; Boulanger 2001; Boulanger et al. 2004).

We extracted DNA from hair roots using the Chelex protocol (Walsh et al. 1991) before 1998 and DNeasy columns (QIAGEN Inc., Mississauga, Ontario) after 1998. Because individuals were "DNA captured" several times, on average, we needed to set a threshold for declaring two different genotypes as two different individuals. Because it was possible to capture full siblings, and these individuals would likely

represent a dyad having the most similar genotypes in our sample, we identified individuals (or distinguished genotypes representing two individuals) statistically using six loci and a P_{SIB} statistic (Woods et al. 1999). Our threshold for acceptance that two genotypes were from two individuals (and not two individuals with the same genotype or full siblings) was a P_{SIB} value of 0.05 (Woods et al. 1999). Individual genotypes were analyzed at 15 microsatellite loci to increase analytical power. Genetic markers used were those previously developed by Ostrander et al. (1993), Taberlet et al. (1997), Paetkau et al. (1998), and Proctor et al. (2002). Specifically, we used G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10U, G10X, MU50, MU59, CXX20, and CXX110. Genotypes were determined with an ABI PRISM[®] 377 automated sequencer and scored with the help of Genotyper® Software (Applied Biosystems, Foster City, California). To minimize the possibility of creating a false individual through genotyping error, samples with similar genotypes were scrutinised for potential errors and rerun for verification, as were any genotypes represented by only one hair sample (likely possibilities for genotyping errors; Gagneux et al. 1997; Goossens et al. 1998; Taberlet et al. 1999; Paetkau 2003). We also ran all 15-locus genotypes through the software program Relatedness (Queller and

Goodnight 1989) to look for similar genotypes that were erroneously considered to be two individuals, and through CERVUS (Marshall et al. 1998; Slate et al. 2000) to look for potential parent–offspring pair members that did not share an allele at each locus because of genotyping error. We reanalysed all similar genotypes so that we had no pairs of genotypes with fewer than three mismatching loci in the final data set. We distinguished grizzly bear from black bear samples and determined sex according to protocols detailed in Taberlet et al. (1993), Woods et al. (1999), and Proctor et al. (2002).

We tested all 15 loci in all local populations for conformance to Hardy–Weinberg assumptions of random mating using the probability test for a deficit of heterozygotes (Rousset and Raymond 1995), and we 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–Šidák method (Sokal and Rohlf 1995). These tests were performed within GENEPOP 3.1 (Raymond and Rousset 1995). To establish that two local populations of bears were not one homogeneous unit, we tested the allele frequencies for heterogeneity using the log-likelihood ratio test (G test; Sokal and Rohlf 1995).

Sex-biased dispersal

We first wanted to test a genetic method for determining sex-biased dispersal (Favre et al. 1997; Mossman and Waser 1999) that compares the interpopulation assignment likelihood ($\ln P$ (Assignment)) between males and females. The sex that disperses the farthest will have, on average, lower assignment likelihoods to its population of capture. We determined population assignments for all individuals using an allele frequency-based assignment test (Paetkau et al. 1995). Because we used average assignment likelihoods between geographic areas, we compared bears inhabiting immediately adjacent geographic areas that were separated by major valleys and human transportation corridors. (Fig. 1*b*; see Proctor 2003).

For each individual, we calculated an index of the assignment likelihood (AIc) from the following equation:

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

where $P(A_{CAP})$ is the probability of assignment to the population of capture and $P(A_{AVE})$ is the average of assignment probabilities to each population. Subtracting the average population assignment probability allows comparison between populations that have different allele frequencies and therefore different average assignment probabilities (Favre et al. 1997; Goudet et al. 2002). In this way, relative assignments, not absolute assignments, are compared. The parameters of interest are the mean and variance of each sex's average AIc values. We tested equality of variances using the F test, and means using a t test (Sokal and Rohlf 1995). A nonparametric t test was used when the variances were unequal. In species with sex-biased dispersal, the sex that disperses the farthest, and is therefore most likely to be the sex of interpopulation migrants, is expected to have lower average AIc values. The dispersing sex is also expected to have the highest variance in AIc values, reflecting a population with immigrant and resident genotypes (Goudet et al. 2002).

We used a likelihood estimator of parent-offspring status among pairwise comparisons of individuals captured throughout our study area (CERVUS; Marshall et al. 1998; Slate et al. 2000). CERVUS compares the likelihoods of potential parents calculated from allele frequencies within the population based on Mendelian inheritance principles. CERVUS develops a "Likelihood of Descent" from the cumulative likelihood ratios (the likelihood of inheriting a particular allele from a potential parent relative to the likelihood of inheriting that allele from a random individual in the population). Rare alleles are therefore weighted more than common alleles. For all potential offspring, CERVUS compares the two most likely parentage candidates (maternal and paternal done separately) by log ratio. It then simulates parents and offspring, developing a distribution of relative log ratios to determine a probability for any given potential parent-offspring relationship. We had no prior parent-offspring information and used a 95% confidence level as our threshold for declaring a putative parent-offspring pair. There are several advantages to using this likelihood estimator: the simulation routine incorporates estimates of the rate of genotyping error, the number and proportion of potential parents sampled, and the proportion of genotyping success. We have biologically reasonable estimates of these parameters. Because most of our samples were obtained from formal population surveys conducted to estimate abundance, we were able to estimate the proportion of potential parents sampled (population estimates suggest that we sampled approximately 50% of the total population) with some confidence. We also know the rate of genotyping success (98%). The parameter that is difficult to estimate is the genotyping error rate. CERVUS incorporates a mechanism to accommodate natural mutations and potential genotyping errors by allowing pairs to mismatch at a few loci and still be considered parent-offspring on the strength of their likelihoods. We entered a relatively low error rate of 0.001 to ensure that parent-offspring dyads were not accepted if the the members mismatched at more than one locus. This minimized our type I error rate but potentially reduced our sample size.

Sex-specific dispersal distance

Female dispersal distance

To estimate the dispersal distance of each gender, we used the average distance between capture locations of individuals of parent-offspring pairs. We excluded any pair thought to be a predispersed offspring traveling with its mother (individuals that appeared as a parent-offspring pair and that were captured together twice). For female dispersal distance, we used female-female parent-offspring dyads. Because age cannot be determined from genetic data, we could not tell which individual was the mother and which was the daughter, but we could tell that one was the mother and the other, the daughter. To calculate the dispersal distance between two individuals, ideally we should have measured the distance between the centers of their postdispersal home ranges (McLellan and Hovey 2001). However, our capture locations were point locations within each home range. Sometimes we captured individuals when the distance between them was less than the distance between the centers of their home **Fig. 2.** Diagram illustrating the method of determination of correction factors and variances for each father–son distance used to estimate the distance between the center of the mother's range and the center of the son's range (male dispersal). Calculations were based on the assumptions that the mother's home range overlaps the father's (i.e., they mated) and the son's postdispersal home range is the same size as an adult male home range. To estimate the correction factor and variance, the procedural steps were as follows: (*i*) assign the father's location to be the origin; (*ii*) select the son's point using a random direction $(0^{\circ}-360^{\circ})$ and a preset distance (our male–male data for each pair); (*iii*) select a mother's range center using a random direction and random distance (maximum is adult male home range diameter plus an adult female home range radius); (*iv*) measure the distance between the mother's and son's home range centers; and (*v*) repeat the procedure 5000 times to generate a mean and variance for each male–male pair.



ranges, and other times when the distance was greater. Given large enough sample sizes, the average of the distances between individuals of mother–daughter pairs can be an unbiased estimate of the average dispersal distance.

Male dispersal distance

Estimating male dispersal distance using genetic techniques is more challenging. In a female–female parent–offspring pair, one individual is the mother and the other the daughter; a male–female parent–offspring pair, however, could be a son–mother pair or a father–daughter pair. Therefore, to estimate male dispersal, we used only male–male pairs. The assumption required in doing so is that the father's location can be used to estimate the mother's location. In essence, we used the distance between the father and the son to estimate the distance between the mother and the son and therefore needed to quantify the bias or a correction factor associated with this assumption.

We generated a correction factor for each father-son pair using 5000 repetitions of a simulation algorithm that used average adult male and female home range sizes from our study area. Males have larger nonexclusive home ranges that overlap several nonexclusive female home ranges (reviewed in LeFranc et al. 1987; Gibeau and Herrero 1998). If a male and a female mated, we assumed that some portion of their home ranges overlapped. We set the hair trap location of one of the males of a male-male pair at the origin and called that male the father; the location of the other male, called the son, was set at the recorded distance. The hair trap that caught the father could have been anywhere in his home range, so he could have encountered and bred the mother anywhere within one adult home range diameter of the hair trap. At most, the center of the mother's home range could have extended up to one adult female's home range radius past the male home range if the two parent's ranges met just at the edges. We therefore simulated the mother's range center by generating a random angle between 0° and 360° and a random distance between zero and the sum of an adult male home range diameter plus an adult female's home range radius. The son's range center, in relation to the father, was simulated by a random direction from the father and the measured distances between individuals of each male-male pair from our data. The distance between the simulated range centers of the mother and son, or the male dispersal distance, was thus measured (see Fig. 2). This procedure was repeated 5000 times, providing a mean and variance of the dispersal distance. Simulation calculations were based on male and female home ranges of 579 and 186 km², respectively (mean values for three radiotelemetry projects within our study area; J. Woods, unpublished data; F. Hovey, personal communication; Gibeau and Herrero 1998).

Results

We genotyped 711 bears (344 females, 367 males) associated with specific location data from 15 geographic areas. Expected genetic variability (H_E) was 0.64 and observed heterozygosity (H_O) was 0.65 across 15 microsatellite loci within our area. There was moderate population structure across all 15 geographic areas ($F_{ST} = 0.050$).

Sex-biased dispersal

As expected, males had significantly lower AIc values (two-tailed *t* test; female mean, 0.225; male mean, -0.219;

Fig. 3. Distances between "capture" locations of individuals of female-female (FF) and male-male (MM) parent-offspring pairs of grizzly bears in southwestern Canada used to estimate average dispersal distance.



t = 2.13, df = 688, p = 0.033), suggesting male-biased dispersal among our study animals. Males also had a greater AIc variance (*F* test; female variance, 6.42; male variance, 7.94; $F_{[328,360]} = 0.809$, p = 0.025), suggesting higher variability in individual dispersal behaviour.

Sex-specific dispersal distance

We found 213 dyads that met the criteria of a parent–offspring relationship. We used 97 of the dyads in our analysis (54 mother–daughter and 43 father–son pairs). One hundred and sixteen dyads were male–female pairs that were not used in our analysis because we could not determine whether the pair was a mother and son or a father and daughter. Although it is difficult to estimate with reasonable certainty the number of parent–offspring pairs that are alive and within our study area, we can compare numbers of male–male, female–female, and male–female pairs we would expect from among the 213 pairs we identified. Assuming a 1:1 male:female ratio, we would expect 53.5 male– male, 53.5 female–female, and 106.5 male–female pairs, close to our observed quantities.

Using the mother–daughter pairs, we found that the average dispersal distance for females was 14.3 km (n = 55, SE = 2.8, 95% CI 8.7–19.9), while the minimum and maximum measured distances were 0 and 78 km, respectively (Fig. 3). Using the father–son pairs (n = 43), we found that the average dispersal distance for males was 41.9 km (n = 43, SE = 9.4, 95% CI 23.0–60.8; Fig. 3). We found that the estimated bias associated with using father–son distances to estimate mother–son distances diminished as dispersal distance increased (Fig. 4).

Discussion

The use of genetic tools to estimate population parameters is a new and evolving methodology. Our use of genetic analysis to detect sex-biased dispersal through asymmetrical assignment probabilities was corroborated by our parent– offspring-derived dispersal distances. These techniques have several advantages and disadvantages for dispersal measurement. Parentage-derived dispersal calculation allows genetic techniques to yield a direct measurement of sex-specific dispersal, an improvement over indirect inferences of gene flow derived from the use of $F_{\rm ST}$ and (or) estimators based on migration rate. When using $F_{\rm ST}$ -based techniques, it is not only difficult to detect sex-specific dispersal, it is also not possible to determine whether gene flow resulted from a few long-distance dispersal events or from more frequent but shorter, stepping-stone-like movements (Dobson 1994), or whether gene flow is a result of dispersal events or temporary movements for breeding purposes (Waser and Elliot 1991).

Our genetic-based method of quantifying dispersal did not require the capture of animals and is thus less obtrusive than either radiotelemetry or other marking methods. We were able to generate relatively large sample sizes because our efficient, noninvasive sampling technique allowed broad genetic sampling that in turn allowed us to detect long-distance dispersal events. This analysis was not the primary reason we collected genetic samples and developed microsatellite genotypes for our study species. Because microsatellite analysis is becoming a common way of addressing a variety of questions across many taxa, other studies may be able to efficiently investigate dispersal using these techniques.

One limitation of our methodology is the assumption that point locations of two individuals can be used to estimate the average distance between them. This limitation is the same as that found with other ways of marking individuals (i.e., tags) and requires sufficient sample sizes to ensure an accurate average; precision will always be inflated.

There are also limitations to using a likelihood estimator for relationship analysis. A portion of parent–offspring pairs estimated by CERVUS may be full siblings (Marshall et al. 1998). Full siblings, like members of parent–offspring pairs, share one half of their alleles, on average, but have a different pattern of allele sharing (Jacquard 1974). Siblings share one allele at each locus one half of the time, both alleles one quarter of the time, and neither allele one quarter of the time. With this allele sharing pattern and 15-locus genotypes, full siblings would have, on average, 3 or 4 loci where **Fig. 4.** Relationship between dispersal distance and the correction factor associated with using father–son distance to estimate mother– son (dispersal) distance. The curve was generated from 5000 repetitions for each male–male pair (\blacklozenge) in our data set of dispersal distance, using the simulation routine described in Figure 1. The y axis is the correction distance required when using the father–son distance to estimate the mother–son (dispersal) distance. Note that as the dispersal distance increases, the correction factor diminishes to zero. The dashed lines are the 95% confidence limits.



they do not share an allele (except when they share an allele not by descent but at a rate reflective of that allele's frequency in the population). CERVUS allows for genotyping errors by considering some parent-offspring pairs to be significant even if the members do not share an allele at all loci. We required that members of a parent-offspring pair share an allele at all except one locus, in that way accounting for some genotyping error but minimizing the chance of falsely considering a full sibling pair to be a parent-offspring pair. We knew of 10 pairs of full siblings within our data set (from radiotelemetry studies), and CERVUS assigned 2 of these as parent-offspring pairs. To further explore the tendency of CERVUS to erroneously assign sibling pairs as parent-offspring pairs, we ran CERVUS under the exact same conditions as our analysis (as though we had no prior knowledge of familial relationships) on a 17-locus microsatellite data set of 539 Weddell seals (Leptonychotes weddelli Lesson, 1826) for which familial relationships were better known (Gelatt 2001). Maternal half siblings were known from capture histories at rookeries, and paternity was assigned using exclusion. Putative fathers shared an allele at all loci. As an example of the exclusionary power of this data set, the second most likely candidate shared an allele at 12 loci, on average. Full siblings were determined as two individuals having the same mother and father. Of nine full sibling pairs, CERVUS assigned one as a parent-offspring pair (11%). Of 93 maternal half siblings, CERVUS did not assign any as parent-offspring pairs. Average expected heterozygosity of this seal population was 0.76, higher than in our data set (0.64), and this likely reflects better power for discriminating familial relationships.

Another limitation of CERVUS is the way in which significance is determined: by comparing the likelihoods between the individual under consideration and each of the two most likely candidate parents. This method assumes that other individuals in the sample are not related, and this may not be true. For example, if CERVUS is comparing an individual with its real mother, and the second most likely candidate is that individual's half sibling, then the real mother may not appear "significantly" more related than the half sibling and may be overlooked, contributing to the type II error rate. The effect of this problem on our analysis was likely that it lowered our sample size by falsely rejecting true parent–offspring pairs. In our data set of 20 known parent–offspring pairs (from radiotelemetry studies), 12 were correctly assigned (60%). In the above data set for Weddell seals, 294 of 382 (77%) known parent–offspring pairs were correctly assigned by CERVUS.

Furthermore, because we do not have age data, some of the relationships that underpin our data may include animals that are in the process of dispersing and that may be, on average, closer than their "final" adult home range will be.

Our dispersal distances for each sex were 40%-50% higher than those reported in the only radiotelemetry-based dispersal study done on grizzly bears in our region. By measuring the distances between the home range center of a mother and those of her dispersed offspring (30 offspring, 12 females, 18 males) over 20 years, McLellan and Hovey (2001) found that females dispersed, on average, 9.8 km from their maternal home range; this value was not significantly different from our value of 14.3 km (two-tailed *t* test for unequal variances; t = 1.40, df = 65, p > 0.05). Our male dispersal estimate of 41.9 km, however, was significantly different from McLellan and Hovey's (2001) estimate of 29.9 km (two-tailed *t* test for unequal variances; t = 2.24, df = 89, p < 0.05). Our longer dispersal distances may be a

result of larger home ranges in much of our study area (Gibeau and Herrero 1998). The male/female dispersal ratio is similar to results presented by McLellan and Hovey (2001, 30/10 = 3; this study, 42/14 = 3).

Patterns of mammalian dispersal derived from comparison of life history and behavioural ecological traits suggest that grizzly bears should disperse long distances (Wolff 1999). A large body is correlated with a large home range (McNab 1963) and long dispersal behaviour (Wolff 1999). Species that evolved in patchy, disturbance-driven or unpredictable habitats may have evolved to move longer distances through unsuitable and (or) naturally fragmented habitat. This contrasts with species that evolved in stable, continuous habitats and have conservative movement patterns through unsuitable habitat (Merriam 1995; Lima and Zollner 1996; Wolff 1999). Habitat generalists may respond better to fragmented landscapes as a result of having to meet their ecological needs from a variety of habitat types, whereas habitat specialists may view complex mosaics as barriers to movement (Laurence 1995; Wolff 1999). Non-territorial, asocial species should be less influenced by social considerations and therefore better able to move freely through the landscape (reviewed in Wolff 1999). These characteristics suggest that grizzly bears should have long-distance dispersal, but our results do not support this hypothesis.

A review of body sizes and dispersal distances of several North American large carnivores reveals that while the grizzly bear is one of the largest carnivores, the bears in our study area have some of the shortest reported average dispersal distances. Black bears (Ursus americanus Pallas, 1780) have home ranges approximately one fifth the size of those of grizzly bears (Aune 1994) and also have malebiased dispersal. Male black bears dispersed 61 km, on average, in Minnesota (Rogers 1987), and 30-200 km in Massachusetts (Elowe and Dodge 1989), but only 11 km in the Kenai Peninsula, Alaska (Schwartz and Franzmann 1992). Female black bears were philopatric in all studies. Male and female wolves in Minnesota dispersed, on average, 88 and 65 km, respectively (Gese and Mech 1991). In Maine, coyotes (Canis latrans Say, 1823) of both sexes dispersed similar distances, 98 km on average (Harrison 1992). In two studies in fragmented California habitat, cougars (Puma concolor L., 1771) dispersed 63 km (Beier 1995) and 85 km (Anderson et al. 1992). Male and female lynx (Lynx canadensis Kerr, 1792) in the Northwest Territories did not have different average dispersal distances (163 km; Poole 1997). While methods for measuring average dispersal distance vary among studies, and most estimates have not been placed in the context of home range diameters, dispersal of grizzly bears in our study area appears to be less than that for many other large carnivores in North America.

The southern interior grizzly bear may not fit the general pattern of carnivore dispersal for several reasons. McLellan and Hovey (2001) suggested that the non-territorial, overlapping home range behaviour and promiscuous breeding system of grizzly bears may have resulted in selection for shorter dispersal. They argued that long-distance dispersal is not required to reduce potential inbreeding effects and competition with close relatives for mates and resources. Our results support McLellan and Hovey's (2001) hypothesis and suggest that grizzly bears do not disperse long distances

from their maternal home range, moving less than the distances predicted from behavioural ecology and life history patterns among mammals (Wolff 1999).

Home range size may contribute to the male-biased dispersal distances of grizzly bears. The larger male home range, likely a strategy to increase mating opportunities, may account for a portion of the longer male dispersal distance. Females have smaller home ranges and, like females of most mammals, are more philopatric to utilize familiar habitat (Greenwood 1980).

There also may be an ecological plasticity component to dispersal behaviour (Waser 1996). Although grizzly bears are in the carnivore family, they are omnivorous, and in interior regions of western North America most populations obtain the majority of their energy from plant matter (LeFranc et al. 1987; McLellan and Hovey 1995; Hilderbrand et al. 1999). Herbivores have consistently shorter dispersal distances than carnivores (Wolff 1999). Increased population structure, or reduced regional connectivity and movement, have been associated with topographical and habitat complexity (Clegg et al. 1998). This may, in part, explain the discrepancy in dispersal behaviour between the northern (Glenn and Miller 1980; Reynolds and Hechtel 1986; reviewed in LeFranc et al. 1987) and southern interior Canadian bears (this work and McLellan and Hovey 2001).

In addition to the ecological and evolutionary forces that influence dispersal behaviour, it is important to consider the more recent forces imposed by humans. Large movements and therefore large home ranges suggest that bears are able to move easily between habitat patches across the landscape. However, in many regions, these movements also bring bears into contact with humans, often resulting in bear mortality (Mace and Waller 1998; McLellan et al. 1999) and ultimately population fragmentation (Proctor 2003). For example, in the past decade, 60 grizzly bears were killed or removed within one transportation and settlement corridor in our study area (BC Highway 3 in the southern Rocky Mountains, Proctor et al. 2002) owing to concerns for human property and safety. Human activity in boundary areas separating subpopulations has effectively constrained longdistance dispersal (McLellan and Hovey 2001) by effectively increasing the distances between the subpopulations from a bear dispersal perspective.

Of particular importance is the asymmetric susceptibility to population fragmentation experienced by sexes that do not disperse equal distances. Because female dispersal distances are relatively short and the dispersal process is gradual (McLellan and Hovey 2001), human-caused fragmentation will make it difficult to retain the female component of demographic connectivity. Limited female dispersal and susceptibility to population fragmentation is reflected in the sex-biased fragmentation of grizzly bears in southern Canada (Proctor 2003).

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