A genetic-based spatial analysis of grizzly bears in Alberta

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Abstract

Grizzly bears are wide-ranging carnivores whose populations extend over large geographic areas (and ignore jurisdictional boundaries) and traditional management units tend to be too small for grizzly bear populations. Effective management can be improved by knowing if bears are spatially structured, naturally or as a result of anthropogenic forces, allowing management strategies to be specifically tailored to groups of bears living in separate sub-populations. This report is a result of a genetic-based spatial analysis of Alberta grizzly bears with the objective of delineating biologically-based sub-populations that may be useful for defining management units. To improve rigour and develop an inter-provincial view of grizzly bear population structure, our analysis included Alberta grizzly bear samples combined with those in adjacent portions of British Columbia from a previous effort. We found that Alberta's grizzly bears form five such groups whose boundaries roughly coincided with the major east-west Highways 3, 1, 11, and 16 in central and southern Alberta. These sub-divisions in Alberta's grizzly bear population may be the basis for delineating biologically-based management units. Managers will need to incorporate these results with jurisdictional, practical, and logistical considerations when contemplating final management unit boundaries. While it is difficult to distinguish natural from anthropogenic fragmentation, these results suggest that the human environment is likely influencing the spatial dynamics of grizzly bears in Alberta. While the boundaries between sub-units do appear to be permeable, further population level work, such as abundance estimates for these units and consideration of connectivity enhancement, would be advisable.

Introduction

Wildlife management in Alberta has traditionally been organized around Wildlife Management Units (WMU). Because of the spatially diverse and dispersed habitat requirements of grizzly bears, the WMU was considered too small to effectively contain a group of individuals that could be considered a grizzly bear management unit. In 1988, Alberta developed bear management areas to improve the spatial coverage of their grizzly bear management units. These BMA's were defined by using existing radio-telemetry data and through expert opinion of biologists. However, recent developments in population genetic techniques have made it possible to explore the existence of biologically-based management unit boundaries using genetic samples from various research projects in the province and those collected during compulsory inspection of hunter kills. This analysis and report were commissioned by Alberta

Sustainable Resource Development to explore the existence of genetic partitioning within Alberta that may form the basis to redefine biologically-based grizzly bear management units within Alberta.

It has been suggested that biological criteria for management units should encompass a group of animals where birth and death rates dominate over immigration and emigration (Moritz et al. 1995). Continuing with this logic, breaks in genetic continuity that result from limits to movement of bears may be relevant management unit boundaries. In many jurisdictions in Alberta and British Columbia a legal grizzly bear hunt necessitates accurate population estimation of a biological meaningful population or management unit for the setting of quotas, trend monitoring, and other management considerations, including potential conservation strategies. Proctor (2003) detected anthropogenic population fragmentation in southeast B.C. and southwest Alberta and knowledge of similar subdivisions, if present in Alberta grizzly bears, would be useful and important for management purposes.

Two common methods have been used to delineate population or management unit boundaries: radiotelemetry and population genetics. Extensive radiotelemetry work may detect population boundaries using cluster analysis of cumulative individual home range and movement data (Bethke et al. 1996; Taylor et al. 2001; McLoughlin et al. 2002). Here we use a recently developed population genetic technique that uses Bayesian model-based clustering of genetic data to delineate groups of individuals into clusters that reflect genetic discontinuities and therefore may be candidates for management units (Pritchard et al. 2000). This technique is relatively objective in that it assumes no *a priori* group membership.

We used 15 locus microsatellite genotype data from 414 grizzly bears from Alberta and 625 from British Columbia in the analysis. We included the B.C. bears to increase rigor and explore connectivity between Alberta and B. C. where samples sizes were sufficient on both sides of the continental divide. Grizzly bears inhabit the western portion of Alberta and as such, inhabit the eastern edge of their North American distribution in southern Canada. Therefore, whether there is significant interchange between Alberta and B.C. has important implications for management.

Methods

Genetic samples and analysis

Alberta genetic samples were obtained from Alberta Fish and Wildlife Division hunter kill inspections (Bob McClymont), the Foothills Model Forest Grizzly Bear Project (Gordon Stenhouse), the East Slopes Grizzly Bear Project (Mike Gibeau), and the Southwest Alberta Grizzly Bear Survey of

1997 (Garth Mowat). British Columbia samples were from various projects included within M. Proctor's (2003) Ph.D. work

Samples were a combination of tissue or hair from physically captured bears, or hair collected on remote DNA hair-grab sampling stations as detailed in Woods et al. (1999). DNA was extracted using Chelex protocol (Walsh et al. 1991) before 1997 and DNeasy columns (Qiagen Inc., Mississauga, Ontario, Canada) after 1997. Black bears were distinguished from grizzly using a species-specific fragment of mtDNA (Woods et al. 1999). Sex was determined (when bears were not handled) using the SRY–ZFX/ZFY system detailed in Taberlet et al. (1993) and Woods et al. (1999) and the Amelogenin locus detailed in (Ennis and Gallagher 1994; Proctor et al. 2002).

Fifteen locus microsatellite genotypes were generated by Wildlife Genetics International, (David Paetkau, Nelson B.C.) and M. Proctor during his Ph.D. work. While 6-locus genotypes are sufficient for individual identification and useful for population surveys estimating abundance and distribution, 15-locus genotypes allow investigation of population level questions such as genetic structure or inter-population movement rates. Details, including specific loci used, can be found in Paetkau et al. (1998) and Proctor et al. (2002). Genotyping errors were minimized through protocols found in Woods et al. (1999) and Paetkau (2003).

Management unit delineation

To detect genetic sub-division within the sample of bears, we used a Bayesian analysis and Monte Carlo Markov Chain (MCMC) cluster analysis (STRUCTURE, Pritchard et al. 2000) that is designed to estimate the genetic clustering of groups of individuals with no *a priori* assumption of group membership. This offers a relatively objective method for detecting genetic structure within a sample of individuals. The optimum genetic clustering is derived from the best fit of the data to one of several models depicting the genetic sub-division. Competing models are derived from results based on assigning a specific number of clusters to the data. That is, you run the program under the assumption of various numbers of groups (K = 2, 3, 4 etc.). The number of clusters that best fits the data has the Baysian-derived highest posterior probability. What this means mathematically is that the winning set of clusters has the highest cumulative probability of assignment of individuals to their respective clusters. Assignment is based on the cumulative probability of occurrence of each individual's alleles to the competing groups. The MCMC algorithm iteratively computes these probabilities one individual at a time. Depending on the outcome of each step in the chain, group memberships shifts slightly. With sufficient repetition and genetic structure, group membership stabilizes. What this means biologically is that, given good study design, and correct interpretation, cluster boundaries may reflect some intensity of genetic structuring, which may be a result of natural or anthropogenic fractures, or inhibitors to spatial interchange. In some cases it may reflect isolation-by-distance, with no real biological barrier. As with many genetic analysis techniques, in areas where genetic structure is weak, power is lacking to detect solid genetic boundaries.

STRUCTURE begins from a random location (that is initial group memberships are randomly chosen), therefore a “burn in” period is used where results are not used in calculating the final results. We used a burn in period of 50,000 iterations and collected data during the following 100,000 iterations. Furthermore, multiple runs were used (5) to ensure results were consistent between runs. Individuals were assigned to the group in which their estimated proportion of ancestry was highest.

There are several ways to interpret STRUCTURE clustering results. Ideally, a set of clusters is identified that clearly has the highest posterior probability. Occasionally, this does not occur, particularly in sample sets where genetic structuring is weak. An alternative method is to view the spatial patterns of clustering as the number of clusters sequentially increases (Pritchard, et al. 2000; Rosenberg et al. 2002). If the clustering has a consistent progression of sub-division as the number of groups increases, then the spatial boundaries between clusters likely have real biological meaning, (i.e. population, subpopulation, or management unit boundaries; N. Rosenberg pers. comm.).

We therefore mapped the results from each sequential increase in the number of clusters to facilitate a comparative examination of cluster development across Alberta and southeast B.C. When cluster sub-division left consistent boundaries, they were considered real. The spatial coverage or the sampling effort within this project is almost continuous. Most sampled geographic areas are immediately adjacent to one another and usually within the reasonable dispersal distance of female and male grizzly bears (McLellan and Hovey 2001; Proctor 2003). Therefore, clustering as a result of isolation-by-distance alone should be minimized.

Population assignments

Once genetic clusters were identified using STRUCTURE, geographically defined groups of animals were created for subsequent testing. This involved drawing a line on a map and placing all individuals on a given side of that line into the same cluster (in the STRUCTURE analysis the clustering is not as geographically discrete). We used an allele frequency-based population assignment test

(Paetkau et al. 1995) on the clusters of individuals resulting from the STRUCTURE analysis. Population assignment results are displayed in graphic plots with a related genetic distance measure D_{LR} (Paetkau et al. 1997) for comparative purposes. Also, the genetic differentiation measure F_{ST} (Weir and Cockerham 1984) is reported for adjacent clusters. Population assignment analysis assumes Hardy-Weinberg and linkage equilibrium. These were calculated for all loci in all resulting clusters using GENEPOP 3.1 (Garnier-Gere and Dillman 1992; Raymond and Rousset 1995). Critical values for these tests were adjusted for the experiment-wise error rate using the Dunn-Sidak method (Sokal and Rohlf 1995).

Results

The comparison of Bayesian posterior probabilities between models did not result in a clear winner. As K increased, the posterior probabilities incrementally increased and appeared to be reaching an asymptote somewhere near or above 26 clusters. In a previous effort (Proctor 2003), the same analysis was run using 814 of the same bears but without the additional Alberta hunter kill samples that instigated this project. That effort yielded a clear winning model that displayed a superior fit between the data and model (Proctor 2003). It was therefore, our conclusion that the inconclusive result of the STRUCTURE algorithm to chose a winning model was a result of the more diffuse sampling pattern represented by the northern Alberta bears. Since there is probably no geographic scale at which groups of grizzly bears are genetically homogeneous, it is not surprising that the program will continue to pick more and more groups apart when the population is distributed in a more or less continuous fashion. It is not uncommon for population genetic programs to yield un-patterned results when confronted with diffuse samples that have very little genetic structure. Therefore, the following results and interpretation are based on patterns of sub-division resulting from the sequential increase in numbers of clusters that were run through the STRUCTURE algorithm as recommended by Rosenberg et al. (2002; N. Rosenberg pers. comm.).

In general, the sub-divisions had a clear geographic basis and remained relatively consistent as the number of clusters was incrementally increased from 2 through 8. That is, each successive sub-division resulted in the splitting of one of the previous clusters. At around 8-9 clusters the sub-divisions would split a previous cluster with little spatial pattern as a result of the algorithm being forced to create a new cluster. After this point, the clusters have less biological and geographical meaning and do not retain their consistency through further subdivisions.

There appears to be 5 genetic clusters of bears that roughly align themselves from south to north within Alberta. This spatial orientation is not surprising as grizzly bears occupy a relatively narrow zone paralleling the Rocky Mountains that form the western boundary between Alberta and B.C. The boundaries separating these clusters are not sharp. The clusters from south to north are:

1. the Southern Rockies South (SRS) south of Highway 3 to the US border,
2. the Central Rockies South (CRS) between Highways 3 and 1,
3. the Central Rockies North (CRN) between Highways 1 and 11,
4. the North Rockies South (NRS) area between Highway 11 and 16, and
5. the North Alberta area (NAB) north of Highway 16.

Table 1 is a summary of sample sizes for the resulting clusters. More specifically, there is a definite separation between northern and southern Alberta bears that breaks in the Banff National Park (BNP) area north of Highway 1. This break remains fairly consistent from K = 2 through K = 9 (Fig 2a-i) although this boundary is not discrete as animals cluster across Highway 1 in 2 groups. Another break that remains consistent is the bears south of Highway 3 in the Rocky Mountains. This cluster appears at K = 3 (Fig. 2b) and remains reasonably consistent through further sub-divisions although the sharpness of this break diminishes at higher values of K. At K = 4 the area between Highways 3 and 1 becomes apparent. North of Highway 1, clustering becomes less consistent. At K = 5 the South Selkirks in B.C. separates off. At K = 6 a band north of Highway 1 is apparent. At K = 7 the central Purcells sub-divides in B.C. At K = 8 an interesting group appears that is characterized by a group of bears that were translocated out of the Revelstoke B.C. area between 1985 and 1995 (Proctor and Neumeier 1995; Note the black cluster of bears around Revelstoke). At K = 9 a somewhat overlapping cluster between Highways 11 and 16 appear in the Jasper National Park area. This area appears as a hybrid of other clusters until K = 9 suggesting that the bears are not a strong genetic grouping. The map of K = 8 or 9 may be the best maps of sub-division before the clusters subdivide into groups with little spatial pattern.

The area between Highways 1 and 11 form a weak cluster, likely a result of less numbers of samples, real genetic mixing, and a history of translocations into the area. The bears in the northern reaches of Alberta north of Highway 16 also appear to cluster together despite their wide geographic separation. The break in the area around Highway 16 also appears to be soft.

The resulting clusters that contained Alberta bears were not generally found to depart from Hardy-Weinberg equilibrium as tested by the heterozygote deficit test. There was one failure in 75 tests (5 loci * 5 clusters). Of 525 locus pairs in 5 clusters, 60 (11%) appeared to not be in linkage equilibrium.

Twenty-six of these failures were locus pairs in the North Rockies South (NRS) cluster between Highways 11 and 16. These failures appear to result from the mixing of bears through extensive translocations or mixing of genetic signatures from several groups. The bears in the NRS area appear to be a less distinct group, and this is reflected in the high failure rate for the linkage dis-equilibrium. STRUCTURE-based clustering puts individuals in groups that should optimize conformance to Hardy-Weinberg equilibrium and linkage equilibrium. However, the purpose of this project is to group individuals in spatial (geographic) clusters that reflect the genetic clusters. Because the genetic clusters may be spread out spatially in several cases, the spatial clusters will therefore contain individuals from several genetic clusters. This mixing of genetic clusters, and a general isolation-by-distance that is known to be prevalent in bears (Paetkau et al. 1997), will likely cause some failures in the HWE and linkage equilibrium tests.

Assignment plots within Figure 3 show the genetic separation between adjacent clusters. A quantification of this separation is encompassed within a D_{LR} genetic distance. Boundaries across Highways 3 and 11 appear to be the strongest with D_{LR} values of 2.79 and 3.37 respectively. For contrast we provide several assignment plots showing the potential range of genetic separation that occurs in southern B.C and Alberta. Figures 3a, 4a, and 4b are various comparisons of the bears south of Highway 3 in the Rocky Mountains. Note the difference in genetic separation between the Southern Rockies South (SRS) bears and bears to the north of Highway 3, CRS, (Fig. 3a) relative to those same bears divided across the continental divide (Fig. 4a) or across the North Fork of the Flathead River in southeast B.C. (Fig. 4b).

Figure 4c is an assignment plot of the South Selkirk (SS) grizzly bear population vs. the Central Selkirk (CS) population across Highway 3A. Note the complete separation across a narrow valley with continuous human settlement paralleling Highway 3A.

Of interest are a few northern bears that appear to assign to southern Alberta. It is likely that these bears were translocated from southern Alberta or are offspring from translocated animals. In particular, the bear in far eastern Alberta (Wildlife Management Unit 500) consistently assigns to southern Alberta. This bear was likely translocated somewhere into central or northern Alberta and wandered east.

Discussion

Considering the wide-ranging habits of grizzly bears, it is interesting that we can detect genetic discontinuities across such short distances as in this project. In the absence of human perturbation, habitat appears continuous along the Rocky Mountain range in western Alberta. Given the high level of human activity in the region it is challenging to distinguish between natural and anthropogenic fragmentation. However, figures 4a and b suggest that the high mountains of the continental divide and large river valleys do not inhibit grizzly bear movement and it follows that anthropogenic forces are probably contributing to fragmentation in Alberta. This is not surprising as Proctor (2003) implicated human-caused mortality, traffic volume, and human settlement as contributing factors to population fragmentation of grizzly bears in southern B.C. using multiple regression to compare 23 immediately adjacent geographic areas with a range of human disturbance.

The boundaries between the identified clusters in this project were generally overlapping, that is bears from each adjacent cluster appear on each side of the boundary. Given the numbers of samples (and bear populations) on each side of border areas, genetic signals would be expected to develop slowly through genetic drift as fragmentation increases. In a previous analysis, Proctor (2003) found only one hard boundary across a thin strip of continuous human settlement paralleling B.C. Highway 3A in the Selkirk Mountains. That fracture separated a small population of less than 100 individuals that had a D_{LR} genetic distance of 14.2 (Fig. 4c; compare to the D_{LR} in this effort that ranged from 1.34 across Highway 16 to 3.37 across Highway 11).

The genetic clusters identified in this project are by no means discrete or distinct. Rather, they represent detectable discontinuities in genetic mixing across a landscape. It should be noted that bears naturally exhibit gradual genetic allele frequency changes across the landscape (Paetkau et al. 1997) that is referred to as “isolation-by-distance”. It appears that grizzly bears in Alberta are experiencing two simultaneous genetic processes. The first process, the natural and ubiquitous isolation-by-distance, is being punctuated by the second, interruptions in movement mediated by human disturbance in the form of highways and their associated settlement. The resulting clusters of genetically similar bears are caused by this reduction in mixing. Supporting the notion of isolation-by-distance underlying grizzly bear spatial genetics, Proctor (2003) found that while human disturbance played a dominant role in fragmentation of grizzly bears in southeast B.C and southwest Alberta, geographic distance was a contributing factor to predicting movement rates of bears between adjacent areas. In this current effort, we found no evidence that the reductions are complete and these bears likely intermix at reduced rates, causing the genetic signal detected in this project.

In an effort to clarify our results, we have presented a conceptual illustration of genetic structure as is suggested by the results (Figure 5). The solid red line represents one hypothesis for describing the current situation in Alberta, where partial fragmentation is creating genetic discontinuities. The areas where the curve has a steeper slope separate geographic regions that are candidates for management units.

Other research has identified that male bears move across Highways 3 and 1. Proctor et al. (2002) identified likely male mediated geneflow across Highway 3 in the Rocky Mountains. Subsequent DNA work has also demonstrated males are moving across this highway (and potentially a female; C. Apps pers. comm.). Radiotelemetry work has demonstrated that males are also moving across Highway 1 in the BNP area (Gibeau et al. 2002) Females have also been reported to cross Highway 1 naturally although very few survive in the long-term (M. Gibeau pers. comm.). Recent work has documented female grizzly bear use of crossing structures in BNP (T. Clevinger pers. comm). Radio telemetry work has also documented male movement across Highway 16 and rare short-term female crossings (Stenhouse and Munro 2001)

Most of the identified genetic discontinuities appear to be related to anthropogenic fractures that may be in the process of forming. For instance, the boundary that is evident in the Highway 1 area. shifts slightly with different models (K = 2 – 8), yet hovers around Highway 1. This behaviour is evidence for geneflow across the highway and with neighboring clusters. Often it is difficult to distinguish between current geneflow and remnant historic geneflow, particularly in larger populations, where genetic signals develop slowly. It does appear that while geneflow is likely occurring across the boundaries identified in the effort, it likely has been reduced from historic levels. Proctor (2003) found a relationship between the amount of human disturbance in fracture areas and the amount of perceived movement, of both sexes. Female movement was particularly limited as human disturbance increased. Given the level of fragmentation occurring in southern Alberta, it would be useful to know how many bears inhabit subdivided habitats.

The cluster between Highways 11 and 16 in the Jasper National Park area appears as a hybrid of individuals from other clusters until K = 9, suggesting that these bears are not a strong genetic grouping. Even at K = 9 this cluster is heavily influenced by bears with genetic similarities to the Northern Alberta cluster. This relationship is evident by the genetic distance (D_{LR} = 1.34), the lowest of the four (Fig. 4) and suggests that Highway 16 may only be a mild fracture. This genetic result is corroborated by radio telemetry data that shows while males (and rarely females) do cross Highway 16, crossings are not common (Stenhouse and Munro 2001). Clusters that appear later in this sequential analysis have less genetic structure (Rosenberg et al. 2002). This area may also be influenced by the history of translocations in Alberta. (see below). Our results show northern Alberta north of Highway 16 as unstructured. This is similar to the lack of structure that Paetkau et al. (1997) found across northern North America. Our results may also be influenced by small sample sizes in many of the local areas in northern Alberta. Increased sample sizes will likely be required to detect any further subdivision in northern Alberta if it exists.

Clustering results may be affected by the spatial pattern of sampling. For instance, clusters on each side of a sampling gap are expected to cluster as a result of the genetic differentiation that builds up slowly over geographic distance, but this does not reflect a real biological fracture between areas (Pritchard et al. 2000). One area that might fit this category is the area immediately north and south of Highway 11 in central Alberta.. However, examination of the clustering at lower values of K (Fig. 2) suggests that the structure between northern and southern Alberta is not solely based on geographic distance and sparse sampling alone. One might expect portions of Northern Alberta to fit this category, however this does not appear to be the case. Despite the small regional sample sizes, sampling gaps, and the lowest rate of linkage equilibrium failure, the north did not sub-divide into several clusters suggesting that the north may approach regional homogeneity. Larger sample sizes would be required to verify this notion.

The failure of program STRUCTURE to reveal any one "winning" set of clusters is likely a function of weak genetic structure in portions of the study area due to natural movements of bears, small samples sizes in the northern part of the province where a few samples were spread over a large area, and an historical translocation effort for problem bears. From 1974 through 2000 there were 230 recorded grizzly bear translocations within Alberta moved, on average, 246 km (Alberta Fish and Wildlife files).

The remarkable consistency of the genetic subdivisions as the number of assumed groups was incrementally increased (K = 1, 2, 3…etc.) suggests that the underlying structure is real and biologically based. This notion is also strengthened by the fact that the analysis included over 1000 individual bears, genotyped to 15 loci. Furthermore, the inclusion of B.C. bears provided a regional perspective and likely more accurate picture of genetic structuring in Alberta. For instance, the inclusion of B.C bears south of

Highway 1 was particularly informative as it substantially increased the southern Alberta sample size and demonstrated the genetic similarity across the continental divide (Fig 4a). This suggests that south of Highway 3 bears regularly move and mate across the continental divide. The divide in this region is less rugged than many areas to the north (B. McLellan pers. comm.) so the genetic similarity found across the divide south of Highway 3 may or may not extrapolate to areas where the divide is more rugged.

In the event that there are more genetic samplings within Alberta in the future, there are several areas that would benefit from larger sample sizes. Two smaller areas are north of Highway 1 in the Alberta Rocky Mountains and the area immediately north of Highway 11. Another is the area north of Highway 16 and this could extend as far as interest allows. In the near future a similar analysis is to be undertaken in northern B.C. with the use of hunter killed compulsory inspection samples, integrated with DNA survey samples throughout B.C. It will be interesting to look at genetic structure and fragmentation in the entire northern region including Alberta and B.C.

Conclusions

In conclusion, five genetic clusters of bears in Alberta were identified that were roughly bounded by the major east-west highways in central and southern Alberta. These sub-divisions in Alberta's grizzly bear population could be used to delineate biologically-based population management units. Managers will need to incorporate these results with jurisdictional, practical, and logistical considerations when contemplating final management unit boundaries. While it is difficult to distinguish natural from anthropogenic fragmentation, these results, and those of (Proctor (2003), suggest that the human environment is likely influencing the spatial dynamics of grizzly bears in Alberta. While the boundaries between sub-units do appear to be permeable, further population level work, such as abundance estimates for these units, would be advisable. Given the pattern that female movement may be limited through human dominated environments (Proctor 2003), future consideration should be given when appropriate and practical to management strategies that promote female connectivity across highways and associated settlement. Alberta's bears form the eastern periphery of the grizzly bear distribution in southern Canada, and as such require surveillance through time to insure persistence.

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Table 1. Summary of sample sizes from each resulting cluster, or potential griaaly bear Management Unit. SRS is Southern Rockies South south of Highway 3 to the US border. CRS is Central Rockies South between Highways 1 and 3, CRN is Central Rockies North between Highways 11 and 1, NRS is North Rockies South between Highways 16 and 11, and NAB is Northern Alberta, north of Highway 16. Our analysis included bears from British Columbia and results suggested that Alberta bears south of Highway 1, in the CRS and SRS, cluster genetically with bears from adjacent areas in B.C.

Population unit	**Total**	**AB**	**BC**
SRS	136	55	81
CRS	186	84	102
CRN	67	67	0
NRS	108	108	0
NAB	99	99	0
MU total	596	413	183
Other bears from BC	443		
Total bears in analysis	1039		

Figure 1. North American current and historic grizzly bear distribution and study area which includes Alberta and southeast B.C.

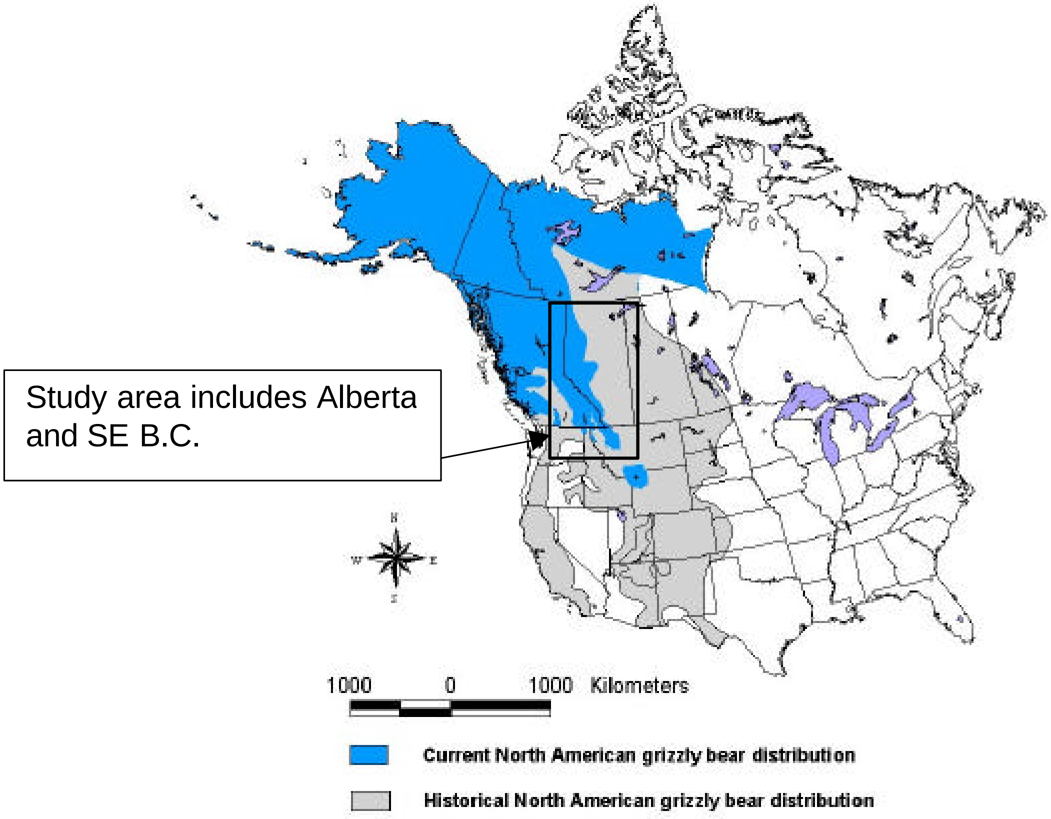


Figure 2a. STURCTURE derived clusters of grizzly bears assuming the number of groups, K, = 2.

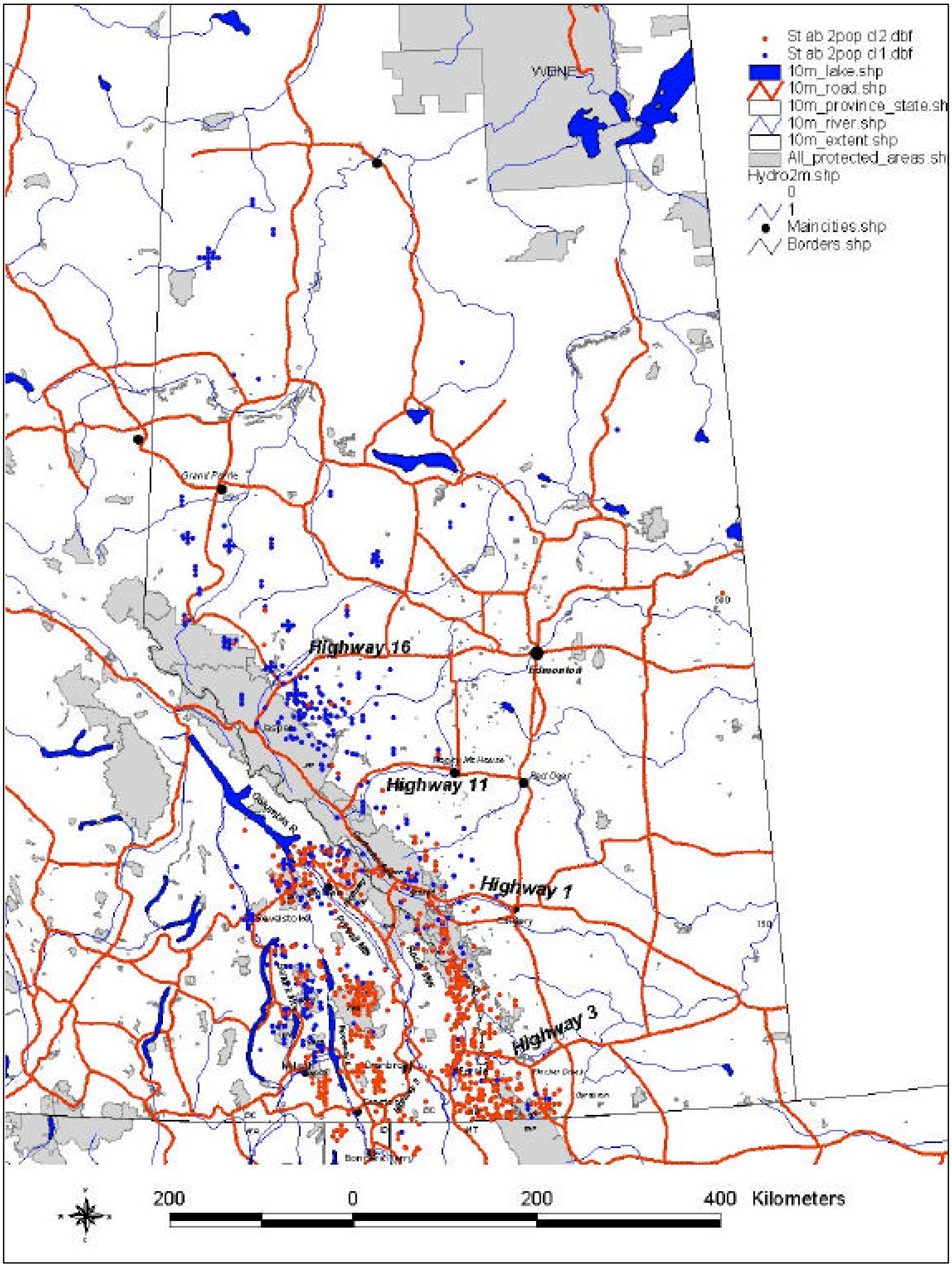


Figure 2b. STURCTURE derived clusters of grizzly bears assuming the number of groups, K, = 3.

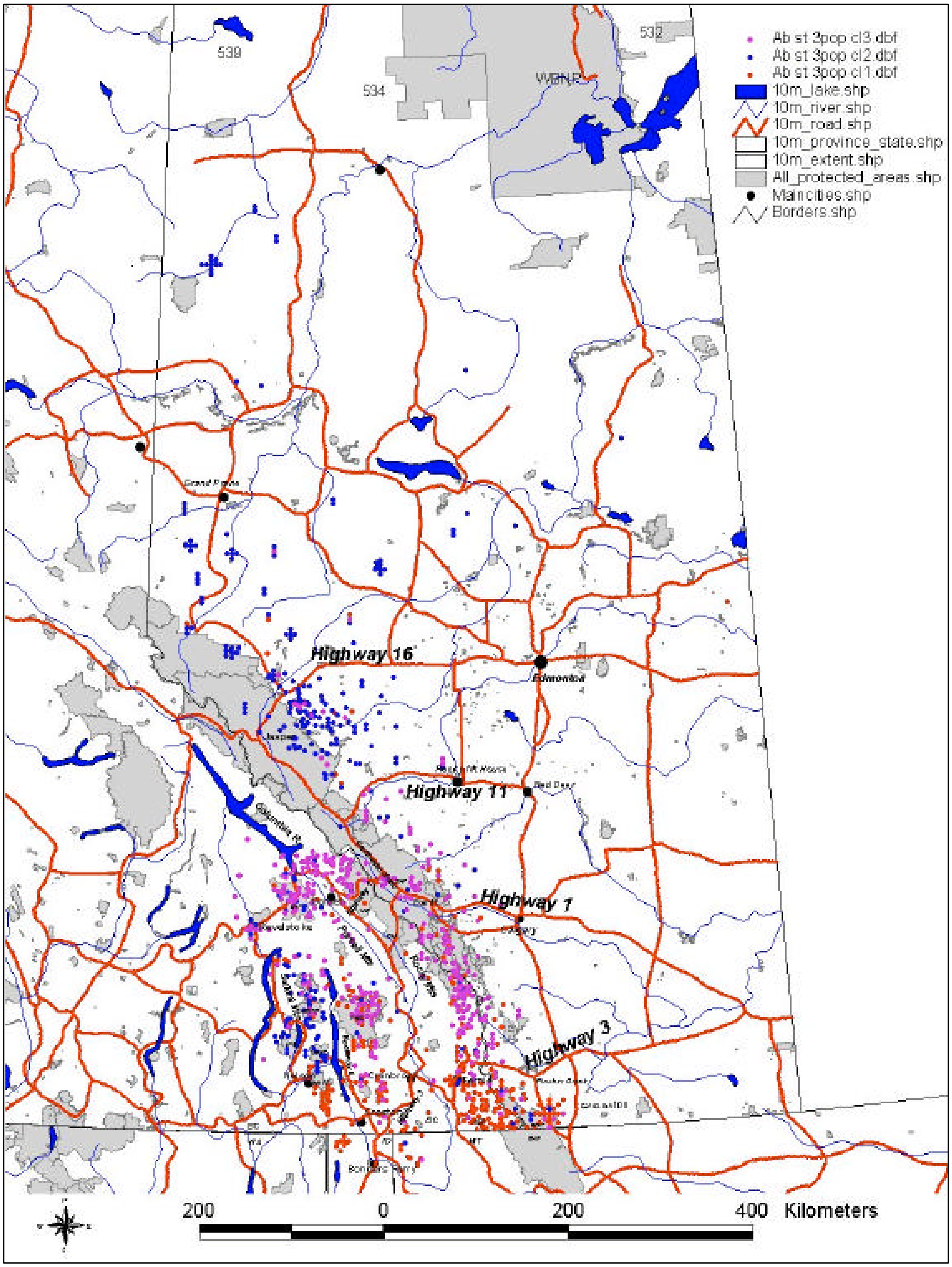


Figure 2c. STURCTURE derived clusters of grizzly bears assuming the number of groups, K, = 4.

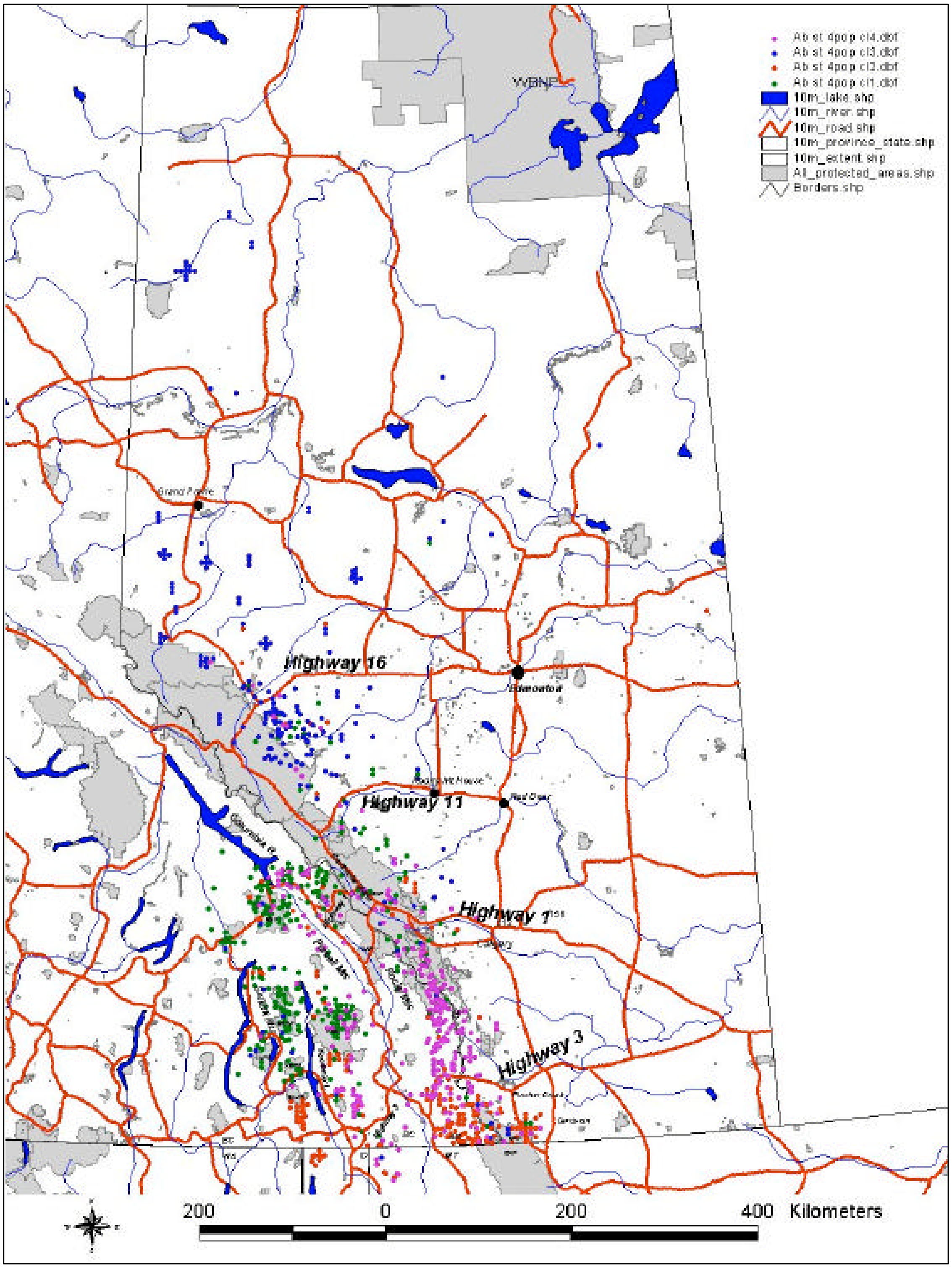


Figure 2d. STURCTURE derived clusters of grizzly bears assuming the number of groups, K, = 5.

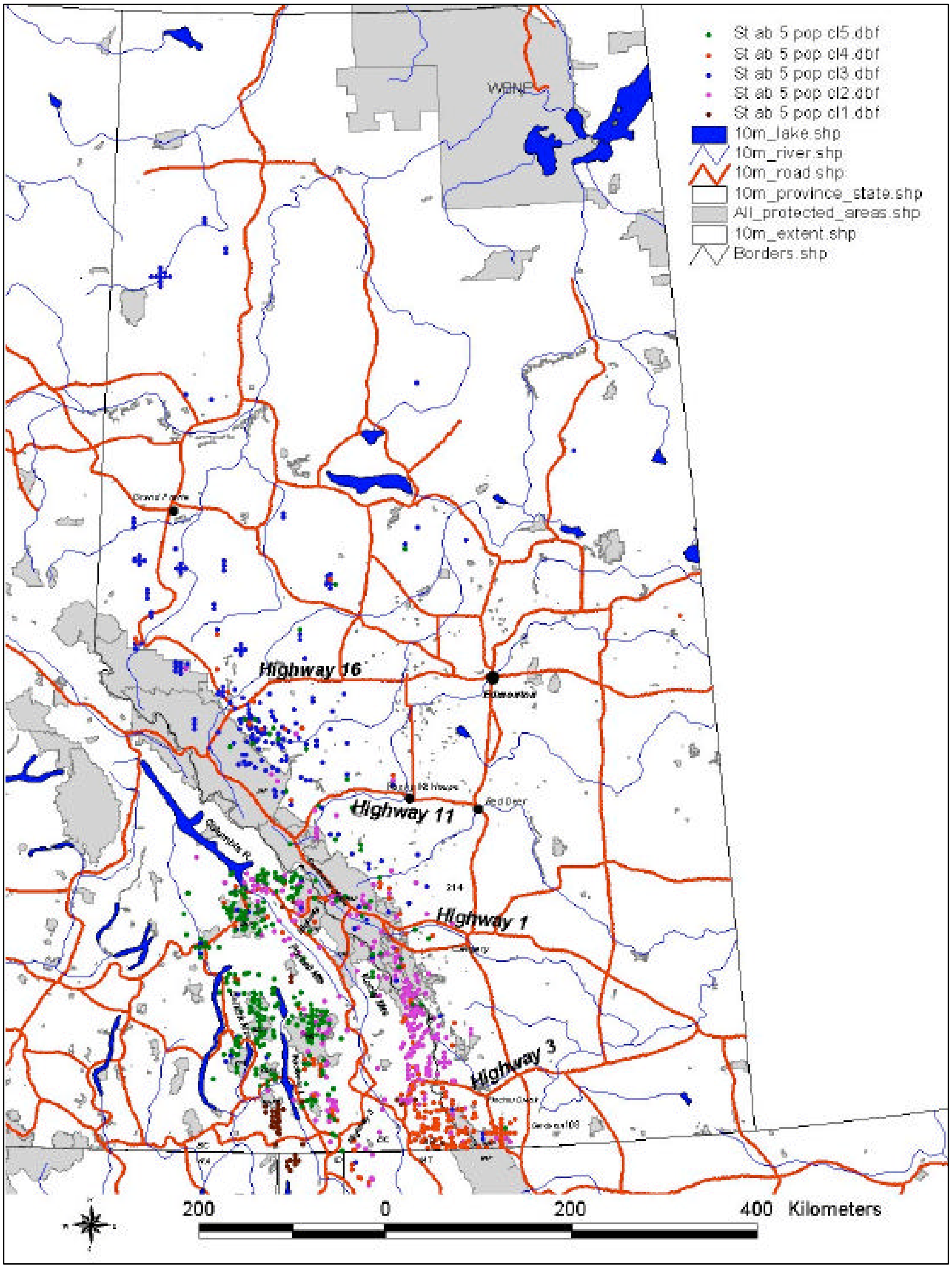


Figure 2e. STURCTURE derived clusters of grizzly bears assuming the number of groups, K, = 6.

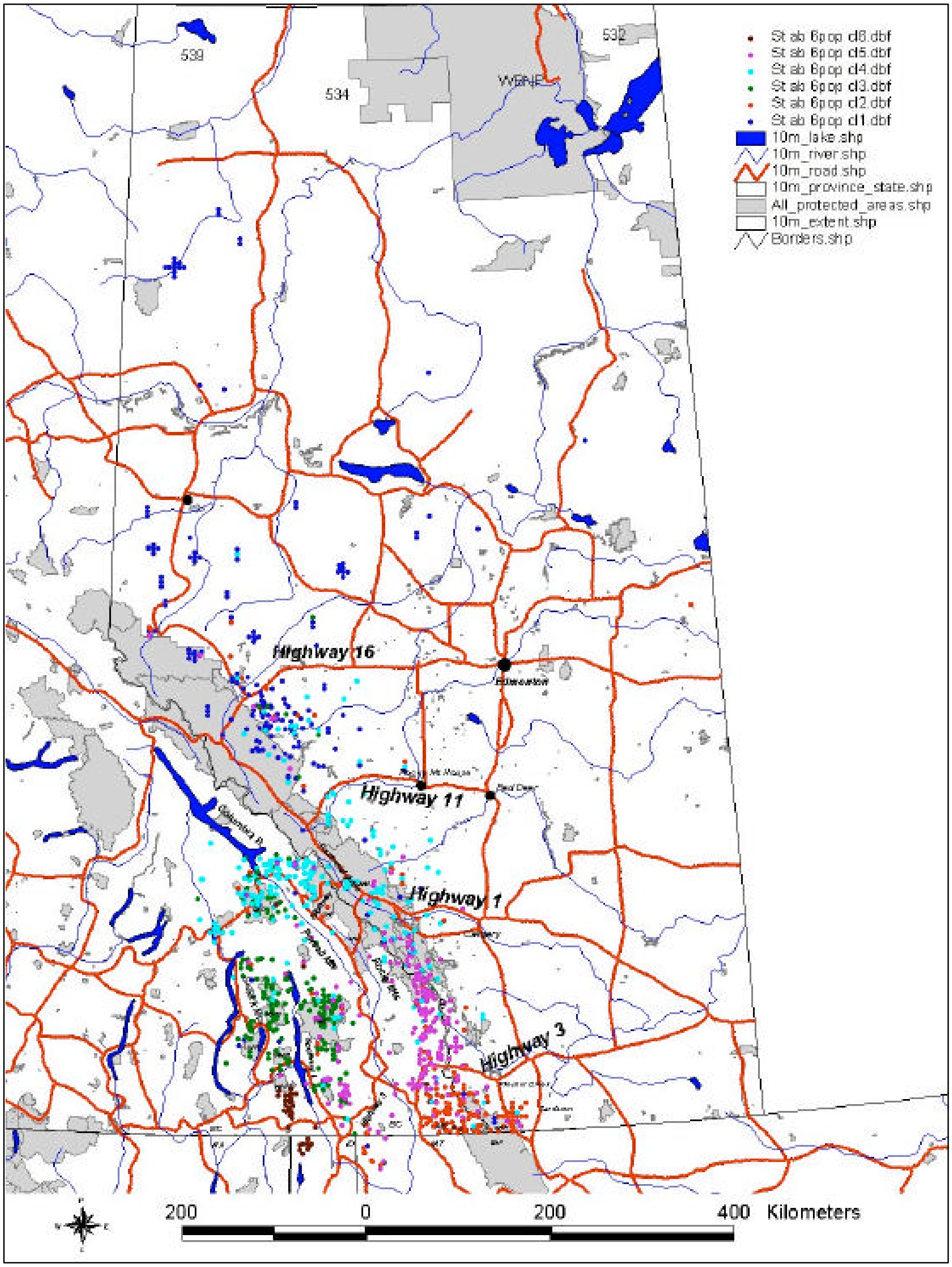


Figure 2f. STURCTURE derived clusters of grizzly bears assuming the number of groups, K, = 7.

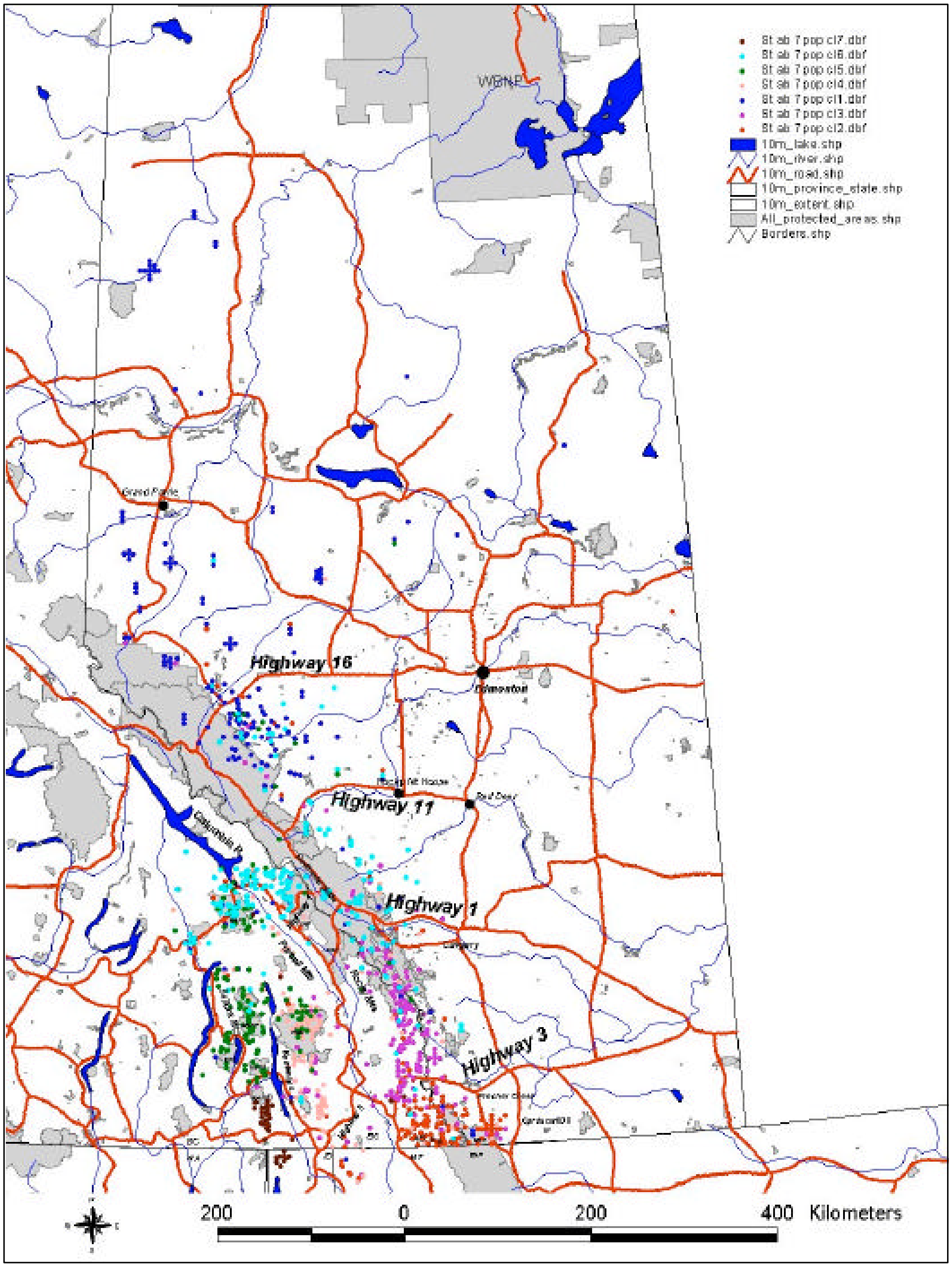


Figure 2g. STURCTURE derived clusters of grizzly bears assuming the number of groups, K, = 8.

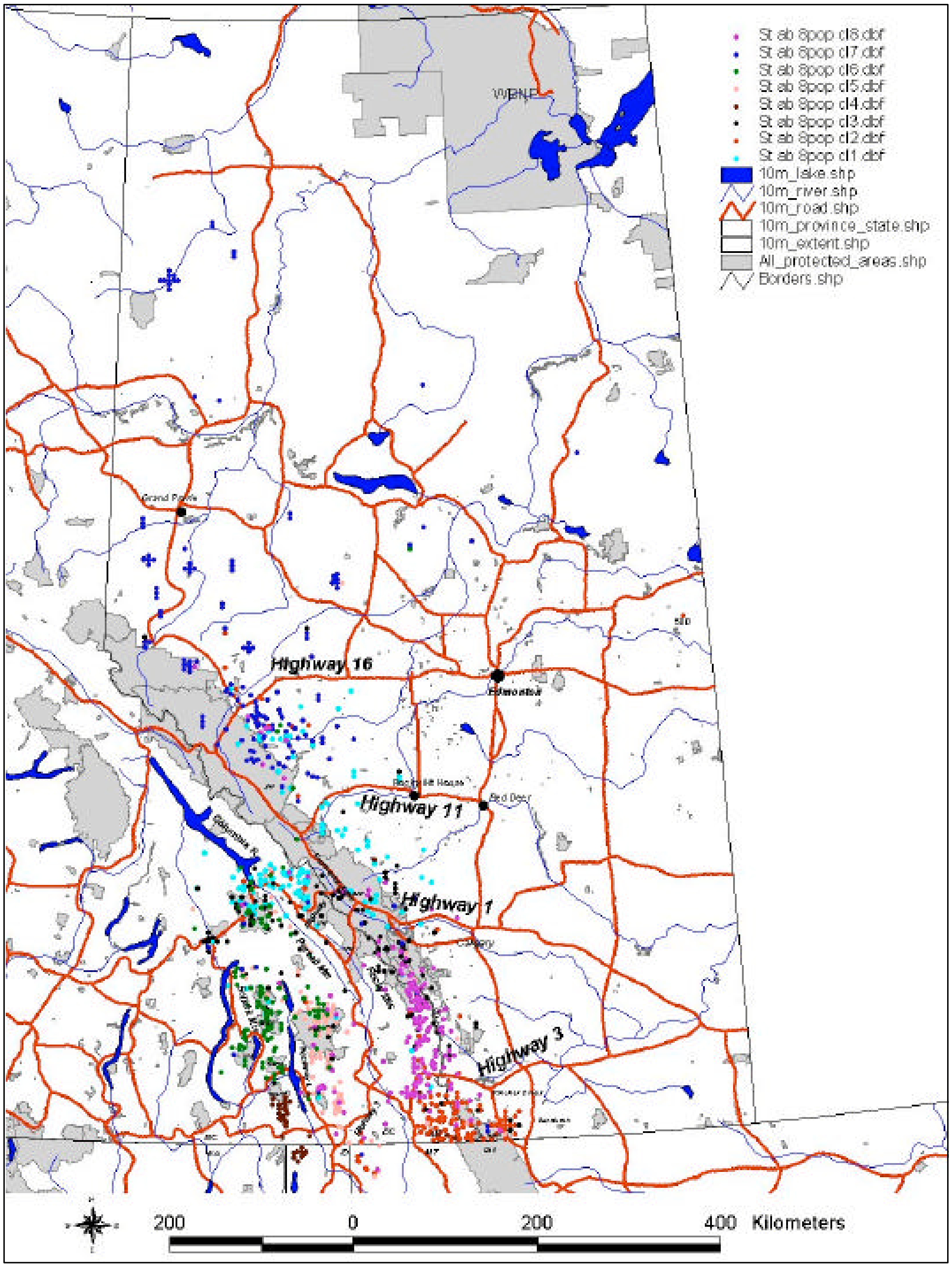


Figure 2h. STURCTURE derived clusters of grizzly bears assuming the number of groups, K, = 9.

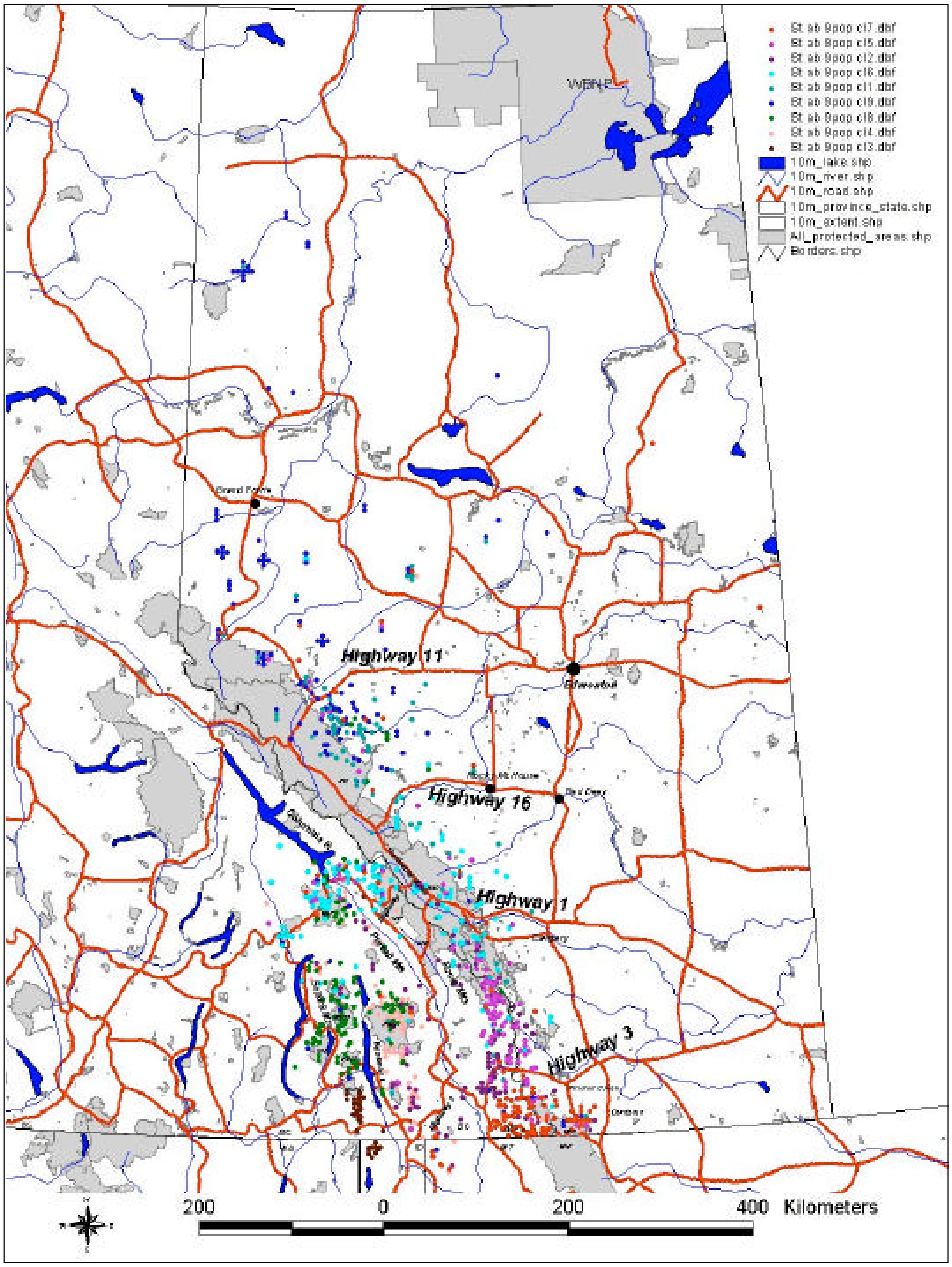
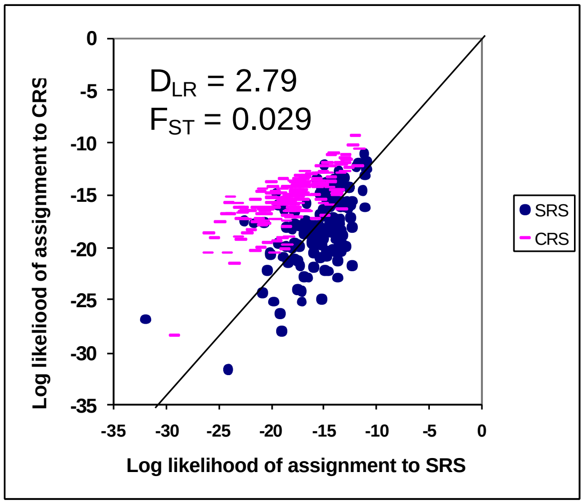
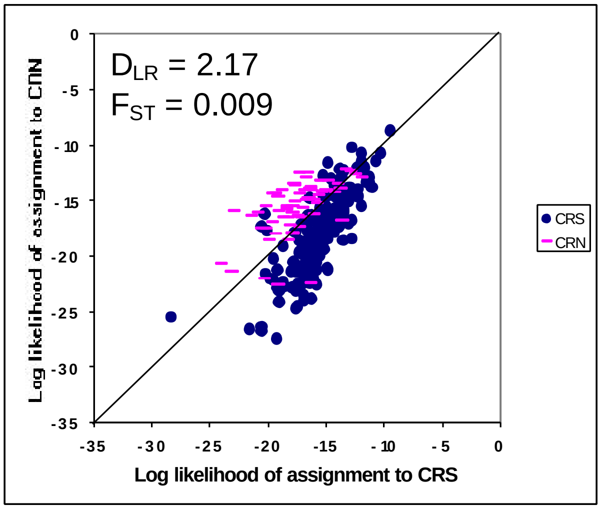


Figure 3. Assignment plots of grizzly bears in 5 adjacent clusters within Alberta. SRS is Southern Rocky South (south of Hwy 3), CRS is Central Rocky South between Hwys 3 and 1, CRN is Central Rocky North between Hwys 1 and 11, NRS North Rockies South between Hwys 11 and 16, and NAB is Northern Alberta north of Hwy 16. DLR is a genetic distance that depicts the average separation of the clusters based on an allele frequency-based assignment test.

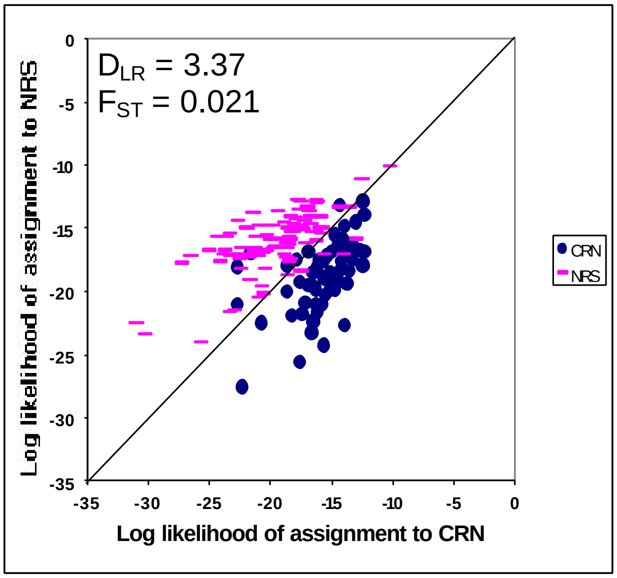
3a. SRS vs CRS across Hwy 3,



3b. CRS vs CRN across Hwy 1



3c. CRN vs NRS across Hwy 11



3d. NRS vs NAB across Hwy 16

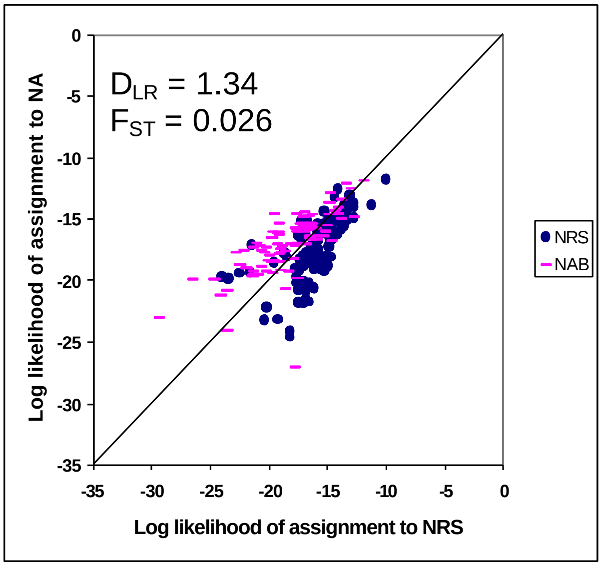
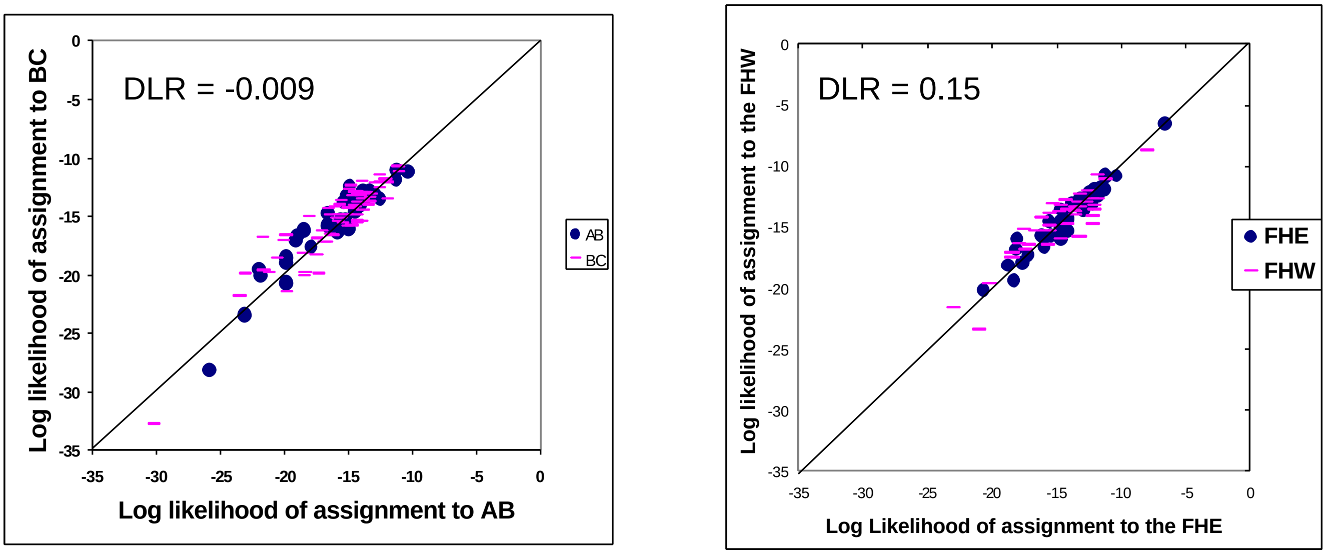


Figure 4. Assignment plots of several areas for contextual purposes. Plot 4a is the bears south of Highway 3 in the Rocky Mountains divided into those captured in Alberta on the east side of the continental divide (AB) and those captured in BC on the west of the continental divide (BC). Plot 4b are bear south of Highway 3 divided into those captures east (FHE) and west (FHW) of the Flathead River. Contrast these assignment plots with Figure 3a, the Southern Rocky South (SRS) bears versus the Central Rockies South (CRS) bears north of Highway 3.



4a. SRS bears across the Continental Divide.

4b. SRS bears across the Flathead River

4c. SS vs CS across BC Highway 3A

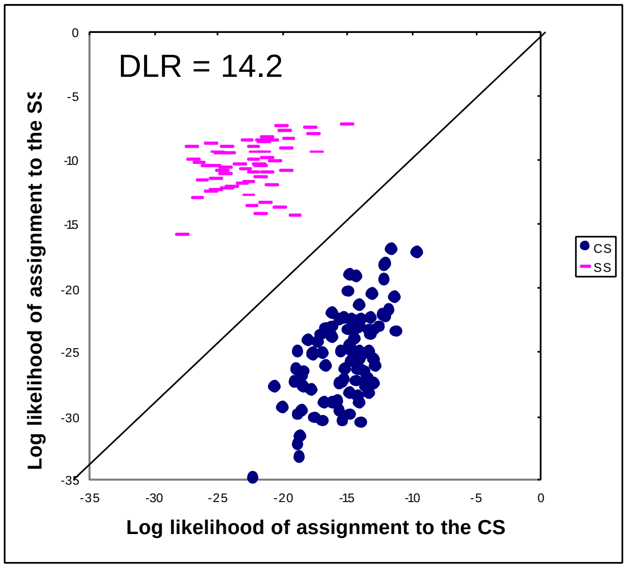


Figure 5. Conceptual illustration of genetic structure south to north in Alberta.
The dashed blue line represents the genetic structure associated with geographic distance (isolation by distance) without biological boundaries. The black double dashed line represents an abrupt genetic boundary, caused by more extensive fragmentation such as that occurring in the south Selkirk Mountains (Fig 4c). In between these extremes is a scenario reflected of the situation in Alberta (solid red line) where the underlying isolation-by-distance is punctuated by areas where partial genetic discontinuities occur resulting in these short steeper slopes (arrow markings).