3. DELINEATION OF BISON POPULATIONS IN WBNP.

The conservation and management of large mammals require a rigorous assessment of population units (Bethke et al. 1996). For example, the number of bison in WBNP declined during the latter part of the twentieth century, dropping in numbers from ≈ 10,000 animals in the late 1960s to ≈ 2,200 animals in 1999 (Carbyn et al. 1993, 1998; Wood Buffalo National Park unpublished data). This decline progressed at different rates throughout the park, with the numbers south of the Peace River declining much more drastically than elsewhere (Carbyn et al. 1993, 1998). There are various hypotheses to explain this decline, including wolf predation, disease (tuberculosis, brucellosis and anthrax), flooding, food limitation, and changes in flood frequency from hydroelectricity production, as well as "combination of factors" hypotheses (Carbyn et al. 1993, 1998). Examination of these hypotheses requires a clear understanding of the structure of bison populations within Wood Buffalo National Park.

Wells and Richmond (1995) defined a population as a group of individuals that are distinct from other groups in at least one of the following aspects: spatial, genetic, or demographic structure. Identification of discontinuity in space is required in order to identify genetic or demographic discontinuities (Wells and Richmond 1995). Population boundaries set arbitrarily can result in biased estimates of immigration and emigration rates (e.g., Figure 1 in Wells and Richmond 1995), which are critical factors determining the dynamics of local populations (e.g., Levins 1969; Pulliam 1988, 1996;

Hanski 1994). Moreover, most models of disease transmission assume random mixing of hosts within a population, and spatial variation in contact rates among individuals can lead to errors in estimating transmission potential of a given pathogen (Anderson and May 1985).

Spatially distinct groups of individuals may be demographically linked, hence forming a metapopulation (Wells and Richmond 1995). Conversely, a demographic discontinuity ensures that population numbers change primarily as function of births and deaths, and not immigration or emigration (Wells and Richmond 1995; Taylor and Lee 1995). Therefore, I use the term "population" to describe either distinct groups of individuals with spatial and demographic discontinuity from other groups, or spatially distinct groups of individuals with substantive exchange to other groups within a metapopulation (Wells and Richmond 1995).

The first criterion for defining a population is spatial discontinuity (Wells and Richmond 1995). Spatial discontinuities in animal distribution can be determined using cluster analysis (e.g., Romesburg 1984). Bethke et al. (1996) showed how cluster analysis of polar bear (*Ursus maritimus*) movements could be used to determine population membership, with the population boundaries set by the overall spatial distribution of polar bears within each population. Taylor et al. (2001) expanded this analysis to delineate polar bear population boundaries in the high Canadian Arctic. Further, McLoughlin (2000) used this method to describe barren-ground grizzly bear (*Ursus arctos*) population structure in the central Canadian Arctic. In the present study, I used cluster analysis of radio-telemetry data to delineate group boundaries for bison in WBNP. I also evaluated exchange rates among these groups of bison in order to evaluate the potential for demographic discontinuity. There are no *a priori* rules as to the degree of exchange that characterizes a metapopulation; therefore, I elected to present the results and interpret them qualitatively. I would define the spatial structure of bison as a metapopulation if evidence for exchange among populations can be demonstrated.

A specific objective of this chapter is to test whether the observed decline in bison numbers in the Pease-Athabasca Delta is the result of emigration of bison from this area to other areas of the park.

3.1 Methods

3.1.1 Monitoring of movements

Details of capture and handling are described in chapter 2. Capture sites were chosen so as to be representative of bison distribution in the Peace-Athabasca Delta, Hay Camp, and Nyarling River areas (Figure 2.1). Bison were relocated using a Cessna 180 fixed-wing airplane approximately every ten days during the spring and every three weeks the remainder of the year. I supplemented the present data by including data from a movement study conducted by Wood Buffalo National Park staff from September 1990 to September 1993 (Wood Buffalo National Park 1995). In the latter study, bison were darted from the ground with carfentanil citrate and xylazine hydrochloride. Eighty-nine radio-transmitters were deployed during the study, from which relocation data were collected from 68 bison. Captures were distributed in the Nyarling River, Hay Camp, Peace-Athabasca Delta, and Garden River areas of the park, as well northwest of the park in the Slave River Lowlands. Bison were relocated approximately every 15 days.

3.1.2 Cluster analysis

In this report I use the term "group" of bison to refer to the results of the cluster analysis. Bison can be grouped at increasingly smaller scales, ultimately to a group of two animals; however, I use the term group to define a number of animals in a relatively large geographical region of the park. Following Bethke et al. (1996) and Taylor et al. (2001), I used agglomerative hierarchical cluster analysis (UPGMA between-linkages method; SPSS 10.05 for Windows, SPSS Inc., Chicago, Illinois, USA) to group bison based on their median, seasonal locations. In this manuscript the term "population" refers to groups of bison that are spatially distinct (Wells and Richmond 1995).

The latitude/longitude coordinates for each bison location were transformed to a flat x, y grid (following Bethke et al. 1996). The origin of this grid was centred at 58° N and 111° W and increased north and west in one-kilometre increments. Winter (7 Nov - 4 May) was defined by the median date of ice freeze-up and break-up reported in Carbyn et al. (1993: p. 60) for the years 1953-1981. The other seasons were defined by modification of those proposed by Komers et al. (1992): spring, 5 May - 30 June; summer, 1 July - 31 August; and autumn, 1 September - 6 November.

I determined the number of groups present in each season by plotting the agglomeration coefficients from the UPGMA cluster analysis for each classification (Taylor et al. 2001). Agglomeration coefficients increase in value as increasingly dissimilar groups are merged. The number of distinct groups was indicated by an abrupt increase in agglomeration coefficients (see Figure 3.1; Taylor et al. 2001). In some cases, the number of groups indicated by the agglomeration coefficients was biologically unreasonable as a result of creation of small groups of bison (<5 bison). In these cases, the bison were arbitrarily designated as part of the nearest group. These small groups were always peripheral to, and not between, two major groups and so the arbitrary designation did not affect the overall classification. I determined the spatial extent of groups by plotting all locations of each bison within each season for each group, and then calculating the 95% fixed kernel utilization distribution contours (ArcView, Version 3.1, ESRI, Redlands, CA; Hooge and Eichenlaub 1997). I assumed that a spatial discontinuity existed for two groups if the 95% utilization contours did not overlap within a season. I determined the overall spatial extent of groups by overlaying the seasonal extents for the entire study period. This composite group range represents the area used by bison in each group over the study. I determined the area used by bison in the north-eastern and south-western areas of the park using the same process based on data from the WBNP movement study (Wood Buffalo National Park 1995).

3.1.3 Exchange rates

I determined the exchange rates of bison among different groups. I defined an "exchange" as a movement from one group's 95% utilization distribution to another group's 95% utilization distribution. A bison was considered "resident" in a group if it was located within that group for at least 50% of the surveys within a season. Exchange rate was calculated as the number of exchanges divided by the number of residents for a given season.

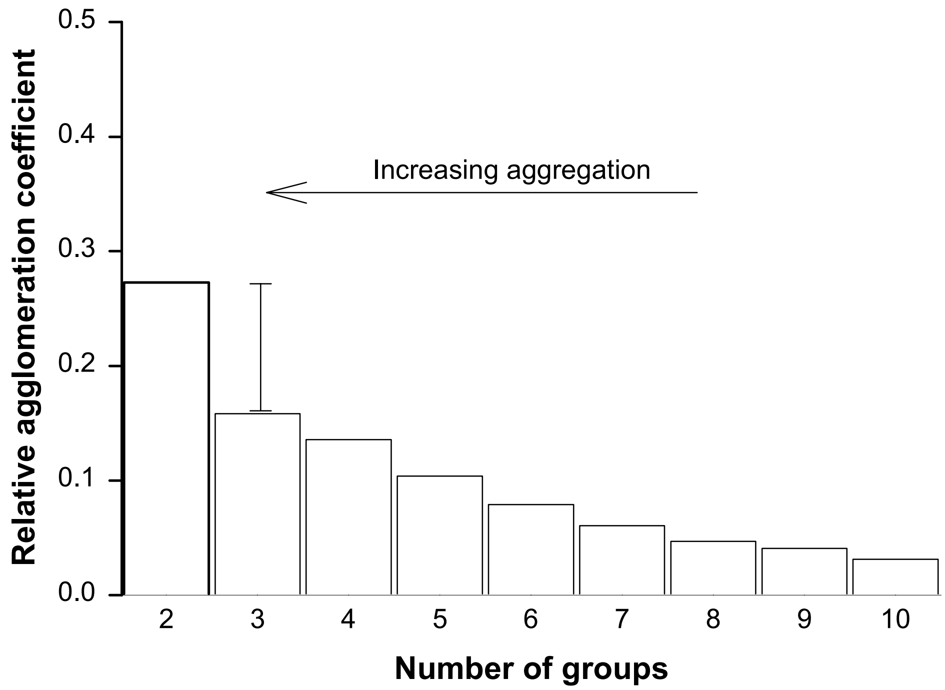

Figure 3.1. Example of how to determine the number of clusters present by the relative agglomeration coefficient. The agglomeration coefficient increases as dissimilar groups are increasingly aggregated. A large change in agglomeration coefficient indicates that two very different groups have been aggregated. In this example, 3 groups are justified by the data.

I supplemented these movement data with data from WBNP bison total count surveys (1980-1999) to determine if there is a significant trend in movement of bison from the Peace-Athabasca Delta to the Hay Camp area of the park. I used the composite group range to classify *a posteriori* bison locations recorded on the total count surveys into populations. I then compared annual changes in absolute numbers of bison between the Peace-Athabasca Delta and Hay Camp area using Pearson product-moment coefficient (Sokal and Rohlf 1995: 559-566). If there is a trend of emigration from the Peace-Athabasca Delta to the Hay Camp, there will be a significant negative correlation between absolute changes in numbers.

3.2 Results

3.2.1 Cluster analysis and population delineation

I deployed 80, 75, and 72 radio-collars on bison in 1997, 1998, and 1999, respectively. The agglomeration coefficients indicated group structure at a minimum of two or three groups of bison (Figure 3.2). The two-group structures indicated that bison in the Nyarling River area were very distinct from bison in the Peace-Athabasca Delta and Hay Camp area. However, three-group structures revealed the distinction among the Nyarling River, Peace-Athabasca Delta and Hay Camp areas (Figure 3.3). Therefore I decided to adopt a three-group structure for data collected in 1997-2000. Hereafter, I refer to these groups as the Nyarling River (north-west), Hay Camp (east-central) and Delta (south-east) bison groups.

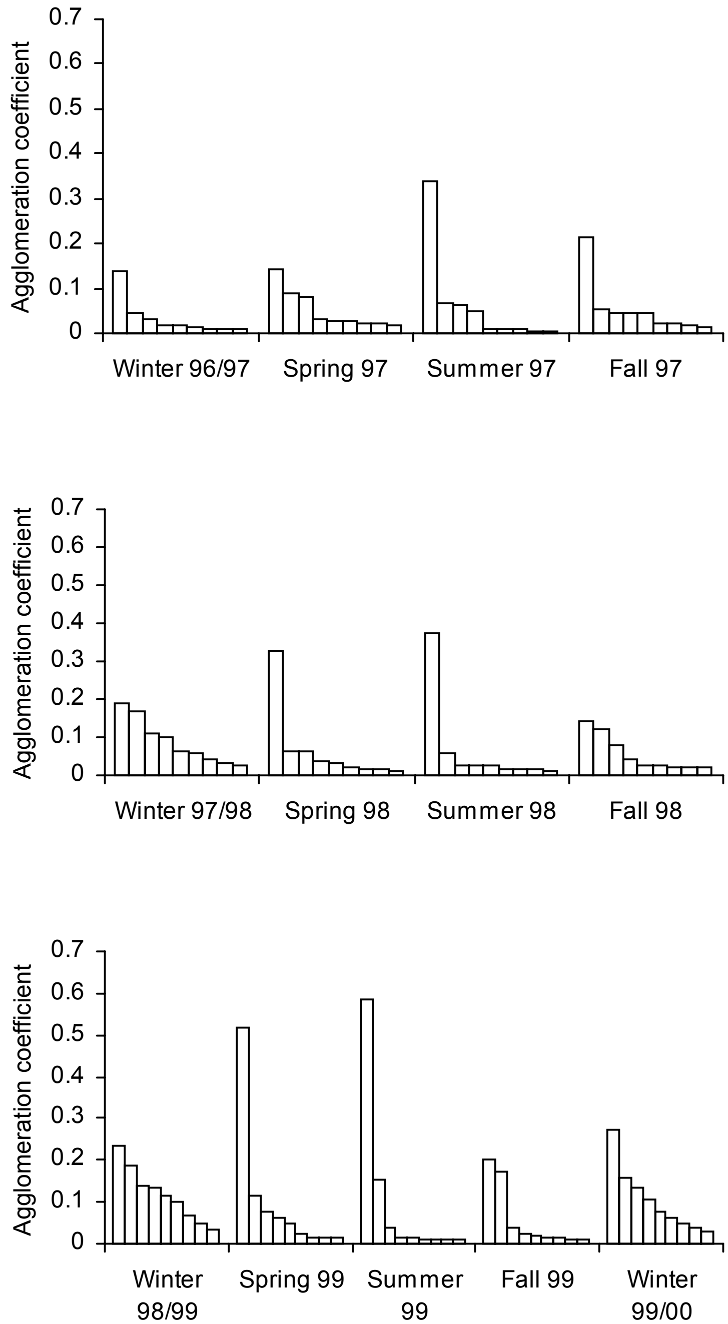

Figure 3.2 Relative agglomeration coefficients for the cluster analysis of bison movements (1997-2000). Note the coefficients have been rescaled so that the agglomeration coefficient for the one group solution is one (not shown).

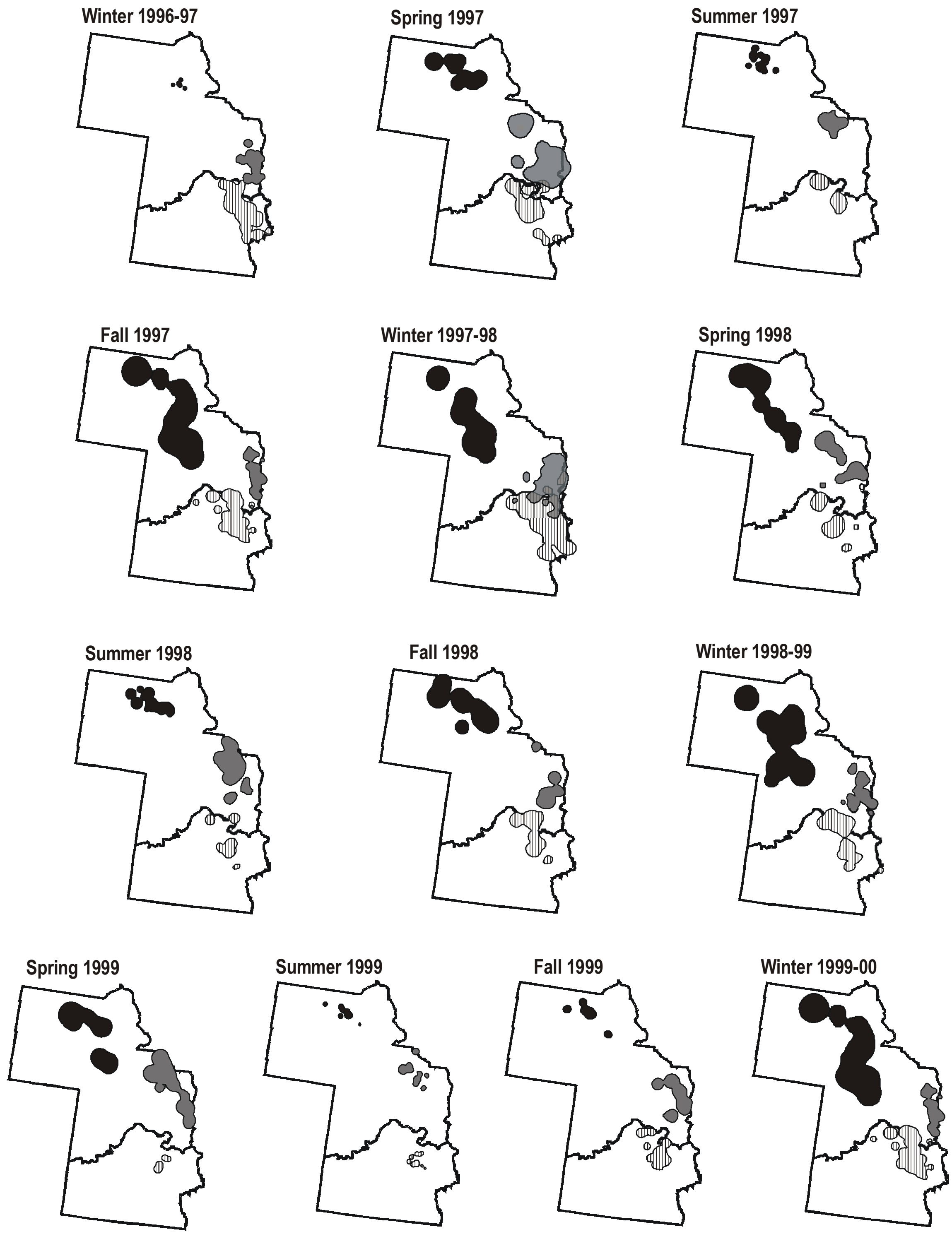

Figure 3.3 95% fixed kernel utilization distribution contours for bison locations within each season for bison populations, 1997-2000.

The 95% utilization distribution for each of these three groups indicated spatial discontinuity among the groups for most seasons (Figure 3.3). The 95% utilization distributions for the Hay Camp and Delta groups overlapped marginally in the spring of 1997 and winter of 1997-98 (Figure 3.3). There was a major flood in the spring of 1997 in the Peace-Athabasca Delta. High waters for the next 12 months resulted in a displacement of bison to the north, resulting in some range overlap. The overlap did not continue through the rest of the study (Figure 3.3). Therefore, I concluded that there was spatial discontinuity among the three groups. Figure 3.4 demonstrates the maximum spatial extent of each of the three groups, which is a composite range for each bison group for the duration of the study.

I used telemetry data from the WBNP movement study (Wood Buffalo National Park 1995) to describe group boundaries for the north-east and south-west corners of WBNP. Radio-collars were not deployed in all areas of the park until winter 1990-91. After this season, the cluster analysis revealed a seasonal group structure of 4-7 groups throughout the park (Figure 3.5). However, the cluster analysis consistently indicated that bison in the south-west and north-east corners were separate from adjacent groups (Figure 3.6). Hereafter, I refer to these as Little Buffalo (north-east) and Garden River (south-west) groups. In combination with the present data, cluster analysis suggested that in all, there are five distinct groups of bison in WBNP.

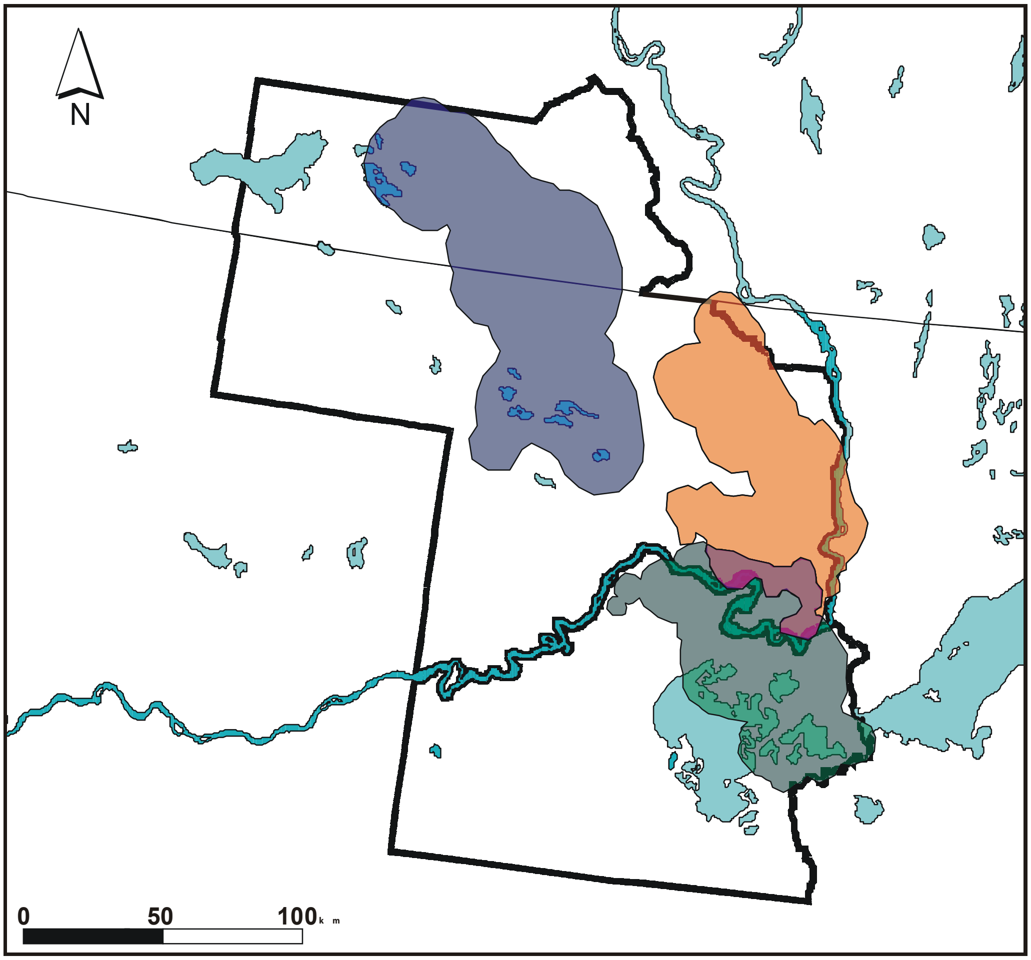

Figure 3.4. Spatial extent of the Delta (south), Hay Camp (central) and Nyarling River (north-west) bison populations in Wood Buffalo National Park, 1997-2000.

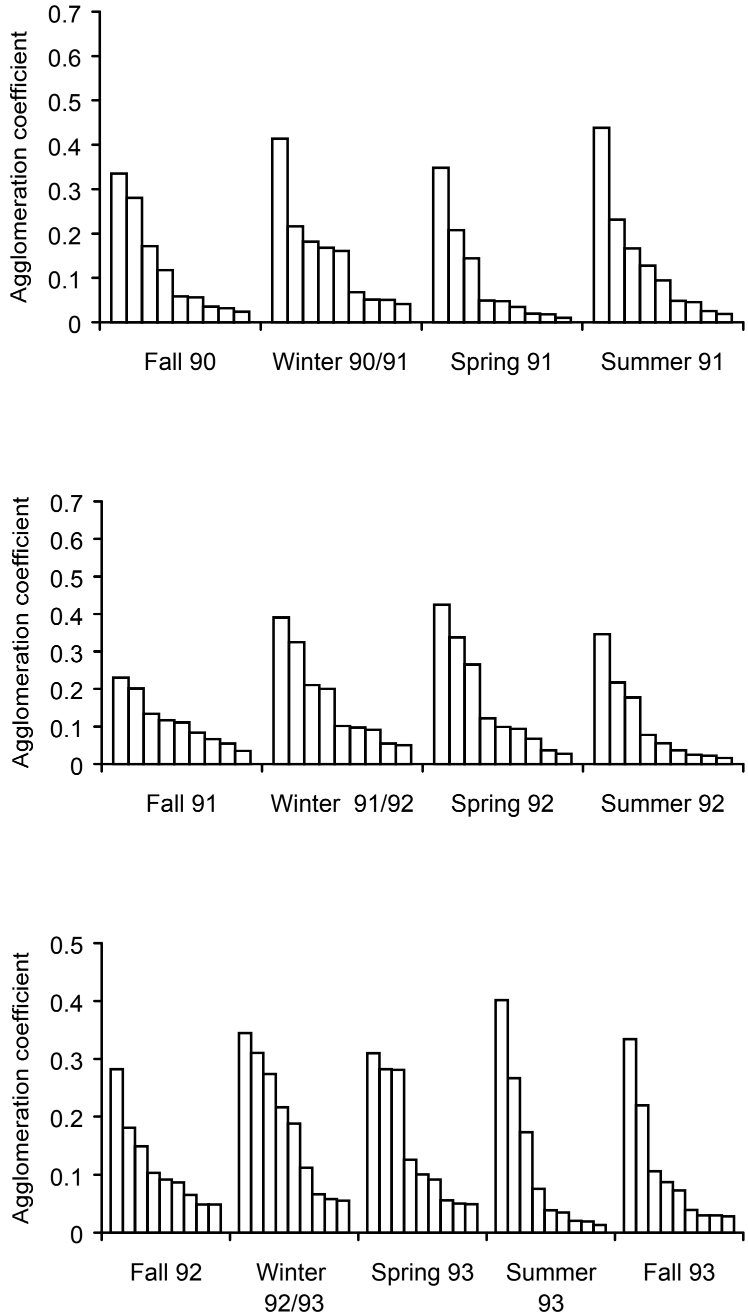

Figure 3.5 Relative agglomeration coefficients for the cluster analysis of movement from the WBNP (1995) movement study. Note the coefficients have been rescaled so that the agglomeration coefficient for the one group solution is one (not shown).

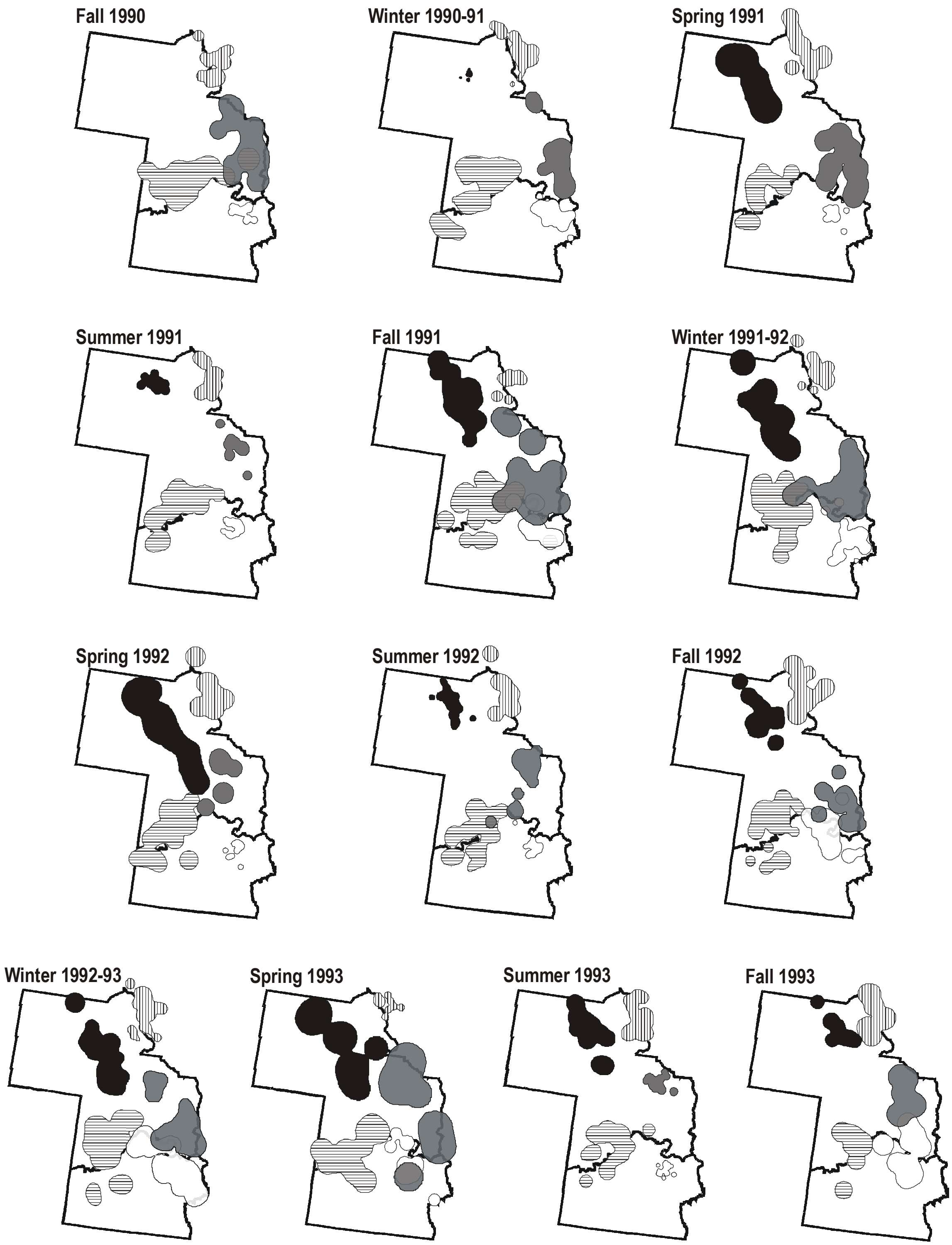

Figure 3.6. 95% fixed kernel utilization distribution contours for bison locations within each season for bison populations, 1990-1993.

3.2.2 Exchange rates

I determined the proportion of bison in a group that dispersed to another group during each season. There were no radio-collared bison that moved from the Nyarling River group to either of the Hay Camp or Delta groups during ~ 60 bison-years of monitoring. Therefore data presented below refer to dispersal movements between the Delta and Hay Camp groups. Further, I excluded from the analysis three unusual dispersals of bison as I was unable to determine the exact season in which the movement occurred. The first of these was a four-year old male that was collared near Baril Lake in the Peace-Athabasca Delta in February 1997. I lost track of it in July 1997, and relocated it on a flight over the south-west corner of the park in March 1999 (Figure 3.7). The collar was found on a snowmobile trail just outside of the park, and other evidence suggested that a hunter had shot the bison. The second unusual movement was that of a 2-year old female collared near Murdoch Creek in the Hay Camp region in March 1997. I lost track of this bison in July 1998 and she was relocated alive in February 1999 near Robertson Lake in the Nyarling River region of the park (Figure 3.8). The third unusual movement of bison was that of another four-year old male that was collared west of Hay Camp in March 1999. He was tracked until late August 1999, at which point I lost track of it. I found it in February of 1999 in the Slave River Lowlands north east of WBNP (Figure 3.9).

There was no movement of bison among groups in late winter 1997 (March 1 - May 5). The largest rate of movement from one group to another was in spring 1997, when 22% (8/37) of the radio-collared bison in the Delta group relocated to the Hay

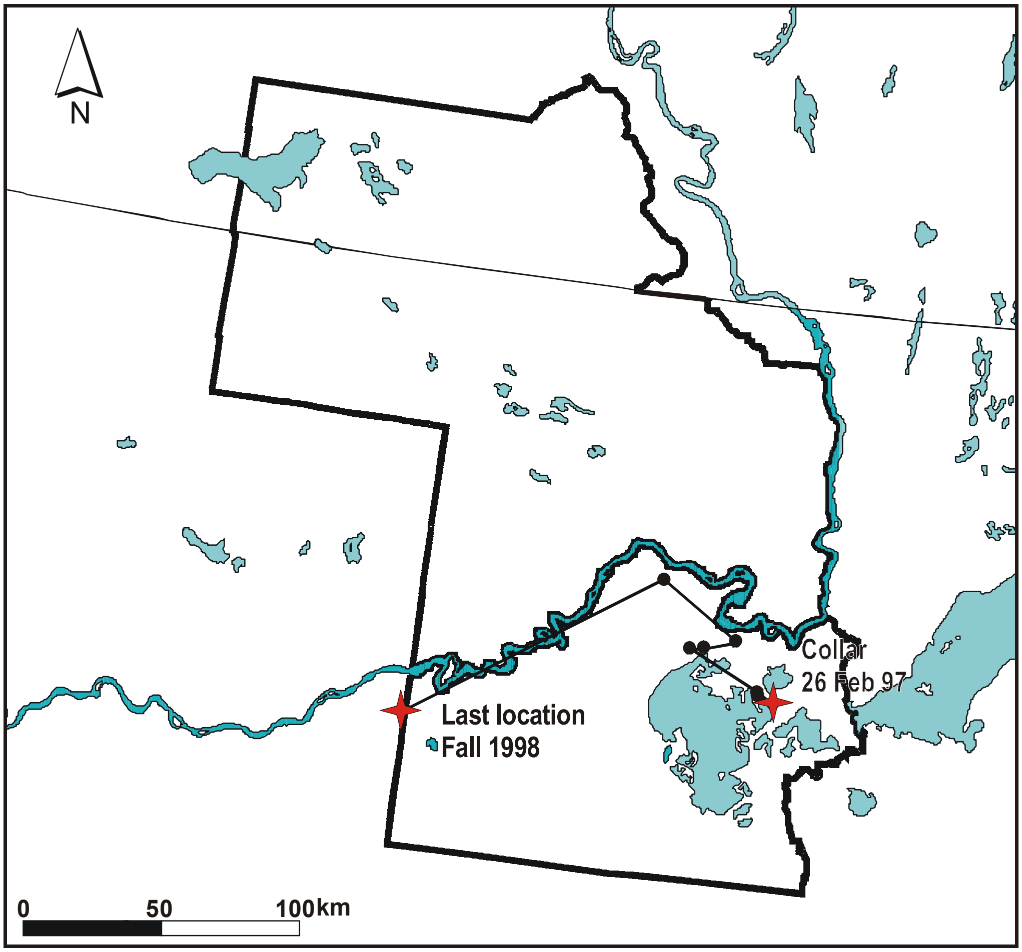

Figure 3.7. Movement of bison 97017 (4 year old male, tuberculosis positive and brucellosis negative).

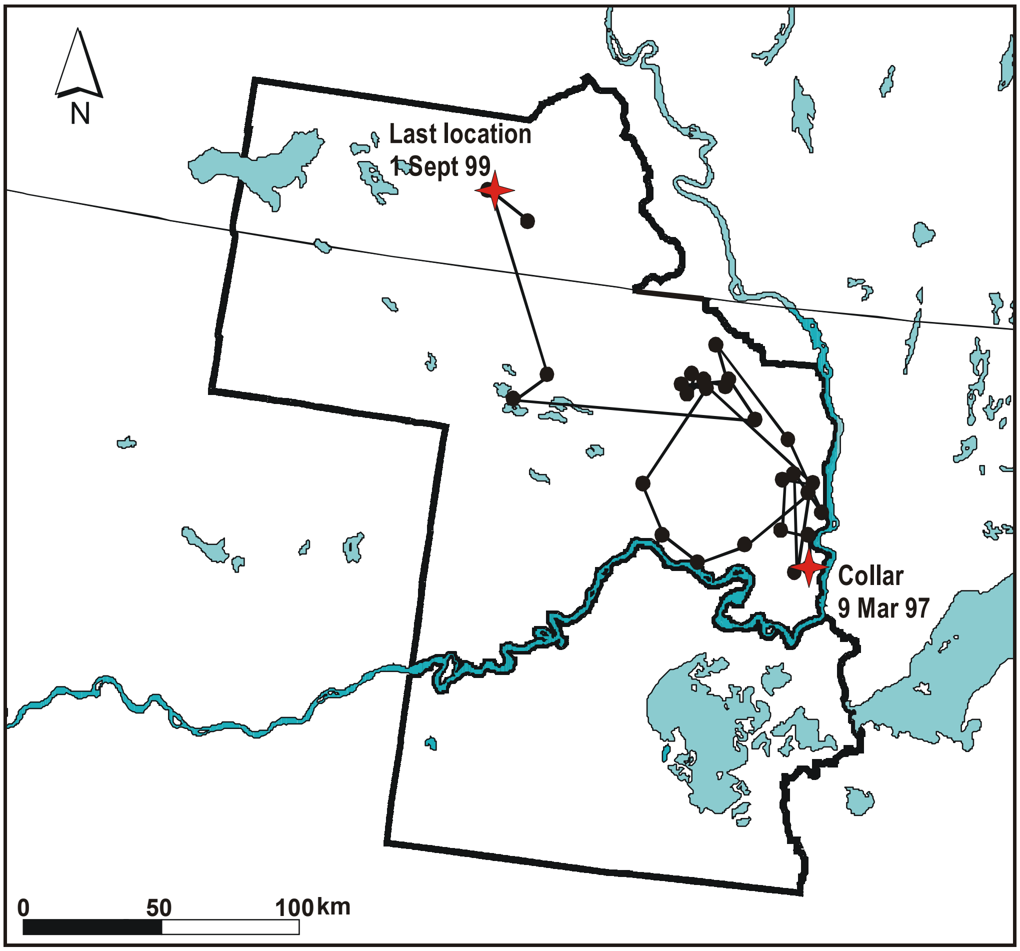

Figure 3.8. Movement of bison 97095 (2 year old female, tuberculosis positive and brucellosis positive).

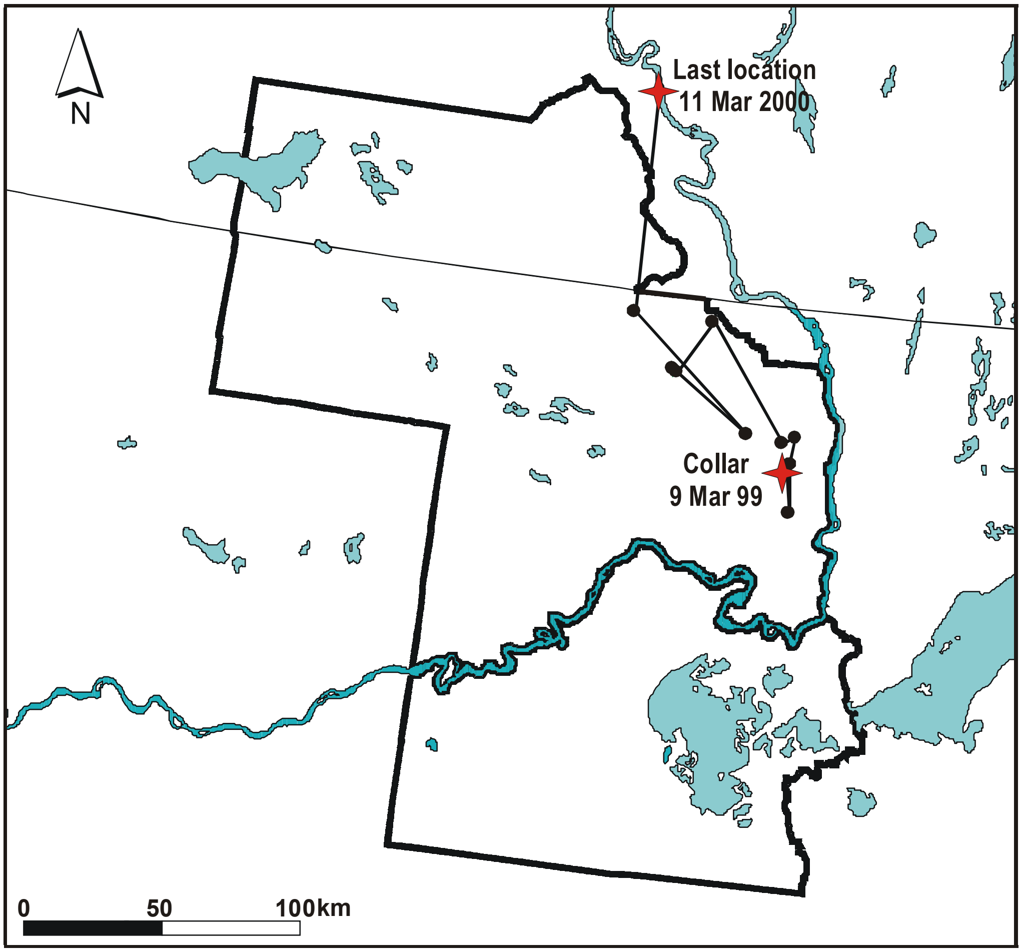

Figure 3.9. Movement of bison 99100 (4 year old male, tuberculosis negative and brucellosis positive).

Camp group (Figure 3.10). This shift coincided with a major flood in the Peace-Athabasca Delta. The following summer, 14% (4/28) of the radio-collared bison in the Hay Camp group moved to the Delta group (Figure 3.10). During the remainder of that year exchange rates from one group to another remained fairly constant at ~5% per season. In 1998/99, movement rates varied from 0 to 13% (Figure 3.11). In 1999/00, there was little movement of bison among the Hay Camp and Delta groups, where only 3% of the radio-collared bison in the Delta group moved to the Hay Camp group in spring, followed by 3% of radio-collared bison in the Hay Camp group moving to the Delta group in the summer and autumn seasons (Figure 3.12). No bison changed groups in the winter of 1999/00. There was no significant relationship between absolute change in bison numbers in the Peace-Athabasca Delta and Hay Camp areas ($r = -0.21$, $p = 0.42$, $df = 17$).

3.3 Discussion

These movement data have implications for managing risk of transmission of tuberculosis and brucellosis to disease-free bison populations in the vicinity of WBNP. I observed movements of two bulls among 14 radio-collared male bison in the 3 to 6 year age class. This is consistent with Larter and Gates (1994), who found in the Mackenzie Bison Sanctuary, NT, that young adult and mature males with no local access to females during the rut had larger home ranges and showed long distance movements to locations with females. Each of these bulls exhibited evidence of infection by bovine diseases (Figures 3.7 and 3.9). A risk assessment conducted by the Canadian Food Inspection Agency concluded that the upper 95% confidence limits for annual probabilities of

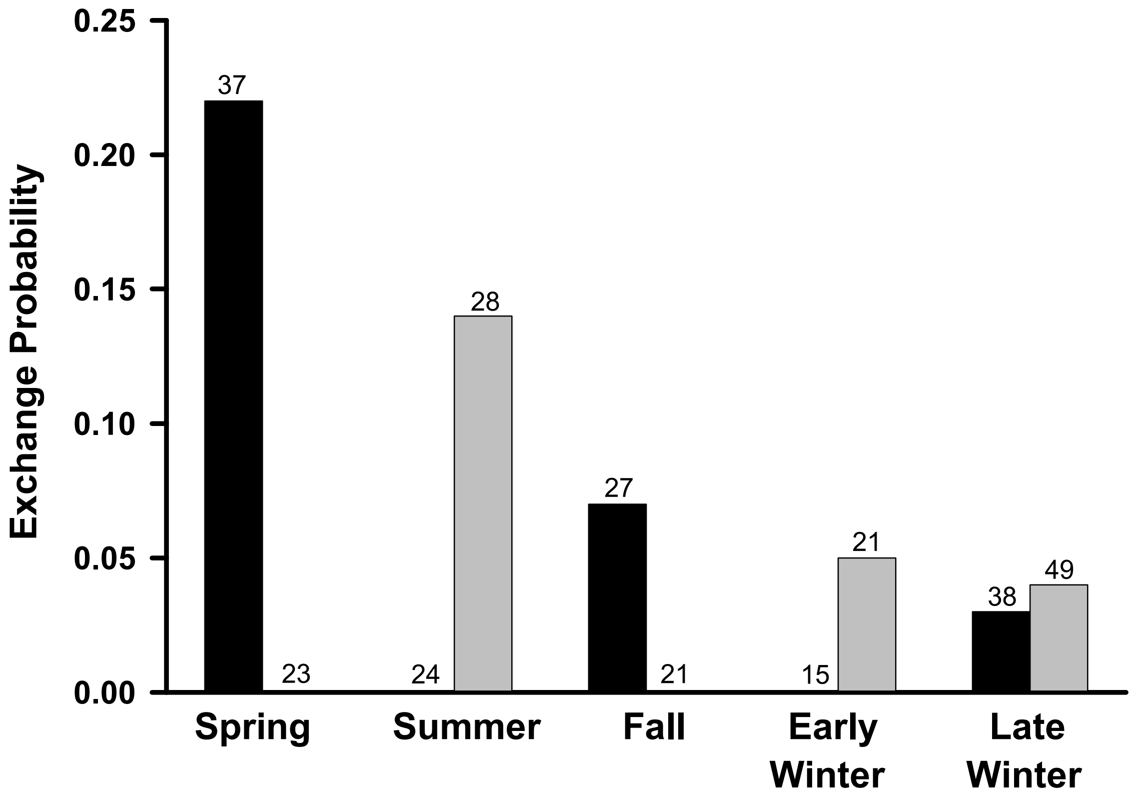

Figure 3.10. Rates of exchange from the Delta to Hay Camp population (dark bar) and Hay Camp to Delta population (shaded bar), 1997-98. Sample size is indicated at the top of each bar.

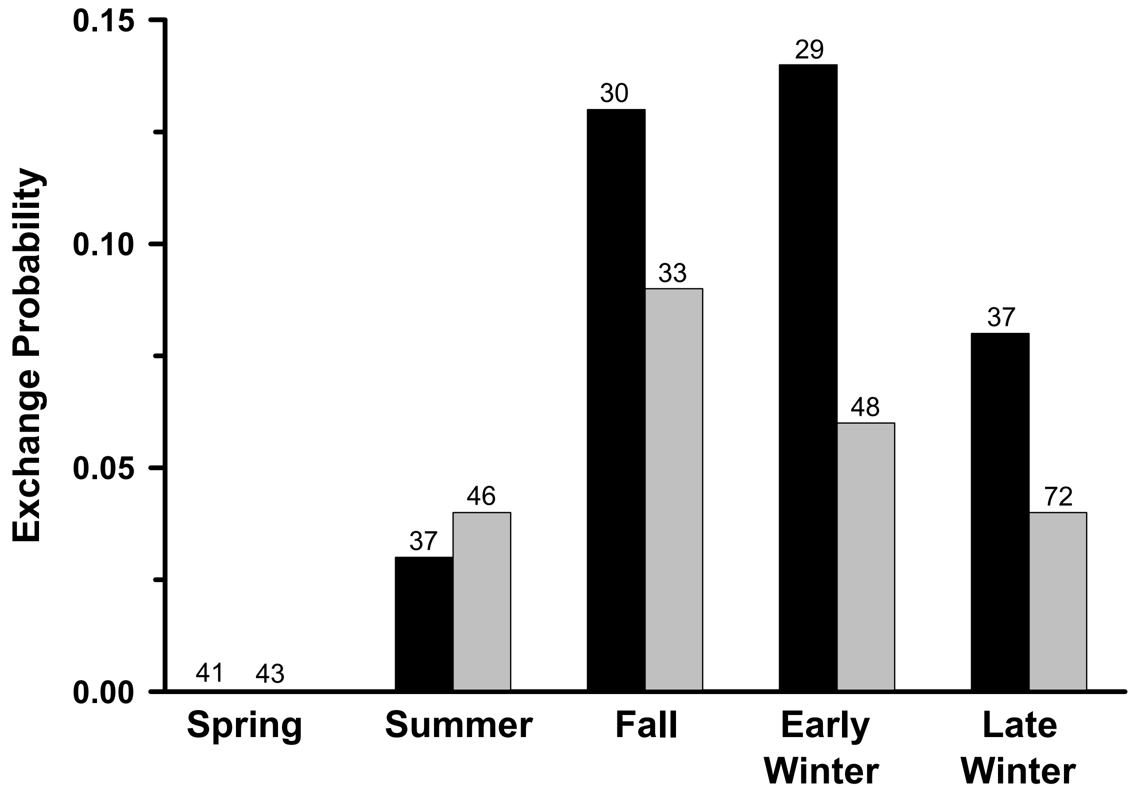

Figure 3.11. Rates of exchange from the Delta to Hay Camp population (dark bar) and Hay Camp to Delta population (shaded bar), 1998-99. Sample size is indicated at the top of each bar.

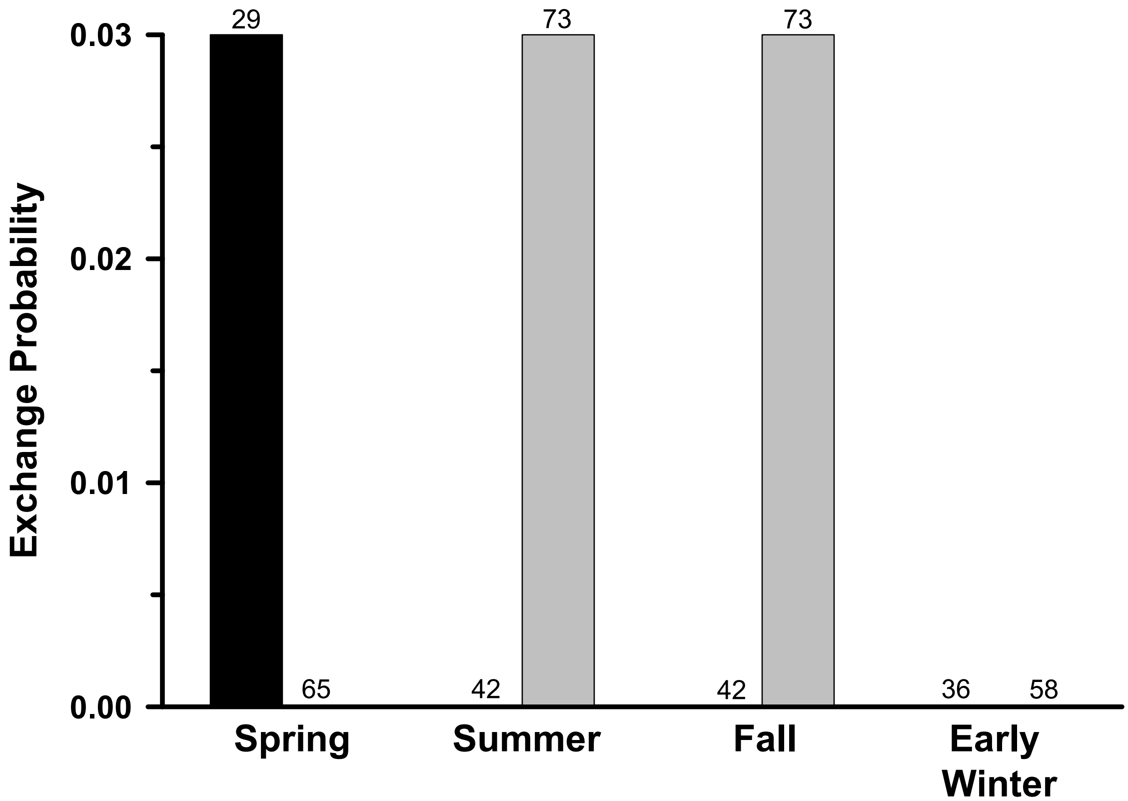

Figure 3.12. Rates of exchange from the Delta to Hay Camp population (dark bar) and Hay Camp to Delta population (shaded bar), 1999-2000. Sample size is indicated at the top of each bar.

introducing tuberculosis and brucellosis to disease-free bison populations were 0.12 and 0.16, respectively (APFRAN 1998). This study was based in part on radio-telemetry data from Wood Buffalo National Park (1995). In that study, park staff monitored movements of only one male <7 years of age; as a result, the risk assessment may underestimate the overall degree of long distance movements of bison. Furthermore, males with home ranges at the periphery of the population were likely under-represented in the sample; these males show long distance movements to associate with females part of the year (see Larter et al. 2001). Bison bulls are among the first to disperse during range expansion, and then are followed by mixed-sex groups of bison (Gates and Larter 1990; Larter and Gates 1994). Further, bull bison often associate in small groups (D.O. Joly and F. Messier, unpublished data; Komers et al. 1992) and so may escape notice if they leave the WBNP boundaries. I have no movement data for bulls in the 3-6 year age class in the Nyarling River population and so cannot assess the risk of movement from this population to the disease-free bison population in the Mackenzie Bison Sanctuary.

Cluster analysis of radio-telemetry data from this study and the previous study (Wood Buffalo National Park 1995) indicate that there are five populations of bison in WBNP according to the spatial discontinuity criteria of Wells and Richmond (1995). This spatial discontinuity is not absolute between the Hay Camp and Delta populations as ecological factors such as floods influence the distribution of bison. Despite the occasional range shift, the spatial discontinuity was stable in most seasons of the study. Sufficient interchanges occurred between the Delta and Hay Camp populations to indicate that these two groups are to some degree linked demographically. I also witnessed movement from these groups to the Nyarling River, Little Buffalo and Garden

River groups, although these movements were more limited (3 dispersals of 232 bison-years where bison were residents of the Hay Camp and Delta populations). Overall, I conclude that each of the groups identified by the cluster analyses should be considered populations within the WBNP metapopulation. The demographic continuity among these populations should be considered in management planning. In all subsequent analyses, I use this population classification in examining demographic and epidemiological characteristics.

I found no significant trend in movement of bison from the Peace-Athabasca Delta to the Hay Camp area of the park; either in the present movement data or in the total count data. There was some movement north from the Delta associated with high waters in 1997, but this movement was balanced by movement south in the following season. Therefore, I reject the hypothesis that the decline of bison in the Delta is the result of emigration.