*Research Article*

# Spatial Population Structure of Yellowstone Bison

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**ABSTRACT** Increases in Yellowstone National Park, USA, bison (*Bison bison*) numbers and shifts in seasonal distribution have resulted in more frequent movements of bison beyond park boundaries and development of an interagency management plan for the Yellowstone bison population. Implementation of the plan under the adaptive management paradigm requires an understanding of the spatial and temporal structure of the population. We used polythetic agglomerative hierarchical cluster analysis of radiolocations obtained from free-ranging bison to investigate seasonal movements and aggregations. We classified radiolocations into 4 periods: annual, peak rut (15 Jul–15 Sep), extended rut (1 Jun–31 Oct), and winter (1 Nov–31 May). We documented spatial separation of Yellowstone bison into 2 segments, the northern and central herds, during all periods. The estimated year-round exchange rate (4.85–5.83%) of instrumented bison varied with the fusion strategy employed. We did not observe exchange between the 2 segments during the peak rut and it varied during the extended rut (2.15–3.23%). We estimated a winter exchange of 4.85–7.77%. The outcome and effectiveness of management actions directed at Yellowstone bison may be affected by spatial segregation and herd affinity within the population. Reductions based on total population size, but not applied to the entire population, may adversely affect one herd while having little effect on the other. Similarly, management actions targeting a segment of the population may benefit from the spatial segregation exhibited. (JOURNAL OF WILDLIFE MANAGEMENT 71(5):1531–1538; 2007)

Mensuration and management of a wildlife population must involve clear identification of the group under consideration. Confusion and misunderstanding may result from a failure to clearly describe the temporal and spatial attributes used to characterize a population (Wells and Richmond 1995). A population is often defined as a group of organisms of the same species with the potential to breed with each other (Krebs 1972). Alternatively, populations may be specified by their geographic extent during specific periods (e.g., winter, breeding, or calving seasons). In this context, the terms herd and population are often used synonymously for many ungulates. Frequently, the only factor defining a population is the occurrence of conspecifics within certain geographic boundaries. Wells and Richmond (1995:461) defined a population as "a group of conspecific individuals that is demographically, genetically, or spatially disjunct from other groups of individuals." These traditional definitions of a population assume a continuous distribution across its range (McCullough 1996). Metapopulations (Levins 1969, 1970) occur when populations of a species exist within a specified geographic range but are isolated from one another or have limited exchange of individuals (Wells and Richmond 1995, McCullough 1996, Akçakaya et al. 1999). This isolation may be due to spatial heterogeneity in environmental factors or anthropogenic causes (McCullough 1996). Within a metapopulation, sets of individuals may be referred to as groups, populations, subpopulations, or local populations (Wells and Richmond 1995, Akçakaya et al. 1999).

Historically, bison within Yellowstone National Park (YNP), USA, were identified as the Mary Mountain, Pelican, and Lamar herds based on winter distributions when numbers were <600 (Meagher 1973). While not geographically discrete year-round, this classification was appropriate for the wintering herds (Meagher 1973) and may have identified a metapopulation. Recent studies have continued to identify Yellowstone bison herds based on winter distributions with little knowledge of the degree of herd exchange (DelGiudice et al. 1994, 2001; Kirkpatrick et al. 1996; E. M. Olexa, United States Geological Survey, unpublished data) although bison numbers had increased to nearly 3,500 by the mid-1990s. An assessment of potential effects of a recently implemented interagency bison management plan assumed that changing spatial population structure (Meagher 1993, 1998; Meagher et al. 1997) has resulted in 2 distinct wintering groups (National Park Service 2000).

Accurate assessments of the effects of natural processes and anthropogenic perturbations on Yellowstone bison require a clear understanding of the spatial structure of the population. Accordingly, our objectives were to 1) identify the spatial structure of bison moving throughout YNP and adjacent lands, and 2) assess levels of exchange between cohesive groups of bison during biologically significant periods.

## STUDY AREA

Our study area included the entire 9,000 km² of YNP and adjacent public and private lands (Fig. 1). Elevations ranged from 1,610 m along the Yellowstone River near Gardiner, Montana, USA, to 3,462 m at Eagle Peak, Wyoming, USA. High plateaus characterized the central portions of the area, and broad river valleys were the dominant feature at lower elevations. Abrupt mountain ranges skirted the park's northern and eastern boundaries.

Although long, cold winters and short, cool summers were typical (Houston 1982), the park experienced 2 climatic
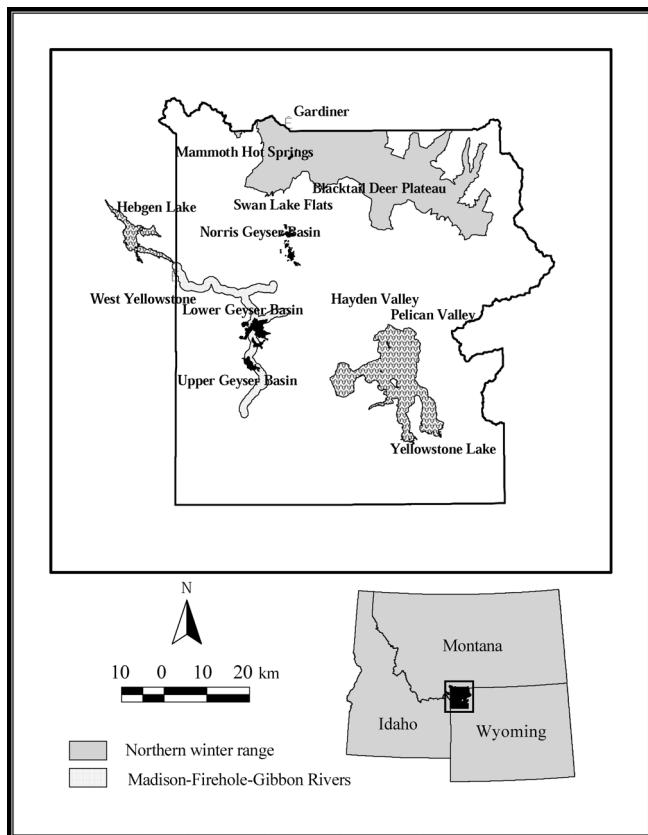
**Figure 1.** Physical features associated with bison spatial distribution in and adjacent to Yellowstone National Park, USA, 1997–2000.

types resulting from its location relative to predominant storm tracks and mountain ranges (Despain 1987). Large valleys and central plateaus experienced a climate similar to the intermountain region to the west and the plains to the east (Despain 1987). Of all precipitation received by these areas, 35–55% was in the form of rain with a peak in May and June (Despain 1987). The southwestern plateaus of the park and the mountain ranges to the north and east experienced a much different climate, characterized by a winter peak in precipitation (Despain 1987). Average annual precipitation ranged from 28 cm near Gardiner, Montana, to almost 97 cm along the Bechler River, Wyoming (Dirks and Martner 1982).

Montane areas were vegetated primarily by coniferous forests or wet meadows (Despain 1987). Whitebark pine (*Pinus albicaulis*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) were common above 2,600 m (Houston 1982). Douglas-fir (*Pseudotsuga menziesii*), juniper (*Juniperus* spp.), and aspen (*Populus tremuloides*) occurred at lower elevations. Douglas-fir also occurred on moist, north-facing slopes associated with valleys dominated by sagebrush (*Artemisia* spp.) steppe communities and dry grasslands (Despain 1987). The central portion of YNP supported primarily dry lodgepole pine (*Pinus contorta*) communities due to coarse rhyolitic soils (Despain 1987, 1990). In 1988, wildfires burned >300,000 ha in YNP (Schullery 1989, Despain 1990). The resulting mosaic of burned and unburned areas was apparent during our study.

Most of YNP's >10,000 geothermal features exist in the southern half of the park with concentrations in the Norris, Lower, Midway, and Upper Geyser Basins (Fig. 1). The Gibbon, Madison, and Firehole rivers that drain these areas were also geothermally influenced. Alum Creek in the Hayden Valley remained free-flowing during winter due to geothermal influence. In the northern half of the park, geothermally influenced areas were found in the Mammoth and Soda Butte areas.

Yellowstone bison numbers increased from <600 in 1967 following cessation of artificial control within the park to approximately 4,000 by 1994. Large-scale reductions along the park boundaries during the winters 1994–1995 through 1996–1997, combined with natural mortality, reduced numbers by approximately 50%. Yellowstone bison numbered 2,105 and 2,444 during the winters of 1997–1998 and 1999–2000, respectively (National Park Service 2000).

## METHODS

### Capture and Radiotracking

We captured and radiocollared Yellowstone bison during October–December 1997 and March 1998. Net-gunning (Barrett et al. 1982) from a helicopter, we sampled adult bison throughout their distribution in YNP as predetermined by aerial surveys. Concurrent research by Aune et al. (1998) provided 6 additional instrumented bison in October 1998. We relocated bison on a 10-day cycle, modified as required by weather and logistic constraints, during November 1997–April 2000. We employed dual H antennas mounted to a Piper Supercub (Piper Aircraft Corporation, Lock Haven, PA) and standard aerial telemetry methods (Gilmer et al. 1981, Mech 1983). The same observer–pilot team conducted all radiotracking flights. Typically, we located each bison once per cycle. All flights occurred during daylight hours, normally in the morning when flying conditions were best. The order of location was opportunistic as dictated by weather and herding behavior. We based location estimates on visual confirmation of instrumented bison, the estimated center of a cohesive group when we could not differentiate instrumented bison or signal strength and direction when we could not observe the target group due to ground fog. Using a Precision Lightweight Global Positioning Receiver (PLGR+96; Rockwell Collins, Cedar Rapids, IA) to record waypoints, we collected Universal Transverse Mercator coordinates for each location as we flew over a bison's position. We typically recorded locations from an altitude of <150 m above ground level. We reduced location error by collecting 3-dimensional fixes, which are often more accurate than 2-dimensional fixes when elevation is uncertain (Moen et al. 1997, Dussault et al. 2001). Mean horizontal location error was <125 m based on similar methodology tested in YNP (Olexa et al. 2000).

### Cluster Analysis

We performed polythetic agglomerative hierarchical cluster analysis on relocations associated with radiocollared bison. Cluster analysis (CA) seeks to classify items based on an analysis of multivariate data patterns (Overall et al. 1993)

and has recently been used to characterize wildlife populations (Bethke et al. 1996, Joly and Messier 2001, Taylor et al. 2001, McLoughlin et al. 2002). In contrast to discriminant analysis, the number of classes and their defining characteristics are unknown a priori (Bayne et al. 1980, Gordon 1999).

We used the Ward's, Complete, Euclidean Sum of Squares (ESS), Mean Proximity, Average Linkage, Centroid, Median, and Weighted Means (WPGMA) fusion strategies. Each method has strengths and weaknesses that depend on the data (Kuiper and Fisher 1975; Bayne et al. 1980; Milligan 1980, 1996; Overall et al. 1993) and the constraints placed on desirable cluster solutions (Fisher and Van Ness 1971, 1973; Milligan 1979; Chen and Van Ness 1994; Gordon 1996). Selection of a single best strategy was not possible because group characteristics (e.g., no., size, and shape) were unknown a priori. We used a suite of fusion strategies because replication of a classification by multiple methods strengthens the validity of the classification (Bethke et al. 1996, Kos and Psenicka 2000, McGarigal et al. 2000). We conducted analyses using ClustanGraphics5 (Clustan Limited, Edinburgh, Scotland).

We pooled all locations except 3 locations of a bull bison that had moved >30 km from YNP. We applied CA to location data grouped into the following time periods: annual, peak rut (15 Jul–15 Sep; Meagher 1973, Gogan et al. 2005), extended rut (1 Jun–31 Oct), and winter (1 Nov–31 May). We selected these periods based on ecological significance and because any attempt to identify population structure must involve temporal as well as spatial criteria. We used the easting and northing coordinates of each relocation as input variables to identify clusters. We standardized the data matrix to zero mean and unit variance prior to analysis (Milligan and Cooper 1988, Bethke et al. 1996). Squared Euclidean distance served as the measure of dissimilarity (Everitt 1993, Gordon 1996), as required by the majority of fusion strategies, and increased as dissimilar groups were combined. A large increase in the resulting fusion value indicated the combining of very dissimilar groups.

Cluster analysis has been faulted for finding structure in data where none exists (Milligan and Mahajan 1980, Pillar 1999). To ensure identified groups were valid, we tested for a lack of significant cluster structure in the data (Milligan and Mahajan 1980). We removed any structure in the data by sampling with replacement from the dissimilarity matrix at the 488-cluster level for the peak rut period and the 500-cluster level for all other periods. We then performed CA on the randomized matrix created from the bootstrap sample. For each fusion strategy, we conducted 1,000 iterations to generate a mean and 95% confidence interval around each fusion value (Wishart 1999).

We tested the null hypothesis that the structure indicated by our analysis did not differ from random. We considered final cluster solutions with fusion values outside the 95% confidence interval significantly different from random and accepted the solution. The number of groups supported by the data was that point prior to the largest statistically different increase in fusion value (Milligan and Cooper 1985, McLoughlin et al. 2002).

## Group Delineation

We did not attribute relocation coordinates to a specific bison until after we identified the spatial structure of the data. Following CA, we defined group membership based on the majority of relocations associated with an individual bison rather than using median relocations in the data matrix (i.e., all of a bison's relocations were assigned to the group containing the majority of relocations for that bison; Bethke et al. 1996, Joly and Messier 2001, Taylor et al. 2001, McLoughlin et al. 2002). We considered a relocation to be cross-classified when its initial group assignment differed from that of the majority of points associated with a bison (Taylor et al. 2001).

We considered groups discrete, for a period, when no bison had cross-classified relocations. We calculated exchange rates for each period as the proportion of bison with ≥1 cross-classified relocation. We identified the population structure of the herd based on the amount and timing of exchange between groups.

## RESULTS

### Radiotracking

We radiotracked 103 bison and secured 3,262 relocations representing bison spatial distribution (annual: 3,262 relocations; peak rut: 488 relocations; extended rut: 1,285 relocations; winter: 1,977 relocations). We collected data over 2,262 bison-months ($\bar{x} = 22$ months/bison, range 2–30 months/bison) and we obtained relocations from 92 (20 M, 72 F) and 94 (20 M, 74 F) bison during the peak and extended rut periods, respectively, and 103 (22 M, 81 F) bison during the winter and annual periods.

### Cluster Analysis

*Annual.*—Analysis of Yellowstone bison distribution throughout the year revealed spatially distinct groups. Most fusion strategies indicated the presence of 2 groups although the Median and WPGMA methods failed to detect any spatial clustering (Fig. 2A). Group membership was similar among methods with a 2-group solution. The Ward's and Complete methods cross-classified 28 relocations of 5 bison. The Mean Proximity method cross-classified 29 relocations associated with the same 5 bison. The ESS, Average Linkage, and Centroid methods cross-classified 29 relocations of the same 5 bison and one additional bison (Fig. 3A). The estimated exchange rate varied from 4.85% for the Ward's, Complete, and Mean Proximity methods to 5.83% for the ESS, Average Linkage, and Centroid clustering methods. Cross-classified bison included 3 females and 3 males.

*Peak rut.*—Analysis of bison relocations collected 15 July–15 September 1998–1999 revealed 2 distinct groups of bison when most breeding occurs. All fusion strategies arrived at the same solution (Fig. 2B). No bison were cross-classified for this time period, which suggests little exchange
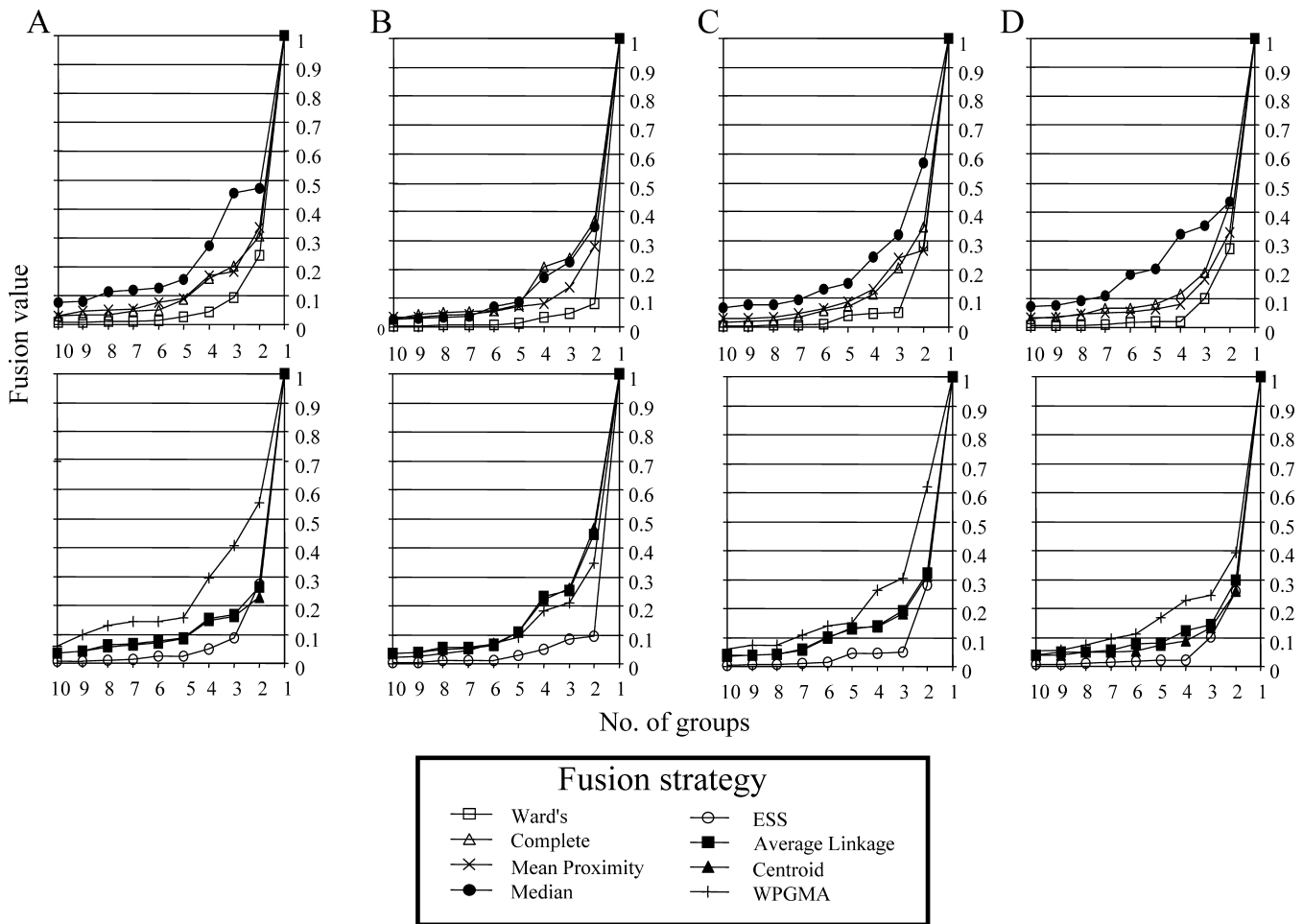
**Figure 2.** Fusion value versus number of groups as determined by 8 clustering methods used to analyze locations of Yellowstone bison, Yellowstone National Park, USA: (A) year-round, 1997–2000, (B) during the peak rut (15 Jul–15 Sep), 1998–1999, (C) during the extended rut (1 Jun–31 Oct), 1998–1999, and (D) during the winter bison management period (1 Nov–31 May), 1997–2000. The number of clusters supported by the data occurs immediately prior to the largest increase in the fusion value. For each method, we standardized fusion values by dividing each by the maximum. ESS = Euclidean Sum of Squares, WPGMA = Weighted Means.

between groups and highlights the strength of the spatial discreteness of each group (Fig. 3B).

*Extended rut.*—Analysis of bison distribution during 1 June–31 October 1998–1999 revealed some exchange of Yellowstone bison during the extended breeding season. Most fusion strategies resulted in a 2-cluster solution, but the Median and WPGMA methods again failed to detect any spatial clustering of locations (Fig. 2C). Four bison (2 F and 2 M) were cross-classified during this period by all methods. The Ward's and ESS methods cross-classified 3 relocations of 3 bison, and the Mean Proximity method cross-classified 4 relocations associated with the same 3 bison (Fig. 3C). The Average Linkage method cross-classified 3 relocations of 2 of the 3 bison cross-classified by the other methods. The Centroid method cross-classified 3 relocations of 3 bison; 2 of which were cross-classified by the other methods. The Ward's, ESS, Mean Proximity, and Centroid methods estimated the exchange rate to be 3.23% for the 2-group solution whereas the Average Linkage method estimated the rate at 2.15%.

The Complete method generated a 2-cluster solution for

this time period that differed from all others. This solution identified a cluster in the Madison–Firehole area and another that included all relocations on the Northern Winter Range and the Hayden and Pelican Valleys. This solution resulted in cross-classification of 57 of 84 bison and we considered it improbable based on observed movements of bison between the Madison–Firehole area and the Hayden Valley.

*Winter.*—Cluster analysis of locations collected from 1 November–31 May 1997–2000, excluding May 2000, produced results consistent with other periods and demonstrated the presence of 2 groups of bison during winter (Fig. 2D). Four of 8 solutions (Ward's, Mean Proximity, Average Linkage, and Centroid) divided the Yellowstone bison population into northern and central herds. The Ward's and Mean Proximity methods cross-classified 19 relocations of 5 bison, whereas the Average Linkage method cross-classified 18 relocations of the same 5 bison. The Centroid method cross-classified 22 relocations associated with these bison and 3 others (Fig. 3D). Bison cross-classified by these methods included 6 females and 2 males. The estimated
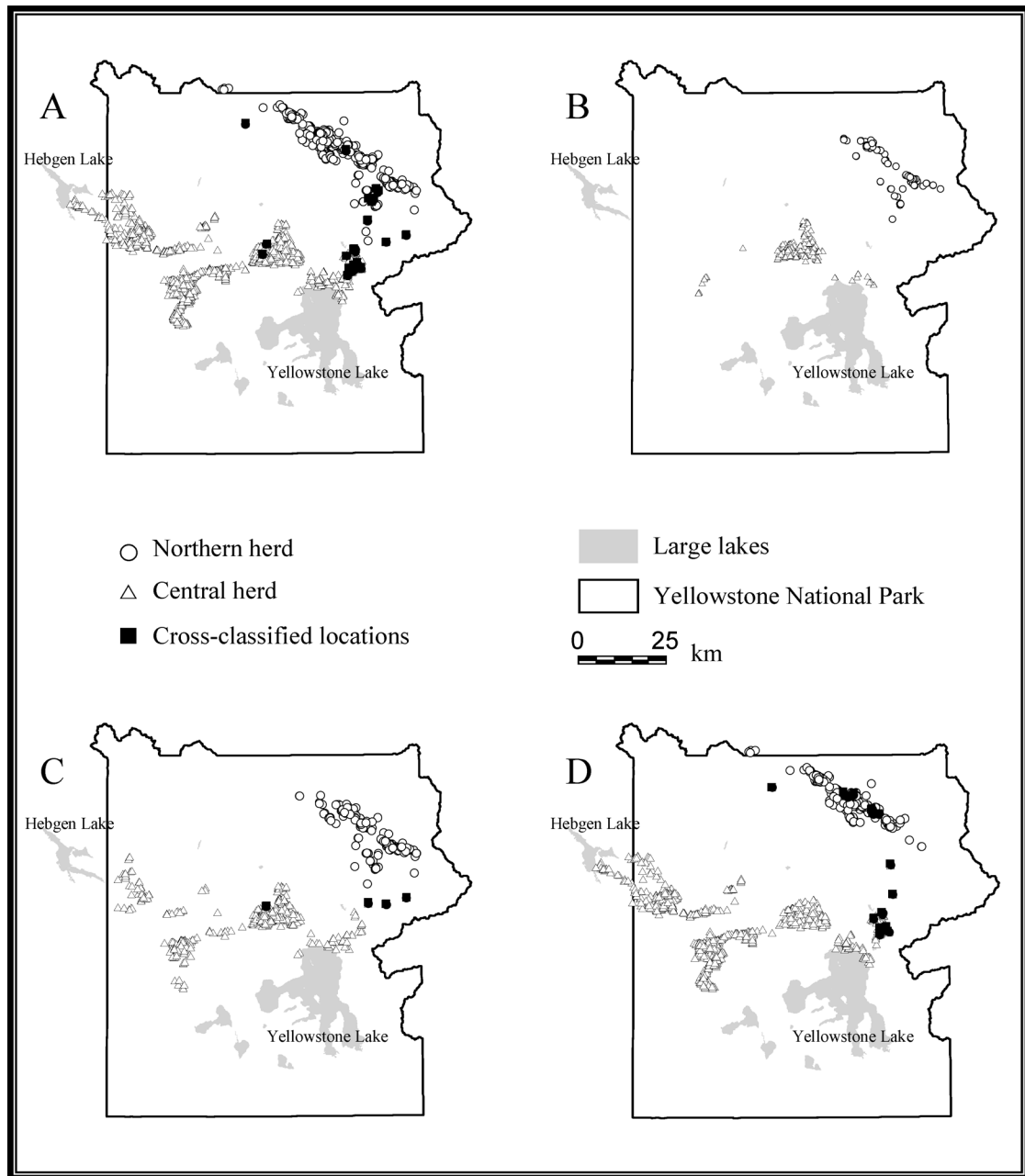
**Figure 3.** (A) Year-round population structure of Yellowstone bison as identified by the Euclidean Sum of Squares, Average Linkage, and Centroid fusion strategies, Yellowstone National Park, 1997–2000. (B) Population structure of Yellowstone bison during the peak rut (15 Jul–15 Sep) as determined by 8 methods of cluster analysis, 1998–1999. No instrumented bison were cross-classified. (C) Population structure of Yellowstone bison during the extended rut (1 Jun–31 Oct) as determined by the Mean Proximity method of cluster analysis, 1998–1999. (D) Population structure of Yellowstone bison during the winter management period (1 Nov–31 May) as determined by the Centroid method of cluster analysis, 1997–2000.

exchange rates were 4.85% for the Ward's, Mean Proximity, and Average Link methods and 7.77% for the Centroid method. The Median method failed to identify any spatial structure. The results of the remaining fusion strategies were not supported biologically. The WPGMA, ESS, and Complete methods generated 2-group solutions that resulted in cross-classification of 19, 40, and 52 of 103 bison, respectively. Of these, the WPGMA grouped all relocations in the Madison–Firehole area with those in the Hayden Valley and the second group included all relocations on the Northern Winter Range and Pelican Valley. This

clustering is consistent with our observed movements of bison from the Pelican Valley north to the Mirror Plateau in early winter but is not consistent with our detected movements of instrumented bison between the Pelican and Hayden valleys continuously throughout winter. The Complete and ESS methods grouped all locations in the Madison–Firehole area and lumped all other relocations into a second group. These latter 2 clusterings (Complete and ESS) cannot be supported biologically as instrumented bison moved regularly from the Hayden Valley to the Madison–Firehole area throughout the winters of this study.

# DISCUSSION

We evaluated the spatial structure of the Yellowstone bison population based on year-round relocations from a sample of uniquely identifiable animals. Our analysis indicates the presence of 2 distinct groups of Yellowstone bison. We designate these the northern and central herds. Our findings support the assertion by Meagher et al. (1997) that historic herd structure (Meagher 1973) has been altered by changes in spatial distribution. Documented differences between the 2 herds with regard to timing of parturition (Gogan et al. 2005), dental wear patterns (Christianson et al. 2005), and age structure (P. J. P. Gogan, United States Geological Survey, unpublished data) support our identification of 2 subpopulations. Differences in timing of parturition may reflect short-term (e.g., a single winter) response to differing ecological conditions in the 2 areas, whereas differences in dental wear patterns and age structure suggest separation for a period much longer than the duration of our study. The degree to which these 2 groups are spatially, genetically, and demographically disjunct may influence the outcome of natural processes and anthropogenic perturbations.

Our year-round analysis revealed that cross-classified bison were distributed primarily in a movement corridor between the Pelican Valley and Mirror Plateau near the eastern border of the park. Those bison cross-classified in the winter management period were distributed predominantly from the Pelican Valley through the same movement corridor to the northern range. The winter period encompasses most management activity driven by bison movements beyond the park boundaries and related to efforts to prevent transmission of brucellosis from bison to domestic livestock. We identified 2 groups, the northern and central herds, during winter. Minimal exchange of individuals occurred between these groups. The spatial distribution of cross-classified relocations showed that exchange during this period continued to occur almost entirely in the upper Pelican Creek and Mirror Plateau areas of YNP. We identified no cross-classified bison adjacent to the park boundaries during our study although 1,084 bison were removed in 1996–1997 under the interagency bison management plan after approaching or crossing park boundaries (National Park Service 2000).

We found consistent agreement among fusion strategies in classifying radiomarked bison into 2 subpopulations with no cross-classification during the rut. Exchange was greatest during the winter management period, and was intermediate during the extended rut. These patterns indicate that bison exhibit high fidelity to a specific range during the rut and lower fidelity in winter. In addition to the spatial separation exhibited by Yellowstone bison, limited exchange of individuals may result in genetic or demographic disjunction. When we assume the rut occurs between 15 July and 15 September, distinct northern and central herds with no exchange are most pronounced. Thus, these 2 groups may function as separate populations. Exchange rates were low during the extended rut. We documented the exchange of only 4 of 87 bison during the extended rut in 1998. Three of

the 4 returned to their original group before the end of that year's extended rut. We were unable to determine the subsequent movements of the fourth bison. We did not detect similar movements by the 65 bison radiotracked during the extended rut in 1999. The extent of genetic exchange between subpopulations cannot be determined without knowing when and where individual bison breed. If bison breed in multiple disjunct groups during a single breeding season, then a single population would exist. However, even if individuals breed in multiple groups, a metapopulation would exist as long as breeding occurs in only one group per breeding season (Wells and Richmond 1995). Such a pattern has implications for conservation genetics.

An analysis of the genetics of Yellowstone bison slaughtered as they left the park in the vicinity of Gardiner, Montana, or West Yellowstone, Montana, between the winters of 1996–1997 and 2001–2002 (P. J. P. Gogan, unpublished data) revealed a genotypic differentiation >75% between bison at the 2 locations (Halbert 2003). Such differences imply long-term separation during the rut. Similarly, exchange of bison between subpopulations at Wood Buffalo National Park, Canada, is limited to the extent that the subpopulations are genetically distinct (Wilson and Strobeck 1999) although genetic material from introduced plains bison (*B. b. bison*; Carbyn et al. 1993) has diffused throughout the park's original wood bison (*B. b. athabascae*) population (Wilson and Strobeck 1999).

The influence of Yellowstone bison population size on the dynamics of spatial population structure is not well understood. We documented 2 subpopulations during a period when Yellowstone bison numbered approximately 2,500. Meagher (1973) identified 3 subpopulations during a period when bison numbered <600. Winter movements of bison from the Norris Geyser Basin area to the Swan Lake Flats area were observed prior to our study during the winter of 1996–1997, when the central herd numbered approximately 2,900 and the northern herd approximately 875 (Taper et al. 2000), and during the winters 2002–2003 and 2003–2004 when total numbers were approximately 4,000 (R. Wallen, National Park Service, personal communication). However, there has been no assessment of spatial population structure at these higher numbers.

The spatial structure and distribution of the Yellowstone bison population are dynamic. Our research coincided with a time of population growth following large-scale culling. Different exchange rates and population structure could be expected with changes in population size. The probability of large-scale movements beyond park boundaries has been tied to population levels in excess of 3,000 (Cheville et al. 1998), and winter exchange rates may change as a function of population size. In November 1996, bison captured and released on the central herd range 13 km north of West Yellowstone, Montana, were recaptured 3 km north of Gardiner, Montana. Similarly, during the winters of 2001–2002 and 2002–2003, groups of bison were observed moving from the Lower Geyser Basin within the range of the central

herd to the Swan Lake Flats and Blacktail Plateau areas of the northern herd range. No such movements were documented during our study. Also, we did not detect movements beyond YNP's southern boundary although they occurred prior to our study (J. A. Mack, National Park Service, personal communication), suggesting that a segment of the Yellowstone bison population may not have been represented. This may reflect conditions during the time of the study or indicate the need for a larger sample of radiocollared bison to detect less-frequent movements.

Given the spatial structure of the population, the results of any research on Yellowstone bison may apply only to the segment studied. Caution should be exercised when comparing segments of the population unless it can be shown that these partitions are representative of spatially or temporally distinct groups. Finally, the validity of previously identified population segments should be cautiously evaluated given the dramatic changes in contemporary size and spatial distribution of the Yellowstone bison population.

## MANAGEMENT IMPLICATIONS

The spatial structure of the Yellowstone bison population should be considered prior to management activities. Management actions, if not applied to the entire population, could impact one population segment and have no effect on the other, due to the disjunct nature of the population. Our results show that winter movements may fail to position a segment of the bison population in proximity to localized management activity. Management actions undertaken during winter will have the greatest impact on the segment of the population directly targeted for management, and may have little, if any, effect on the other herd. Alternatively, management activity targeting a single population segment may benefit from the spatial segregation exhibited. The possibility of reducing a herd below the level needed to maintain the effective genetic population size of 50–500 bison (Franklin 1980, Soulé 1980, National Park Service 2000) cannot be ignored given the limited spatial overlap of the 2 herds during the rut and uncertainty regarding the timing and location of breeding activity.

## ACKNOWLEDGMENTS

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