The Phenology of Space: Spatial Aspects of Bison Density Dependence in Yellowstone National Park

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ABSTRACT

The Yellowstone bison represent the only bison population in the United States that survived in the wild the near-extermination of the late 1800's. This paper capitalizes on a unique opportunity provided by the record of the bison population of Yellowstone National Park (YNP). This population has been intensely monitored for almost four decades. The analysis of long-term spatio-temporal data from 1970-1997 supports the following conclusions. 1) Even though the Yellowstone bison herd exhibits an extended period of what appears to be linear growth, this pattern can be explained with classical density dependent dynamics if one realizes that perhaps the primary response of the herd to increased density is range expansion. 2) Several spatial aspects of social behavior in the YNP bison may be behavioral adaptations by the bison to environmental changes. These behavioral strategies may buffer, temporarily at least, bison population dynamics from the immediate repercussions of possible environmental stress and habitat deterioration. 3) Bison ecological carrying capacity for YNP is on the order of 2800 to 3200 animals. 4) There do appear to be indications of changes in the bison dynamics that are associated with increasing use of sections of the interior road system in winter. 5) The possibility of habitat degradation is indicated.

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INTRODUCTION

There are less than a dozen free-ranging bison populations, and most of those are only several hundred or less in size. These smaller free-ranging populations are managed for a specified population size, usually to avoid conflicts with other land–use objectives. Most bison are maintained on fenced lands and managed for predetermined maximum population size, and sometimes structure and productivity (Shaw and Meagher 1999). Consequently, few studies of the population dynamics of free-ranging bison have been made. However, Van Vuren and Bray (1986) analyzed a seven-year expansion phase in the Henry Mountains, UT herd prior to that population reaching a level agreed upon by the responsible management agencies (Hodson and Karpowitz 1998).

It has long been recognized (Meagher, 1986) that long-term analyses of the population dynamics and factors that naturally regulate free-ranging bison was a major research need. The several extant large populations over 2000 bison appear to afford the best opportunity for such analyses. Study of these herds has potential not only for yielding insight into current population dynamics, but also into the land-use patterns and behavioral ecology of the free-ranging herds that existed a century and a half ago.

There are several Canadian populations. There is the expanding Mackenzie herd (Calef 1984, Gates and Larter 1990, Larter et al. 1993), and two declining populations, in Wood Buffalo National Park (Carbyn 1993) and in the adjacent Slave River lowlands (Van Camp and Calef (1988). Population

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information available from these Canadian herds has been variable in time, and quality.

This paper capitalizes on a unique opportunity provided by the record of the bison population of Yellowstone National Park (YNP). This population has been intensely monitored for almost four decades. There does not appear to be another comparable data set in existence for a very large highly gregarious herbivore (G. Caughley pers. comm. to MM). This population has a long historical record with some information dating back to 1860 (Meagher 1970, 1973). Further, the YNP bison herds have been the subject of long-term detailed and continuous ecological study since 1963. Information spanning 1963-1968 was published in Meagher 1970, 1971, 1973. Overviews of population changes in the last two decades were published in Meagher (1998) and Meagher et al. (1997).

The Yellowstone bison represent the only bison population in the United States that survived in the wild the near-extermination of the late 1800's (Meagher 1970, 1973). As such, they serve as a symbol, an icon for many people, nationally and internationally. They are free-ranging, without boundary or internal fences, but they are affected by management concerns inside and outside the park. Present management might be termed a mostly hands-off approach within the park. However, outside the park they are in conflict with other land-use objectives that have generated concern and controversy. The presence in the herd of the livestock disease brucellosis, introduced into North America by cattle (Meagher and Meyer 1994), has been an issue that has

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resulted in litigation and the development of a full Environmental Impact Statement (EIS) (National Park Service, 2000a) for bison management in the region.

Within the park, long-term field data have indicated that changes in bison spatial dynamics have occurred during the period of development of a program of human use of the park's interior in winter. This has led to the hypothesis that park winter use may have played a major role in changes in the bison population. Consideration of the ecological effects of winter use and associated management implications has also been a part of litigation resulting in preparation of a winter use EIS (National Park Service 2000b). The population consequences for the Yellowstone bison may be enormous, and require the best possible information.

Here, we have undertaken a detailed analysis of the long-term population dynamics of the Yellowstone bison. Our primary goals in this section of our work have been 1) to determine if the Yellowstone National Park bison herd is subject to natural density dependent population regulation, 2) to investigate spatial aspects of natural regulation in bison, 3) to determine an ecological carrying capacity for the herd, and 4) to seek indications in the bison space-time series of whether or not changes in bison dynamics are associated with the increasing bison use of sections of the interior road system in winter.

METHODS

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DATA ACQUISITION AND PROCESSING

Fig. 1 near here.

The study area encompassed most of Yellowstone National Park (Fig. **1**). Aerial survey efforts concentrated on the locales used by the mixed groups (cows with young, usually some mature bulls; Fuller 1960), Historically, the winter locales used by bison occupied three areas designated the northern range (Lamar Valley), Pelican Valley, and Mary Mountain (Meagher 1970, 1973). The latter encompassed both the centrally located Hayden Valley and the Firehole to the west as one wintering unit because of the movements in both directions across Mary Mountain. Beginning in the 1980's as bison use patterns began to change, the *west side* was considered as part of the Mary Mountain geographic unit. Because adult bulls may wander widely (Meagher 1970, 1973), extra efforts were not made to locate these scattered individuals. The study area is described generally in Meagher (1970, 1973). Meagher and Houston (1998) provided a broad description of geology, climate, vegetation, wildlife, and park management.

The data we analyze span 1970 through July 1997. There were four aerial surveys per year (Piper supercub, same pilot and observer with few exceptions), weather and desired timing permitting from 1970 through 1990. Thereafter surveys increased to 9-10 per year, circumstances permitting, for a total of 151. (Two surveys were not complete; these were made to verify Pelican

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area calf numbers (flight 3, June 3, 1970) and the Mary Mountain winter-spring distribution change (flight 11, May 1, 1972. Flying weather required reasonably wind-free, clear-to-partly-cloudy conditions. Occasionally wind and/ or ground fog over open valleys dictated a survey could not be completed in one day, in which case the rest of the areas usually were flown the following day. For analysis, these pairs of flights were merged and considered a single flight. Further, flights usually were broken only between the major geographic wintering areas of the northern and central regions. There are indications (to be discussed below) that there is little population transfer between these areas in general. Also, during the earlier years the bison numbers observed on flights over the northern range by an elk researcher (D. B. Houston) occasionally were used when the timing was suitable, rather than duplicate the effort. Surveys were intended to locate all visible bison within the YNP with the exception of wandering bulls that were beyond population-use areas in unknown and unpredictable sites. An exceptionally sharp-eyed pilot (D. Stradley) made the overall and calf counts. The observer (MM) cross-checked and recorded those numbers, locations, groups size and cohesiveness, general conditions, and miscellaneous data such as mortality, travel routes, and so forth. All initial data entries were recorded manually and transferred to field notebooks as soon as possible, usually the same day. Over the course of 27 years of data collection, 11 field journals were cataloged with detailed information concerning seven key variables: location, group size, demographics, dispersion, group shape, snow cover, and habitat use. Processing the data occurred in three major steps. After agreeing on a

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spreadsheet format, data was hand translated by the original observer (MM) from journal to spreadsheet outline. Location descriptions were translated into UTM coordinates by the original observer (U.S. Geological Survey Topographic Map of Yellowstone National Park, Wyo.-Mont.-Idaho. 1961ed. with 10 km UTM grid overlay***)***. Secondly, the data was entered into a computer spreadsheet. Upon completion, on December 15, 1998, over 22,000 lines containing 25 variables had been entered into the data set. Finally, the electronic data set was checked and validated as thoroughly as possible. Because of the massive size of the data set, several methods of checking were implemented. Data transformations looked for spatial continuity in observation sequence. Furthermore, each flight was summarized for the number of observed bison. All anomalies suggested by the transformations and summaries were back-checked to the original observer's log. Five major passes were made to reconcile our computerized data representation with all aspects of the aerial surveys recorded in the field notebooks. This work was completed on September 2000.

The precision of the location description translation process was checked for a random sample of a hundred and fifteen observations, stratified over the five principle localities. For each observation, a maximum deviation from the assigned UTM coordinates consistent with the observer's description was determined in both east/west and north/south directions. From these a maximum possible error was calculated for each sampled observation. The mean maximum possible error was found to be only 0.324 km (s.d. 0.156) with no significant difference among localities. Errors of this magnitude are

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inconsequential for all analysis performed in this study. Fig. 32 plots all bison observations made during the study. The points in this figure have radii about 50% larger than the mean maximal error. The second pass through the notebooks also gives us a check of our transcription accuracy. Of the 230 transcribed UTMs, 229 agreed exactly with the spreadsheets. The final UTM had a small discrepancy in trailing digits amounting to an error of about a quarter of a kilometer. Errors of this magnitude would not be caught by our continuity checks.

Analysis

Fig. 2. Near here.

Population size represented by yearly maximum count

As Fig. 2 indicates there is considerable variation in bison counts within years. This variation is too large to represent actual population fluctuations given bison reproductive capacities. Further, the within year pattern of counts is not consistent with bison life history with highest counts occurring towards the end of the year rather than at the end of the calving season. Therefore, we use as an index of population size for a given year the maximum count made in that year. The year-to-year continuity exhibited in Fig. 3 indicates that this measure is likely to be accurate. Quantitative measures of bias in this measure are developed and discussed below.

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Fig. 3. Near here.

Areas estimated by kernel density estimation

Kernel density estimation (Silverman 1986; Scott 1992) is the most accurate range estimation technique currently available. There is still debate over the use of adaptive versus fixed kernels (Worton 1989 a,b, 1995; Seaman and Powell 1996). The issues involved are reviewed by Fortin et al. (2001). We utilize a fixed kernel whose window width is based on the optimal jackknife cross-validated window width for a fixed kernel. As discussed by Seaman and Powell (1991) the jackknife cross-validation determination of kernel window width has difficulty when multiple observations are recorded for single locations. We follow one of the Seaman suggestions for correcting this problem by adding small random jiggle (s.d. 1 km) to each bison location. Range size is operationally defined as the area contained by the 95% contour.

Areas occupied by the population on each air survey.

Fig. 4. Near here.

Each flight generates a range estimate. There is considerable seasonal variability in the area occupied by the population (Fig. 4). The units of area in Fig. 4 are square kilometers.

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The maximum area occurs in winter, generally in January or February. We operationally define the area associated with a year-to-year transition as the maximum area used by the bison in the period from June of one year to June of the next. This area is indexed by the first year of the transition.

Minimum areas occur during the breeding season in late summer. Our minimum area is defined as the minimum area occurring in a calendar year.

Minimum Winter Densities

Our a priori belief is that density dependence in Yellowstone bison occurs primarily in winter. Thus, we calculate densities as maximum count divided by maximum winter areas. Our results do not depend critically on the seasonal area used. Although there is a strong seasonal pattern in use of range areas, seasonal ranges are highly correlated over years.

Sightability estimation

Heretofore, we have been using the maximum count for a year as our estimate of population size. A set of replicated counts contains more information than just the maximum count. The distribution of observations contains information about sightability and hence about the true population size. As an illustration, lets consider the simple case of constant sightability. If a population has a size N, and an observer has a probability, P, of observing any individual animal, total counts will then follow a binomial distribution with parameters N and P. The expected mean count would be N*P and the expected variance among counts would be N*P*(1-P). Using the method of moments and equating

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observed means and variance with their expectations yields two equations that can be solved for the two unknowns N and P.

The above assumes that the probability of sighting animals is constant over all replicate counting episodes. For many organisms, and certainly for the YNP bison, this is not a tenable assumption. A more reasonable assumption, which is likely to apply to a broader class of data sets, is that there is a common distribution that sightabilities active during each count are drawn from. A flexible distribution often used to describe probabilities is the beta distributions. If one assumes that sightability is drawn from a beta distribution then with the binomial sampling inherent in each count, then replicate counts will be distributed as a compound distribution known as a beta-binomial (McCullagh and Nelder 1989).

Although one can explicitly write out the probability density function of the beta-binomial, one cannot find a maximum likelihood solution for the population N. This is because N represents the boundary of possible observations. Maximum likelihood theory does not handle boundary parameters well. In this case, if one tries to estimate N by maximizing the likelihood, the estimate either goes to infinity or to the observed count.

An alternative estimation technique was invented in the early 1980s called the Maximum spacing product (Cheng and Amin 1982; Ranneby 1984). This method was explicitly designed for boundary problems. This method has not been employed often, primarily because it is massively computational. The estimation is based on an optimization that at each step requires numerical integration.

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We implemented the algorithm on the Montana State University's Center for Computational Biology thirty-two processor super computer, and were able to obtain results. A paper by Mark L. Taper and Brian Dennis describing these procedures in detail is in preparation.

To utilize the beta-binomial model, we need replicate counts that all estimate the same population size. Thus, we restricted ourselves to counts that occurred between August 1 and December 31 for each year. This is a period after the pulse of peri-natal mortality and before winter mortality. Over the time course, there is no discernable tendency for a year's maximum count to fall in any particular portion of this period. This gives credence to the assumption that sightabilities are drawn from a single distribution.

The estimation requires a large number of replicate counts to achieve good results. We can greatly improve our efficiency by assuming the sightabilites for counts from a number of years are all drawn from the same distribution.

Results

Protracted growth

The most striking feature of the population growth presented in Fig. 3 is the protracted period of positive growth. In a two-decade period from 1970 until 1980, the population suffered only four years in this period with negative growth rates. This extended period of positive grow is demonstrated whether one represents growth as a yearly exponential growth rate ($r=\ln(N_{t+1}/N_t)$, Fig. 5) or as an additive growth increment ($\Delta N= N_{t+1}-N_t$, Fig. 6).

Fig. 5. Near here.

Fig. 6. Near here.

Density dependence

Density dependence regulation is a negative relationship between growth rate and population density. Visual inspection of Fig. 7 confirms such a negative relationship, as does the regression analysis in Table 1. Standard regression significance tests are not appropriate for the analysis of population dynamics (Dennis and Taper 1994), and therefore the P values have been deleted from the Table. The P-value for the Dennis and Taper Parametric Bootstrap Likelihood Ratio test (PBLR) is estimated as 0.067 using a bootstrap of 40,000 trials. Although we believe that density is the appropriate scale on which to test for density dependence as apposed to raw counts, in this case, the significance of the test is not dependent on our having transformed counts to densities. An even lower P-value (0.0056) was obtained when we tested the relationship of r and maximum counts. The estimation of maximum area introduces added error variability in the density estimates beyond that found in the raw counts. Surveys are taken only intermittently. It is extremely unlikely that the winter's maximum area actually coincides with a flight. Measurement error in the independent variable in a regression will generate a bias that reduces the steepness of slope (Taper and Marquet 1996), and may reduce power in testing for density dependence if very large.

Fig. 7. Near here

Table 1. Near here

Fig. 7, which plots growth rate against bison minimum winter density, indicates density dependence in the population. Nonetheless, there is considerable residual in Fig. 7 and Table 1 unexplained by density. A number of the extreme growth rates are associated with known extreme environmental events such as hard winters, late springs, or major firestorm. Although not all major environmental events appear as outliers (e.g. 1982), this pattern suggests environmental events play a role in bison population dynamics as well as density. Environmental covariates will be investigated more fully when the historical winter severity data set becomes available.

Fig. 8. Near here.

Fig. 8 allows us to estimate an ecological carrying capacity by relating the density (5.2 bison per square kilometer) at which a zero growth rate is achieved to the number of bison expected for such a density. If we include all observations, we estimate a carrying capacity of about 3200 bison for Yellowstone Park. This number must of course be taken with a grain of salt. It essentially assumes that a bison impermeable barrier is erected around the park. This has been the case in the last decade, and the effects of management reductions at the park boundaries are included in this estimate. A further implicit assumption is that environmental conditions and habitat quality will continue as they are into the future.

Expansion

The area occupied by the Yellowstone bison herd has increased steadily over the period of this analysis (Fig. 9).

Fig. 9. Near here.

Fig. 10 plots the area occupied by the Yellowstone bison herd in winter against herd size. The correlation is obvious and striking. The conclusion we draw is that one of the major density dependent responses bison exhibit is range expansion. As population size increases, range will increase – if it can. This observation allows us to estimate another number we might call a social or management carrying capacity, where bison densities are low enough that ecological conditions do not produce pressures for range expansion that outweigh the species' natural tendency for aggregation. One might call this balance a bison "comfort level". In 1984, the bison herd expanded to the borders of Yellowstone Park and began to suffer management reductions. The herd's maximum range that winter is estimated at 675 sq. Km. Using Fig. 10 we can estimate a herd size of approximately 2800 animals below which we would not expect ecological impetus for significant wandering beyond park boundaries under current environmental, habitat, and management conditions. Nonetheless, if the bison use of their habitat has a substantial learned component, there may be a long period of hysteresis after the bison herd has been reduced to this level during which management action may still be necessary if the herd is to be maintained within the park's boundaries. The figure of 2800 may be somewhat high. In 1984, winter conditions were very favorable (two years of warm winters and wet springs). The density of animals sustainable under those conditions may have been higher than under conditions that are more normal.

Fig. 10. Near here

We have only indirect evidence in the data set for habitat degradation. Nonetheless, these figures indicate the current population is possibly being maintained at a level above the population's "comfort level". Further, the population has gotten as large as 50% above this "comfort level". We believe it is therefore reasonable to consider the risk of degradation.

Impacts of human use of interior roads in winter

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In Fig. 11 we see population density as a function of year over the study period.

Fig. 11. Near here.

Remember, from 1970 until about 1990, population size is more or less steadily increasing. What is apparent in Fig. 11 is that until about 1981, as population size increased, density increased. After about 1981, we have a shift in this relationship, and density remains roughly constant as both population size and herd range increases. One interpretation of this pattern is that the Yellowstone bison herd was more constrained on the winter landscape before 1981 than it was afterwards

Although over-snow vehicle use of interior park roads began much earlier (Yochim, 1998), such use increased steadily and expanded geographically during the 1970's. By the late 1970's, east side roads, including East Entrance, were being groomed several times a week, and being used daily (Meagher, unpublished data; Nat. Park Service snowmobile briefing books, 1976-1978, YNP research library). MM (Meagher 1998; Meagher et al. 1997) expressed the belief that the YNP bison appeared to reach ecological carrying capacity and fully occupied their habitat for the environmental conditions circa 1981.

This analysis does not directly implicate over-snow vehicle use and road grooming, it is possible that some other environmental, habitat, or behavioral change occurred at this time to reduce the constraints on the bison population.

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Nonetheless, the coincidence of spatio-dynamic transition with the increased use of interior park roads by over-snow vehicles lends support to this hypothesis rather than detracts from it.

Loose linkage of northern and central ranges

There is considerable spatio-temporal variation in bison abundance.

Fig. 12: Near here.

Fig. 12 plots smoothed curves of the proportional distribution of YNP bison among the five localities of Hayden Valley, the Firehole , west side areas, Pelican Valley, and the northern range. The raw data for this figure are the counts of bison in these localities recorded in the 149 complete flights by MM standardized by the total count for each flight. The flight standardization adjusts both for the population trend over the study period, and seasonal variation in sightability. The figure was produced in Systat 9 using a DWLS smooth with a tension of 1.

Bison habitat selection follows a trend throughout the year. Winter usage by bison is scattered through the park. Bison numbers concentrated on the northern range, Pelican Valley, and Mary Mountain (Hayden Valley, Firehole, west side). Prior to 1981, Hayden Valley and the Firehole traditionally had been a fluid wintering situation, with the bulk of the bison beginning winter in Hayen Valley and shifting to the Firehole during the season. (Meagher 1970, 1973,

1976) There was no use of the west side in this period. Bison begin to congregate through the spring and early summer until the rut where over half the total YNP bison population and three quarters of the central herd is located in Hayden Valley. Following the rut, bison disperse back to their winter usage areas.

Fig. 13 Near here

When the Pelican Valley, Hayden Valley, the Firehole , and west side groups are combined to form a central assemblage, the data show bison proportions remaining almost constant throughout the year (Fig. 13). The fairly steady proportions suggest that YNP has two largely independent herds of bison with a small amount of seasonal exchange over the study period.

These spatial relationships can be further documented in a correlation matrix. Table 2 lists the correlations among population sizes in the five geographical locations in YNP; four sites in the central range and the entire northern range. In order to adjust for population trend, all counts are standardized by that flights total count. The pairwise P=0.05 critical value for correlations with 149 observations is 0.162, while the Bonferoni corrected tablewide P=0.05 critical value for a table of 10 correlations is 0.230.

Table 2: Near here

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Table 2 indicates that there are marginal negative correlations between the northern range and both the Hayden and Firehole regions of the central range. These negative correlations may indicate a low level of exchange between the northern and central ranges through these sites. This would be in keeping with the observed bison numbers on the Mirror Plateau and in the region between Norris and Gardner 's Hole (Meagher 1970, 1973; MM unpublished data; J. Mack unpublished data; CLJ per. obs.).

These exchanges can be seen directly in the reciprocal changes in numbers between the northern herd and Pelican Valley that pepper the record (see Figs. 14 and 15).

Fig. 14 Near here.

Fig. 15 Near here.

Although Fig. 14 indicates that the magnitude of these exchanges has remained roughly the same, Fig. 15 shows that the proportional impact on the northern range has decreased as the populations have grown.

Figs. 14 and 15 can be used to make at least two other points about the period from around 1989. First, there is a dramatic increase in the use of the west side by the central herd, and, second, minimum winter occupancy of Hayden Valley decreases during this period. This decrease in the winter use of Hayden Valley may represent an environmental degradation signal.

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These statements about population transfer between the northern and central regions can be further quantified. For pairs of time-series where the only variation in population estimates results from measurement error and population exchange, it can be easily shown that the variance of the net number of individuals exchanged between the two populations per interval can be estimated as minus the cross-covariance of the differenced time series.

As discussed above, it is reasonable to assume that true population size in these bison herds changes minimally during the period from August 1 to December 31. Thus, these periods would be reasonable candidates for estimating exchange between the northern and central herds except number of counts within each year is far to low to be used to estimate a covariance reliably. To overcome this problem, we standardize each observation by the maximum total count (northern and central regions summed) for its year. This creates comparable quantities that can be averaged over multiple years. Covariances of the scaled differenced time series were calculated for each decade. The square root of minus each of these covariances is a coefficient of variation like quantity that estimates the standard deviation of exchanges as a proportion of total YNP herd size.

There are 38 useable pairs of differences over the entire time series, 10 in the decade of the seventies, 8 in the eighties, and 20 between 1990 and 1997. The standard deviation of proportional exchanges was 9.1% in the seventies, and 2.4% in the nineties. The covariance between the scaled differenced time series was positive in the 1980s, and thus cannot represent exchange. This highlights some of the limitations of these calculations. An assumption of the estimate is that the measurement errors in the northern and central regions are uncorrelated. Correlated measurement error would mask exchange. The positive covariance in the eighties is generated by a single flight (flight 62, 11/30/83). The original flight records confirm that counting conditions were suboptimal for both regions on that flight. Without this transition, the remaining scaled differences in the eighties also exhibit a weak but negative covariance between the two regions (standard deviation of proportional exchanges=0.8%).

One can get an indication of the direction of exchanges by taking differences between the two differenced time-series. This indicates that in the seventies all estimated exchanges during the observation period of August 1 through December 31 were from the northern region to the central region. However, during the nineties the observed exchanges were in both directions.

Because it appears the northern and central herds have only a weak connection, independent analysis of these two segments of the population adds further insight.

Fig. 16 near here

Fig. 17 near here.

Both Fig. 16 and Fig. 17 show sustained and parallel population growth throughout the entire period, particularly when one considers the 569 bison removed from the northern herd in the winter of 1988-1989. Further, the regressions of growth rate versus minimum population density in the two regions yield very similar estimates of the intercept (intrinsic growth rate) and slope (strength of intra-specific competition). However, because there is much more residual variability in the northern range the regression is not significant for the northern range. This increased variability in the northern range is potentially interesting. It could be nothing more than an artifact of smaller sample sizes in the northern herd. This is not a likely explanation, because measurement error would tend to reduce the slope of the regression and the northern herd has demonstrates a slightly steeper slope. Another explanation is that the low level exchanges between the two regions have a greater impact on estimated growth rates in the northern herd because of its smaller size. On the other hand, this greater variability may indicate that the northern herd is actually more susceptible to environmental variation. The thermal features utilized by the central herd in winter may buffer the central herd from extreme winter conditions. This is a hypothesis that can be more fully explored once winter severity data is available.

Table 3. Near here.

PBLR 2 Tailed Test $P<0.2$ based on 40000 bootstrapped time-series

Table 4 near here.

PBLR 2 Tailed Test $P<0.73$ based on 40000 bootstrapped time-series

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The most striking difference between the central and northern ranges is seen in the pattern of density increase through time. As shown in Fig. 18, the pattern of the central range mirrors that shown for the total population in Fig. 11.

Fig. 18 near here.

However, in the northern region (Fig. 19) densities show a gradual increase through time. Road grooming activity and over snow travel by people is concentrated in the central region, and thus the discrepancy in the density patterns through time is consistent with a causal influence of interior winter road use.

Fig. 19 near here.

Observed bull proportions through time.

Bulls are identified in the data record. However, this record was made in aerial surveys. Identification of bulls from the air is not as clear as from the ground. In the Meagher record, animals with uncertain sex were classified as “unknown”. Thus, the observed proportion of bulls will in general underestimate the true proportions. Furthermore, as Fig. 20 indicates the ability to discriminate the sexes varies over the year. Discrimination ability is lowest during the breeding season when it is difficult to get an uninterrupted view of many animals because of the tightly knit groups at this time.

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Fig. 20 near here

Fig. 21 plots the proportion of all observations for a year that are bulls for the central and northern regions. This figure indicates that there is no trend in bull proportions over the study period. However, bull proportions will respond to episodic environmental conditions with a rapid rise. In between these acute events, bull proportions gradually declines to a background level of about 10%. The large year-to-year fluctuations in the observed proportions almost certainly have to do with changes in the timing of counts and thus in the ability to discriminate the sexes rather than upheavals in the demography. In the 1990s, when counts were made much more frequently throughout the year, these fluctuations are absent.

Fig. 21 near here

Social aggregation

Group size

Group size is heteroscedastic and not normally distributed. An analysis of Box/Cox transformations indicates that the square-root transformation is a useful transformation, improving both normality and reducing heteroscedasticity.

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Seasonal patterns

Fig. 22 plots the square root of mean group size by bimonthly blocks. Error bars are scaled to the standard errors. Bison mean group size shows a clear seasonal pattern. Peak group size occurs during the breeding season in August, while minimum mean group size occurs in the early spring.

Fig. 22 near here.

Changes by decade

The changes in mean group size are presented in Fig. 23. The 1980s have a slightly greater mean group size than do the 1970s, but this difference is not significant. The mean group-size in the 1990s is significantly less than that of the 1980s. However, over all, all three decades are quite similar in mean group size.

Fig. 23 near here.

Shifts in seasonal patterns by decade

The seasonal pattern presented in Fig. 22 is a composite of all data from the entire time course. When seasonal patterns are viewed by decade (Fig. 24), all decades of course retain the peak in group size during the late July/early August breeding season. The decades do differ in how quickly mean group size declines after the peak. The decline in the 1980's is slowest, while the decline in the 1990s is most rapid. The 1970s are clearly intermediate. Unfortunately,

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because there were few late summer counts in the 1970s, it is difficult to say whether the 1970s are more similar to the 1980s or the 1990s.

Fig. 24 near here.

The changes in group size through time and the seasonal shifts in group size through time may be subtle signals of environmental degradation. In this interpretation, the forage base is less able to support large groups during the breeding season. This concept that the population density of a mobile species could be used as a measure of the unfavorableness of the local environment was pioneered by Morisita (1970). Unfortunately, his quantitative measures of "environmental density" were developed for species with either repulsive or congregation behavior, but not both.

Dispersion

We have another window into bison aggregation behavior in the dispersion variable. This variable describes the average inter-animal distances in groups, and takes values 1, 2, and 3. Thus, the most cohesive groups are coded 1 while the most dispersed groups are coded 3.

There are a few caveats that must be raised about this variable: 1) Inter-animal distance was not measured in a quantitative fashion, but does represent the gestalt impression of an experienced researcher. 2) Group sub-structure makes this a difficult variable to estimate and interpret. 3) Not all group observations have a recorded dispersion. It is obvious that these are not "missing at random". Instead, small groups have a greater probability of missing the dispersion variate than do large groups. Non-randomly missing variables can skew statistical analysis, but because less than 5 % of observations are missing the dispersion variable, this in not likely to be too much of a problem.

Group size/Dispersion negative association

Averaging over all data, there is a clear and significant negative correlation between group size and dispersion (Fig. 25). In general, large groups are tightly cohesive, and small groups are more dispersed.

Fig. 25 near here.

Increase in large dispersed groups through decades.

Over the decades, groups of dispersion 1 and 2 remain more or less constant in size. However, interestingly, the mean group size of highly dispersed groups increases significantly (see Fig. 26).

Fig. 26 near here.

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Seasonal changes in dispersion through the decades.

Fig. 27 shows group size as a function of season, dispersion, and decade. During the 1970s and 1980s, tightly cohesive groups (dispersion=1) peak in group size during the August breeding season, groups with dispersion=2 peak in size during the fall, and highly dispersed groups have approximately constant group size over the year. In contrast, during the 1990s, the peak group size for groups with dispersion=2 shifts forward to the breeding season, while a clear peak in group size of dispersion class 3 also appears during the breeding season.

As with the changes in group size, the changes in the group dispersion patterns may indicate that a change in the forage base is forcing the YNP bison into less cohesive groups during the breeding season than is their natural predilection. They also seem to be breaking their social bonds earlier in the season in the 1990s than they did in either of the preceding decades.

Fig. 27 near here.

Photographic Record of Habitat Changes

Some information on apparent habitat degradation in YNP generated by bison land use can be garnered from the comparison of photographs taken over a span of 85 years.

Fig. 28 near here.

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Fig. 28 (a,b,c,d) lookss south across Fountain Flats in the Lower Geyser Basin, Firehole area. Dates: Sept.1912, 26 Aug.1971, 6 July 1991, 20 Aug.1997. Photos by (a). U.S. Army Engineers. Photos (b-c) by M. Meagher, (d) by M. Meagher/ R. Renkin.. Views a-c Meagher and Houston (1998:plate 32:76-77).

The comparative views show an extensive geothermally-influenced flat that had been an important wintering area for bison at the time the park was established (Meagher 1970, 1973). However, bison were exterminated from the Mary Mountain complex sometime in the mid-1890s (Meagher, 1970, 1973). Seventy-one bison were reintroduced to the area from the northern range in 1936 (Skinner and Alcorn, 1942-1951). Thus bison had been absent from the area of these photographs for almost two decades when the first picture was taken, and had been present seasonally for 35, 55, 61 years at times of the second, third, and fourth photographs respectively. This area has also been subject to variable mixed grazing throughout the entire period (horses, dairy cattle, elk). Note the grazers in the 1912 photograph are cattle. Further, it should be recognized that climate has not been constant over the period of these pictures. The area generally was much cooler and wetter during the 1890s (Meagher and Houston 1998) and those influences are reflected in the Fig. 28a. Thereafter the general climatic trend was to warmer and drier conditions. Between views b and c conditions varied annually but the winter of 1990-1991 was roughly 75% of the long-term average for the Old Faithful snowcourse. This is reflected in the 1991 retake (view c), with more areas of whitish-appearing geothermally-influenced soils exposed. However, after 1991 it became increasingly apparent during air surveys that more than climatic trend might be involved. There appears to be little difference between views c and d, but the climatic conditions, especially winter precipitation as snow, were quite different. Compared to the below-average snowpack conditions of winter 1990-1991, the snowpack for 1996-1997 was exceptional. The Old Faithful snowcourse record showed 241% of the long-term average for the January 1, 1997. During the summer, moisture and temperature conditions combined for an excellent vegetative growing season. Yet, the 1997 view looks comparable to the 1991 view, recognizing that the 1991 scene was photographed earlier in the season, while the timing of the 1997 view reflected the maximum expression of growth in grasses, grass-like plants such as sedges (*Carex* sp), and forbs.

Estimated sightability

The central range

We begin the sightability analysis by checking the assumption that sightabilities are drawn from a common distribution. We do this by fitting the beta-binomial observation model to 5 year blocks of data. The estimated mean sightabilities are shown in Fig. 29. The estimates for the last 5 blocks are very consistent indicate that for this period, it is reasonable to assume a constant mean sightability.

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Fig. 29 near here.

We confirmed that the transition in sightability is between 1974 and 1975 as shown in Fig. 29 by comparing estimates for a 4 year block from 1970-1973, and the 5 year block from 1974-1977 with the 1970-1974 and 1975-1979 blocks. In the 1970-1974 “learning period” the estimated mean sightability was 0.70 with a variance in sightability of 0.049. After 1974, estimated mean sightability is 0.88 with a variance in sightability of 0.014.

Fig. 30 near here.

Fig. 30 plots population sizes estimated by the beta-binomial observation model and maximum counts by year for the central range. Note that after 1974, the discrepancies between the two sets of estimates are small. Naively, one might think that the difference should be 12 per cent. This is in fact the discrepancy when the maximum count is based on a single observation. However, because in general the maximum count is the highest of several observations per year it does considerably better than the mean sightability.

The northern range

A similar pattern is found in the northern range. The “learning period” extends to 1975, but in the residual seems to be satisfactorily described by a single distribution. Sightability is lower in both periods than it is in the corresponding period for the central range. Mean sightability in the 1970-1975

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period is estimated as 0.46 with a variance in sightability of 0.096. In the period from 1976-1997 mean sightability is estimated as 0.77 with a variance in sightability of 0.053.

Fig. 31 near here.

Fig. 31 shows the beta-binomial observation model population estimates and the maximum counts plotted against year for the northern range. In this case, due to the much lower estimated sightability in the “learning period”, there is considerable difference between the maximum counts and the estimated population sizes for the 1970-1975 years.

One consequence of the low sightabilities in the northern range during the 1970-1975 period is that the densities shown in Fig. 19 for this period are probably too low. Given this is the case; density in the northern range may be more or less constant over the entire observation period.

We do not actually make this correction because density is the ratio of population size to area occupied. While we have developed a correction for population size, we do not have any explicit way of knowing how the locations of the unobserved individuals would affect our estimate of area utilized.

DISCUSSION

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It is apparent that over the time spanned by the Meagher data the Yellowstone bison population has undergone major changes in numbers, distribution and seasonal movements, range expansion, and density dependent dispersal. The use of sections of the winter road system of the park's interior as travel linkages, possible habitat degradation and potential effects on other species are addressed in this report. Because these various topics are interrelated and the causal factors interactive, the description is complex.

Numbers

Bison numbers park-wide generally increased after the cessation of management reductions in 1965-1966, left a park-wide population of 397 in 1967 (Meagher 1970, 1973). In 1970, at the beginning of the time-series analyzed, the park-wide population was 476 (Appendix Table 1). The population increase continued until 1994 (Figs. 2 and 3), with a high count of 4114, after which a decline began, followed by the sharp decrease in 1997 to 2992. Causative factors and influences for these changes has varied over time and between geographic locales.

Northern winter range numbers increased (Appendix Table 3) after the last management reduction there in the winter of 1964-1965 left less than 100 bison (Meagher 1973). The winter of 1975-1976 was severe, with a very dense snowpack that formed the lower layers after two arctic storms followed by thaws occurred during the middle part of November. Winterkill was limited, with 7 recorded inside the park and 8 shot outside. Instead, the bison responded by

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moving. Conditions appeared to generate a stress dispersal and range expansion (Meagher 1989). Subsequent numbers have been variable but higher than the roughly 200 bison (max. count 182, flight 30) that comprised the population at the beginning of the 1975-1976 winter. Management removals by the State of Montana outside the park's north boundary that began in 1985 (88 removed that year) have complicated the numerical record, as have shifts between the northern and central herds (see below).

The decade of the 1970's appeared to be one of interior population units (Mary Mountain, Pelican Valley) fully occupying their winter habitat after the management reductions of the 1960s. Combined numbers totaled 2067 (Appendix Table 2) prior to onset of winter. Mortality for winter-spring 1982 in the park's interior was the highest recorded (303) during the study. For four years afterwards combined numbers for the two units totaled less than 2000 (Appendix Table 2***).*** Numbers again increased until the winter of 1988-1989, after the fires of 1988 combined with drought and an above average snowpack (130% on the Lake snowcourse for March 1, 1989). The combined numbers then decreased by about 200 bison (Appendix Table 2). Interestingly, in contrast to the apparent effects (above) of winter in 1981-1982, the population decrease occurred for one year only. Also, recorded combined mortality for Mary Mountain and Pelican totaled 296 bison, in spite of a park-wide population that had a nearly 150% increase compared to 1981-1982 (Appendix Table 1). Thereafter, numbers increased in the interior to a combined count of 3376 in 1994, after which decline

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began (Appendix Table 2). A combination of changes in distribution and range expansion (see below) appears to have been involved.

Distribution and seasonal movements

Distributional analysis focused on mixed groups. Separated males, usually adults, often travel widely and are considered *"wanderers"*(see **Data collection**). Historically, the bison mixed groups of YNP centered on the three winter locales of Pelican area, and Mary Mountain (Hayden Valley-Firehole), and the northern range (Meagher 1970, 1973). After extermination within the park except for the Pelican area, bison were reestablished on the northern range in 1907 (the old Buffalo Ranch), and from there, hauled by truck to reestablish the Mary Mountain population unit in 1936 (Skinner and Alcorn 1942-1951).

Through the 1970s, after bison again occupied the several winter ranges within the park, the distribution continued to focus on these several winter ranges with a repetitive and fairly predictable pattern of seasonal movements (Meagher 1970, 1973). The predominant patterns are described here briefly for comparison with the changes that began in the 1980s and continued into the 1990s.

Northern range bison (Lamar) mainly wintered in the lower Lamar Valley east of the Yellowstone River at Tower to the Lamar Canyon (e.g. flight 16, 2/14/73) until 1975, when winter range expansion began as numbers increased (Meagher 1989). See **Range expansion** below. By the last week of May or the first week of June, the northern range bison moved 19-24 km eastward to the lower subalpine meadows of the Cache-Calfee ridge of the east boundary

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Absaroka Mountains (e.g. flight 13, 6/14/72). As summer progressed into breeding season the last half of July they moved further up the ridge, reaching the crest of the east boundary at 2900-3000 m most years (e.g. flight 14, 7/29/72, where they intermixed with the Pelican bison. By early August, some groups would come down the ridge and cross westward to the rim meadows of the Mirror Plateau. Although groups sometimes visited the Lamar Valley briefly, they did not linger. Shifts back and forth between the Mirror Plateau and the Cache-Calfee ridge occurred until storms brought the bison down to the Lamar Valley for the winter, usually by late November (e.g. flight 15, 11/28/72).

The Pelican area bison wintered mainly in the eastern two-thirds of Pelican Valley (e.g. flight 16, 2/14/73). However, as winter progressed, groups began to fragment and mixed group members would be located as singles or a few animals, commonly in geothermally-influenced sites where snow depths are less and some ground may remain snow-free (Meagher 1973: Fig. 46, p. 103). Shifts toward summer range usually began during the first week of June with groups moving to upper Pelican Valley (e.g. flight 24, 6/10/74). Later, sometimes as late as mid-June, groups would cross the Mirror Plateau and the upper Lamar River, and move also to lower subalpine meadows of the Absaroka Mountains. From those areas they would mimic the shifts of northern range bison (see above) and intermix with those groups to some degree (e.g. flight 25, 7/29/74). During this time, bison that had wintered on the northern range could not be distinguished as individuals within the groups. After shifting back to the rim meadows of the Mirror Plateau, bison moved for the winter to Pelican Valley,

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usually during the first two weeks of November. Movements did not occur westward

Hayden Valley and the Firehole functioned in winter as two parts of one geographic unit, which we term the Mary Mountain complex . In most years, some bison groups appeared on the Firehole side by early fall (e.g. flight 5, 10/14/70), but the majority stayed in Hayden Valley most of the winter. As numbers increased in the 1970's, two-thirds to three-quarters of the Mary Mountain bison would begin the winter in Hayden Valley, but as winter progressed and snow depth and density increased, the reverse distribution would occur as bison groups moved into the Firehole. Movements westward across the Mary Mountain divide continued throughout winter (e.g. flights 15, 16 and 17 on 11/28/72, 2/14/73 and 5/29/73). Occasionally, groups moved back to Hayden Valley during the winter, or shifted back and forth (Aune 1981; Meagher 1970, 1973). All the Mary Mountain bison concentrated during the breeding season in Hayden Valley, but stayed west of the Yellowstone River (e.g. flight 19, 7/27/73).

Beginning in the 1980s, winter use patterns for the bison underwent a westward expansion (see **Range expansion** below). Although on the northern range, the bison continued to use the Lamar Valley areas, movements westward to lower elevations became predictable. Because of the existence of the park's boundary and different management objectives outside the park, bison were either hazed back into the park or shot. These practices effectively truncated the herd's natural expansion at the park boundary (e.g. flight 59, 2/6/83). If this were not the case, the changes suggested that this population unit would be one that

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migrated more readily according to winter conditions (comparable to the northern Yellowstone elk, Houston 1982), and that mixed group use might be infrequent in the Lamar Valley toward late winter.

Numbers that began the winter in the Pelican area became higher, changing from the nearly 400 that wintered there at the beginning of the 1980's to generally higher numbers, such as the 547 recorded for November 19,1987, 585 on December 6,1990, 730 on November 3,1991, and an incredible 1123 for flight 125 in December 1994. Bison continued to use the Pelican area as winter range. However, their numbers became more variable year to year. Further, the numbers of bison in the Pelican area would decline throughout each winter during this period. (see **Range expansion** below) Although winter use of the Pelican area by bison continued, the ease with which bison left the area and moved to the Mary Mountain complex resulted in the Pelican area becoming a part of what is now designated as the central herd for analysis purposes. Functionally, by the mid-1990s, the Pelican area was no longer serving as winter range as it had in the past (compare flight 134, 2/11/96 with flight 28, 2/17/75) .

Summer range use patterns changed rather abruptly for the northern range and Pelican area bison. Flight 61 (7/22/83) was the last aerial survey during which bison were seen as high as the east boundary meadows. Information provided every summer from the frequent grizzly bear air surveys (D. Stradley, pers. comm. to MM) and from the park's air operations office (which supervised the park 's summer contract helicopter) also never reported seeing groups there after 1983 (pers. comm. to MM). Although bison mixed groups had been seen briefly (12-24 hrs.) in past years sometimes in summer in the Lamar Valley, apparently traveling through (Meagher 1970, 1973), in 1984 large aggregations became an annual feature of breeding season. For example, flight 65 of 8/9/84 located approximately 400 bison down along the Lamar River. Nineteen-eighty-five was the last summer some bison groups apparently from the Pelican wintering area (based on location and timing) were seen east of the upper Lamar River (D. Stradley, pers. comm. to MM). Thereafter, bison that wintered in the Pelican area apparently ceased to cross the Mirror Plateau in spring, summering only on the Mirror Plateau and mixing to some extent (judging by aerial counts and distribution) with northern range bison in the Lamar Valley during at least a part of the breeding season. Numbers using the Mirror Plateau generally decreased as the Pelican wintering distribution became a fluid situation throughout the winter, compared to the situation that prevailed during the 1970's (see **Range expansion** below).

In general, the use of the Hayden Valley-Firehole parts of the Mary Mountain complex for winter range resembled that of the earlier period. As numbers increased, so did the distribution to the west of the Firehole, termed the *west side (*e.g. flight 75, 2/6/87*) (*see **Range expansion** below) . Numbers seemed to become more variable for locations, with a lot of moving around, especially between the Firehole and the west side.

Functionally, with the winter of 1991-1992, Hayden Valley no longer served as winter range in terms of numbers of bison and length of stay as compared to the earlier period (compare flight 91, 2/7/91 with, say, flight 45, 2/16/79).

In summer, for the Mary Mountain geographic unit, the general pattern prevailed of most bison that wintered in the several parts aggregated in Hayden Valley during breeding season (flight maps throughout the study, dated late July-early August, e.g. flight 138). However numbers there at the peak of breeding season about the end of July increased greatly. For July 29, 1981, 1461 bison were counted in Hayden Valley, 1609 on August 1, 1985, 2035 on July 31, 1987, 2585 on July 25, 1992, and 2775 on July 22, 1994. This last number was the highest recorded in Hayden Valley during the study.

Finally, a comparison of numbers and distribution of the Mary Mountain complex between the early 1980s and the end of the 1990s is striking. For December 9, 1981 (flight 55) the park-wide total was 2397 bison, with 1517 in the Mary Mountain geographic unit. After the mortality that occurred in winter-spring 1982 (see **Numbers** above), the November 14, 1982 (flight 58) total was 2245 with 1356 bison in the Mary Mountain areas of Hayden Valley and the Firehole. There were no bison west of the Firehole for those counts. In contrast, for December 4, 1997 (J. Mack, unpub. data), the park-wide count was 2105 bison. Of these, 1347 were in the Mary Mountain complex but 352 were <u>west</u> of the Firehole. Similarly, for December 10, 1998 (J. Mack, unpub. data), the park-wide count was 2203, with 1418 in the Mary Mountain complex. On this survey, 653 bison were in west side areas <u>west</u> of the Firehole. In sum, population size was

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comparable between the early 1980s and the end of the 1990s, but the proportion utilizing the west side had increased from nothing to hundreds.

Range expansion

Range expansion westward by northern range bison began the winter of 1975 when a mixed group moved to the meadows at Tower Junction (Meagher 1989). Thereafter as numbers continued to increase so did winter range expansion. The drainage of the Yellowstone River (Fig. **1**) forms a topographic and environmental gradient west across the northern winter range and northward into Montana. A range expansion could be anticipated to lower elevation wintering areas that have less snow.

The northern range bison probably would continue to increase in numbers and expand their range to form a population that extended northward into the Yellowstone River valley (Montana) to mimic the population that existed shortly before the park was established in 1872 (Meagher 1970, 1973). However, because of present-day conflicts with different land-use objectives north of the park's boundary, this has not been and will not be allowed (NPS 2000a).

The range expansion westward that has occurred in the park's interior is less predictable by comparison. No expansion occurred from Pelican Valley toward Hayden Valley between 1900-1936 although wild bison survived in the Pelican area and numbers increased after protection was ensured about 1900 (Meagher 1970, 1973) The two wintering valleys are approximately 18 km apart using the route westward through Fishing Bridge junction and north along the

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Yellowstone River. Trails in the snow made by a few bulls were seen in 1968 and a mixed group of about two-dozen was reported for 1956-1957 (Meagher 1970, 1973). More likely, the date was 1955-1956 (a hard winter according to snowcourse records), and this was a one-time-only exploration (see **Winter road use** below). During the earlier part of this study, bison would sometimes move directly from Pelican Valley through the Turbid Lake hot springs area to the geothermally-influenced Mary Bay on the shore of Yellowstone Lake, usually during April when the valley was still covered with deep winter snows, However, before 1980 mixed groups were not found west beyond the scattered geothermal areas on lower Pelican Creek, nor did they move westward along the lakeshore from Mary Bay. But on February 24, 1980 (flight 49) a mixed group was located several km. further west of Mary Bay but adjacent to the snow-packed road, and on February 22, 1981 (flight 53) a group was located for the first time near the mouth of Pelican Creek (see **Winter road use**), which indicated the beginning of a range expansion. Annually the aerial surveys over the Pelican area in late winter would find that the bison in this area would begin to break into smaller groups and scatter more widely. Pelican Valley is the harshest wintering area (snow depth and density, coupled with wind) for bison in YNP, and apparently in North America (Meagher 1970,1971,1973, 1976). Thus, winter conditions will be severe there for bison, relatively, even when snowcourse records are average or below average.

The Pelican area bison continued to expand their winter range westward, initially with more bison wintering on lower Pelican Creek near the mouth.

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Approximately 100 were located there February 18, 1982 (flight 56). On February 6, 1983 (flight 59), 30 were about one km north of Fishing Bridge on the east bank of the Yellowstone River. By February 1985 (flight 67), numbers and distributions suggested that some bison had moved the entire distance from Pelican Valley to Hayden Valley. The process of more bison moving further each winter was quite apparent by February 1988 (flight 79). As the frequency of air surveys increased in 1991, it became apparent that movement of bison groups from Pelican Valley to Hayden Valley continued throughout the winter, because Pelican area numbers decreased with each flight. For example, 730 bison were counted on November 3, 1991 (flight 95), but decreased to 235 by June 9, 1992 (flight 101). No significant winterkill was recorded, and the winter generally was below average on the Lake snowcourse (42% for April 1).

In spite of this expansion west and north to Hayden Valley, bison did not abandon the winter range in Pelican Valley. However, those that moved became a part of the Mary Mountain geographic unit, and remained with that unit into breeding season in July-August. They would then begin to move back to Pelican Valley, resulting in bison use by September of what had been winter range only (e.g. August 29, 1992, flight 103, 98 bison in mixed groups in central Pelican Valley).

For the Mary Mountain unit, range expansion began with the winter of 1981-1982. This winter was slightly above average severity with 112% of normal for February 1 at the Old Faithful snowcourse. The early winter aerial count was 1517 bison on December 9, 1981 (flight 55). For the first time during this study, on February 18, 1982 (flight 56), 49 bison were seen at Madison Junction. A review of subsequent air surveys showed a constant increase in numbers and amount of time during the year that bison were located west beyond the Firehole, even though numbers located there were variable between flights.

To summarize this section, bison numbers and distributions have shifted westward overall. This is especially striking in the central herd. When the Pelican bison began to move westward, they had a "domino" effect. Hayden Valley was already occupied by the numbers of bison that were "comfortable" at a given time. When more bison arrived, this bumped the system up, and for bison, the solution was to move westward to the Firehole, which was the traditional shift as winter progressed. In turn, these increased numbers on the Firehole led to the shift westward and northward from Madison Junction. But, more bison survived within the park, so the whole process developed a positive feedback leading to the recorded high count of 4114 in 1994. Thereafter total park numbers decreased, and this decline was accelerated in the severe winter of 1996-1997 as bison moving outside park boundaries were removed from the population by management action.

Density dependent dispersal

A review of the recent synoptic volumes in the field make it clear that little attention has been paid in the recent theoretical literature on spatial processes to density dependent dispersal and particularly to its consequences. Shigesada and Kawasaki (1997) devote only a paragraph to the process despite having written several of the few papers on the subject (Shigesada et al. 1979, 1980).

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Turchin (1998) devotes only slightly more space to repulsive interactions citing the Shigesada et al. papers and adding Gurtin and McCamy (1977) and Aronson (1980). Hanski and Gilpin (1997) has only one paper (Stacey et al. 1997) that discusses the phenomenon (see also Stacey and Taper, 1992). Neither Tilman and Kareiva's (1997) volume nor Maurer (1994) mention density dependent dispersal at all. However, despite this lack of theoretical interest in density dependent dispersal, it is seems clear that the bison range expansion under study is not the result of a diffusive process, but is the result of a density dependent dispersal. Typically in a diffusive process, the area occupied by a population grows quadratically with time. Fig. 9 demonstrates that growth in area is only linearly with time.(Shigesada and Kawasaki, 1997), this is in keeping with Aronson's prediction that the growth in area should be slower in the case of density dependent dispersal than in the case of density independent movements. In a diffusive process, individual movements are random in direction and constant in probability. Further, in diffusive spread, the locus of current dispersal serves as a starting point for future dispersal. But, as described above the YNP herds coalesce each year in their breeding grounds. The animals then expand throughout the year directed by their knowledge of the landscape and driven by density. Guo et al. (2001) in a modeling exercise comparing density dependent and density independent dispersal find substantial differences in the behavior of the spatial population dynamics of models having these two forms of dispersal. One finding in Guo et al. is that the area utilized by a species with density dependent dispersal should be more sensitive to environmental fluctuation than

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for species with density independent dispersal. Another relevant prediction from Aronson (1980) is that the boundaries of species with density dependent dispersal should be much sharper than species with density independent dispersal.

Density dependent dispersal is not the only process shaping the bison Congregation has a much richer theoretical literature than does density spatial distribution, congregation behavior is also clearly important (see extensive reviews in Shigesada and Kawasaki (1997) and in Turchin (1998). What is missing from the literature is a treatment considering the balance between these two forces. It seems apparent that progress in modeling bison spatial distributions will only come from models incorporating both important features of bison spatial biology.

Winter road use

Bison are legendary for their ability to develop travel routes that left well-entrenched trails across the landscape. As reviewed by Roe (1970) historical accounts indicated considerable variability in route existence and quality according to the locale and habitat reported, but in places bison trails were the best routes and were preferred for use by people. Route existence and quality undoubtedly reflected local land-use patterns of the bison, which is true also for YNP. When bison move as a grazing front (McHugh 1958) travel trails would not be created. But when they travel with a destination in mind they create heavily used trails (Meagher 1973:Fig. 50, p. 107), because commonly they travel in line.

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In snow these trails can become well-defined trenches (Meagher 1973:Fig. 25, p. 73). During the northern range expansion, travel routes could be seen easily in winter from the air (Meagher 1989).

Bison are demonstrably stolid by temperament (Meagher 1998) and in the popular perspective may be judged as stupid (Roe 1970). Indeed, this stolid temperament was the basis for the “stands” described by the buffalo hunters of the Great Plains (e.g. Mayer and Roth 1958; Roe 1970). The combination of temperament and travel mode suggests that they are well suited for the use of sections of roads at times. Indeed, a group of two-dozen bison was observed in spring 1963 (MM pers. obs.) traveling the bare paved road westward through the Lamar Canyon. By comparison, elk were never seen to behave comparably during 40 years of fieldwork (MM pers. obs.). For stolid-tempered bison, parts of a road system can provide an easy travel route. Several times during the first decade of this study bison were seen on roads during air surveys. On February 14, 1973 (flight 16) 13 were on the bare pavement at Mud Volcano. Beyond the geothermal area, deep snow would have precluded further travel. On flight 23 (April 24, 1974, after the snowplows had opened that section of road during spring plowing) two small groups of eight and four each were eastbound on the road at Sedge Bay. On May 1, 1976 (flight 33) 3 bison (likely bulls) were on the plowed road north of the Lake-Fishing Bridge junction. Road use such as the foregoing is likely to be critical during stress induced exploratory dispersal. Without a prior destination, exploratory travel is likely to utilize the energy efficient plowed or snow-packed roads.

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For a road section to serve as a good travel route, it appears that there are tradeoffs between the effort of travel and the benefits to be had. For example, on March 24, 1992, approximately 60 bison were seen by the park's snowplow crew to leave Mary Bay near Pelican Valley, travel west and then north on the plowed through Hayden Valley to Canyon Junction (J. MacDonald pers. comm. to MM). They then forced a trail northward through the unplowed snow that still covered the road that crosses Mount Washburn, reaching the northern range where the habitat was becoming snow-free. The plow crew followed the trench all the way as they opened that road later. It would appear that some adult cows, the leaders, were destination-oriented and headed north to a previously occupied locale. However, this movement did not become repetitive. Apparently the trade-offs of effort to reach a desirable destination, coupled perhaps with a lack of foraging sites en-route, resulted in what could be called an exploratory movement.

A similar situation prevailed for winter movements from Pelican Valley to Hayden Valley prior to the 1980's (see **Distribution and movements** above). In contrast, the route the bison use between Hayden Valley and the Firehole became a common one. Although this route traverses high ground and must be broken out in deep snow at times, it apparently offers the following advantages. Between Hayden Valley and the high ground of Mary Mountain the terrain slopes upward gradually. The route crosses fairly extensive geothermal areas on the east side, some of which offer at least limited forage, and certainly ease of movement. When west bound in winter, the dominant direction (see **Distribution**

and movements above), the route drops down across a relatively steep slope to arrive at more geothernally-influenced habitat. In addition, Nez Perce Creek remains open mostly because of warm water influx, and offers ease of travel.

The above review suggested that snow-packed interior winter roads that existed prior to the stress-induced movements by the Pelican area bison encouraged the beginnings of bison population adaptation in YNP to use of road sections as energy-efficient linkages between suitable locales and foraging sites to which movements might not otherwise become repetitive, especially by mixed groups. In the case of the Pelican bison, repetitive air surveys over time made it obvious that those bison did not access the area of the mouth of Pelican Creek by traveling down the drainage from Pelican Valley to Yellowstone Lake. Rather, they moved directly southward from the valley to Mary Bay via geothermal areas at Turbid Lake. Their trails could be monitored from the air. From Mary Bay, with the impetus first to explore because of harsh conditions and relatively limited forage at Mary Bay, they moved west. Movements escalated (see **Range expansion** above). As bison learned travel routes and destinations, more survived by moving to less-harsh conditions, and numbers increased. It appears that the impetus for the population change was triggered by the development of snow-packed energy-efficient interior roads. These were established shortly before the interactive factors of bison numbers combined with increasingly severe winter conditions (ECC for the particular circumstances) produced exploration. From a bison perspective, move and live if possible, or die.

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As bison numbers increased and population shifted westward, road use elsewhere became apparent. Nine hundred and sixty eight bison in 132 separate observations were seen on roads during aerial surveys between 1980 and 1997. Fig. 32 showing all observations clearly indicates that the only bison use of the region between the Firehole and Mammoth is associated with the west-side road.

Bison removal records (YNP bison management office) coupled with air survey results (MM) allowed an estimate of numbers of bison moving north on the road during the harsh winters of 1994-1995 and 1996-1997. In December 1994 (flight 125), 694 bison were recorded for the northern range. For May 9, 1995 (flight 129), 649 bison older than new calves were counted. Yet, 307 bison were removed by management action near Gardiner, Montana. A comparison of these numbers indicated that 250-300 bison must have moved north from the park's interior on the west side road. Similarly, an estimate of movement north on the road of 320-350 bison was derived for the winter of 1996-1997. On October 31, 1996 (flight 141), a northern range count showed 775 bison. On February 21, 1997 (flight 145), 194 were counted, and on March 11, 1997 (flight 146), 222 were counted. During the winter, 1123 bison were removed by management actions (including 39 live-shipped from the park for research), with 765 of these taken from the area near Gardiner, Montana.

An additional factor is relevant here. It is apparent that bison could survive by breaking social bonds and scattering in to small sites where a few animals could survive (see **Distribution** above). However, the gregariousness of bison is the stuff of legend—the huge aggregations reported for the Great Plains (Roe

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1970). Over time, it has become apparent that when bison are free-ranging and can move, they will move to stay together and maintain their social bonds, rather than scatter. This factor is fundamental to the ease with which bison began to use sections of road. When bison did this in the Pelican area, more of the population survived, and more bison moved to Hayden Valley. But, Hayden Valley was occupied, so more bison moved west, and developed habitual usage of road section usage, foraging sites, and attractive destinations. The population increased greatly, and shifted westward.

Stolid temperament, gregariousness, and the harshest wintering conditions (Pelican area), coupled with the establishment of a winter road system that produced improved travel linkages between places that bison wanted to be combined to produce the population changes we analyze. The ability of bison to learn dictated that they not only moved from harsh conditions, but over time learned to move to earlier spring greenup—just as the Pelican bison used to do when annually they crossed the Mirror Plateau to the slopes of the Absaroka Mountains of the upper Lamar country.

Habitat degradation in the photographic record

The photographic record (Fig. 28) documented a visual change in habitat during the period 1912-1997. This area is winter range for both bison and for a part of the Madison-Firehole elk. Elk numbers for the entire Madison-Firehole population appeared to be relatively constant at about 800-1000 from 1965 (Aune 1981 page19; Cole 1983 page66) through 1988 (Singer 1991 page 343;

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Singer and Mack 1993 pages78-79). Neither climate nor bison numbers have shown constancy. However, if the general trend to a warmer drier climate was the only factor involved, then the exceptional growing conditions of the season of 1997 should have shown a more extensive and dense vegetative cover, but this did not occur. Visually, conditions appeared comparable to those of 1991 when moisture conditions (winter snowpack,) were below average. Furthermore, from a descriptive perspective, to the experienced eyes of the long-term aerial survey team (Meagher and Stradley) conditions worsened between the end of June 1997 (flight 150) and the end of July 1997 (flight 151).

Regrettably neither soil nor vegetation transects exist for the area that pre-date the changes in bison distribution and time spent throughout the year. However, because of the increased amounts over time of the exposed whitish geothermal soils, these sites became a focus of interest. The soils of this flat are derived from parent materials comprised of hydrothermally-altered volcanic rocks and secondary mineral deposits from magmatically-heated groundwater (Wilson 1996). The area is characterized as being a neutral chloride alluvial area, with soils forming in siliceous deposits that are either hard platy materials or soft, slightly thixotropic deposits.(Thixotropic applies to certain clays in an alkali chloride solution that act as gels that become fluid when stirred or agitated, then set again when agitation ceases; Barnhart and Steinmetz 1986). Wilson (1996) further describes the soils as saturated with groundwater at ambient temperature, with both inorganic and biogenic silica deposits that accumulate to form soft, low-density aggregates of diatoms, plant opal, and inorganic flakes of opal-A. The matrix of this soil is white with upper horizons darkened by organic matter accumulation. The increase in expanses of white in the photographs suggests a loss of organic materials and a compaction of the gel matrix. Field reconnaissance showed that the white, exposed soils occur at sites that are lower by some centimeters relative to the areas that support vegetative cover. Preliminary infiltration tests showed that water passed relatively quickly into the soils where vegetation grew but pooled on top of the bare white soils by comparison. Furthermore, these sites with pooled water served to concentrate salts, with a potential for additional negative effects on adjacent vegetated sites. This information suggests the need for further research (A. Rodman pers. comm. to MM).

Bison numbers and presence during the years have changed dramatically since the 1971 photograph. Seventy-five bison were counted in the Firehole area on flight 6 of February 22,1971, with 286 by May (flight 7). Subsequent mid-winter and spring counts were variable but increased with mid-winter counts 0f 700-800 by 1980., and 838 on February 22,1981. On - February 7,1991 (flight 91) 516 were recorded but more moved in, as shown by a count of 1020 on May 16, 1991 (flight 92). Because of considerable movement in from Hayden Valley, and back and forth between the Firehole and the west side, numbers became more variable between flights and between comparably-timed flights but between years. However, on March 30,1995 (flight 128) 1186 were recorded from the air but with an additional 305 on the west side. On May 9, 1995 (flight 129) 976 were counted on the Firehole, and 860 on the west side. A review of all counts underscored that bison numbers and presence during much more of the year indicated a very large increase in bison use occurred during the 1980s, and especially the 1990s.

We suggest that the mechanical impact caused by greatly increased numbers of bison with their large cloven hooves and their presence for more of the year has led to compaction of these soils. The process would be facilitated by the combination of the mildly thixotropic characteristics of these soils coupled with both inorganic and biogenic silica in the soil matrix. The interaction of these factors apparently constitutes a soil change accompanied by a decrease in vegetative cover and forage for bison. Also, because the geothermal areas serve as a survival margin because of less-to-no-snow (Meagher 1970, 1973; Meagher and Houston 1998), bison concentrate at times in winter on these sites even when vegetative cover has decreased, causing the compaction process to continue. Compaction can continue in these areas even in winter, because expanses of the ground are kept from freezing by geothermal heat.

Effects on other faunal species

Bison are the only large ungulate population that winters in the areas of Pelican and Hayden valleys. Both bison and elk (*Cervus elaphus)* winter on the Firehole and west side areas. On the northern range, elk, bison, and 4 other species of ungulate populations winter (Houston 1982). However, only elk appear to be a species of possible concern for interspecific competition. On Yellowstone's northern range, elk and bison showed a pronounced ecological

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separation (Houston 1982) and lack of competitive interaction (Singer and Norland 1994) even though both species increased during the several study periods. Elsewhere there appeared to be considerable niche separation between elk and bison (Cairns and Telfer 1980, McCullough 1980, Telfer and Cairns 1979, Wydeven and Dahlgren 1985). However, these latter areas are fenced and large ungulate numbers are managed at levels probably below ecological carrying capacity. Niche overlap can be expected to increase as population sizes increase.

This question may require future evaluation for the Firehole and west side areas of the central part of YNP because of the bison population changes analyzed here. While bison numbers park-wide roughly doubled between 1980 and 1994 (see **Numbers**) the proportion of the total more than doubled for the population using the these areas (see **Distribution**). Additionally, the more recent aerial surveys documented the presence of bison in these locales for much of the year, not just winter. The relatively deeper snows of the park's interior would preclude populations of wintering bison and elk were it not for the presence of geothermal features and their influence on habitat as a survival factor (Craighead et al. 1973; Meagher 1970, 1973; Meagher and Houston 1998). These animals concentrate on these sites during more severe conditions (see **Habitat degradation in the photographic record** above**).** Ferrari (1999) found a spatial range overlap between the two species of 53-76%. The additive effects of the on-going changes in the bison population suggest that negative

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impacts upon elk might occur that would not otherwise be a consideration. We can only raise that question here; an answer will require future research.

Bison as a food source for threatened and endangered species may be affected also by changes in population distribution. Winterkilled bison are an important source of high-quality food for bears emerging from winter dens (NPS 2000a:76). Winterkill of at least a few bison (usually bulls) occurred on all winter ranges every year, but numbers increased considerably with severe winters (Meagher 1970, 1973, 1976). The first large episode of winter-caused mortality occurred during this long-term study the winter of 1981-1982. That winter was slightly above average in severity according to snow course data, but it occurred following two very mild winters (NPS 1984). Spring-early summer field surveys recorded 306 winter-killed bison carcasses; 66 of these were in the Pelican Valley area (NPS 1984:94-95). A recheck of carcasses throughout summer-fall indicated that all had been utilized to some extent by grizzly bears except some adjacent to roads where disturbance discouraged bear use. The actual mortality for the Pelican area was estimated from aerial bison counts to be much higher, between 200-250 bison. The biomass available to be utilized by grizzly bears was estimated to be at least 140,600 lbs. More recently, with the reintroduction of the gray wolf to YNP, four of 14 known kills of bison by wolves occurred in the Pelican area 1997-1999 (Smith et al. 2000). We cannot predict the specific effects, but in the absence of a wintering elk population in the Pelican Valley area, the changes that have occurred in bison numbers and distribution in recent years are likely to be particularly important in the future.

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Conclusions

The analysis of long-term data supports the following conclusions.

1. Regulatory mechanisms.

Even though the Yellowstone bison herd exhibits an extended period of what appears to be linear growth, this pattern can be explained with classical density dependent dynamics if one realizes that perhaps the primary response of the herd to increased density is range expansion. This response is seen throughout the history of the northern range bison. A secondary response in the harsh winter environment of the interior of YNP, seen in the 1970s, was to increase densities and incur winter mortality at irregular intervals in the absence of the physical ability to undergo range expansion. In this instance, the interior of YNP function as somewhat of an anomaly, because the annual winter snows would preclude population occupancy were it not for the geothermal history of YNP.

2. Spatial aspects of natural regulation.

However, several changes observed in the bison use of the Yellowstone landscape may be behavioral adaptations by the bison to environmental changes. These adaptations encompass the ability to lengthen or even break social bonds and form smaller groups than the highly gregarious bison “prefer”,

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and eventually to scatter as a few animals and individuals. These behavioral strategies may buffer, temporarily at least, bison population dynamics from the immediate repercussions of possible environmental stress and habitat deterioration.

3. Ecological carrying capacity.

The density dependent patterns of growth and range expansion lead us to estimate two separate carrying capacities for the bison herd in YNP. First there is an ecological carrying capacity that represents what we might expect the park to support if it were isolated or if the management reduction wall is maintained. This number is on the order of 3200 bison. A second capacity, which might be better called a social or management capacity, is about 2800 bison. This is a level below which we would expect bison to only rarely leave the park due to ecological pressures. Both estimates should be regarded as indications rather than hard numbers, and may be high by as much as four or five hundred bison. Both estimates presuppose environmental conditions will remain as they have been in recent years and, contrary to the indications given above, habitat degradation will not occur.

4. Effects of bison use of interior winter road sections as travel linkages.

There do appear to be indications of changes in the bison dynamics that are associated with increasing use of sections of the interior road system in winter.

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5) The possibility of habitat degradation is indicated. The signals of range degradation that we have identified in the data are 1) a decrease in the winter use of Hayden Valley.; 2) a decrease in mean group size through time; 3) an increase in the group size of highly dispersed groups; and 4) an earlier breakdown in the 1990s of the breeding season aggregation. 5) Increase over an 85 year photographic record of bare ground in the Lower Geyser Basin of the Firehole area.

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(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

Literature cited:

Aronson, D. G. 1980. Density-dependent interaction-diffusion systems. Pp161-176 In *Dynamics and modeling of reactive systems.* (W. E. Stewart, W. H. Ray, and C. C. Conley editors) Academic Press, New York.

Aune, K.F. 1981. Impacts of winter recreationists on wildlife in a portion of Yellowstone National Park. MS thesis. Montana State University. Bozeman. 110 pp.

Barnhart, R.K. and S. Steinmetz, eds. 1986. *Dictionary of science*. Hammond-Barnhart. Maplewood, NJ. 740 pp.

Cairns, A.L. and E.S. Telfer. 1980. Habitat use by four sympatric ungulates in boreal mixedwood forest. J. Wildl. Manage. 44:849-857.

Calef, G.W. 1984. Population growth in an introduced herd of wood bison *(Bison bison athabascae)*. Pp. 183-200. In: *Northern ecology and resource management*. R. Olson, F. Geddes, and R. Hastings, eds. U. Alberta Press. Edmonton. 438 pp.

Carbyn, L.N. 1993. Wolves, bison, and the dynamics related to the Peace-Athabascae delta in Canada's Wood Buffalo National Park. Circumpolar Research Series No. 4. Canadian Circumpolar Institute. U. Alberta, Edmonton. 270 pp.

Cheng, R. C. H., and N. A. K. Amin. 1983. Estimating parameters in continuous univariate distributions with a shifted origin. J.R. Statist.. Soc. B. 45:394-403.

Cole, G.F. 1983. A naturally regulated elk population. Pp.62-81. In: Symposium on natural regulation of wildlife populations. F.L. Bunnell, D.S. Eastman, and J.M. Peek, eds. Proceedings of the NW Section of the Wildlife Soc., March 10, 1978,

(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

Vancouver, B.C. Forest, Wildlife & Range Exper. Station. Univ. Idaho Proceedings. 14, Moscow, ID. 225 pp.

Craighead, J.J., F.C. Craighead, R.L Ruff, and B.W. O'Gara. 1973. Home ranges and activity patterns of non-migratory elk of the Madison drainage herd as determined by biotelemetry. Wildl. Monogr. 33.

Dennis, B.; **Taper, M.L**. (1994) Density dependence in time series observations of natural populations: Estimation and testing. Ecological Monographs 64(2) 205-224.

Ferrari, M.J. 1999. An assessment of the risk of inter-specific transmission of *Brucella abortus* from bison to elk on the Madison-Firehole winter range. M.S. thesis. Montana State Univ. Bozeman. 43 pp.

Fortin, M.-J., T. Keitt, B. Maurer, M.L. Taper, D. Kaufman, and T. Blackburn. 2001. Species ranges and distributional limits: pattern analysis and statistical issues. Ecology Special Feature (submitted)

Fuller, W.A. 1960. Behavior and social organization of the wild bison of Wood Buffalo National Park, Canada. Arctic 13:3-19.

Gates, C.C. and N.C. Larter. 1990. Growth and dispersal of an erupting large herbivore population in northern Canada: the Mackenzie wood bison (*Bison bison athabascae)*. Arctic 43:231-238.

Guo, Q., M. L. Taper , M.M. Schoeneberger, and J.R. Brandle. 2001. Spatial-temporal Population Dynamics across Species Range: from Center to Margin. Ecology special section (submitted).

(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

Gurtin, M. E. and R. C. McCamy. 1977. On the diffusion of biological populations. Math Biosci. 33: 35-49.

Hanski, I. A. and M. E. Gilpin. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press Inc., San Diego. 512 pp.

Hodson, R. and J. Karpowitz. 1998. Utah's Henry Mountain bison herd: management by hunting. Pp. 229-232. In: *International Symposium on bison ecology and management in North America*. L.R. Irby and J.E. Knight, eds. Montana State University, Bozeman.

Houston, D.B. 1982. *The northern Yellowstone elk: ecology and management*. Macmillan Publishing Co., New York. 474 pp.

Larter, N.C., A.R.E. Sinclair, and C.C. Gates. 1993. Dynamics of the Mackenzie wood bison population. Pp. 260-270. In: *Proceedings, North American public bison herds symposium*. R. Walker, compiler. Custer State Park. Custer, SD.

Maurer, B. A. 1994. *Geographical population analysis: tools for the analysis of biodiversity*. Blackwell Scientific Publications, Oxford. Pp 130.

Mayer, F.C. and C.B. Roth. 1958. *The buffalo harvest*. Sage Books. Denver, Colo. 96 pp.

McCullough, Y.B. 1980. Niche separation of seven North American ungulates on the National Bison Range, Montana. Ph.D. dissertation. Univ. Montana, Missoula. 226 pp.

McCullagh, P. and J. A. Nelder 1989. *Generalized linear models*, 2nd edition. Chapman & Hall. New York. 511 pp.

(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

McHugh, T. 1958. Social bevavior of the American Buffalo (Bison bison bison). Zoologica 43. Part1. March 1958. 40 pp.

Meagher, M.M. 1970. The bison of Yellowstone National Park: past and present. Ph.D dissertation. Univ.Calif., Berkeley. 172 pp.

Meagher, M. 1971. Snow as a factor influencing bison distribution and numbers in Pelican Valley, Yellowstone National Park. In: Proceedings, Snow and Ice Symposium, Iowa State Univ. Ames, Iowa.

Meagher, M.M. 1973. *The bison of Yellowstone National Park*. National Park Service Scientific Monograph 1. U.S. Gov't. Print. Office. 161 pp.

Meagher, M. 1976. Winter weather as a population regulating influence on free ranging bison in Yellowstone National Park. Pp 29-38 in Research in the Parks. Trans. Natl. Park. Centential Symp. Amer. Assoc. Adv. Sci. Dec. 28-29 1971. Ser. #1 USGPO. Wash DC 232 pp.

Meagher, M. 1986. *Bison bison.* Mammalian Species 266:1-8.

Meagher, M. 1989. Range expansion by bison of Yellowstone National Park. J. Mammal. 70:670-675.

Meagher, M. 1998. Recent changes in Yellowstone bison numbers and distributions. Pp 107-112 in *International Symposium on Bison Ecology and Management*. L. Irby and J. Knight eds. June 4-7. Bozeman MT.

Meagher, M. and D.B. Houston. 1998. *Yellowstone and the biology of time*. Univ. Oklahoma Press. Norman. 287 pp.

Meagher, M. and M.E. Meyer. 1994. On the origin of brucellosis in bison of Yellowstone National Park. Conservation Biology 8:645-653.

(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

Meagher, M. S. Cain, T. Toman, J. Kropp, and D. Bosman. 1997. Bison in the Greater Yellowstone Area: Status, Distribution, and Management. Pp 47-5 in : *Brucellosis, bison, elk, and cattle in the Greater Yellowstone area*. E. T. Thorne, M.S. Boyce, P. Nicoletti, and T.J. Kreeger,Edis. WY Game and Fish Dept. Cheyenne.

Morisita, M. 1971. Measuring habitat value by the “environmental density” method. Pp 379-401 in *Statistical Ecology*, vol 1. (ed. G. P. Patil, E. C. Pielou and W. E. Waters). Pennsylvania State University Press. University Park, PA.

National Park Service (NPS). 1984. Fishing Bridge and the Yellowstone ecosystem. A report to the Director. NPS. U.S. Govt. Print. Office. Region 8. 151 pp.

National Park Service (NPS). 2000a. Bison management plan for the State of Montana and Yellowstone National Park. Executive Summary and Final Environmental Impact Statement. NPS D-655a/August 2000. U.S. Gov’t. Print. Office. 2000-592-691/12007 Region 10. 97 pp.

National Park Service (NPS). 2000b. Winter use plan for the Yellowstone and Grand Teton national parks and John D. Rockefeller, Jr., Memorial Parkway. Summary and Final Environmental Impact Statement. NPS D-758A, August 2000. Denver Service Center. NPS. Denver, CO. 12 pp.

Ranneby, B. 1984. The maximum spacing method. An estimation related to the maximum likelihood method. Scand. J. Statist. 11:93-112.

Roe, F.G. 1970. *The North American buffalo. A critical study of the species in its wild state*. 2 nd ed. Univ. Toronto Press. 991 pp.

(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

Scott, D.W. 1992. *Multivariate density estimation: theory, practice and visualization*. Wiley. New York. Pp 317.

Seaman, D.E. and R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77: 2075-2085.

Seaman, D.E. and R.A. Powell. 1998. Kernel home range estimation program (KernelHR) version 4.28 documentation. North Carolina State University.

Shaw, J.H. and M. Meagher. 1999. Bison. Pp. 447-466. In: *Ecology and management of large mammals in North America*. S. Demarais and P.R. Krauseman, eds. Prentice-Hall. New York. 778 pp.

Shigesada, N. and K. Kawasaki. 1997. *Biological invasions: theory and practice*. Oxford University Press. Oxford, 205 pp.

Shigesada, N., K. Kawasaki, and E. Teramoto. 1979. Spatial segregation of interaction species. Journal of Theoretical Biology 79, 83-99.

Shigesada, N., K. Kawasaki, and E. Teramoto. 1980. Spatial distribution of dispersing animals. Journal of Mathematical Biology 9, 85-96.

Silverman, B.W. 1986. *Density estimation for statistics and data analysis*. Chapman and Hall, London, England. Pp 175.

Singer, F.J. 1991. The ungulate prey base for wolves. Pp. 323-348. In: *The greater Yellowstone ecosystem*. R.B. Keiter and M.S. Boyce, eds. Yale Univ. Press. New Haven, CT. 428 pp.

Singer, F.J. and J.A. Mack. 1993. Potential ungulate prey for gray wolves.pp.75-102. In: *Ecological issues on reintroducing wolves into Yellowstone National Park*. R.S.

(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

Cook, ed. Scientific Monograph NPS/NRYELL/NRSM-93/22. Nat. Park Service. Denver, CO. 328 pp.

Singer, F.J. and J.E. Norland. 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. Canad. J. Zoology 72:1383-1394.

Skinner, C.K. and W.B. Alcorn. 1942-1951. History of the bison in Yellowstone Park. Typed report. Archives, Yellowstone National Park. 57 pp.

Smith, D.W., L.D. Mech, M. Meagher, W.E. Clark, R. Jaffe, M.K. Phillips, and J.A. Mack. 2000. Wolf-bison interactions in Yellowstone National Park. J. Mammal. 81:000-000.

Stacey, P.B.; Johnson, V.A.; and **Taper, M.L.** 1997. Migration within metapopulations: The impact upon local population dynamics. Pages 267-291 in I Hanski and M. Gilpin eds. *Metapopulation Dynamics: Evolution, Ecology and Genetics*, Academic Press.

Stacey, P.; and **Taper, M.L**. (1992) Environmental variation and the persistence of small populations. Ecological Applications 2(1):18-29.

Taper, M.L.; Marquet, P.M. 1996. How do species really divide resources? Am. Nat. 147:1072-1086

Tilman, D. and P. Kareiva (editors). 1997. *Spatial ecology: The role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton. Pp 368.

(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution In animals and plants*. Sinauer Associates, Inc. Sunderland. Pp 396.

Telfer, E.S. and A. Cairns. 1979. Bison-wapiti interrelationships in Elk Island National Park, Alberta. Pp. 114-121. In: *North American elk: ecology, behavior and management*. M.S. Boyce and L.D. Hayden-Wing, eds. Univ. Wyoming. Laramie.

Van Camp, J. and G.W. Calef., 1988. Population dynamics of bison. Pp. 21-24. In: *Bison ecology in relation to agricultural development in the Slave River lowlands*, NWT. H.W. Reynolds and A.W.L. Hawley, eds. Canad. Wildlife Service Occasional Paper N. 63. Edmonton, Alberta.

Wilson, M. 1996. Hydrothermal soil studies. pp. 320-324 (appendix). In: *Soils of Yellowstone National Park*. A. Rodman, H. Shovic, and D. Thoma.YCR-NRSR-96-2. Yellowstone Center for Resources. Yellowstone National Park. Wy. 324 pp.

Worton, B.J. 1989a. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168.

Worton, B.J. 1989b. Optimal smoothing parameters for multivariate fixed and adaptive kernel methods. J. Statist. Computing and Simulation 32: 45-57.

Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. J. Wildl. Manage. 59: 794-800.

Wydeven, A.P. and R. B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. J. Wildl. Manage. 49:805-813.

(If viewing electronic version **CLICK HERE** to return to the Table of Contents)

Yochim, M.J. 1998. The development of snowmobile policy in Yellowstone National Park. MS. Thesis, University of Montana, Missoula 192 pp.

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Tables

Table 1. Regression table for full data set.

```
Dep Var: R    N: 27    Multiple R: 0.430    Squared multiple R: 
0.185

Adjusted squared multiple R: 0.152    Standard error of estimate: 
0.119

Effect      Coefficient    Std Error     Std Coef Tolerance     t
CONSTANT            0.235        0.075        0.000      .   
3.136
MIN_DENSITY      -0.045        0.019       -0.430     1.000   - 
2.382

                        Analysis of Variance

Source          Sum-of-Squares   df  Mean-Square     F-ratio
Regression               0.080     1        0.080       5.673
Residual                 0.354    25        0.014
```

Table 2: Site Pearson correlation matrix

	PELICAN	FIREHOLE	HAYDEN	WEST SIDE	NORTHERN
PELICAN	1.000				
FIREHOLE	0.288	1.000			
HAYDEN	-0.370	-0.871	1.000		
WEST SIDE	-0.177	0.280	-0.606	1.000	
NORTHERN	-0.182	-0.200	-0.060	0.091	1.000

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Table 3: Central growth rate vs. minimum density

```
Dep Var: Rate  N:27   Multiple R:0.341  Squared multiple R: 0.116


Effect         Coefficient    Std Error     Std Coef Tolerance
CONSTANT             0.196        0.082        0.000      .
MIN_DENSITY         -0.034        0.019       -0.341     1.000

                             Analysis of Variance

Source             Sum-of-Squares   df  Mean-Square     F-ratio

Regression                 0.053     1        0.053       3.290
Residual                   0.404    25        0.016

Durbin-Watson D Statistic     1.613
First Order Autocorrelation   0.006
```

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Table 4: Northern growth rate vs. minimum density

```
Dep Var: R   N: 27   Multiple R: 0.176   Squared multiple R: 0.031


Effect        Coefficient    Std Error     Std Coef Tolerance

CONSTANT            0.212       0.196       0.000     .
MIN_DENSITY        -0.053       0.059      -0.176    1.000

                           Analysis of Variance

Source           Sum-of-Squares   df  Mean-Square     F-ratio
Regression               0.071     1       0.071       0.796       0.381
Residual                 2.245    25       0.090

Durbin-Watson D Statistic     2.890
First Order Autocorrelation  -0.491
```

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Figures:

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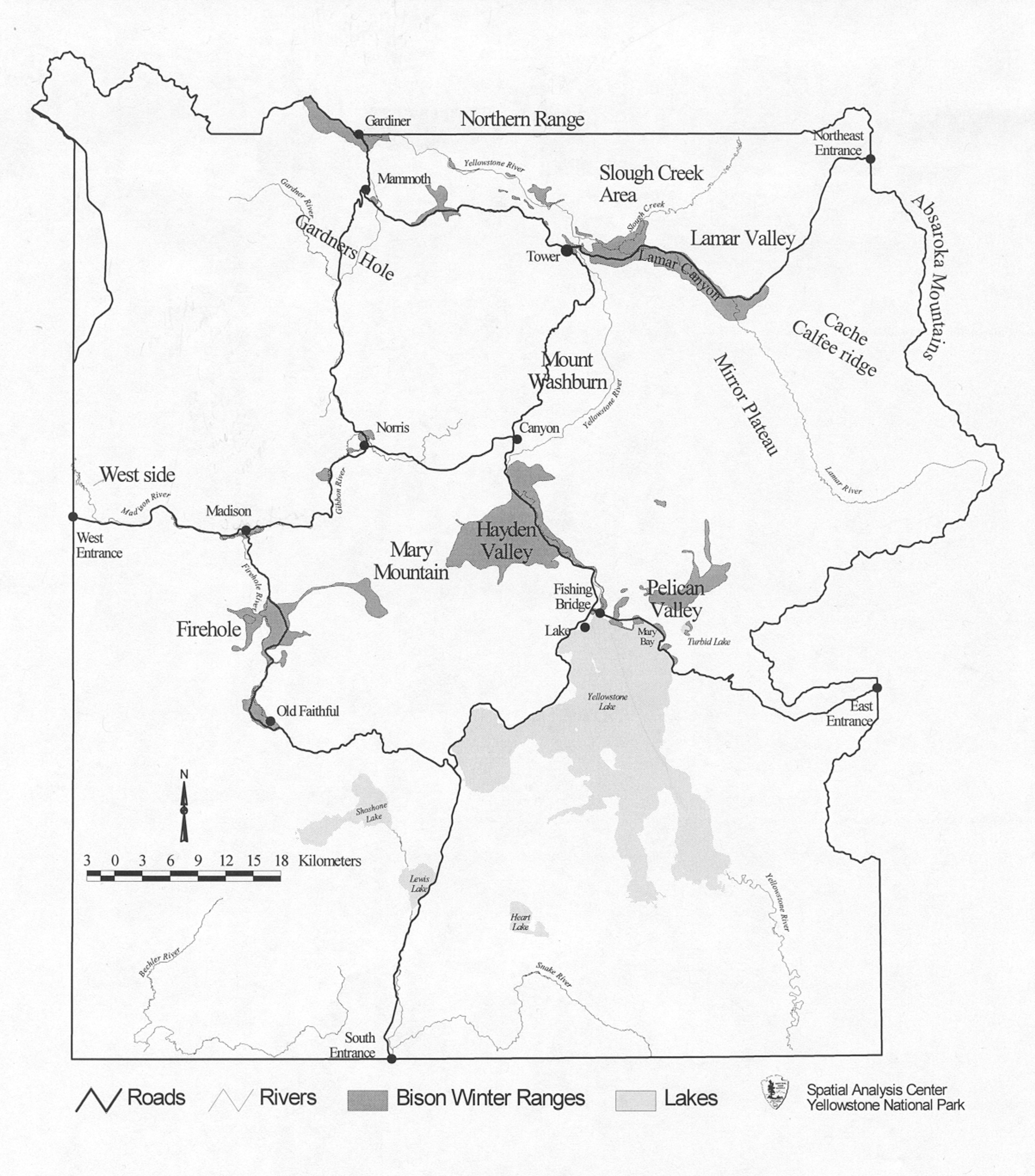

Fig. 1: Map of study area in YNP showing key bison winter ranges and park road system.

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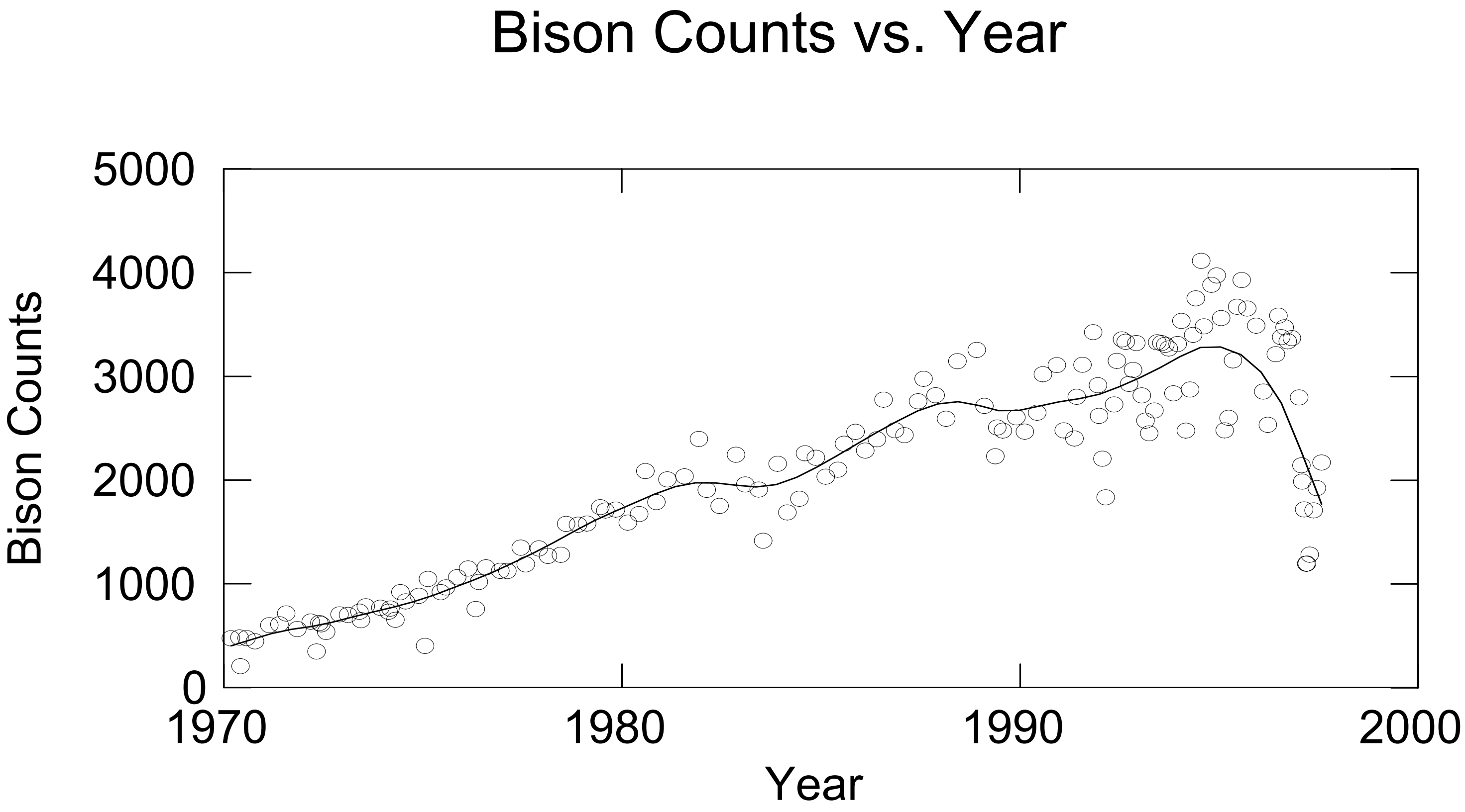

Fig. 2: Total counts for each flight plotted versus time.

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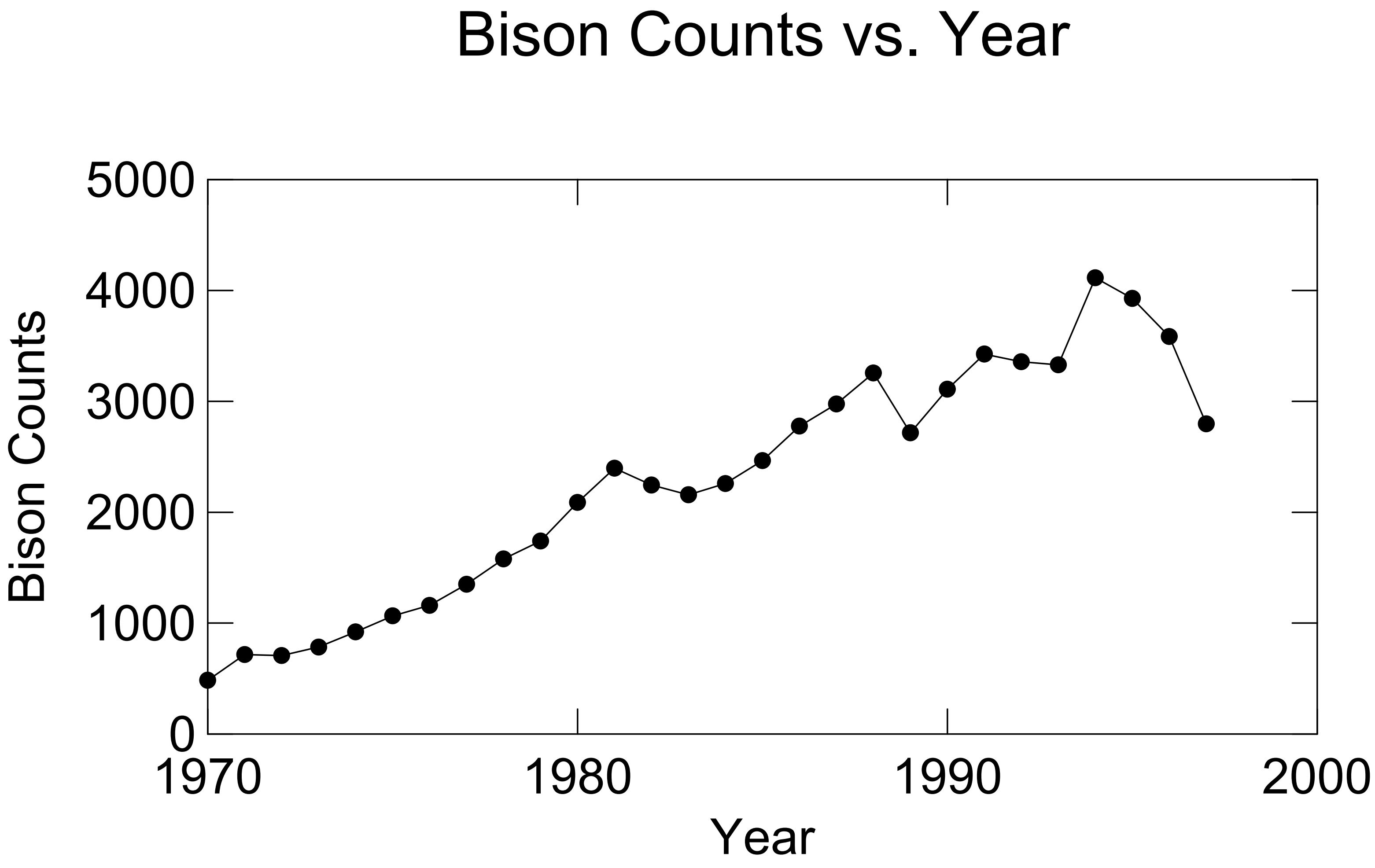

Fig. 3: Maximum yearly count plotted versus year.

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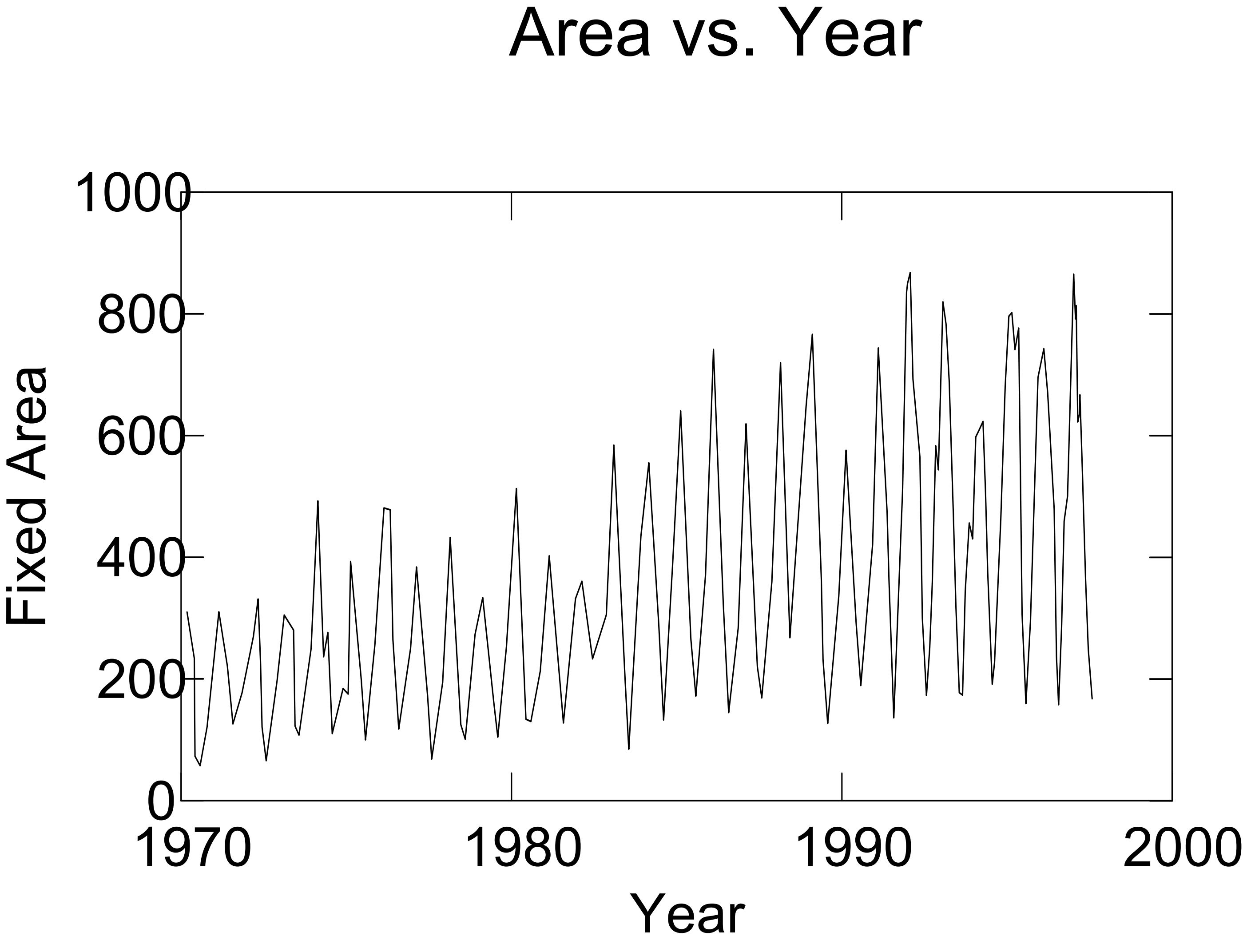

Fig. 4: Area occupied by herd plotted against time.

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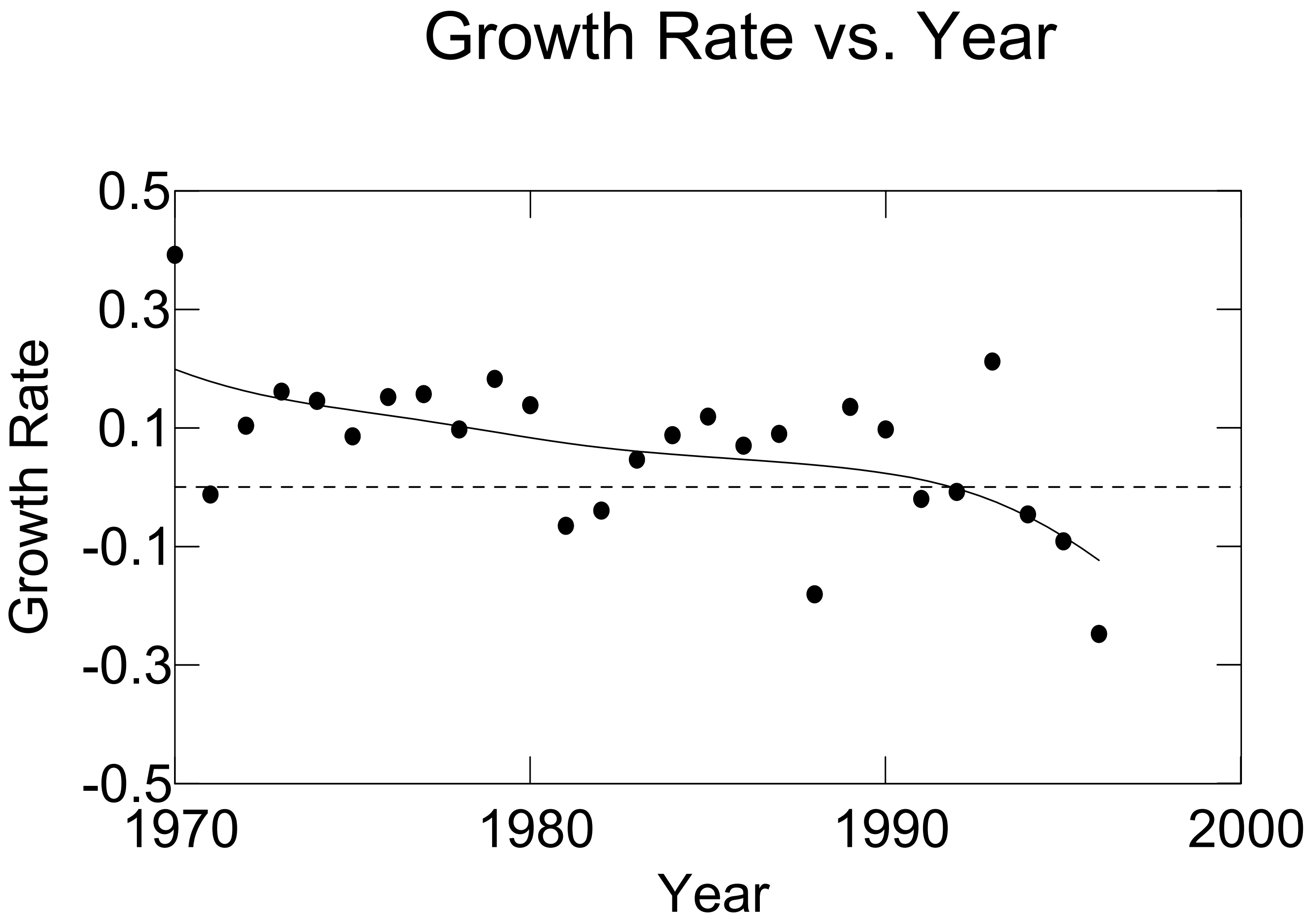

Fig. 5: Per capita growth rate plotted versus year

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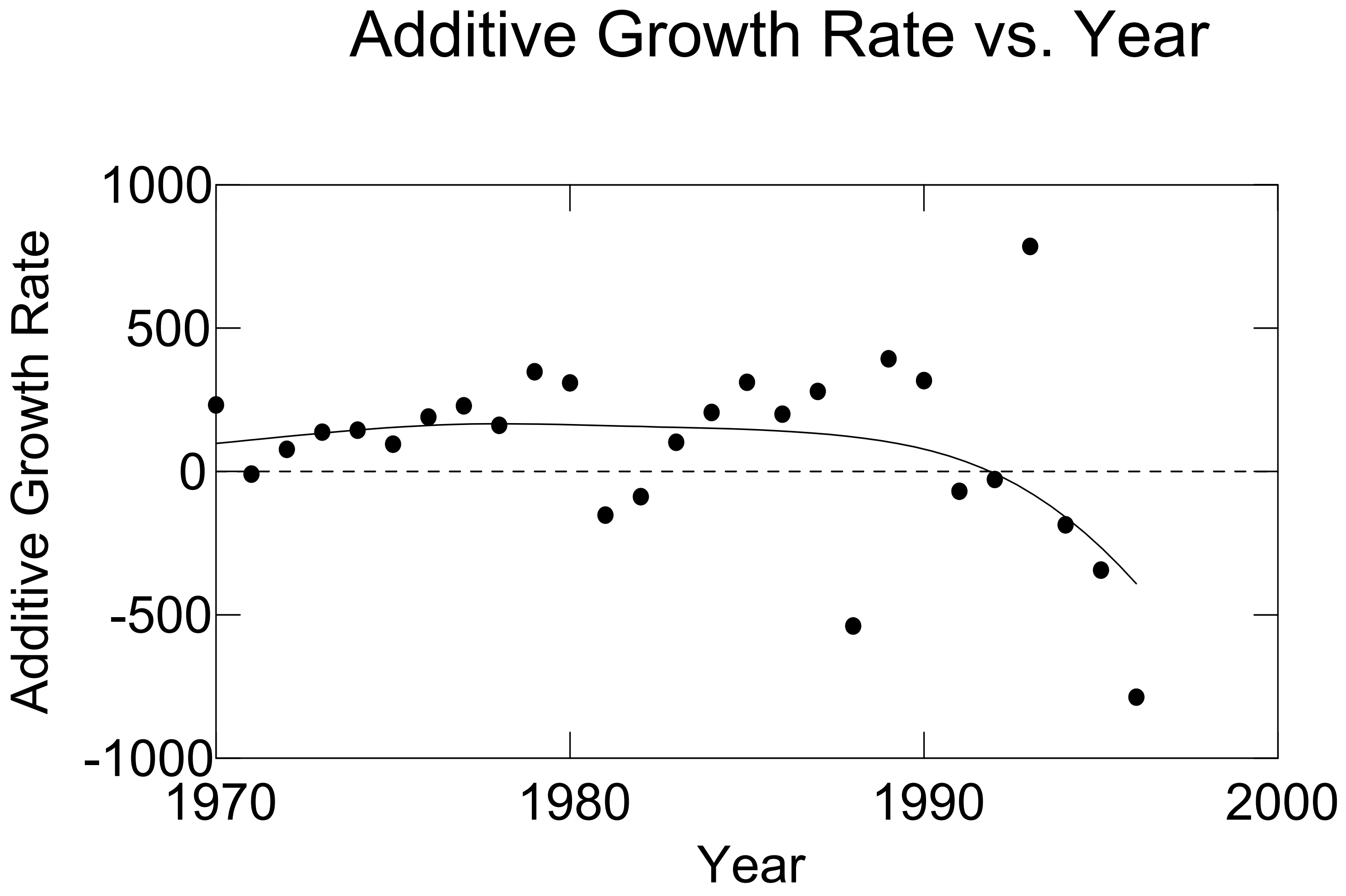

Fig. 6: Additive growth rate plotted against year

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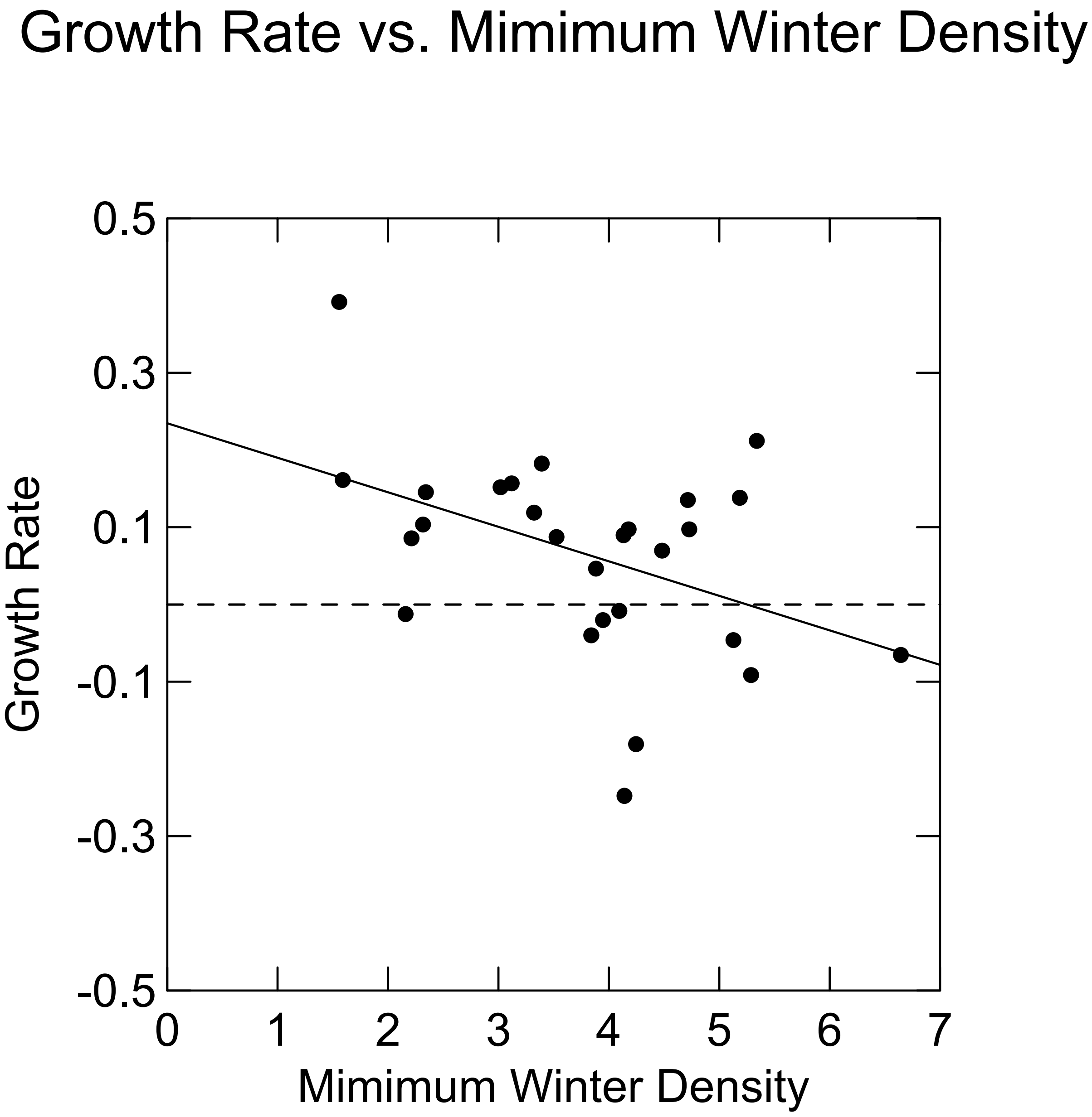

Fig. 7: Per capita growth rate plotted against minimum winter density

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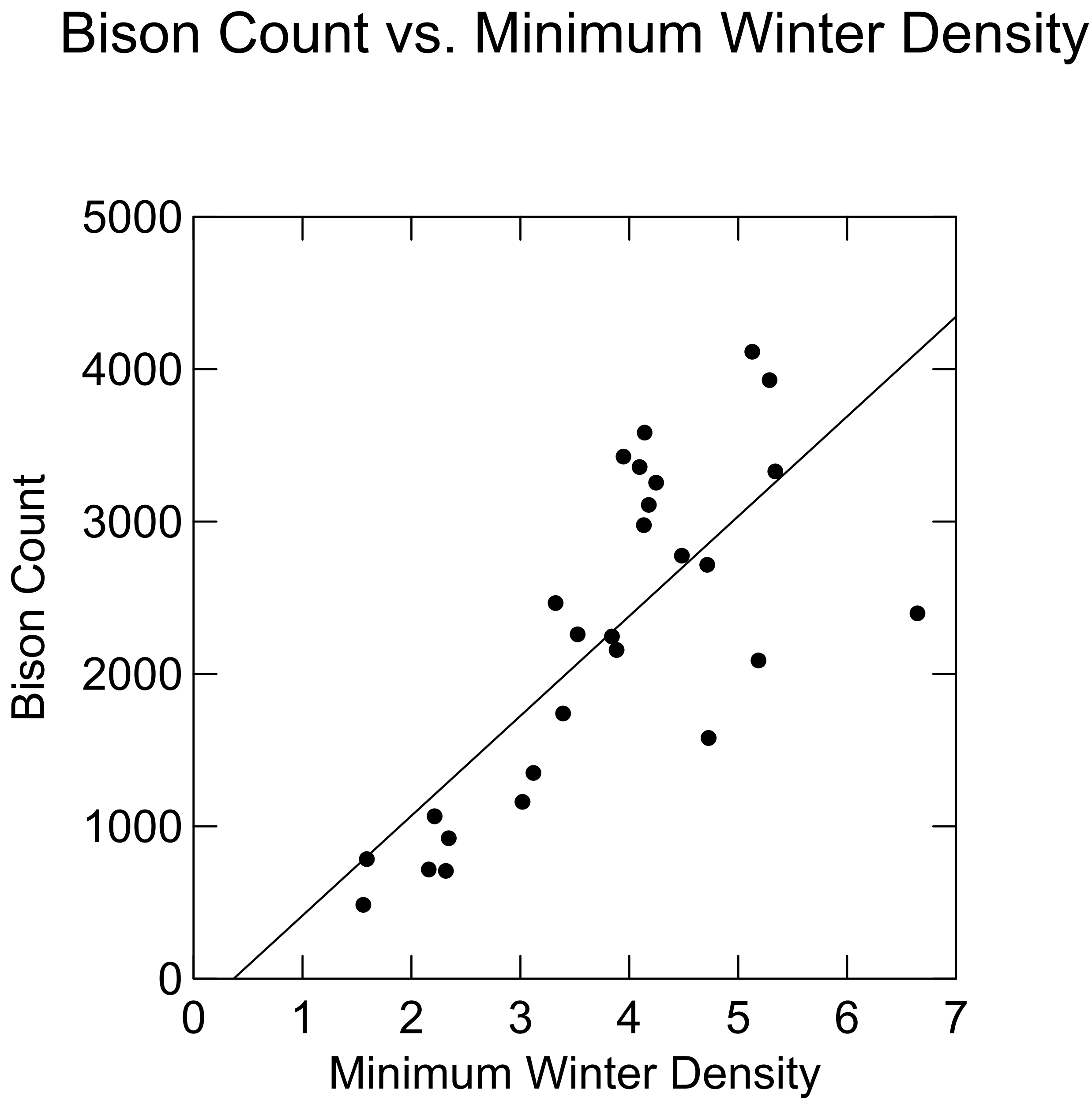

Fig. 8: Total bison count plotted against minimum winter density.

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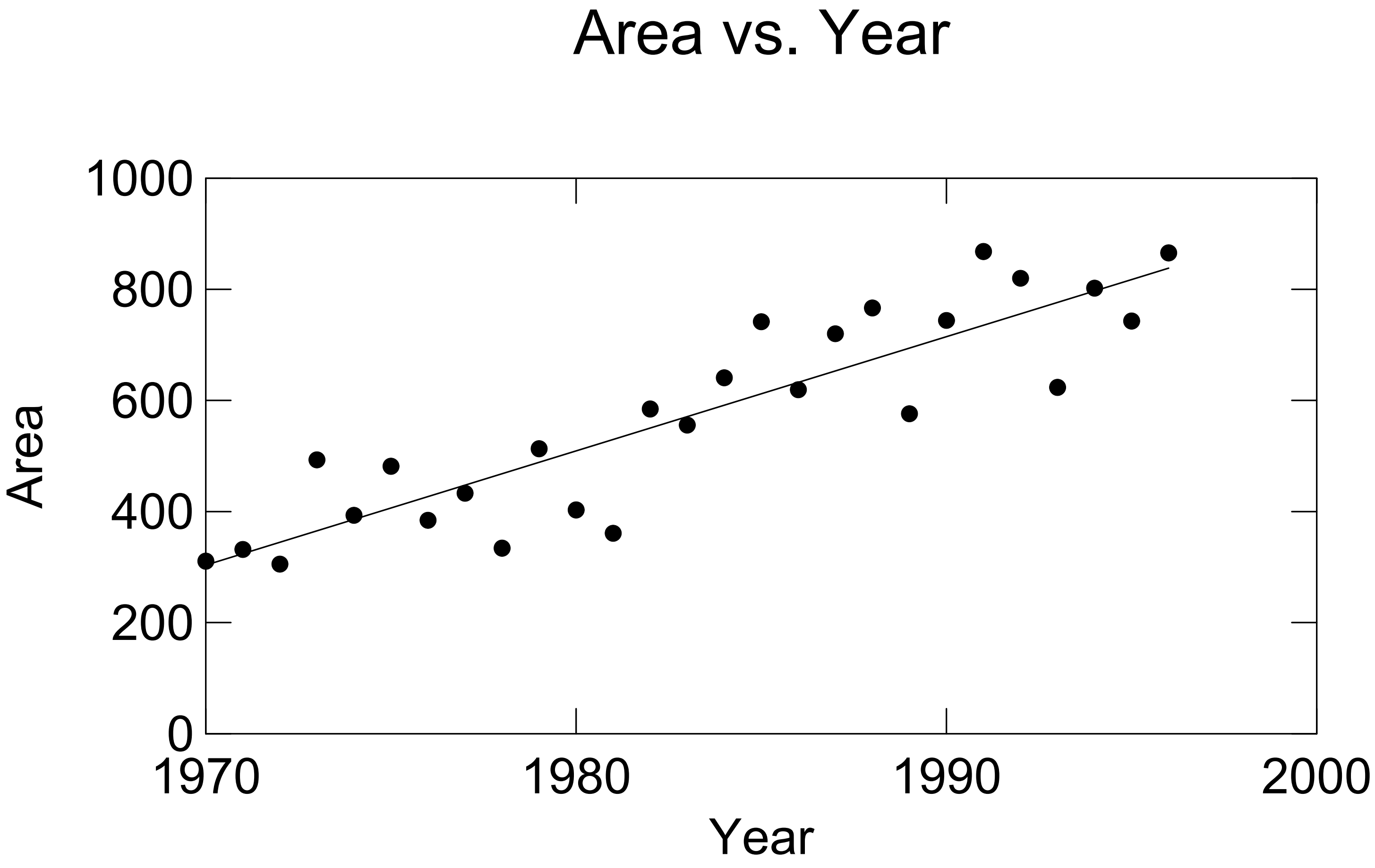

Fig. 9: Maximum winter area occupied by the herd versus year.

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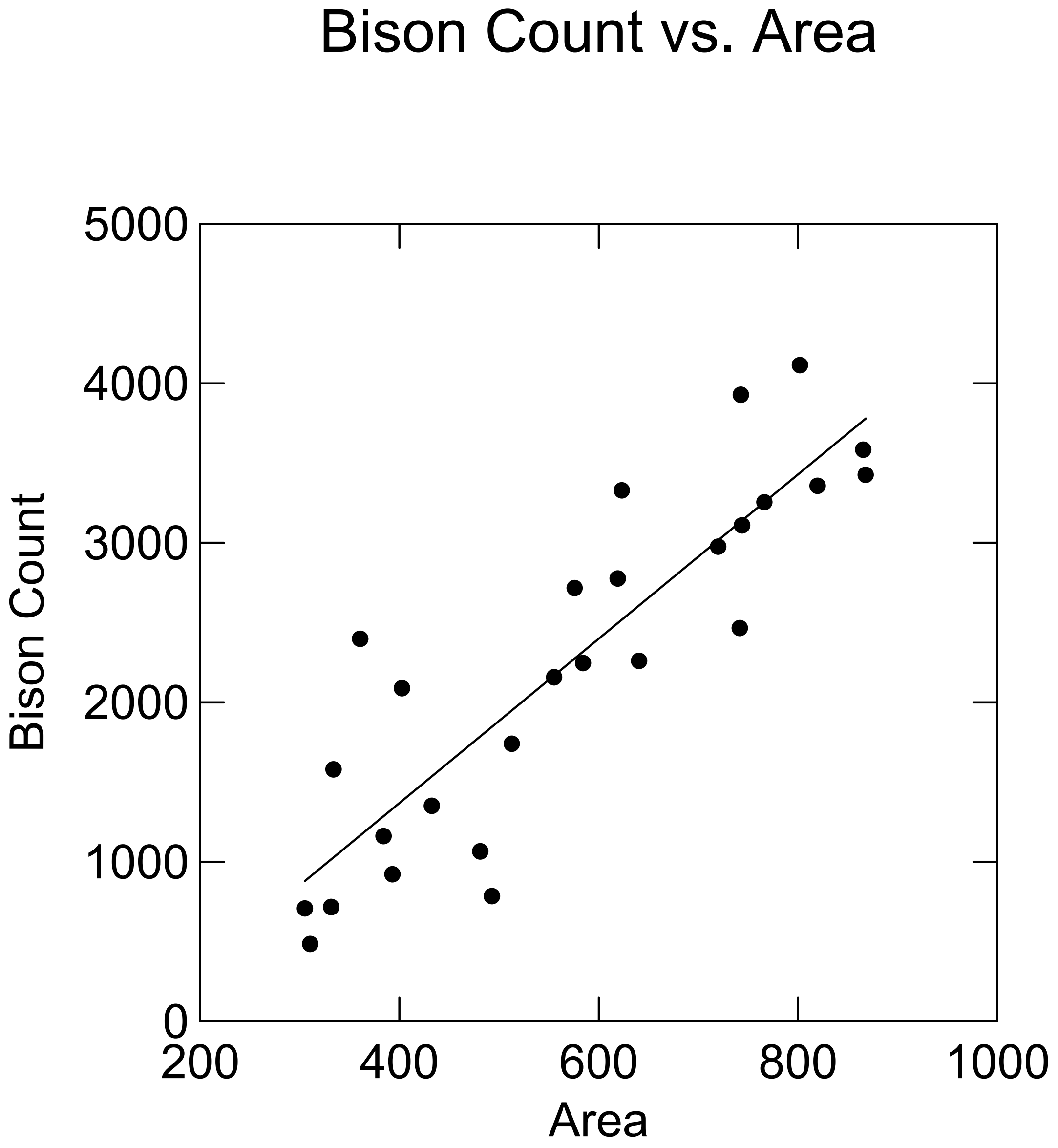

Fig. 10: Total bison count plotted against maximum winter area.

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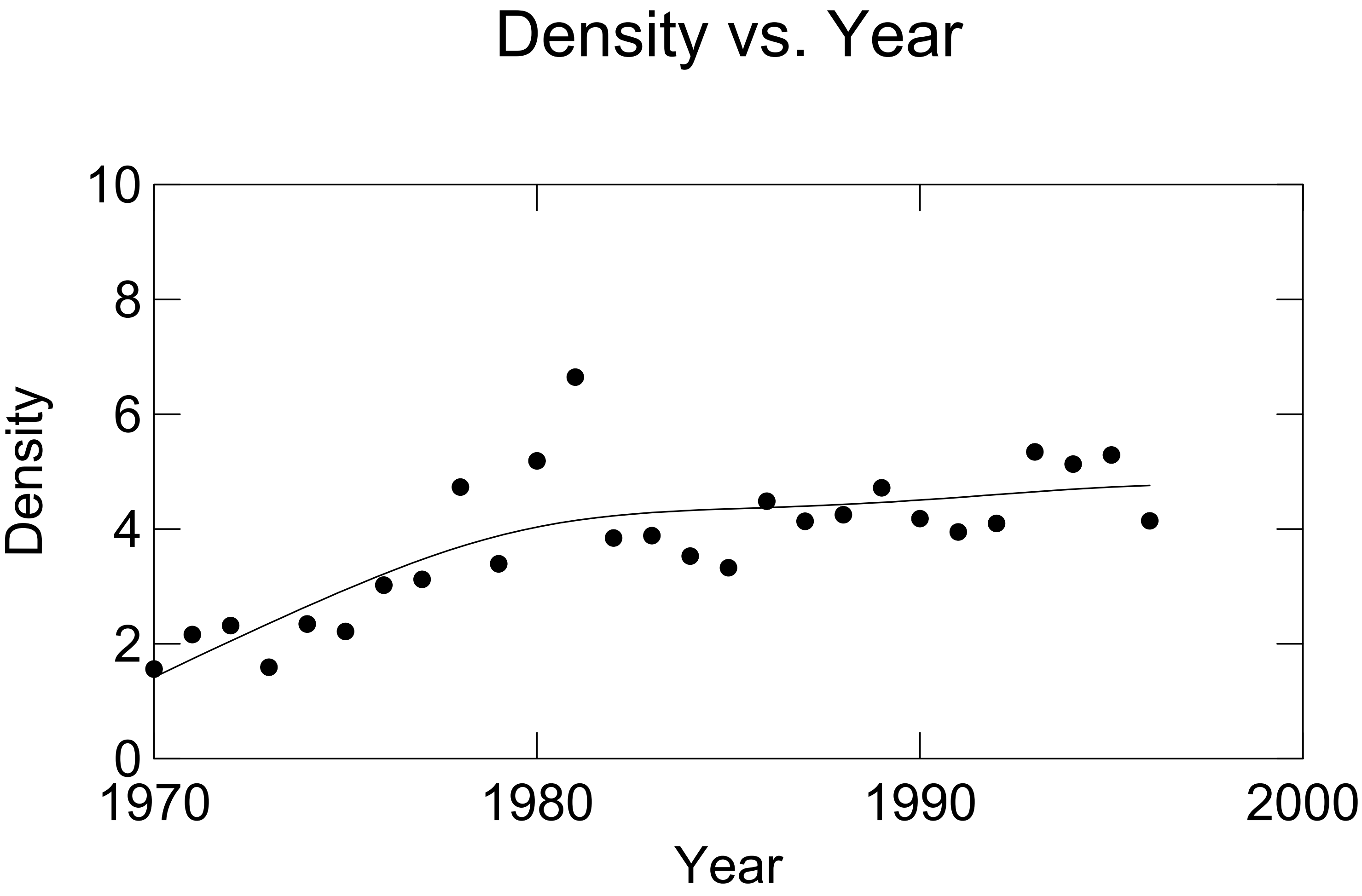

Fig. 11: Minimum winter density plotted against year.

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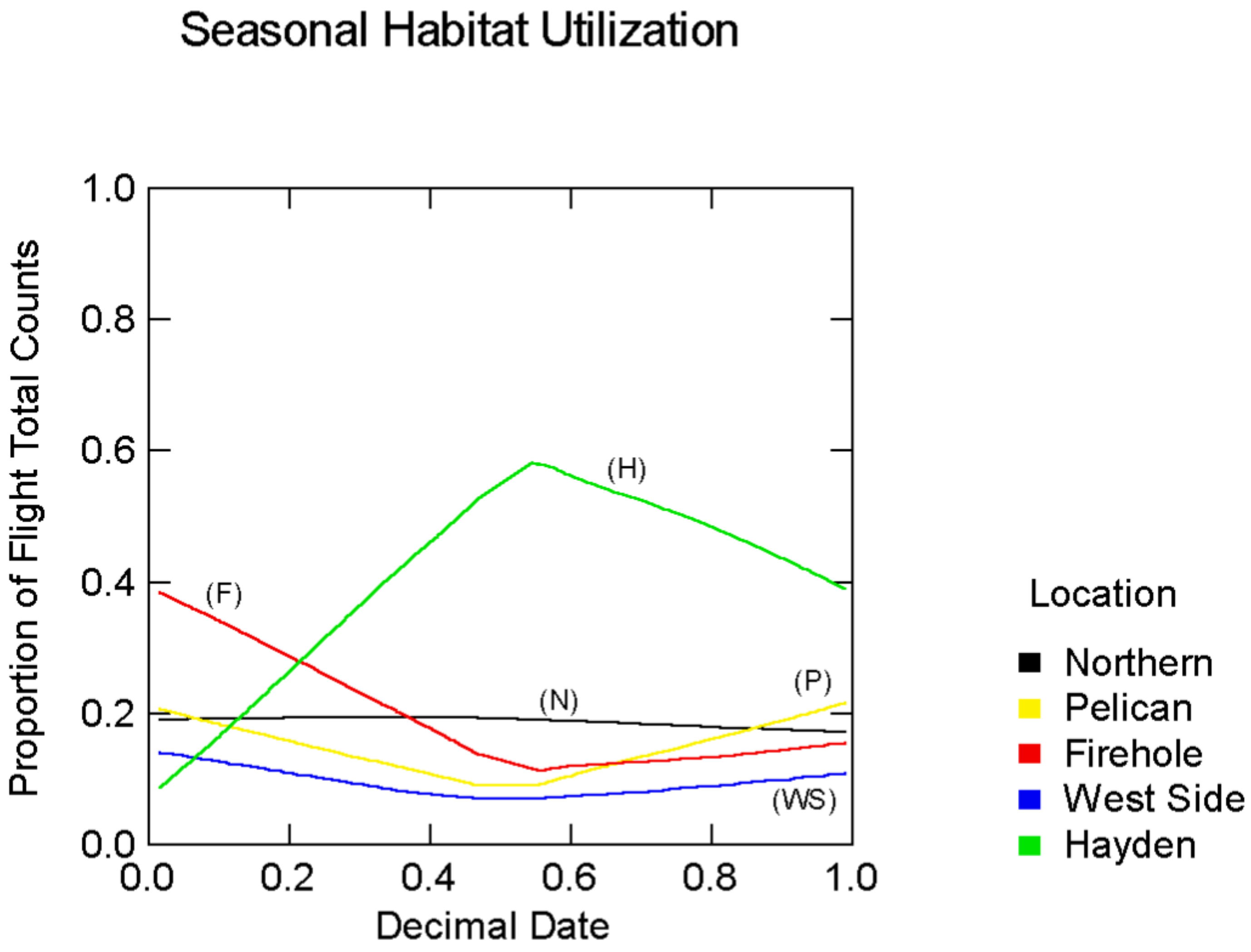

Fig. 12: Seasonal distribution of total bison population amongst the five principal regions

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Seasonal Bison Proportions (Northern and Central)

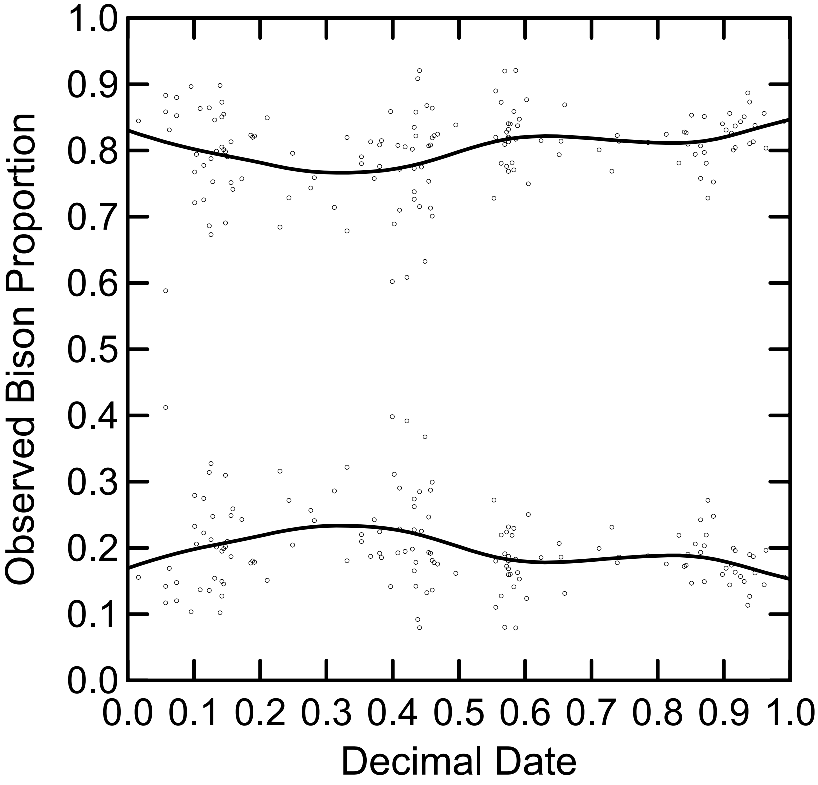

Fig. 13 Population proportional distribution between the northern and central ranges

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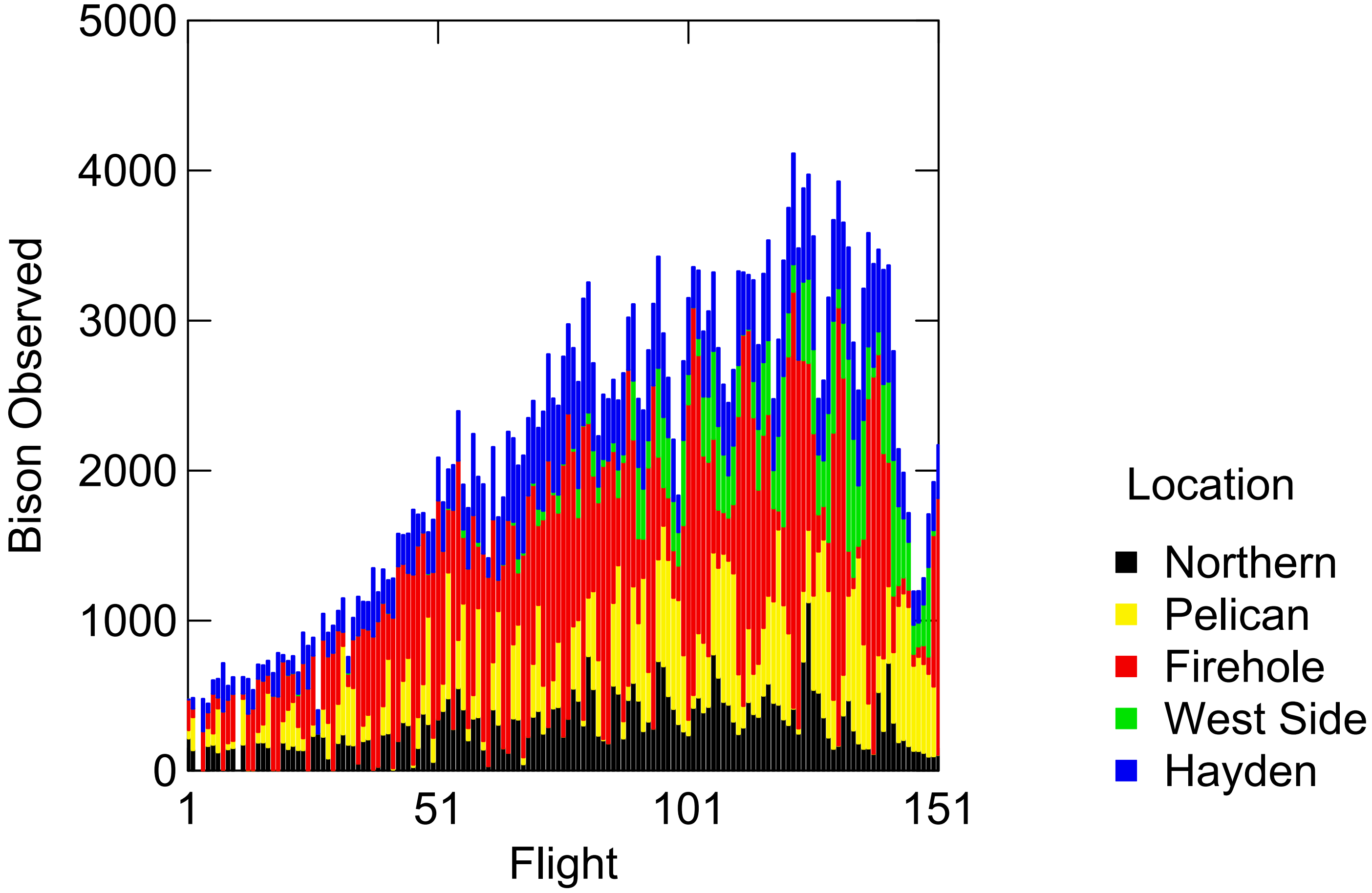

Fig. 14: Stacked bar graph of regional counts versus time.

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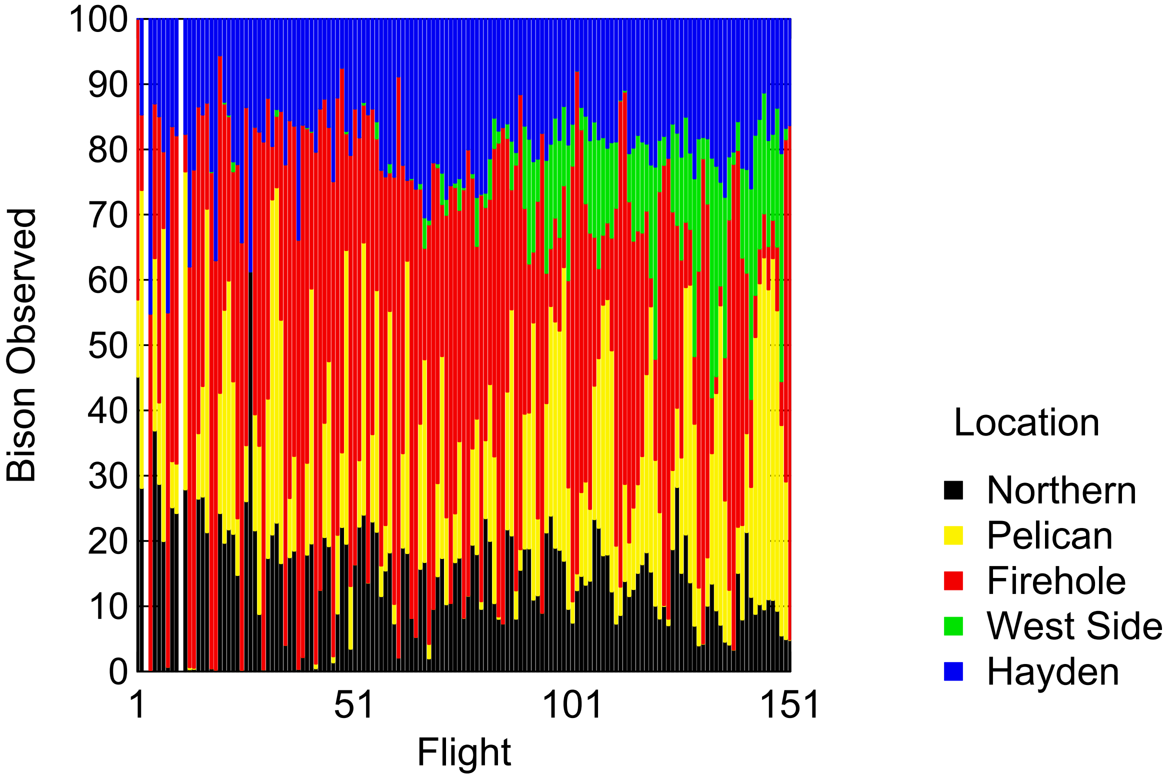

Fig. 15: Stacked bar graph of proportion of total count in each region versus time.

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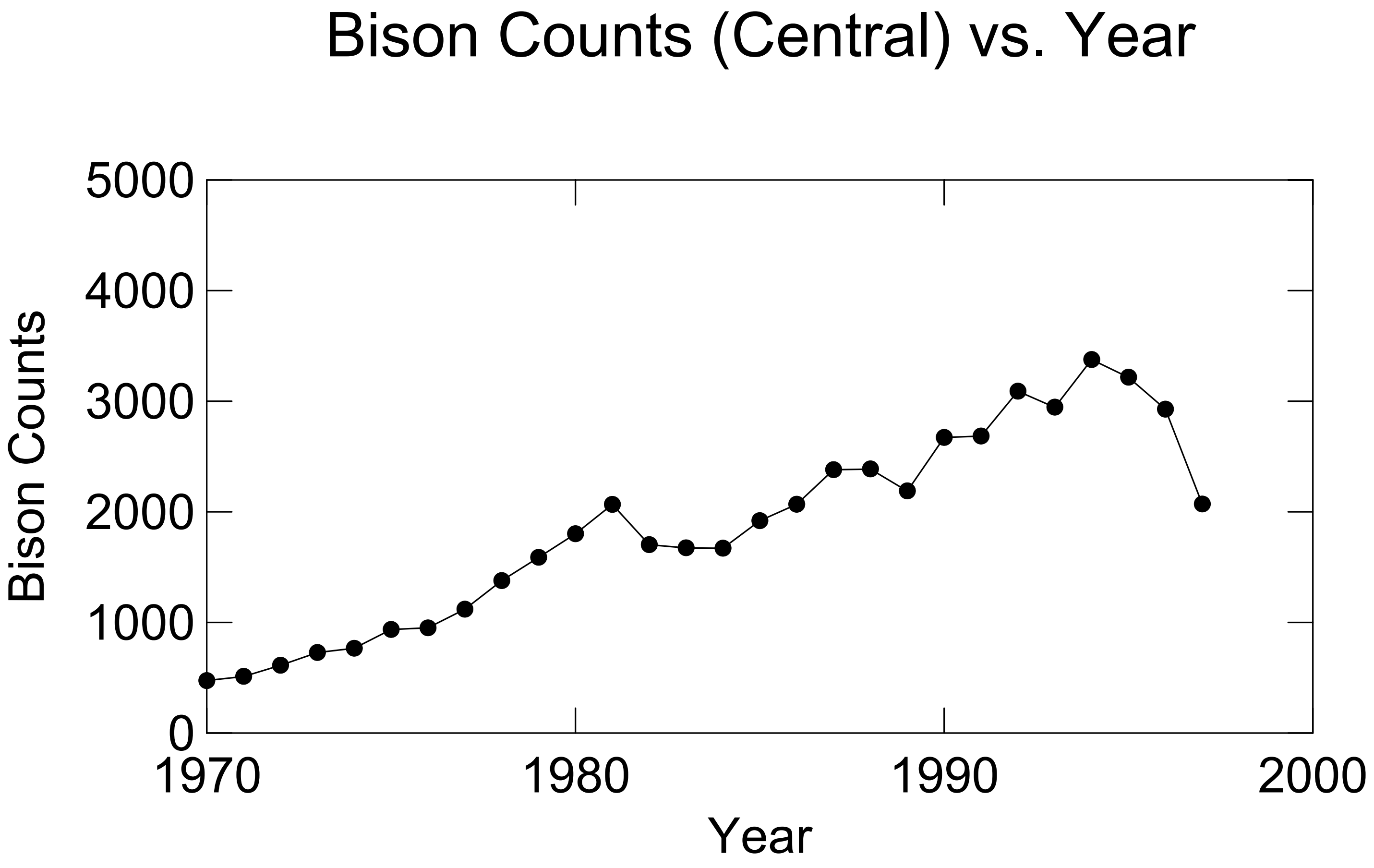

Fig. 16 Central herd maximum bison counts versus year

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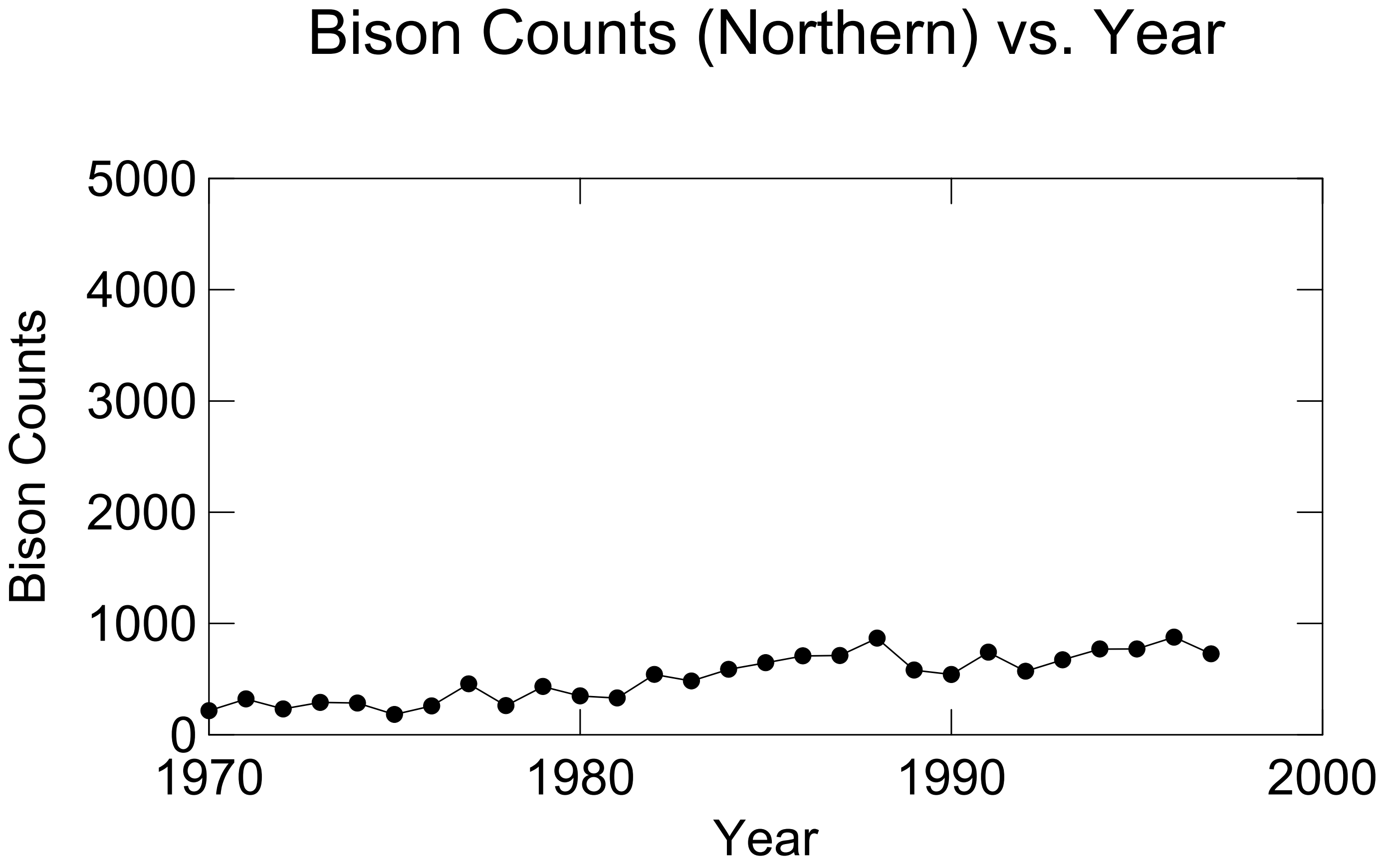

Fig. 17 Northern herd maximum bison counts versus year.

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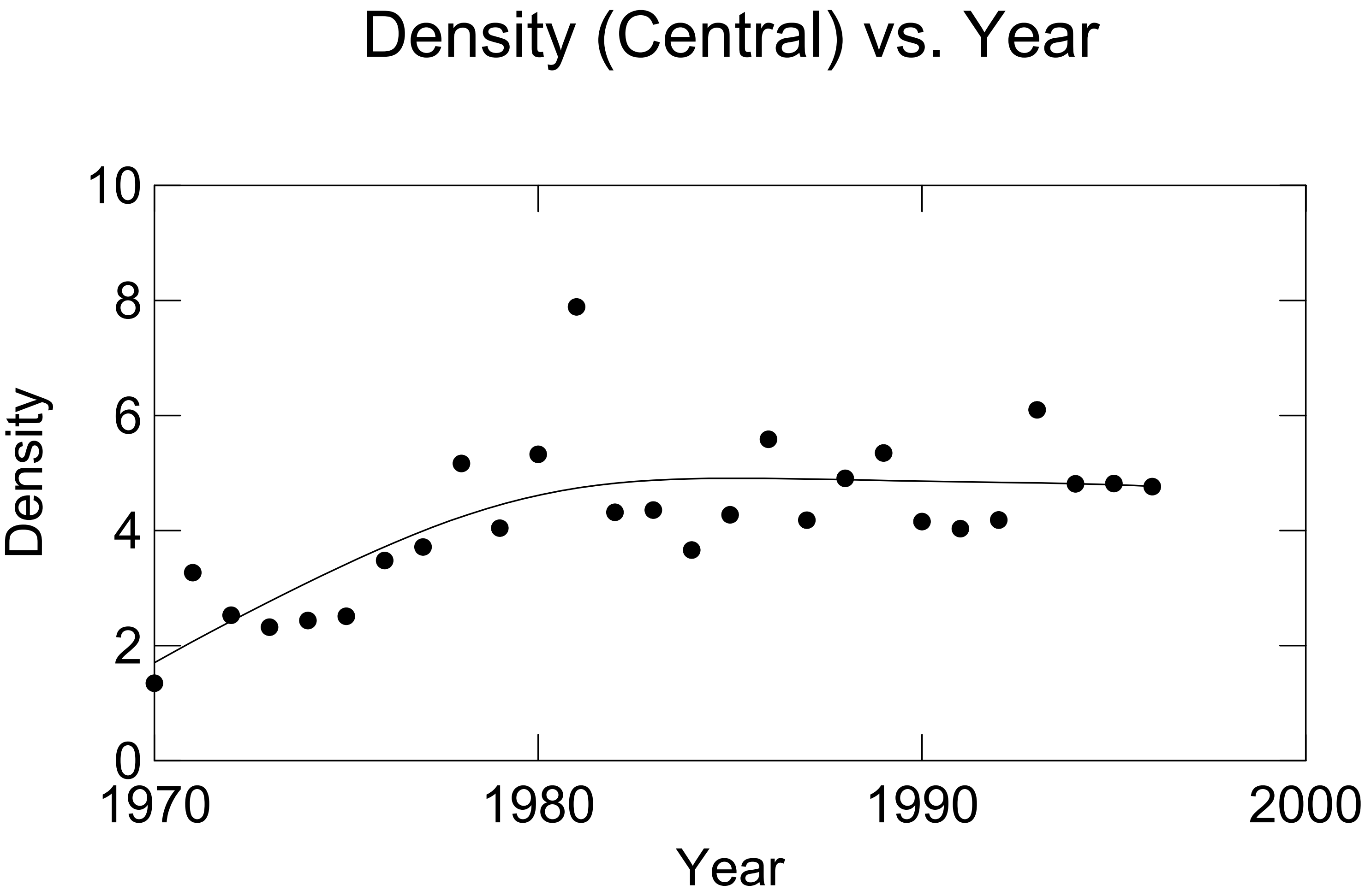

Fig. 18 Central densities (bison per square kilometer) versus year

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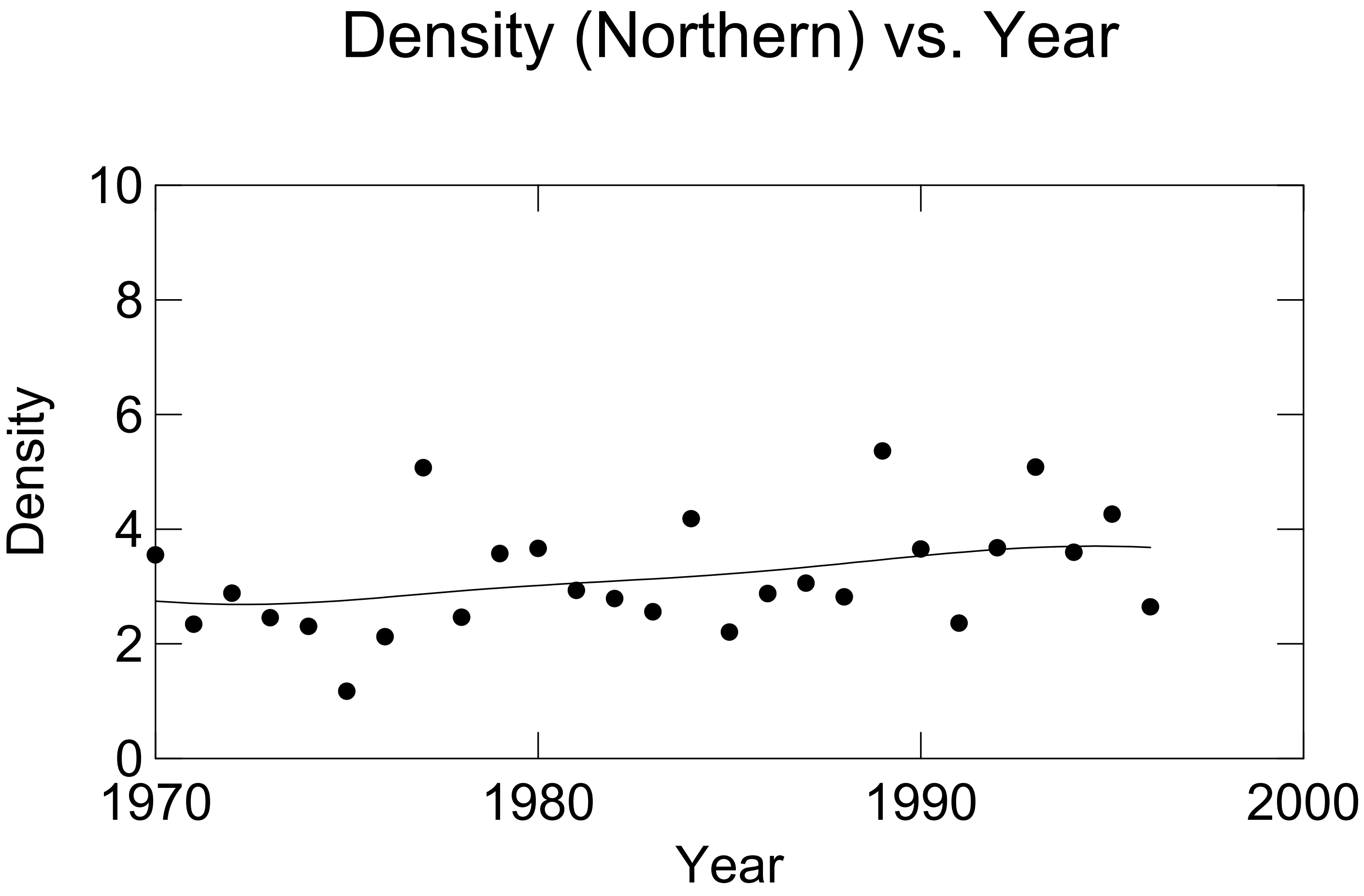

Fig. 19 Northern densities (bison per square kilometer) versus year

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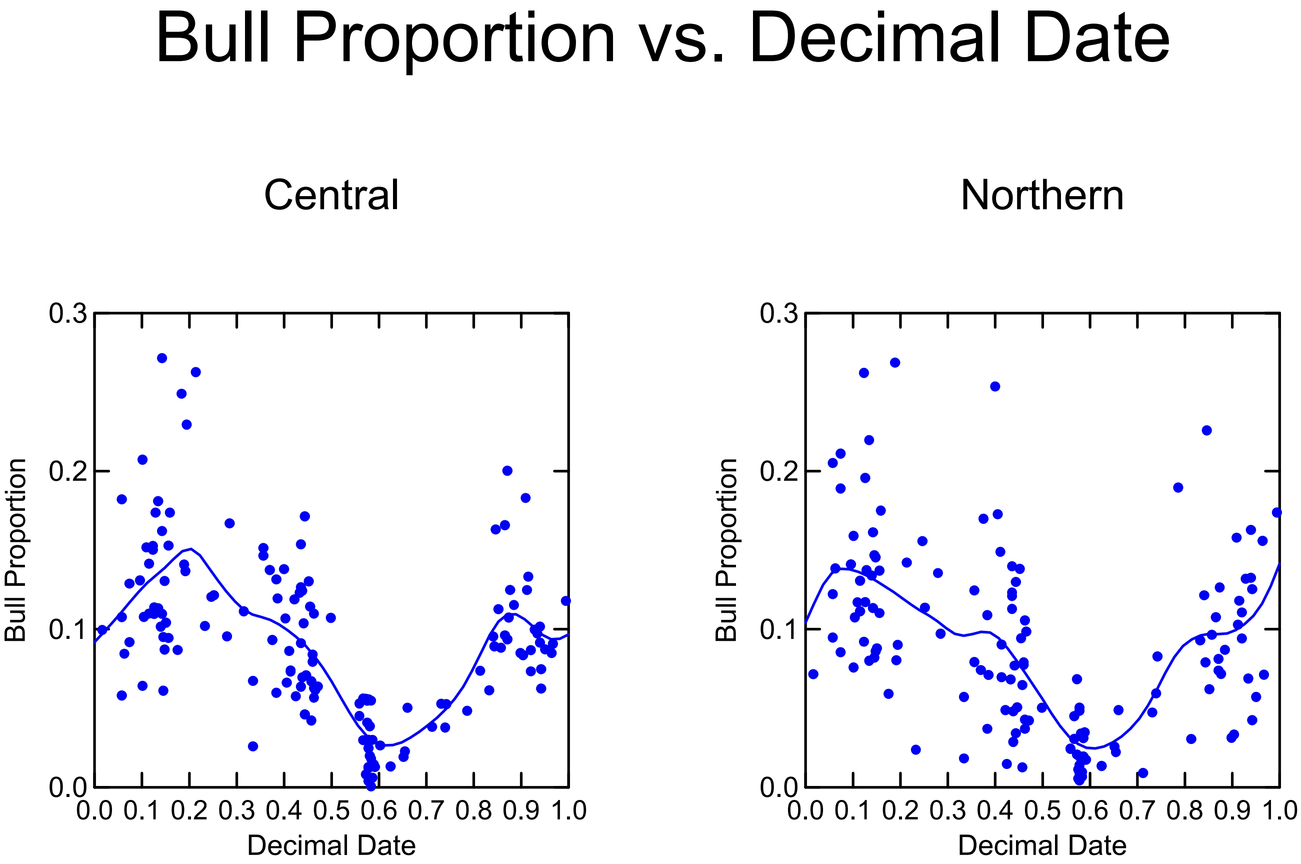

Fig. 20. Seasonal variation in observed bull proportion. All flights plotted.

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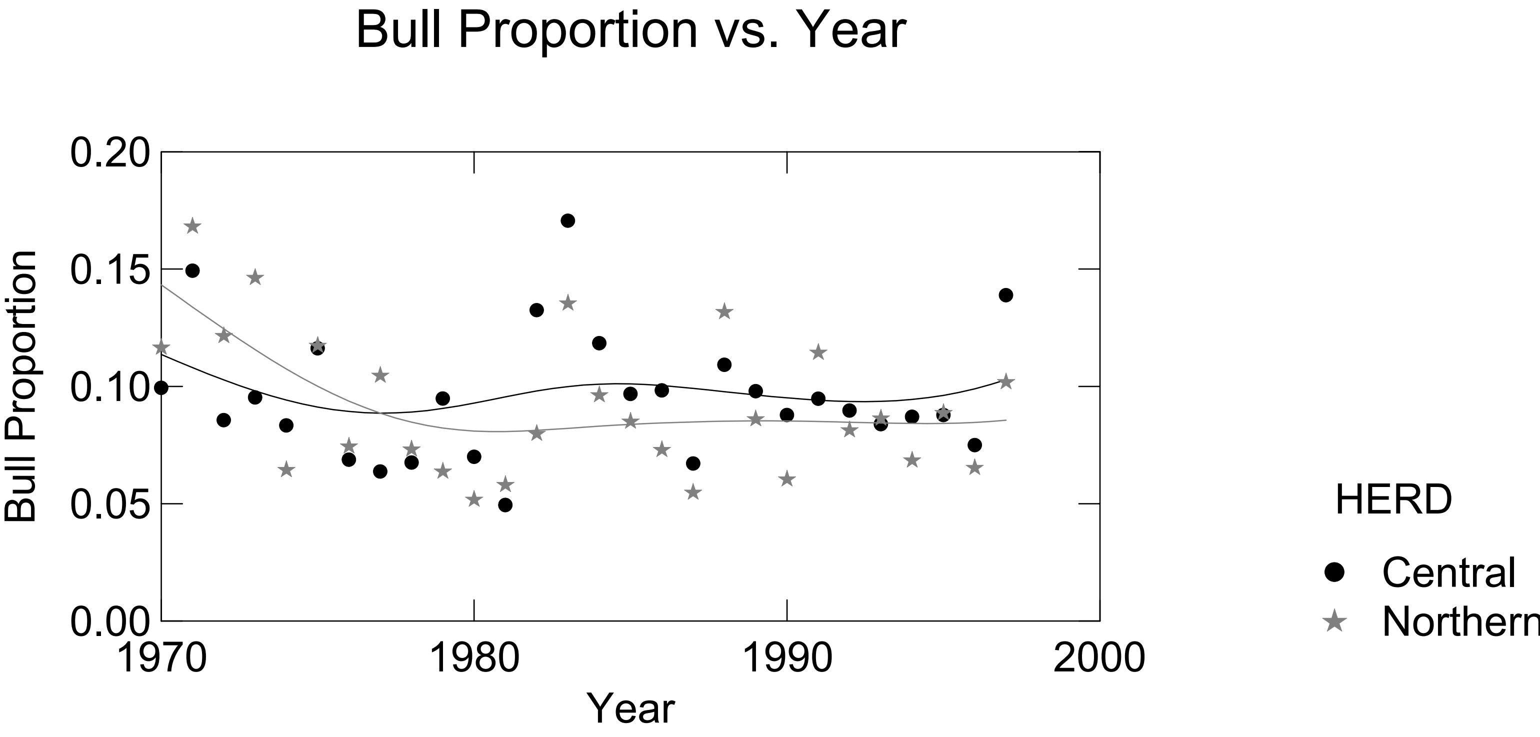

Fig. 21. Mean observed proportion of bulls versus year

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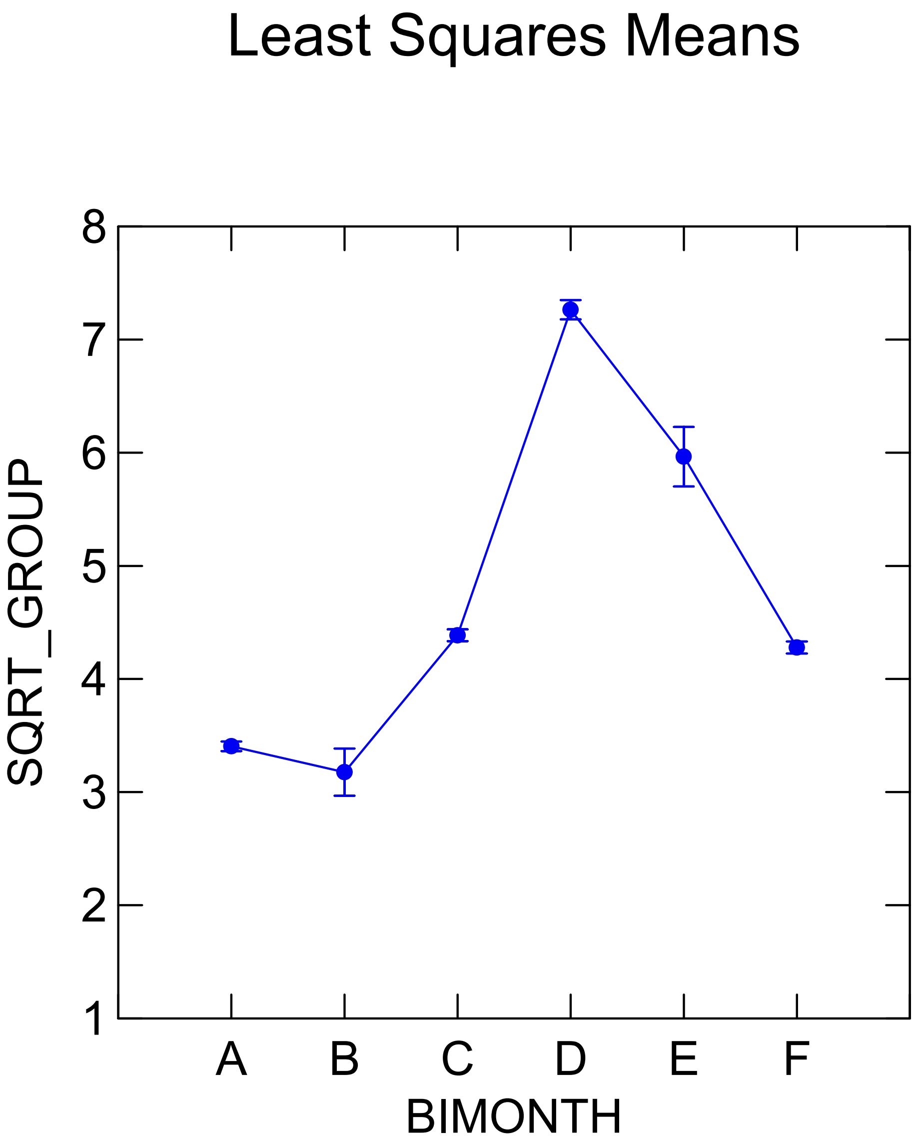

Fig. 22. Seasonal changes in square-root transformed group size.

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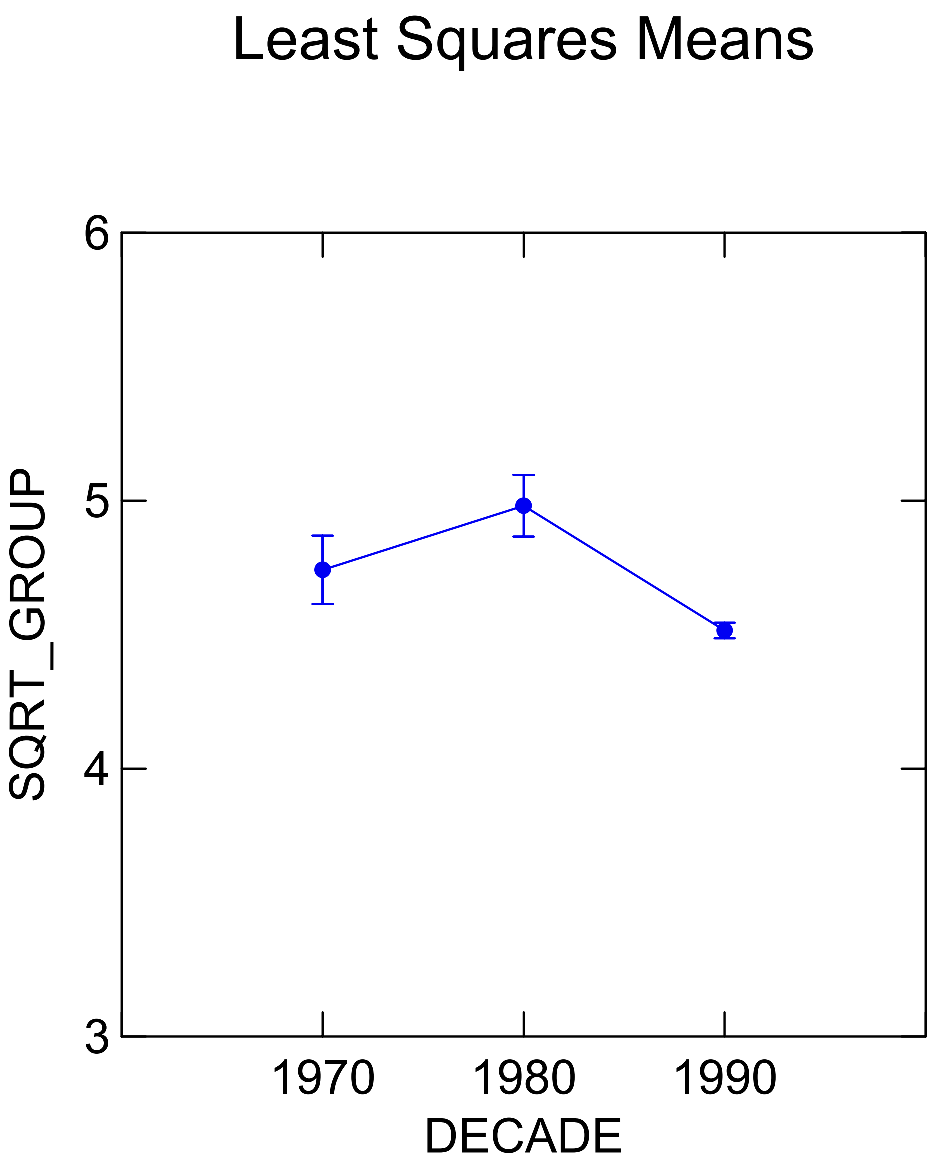

Fig. 23. Decadal changes in square-root transformed group sizes.

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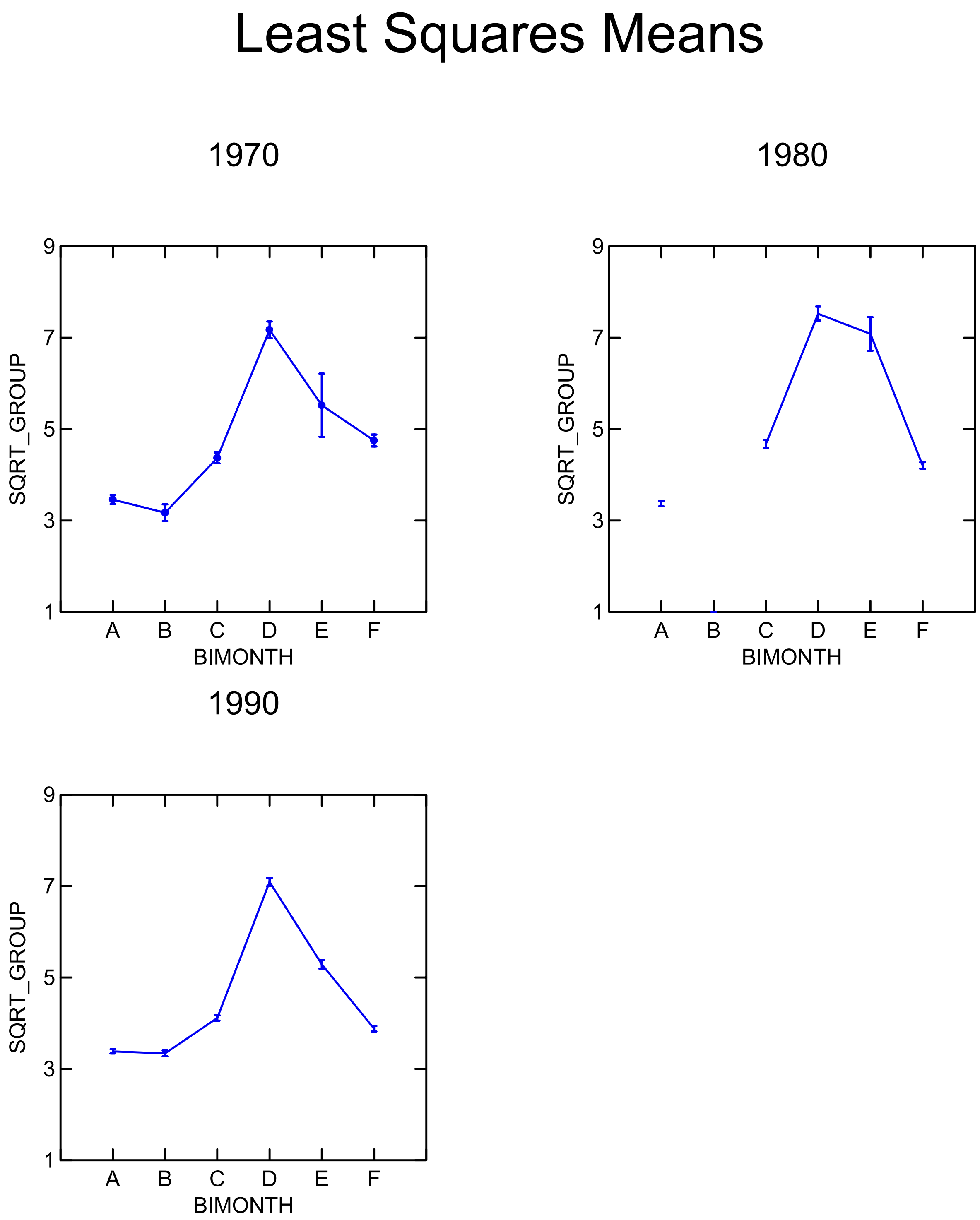

Fig. 24. Decadal changes in the seasonal pattern of group size

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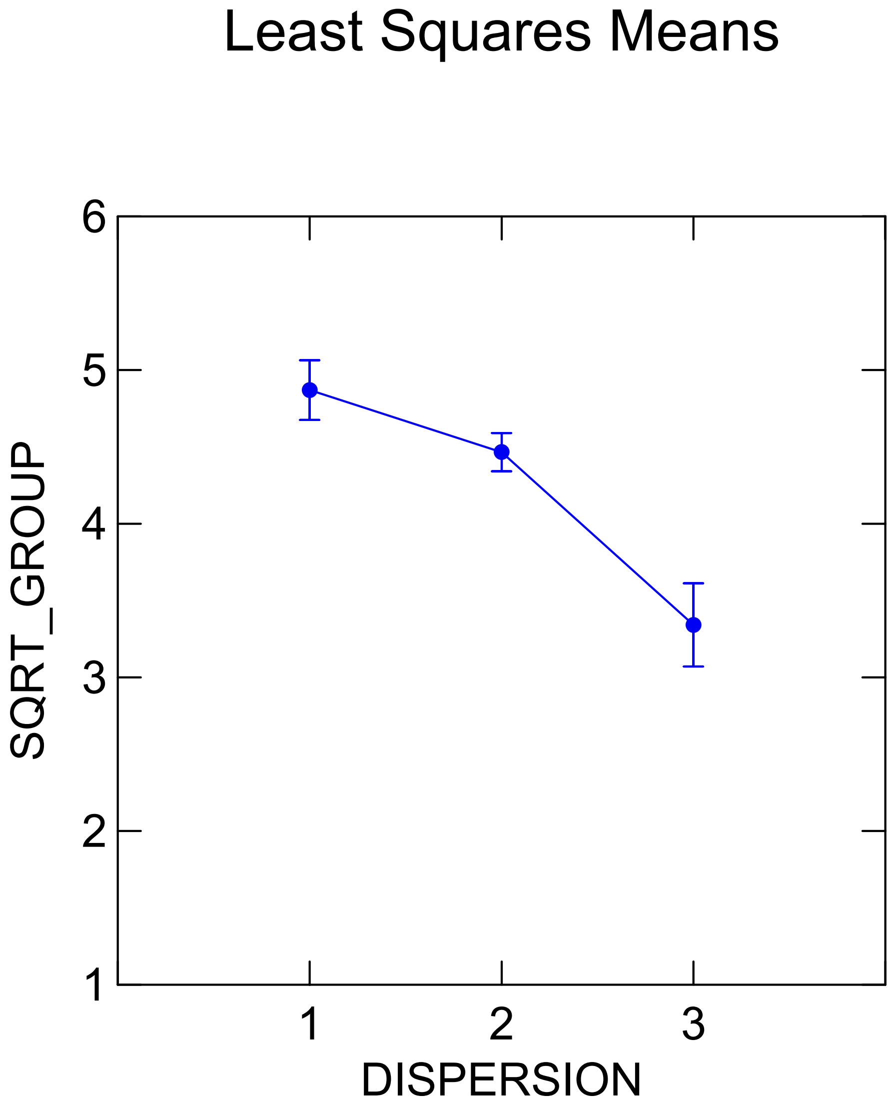

Figure 25. Square-root transformed group size and dispersion

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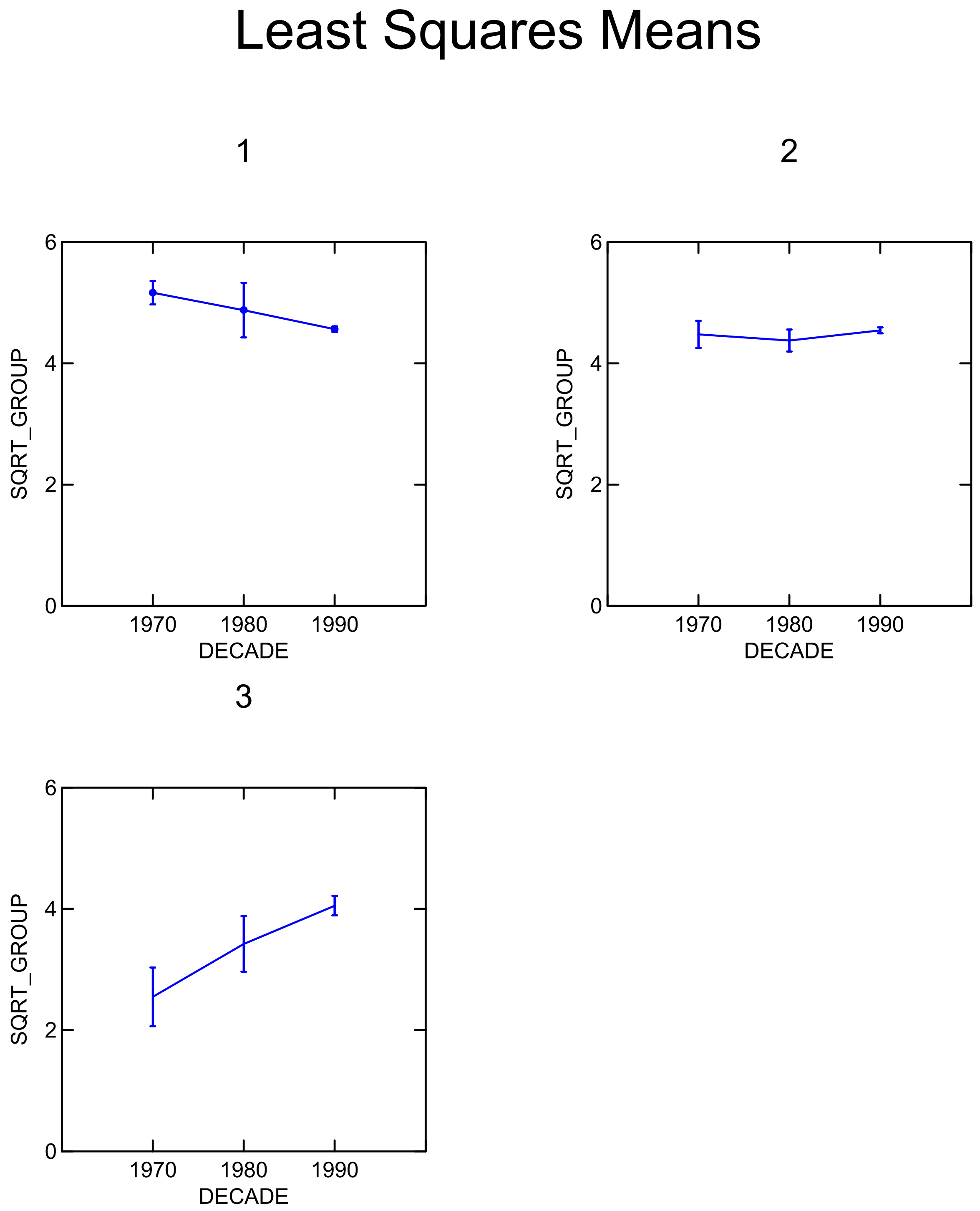
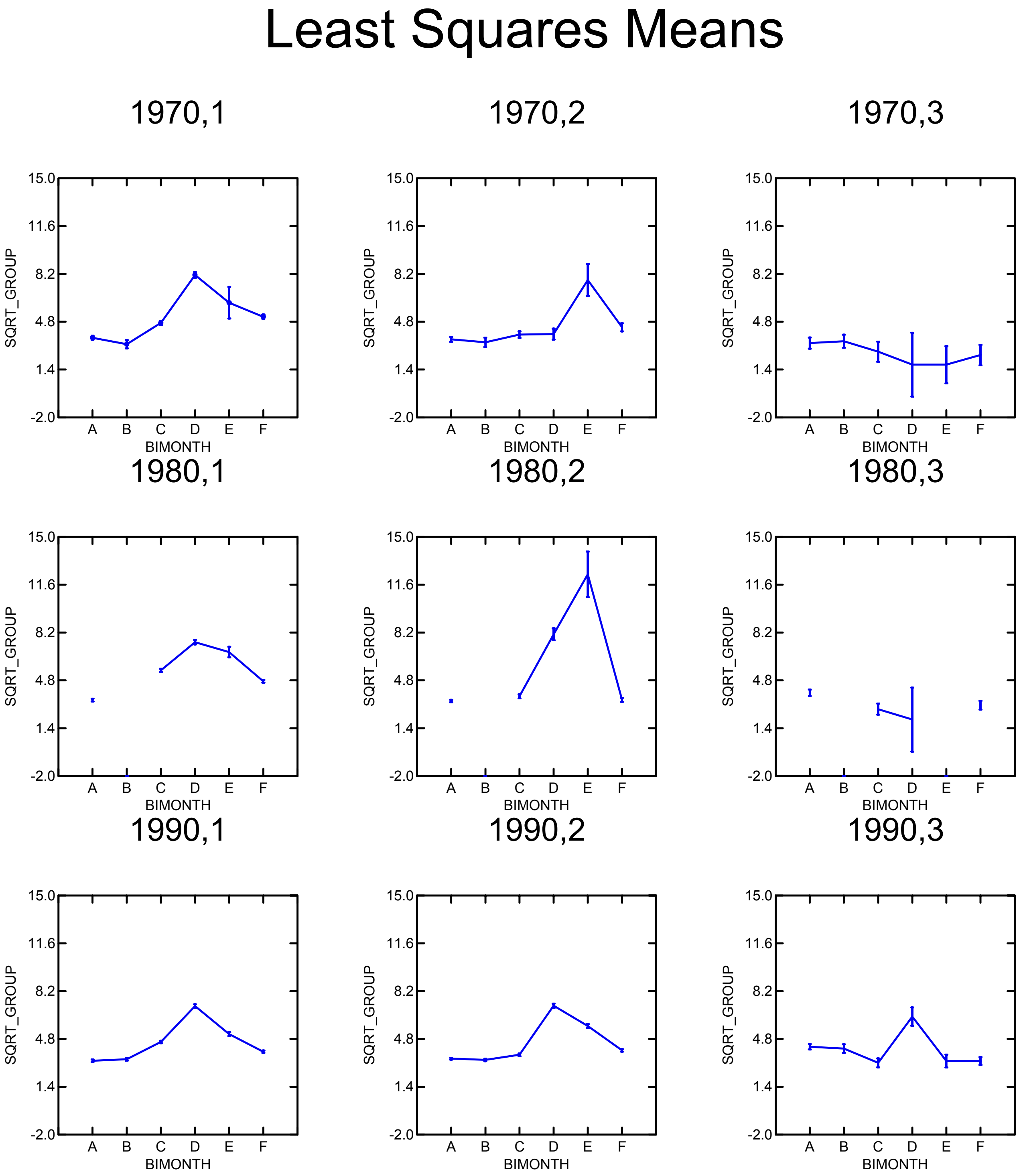


Fig. 26. Square-root transformed group size by decade and dispersion.



Least Squares Means

1970,1

1970,2

1970,3

1980,1

1980,2

1980,3

1990,1

1990,2

1990,3

Fig. 27. Decadal changes in the seasonal patterns of group size and dispersion.

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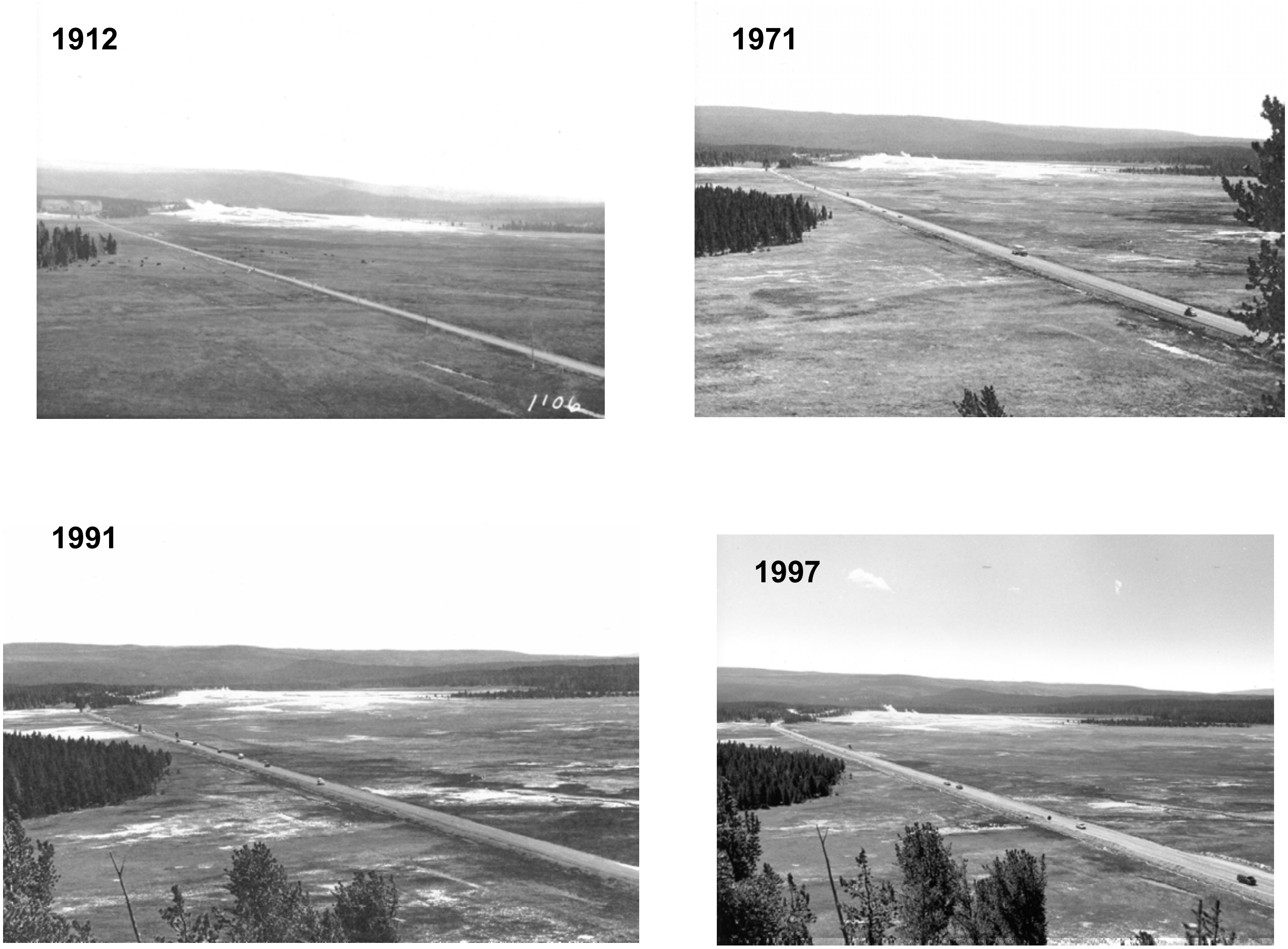

Fig. 28 (a,b,c,d). Views south across Fountain Flats in the Lower Geyser Basin, Firehole area. Dates: Sept.1912, 26 Aug.1971, 6 July 1991, 20 Aug.1997. Photos by (a). U.S. Army Engineers. Photos (b-c) by M. Meagher, (d) by M. Meagher/ R. Renkin.. Views a-c Meagher and Houston (1998:plate 32:76-77).

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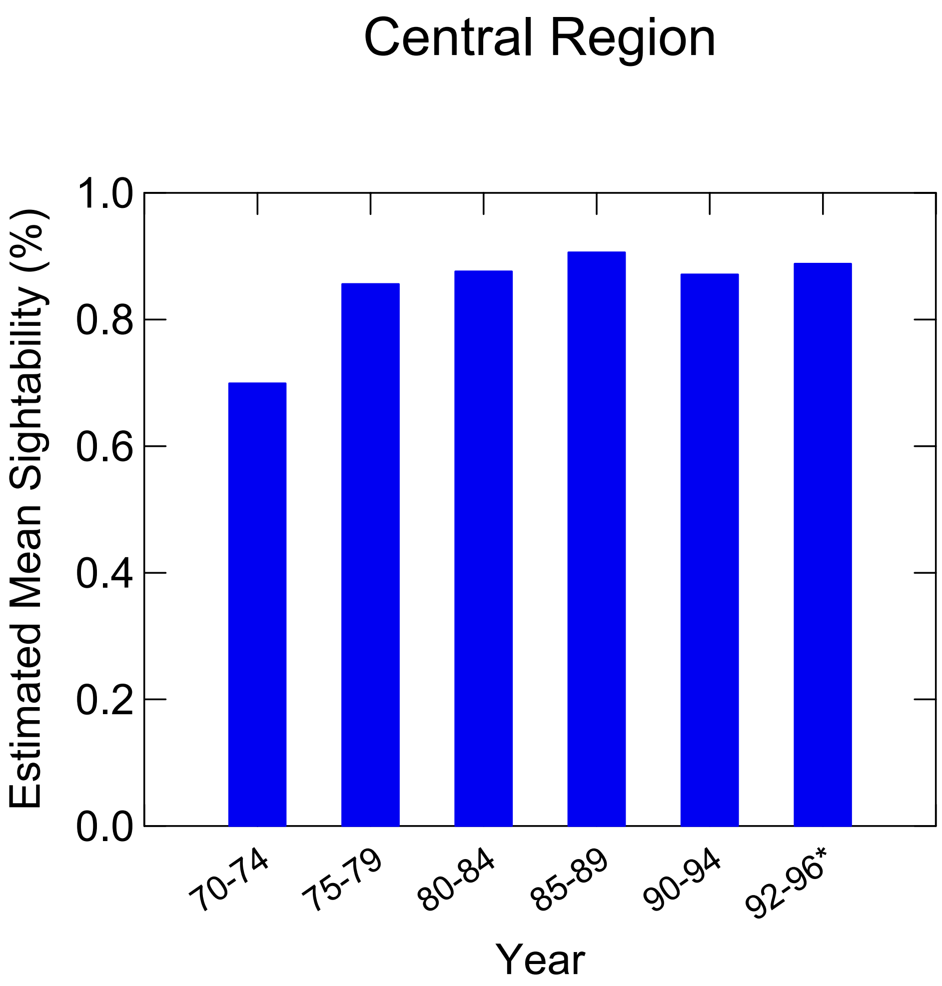

Fig. 29. Central range estimated sightability for 5 year blocks of data.

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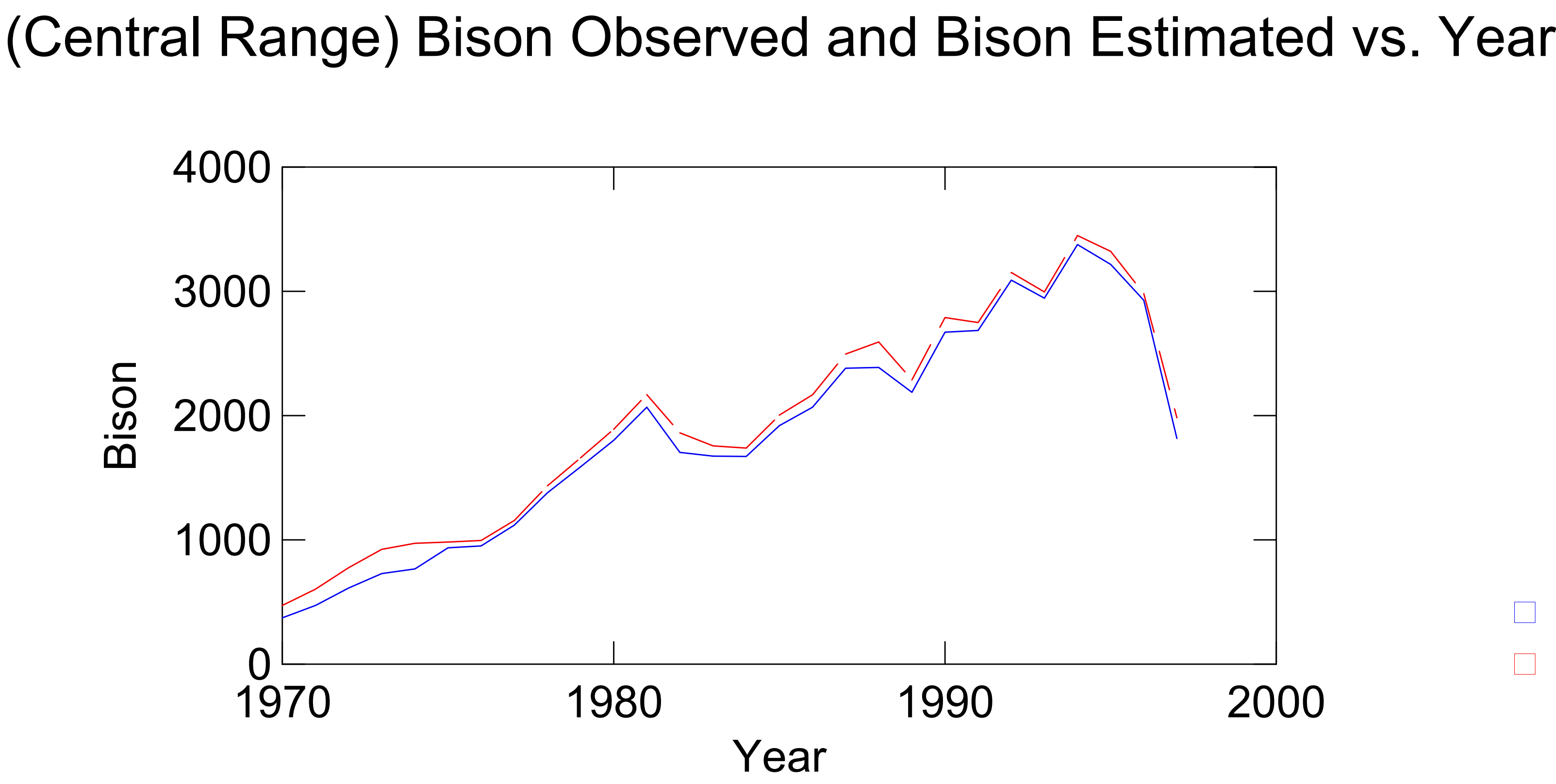

Fig. 30. Central range observed and estimated bison numbers.

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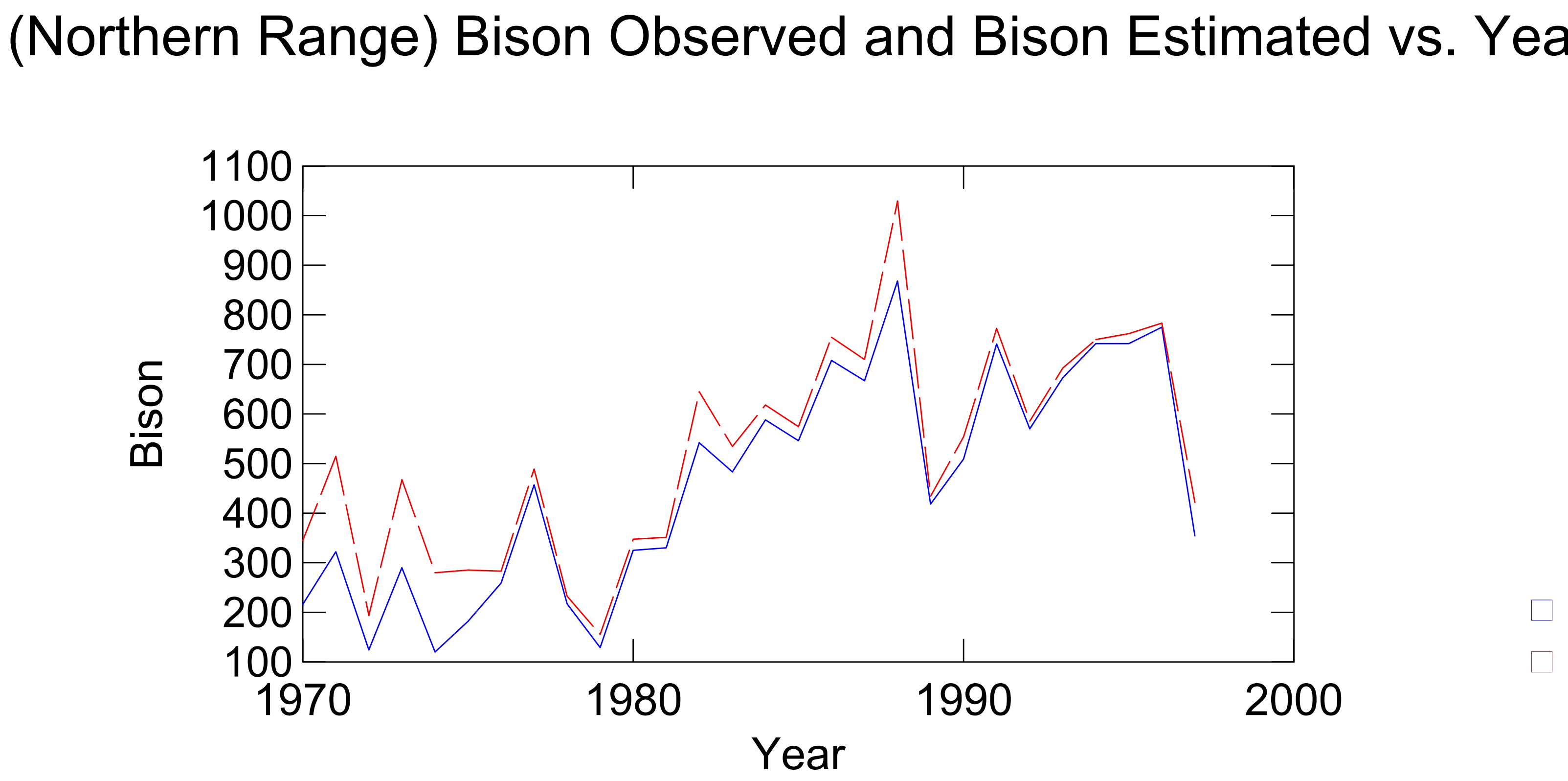

Fig. 31. Northern range observed and estimated bison numbers.

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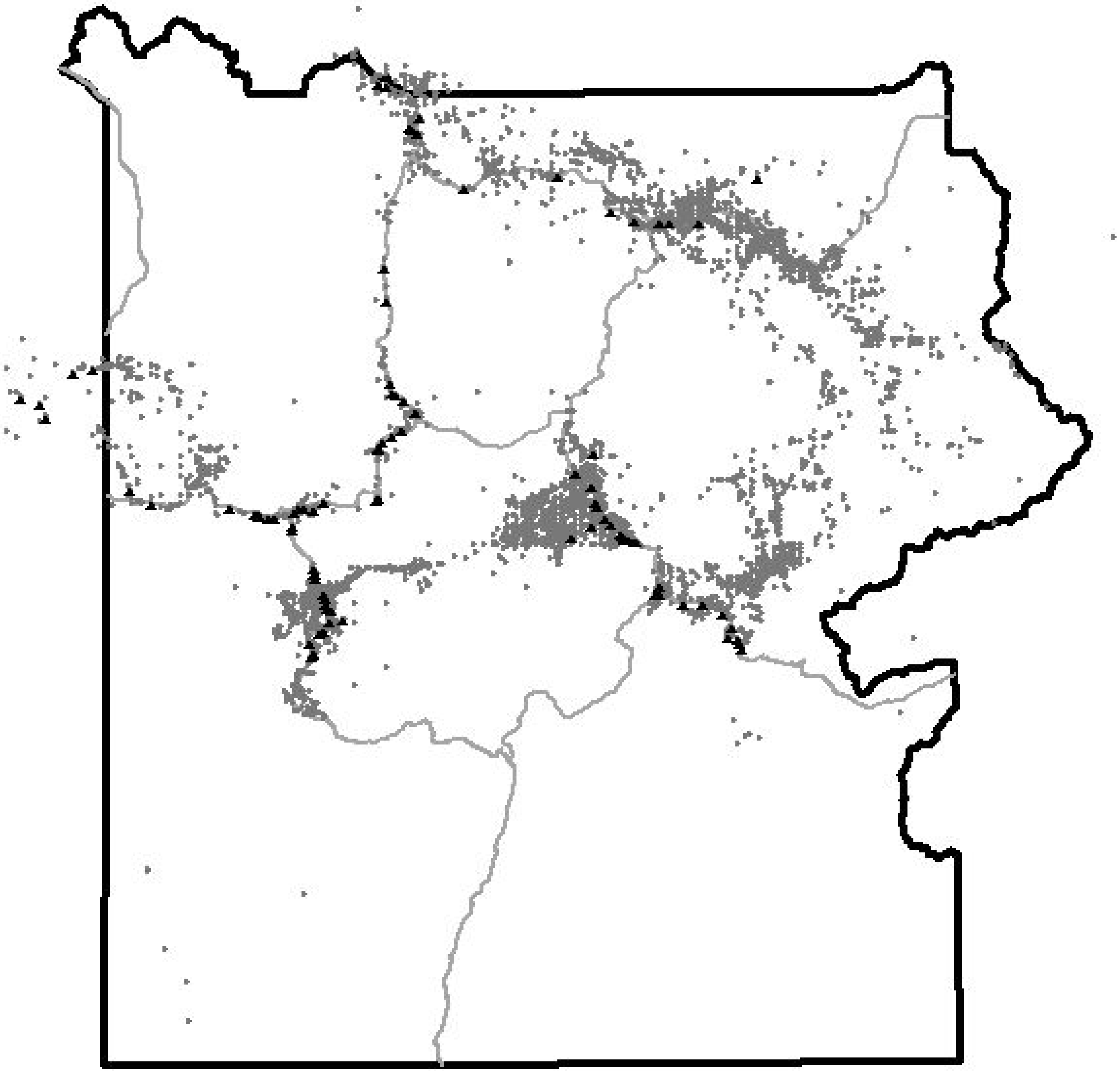

Fig. 32: Locations of all bison observations (January 1970-July 1997). Triangles represent observations of bison roads.

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Maps

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Appendix 1: Yearly summary statistics.

Tables A1 to A3 present yearly summary statistics for the combined, Central and Northern bison herds. The variables are **N**, the maximum count, **AREA,** the maximum area, and **RATE**, the observed growth rate. The Central and Northern numbers do not add to the combined. This is because the maximum counts for the component regions do not necessarily occur on the same flight as the maximum count for the combined regions. If one were to accept the isolation of the Northern and Central herds as complete, then a more accurate estimate for the combined population size would be the sum of the maximum counts for the two herds. We have not chosen this option because of the evidence of low levels of difficult to quantify population exchange between the two regions.

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Table A1: Combined Northern and Central Herds.

YEAR	N	AREA	RATE
1970	484	310.486	0.39159
1971	716	331.515	-0.01264
1972	707	305.11	0.10337
1973	784	492.862	0.16105
1974	921	393.058	0.14527
1975	1065	481.182	0.08544
1976	1160	384.04	0.15168
1977	1350	432.571	0.15668
1978	1579	333.863	0.09709
1979	1740	512.844	0.18232
1980	2088	402.582	0.13801
1981	2397	360.649	-0.06551
1982	2245	584.376	-0.03998
1983	2157	555.342	0.04620
1984	2259	640.546	0.08726
1985	2465	741.532	0.11881
1986	2776	619.123	0.06956
1987	2976	719.876	0.08961
1988	3255	766.252	-0.18103
1989	2716	575.824	0.13514
1990	3109	743.841	0.09709
1991	3426	867.938	-0.02034
1992	3357	819.714	-0.00837
1993	3329	623.225	0.21172
1994	4114	801.962	-0.04626
1995	3928	742.652	-0.09165
1996	3584	865.416	-0.24793
1997	2797		

Table A2: Central Herd.

YEAR	N	AREA	RATE
1970	474	352.223	0.07711
1971	512	156.745	0.17840
1972	612	242.258	0.17356
1973	728	313.833	0.05088
1974	766	314.518	0.20043
1975	936	373.155	0.01589
1976	951	273.482	0.16267
1977	1119	301.395	0.20819
1978	1378	266.725	0.14184
1979	1588	392.999	0.12586
1980	1801	338.234	0.13775
1981	2067	262.036	-0.19370
1982	1703	394.492	-0.01717
1983	1674	384.276	-0.00179
1984	1671	456.613	0.13838
1985	1919	448.941	0.07477
1986	2068	370.252	0.14093
1987	2381	569.683	0.00251
1988	2387	486.539	-0.08704
1989	2188	409.16	0.19983
1990	2672	642.977	0.00485
1991	2685	665.73	0.14049
1992	3090	738.867	-0.04806
1993	2945	482.927	0.13658
1994	3376	701.515	-0.04855
1995	3216	667.604	-0.09381
1996	2928	614.549	-0.34677
1997	2070		

Table A3: Northern Herd.

YEAR	N	AREA	RATE
1970	216	60.827	0.39927
1971	322	137.632	-0.32781
1972	232	80.526	0.22314
1973	290	118.205	-0.01739
1974	285	123.828	-0.44848
1975	182	155.418	0.35282
1976	259	122.087	0.56785
1977	457	90.126	-0.56016
1978	261	106.057	0.50621
1979	433	121.18	-0.21566
1980	349	95.276	-0.05597
1981	330	112.642	0.49617
1982	542	194.352	-0.11524
1983	483	188.83	0.19671
1984	588	140.62	0.09561
1985	647	293.566	0.09009
1986	708	246.283	0.00563
1987	712	232.885	0.19811
1988	868	308.1	-0.40144
1989	581	108.344	-0.07133
1990	541	148.104	0.31458
1991	741	314.051	-0.26236
1992	570	155.159	0.16610
1993	673	132.447	0.13464
1994	770	214.18	0.00129
1995	771	180.922	0.12881
1996	877	331.773	-0.18758
1997	727		

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