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Dynamics of Ungulate Populations in Elk Island National Park

by

Charles Bertram Blyth ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

Department of Agricultural, Food and Nutritional Science

Edmonton, Alberta
Fall 1995

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ISBN 0-612-06446-8

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Degree: Master of Science

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Dynamics of Ungulate Populations in Elk Island National Park submitted by Charles Bertram Blyth in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

Population dynamics of plains bison (Bos bison bison), wood bison (B. b. athabascae), elk (Cervus elaphus canadensis), moose (Alces alces andersoni), white-tailed deer (Odocoileus virginianus) and mule deer (O. hemionus), at Elk Island National Park, were described by time series analysis of historic data from 1906-85 and data collected during this study from 1986-94. From this analysis, delayed density-dependence was suggested and curves describing the relationship of density and both per capita and unit area rates of increase were created. These curves were characterized by inverse density-dependence at low densities, lagged density-dependence, and variation in maximum sustained yield (MSY) and ecological carrying capacity (K). Rates of increase of moose were influenced by combined moose and elk density and also the winter tick (Dermacentor albipictus). Ecological carrying capacity of bison was correlated with the proportion of grassland habitat in the park. Density-dependence was not evident for deer. Deer were influenced by external regional population change because, unlike the other species, they move freely across the boundary of this fenced park. The mean rate of increase (λ = 1.19) was the same for each species in the 136^2 Main Park, from 1906-93. In the smaller 59 km^2 Isolation Area, from 1959-93, mean rates of increase were (λ = 1.17) for elk, (λ = 1.22) for moose, (λ = 1.25) for wood bison and (λ = 1.19) for white-tailed deer. Long term trends, periodicity, and intrinsic rates of increase were also described for each species. Intrinsic and maximum rates of increase were consistent with or higher than seen in previous studies. For elk, bison and moose, low frequency and high frequency periodicity was detected and was remarkably similar to that seen in other studies. Long term trends detected in rates of increase (λ) for elk were correlated with successional trends in vegetation. Biomass densities achieved in Elk Island provide evidence of the highly productive nature of the aspen parkland and confirm the reported pristine abundance of ungulates. Total ungulate biomass density estimates of 52.9 - 91.5 kg/ha, yielding 10.6 - 18.3 kg/ha/yr, were proposed from the range of MSY estimates derived for each species. Analysis of the grazing system, historic population management programs, and the most recent adaptive experimental management conducted during this study, provided evidence of effects of ungulate populations upon ecosystem dynamics. Management recommendations for the maintenance of ecological integrity were made based on the understanding of ungulate population dynamics realized by this study.

ACKNOWLEDGEMENT

I would like to express appreciation to Mr. J.N. Willman Chief Park Warden of Elk Island National Park. His management of the entire resource management program, afforded those involved the working atmosphere and resources needed to complete the years of detailed study, writing and commitment to pursue the program of adaptive management required to validate the research.

I also thank Dr. R. J. Hudson, my supervisor, a man whose writing and research I have always admired. I appreciated his constant enthusiastic support over the ten years it took to do this research.

Many staff members of Elk Island's Resource Conservation section and the University of Alberta contributed much needed time, effort and discussion. In particular, I would like to thank Wes Olson, Norm Cool, from Elk Island and also Dr. R.T. Hardin, Dr. W. Samuel, Dr. W. L. Adamowicz and the clerical staff of the Department of Animal Science at the University of Alberta. I also extend my appreciation to E.S. Telfer from the Canadian Wildlife Service for his assistance.

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ARIMA	autoregressive integrated moving average; a statistical model which may use seasonal and non-seasonal autoregressive, or moving average terms to identify and predict periodicity in a time series.
a_t	white noise; completely random series generated from independent identically distributed variables; all possible periodic oscillations or frequencies are present with equal power or variance.
K	ecological carrying capacity; natural limit of a population set by resources in a particular environment; the asymptote, or plateau, of the logistic and other sigmoid equations for population growth.
MSY	maximum sustained yield; the population numbers or density the produces the maximum number of new individuals (for offtake)
N_t	number of individuals in the current year.
N_{t-1}	number of individuals in the past year.
r	annual rate of population increase.
$\underline{r}$	exponential rate of population increase; $\underline{r} = \ln\lambda$.
r_m	intrinsic rate of increase; when resources are not limiting the annual rate at which ungulate populations with stable age distributions increase
r_{max}	maximum annual rate of population increase.
S	number of individuals removed, by management, from the population.
W	mean adult body weight.
α	population noise or error; the random component of population change within a constant environment.
β	environmental noise or error; the random component of population change caused by environment.
γ	measurement noise or error; the random error caused by estimation of r and N because they cannot be measured accurately.
λ	finite population multiplier; $\lambda = 1 + r$.

INTRODUCTION

First described by European fur traders as the transitional area between the boreal forests to the north and great plains grasslands to the south, the Aspen Parkland served as critical habitat for millions of large ungulates, which provided a subsistence and economic base for native people (Ray 1974). Today only 5-10% of Canada's parkland has not been altered or destroyed (Fehr 1984). One unique remnant is preserved in Elk Island National Park which contains within its fenced boundaries populations of plains bison (Bos bison bison), wood bison (B. b. athabascae) elk or wapiti (Cervus elaphus canadensis), moose (Alces alces andersoni), white-tailed deer (Odocoileus virginianus) and mule deer (O. hemionus). An 89 year uninterrupted record of ungulate populations at Elk Island provides a rare opportunity to gain insight into density-dependent population dynamics of coexisting ungulate species. It also offers a significantly large data set from which to describe temporal variability within species populations by use of time series analysis. Despite this potential, there have been few formal publications and they are limited to individual species within a relatively short period (Flook 1970, Blood 1974, Telfer and Scotter 1975, Telfer and Cairns 1979).

A significant body of literature discusses theoretical population dynamics. Discussed are the expected dynamics of populations regulated primarily by abiotic density-independent conditions and those limited by density-dependent intraspecific and interspecific interactions (Caughley 1976, May 1981, Noy-Meir 1981, Schaffer 1986). Closely tied to this is the theoretical concept of carrying capacity which has also been thoroughly reviewed (MacNab 1985).

There is also a growing body of long-term empirical studies of population dynamics but these are largely limited to microtine rodents (Krebs and Myers 1974, Henttonen et al. 1985, Brown and Heske 1990). These species having short life-spans and high reproductive rates are most productive at densities below 50% of ecological carrying capacity (K). Ungulates having low reproductive rates, long life-spans and being resource limited are usually most productive (MSY) at densities closer to (K). This was confirmed by Fowler (1981) in 23 of 27 cases reviewed and by Skogland (1986) who listed food limited density-dependent responses for over 12 ungulate species. This principle has formed the basis for some notable models of trophic interactions and many harvest strategies employed in the management of hunted game populations, game farms, and fenced large mammal preserves (Caughley 1976, Noy-Meir 1975, Eberhardt and Siniff 1977, Houston 1982, Skogland 1986).

This ongoing study began in 1983 to develop a vegetation and ungulate management plan for Elk Island National Park. The specific objectives of this study were to: (1)describe the population dynamics of the five coexisting ungulates - plains bison, wood bison, moose, elk and deer; (2)characterize density-dependent population regulation; (3)relate man-caused mortality, successional changes in vegetation, parasites, disease, and climate to population dynamics; and (4)define carrying capacity with respect to maintenance of the ecological integrity of Elk Island National Park. The strategy consisted of two main parts: models developed from detailed description/time series analysis of population dynamics and; a continuing program of adaptive management designed to test model assumptions and predictions.

STUDY AREA

General Characteristics

Elk Island National Park is situated approximately 30 km east of Edmonton in the Beaver Hills of central Alberta, Canada. It is bisected by a highway into the "Main Park" area covering 136 km^2 and immediately to the south the smaller 59 km^2 "Isolation" or "Wood Bison" Area. Each is completely enclosed by a 2.2 m paige wire ungulate fence (Fig. 1). Elk Island is situated on the northern portion of the Cooking Lake Moraine that rises 30 to 60 meters above the general level of the surrounding Alberta plains. Also known as the Beaver Hills, the landscape is a complex mosaic of small hummocks, prairie mounds, and linear ridges with some interspersed flat lying glaciolacustrine areas (Jennings 1984).

Surface water flow and storage are constrained within five local drainage basins that drain from the park to the North Saskatchewan river. Several large shallow lakes and many small lakes are present in the many depressions of the hummocky topography. This topography coupled with the abundant aspen vegetation has allowed beavers to dam and greatly reduce surface water flow. The associated flooding resulted in a loss of nearly 7% of the land area between the years 1950 and 1983 (Blyth and Hudson 1987). The key characteristic of the water resources is that of the broad and frequent land interface. This contributes to the physical diversity of the area and allows a range of hydric regimes to occur over short distances.

The general region is characterized by Chernozemic and Solonetzic soils. In contrast, the specific local conditions in the Cooking Lake Moraine have resulted in predominantly Luvisolic soils. This formation of Orthic Luvisols beneath aspen forest and Dark Gray Luvisols beneath grasslands, is predisposed by the heavy clay subsoils that abound (Crown 1977). Where deep sand deposits occur, such as those found southeast of Astotin Lake, Eluviated Eutric Brunisols have developed and in areas of poor drainage Luvic Gleysols typically occur. With further organic accumulation, Typic Fibrisols and Teric Mesisols are also found (Crown 1977).

In one area, the "Soapholes," groundwater discharge has brought a concentration of soluble salts to the surface. Here a Gray Solodized Solonetzic soil has developed. Although common throughout much of the region, it is locally rare owing to the generally low concentration of salts in the soils of the park.

Elk Island falls within the same climatic zone as Edmonton (MacIver 1981). The climate station record for Elk Island is comparable with that of 'Edmonton International' which is the representative climate station of the transitional grassland ecoclimatic region (Ecoregions Working Group 1991) (Fig. 2). The climate in the Edmonton region is northern mid latitude continental and as such, is subject to large contrasts in daily and seasonal temperature. At Elk Island the coldest and warmest months of the year are December and July with mean minimum daily temperatures of -16.3°C and mean maximum temperatures of +22.6°C, respectively. The total yearly precipitation averages 487 mm, 78% occurring as rainfall. The average winter, as defined by below freezing daily mean temperatures, lasts from November 16 - March 17. Average annual snowfall is 106 mm usually resulting in accumulations of approximately 20 cm at the end of January and February.

Weather records from the city of Edmonton describe the yearly variability of the region's climate since 1880. The 1880-90 period was cool but dry. Over the next 80 years the general trend was toward a more moist and warm climate. Mean minimum temperatures, total degree days and frost free period increased as did snowfall and precipitation. Notable exceptions to the general trend were the 1900's and 1920's which exhibited low precipitation, temperature and growing degree days. The 1960's had lower summer precipitation but above normal temperatures. Of special note are the great amounts of rainfall (100-150% of normal) which occurred during the 1930's when much of the central North American grasslands experienced extreme drought (Mackay 1977).

Elk Island is geographically situated in a transitional region between the prairie to the south and boreal forest to the north. Its vegetation has been variously described as Mixedwood Boreal forest (Rowe 1972, Polster and Watson 1979, Strong and Leggat 1982), Parkland Prairie (Moss 1955), Parkland-Boreal Forest Transition (Zoltai 1975, Reid 1986), Aspen Parkland (Bird 1961), Aspen Grove (Knapik and Coen 1978) Transitional Grassland (Ecoregions Working Group 1991) and Fescue Grassland (Wright and Bailey 1982). Common to all classifications is the recognition of aspen forest in various stages of succession and abundance with the presence of some boreal and prairie species, such as spruce and fescue.

The 15 primary communities that together comprise the vegetation of Elk Island and their successional relationships were described by Reid (1986). They include six forest communities; Populus tremuloides/Corylus cornuta/Aralia nudicalis, P. tremuloides/P. balsamifera, P. balsamifera/C. cornuta/A. nudicalis, Betula spp. /A. nudicalis, Picea glauca/A. nudicalis, P. mariana/Ledum groenlandicum/Sphagnum spp., 3 Shrub communities; Symphoricarpos spp./Poa pratensis, Salix spp./Calamagrostis canadensis, and L. groenlandicum/Vacinium spp./Sphagnum spp., 3 Grassland communities; P. pratensis/Achillea millefolium, Puccinellia distans, Bromus inermis/P. pratensis, and 3 wetland communities; Carex spp., Carex spp./Salix spp. and Typha latifolia.

The vegetation is dominated by aspen forest communities that comprise approximately 70% of the surface area of the park. This present vegetation cover is a result of rapid succession from grasslands to aspen forest during the late 1930's and 1950's (Blyth and Hudson 1987). The decline of grasslands from nearly 40% of the total surface cover in 1923 to < 2% today, provides evidence of the significant ecological change in this century (Fig. 3). Study of the pollen assemblage and records of early explorers also describe the protohistoric vegetation as having been less dominated by Aspen forest and characterized by frequent fires (Vance 1979, Vance et al 1983, Thomas 1977, Coues 1965, Spry 1968 and Hind 1859).

Predators such as the wolf, grizzly, black bear, cougar, lynx, wolverine and foxes were all historically present within the region. All these predators were trapped in the Beaver hills during the 1800's. Today, only the coyote and lynx occur in relative abundance with the cougar and red fox being extremely rare. Collectively, the entire predator component is assumed to have little effect upon the large ungulate population. Coyotes prey upon white-tailed deer but their effect on the population is believed to be negligible.

Diseases and parasites have been and are important components of Elk Island. The winter or moose tick (Dermacentor albipictus) has since 1933, been associated with mortality and declines in the moose population at Elk Island. Brucellosis (Brucella abortus) was detected in the park's plains bison population in 1947 and remained a significant disease until its elimination from the population in 1972. Tuberculosis (Mycobacterium bovis) discovered in the park's wood bison resulted in destruction of all females and the hand rearing of salvaged calves. This potentially serious disease was thus successfully eliminated.

Use and Management by Man

By the altithermal period, approx. 4000BP, Plains Indian cultures had emerged. Their presence continued in the Elk Island Region throughout the evolution of the aspen parkland that followed. Records of early Europeans in the area suggested that harvesting of bison to feed, cloth and shelter the large winter concentrations of people were an important activity. A second important activity was the use of fire. Many early explorers noted that the native people regularly set fires that burned seemingly out of control over large regions (Lewis 1983). The Beaver Hills was no exception and were described as an area where fires were frequently set. The purpose was to burn the forest to increase game populations. This practice was viewed with horror and actively discouraged by Europeans.

The Beaver Hills region was, as the name implied, rich in furbearing species such as the beaver. For this reason and the local abundance of large game for food, Fort Edmonton and Fort Augustus were established in 1795. By 1815, only twenty years later, the fur trade had nearly exhausted the country of beaver. Subsequently, the forts concentrated on the provision of large quantities of game meat. The journals of Kane, Palliser, Hector and McGilvary provide many references to the numerous bison, moose, deer, and elk being supplied from the Beaver Hills (Losey 1978).

By the late 1860's, bison were almost eliminated and other large ungulates were reported as scarce. Local native tribes, no longer able to support themselves, requested government assistance and were moved away to reserves. Early conservation efforts failed. Consequently, the plains bison disappeared and elk were reduced to only a few remnant populations. During the next thirty years, the Beaver Hills remained untouched, few ungulates grazed, few fires occurred, and little land was cleared. The result was likely a rapid succession to aspen forest. Later these forests were viewed as a valuable resource and thus six townships of land were withdrawn from settlement. In 1895, whatever forests had developed were destroyed by a large fire of human origin. In 1899, further action was taken to set aside the land as "The Cooking Lake Forest Reserve." The elk population, still present in the area, was considered one of the last populations in Canada. Although the forest was now within the legal protection of a reserve, this did not include protection of wildlife. Commercial hunting was no longer a threat but was replaced by settlers who hunted for both meat and sport.

In 1906, a group of five local residents offered under bond, to enclose at least 20 elk in a proposed reserve or park if the Government of Canada would legally designate the land. The offer was accepted and in July 1906, "Elk Park" was established. With elk, mule deer, and moose secured within its fenced boundaries, Elk Park became the first federally controlled area in Canada to be enclosed as a sanctuary for ungulate species.

Elk Park was legally designated as a Dominion park with the name Elk Island in 1913. As such, it was informally referenced as an "animal park" as opposed to a "scenic park." Management of the park was specifically directed at the ungulates. Cutting hay within the park to feed the animals and eradication of predators were excepted practices at this time. Orphaned moose, deer and even one elk obtained from outside the park were carefully hand-reared. Births, deaths and total animal numbers were carefully recorded.

Perhaps more than anything else, the introduction of plains bison determined the course and style of management of the park. In 1907, 377 plains bison were placed in Elk Island on a temporary basis before being shipped to the Dominion Buffalo Park in 1909. Not all were translocated and those left behind formed the basis for a population that grew to require a substantial degree of management. This included capture, feeding, culling and other forms of husbandry normally associated with cattle.

Each year as the populations of ungulates grew, more hay was required to feed the bison in winter. Native range was also perceived, by the Superintendent, as overgrazed by the elk and moose that were not being fed (Coxford 1917). Recommendations to expand the park were accepted and in 1923, an adjacent 94 km^2 area to the south was added to the original 42 km^2. This new area was largely grassland and aspen groves that provided new diversity to the park's vegetation. The bison, which favoured grasslands, now appeared to spend more time in this new southern area.

Immediately after park expansion, livetrapping of moose and elk was attempted at the request of the Dominion Commissioner for Parks who noted an excess number of ungulates compared to other parks (Harkin 1924). At the park, the numbers were not seen as excessive since Elk Island had just more than doubled in size. This and inadequate facilities resulted in a failure to achieve a reduction in animal numbers. The first real discussions of large ungulate carrying capacity came in 1928. Although Elk Island's populations were below the proposed carrying capacity of 1,400 to 1,500 for bison, it was decided that small annual population reductions were required as a preventive measure. Other wildlife-oriented Dominion parks also experienced population increases viewed as detrimental to the range and the animals themselves. They reacted by constructing abattoirs and reducing populations by slaughter. This method was used at Elk Island to remove a small number of bison, moose and elk.

In 1930, Elk Island was re-designated a "National" park. Although this provided new legal direction, little change occurred in management direction. Later that same year, the Superintendent proposed to reduce populations of large ungulates again by slaughter. This time, the proposal was rejected by officials in Ottawa. The reason was that meat prices were depressed and Elk Island's bison population was not yet at carrying capacity. In the years that followed, meat prices and other concerns meant continued delay of further slaughter operations. Even in 1935, when a slaughter was finally conducted, sufficient numbers were not removed due to poor carcass quality. The following winter with the populations of bison and elk each over two thousand, significant winter mortality and associated public criticism resulted in the retirement of the first Superintendent, A. Coxford and his replacement by a veterinarian, Doctor B. I. Love.

Large populations and yearly programs of slaughter and livetrapping perhaps best characterize resource management of the 1940's and 1950's. In 1949, the park was expanded. This new area was fenced separately as a quarantine area for brucellosis eradication. Hay production capacity within the park was increased during this period. In many roadside meadows, brushing and reseeding with agricultural species was carried out. In 1939, a program of spruce tree planting started. This practice, which contributed to today's more boreal appearance of the park, continued until the late 1950's.

At the end of the 1950's, the Canadian Wildlife Service began to support research and provide park management with advice concerning the natural resources. This sponsorship resulted in the first comprehensive study of the vegetation and ungulates (Holsworth 1959). Unfortunately the results of this research were largely ignored and as a result the newest Superintendent, H. R. Webster began to carry out a strategy aimed at restoring the area to a boreal environment. This included the philosophy that a population of bison was perhaps an unnecessary component of the park's ecosystem. Because of his beliefs, the ungulate populations were reduced by over 45% in the winter of 1959 followed by more large slaughters over the next two winters. The density of large ungulates was now as low as it had been in the mid 1920's when the park was first expanded. With fire excluded from the park and lowered densities of bison, elk and moose, rapid aspen succession eliminated much of the grassland and groveland areas from the park.

In the next 18 years from 1960 to 1978, 6 more Superintendents grappled with the difficult decisions of appropriate animal numbers and the maintenance of the natural character of the park's vegetation. These considerations were further complicated by the rapid expansion of reintroduced beaver populations in the 1960's and the fact that since 1965 the park had maintained a wood bison population in the separately fenced southern portion of the park.

In 1978, agreement was reached on the first formal management plan. Shortly after that a process of resource management planning was begun, spawning a comprehensive suite of inventories, and the data used in this study. Today, park management is committed to the preservation, and restoration of the natural ecological processes of change in order to maintain the temporal and spatial characteristics of the native aspen parkland grazing system. Its current aim is to allow ungulate populations to be determined largely by ecological carrying capacity subject to the constraints imposed by land area, the surrounding fence, absence of effective predators, justifiable public reaction to substantial animal losses, and protection of endangered species.

METHODS

Population Census

Since the park's establishment, regular counts of the large ungulate populations have been conducted and carefully recorded. During the early history of the park, yearly reporting of animal numbers was required for submission by the Park Superintendent to Ottawa. These numbers were obtained by ground counts conducted on horse, by foot and by roundup, capture and feeding of many of the park's large ungulates. These estimates were believed to be accurate given the small size of the area being surveyed. This yearly report was replaced in the late 1920's with a monthly report of population numbers that required the notation of all mortalities, removals (slaughters and live removals), additions (reintroduction), and births. Although the park area had been enlarged significantly, the open grassland environment made ground census easy. These reports did not account for all additions and deletions to population totals but yearly ground surveys and roundups updated the population totals.

In the late 1950's the monthly reporting of animal numbers was confirmed or adjusted by annual aerial surveys. Initially these surveys were conducted by fixed wing aircraft however, since 1969 they have involved a Bell 206 helicopter (D. Gilbride, Annu. Air Survey Rep., Elk Is. Nat. Park, 1984). Each of the two separately fenced areas of the park is completely covered by 0.5 km wide east/west transects resulting in a total count of each species. Animals observed are classified as adult, yearling or calf and are described as male or female. This and the requirement of the survey for overcast sky conditions, snow cover, the very open nature of the vegetation, and the short duration of the survey (Main Park 6 hrs., Isolation Area 3 hrs.) resulted in a very low estimate of error. This was confirmed by successive surveys conducted before and after removal of known numbers of each species. In recent years the number of elk observed has been adjusted based upon group size and forest cover following the method described by Samuel et al. (1987).

In the late 1970's, population structure and relocation records for bison and relocation records for the other large herbivores were compiled. The bison population structure records were updated by annual roundup operations where each individual was weighed and ear tags were recorded (Reinjtjes 1991). These records from 1960 to the present provided a demographic record of the bison handled and shipped from or slaughtered at Elk Island. Elk and moose population structure were derived from aerial census and classified ground counts.

Data Acquisition

The data for the analyses were obtained from: (1) Elk Island National Park (Historic) Files E.181 to E.331. and 63/7-A2 to A4, found in the National Archives of Canada, and at Elk Island National Park; (2) active resource management files at Elk Island National Park; (3) warden wildlife records stored in the Canadian Soil Information System (Can.S.I.S.) computer data base; (4) annual air survey reports (1959-92); (5) the annual "ecosystem status" reports (1985-93); (6) population structure, ear tag and relocation ledgers; (7) post mortem record ledgers from annual slaughters (1928, 1935-1981); and (8) published reports. From these sources, demographic data were collected and verified for plains bison in the Main Park (1909-86), wood bison in the Isolation Area (1965-86), moose numbers in the Main Park (1909-86) and in the Isolation Area (1960-86), and elk numbers in the Main Park (1906-86) and in the Isolation Area (1960-86).

For each year, an estimate of the population before removal of individuals (N_t) and after (N_t-S) was derived. The ratio of N_t and the post removal total of the previous year (N_{t-1}-S) was used to derive λ, the finite population multiplier, which is defined as $\lambda=1+r$. It is this annual rate of change (r) which is usually referred to throughout the text. This method, used by Eberhardt (1987), was selected because population surveys were usually conducted during the winter just before or just after each population reduction. This allowed an analysis of demographics with and without the reductions imposed by management. During periods of initial population growth, when populations were free from such reductions, the exponential rate of increase was calculated by regressing the natural logarithm of population numbers against time. This exponential rate of increase ($\underline{r}$) and λ can be related by the function $\underline{r} = \ln\lambda$. Low natural mortality, detailed monthly accounts of mortality and accounts of animals slaughtered and removed made population estimating relatively easy. In a few instances, conflicting numbers were resolved by written assessments found in park files. Throughout the record, only three years were derived through extrapolation. This included the years 1913-14, 1963-64, and 1989-90 (Main Park).

Changes in vegetation and available habitat for ungulates were documented by a review of air photography for the years 1924, 1950, 1962, 1972, and 1983 (Blyth and Hudson 1987). Boundary fences locations, surface water area and additions to the park [illegible] included thus documenting the total terrestrial habitat available to the ungulate populations. These available area estimates were used for calculating the population density (#/ha) for each year (Appendix 1 and 2).

Bison population records after 1960 represent the best data describing age and sex because of branding and tagging which allowed identification of individuals during yearly roundups. Regular post mortem data recorded during slaughters (1935-81) provided records of actual age on other species but did not provide absolute age breakdowns on the entire population. These slaughters also provided data regarding live and dressed weight, fecundity, disease, and condition. This information was available in slaughter record books and slaughter reports that were routinely written following most slaughters. Together population structure, weights, and demographics formed the basis for biomass density estimates and allowed the validation of estimated average weights proposed by Telfer and Scotter (1975). This provided the primary time series data set for investigation of density-dependence.

Supporting information that described parasites, predators and diseases were derived from data in park files and in recent years, published reports. The results of blood testing and post mortem inspection for brucellosis and tuberculosis were recorded routinely as required by the Canadian Health of Animals Branch. Winter tick infestations were recorded in monthly and yearly animal reports whenever severe hair loss was observed in the field or ticks were found on dead or slaughtered animals. Necropsy reports found in park files and parasite investigations of slaughtered animals were used to describe the other parasites and diseases.

Comparative information concerning browse and herbage use by the ungulate populations was obtained from existing published and unpublished surveys. Range condition information was derived from subjective assessment reported in monthly and yearly reports located in Elk Island park files. Quantitative data were derived from reports by Holsworth (1959) and Bouckhout (1971). Both studies were only undertaken during a single season and permanent transects were not established. In 1972, the Canadian Wildlife Service established permanent browse transects that were measured again in 1974, 1976, 1979, 1981, 1983, and 1984. The method for this survey is outlined in Telfer (1972). In 1985, a new method of browse survey was adopted (Olson and Blyth 1985). Descriptions of herbage production and use were gleaned from a few existing reports and from permanent plots monitored yearly since 1984 (Stromsmoe 1991). Supplemental feeding of bison, and to a small extent other large herbivores, was described by compiling all of the monthly feeding records into yearly totals. These monthly records were obtained from Superintendents reports, park farm records, and yearly reports of the Dominion Commissioner of Parks.

Supportive information describing the climate is based upon the weather records of several stations in the Edmonton area situated approximately 45 km west of Elk Island. These climate records begin in 1883 and thus provide a record of suitable length for comparison with vegetation and herbivore dynamics at Elk Island. The operation of a weather station at Elk Island began in 1966 but until the spring of 1980 only sporadic records were made. Subsequently, continuous records of temperature, pressure, humidity, precipitation, and snow depth are available. These records were obtained from the Climate section of the Atmosphere and Environment Service of Environment Canada, in Edmonton. Some other specific short term records were also available. Winter severity data including snow depth and crusting in various habitats at Elk Island were collected for two separate winters (VanCamp 1975, Welch 1982).

Analytical Procedures

Statistical procedures were consistent with Shumway (1988) unless stated otherwise. Analyses were conducted using the Statgraphics statistical analysis computer software (STSC, Inc. 1991).

For each large ungulate species, time series data for density and r were plotted on the axis of time to aid in the selection of appropriate statistics and to search for obvious patterns. Frequently, the variation of population dynamics as a function of density was not easily seen especially in the 80 year time series. This was not unexpected as density should interact with productivity to establish a general pattern or signal while α (population), β (environment), and γ (measurement error) noise would be expected to cause high-frequency variation around that pattern (McCullough 1990). If succession or long-term climatic change affected this relationship, a long term change or low-frequency variation across the entire data set would be expected and might also obscure the density-dependent relationship.

The Fast Fourier Transform procedure was applied to decompose the variance of the data into contributions over a range of frequencies (Goertzel 1960). To decide if this variance was random or represented statistically valid cycles, an Integrated Periodogram procedure with 75% and 95% Kolmogorov-Smirnov bounds of the uniform distribution of ordinates, was used. This statistic was particularly valuable in describing both long-term density-dependent cycles and shorter term cycles that created noise or variance around the pattern of density-dependence (Box and Jenkins 1976).

For low frequency variance, polynomial filters of each time series were conducted if required and analyzed for trends as suggested by Shumway (1988) . This and the analysis of autocorrelation and partial autocorrelation were important in determining if differencing was required for statistics that required stationary means. A discussion of this theoretical requirement of stationarity can be found in Hannan (1970).

Cross-correlation was used to estimate the correlation between r at time $_t$ and density at time $_{t+1}$ as a function of lag $_i$. After characterizing the frequency aspects of density and r, and the estimated cross-correlation, filters were applied to produce an output with emphasis on the frequency where density-dependence appeared to operate (Shumway 1988). In each case, a variety of weighted and unweighted filters were tested with the most appropriate filter selected for each individual time series. Successive filtering was applied based on the appropriate lag times, if suggested by cross-correlations. Descriptions of all the filters used can be found in Kendall and Stuart (1961)

For moose in the Main Park, a primary filter (the four term lagged mean composed of the present and past three years) followed by Spencer's 21 term weighted filter was applied. Net rate of population change was filtered in one stage by Spencer's 21 term filter. In the Isolation Area, the shorter period of record and cycle, precluded the use of the same long term filter. Instead successive filters of five and three terms were applied to the appropriately lagged density and r.

For plains bison, Spencer's 15 term filter was applied to both r and the lagged mean density of the present and previous year. For wood bison, a simple unweighted three term filter was used. Following their introduction in 1965, they were initially held in corrals where they were artificially fed. In 1969, discovery of disease resulted in the slaughter of almost all female adults and the hand rearing of that years calf crop. Owing to these intensive animal husbandry practices associated with the early wood bison recovery program, the analysis of density-dependence in wood bison was conducted only on post 1969 data.

Lagged density for the previous 2 years was compared to the rate of population change for Elk. A significant fifth order polynomial trend was detected and removed. Spencer's fifteen term filter was used to remove noise from the data. Successive 3 term filtering was also used to analyze elk data prior to 1950 and Henderson's five term filter was used for the remaining years.

From the filtered r and density time series, productivity curves were developed by plotting the x-y ordinates. The shapes of these curves were then described and plotted as 2nd-order polynomial regressions. In each case, productivity curves developed from filtered time series were tested using a variety of filters to ensure that the shape of the curve was not influenced unduly by the filter itself. From each productivity curve, carrying capacity (K) was described as the point where mortality balanced recruitment while MSY gross or economic carrying capacity was derived from the peak of the curve where production was maximized (Caughley 1977, Gross 1969). For bison and elk the point at which K and MSY occurred radically and rapidly shifted to new locations. This highlighted the need to separately analyze certain periods of each time series. In practically all cases, management history, parasite infestations or plant succession provided a basis for division of each time series and often provided a relevant explanation for the changes in K and MSY.

Predicted population trajectories based upon past r patterns were characterized by ARIMA time series analysis (Box and Jenkins 1976). These models contain autoregressive and moving average components, with trends accounted for by differencing if required. Statistical adequacy was determined through inspection of residual autocorrelations and probability (t-value) to ensure that residuals were attributable to white noise. Models selected were those deemed to be statistically adequate and most parsimonious (having the greatest degrees of freedom and the fewest terms).

Model Validation

Following the time series analysis and characterization of density-dependence, I evaluated alternative population management methods and objectives, specifically new population reduction techniques, amounts and timing of management intervention. In general, park management sought greater reliance upon self-regulation of the moose and elk populations (Blyth and Hudson 1987). This period of adaptive experimental management beginning in 1984 allowed testing of model assumptions with ungulate populations at different densities and under management regimes not previously experienced.

In the Main Park area, assessment of carrying capacity and the potential for greater self regulation of moose and elk populations was tested under a regime of carefully controlled bison numbers. The Main Park moose population, which had historically been subject to slaughters when deemed to be over carrying capacity, was instead allowed to find its own density. Active intervention was reduced significantly being restricted to some livetrapping, slaughter of individuals for moose tick research and reproductive suppression by administration of synthetic prostaglandins to mature females. The objective was to ameliorate the rate of increase during the initial population growth phase (1985-88) and then allow the population to seek its own density. The elk population was subjected to only small population reductions that allowed a gradual increase toward ecological carrying capacity. Plains bison were, held within set limits through biannual population reductions. Consequently, elk became more numerous than bison for the first time in the history of the park.

In the Isolation Area, the dynamics of elk and moose populations in a partially open system with a high density of bison was assessed. "Jump rails" placed in the fence allowed the elk and moose to leave and enter the park to an area of lower elk and moose density while containing wood bison within the park. The Wood bison population, managed at MSY to produce the maximum number of individuals for reintroduction to other locations, was allowed to exceed this density for a brief period testing the potential density at which K might exist. Response of each population to this period of adaptive experimental management was compared to mathematical models of density-dependence and ARIMA forecasts derived from the previous periods. Deviations were used to validate the models and provide inferences regarding causation.

RESULTS

Moose

Historical Abundance.-- The present distribution of moose may have been established 2,000 years BP (Telfer 1984). In central Alberta, the subspecies was A. a. andersoni. The Beaver Hills area was probably near the southern limit of moose in central Alberta owing to a lack of forest cover and summer temperature that generally limit present moose distribution (Kelsall and Telfer 1974, Renecker and Hudson 1986). Moose were nevertheless abundant and provided a substantial year-round food source to the native people and first Europeans (Losey 1978 and Ray 1974). Given that the local vegetation was both dynamic and diverse, because of fire and grazing by other large herbivores, moose populations probably varied through both space and time. Historical densities in the aspen parklands of central, Alberta may have been about 0.01/ha (Telfer pers. com.). Lynch (1975) describes densities from 0.39/km^2 to 1.39/km^2 in areas of Alberta from 1958 to 1975. Telfer (1984) describes better boreal and coniferous/deciduous transition ranges as supporting regional averages of one to three moose/km^2.

In the late 1700's, moose were regionally abundant in the area of Fort Edmonton, 48 kms west of Elk Island. Hudson Bay records suggest a substantial local population of moose that were harvested during all seasons but were probably not substantially depleted from 1795-1800 (Losey 1978). Moose were secondary to bison as a source of food for both native peoples and Europeans. In the mid 1800's, this secondary use changed with the depletion of the local bison populations. The result was a severe reduction and shortage of moose (Losey 1978).

By the time Elk Park reserve was established in 1906, very few moose remained in the Beaver Hills. The fenced area around Astotin lake, which formed the park itself, only enclosed two or three individuals in 1907. This led to the acquisition and reintroduction of several individuals over the next few years.

Moose were first reintroduced to Elk Island during the summer of 1909, and included a total of three individuals from unknown locations (Coxford 1910). The following summer two, 2-year olds were added. The total park population was cited by Coxford (1911) as five animals suggesting that no other than those introduced were believed to be in the park In 1911, several moose including nine from Banff, three from Lesser Slave Lake and two from an unknown location were added to the park population (Coxford 1912). That year (1911), the total number of moose was listed as 19, which again only included those animals introduced to the park. All introduced moose were held in the bison paddock on the west side of Astotin lake. Superintendent Coxford stated that "what moose were in the park previous to 1911 are running in the large timbered part of the park . . . "

Dynamics 1909-85.-- Over the entire period, periods of rapid and sustained growth resulting in high populations were followed by periods of net loss or decline. Four such periods, 1909-40, 1941-60, 1961-70, and 1971-84, occurred in the Main Park and two 1959-70, and 1971-85, in the Isolation Area. The first period of sustained growth (1909-38) was followed by a decline to 1940. From 1940-48, the population expanded and then gradually declined with several slaughters to a low point in 1960 During the next eight years, rapid growth of the population reoccurred followed by natural decline and slaughters to 1970. The period of growth (1970-80) was irregular owing to frequent slaughters and was followed by population decrease until 1984.

In the Isolation Area, concurrent periods of growth and decline occurred with those in the Main Park (1959-85). From 1959-70, population dynamics in the Isolation Area showed less amplitude and cycled one year earlier. From 1970-85, greater amplitude was displayed than in the Main Park area but again the cycle of growth and decline was one year earlier.

Since 1933, five major infestations of the winter tick were recorded in the moose populations at Elk Island. Peak infestations likely occurred in 1933, 1937, 1948, 1968, and 1981 based on reports of tick-caused alopecia on moose. In addition elk were also reported with tick-caused alopecia in 1937 and 1948. The period from 1977-90 is described in several studies (Samuel 1978, Glines 1983, Drew 1984, Samuel and Welch 1991). Each outbreak occurred after rapid increases in moose numbers and in each case significant tick numbers and alopecia were associated with subsequent population declines (Fig. 4).

In the first four periods, the population continued to decline until both slaughter and the mortality associated with the winter tick resulted in a relatively low moose population. After 1980, population reduction by slaughter or trapping was suspended and thus the moose population decline, associated with ticks, and the subsequent recovery, occurred without interference by man. In spring 1981, the number of moose with alopecia was low while tick numbers and mortality were high. This indicated that hair loss might not be strictly tied to tick numbers and mortality (Samuel Pers. Comm. 1986).

Including all periods of gain and loss, the mean r from 1911-85 was 0.20 ± 0.03 while the median was lower at 0.17 in the Main Park. The mean r occurred during only 16.5% of the years. This and the interquartile range of 29.3% describe a variable rate of population growth. In the Isolation Area the mean r was higher at 0.24 ± 0.06. The slaughter rates were 0.93 ± 0.02 in the Main Park and 0.13 ± 0.03 in the Isolation Area.

The mean standing biomass of the Main Park moose population from 1909-85 was 8.75 ± 0.543 kg/ha/year, which is equivalent to 0.028 ± 0.0014 moose/ha/year or 37.03 ha/moose/year. This density was achieved despite mean yearly slaughters of 0.91 ± 0.174 kg/ha/year and annual production of 1.14 ± 0.23 kg/ha/year. The maximum biomass occurred in 1937 when 23.32 kg/ha of moose was supported in the Main Park. This is equal to a density of 0.077/ha or 12.9 ha/moose. Over this 76-year period, slaughters and live removals occurred in over one third of the years. All but one of these 26 population reductions occurred during the period 1938-85. From 1938-85, a grand total of 2,491 moose (0.224 moose/ha, 69.15 kg/ha) were harvested in the Main Park. When averaged over this 48 year period harvests occurred in 52% of the years at a mean rate of 99.64 moose/harvest (28.6% of the total population/harvest, 0.009 moose/ha/harvest, 2.7

kg/ha/harvest). On an annual basis this equalled 51.89 moose/year or 1.44 kg/ha/year when averaged over this 48-year period. Perhaps many more could have been harvested if significant natural mortality had not removed many individuals from the population.

In the Isolation Area the mean standing biomass was 8.75 ± 0.664 kg/ha/year that is equivalent to 0.026 ± 0.002/ha/year or 40 ha/moose/year. Annual population growth (r) averaged 0.24 or 1.31 ± 0.405 kg/ha/yr. The maximum biomass supported was 15.85 kg/ha at the end of 1967. This was equivalent to a density of 0.052/ha or 19.23 ha/moose. A grand total of 496 moose were removed from 1959-85 in the Isolation Area. This is equivalent to a total of 31.75 kg/ha or 0.105 moose/ha. Slaughters and live removals were carried out during 11 of 26 years or 42% of the years. During this period an average of 45 individuals or 2.8 kg/ha were removed from the population because of each slaughter. Annually, this equaled 19.84 moose/year or 1.27 ± 0.38 kg/ha/year. A detailed description of the population dynamics for the Main Park and Isolation Area moose populations follows.

In 1912, the first moose calf was born to the introduced portion of the population. This small increase was attributed to the very young nature of this population as practically all moose had been brought to the park as calves. One moose was reported dead and one female was shipped to a zoo in Washington, D.C. leaving the park total recorded as 19 that same year. This suggests that the mortality occurred in the non-introduced portion of the population. A more substantial increase was predicted by the Superintendent for the next year. That following year another three moose were provided by the province of Alberta (Coxford 1913). These moose and three calves born that year brought the total population to 12 males and 14 females. The three calves represented an r = 0.16. In 1914, another five calves increased the entire park population to 31. This r = 0.19 represented a healthy incremental growth of the park's moose population. Further increases during the next two years of seven and eight represented rates of population increase of 0.23 and 0.21 respectively. This resulted in a total population of 46 moose in 1917. These years (1912-18) were a period of exponential population growth with r = 0.185 ± 0.015.

Poaching, natural mortality and poor range condition from overcrowding were first noted in 1917. Then the total number of moose was recorded as 46 (0.014/ha, 4.24 kg/ha). Over the next seven years, the growth rate of the park's moose population was less than half that of the previous period, perhaps because of the poaching and range conditions. The mean r from 1918 to 1923 was 0.076 ± 0.007. The population total by 1922 had increased to 70 (0.021/ ha, 6.45/kg/ha) (Fig. 4).

With park expansion in 1923, the density of moose dropped to 0.007/ha and the previous period of declining population growth ended abruptly. In 1923, r increased to 0.31 from the 0.10 the previous year. This and the next five years averaged 0.43 and by 1928 the population had reached a total of 357 (0.035/ha, 10.75 kg/ha). The first slaughter of moose was conducted in the winter of 1928. This reduced the total population by 130 and the density to 0.022/ha. The reduction in moose numbers was short lived and by the following winter the population had increased to 400 (0.039/ha). During the next three years the population grew by 0.18, 0.6, and 0.10. This represented a slowing of the growth as the population reached a peak of

550 (0.05/ha) by 1932. Including the 1928 reduction, the mean r (1924-32) was 0.218 ± 0.056. Clearly, the period 1924-32 represented a superior population growth over that of the previous period. For the longer period of 1912-32, the r was 0.177 ± 0.023.

Following the winter of 1932-33, the moose population declined drastically (r = -0.28 and -0.08) to 366 individuals (0.036/ha) by 1934. This decline was brief and again the population increased at a rate of 0.37 and 0.52 that resulted in a peak population of 775 (0.067/ha, 23.32 kg/ha) by the end of 1937. Slaughters were conducted that winter removing 160 thus reducing the density to 0.053/ha. In addition, the population declined by a further 0.29. At the end of the next year (1938), a second slaughter was undertaken which reduced the population to a density of 0.030/ha. Again despite the slaughter, the population subsequently declined by 0.29. A third slaughter in as many years reduced the population to 113 (0.009/ha) by the beginning of 1940. The population now responded by increasing at an r = 0.09. The moose population was at a similar size and density to that of 1924, which set the stage for another period of population growth.

From 1940 to 1947, the mean r was 0.38. This resulted in a peak population of 487 (0.042/ha, 12.82 kg/ha). The actual rate of population growth from 1940 to 1948 was 0.191 ± 0.026. This is far below r owing to slaughters of 105 and 110 that reduced the populations in 1944 and 1945.

After 1947, the moose population again declined. In 1948, with r = -0.22 and the slaughter/trapping of 127 individuals the population was reduced to 272 (0.023/ha). This decline occurred at a density similar to that of 1931. Following these removals and concurrent natural decline, a period of relative stability developed. Together the mean r = 0.11 and mean annual population reductions (S) = 0.11 maintained an average density of 0.027/ha or 9.24 kg/ha from 1949 to 1959.

In 1949, the Isolation Area was added to the park. The existing population of moose was removed from the area to leave the area free of any diseased animals. However, by 1959 a population of 80 moose (0.014/ha) was present in the area (Fig. 5). As all moose had been reportedly removed before 1949, individuals from outside the park probably entered this area or a small number, perhaps five to ten, remained to found the population counted in 1959.

At the end of 1959, a slaughter of 149 individuals reduced the Main Park population to 83 (0.007/ha). This extremely low density was again identical to that of 1924 after the expansion of the Main Park. Again the population responded with a high mean r = 0.41 from 1960-67. From the peak population of 627 (0.059/ha, 18.08 kg/ha) at the end of 1967, the population was reduced by slaughter of 134, 209, and 104 in 1967, 1968, and 1969, respectively. Population growth (r) also declined to 21.7% and 6.1% and -6.66% during these years. By 1971 the Main Park population was 280 (0.026/ha). A net decrease beyond the slaughters did not occur as during the previous periods of population decline.

Meanwhile, a similar population growth and reduction by slaughter occurred in the Isolation Area. The population here began from a higher density in 1961 (0.014/ha) but did not reach as high a density (0.052/ha) at the end of 1967. Over this period the mean r in the Isolation Area was 24.98%. Despite the higher r in the Main Park, larger slaughters resulted in a mean annual net population increase of 0.209 ± 0.046 similar to the 0.195 ± 0.029 of the Isolation Area during the same period (1961-68). In the Isolation Area, the r = 0.6, -0.11, and 0.32 in 1967, 1968, and 1969, respectively resulted in the population following a similar but moderated decline with recovery occurring one year earlier. This pattern was repeated during the early 1980's.

The remaining years in the Main Park are very complex. From 1970 to 1980, the r of the Main Park moose population averaged 0.29. During the first four years (1970-74), the population was stabilized by large yearly slaughters. However, after only a small slaughter of 40 in 1975, and no removals the following year the population grew very rapidly to reach 449 (0.040/ha). Again large slaughters were conducted in each of the next two winters reducing the population to 175 (0.015/ha) in the winter of 1977-78. During the next three years the population responded again with rapid population growth rates (r) of 0.34, 0.56, and 0.31 resulting in a total of 380 (0.034/ha) in 1980. Following this, the population declined by 0.27 beyond the 163 removed by trapping and slaughter during the winter of 1980-81. In the next two years the population increased by 0.14 and then declined by 0.31. Thus by the end of 1983 a low of 148 (0.019/ha) had been reached.

The dynamics of moose in the Isolation Area (1970-86) is not as complex. Except for a brief decrease in total number during 1972-73 due to slaughter, the population expanded from 62 (0.016/ha) in 1970 to 225 (0.047/ha) at the end of 1976. Over this period the growth rate of the population (r), not including slaughters, was 0.41. This was significantly higher than the r = 0.29 observed for the same period in the Main Park. By 1976, the Isolation Area moose population thus attained a higher density than in the Main Park despite having started from a lower density in 1970.

A period of population decline began in 1977 and continued until 1983 in the Isolation Area. Unlike the Main Park population, growth was not experienced after the slaughter at the end of 1976. As a result the Isolation population reached a lower density than the Main Park and reached it one year earlier. The population decline of 0.70 experienced in 1982 was the most severe on record. Despite the increased amplitude of the Isolation population the cyclicity of the population remained one year ahead of the Main Park.

Time Series Analysis and Density-Dependence.-- From 1909-85, the mean r and density in the Main Park remained stationary. This is confirmed by the character of the estimated autocorrelation and partial autocorrelations of the annual rate of moose population growth in the Main Park (Fig. 6). The absence of long-term trend toward either increasing or decreasing productivity suggested that nonseasonal differencing was not necessary to compare density and population rate of change. This is surprising in view of the general change in forest succession that occurred over the period of record.

A cycle of 15.6 years for the Main Park and 13 years for moose in the Isolation Area moose populations was suggested by the 'Fast Fourier Transformation' procedure (Fig. 6 & 7). Estimated autocorrelations indicated different periodicities of 18 and 11 years respectively. The latter were confirmed by ARIMA models and are believed to be the best estimates. Both the shorter cycle and a greater variability in the smaller Isolation Area perhaps demonstrates the effect of system size.

Cross-correlation was conducted to search for density-dependence. In the Main Park, the current and the past three years density (N_t...N_{t-3}) had a strong negative correlation with r_t. The strongest correlation was seen in the two previous years with coefficients of -0.38 and three years previous with a coefficient of -0.33. The cross-correlation of density with r for all of the three years previous exceeded that of the current year that was -0.30. All other lags showed low correlations but continued to show strong periodicity (Fig. 6).

The evident periodicity and the lagged response of r to density suggested that the population dynamics may follow that of a limit cycle. A phase plot of density vs. r with high frequency variability removed, revealed that the trajectory of density vs. r, although cyclic, does not exactly repeat itself. This suggested the population was either quasi-periodic to chaotic or attempting to return to a point attractor but appearing to cycle owing to constant disturbance.

Density-dependent curves describing per capita (r) and per unit area (#/ha/yr) rates of increase for the Main Park moose populations as a function of lagged density were constructed (Fig 8). They represent the relationship between the pattern of density and r with the high frequency variability or "white noise" removed. The specific r was almost linear for the two major periods of increase and decline (1909-40 & 1960-80). However, there appeared to be a minimum viable number below which r declined. Theoretically, r should increase toward a lower density only declining when numbers are so low that reproduction is impossible. The MSY in terms of absolute numbers (economic carrying capacity) occurred at a density of 0.028/ha for the two cyclical periods of 1909-40 and 1960-80. During the intervening cycle (1941-60), MSY occurred at a lower density of 0.021/ha. The ecological carrying capacity K (the point at where mortality balances recruitment) occurred at a density of 0.053/ha during the periods 1909-40 and 1960-80 and at 0.033/ha from 1941-60. For the first and third periods of growth and decline, the MSY was approximately 0.50 K rather than >0.50 K as expected. The second major period is more curvilinear like the expected shape for a large ungulate productivity curve. In this period, MSY is 0.6 K. Thus, only the second cycle displays the nonlinear density-dependence proposed by Fowler (1981) for K-selected animals such as ungulates, which results in an MSY greater than 0.5 K.

In the Isolation Area, the same density-dependent r as for the Main Park was derived for 1960-80. However, the years 1980-85, showed a density-dependent decline and recovery that were not lagged with density and had a much lower K than seen previously. Thus, this period of decline and recovery can best be described by a relationship similar to that for the second period of growth and decline in the Main Park moose population (Fig. 8.). Moose in the Main Park and Isolation Area had similar density peaks but the Main Park lagged one year behind. Even the second peak in the Isolation Area that characterized the 11-year period had a similar analogue in the Main Park population that displayed a small period of increase during the overall longer period of population decline.

In contrast, the Isolation Area showed a different lagged density-dependence from 1960-72. Instead density in the present and previous year had the strongest cross-correlation with r. After this period, the relationship of density and r changed to a lagged density-dependence similar to the Main Park (Fig. 7). A phase plot of density vs. r for the Isolation Area moose population is consistent with this finding in that it shifts from linear to an orbital relationship. This change in lag dependence and the short period of record made the dynamics appear chaotic.

For forecasting moose population in the Main Park, a first order seasonal moving average model was selected after first order seasonal differencing - ARIMA $(0,0,0)(0,1,1)_{18}$. The seasonal moving average was estimated at 0.5149 ± 0.13 ($P = 0.0005$). There was no temporal structure in the first 20 residual autocorrelations (Chi-square = 8.7, $P > 0.05$). The addition of a first order nonseasonal moving average marginally increased the statistical adequacy but was rejected as it was not parsimonious.

The resulting model:

$$Y_t - Y_{t-18} = a_t + [-0.5149_{18} Y_{t-18}]$$

attributes statistical dependence solely to the random impact of the previous population cycle $_{(t-18)}$ to forecast the annual rate of population change. All other variation is attributed to white noise a_t. The resultant forecast shows a highly variable annual rate of population change with very wide 95% confidence limits around a distinct cyclical pattern (Fig. 9). The requirement of seasonal differencing, as suggested in the ARIMA model selected, suggests that moose population growth or decline is drifting or trending in 18 year cycles or steps. This supports the previous density-dependent analysis where K and MSY shifted to different densities during some periods.

In the Isolation Area, a mixed model composed of a first order seasonal moving average and a second order non-seasonal moving average was selected after first order seasonal differencing - ARIMA $(0,0,2)(0,1,1)_{11}$. The seasonal moving average was estimated at 2.21 ± 0.44 ($P = 0.0003$). The non-seasonal moving average estimated at -0.71 ± 0.22 ($P = 0.0078$) contributed less to the model but was retained as it was considered parsimonious. Alternatively the constant or mean did not contribute significance to the model and was thus eliminated. The model selected is thus described as:

$$Y_t - Y_{t-11} = [-0.02950_1 Y_{t-1} - 0.71479_2 Y_{t-2}] + [2.21045_{11} Y_{t-11}] + a_t.$$

A plot of the model's forecast and analysis of the integrated periodogram of residuals proved that most periodicity had been accounted for by the model (Fig. 10). The Chi-square test statistic was equal to 1.71 ($P > 0.05$) also suggesting little temporal structure remained in the residuals. Like the Main Park, the seasonal component of the model attributes statistical dependency to the random impact of the previous population cycle $_{(t-11)}$. In contrast to the Main Park, the non-seasonal component of this model also attributed statistical significance to the random impact of the current and portions of the two previous years $_{(t-1)+(t-2)}$.

<u>Response to Management 1985-92.</u>-- The period of population decline, ending in the early 1980's, represented the completion of the third major period of cyclical increase and decline in the Main Park moose population. In all three periods, slaughters at periods of peak moose numbers appeared to do little to

prevent decline. It was also considered that these population reductions might affect the dynamics of the population. Thus, it was decided to allow the moose population to progress through its next major cycle with management actions being taken only to partially mitigate the rate of increase and test alternative methods of population reduction. The response of the population provided valuable additional data and served as a process of validation.

The population was allowed to expand during the first year of population growth (1984). That year, moose in the Main Park increased substantially, r = 0.49. The following year, 1985, the population again increased by 0.33. In the winter of 1986, the first attempts to reduce the rate of increase were undertaken with a very minor intervention, removing 3% of the population through livetrapping. In the following season, the population increased by r = 0.24. This was the third successive year of increase however, r was declining each year. The population was then reduced by 11%, through livetrapping, and through slaughter of individuals for moose tick research. The intention was to reduce the annual increment by approximately one half.

That same winter, chemical reproductive inhibition was also administered to 59 (approx. 23% of the mature cows) to reduce the rate of increase. Based upon study of 19 known individuals Cool (1987) estimated that 84% of the individuals (50) mature cows could have been prevented from calving. The following year, only 16 calves were observed and the cow/calf ratio of 100:23 was lower than the 100:67 the year before or the 100:47 the year after. That year 18% of the moose were reported with significant alopecia and the population census showed that the moose population had declined by r = -0.19. Mortality occurred over a longer period, rather than the usual concentrated spring die-off (Deering and Olson 1987). Chemical inhibition of reproduction was expected to only slightly reduce the rate of increase. This and the lack of observed mortality, resulted in a slaughter before the census thus reducing the population by a further 14.5% from 256 to 199. In summary, the unexpected natural decline, higher than expected effect of the chemical control of reproduction, and livetrapping resulted in a reduction of the total population by 47%.

The following year (1988), the moose population census showed a further natural decline of r = -0.07 to 186. From this point all population management was indefinitely suspended. Over the next three years, the population increased at a decreasing r = 0.24, 0.19 and 0.02 respectively to an estimated population of 282 (0.026/ha) in January 1992. In the winter months that followed, significant mortality and substantial hair loss from ticks was observed.

Mean r of moose population in the Main Park was 0.10 during the most recent decade, less than half of the previous 76 year period. Thus, reducing the mean r for the entire period of record to 0.19 ± 0.03. Consistently, population growth at MSY was significantly lower than previous periods (Fig. 11). MSY occurred at a density of ≈0.018 moose/ha and K at a density of ≈0.025 moose /ha. The density at which MSY occurred was similar to the previous period (1940-60) when high densities of elk coexisted. K was lower, being closer to that displayed during the previous period, 1981-86.

Crosscorrelation of combined moose and elk density failed to provide a good correlation with moose population growth in either period. Periodicity significantly increased with the population appearing to reach peak numbers every seven years in the most recent period. During this last decade, only 85 individuals were removed from the population. This represents a significant decrease in the degree of management through active population reduction being only 2.4%/year compared to the long term average of 9.5%/year. In summary, the frequency of the Main Park moose population cycle increased while the mean density (0.022 moose/ha), and amplitude declined during the most recent period

A comparison of the phase plot of r and density clearly portrays these dampened occilations as an inward spiral suggesting the population approached a stable point at a density of ~0.025/ha (Fig. 11). Filters were not required as there was very little high frequency variation. The dynamics suggest that the cyclical nature of the previous period (1906-85) may have been that of a population attempting to reach ecological carrying capacity (point attractor) but appearing to cycle owing to the disturbance caused by management.

A demographic summary of the entire 87 year period of record, including this most recent period, is provided in Table 1. The inclusion of these most recent years marginally reduced the mean pre-reduction population density to 0.028 ± 0.001/ha and numbers removed by management to 31 ± 6/yr.

The period of population decline, ending in 1982, also represented the end of the second documented period of cyclical increase and decline in the Isolation Area moose population. As during previous cycles in the Main Park, the Isolation moose population was also reduced through slaughter and trapping when numbers were judged to be in excess. In the Isolation Area, these population reduction measures also failed to prevent population decline - being instead additive to the decline. Thus, it was decided to allow the moose population to progress through its next cycle, with management actions taking the form of changes to the park perimeter fence. The changes were designed to allow moose to leave and enter the park at a few locations. Also a small population reduction when the moose population was believed to be at low numbers was planned.

From 36 individuals in 1983, the population grew very rapidly over the next four years (r = 0.69, 0.61, 0.46 & 0.49) reaching a total of 207 (0.04/ha) by 1987. Given the previously documented 11 year population cycle, it was expected that a population decline would occur in the next two years. Modifications to the fence were made to allow movement of moose in and out of the park in May 1987. The following year, a natural decline (r = -0.28) in the population occurred. In addition to this decline, a 9% net emigration of the total population occurred through the modified fence (Cool 1989). This point of decline occurred one year earlier than expected with less than half of the decline attributable to the modifications to the fence. In the next two years, the population continued to experience a net decline, reaching a low of 91 individuals in the early winter of 1989/90. Later that winter (March 1990), 14 moose (-15.4% of the population) were removed resulting in a population of approximately 77 (0.016/ha). Kidney/ backfat indices from these 14 individuals suggested a population of moose that were carrying significant amounts of stored energy into the winter and urea cortisol levels suggested that they were not nutritionally stressed (Cool

1991). Tick-related hair loss was also not reported for this winter. From these indices and because of the artificial reduction of density caused by the removal of these 14 individuals, it was predicted that the population was poised for a new period of increase thus completing the moose population cycle after only eight years. In the following two years, the population as expected grew substantially (r = 0.46 and 0.30 respectively). Unfortunately, detection of tuberculosis in game farms in the region forced the closure of the fence modifications during 1991 thus eliminating the possibility of further analyzing the population dynamics resulting from emigration.

The mean r = 0.20 was lower and density of 0.028/ha was slightly above the mean of the previous period. The frequency of the population cycle increased while the magnitude decreased. Population densities at which MSY and K were reached remained similar to the previous period (1973-86)(Fig. 11). Unlike the Main Park, the population dynamics in this area appeared to remain more cyclic not experiencing the same degree of dampening perhaps because of the population reduction carried out when the population was at a low. The inclusion of these most recent years in the average for the entire 33 year period increased the mean pre-reduction density to 0.027 ± 0.002/ha while decreasing the average numbers of moose removed by management to 18 ± 7 and the mean r to 0.22 ± 0.06 (Table 1).

Bison

Historical Abundance.-- B. b bison probably reached maximum population numbers and densities after about 2,500 years BP, when full development of the primary range was attained (McDonald 1981). Estimates of pre-European bison populations range from 75 million (Seton, 1929) to 35 million (McHugh, 1972). Density estimates derived from these calculations by Roe (1970), relates values of 0.05/ha for the plains, 0.12/ha for prairie, and 0.019/ha for forest environments. Locally, Kane (1968) estimated 15,000 bison between Edmonton and Beaverhill lake in December of 1847. Given that this area is approximately 1400 km^2 the density would have been approximately 0.11/ha. These estimates compare realistically with the densities recorded at modern Elk Island that have varied from below 0.02 to over 0.2 per ha (Fig. 12).

Moodie and Ray (1975) reviewed primary accounts of fur traders and missionaries, and found that a regular migration into the parkland in winter, and back onto the prairie in spring and summer, was characteristic of plains bison movements in the region. They concluded that migration into the parkland in winter was initiated by the need for shelter, with specific spatio-temporal manifestations of this general movement being conditioned by mild winter spells, heavy snow, hunting pressures and fires. It appears likely that immediately following European exploration the Beaver Hills supported a residual population of plains bison which during the winter was substantially increased with the arrival of numerous wintering plains bison from the south and in some instances the wood bison to the north (Losey 1978, Blyth and Hudson 1987). Morgan (1979) suggests a geographic convergence of bison onto the summer range (the prairie) and a corresponding geographic divergence onto the winter range (the parkland). She also notes that movements to the summer range entailed a gradual dispersal of smaller populations while movements to the winter range involved a gradual convergence and amalgamation of populations into specific localities (such as the Beaver Hills) suited for winter habitation. The seasonal movements of native peoples reflected this as they obtained vital winter foods via. bison pounds constructed in areas such as the Beaver Hills during winter. Hudsons Bay Co. records from Fort Edmonton suggest that this state of equilibrium between bison and man, the hunter, was still present at the end of the 1700's in the Edmonton - Beaver Hills area.

With the establishment of fur trading forts, such as Fort Saskatchewan and Fort Edmonton, native subsistence hunting was replaced with commercial hunting by both Europeans and natives. This led to the decline of local populations during the mid 1800's. By the late 1880's the plains bison was almost extinct and had been eliminated from the greater region surrounding what is today Elk Island National Park. Over thirty years passed before plains bison were again to graze in the grasslands of the Beaver Hills.

At the turn of the century, only one major free roaming population of plains bison was left. They were located in Yellowstone National Park, Montana. Several privately owned herds were also held in captivity or semi-captivity. The largest privately-owned plains bison population was owned by Michel Pablo of Ronan, Montana. This population originated from four yearlings brought to the area by their former owner Walking Coyote. The exact location of their origin will probably never be known but they may have originated from several hundred miles northeast near or across the Canadian border. Although the bulk of this population originated from this source, 26 head of plains bison were also obtained from "Buffalo" Jones and added to the population. These animals were descendants from plains bison near Winnipeg Manitoba, Battleford Saskatchewan and Texas.

Known after their more recent owners, Michel Pablo and Charles Allard, the Pablo-Allard herd, had by 1906 grown to well over 600 individuals. Faced with loss of his grazing lands, the surviving partner Michel Pablo sold the entire population to the Canadian government. It was originally intended that these bison would be shipped to Wainwright, Alberta. However, fencing had not been completed therefore, an interim location was found. That location was the newly fenced Elk Island park.

On June 3, 1907, 190 plains bison, consisting of "103 bulls, 17 stags (presumably steers), 39 cows and 27 calves," arrived at Elk Island (Douglas 1909). These animals were shipped from Montana and Banff by rail and unloaded at Lamont, Alberta. Those from Banff originated from the Bedson, Corbin, and Goodnight private herds. From the rail yards at Lamont to the northeast corner of Elk Island a long alley had been constructed of 2.2 meter paige wire. Up this alley the bison were driven to their new home in Elk Island. In total 206 had been shipped, three died during shipment, one yearling died in the alley, and 16 bulls, two stags, eight cows and six calves were sent back to Banff. On the night of their arrival, 11 individuals drowned. This left 171 bison safely installed at Elk Island with only two mortalities occurring over the summer that followed.

On October 10, 1907, the second shipment from Montana arrived. It consisted of 44 bulls, 119 cows and 48 calves. From this shipment of 211 animals, five were recorded as having died during handling which left 206. Together 377 were now assembled at Elk Island. Records show "24 calves few days old frozen (Temp. 60 below)." By the position of this reference in the report ledger of Howard Douglas, it appears that this pertains to animals from the October shipment. Logic would dictate that this was concerning the calf crop from the spring of 1908. Increases in the population were recorded as approximately 40 during 1907-08 and 10 during 1909.

By 1909, Wainwright National Buffalo Park had been completely fenced. In late November 1909, the bison population at Elk Island was rounded up and driven to the northeast corner of the park. Here they were held all night by riders on horses until the next morning when they were to be moved north down the temporary alley to Lamont that had again been constructed. Of the 402 animals on hand at Elk Island on November 30, 1909, 325 were shipped, and six were killed during this shipment. On December 31, 1909 a total of 71 bison could have remained within the park. This is described in park records as "42" plus "6 in the bush" and "23 unaccounted for." All accounts after that refer to only 45 bison remaining in the park suggesting that 26 bison were never accounted for (Coxford 1911).

Over this brief period (June 1907 to Nov. 1909) densities had exceeded 0.12 bison/ha and biomass had exceeded 55 kg/ha (Fig. 12). These values are averaged over the entire park but they spent much of their time confined in a grassland area on the west side of Astotin lake where they were fed and extensively handled. The trauma of shipment to the park, the unfamiliarity with the area and winter severity all appears to have contributed to a very poor calf crop (6-12 calves/100 cows) and a low r of 0.02-0.05 during these years.

Whether these animals were impossible to round up or were left in Elk Island by a deliberate accident may never be known. Roundup participants such as M. H. Butler suggest the latter (Scace 1976). Regardless, they immediately became a valuable resource and were the foundation of today's plains bison population at Elk Island.

One very interesting record that bears mention is the introduction of two (2) plains bison from the Edmonton Zoo to Elk Island in July of 1948. It is not known whether these bison had originated from Elk Island and were being returned or were from another source. If they were from a population with a different origin from that of the park then this represents a possible infusion of new genetic material to the population.

The wood bison, like the plains bison, were nearly eliminated during the late 1800's. The only major population was in the area that is today Wood Buffalo National Park. Under the protection of legislation passed by the Dominion government in 1887 and later in 1922 under Wood Buffalo Park the wood bison population was maintained.

In Buffalo National Park, near Wainwright, Alberta, widespread infection of the plains bison with bovine tuberculosis and brucellosis occurred. To deal with this problem, the park needed to eliminate diseased animals. It was felt that if these infected animals could be relocated to a larger area the diseases would dissipate. Despite many opinions to the contrary, the plan was approved. Thus 6,673 plains bison were shipped to Wood Buffalo National Park, from 1925-28. These descendants of the Pablo-Allard herd, which had been originally shipped to Wainwright via Elk Island were now free roaming with the native wood bison. Both extensive interbreeding and disease transmission resulted thus, Wood Buffalo National Park became the home of a hybrid and diseased bison population.

In 1959, an isolated population of what was believed to be pure, disease free wood bison were discovered (Banfield and Novakowski 1960). In 1963, nineteen and in 1965, forty individuals were captured and transported to holding corrals near Fort Smith (Gates et al 1992). Sixteen of these formed the basis of the large population presently occupying the MacKenzie bison sanctuary. In August 1965, 24 individuals, were shipped from Fort Smith to the Isolation Area of Elk Island. One animal died in transit and two others died that same year leaving 21 animals to form the basis of the Elk Island Wood Bison population (Gates et al 1992). These animals were originally believed to be pure wood bison. However, subsequent analyses have shown the Elk Island population to contain some plains bison characteristics (van Zyll de Jong 1986).

Plains Bison Dynamics 1910-86.-- Over the entire period of record, the average population during the fall (before reduction) was 850.59 ± 63.99. This is equivalent to a density of 0.077 ± 0.005/ha or 34.8 ± 2.19 kg/ha. The mean rate of population change (r) was 0.20 ± 0.02 from 1907 to 1987. This resulted in a total population increment of 10,428 individuals or 137.21 ± 14.76/year. The total number of individuals removed by slaughter, sale and donation were 10,091 over the same period that resulted in an average population reduction of 12.36 ± 15.99% or 131.05/yr. This is equivalent to a density of 0.011 ± 1.82/ha/year or biomass removal rates of 4.98 ± 0.94 kg/ha/yr. On average each hectare of the park had 0.875 or 393.89 kg of plains bison removed by slaughter, sale and donation from 1907 to 1987. A detailed description of the population dynamics follows.

From a founding population of 45 individuals (0.014/ha), in 1910, the park plains bison population began a slow but steady period of growth reaching 195 individuals (0.159/ha) by 1919. This period of growth occurred at an r = 0.161 ± 0.013. The close fit (r^2=0.99) of these ten years to the regression,

$$Y = 37 * \exp(0.161 * x)$$

is comprised only marginally by the lower values of the years 1916 and 1918. These two years display population growth rates (r) of only 0.06 and 0.13 respectively which contrasts with the ten year mean r of 0.165 ± 0.029. It is interesting that the two best years of population growth, 1917 and 1918, immediately followed the two poor years with observed increases of r = 0.26 and 0.29 respectively.

The population of bison, described in 1920 as 202 individuals, represented a density of (0.062/ha) 27.75 kg/ha. The Park Superintendent, recognizing that overcrowding would soon result, recommended park expansion. During the next two years moderate population growth (r = 0.14 & 0.17) caused the plains bison population to reach 270 individuals (0.082/ha, 37.10 kg/ha), just before park expansion in 1922. Expansion of the park from 3,275 ha to 11,470 ha of available range achieved an immediate reduction of bison population density to 0.025/ha (11.456 kg/ha). The resulting population growths (r = 0.08 & 0.09) during the next two years were well below what might have been expected considering the lowered density and new environment afforded by park expansion. In the third year following park expansion the population did begin to increase more rapidly (r = 0.26). This productivity continued with a mean r = 0.20 over the next five years. This resulted in a population of 823 individuals (0.071/ha or 32.29 kg/ha) by the beginning of 1929. Slaughter that year of 225 individuals (0.019/ha or 8.82 kg/ha) then reduced the population to 598 (0.052/ha or 23.46 kg/ha). From 1920-29, population growth can be characterized by an exponential rate of increase of 0.157 ± 0.02, closely fitting the regression:

$$Y = 163 * \exp(0.157 *x)$$

with an r^2= 0.98. This r was similar to the previous ten-year period. The mean population rate of change (r) over the same period was 0.17 ± 0.02. The most significant increase over this period was r = 0.33 experienced in 1927.

Following the slaughter of 1929, park managers allowed the population to increase for seven years before again intervening with slaughters. During this period the population grew from 716 (0.062/ha) in 1930 to 2,479 (0.216/ha) in 1936. The 1936 population was the largest ever supported at Elk Island, representing a live biomass density of 97.25 kg/ha. This period was characterized by excellent and consistent incremental rates of population increase until 1935. The winter deaths of 116 individuals and the small increase (r = 0.03) during the spring of 1936 suggested that a density-dependent natural decline may have been eminent. That winter (1935-36), park managers slaughtered 500 (0.043/ha or 19.05 kg./ha) old and sick individuals, probably preempting any such decline. This seven-year period (1930-36) can be characterized by r = 0.213 ± 0.018 which was significantly greater than the previous 20 years. Again the census data closely fits (r^2=0.99) the regression [Y = 565 * exp(0.213 * x)] derived for this period. The mean annual rate of population change (r) for this period was 0.24 ± 0.03. The entire period of 1910 to 1935 showed sustained population growth after the population exceeded 700 individuals (0.064/ha). The sex and cow/calf ratios show an increase in the proportion of females and increased numbers of calves per female over this period (Fig. 13). This is consistent with the general increase in population growth. From 1935 to the present the plains bison population has been carefully controlled making this the last period of uncontrolled exponential population growth.

Regular large scale slaughter programs were carried out with the removal of 800 individuals (0.069/ha or 31.38 kg./ha) in the winter of 1938-39. This followed three years of poor population growth (r = 0.03, 0.05, and -0.10) and low calf/cow ratios. This major reduction lowered the population to 995, a density of 0.087/ha. It also altered the sex ratio in favour of males. From 1940 to 1952 the population fluctuated from slightly below 1,000 to nearly 1,800 and averaged 1,350 (0.117/ha or 52.99 kg/ha). Slaughters of over 500 bison were undertaken nearly every other year to control the population within these limits. Each of these slaughters removed 30-40% of the entire population. This equalled an average biomass removal of 12.04 kg/ha during the years of slaughter or an average of 7.02 kg/ha/yr. During this period, r improved averaging over 0.21 between 1940 and 1952. This was a marked increase in productivity over most of the previous periods.

During this period, dressed weights of the male bison cohorts also increased suggesting improved animal condition at lower population densities (Fig. 14). The dressed weight of two-year-old male bison was significantly crosscorrelated (-0.55) with bison density during the previous year. The slope of the line, describing weight change as cohorts graduated to the next age class, increased when the park was expanded in 1951 also showing the effect of lowered bison density on body size.

From the late 1940's to the early 1960's, brucellosis was present in plains bison. Slaughters described previously were associated with programs intended to control the disease. In the winter of 1947, six out of 37 bison were seropositive for the disease. The park attempted to salvage and isolate a group of disease free-bison and depopulate the Main Park area. During the next few years, most of the bison were rounded up and tested; seropositive animals were slaughtered.

In April 1951, 75 seronegative plains bison were introduced from the main population (north of Highway 16) to the eastern portion of the Isolation Area. This initial stocking density was 0.036/ha in the new 2,062 ha available to the park's population. By December 1958, this isolated population had grown to 520 (0.252/ha). This growth included both calves and some further introductions of seronegative individuals from the main population to the north. This was the highest density of bison ever supported at Elk Island. This density may appear large in comparison to that reached by the Main Park population in 1935, but few other ungulates existed in the Isolation Area thus little or no competition would have resulted. Unfortunately brucellosis soon became prevalent in this area. Isolation having failed, slaughters followed and the population was reduced to 415 by February of 1959 and further reduced to 236 (0.114/ha) by September 1960. In 1961, the remainder of the Isolation Area was opened allowing the population to range within 16,686 hectares.

In 1959, after 12 years of testing and slaughter of reactors, 52% of the bison tested were seropositive. A different protocol was clearly needed to eradicate the disease. This took the form of a massive population reduction followed by vaccination of young age classes and removal of seropositive individuals. Finally in 1964, all nonvaccinated and seropositive animals were removed. That same year, actions were undertaken to completely remove the plains bison from the Isolation Area. Numbers were reduced to 221 in October of 1964 and 136 by April of 1965. By the late spring of 1965, the entire population was removed from the Isolation Area. Some were moved back to the main population and others were slaughtered.

During the period 1951-65, the rate of increase (r) of the park's plains bison population ranged from 0.09 in 1954 and 1962 to 0.33 in 1956. The low rate in 1962 may be a result of management actions being taken to eliminate brucellosis in the Isolation and Main Park populations. The average r of the population remained consistently high at 0.20 for 1951-55, 0.24 for 1956-60, and 0.21 for 1961-65. This occurred despite evidence that brucellosis was reducing the calving rate (Corner and Connell 1957).

Population reductions occurred during 12 of this fifteen-year period (1951-65) and averaged 305/reduction (25% of the population per reduction) or 244/yr (8.11 kg/ha/yr). This reduced the total population from 1,440 (0.125/ha) in December 1952 to 519 (0.049/ha) by the spring of 1965.

From 1966-73, population productivity was excellent (mean r = 0.27) with significant slaughters and live sales (21.4%/yr, 5.16 kg/ha/yr). Consequently the population increased gradually to 831 individuals (0.079/ha or 35.7 kg/ha) by 1972. In that same year the population was officially declared brucellosis free as no suspected cases had been detected since 1969. Elimination of the disease and the age structure resulting from the slaughter of all old nonvacinated animals may have both been factors contributing to this outstanding period of population growth.

From 1973-81, the mean r was only 0.17. The general low rate of increase and the concurrent 14.45% (3.25 kg/ha) average yearly reductions resulted in a decline in numbers to 421 (0.038/ha) at the end of 1979. The average prereduction population was 501.9 at a density of 0.046/ha or 20.77 kg/ha. Population structure and cow/calf ratios from 1950-80 were highly variable but followed a general trend of increasing proportion of males and calves (Fig. 13).

The period from 1982-87, saw a return to increased productivity (mean r = 0.23). During this period the population was maintained within the 450 - 600 limits prescribed by the park's bison management plan through the removal of 610 (122/yr, 0.011/ha/yr, 505 kg/ha/yr). As a result the average prereduction density was 0.048/ha. During the twenty years, 1967 to 1987 the mean r was 0.22.

Wood Bison Dynamics 1965-85.-- Over the entire period the mean r was 0.27 ± 0.06. The actual rate of increase varied less than suggested by the standard error. The initial period of growth from 1966 to 1969 exhibited several extreme anomalous values. This was primarily due to the large proportion of females in the initial population and later the destruction of T.B. infected females. The average density, before each annual reduction, was 0.019 ± 0.0025/ha/year that resulted in a biomass of 9.23 ± 1.25 kg/ha/yr. The total number of wood bison removed or killed during handling from 1965-83 was 211 representing an average offtake of 1.12 kg/ha/yr. On average the wood bison population was demonstrably more productive than the plains bison, from 1966 to 1983.

The foundation population of wood bison began from 21 individuals (five males & 17 females). In 1966, one calf was born and no mortalities occurred. The following year 12 calves were born (r = 0.59) and one additional calf was flown to Elk Island from Wood Buffalo N.P.. The one additional calf had an umbilical hernia but only survived until 1969 when it was slaughtered. Later that same year one calf was found dead in a winter storm and another broke its neck.

A total of 18 calves were born in 1968 but one was destroyed and another died shortly after birth. Resulting calf cow ratios were very high (Fig. 16). Another calf, which had been removed from its diseased mother, was shipped from Wood Buffalo to Elk Island in October 1968. During the first four years the proportion of males gradually increased to 73 males:100 females by 1968. Later that same year brucellosis and tuberculosis were discovered in the population at Elk Island.

In 1969, 11 calves, including six males and five females, were successfully removed from all the diseased cows. Three died at birth. These cows were then destroyed and burned. All orphaned calves were then disinfected and hand reared. Three of these calves died of natural causes. In March of 1969, the entire population was separated into two groups, those remaining from the original 22 and the remainder that included those calves born at the park and those shipped after 1966. All of the original animals were then destroyed. This left a population of only 32 wood bison (0.0067/ha) at the end of 1969. This management action not only reduced the population but also reversed the sex ratio, which by 1970 was 147 males: 100 females.

A two year old had also been acquired in a trade with a private owner of wood bison, Al Oeming. This animal was of suspect health and genetic purity so it was held separately from the remainder until, one day having escaped from its corral, it was shot.

During the next few years, population growth was marginal, with only two calves being born in 1970, and 11 during each of the next two years. Handling resulted in deaths of three to four individuals each year. By 1976, the population reached 114 (0.024/ha or 11.55 kg/ha) from which four calves were shipped to the Calgary Zoo. Another healthy increase of 28 calves in 1977 provided sufficient numbers to allow a second shipment of 12 animals to Toronto, Ontario and Cochrane, Alberta (Schwanke 1979). The r̲ of the wood bison population from 32 animals in 1969 to 150 in 1977, was 0.188 ± 0.017 (r^2=0.99). This period of population growth not significantly different from a similar period of growth exhibited by the park's plains bison from 1910 to 1919.

Thirty-eight animals were shipped from the population in 1978 as the Elk Island population was now being used as a source population for reestablishing other wild populations (Schwanke 1979). Some animals from unsuccessful attempts were returned. Another 10 animals were destroyed for taxonomic purposes or died during handling operations which left a total of 102 wood bison at the end of 1978. In 1980, 30 calves were born (r = 0.22). A mixed population of 44 was shipped to the Nahanni Butte, N.W.T. and other locations that same year leaving a population of 110 animals by February 1981. In 1981, 29 calves were added to the population representing another healthy increase (r = 0.26). Increases of r = 0.24, and 0.33 during the next two years resulted in a population of 180 individuals in 1983. These incremental increases were larger and more consistent than that displayed by the plains bison population over any similar period. Figure 15 shows this very consistent yearly increase from 1971-83. In 1984 and 1985, r declined to 0.21 and 0.09 respectively. It marked the end of this 13-year period of remarkably stable population growth.

Live weights of wood bison from 1968-86 exhibit several unique short term trends. Mean weight of calves declined from 216 kg for males and 221 kg for females to 184 kg and 167 kg respectively. Yearlings also showed a decline in average weight but this trend becomes less evident in successively older age classes. In fact, male 2.5 and 3.5 year old cohorts increased in weight from 1980-86 but remained below the weights recorded in the early 1970's. This trend toward lighter individuals may reflect limiting resources as population size increases or the effect of the intensive animal husbandry conducted during the early years of the wood bison recovery program at the park.

Time Series Analysis and Density-Dependence. -- The Autocorrelation and partial autocorrelations for the annual rate of plains bison population growth showed stationarity across the entire period of record (Fig. 17). Consequently, raw undifferenced data were accepted for comparison of r and density. Fast Fourier Transformation procedure revealed a strong 13 year cycle that was also visually evident in the estimated autocorrelations. If the variability in this frequency range is removed through seasonal first order differencing the residuals retain a two year cycle. Wood bison did not exhibit any long term periodicity, no doubt owing to the shorter period of record and management history. The wood bison did however, exhibit a clear short term cycle of two years as evidenced by Fast Fourier Transformation. This strong alternation of good and bad years of growth is visually apparent in the wood bison data. For plains bison it describes the 'noise' obscuring the significant 13 year pattern (cycle).

Cross-correlation displayed a significant negative correlation between r and second order detrended density during the present $_t$ and of previous year $_{t-1}$. For the shorter history of the wood bison a similar lag dependence was also detected (Fig. 18). Next an appropriate filter was applied to r and lagged density for plains bison to remove white noise. A general relationship between the pattern of r and density was evident but it appeared to shift in response to management. A phase plot of density vs. r clearly shows that each period of population growth and decline follows a different trajectory (Fig. 17). This may suggest a sensitivity to initial conditions consistent with deterministic chaos. This suggested that an analysis of discrete periods would be appropriate. From these analyses density-dependent curves describing per capita r and per unit area rates of increase (#/ha/yr) for the plains and wood bison populations as a function of lagged density were constructed (Fig. 19).

Both wood bison and plains bison population rates of change (r) are severely altered from a linear relationship with reduced productivity at lower population densities (Fig. 19). The resulting per unit area rate of increase is again quite typical of a large herbivore with MSY ranging from 0.71 to 0.93 of K for the various periods examined.

From 1910 to 1922, MSY occurred at approximately 0.07/ha while K was at 0.7/ha. The second period of analysis was that of 1922 to 1940. In 1922, the addition of a large area of grassland lowered the density of plains bison from 0.07 to below 0.04/ha. From this point until the mid 1930's the population increased dramatically to over 0.2/ha. After this large winter mortalities and slaughters reduced the population to approximately 0.09/ha in 1940. Park records of overgrazing and starving animals during this peak confirm that resources were limiting. As during the previous period, lagged density of one year was evident. In the latter period, the MSY of 0.14/ha and K of 0.18/ha portrays the expected productivity curve for a large herbivore limited by resources (Fig. 19). It also indicates that the plains bison were much more productive than during the previous period.

From 1941-60, the plains bison population was held between 0.08 and 0.12/ha, near the MSY derived for the previous period, 1923-40. The population was maintained at this density by large annual slaughters and feeding. At the beginning of this period, the proportion of grassland began to decline as aspen forest expanded and thus larger quantities of hay were required for winter feeding. Park records show that the population was in fact being managed for high productivity. The mean rate of growth was the highest of the four periods analyzed. Unfortunately control of the population within a narrow density range, near MSY, did not allow K to be adequately described. Brucellosis was identified during this period but it did not severely influence productivity. At the end of this period the bison population was dramatically reduced to eliminate this disease. Any density-dependent relationship is masked by the substantial decline in productivity that resulted from the large scale of this slaughter.

From 1961-75, mean r of the plains bison population was 0.22. The period from 1961 to 1970 is characterized by a rapid increase in per unit area rate of increase and density (MSY of 0.016/ha/yr at 0.055/ha). After this, two major changes in management approach caused a decline in productivity to -0.01/ha/yr by 1975. This included the shift from slaughter to live sale for reducing the population that shifted the sex ratio from a female dominated to a male dominated population and the closure of the park farm and the cessation of large scale winter feeding.

From 1975-86, plains bison numbers again increased and then declined slightly. In this period a clear relationship between per unit area rate of increase and density was expressed with MSY of 0.008/ha/yr occurring at 0.037/ha. As a result, mean r = 0.20, which was close to the average for the entire period of record. From 1970-86, wood bison population growth rate was remarkably consistent functioning at or below what was an MSY of ~230 (0.05/ha). As a result the wood bison population was somewhat more productive with an average annual population increment of over 25%.

Unlike moose where the increasing forest cover through time appeared to have little influence upon population dynamics, density-dependent relationships for plains bison were closely tied to available grassland habitat. As the proportion of the park in grassland habitat decreased the population density K also decreased. Although MSY and K were derived from only six periods, a strong linear relationship is apparent (Fig. 20).

An ARIMA model that attributes statistical dependency simply to a constant or mean was found parsimonious for plains bison. This implies that the annual rate of population change exhibits a flat noisy type of stochastic behaviour "white noise," occurring at a constant or mean level. As such it is described as:

$$Y_t=18.39+a_t$$

where a_t is white noise. The standard error of the estimate of the mean was 1.36 with no significant temporal structure remaining in the first 20 residuals (Chi-square = 12.8, $P > 0.05$). Seasonal autoregressive or moving average terms in the model were absent despite the strong periodicity previously described. Differencing was not required again suggesting absence of a trend or any systematic change in the annual rate of population increase throughout the period of study.

The wood bison annual rate of population change is also best characterized by an ARIMA model that does not require differencing and that attributes a significant degree of statistical dependency upon a constant - ARIMA $(0,0,0)(0,0,0)_2$C. The resulting model for the wood bison rate of annual population change:

$$Y_t=24.34+a_t$$

predicts based upon a current random shock a_t, and a constant that is the mean rate of population growth. The standard error of the estimate of the mean was 1.29. More complex models with first order seasonal moving average terms and first order autoregressive terms were statistically valid but did not contribute significantly to the model and were thus not included.

Response to Management 1985-93.-- During this period the plains bison population was maintained within prescribed limits believed to be well below ecological carrying capacity. Being maintained at these densities, ranging from 0.03 - 0.04/ha, exceptional average annual population growth increments resulted (r = 0.26). During four of these six years r even exceeded 0.30. This productivity was higher than predicted by the mean of the ARIMA model but well within the standard error of the white noise.

Comparison of density and per unit area rate of increase realized in this period compares closely with the expected point of MSY described from previous periods (Fig. 21). Consistent with this, calving rates among cows older than three years of age ranged from 84 to 93% ($\bar{x}$ = 87%). Sex ratios of calves surviving to six months was virtually even at 101 males:100 females. The year 1986, displayed very poor population growth and is an exception to the generally high productivity. During the previous summer grassland biomass production was the lowest recorded (Blyth et al. 1993).

Maintenance of the population at a density near MSY required significant management intervention through live removal of 125 bison/yr (4.26 kg/ha/yr). Consisting of mostly calves, yearlings, and adult males, these population reductions were done with the objective of reducing the numbers of those cohorts that would be most affected in an ecological setting where predation and dispersal were operating as mechanisms of population regulation. Calves and yearlings were removed in even sex ratios thus ensuring that the sex ratio of the population was not artificially affected.

A demographic summary of the entire 86 year period of record, including this most recent period, is provided in Table 1. The inclusion of these most recent years did not significantly affect the values because the population was managed at close to mean densities.

In 1985, the wood bison population was being managed near MSY (232, 0.049/ha), with the primary objective of maintaining a productive nucleus for establishing new populations. The population growth rate (r = 0.08) and a calving rate of only 41% (the lowest recorded rate), suggested that this estimate of MSY (0.05/ha), derived from previous years, was too high. Low vegetation biomass productivity in the upland grasslands that same year may explain the unexpectedly low wood bison population growth rate (Blyth et al. 1992). Continued population management over the next two years at approximately the same density with resultant r of 0.19 appeared to suggest that MSY was at or near the prediction given normal amounts of vegetation biomass productivity.

In 1988, wood bison were down listed from the "rare" to "threatened" status. In the brief period that followed, the demand for relocation dropped and the population increased allowing an assessment of

MSY and K. The population dynamics that resulted appear to prove that the point of MSY and K both occurred at higher densities than expected (Fig. 21). Feeding of the wood bison population for as many as 40 days during the winter while handling (Olson and Westhaver 1988) and excellent vegetation biomass productivity during these summers (Stromsmoe 1992) offers possible explanations. Most recently the relationship between density and population growth shows a strong lag with growth being lower than the 1987 - 89 period.

The mean r for the wood bison population from 1986-91 was 0.21. This was significantly lower than the mean r = 0.27 o. previous period. Compared to the ARIMA prediction this was beyond the standard error of the estimate but was well within the standard error of the white noise variance 24.34 ± 4.02.

A demographic summary of the entire 34 year period of record, including this most recent period, is provided in Table 1. The inclusion of these most recent years reduced the mean r to 0.25 ± 0.02, increased the mean pre-reduction density to 0.033 ± 0.004/ha and increased the mean numbers of wood bison removed by management to 19 ± 5/yr.

Elk

Historical Abundance.-- Accurate estimates of natural densities of elk in the aspen parkland are not available, however qualitative descriptions present a picture of large populations second only to the bison. At the time of the first European settlement and establishment of the first trading posts in central Alberta, elk were present throughout Alberta to just south of the Northwest Territories (Stelfox 1964). The populations of elk were described as abundant throughout the year in the Edmonton area at the end of the 1700's (Losey 1978). Elk were hunted by the native peoples as supplementary food to their mainstay, the bison. Apparently its meat left an unpalatable taste as the fat congealed on ones teeth and thus native people preferred bison, moose and deer (Ray 1974). Consequently the depletion of elk numbers in the prairies did not begin until after the bison became scarce and as a result of supplying meat commercially to European consumers in the forts and early settlements. By 1894, elk had been greatly reduced and were practically eliminated north of the North Saskatchewan river (Bryant and Maser 1982). Populations were now discontinuous with many small groups existing in isolated locations. At the turn of the century small populations remained in the Brazeau river valley, Saskatchewan river valley, and the Beaver Hills.

The remaining population of 75 elk in the Beaver Hills was noted by Territorial Game Warden, W. H. Cooper, who advised his member of parliament of the need to protect this population (Scace 1976). He described this population as the largest existing population in Canada outside "the unexplored forests of the north" (Lothian 1979). During the winter that followed (1903-1904), at least 20 elk were killed and plans were being made for more hunting the next winter (Lothian 1979). Fortunately a petition was signed by local residents in April 1904 that requested the protection of the remaining elk in a fenced enclosure of about 41 km^2. Action was then taken by the Department of the Interior to withdraw the land from settlement. By June 1907, the fence surrounding the park was completed. It enclosed elk that were probably already present and others "driven" in from the south (Williams 1967).

Dynamics 1907-85.-- Over this entire period of record, the average population size during the fall (before reduction) was 511.1 ± 43.2 in the Main Park. This was equivalent to a density of 0.05 ± 0.004/ha or 12.19 ± 0.93 kg/ha. The total population increment was 6,120 individuals that can be described as 77.47 ± 14.00/year (r = 0.19 ± 0.02). From 1940-85, the mean r = 0.25 was significantly higher and contrasted to the previous period that averaged 0.15.

The total number of individuals removed by slaughter and donation was 5,471 over the 57-year period from 1928-85. During this period, population management was conducted in 38 of the 57 years or 66.6% of the years. On average 143 elk (0.013/ha, 3.12/kg/ha) were removed during each man caused population reduction (20.4% of the total population). The reduction of the elk population by slaughter and live removal occurred at a rate of 68.39 ± 12.06 elk/year. This was equivalent to a density of 0.006 ± 0.001 elk/ha/year or a biomass removal rate of 1.48 ± 0.26 kg/ha/year. In total each hectare of the Main Park had 0.49 elk or 118.7 kg of biomass removed by slaughter and live removal since 1906.

The elk population in the Isolation Area of Elk Island averaged 43.11 ± 8.11 individuals from 1959-85. This was equivalent to an average density of 0.009 ± 0.002/ha or 2.21 ± 0.41 kg/ha. This population was, throughout its history, significantly smaller than the Main Park population. The mean r = 0.15 was also lower than the Main Park elk population (1940-85) but was equivalent to the Main Park population before 1940. The total number of elk removed by trapping and slaughter was only 3.7/year for a total of 102. On average each hectare of the Isolation Area has had 0.021 elk or 5.2 kg of biomass removed by slaughter or live removal since 1960. A detailed description of the main and Isolation Area elk populations follows.

At least 24 elk were within the park according to statutory declarations made by the original assistant caretakers of the park. This represented an initial density of 0.007/ha (1.47 kg/ha). These animals formed the foundation stock of today's Main Park population.

In total, 26 and 30 elk were counted during 1909 and 1910. In the fall of 1910, one female was introduced from an unknown location. It is assumed that this individual was of local origin otherwise specific reference probably would have been made. The population was reported to be in good condition during the next few years but only marginal increases and some declines in numbers occurred. By 1915, only 50 elk were reported. This represented a mean r = 0.15 during the first 10 years of population growth. After 1915, two very productive years followed (r = 0.50 & 0.33). This increased the population to 100 individuals (0.03/ha) with a sex ratio of 66 males:100 females. From this point until 1922, population growth followed an erratic pattern with r as high as 0.42 in 1919 and as low as 0.03 in 1918. In 1922, the population declined (r = -0.06) to 200 elk (0.061/ha, 14.77 kg/ha). This decline and expansion of the park area the following year resulted in a substantially lower density of 0.018/ha (4.56 kg/ha) (Fig. 22).

When plans for the park expansion were first conceived, it was hoped that a small group of elk outside the park could be included and that the additional land would increase the productivity of the population. The addition of new elk was not recorded and the r that following year was 0.18. However, the next two years were very productive with increases of $r = 0.40$ and 0.29 respectively. As a result, the population reached a total of 400 individuals (0.039/ha, 9.66 kg/ha) by the winter of 1924-25. From the origin of the park to 1924, growth of the population can be described as an exponential increase of $\underline{r} = 0.146 \pm 0.025$.

In contrast to bison and moose populations, the elk population only increased from 400 to 467 (mean $r = 0.04$) from 1924-31. This net increase of only 67 animals included a slaughter of 24 animals (5% of the total population) in 1928 and one year of natural decline of 33 animals ($r = -0.06$) in 1930.

The next four years that led up to 1935 were extremely productive. The mean annual population increase ($r = 0.44$) resulted in a massive population growth to 1,979 individuals by 1935. This represented a density of 0.197/ha (47.79 kg/ha). The 1931-35 increase can also be described as an exponential increase of $\underline{r} = 0.358 \pm 0.013$. In the winter of 1935-36, a significant winter die-off of elk was recorded. Estimates of 250 to 300 dead elk were made by park officials. Estimated losses for all species of large ungulates were 500 to 600 (Love 1955). In relation to other species, the elk population experienced the greatest mortality in that particular winter. Despite this, the calf crop the following spring was significant enabling an actual net increase ($r = 0.01$). During the next three years, large slaughters of 500, 183 and 101 elk were carried out to reduce the population density to prevent winter mortality. This desired effect was not immediately realized as the population further declined ($r = -0.15$ & -0.43). The resulting populations returned to densities similar to that of the mid 1920's. In fact, the post slaughter population in 1939 was 473 (0.04/ha).

The stage was set for a repeat of the 1925-35 population growth that featured an initially low annual increment followed by a sudden population explosion. Heavy natural mortality of males and the large slaughters not only reduced the population but also created a sex ratio of 51 males:100 females by March 1941. Initial population growth from 1939 to 1942 was low, (mean $r = 0.05$). Then annual population growth became substantial with $r = 0.41$ in 1944 and $r = 0.51$ in 1946. The resulting populations during this time were not as large as during 1935 due to slaughters of 350 (1943-44) and 160 (1945-46) elk (Fig. 22). Nevertheless the population reached 851 or 0.074/ha (17.95 kg/ha) by 1947. The sex ratio by this time had also been changed by these slaughters to 89 males:100 females.

Mindful of the previous large populations and associated mortalities, the park staff now undertook annual slaughters to control the elk population. Even with yearly slaughters of 50 to 200 elk (3.33/kg/ha/yr) the population gradually increased to 1,149 (0.098/ha or 23.71 kg/ha) by 1957. At that point several larger slaughters were carried out to reduce the size of the population. From 1957-61, 1,205 elk were slaughtered, reducing the Main Park elk population to 154 (0.013/ha) with a sex ratio of 72 males:100 females. From 1947-61, mean $r = 0.21$ while 2,383 animals were removed at a rate of 183.3/year (3.66 kg/ha/year). During this period, 77.2% of the animals were removed by slaughter while 22.8% were removed by capture (Flook 1967).

Over the same time, a small population of elk was present south of Highway #16 in the Isolation

Area. As with moose, an unsuccessful attempt was made to eliminate all elk from this area by slaughter in 1948. By 1959, 90 head of elk (0.019/ha, 4.57 kg/ha) were counted in the area. A slaughter of 80 head was carried out in 1959-60 and as a result the elk population in the Isolation Area was again virtually eliminated. For the next 18 years, the population remained below 25 head only increasing to 54 because of transplanting 29 individuals from the Main Park in 1977 (Fig. 23). From 1977-79, the 29 transplanted elk were separately confined to a 10.36 km^2 area in the southwest corner of the Isolation Area. Here they were present in a density of 0.048/ha in 1977 and with an increment of seven reached a total of 36 (0.006/ha) in 1978. In 1979, the gates of this separately fenced area were opened allowing the transplanted and preexisting populations to become one. The resulting total population was 73 (0.015/ha).

From 1980-85, the Isolation Area elk population grew from 75 to 137 (0.029/ha.). This included a live removal of 11 individuals in 1984. Throughout this period and the previous 10 years, r in the Isolation Area was highly variable. This was possibly due to emigration and immigration between the park population and the adjacent Blackfoot grazing reserve to the south. When such a small population is under consideration even small transboundary movements could greatly affect the population size. The mean r of 0.15 ± 0.11, and the paultry removal of only 22 elk during 25 years of population growth provides support for such a conclusion.

After the major population reductions of the late 1950's the Main Park elk population began a rapid increase. In 1961, 1962 and 1963, the annual population increase (r) was 0.49, 0.30, and 0.47, respectively. Pregnancy rates were between 93% and 97% (Flook 1967). Two poor years with r = 0.04 and -0.09 followed but only briefly restrained the general trend of excellent population productivity. By 1974, a total of 570 elk were present in the Main Park. An excellent mean r = 0.26 allowed an increase of 416 (34.6/year) over 12 years despite the slaughter of 508 elk (42.33/year, 1.01 kg/ha/year).

The eleven years of population growth before 1985 in the Main Park population was again characterized by healthy population increases (mean r = 0.22). By 1985, the population had reached 643 (0.059/ha) despite the removal of 628 animals at an average rate of 62.8/year (1.38 kg/ha/yr). In this period population increase was mitigated not by slaughter but primarily by trapping and removal of live elk. The larger portion of males removed by this method resulted in a sex ratio of 30 males:100 females. This represented the lowest portion of males in the population since 1914 and a sex ratio similar to that found in other populations (Green 1950, Taber et al. 1982).

Time Series Analysis and Density-Dependence.-- The population dynamics of the elk population in the main area of Elk Island superficially resembles that of the plains bison population for the same area and time. However, unlike bison, the annual population growth rate continuously increased over the 80 years of record and displayed an abrupt and permanent upward shift after 1940. This increasing r and density are represented as 5th order polynomial trends (Fig. 24). When r is viewed vs. density in a phase plot, the trajectory appears quasi-periodic, both increasing but out of phase. Of the ungulates in Elk Island, only elk displayed this long term trend toward increasing productivity.

Within this trend a strong periodic component at a frequency of 0.103 cycles per year (≈ 10 years per cycle) was detected in the undifferenced data. With this 5th order polynomial trend and noise removed, the phase plot of density vs. r follows a trajectory consistent with quasi-periodic or chaotic dynamics about a point attractor (Fig. 24). This clearly shows that the periodicity detected does not exactly repeat itself.

Besides the general trend of increasing productivity and ten-year periodicity, a minor periodicity was also detected in the frequency of 0.41 cycles per year (2.4 years per cycle). This minor periodicity was significantly enhanced when nonseasonal differencing was applied to remove nonstationarity created by the long term trend in the data. As in the periodogram, Fast Fourier Transformation of the nonseasonal differenced rate of population change also suggested similar periodicity of 2.5 years.

The dependence of per capita or per unit area rate of increase and population density was confirmed through Cross-correlation (Fig. 24). This procedure provided evidence that the lagged density of the past two years had the greatest correlation with net productivity. Despite accounting for this lag and removal of high frequency periodicity, clear relationships between population growth and density were not visually evident across the entire period of record. This was not surprising given the dynamics described previously. It was thus necessary to conduct analysis of discrete periods to derive density-dependent productivity relationships (Fig. 25).

From 1906-22, the elk population increased from an initial density of 0.006/ha to over 0.06/ha. In this period r showed a marked reduction at densities below MSY. Although population growth widely varied from year to year, an initial period of increased productivity was followed by decline. From the lagged density and filtered net growth rate data, both per capaita and per unit area productivity curves were constructed (Fig. 25). The resulting MSY at ~0.06/ha, and K at ~0.12/ha describes a population where most density-dependent change occurs near 0.5 K. This is lower than expected for a large ungulate herbivore that should have an MSY > 0.5 of K. Elk were neither provided with supplementary feed nor slaughtered nor relocated. However, during the latter years of this period, poaching may have been a significant problem.

In 1922, the addition of a large grassland area to the park reduced the density of elk to nearly 0.02/ha. The population rapidly grew to over 0.2/ha in the mid 1930's. Natural mortality and slaughters reduced the population to approximately 0.04/ha by 1940. The per unit area productivity curve derived displays an MSY at 0.08/ha and K at 0.14/ha. Both values are much higher than the previous period. However, MSY remained close to 0.5 K. This contrasts sharply with the plains bison where the productivity curve shifted to the expected K-selected shape during this period. Like the plains bison, the elk were considered resource limited and were slaughtered after reaching these "high" numbers but, unlike plains bison, the elk were reported to be heavily infested with winter ticks.

From 1941-60, the elk population gradually increased but, for the most part was held between 0.04 and 0.08/ha. This period, where elk numbers were held near MSY by slaughtering excess numbers and feeding, produced a similar productivity curve to that of the plains bison population that was also being maintained at or near MSY densities. The result was a period of very high productivity (mean r = 0.22 ±

0.04). The density at which the MSY occurred dropped slightly to 0.07/ha while K declined to 0.10/ha. As a result MSY was 0.7 of K. This relationship was now closer to that expected for elk. Whereas K may have declined because of succession of much of the park's grassland to forest, maintenance of the point of MSY may have been a result of culling and feeding.

At the end of the 1950's, slaughters reduced the numbers of elk to < 0.02/ha. Densities then gradually increased to 0.06/ha by 1985. This resulted from a mean rate of increase (0.24 ± 0.04) that marginally exceeded the numbers of individuals removed by slaughter and trapping. In the latter part of this period, trapping replaced slaughter entirely. Consequently, growth exceeded the number reduced by trapping. The relationship between density and population growth rate appeared to have been altered and was extremely difficult to characterize during this period. Polynomial filtering of the second order, showed that as the population density increased the rate of population growth declined. Given the frequent small reductions of animal numbers caused by trapping and some larger reductions by slaughter only density-dependent relationships below MSY could be described for the period, 1960-84 (Fig. 25).

For the Main Park elk population, an ARIMA model that primarily attributes statistical dependency to a constant or mean and secondarily to a first order seasonal moving average was selected as it was considered parsimonious - ARIMA $(0,0,0)(0,0,1)_6C$. Although previous analysis of periodicity suggested a strong 10 year cycle and a weaker 2.4 year cycle, analysis of the autocorrelations and partial autocorrelations suggested that a seasonality of $_{t-6}$ would be appropriate. This may be a result of the harmonic effect of the two cycles, six being approximately double that of 2.4 and half of 10. Differencing although suggested by the general increase of r throughout the data set, was found to exaggerate the spiking in the autocorrelation and partial autocorrelation and was thus considered to represent an unnecessary overdifferencing.

This model describes a flat noisy type of stochastic behaviour occurring at a constant or mean plus a minor effect resulting from the random impact of the previous period $_{t-6}$. The standard error of the estimate of the mean was 1.39 (P = 0.00). The seasonal moving average was estimated at 0.34726 ± 0.11 (P = 0.003). As such, it is described as:

$$Y_t=19.18463+[0.34762_6 Y_{t-6}]+a_t$$

where a_t is white noise. A plot of the model's forecast and analysis of the periodogram of residuals suggested that some periodicity was not yet accounted for in the frequency of 0.1 cycles per year (~10 years per cycle). The Chi-square test statistic of 10.6 (P > 0.05) of the first 20 residuals and the retention of the cumulative sum of residuals within the 95% Kolmogorov-Smirnov bounds of the integrated periodogram argue that this remaining cyclicity is not significant (Fig. 26).

Response to Management 1985-91. -- Following the previous analysis, the elk populations in both the main and Isolation areas of Elk Island were allowed to gradually increase toward ecological carrying capacity (K). The population in the Main Park was expected to follow a density-dependent relationship similar to that of 1941-60 because the population dynamics at densities below MSY from 1960-83 were similar to this period. It was expected that MSY would occur at densities of 0.07 - 0.08/ha and that K would occur at 0.09 - 0.10/ha. In the Isolation Area, modifications in the perimeter fence would test density-dependence in an environment where immigration and emigration would be possible. In addition, population data for the Isolation Area population would provide for a time series data set of significant length thus allowing for comparison with the Main Park population.

From 1984-87, the Main Park elk population increased from 519 to 832. During these first four years excellent rates of increase ($r = 0.24$, 0.20, 0.36 and 0.26) occurred. MSY appeared to occur at 0.056/ha when the population grew by 219 ($r = 0.36$). In 1988, the population having reached a density of 0.088/ha, the population rate of increase suddenly declined to 27 ($r = 0.03$). This density was initially viewed as near K. As a result the population was reduced by livetrapping from 959 to 847. During the next two years, continued management maintained the population below 900 (0.081/ha). The population responded with rates of increase near average ($r = 0.19$ and 0.20). In 1991 the population was again allowed to increase to 992 (0.091/ha$_{t}$, 0.084/ha$_{t \quad t-2}$) resulting in a reduced rate of increase ($r = 0.10$). At this time MSY was approximately 0.065 to 0.075/ha$_{t \quad t-2}$. Ecological carrying capacity was in the range of 0.09 to 0.085$_{t \quad t-2}$ (Fig. 27). In the remaining two years, 1992 and 1993, higher than expected rates of increase occurred. It remains to be seen if these years represent anomalies in the general relationship of density and rate of increase (noise) or are indications of a real shift in K.

Although the density-dependent relationship was similar to that of 1941-60 as predicted, the most recent period was generally less productive and required less intervention to control the population. During the 7-year period, 1950-57, the population grew from 674 to 1,149. The mean r during this period was 0.25 and 111 individuals were removed on average each year. From 1985-92, also a 7-year period, the population grew from 643 to only 945. This occurred despite lower rates of population reduction of 92.5/year owing to a reduced general rate of increase ($r = 0.17$).

During the same period (1984-86) the Isolation Area elk population also increased rapidly. Annual rates of increase (r) of 0.28, 0.39, and 0.36 allowed the population to grow from 122 (0.026/ha) to 165 (0.035/ha) despite the removal of 48 individuals. In 1987 and 1988, the population continued to rapidly increase ($r = 0.42$ and 0.31). These increases represented a per unit area rate of increase of 0.02/ha/yr at densities of 0.048/ha and 0.068/ha. From this MSY density (0.05-0.06/ha), the rate of increase sharply declined in 1989 and then marginally increased in 1990. K was estimated at 0.08/ha. Together these years showed remarkably unlagged, noise free, density-dependence with MSY being > 0.5 of K (Fig. 27).

In comparison with the Main Park, the densities at which MSY and K occurred were very similar despite transboundary movements of the elk between the Isolation Area and the Blackfoot grazing reserve. In 1991, the jump rail that allowed this emigration or immigration was closed. Over the next two years, productivity was greater than expected. These two years appear to suggest that as a result both MSY and K densities have been shifted. It is possible that a lagged density-dependence, similar to the Main Park, may have been established because of fence closure. Several more years of population data will be required to detect if this represents a permanent shift in MSY and K, a change to lagged density-dependence, or β noise in the data caused by climate or other factors.

Deer

Historical Abundance.-- The first historical records of deer in the Beaver Hills state that mule deer were the dominant deer species in the immediate area. The white-tailed deer was not historically abundant in the area but was found further south. Both species were found throughout the parkland but numbers were probably never large due to competition from bison, moose and elk (Webb 1967). Before European contact, densities of deer within this range were estimated to be 0.077/ha (Seton 1929, Halls 1984). Deer like the other species were originally a source of food and other materials to the native inhabitants. They suffered a similar fate to the other large ungulates when their meat became a commercial source of supply to the early fur trading posts in the region, but may have increased briefly due to the elimination by hunting of their principle competitors. References to historical abundance or density are difficult to assess but sources suggest that the populations during the late 1800's were at a low following a large die-off due to winter severity that affected all large ungulates (Hewitt 1921, Seton 1937 and Soper 1951). Establishment of parks, such as Elk Island, and the first efforts of game preservation were all viewed as positive steps toward establishing the previous populations (Hewitt 1921). At the time of park establishment, mule deer were comparatively few and their presence in the original fenced park was viewed as an asset. With the original elk population, they were described as having been present when the park area was fenced.

Dynamics 1906-86.-- From 1906 to the mid 1950's, the mule deer population size averaged 118 ± 12.37 (0.016/ha; 0.82 kg/ha). The population was relatively unproductive, with a mean r of only 0.04 ± 0.05. No population reductions by either slaughter or live removal were conducted during this period. During the period 1951-59, white-tailed deer replaced the mule deer population. From 1951-84, the mean white-tailed deer population was 62.97 ± 7.37 (0.005/ha; 0.28 kg/ha) in the Main Park. Excluding the years 1951-59, the mean r was 0.21 ± 0.12. In contrast to the previous mule deer population the Main Park white-tailed deer population was more productive and exhibited a higher degree of variability. Population reductions through slaughter were minor (0.019 kg/ha/yr). During the same period, the mean Isolation Area white-tailed deer population was 133.6 (0.028/ha, 1.41 kg/ha). Density in this area exceeded that of the Main Park while the mean rate of increase was the same (r = 0.21 ± 0.10). A detailed review of deer population history follows.

The founding mule deer population numbered 35 in 1906. Within the confines of this preserve surrounding Astotin lake, they were present at a density of 0.010/ha (0.53 kg/ha). By 1910, the population had declined to an estimated 30 (0.009/ha). A period of slow growth followed allowing the population to reach 100 (0.030/ha) by 1917. The mean r was 0.12 for this first decade. The next six years, before park expansion, were even less productive with a mean r of only 0.05. This entire period was very unproductive for mule deer but in comparison to extralocal and North American populations that were declining, the Elk Island population was very productive (Fig. 30).

The original mule deer population freely moved under or over the surrounding park fence, as they do today. Deer leaving the park would have been subject to the uncontrolled hunting that occurred at this time and this may have forced them to seek refuge within the park. Soper (1951) commented that, within the confines of the park, mule deer had gradually increased in number, inferring that outside the park they had not.

The addition of the new area, in 1923, caused the mule deer population to increase dramatically. This may have been the result of the new range and lowered densities, but more likely it was a result of preexisting populations in this new area. The preexisting population in the new area was probably present in a much lower density thus the total number increased from 150 to 300 but the density declined from 0.045/ha to 0.029/ha. This total park population of 300 was to be the highest number of mule deer counted during the entire history of the Main Park. As other ungulate populations began to rapidly expand following park expansion, the mule deer population declined to a total of 200 (0.019/ha) by 1929 and then increased very marginally at an r = 0.03 (1929-35) and 0.06 (1935-38).

Other large ungulates experienced drastic declines both natural and man induced beginning in the winter of 1935-36, but the mule deer population increased. This was short-lived as a massive decline in the winter of 1938-39 reduced the population from 260 (0.024/ha) to 27 (0.002/ha). At the time this was the lowest density of mule deer on record for the Main Park. It is unknown what proportion of this decline can be attributed to emigration.

From 1939-44, mule deer populations remained virtually unchanged. Large slaughters were being conducted to reduce the populations of the other large ungulates and although the deer themselves were not slaughtered it is possible that many may have left the park because of these activities. This stable and low population suddenly tripled in only two years resulting in a population of 72 in 1946. Poor population surveys or immigration are possible explanations. After this, the population of mule deer now experienced 10 years of steady population growth (mean r = 0.20). During this period the first mammal inventory of the park was conducted which described this healthy increase in the population (Soper 1951).

In 1947, the Isolation Area was added to the park. This separately fenced area was initially cleared of all ungulates but the ability of the deer to enter and exit the park fence meant a rapid recolonization of the area. From this date the Isolation Area has maintained a substantial population of deer that during most times has far exceeded the density found in the Main Park (Fig. 28).

Throughout much of North America, the white-tailed deer dramatically increased in the 1940's and 1950's and had been moving steadily northward displacing mule deer from much of it's range (Soper 1951). In central Alberta, these increases were mainly due to a series of wet years and elimination of prairie fires that increased the proportion of aspen forest (Webb 1967). The movement northward was probably facilitated by the white-tailed deer's ability to exploit agricultural crops and thus they moved northward with postwar homesteading (Wishart 1984). In 1951, the first white-tailed deer was seen in the park and by the summer of 1959 not one mule deer was observed (Holsworth 1959). During this period, numbers decreased from 96 to 50 (0.004/ha) in the Main Park while in the Isolation Area the population had increased to 150 (0.03/ha). Holsworth (1959) speculated that this resulted from the lack of competing ungulates, especially elk, in the Isolation Area. The deer, being able to freely move under the fence, chose to inhabit the less browsed Isolation Area were fewer competitors, such as elk, existed.

Although a few mule deer and mule/white-tailed deer hybrids were periodically observed in the park after 1960, the population was after that described in park records as a white-tailed deer population. After white-tailed deer dominated the park, the yearly variability and general productivity both increased dramatically. As a result large and apparently erratic changes in population densities were observed from year to year. Many of these changes were of such magnitude that they could only be accounted for by immigration, emigration or inconsistent surveys.

In the 1960's the first slaughters of deer began on a modest scale removing an average of 0.12 kg/ha over three years. At the beginning of 1964 the Main Park population numbered 64 (0.006/ha; 1.46 kg/ha) and the Isolation Area population numbered 140 (0.029/ha; 1.46 kg/ha). By 1967, both deer populations declined without slaughter leaving only 34 (0.003/ha) in the Main Park and 76 (0.015/ha) in the Isolation Area. This decreases were followed by an equally dramatic increase to 74 (0.007/ha) in the Main Park and 265 (0.055/ha) in the Isolation Area by 1969. These patterns continued with similar peak populations also resulting in 1973 and 1982. Annual population change varied from r = 2.0 to -0.60. In both the Isolation Area and the Main Park the pattern and yearly variability was similar or lagged (Fig. 28). Throughout most of the period white-tailed deer population density was higher in the Isolation Area. However, because of increasing numbers in the Main Park the populations in both areas reached a similar density of 0.015/ha by 1984.

Time Series Analysis and Density-Dependence.-- Estimated autocorrelation and partial autocorrelations of the annual rate of population growth and density of the white-tailed deer populations indicated stationarity before 1985. A comparison of the population dynamics of the mule deer dominated population before 1950 and the white-tailed deer population after that showed an abrupt and permanent change in productivity. From this perspective, the entire record of the Main Park deer population was not stationary. It was thus analyzed as two separate data sets.

Fast Fourier Transformation, periodograms, and inspection of autocorrelations all failed to indicate any form of periodicity in either of the white-tailed deer populations or the pre 1950 mule deer population. In addition, crosscorrelation of density and per capita r failed to show any direct or lagged correlation. Phase diagrams of density and per unit area productivity also confirmed that there was no density-dependent relationship.

Consistent with this, the selected ARIMA model:

$$Y_t=19.92+a_t$$

attributed statistical dependence solely to a constant or mean with the remaining quite substantial variability (SE ± 10.07) attributed to white noise. This $(0,0,0)(0,0,0)_2C$ model demonstrated no requirement for differencing nor seasonality. Although not particularly enlightening, the mean derived through this method is similar to the mean r calculated if the period of white-tailed deer colonization (1951-59) was eliminated (Table 1).

Response to Management 1986-92.-- During this period the white-tailed deer populations in both areas continued to fluctuate without direct management intervention. The Isolation Area deer population had been expected to decrease through emigration given the increasing densities of the other ungulates. Instead the mean density remained constant leaving the density for the entire period of record (1960-92) unchanged at 0.028 ± 0.002/ha. The population also exhibited greater stability with less yearly variation in population density and a reduced r of 0.14 ± 0.16 during this most recent period (Fig 28). This lowered the mean r for the entire period (1959-93) to 0.189 ± 0.098.

In the Main Park the population increased to 279 (0.026/ha) resulting in a similar density to that of the Isolation Area (0.028). This had been expected as the other ungulate populations had reached similar densities in both areas and given the ability of the white-tailed deer population to leave or enter the park. It was however, not expected to have resulted from an increase in the Main Park population. This increase in the most recent period increased the mean density in the Main Park to 0.008/ha for the entire period of record (1953-92). Yearly variability of population density increased marginally while the variability and r declined to 0.16 ± 0.15 during the period 1985-92. As a result the r for the entire period of record (1960-92) was 0.197 ± 0.099.

Ungulate Guild

Main Park Area.-- From the time when plains bison were introduced to Elk Island until 1984, the numeric ratio of the four principal ungulates remained remarkably constant. Plains bison (0.082/ha) dominated followed by elk (0.05/ha), moose (0.029/ha) and deer (0.01/ha). Two exceptions to this general rule occurred. The first during a brief period around 1930 when poor elk productivity allowed moose numbers to exceed elk. The second during the late 1960's when very sharp increases in moose numbers allowed a similar brief period in which moose numbers exceeded elk. After 1984, elk were more abundant than moose and plains bison (Fig. 29). This was preceded by the gradual and steady increase in elk numbers from the extremely low numbers following the large reductions of 1959.

A comparison of relative population biomass for each species before 1985, revealed that mule deer and moose had a loose association while white-tailed deer and moose remained closely correlated at 8 kg/ha (moose) vs. 0.2 kg/ha (deer). Elk and deer had a similar relationship centring on 15 kg/ha (elk) vs. 0.25/kg/ha (white-tailed deer). In relation to moose the elk population was approximately 2 kg/ha higher, and centred on a proportion of 10 kg/ha (elk) vs. 8 kg/ha (moose). Plains bison were, in relation to both moose and elk, centred along a linear axis with the result that a common range of relative biomass proportions developed. Bison as compared to elk ranged from 45 kg/ha (bison) vs. 15 kg/ha (elk) to 20 kg/ha (bison) vs. 7 kg/ha (elk). Moose, on the other hand, varied between 10 kg/ha and 4 kg/ha given the same bison biomass.

The total biomass of all large ungulates combined is presented in Figure 29. An initial peak in biomass (61 kg/ha) was experienced with the temporary introduction of plains bison. When shipment of most of these bison occurred in 1910, the park was left with a meagre 9 kg/ha of large ungulate biomass. A period of exponential growth followed in all species. Thus, in twelve years 60 kg/ha of biomass was supported by the park. Park expansion resulted in a lower biomass density of 18 kg/ha. Again exponential growth occurred and thirteen years later, in 1935, the largest biomass ever supported in the park (161 kg/ha) resulted. Natural mortality and slaughters reduced this to 56 kg/ha in the short span of five years. Over the next twenty five years continued annual slaughters maintained an average biomass of 67.7 ± 1.6 kg/ha until larger reductions in 1959 and 1960 reduced the biomass (23.6 kg/ha). From this low, the biomass increased quickly and then was again stabilized through a period of reductions by slaughter and live removal. During this ten-year period (1964-74), the average biomass was 46.4 ± 2.8 kg/ha. From 1975-85 the mean biomass was lower and less variability (37.2 ± 0.8 kg/ha). Since 1985, total herbivore biomass of 35 kg/ha has increased to that of 63.80 kg/ha in 1992. This is a result of the most recent management regimes.

For the entire period of record the annual biomass production in the Main Park averaged 8.4 ± 1.1 kg/ha/yr this was composed of 63% plains bison (5.3 ± 0.5 kg/ha/yr), 24% elk (2.0 ± 0.3 kg/ha/yr), 13% moose (1.1 ± 0.2 kg/ha/yr), and <1% deer (0.04 ± 0.03 kg/ha/yr). Ungulates removed by management, through both slaughter and live removal, totalled 19,199 (645 kg/ha; 7.5 kg/ha/yr) for the entire period 1906-93 in the Main Park. This does not include the removal of the initial plains bison population, in 1910. The mean amounts of biomass removed from 1910-60 were slightly over 14 ± 2 kg/ha. From 1960-85, the management required to affect control of a new lower population (7.3 ± 1.0 kg/ha/yr) was almost half of that required during the previous twenty-five years. Recently (1986-93), management was further reduced to 5.7 ± 1.3 kg/ha/yr. Ignoring the early period of population growth, during which management intervention was minimal and considering only the post 1935 period the yearly mean population management was 10.96 kg/ha/yr. The contribution of each species to the total number of ungulates removed was similar to that of the relative population size, with bison contributing the largest proportion of the total (53.51%), followed by elk (32.28%), moose (13.42%) and deer (0.1%). The biomass harvested was composed of 67.9% plains bison, 20.9% elk, 11.08% moose, and 0.1% deer. Moose biomass removed was also lower than the total live standing biomass suggested due to significant periodic natural mortality. The deer biomass harvest was extremely low because, as noted previously, this species is not managed due to it's ability to move freely in and out of the park

Isolation Area.-- The relative abundance of the Isolation Area ungulates varied widely before 1987. At various times moose, deer, plains bison, and wood bison all numerically dominated the total large ungulate population. This is in direct contrast to the stable ratio of large ungulate numbers in the Main Park before 1984. Besides the unstable proportions of each herbivore, the Isolation Area also contrasted with the Main Park in several other respects. The most important difference was in the relative proportion of deer which, at 0.028/ha, were more abundant in relation to both the Main Park and other herbivores in the

Isolation Area. Moose density was similar in both areas but represented a greater proportion of the total ungulate numbers in the Isolation Area. Elk numbers, were until recently very low, both in absolute and relative terms. Before 1989, high deer numbers in the Isolation Area correlated with low numbers of elk as did the reverse proportions observed in the Main Park.

Since 1987 the elk population size has exceeded that of wood bison population and the resulting relative order of numerical abundance (1.elk, 2.wood bison, 3.deer and 4. moose) has remained constant. This was the result of the elk, moose and deer being allowed to reach ecological carrying capacity and the wood bison population being kept at a lower MSY density.

The relative contribution of each species to the total large ungulate biomass is clearer. Initially the Isolation Area was strictly used to "Isolate" plains bison. The requirement to remove all the other species from the area logically resulted in an ungulate biomass (57 kg/ha) almost totally dominated by the 52 kg/ha of plains bison. This proportion was maintained until all plains bison were removed in favour of wood bison. Over time, moose had increased and at the time of wood bison reintroduction dominated the biomass of the Isolation Area. They remained dominant until the wood bison population increase exceeded the total biomass of moose in the late 1970's. Elk biomass was very low and only just recently exceeded that of moose. Deer although numerically very abundant, still represented the smallest biomass, except during the period 1960-75, when elk were the lowest contributors to the total biomass of the Isolation Area.

From 1960-85, the total herbivore biomass averaged 24.4 ± 1.4 kg/ha in the Isolation Area. This was nearly half that of the Main Park that during the same period averaged 42.7 ± 1.3 kg/ha. From a low of 12 kg/ha in 1964, a rapid increase in moose and wood bison allowed the total biomass to increase to 22 kg/ha by 1967. This was to be only a brief peak in biomass as moose were reduced by tick-related mortality and slaughter while wood bison were reduced due to the destruction of T.B. infected individuals. Thus, by 1970, the total biomass was reduced to 9 kg/ha. Following this all herbivores increased rapidly reaching a total biomass of 28 kg/ha in 1976. The next seven years (1976-83) featured a stable biomass because of slaughter and donation of wood bison and moose. During this time the biomass averaged 27 ± 0.5 kg/ha. By 1985, the total biomass had reached 37 kg/ha due to the delay of wood bison donations and recent increases in both the moose and elk populations. From 1986-92 the biomass averaged 58.5 kg/ha. This period of increased biomass, resulting from the most recent management regime, represents a biomass density consistent with the Main Park. This most recent biomass density has a strong influence on the mean of the entire period (1960-92) which was 28.77 kg/ha.

In the Isolation Area annual biomass production averaged 5.0 ± 1.2 kg/ha/yr composed of 59% wood bison (3.0 ± 0.4 kg/ha/yr), 23% moose (1.2 ± 0.4 kg/ha/yr), 17% elk (0.9 ± 0.3 kg/ha/yr), and 1% deer (0.08 ± 0.1 kg/ha/yr). Numbers removed by management totalled 1,502 (98.5 kg/ha; 3.3 ± 1 kg/ha/yr) from 1960-92. This was composed of 1.8 ± 0.5 kg/ha/yr of wood bison, 1.0 ± 0.3 kg/ha/yr of moose, 0.3 ± 0.1 kg/ha/yr of elk, and 0.07 ± 0.04 kg/ha/yr of deer (Fig. 29). This biomass consisted of 59% wood bison, 30% moose, 9% elk, and 2% deer. The large contribution of moose and deer, to the total harvest, results from the consistent presence of these species in large numbers. The wood bison and elk have only recently reached proportions where population reduction was required. Thus, they are proportionally low in their contribution to the total harvest. In both relative and absolute terms, the Isolation Area population management was well below that of the Main Park.

DISCUSSION

Evaluation of the Data

Many ungulate populations show highly variable and apparently unpredictable changes in density. This should not be surprising in that even simple population models often show a variety of behaviour including chaotic, cyclic, aperiodic and equilibrium (Noy Meir 1975, Caughley 1976). Pimm (1991) states, that despite all the good reasons for ecologists to appreciate the importance of these complicated population dynamics, studies have often only been of interest to theoretical ecologists. The reason, he concludes, is the failure of field ecologists to view population change over periods long enough for complex dynamics to unfold. For ungulates, a limited number of cases are available to provide such an understanding. This includes the notable examples of moose/wolf interactions of Isle Royale, ungulate populations of the Northern Yellowstone, elk of Jackson, Wyoming, white-tailed deer of George Reserve in Michigan and the guilds of grazing ruminants of the Serengeti and Lake Manyara in Africa (Peterson 1977, Houston 1982, Boyce 1989, McCullough 1983, and Leuthold and Leuthold 1976, respectively). Of these, none provide a record of ungulate population dynamics as lengthy and comprehensive as that for Elk Island. The 87 years of records for the Main Park, and 34 years of comparative data for the smaller Isolation Area, are arguably the best example of complex population dynamics of an entire ungulate guild.

Population census and management data obtained from detailed park records allowed complete reconstruction of population dynamics of bison, elk, moose and deer at Elk Island. The wealth of information available and consistent annual reporting allowed reconciliation of anomalous records. Population estimates permitted confident detection of the rate of population change and densities of ungulates. Previous authors (Telfer and Scotter 1975, Holsworth 1959) cited the extremely high numbers of elk and bison in the late 1930's but believed these numbers to be overestimated (Telfer Pers. Comm. 1987). However, a review of the entire set of yearly estimates leading up to these peak populations, the observed mortality and known numbers removed at the end of this period, supports these numbers. For the remainder of the period there appears little question about the accuracy of the estimates. The removal of a large proportion of the ungulate populations each year and annual aerial surveys validate these population estimates. Actual rates of change of ungulate numbers are often difficult to document from population estimates obtained from aerial surveys because estimates may be inaccurate and/or imprecise. For Elk Island, the consistency of survey conditions, the complete coverage, short duration of the survey required, open nature of the vegetation canopy during winter, and periodic surveys of the populations before and after removals appear to have resulted in both accurate and precise estimates. Analysis of the surveys conducted since 1979, when georeferenced group size and canopy coverage information were available, confirm that 80-90% of the ungulates were observed. This precision was more than adequate for statistical analysis by time series methods.

The long record in the main and Isolation areas of Elk Island provided excellent temporal control for time series analysis. For the Main Park, consistent population estimates were available for all but three years, 1913-14, 1963-64, and 1989-90. In these three cases, numbers were derived from the years before and after, through extrapolation. The first two periods were easy to extrapolate in this matter given that both years occurred during periods of low numbers with consistent exponential rates of population growth. For 1989-90, population removals helped in reconstructing the population numbers. Extrapolation of population numbers in these three years did not appear to compromise the validity of these data as an 87-year time series. The Isolation Area surveys were inconsistent before 1960 and did not provide a valid data set for time series analysis. However, from 1960-93 the surveys provided an excellent 34-year time series.

Good spatial control also was evident in the population estimates for elk, bison and moose. Park records and observations made by the author, during the last 15 years, suggest that the perimeter fence prevents transboundary movements of bison and elk. Moose, although occasionally seen breaching the park perimeter fence, are also effectively contained within the park. In contrast, white-tailed deer are frequently observed moving in and out of the park. This lack of spatial control is apparent in the highly variable yearly population estimates. This α noise (population error) is significant and must be considered when drawing conclusions with respect to white-tailed deer.

Merit of the Time Series Approach

e search for deterministic patterns in ungulate populations, observed at different points in time, has often led to problems in both modelling and inference. In particular, the characterization of density-dependence in real populations has been notoriously difficult (Crowley 1992). To overcome many of these problems, ungulate population dynamics have been analyzed by a variety of techniques (Slade 1977, Clutton-Brock et al. 1985, Gaston and Lawton 1987, Pollard et al. 1987, Vickery and Nudds 1991). The validity and appropriateness of these techniques have been reviewed by several authors (Williamson 1972, Caughley 1977, McCullough 1990, Eberhardt and Simmons 1992, Pimm 1991, Hastings 1993). The obvious correlation introduced by sampling adjacent time points can severely restrict the applicability of statistical methods that depend on the assumption that the adjacent observations are independent and identically distributed. Recognizing this, time series statistical approaches are considered an appropriate, but underutilized tool for study of ungulate population dynamics (Sauer and Boyce 1979, McLaren and Peterson 1995). Studies have been mainly limited to microtines and other species where significantly longer uninterrupted data sets are available (Steen et al. 1990, Turchin 1990, Bautista et al. 1992).

Time series analysis in both the time and frequency domains allowed detection of patterns of density-dependence that would have otherwise been lost in the noise (α,β) or drifting (non-stationarity). The importance of removing noise through filtering or simple averaging cannot be overemphasized.

Frequently, characterization of underlying phenomenon would have been lost in the apparently exogenous random effects. Similarly stationarity was an important consideration in the characterization of Elk Island populations. The detection of a constant mean throughout a time series was essential for the application of many techniques required to detect periodicity, and density-dependence. Alternatively, the absence of a stationary mean also showed important underlying forces effecting the time series.

Spectral analysis provided the means for formalizing dependence or correlation between adjacent points. Although one may have obtained indications regarding different periodicity's and the extent of their contributions through visual analysis, a more precise identification and assessment of the statistical significance were obtained through Fourier transform and estimated autocorrelation. The identification of the most appropriate ARIMA model provided insight into the relative contributions of noise, patterns and trend components to the rates of population change. It also made it possible to integrate seasonal and annual changes in the same model. However, ARIMA forecasting was of limited utility. This was because it merely related the present or future value of a time series to a collection of values from the past. It did not explicitly incorporate a density-dependent function and was unrealistic where ecological conditions changed. This shortcoming was also noted by Merrill and Boyce (1988) who nevertheless found this method good for short term projection of elk and bison populations.

Finally, cross-correlation proved to be essential for detecting density-dependence in that population rates of change lagged behind density. The necessity of these basic time series methods for clear interpretation of temporal variation and detection of density-dependence in Elk Island, suggests that a better understanding of other ungulate populations may be gained from this approach. This is especially true where measurement error because of poor surveys (γ noise) or when ungulate populations are fluctuating below carrying capacity where environmental forces (β noise) exert a greater influence.

Biomass Density of Ungulates

When explorers first observed the aspen parkland, they described an area of abundant wildlife. Vast herds of bison roamed its periphery during the summer and sought shelter within wooded portions during winter. Large populations of other ungulates such as elk, moose, antelope, and deer also inhabited the ecosystem (Bird 1961). The presence of fire was evident to these early visitors as it was frequently applied by native peoples (Lewis 1982). These trophic and pyric factors have determined the dynamic character and extent of the ecosystem (Maini 1960, Fehr 1984, Campbell et al. 1994).

Despite historical references regarding the great abundance of ungulates in the pristine aspen parkland, quantitative data are sparse. This is because few intact examples of aspen parkland, with its native ungulate guild, remain for study. Estimates of biomass densities derived from my review of historic abundance suggest that the parkland may have supported 9 - 54 kg/ha of plains bison, 0.25 - 1.2 kg/ha of deer, 1.24 - 3.1 kg/ha of moose and 0.3 kg/ha of antelope. Reasonable estimates of elk biomass densities are lacking. Linear programming models of resource allocation by Hudson (1981) predicted the density of elk to be 0.03/ha (7.26 kg/ha) along with 0.03/ha (9.3 kg/ha) of moose and 0.07/ha (31.5 kg/ha) of bison.

Hudson and Blyth (1984), using a similar model, calculated that a maximum of 0.14 elk/ha (33.9 kg/ha) could be supported in the aspen parkland if fewer bison and no moose were present. This compares to 0.12-0.14 elk/ha (29-34 kg/ha) in areas such as the Northern Yellowstone winter range (Houston 1982). From these models and historic records I estimated the total equilibrium biomass density of the aspen parkland ungulate guild could have been 18 - 93 kg/ha.

The ungulate guild at Elk Island provides a modern analogue for comparison to this estimate. Telfer and Scotter (1975) noted that the Main Park supported a similar range of 22.5 - 98.2 kg/ha of native ungulates from the late 1950's to the early 1970's. From their analysis of vegetation production they proposed that the park could sustain 31.9 kg/ha of bison, 14.0 kg/ha of moose and 11.1 kg/ha of elk (total biomass of 57.1 kg/ha). At these densities they predicted a 20% (11.41 kg/ha/yr) yield or rate of removal of the total ungulate biomass. In fact my study found the average standing stock from 1906-93 to have been 56.0 kg/ha but the annual yield was only 13% (7.5 kg/ha/yr). Annual yields of 14.2 kg/ha (20%) were realized during the 25 years before 1960 when standing stocks of ungulate biomass was 67.7 ± 1.6. Since 1985, population harvests were reduced for elk and eliminated for moose. This and the lower relative abundance of moose probably account for the lower yield than forecast by Telfer and Scotter (1975). This lower relative contribution of moose to the annual yield is consistent with the predictions of Hudson and Blyth (1984).

A range of possible ungulate biomass estimates for the aspen parkland is proposed from the range of MSY densities derived for each species at Elk Island (Table 1). From these MSY values, the biomass of ungulates could range from 52.9 - 91.5 kg/ha perhaps yielding 10.6 - 18.3 kg/ha/yr. Similarly the total biomass of ungulates at ecological carrying capacity could range from 76 - 134 kg/ha. The 161 kg/ha of ungulate biomass supported in 1935 also suggests the maximum densities that might be supported in the aspen parkland. However, significant supplementary forage was provided during the winters when this extreme biomass was supported at Elk Island.

The proportion of total ungulate biomass in the Main Park was dominated by bison followed by elk, moose and deer in descending order. This is the same order as that suggested for resource partitioning and social dominance with respect to these four species at Elk Island (Cairns 1976, Telfer and Cairns 1983). It is also the same as expected based on historic accounts of the pristine aspen parkland ecosystem. The deer population represented only 1% of the total biomass. This is important to consider because in many areas of North America, deer are the only remaining members of the original ungulate guild (Table 3). In these areas, the density of deer (0.01-0.4) is greater than or equal to Elk Island's deer population but far less than the biomass of the entire ungulate guild.

Biomass densities of Elk Island can be compared to three other aspen parkland areas with intact or partially intact native ungulate guilds. At the former Buffalo National Park, located approximately 200 km's east of Elk Island in a dryer area of the aspen parkland, approximately 49 - 75 kg/ha of bison, elk, moose and deer were supported from 1928-33 (Harkin 1933). Here, biomass densities were similar to Elk Island but moose comprised <1% (0.3 - 0.6 kg/ha) of the total. In the Cooking Lake-Blackfoot Recreation Area (CLBRA) immediately adjacent to Elk Island, Telfer and Scotter (1975) reported moose, elk and deer biomass densities of approximately 30 kg/ha along with 347 animal unit months of cattle grazing. They noted that Elk Island supported almost 45% more grazing by the native ungulate guild than the CLBRA did cattle, and 18% more than for cattle and native ungulates in combination on the latter. Today the CLBRA supports far fewer native ungulates (8.75 kg/ha) owing to intense hunting pressure and the replacement of the aspen parkland with tame pasture in several areas for use by cattle. At Riding Mountain National Park (RMNP), in west central Manitoba, peak elk densities of 13.9 kg/ha (70.1 kg/ha on 'concentrated elk range') and moose densities of less than 0.3 kg/ha were reached before dramatic population declines occurred in 1946 (Banfield 1949). From 1950-87, 2.3 - 8.1/kg/ha of elk and moose was supported (Rounds 1977, Carbyn 1989). Deer were not counted but contributed less than 2.5 kg/ha. Here, bison were present as a small display herd and were not free ranging. In this situation, the absence of bison and hunting around the perimeter of this unfenced park probably accounted for the lower biomass densities. The comparison of these areas with Elk Island implies the importance of bison as the major contributor to ungulate biomass in the aspen parkland.

Prince Albert National Park (PANP), located mostly in the southern boreal mixed-wood forest in central Saskatchewan, also contains remnants of aspen parkland and its native ungulates at its southern margin. Peak elk densities of 3.63 kg/ha and moose of 1.55 kg/ha were reached in 1940 (Tarleton 1988). In recent years, substantial losses of animals to the surrounding area resulted in very low densities. In 1990, the total biomass density of elk, moose and deer was 1.6 kg/ha in the southern section of the park and only 0.49 kg/ha in the northern section (Theberge et al. 1993). In addition, a small herd of bison is now inhabiting a small aspen parkland area in the south of the park at a density of 0.9 kg/ha (Frandson Pers. Comm. 1994). The data from PANP show that the aspen parkland areas are more productive than the boreal.

The ungulate biomass supported at Elk Island is high when compared to other natural grazing systems in North America. Grassland ecosystems such as the Mixed Prairies of South Dakota (36.4 kg/ha), the Northern Yellowstone winter range (43 kg/ha), and the Mixed Tallgrass-Forests of the Wichita Mountains N.W.R. (17.8 kg/ha) are comparable to the lowest estimates of standing stock for the aspen parkland (Waldrip and Shaw 1979, Houston 1982, Redmann 1982). Ungulate biomass density is similar to several notable ungulate guilds in East Africa. The Tarangire (101.7 kg/ha), Serengeti (63.4 kg/ha) and East Tsavo N. P. (44.5 kg/ha) provide examples that compare to the range of biomass densities supported by the aspen parkland at Elk Island (Leuthold and Leuthold 1976, Fritz and Duncan 1994).

Ungulate biomass density at Elk Island is supported by a productive plant community. Estimates of this primary productivity or plant biomass for Elk Island and other aspen parkland areas were described by Blyth and Hudson (1987). The standing crop or total biomass of plants in the parkland can be as high as 180,000 kg/ha in heavily forested sites. In the upland sites dominated by grasses and forbs, total above ground biomass has varied from over 4,000 kg/ha to nearly 7,000 kg/ha. Sedge meadows have standing crops of nearly 10,000 kg/ha (Blyth et al. 1993). The trophic pyramid can be described as a base of plant biomass ranging from 5,000 - 180,000 kg/ha which at Elk Island has supported the ungulate biomass noted. This ungulate biomass even in the peak ungulate densities of the mid 1930's was only 0.0009 - 3% of the plant biomass.

Primary productivity of shrubs ranges from 24 - 348 kg/ha, sedges from 3,266 - 6,813 kg/ha and grasslands usually produced over 5,000 kg/ha. Consumption of this primary production by the ungulate guild was calculated by Blyth and Hudson (1987) as a function of metabolic weight and using the ungulate population dynamics data from Elk Island. They determined that consumption of the primary productivity by the ungulate guild may have been as low as 150 kg/ha/yr in 1910 to as high as 1,200 kg/ha/yr in 1936. In the most recent decade the ungulate biomass of 30 - 60 kg/ha was estimated to have consumed 240 - 480 kg/ha/yr of plant biomass. Monitoring of vegetation during this period documented that 50 - 70% of the grass and forbs, 8 - 40% of the sedges, and 15 - 55% of the shrub production was consumed (Blyth et al. 1993, McDougall 1993, Osko 1993). These amounts of herbivory were reported as acceptable for the maintenance of ecological integrity. The average ungulate biomass of 56 kg/ha is estimated to have consumed 448.5 kg/ha of primary production to produce the mean annual increase of 8.38 kg/ha of ungulate biomass. This represents a foraging efficiency of 1.9%. During the 25 years before 1960, the average annual yields were achieved through a foraging efficiency of 2.6%. Given the amounts of primary production and observed utilization, the biomass densities and yields of ungulates observed by my population analysis seem reasonable. The aspen parkland trophic structure can be described as substantial and productive primary productivity capable of withstanding substantial rates of herbivory by efficient secondary producers thus supporting secondary production greater than or equal to many other grazing systems.

Rates of Increase

Ungulate population dynamics are often considered from one of four different perspectives. The first view is that population dynamics result from essentially random changes in environmental conditions. The ARIMA models of bison and white-tailed deer at Elk Island attribute population changes to a constant plus noise. These models can be considered as support for this theory if one ignores evidence of density-dependence. This theory fails to consider the role of ecological interactions with resources, management practices and predators or disease shown for many populations including Elk Island.

The second view holds that changes in density can be attributed to a simple equilibrium plus noise. It proposes that there is an equilibrium density to which populations return after disturbances imposed by the environment (noise). Many ungulate populations show this tendency to increase when rare and decrease when overabundant, but this idea does not capture the complexity that results from the lagged density-dependence observed at Elk Island. It also fails to predict the range of responses that different populations at Elk Island exhibited following environmental influences.

The third view is that population dynamics may be driven by deterministic processes that cause complex population changes with environmental noise adding a further component of variation. The prevalence of such complex changes is currently a matter of debate. Studies of some populations do not support this theory, but it has been argued that this may be a limitation of the techniques used to detect complex dynamics. In particular, supporters of this theory state that it cannot be proved without very long time series. In fact, support for this comes from the lengthy time series at Elk Island, where population cycles, delayed density-dependence, and other complex dynamics are prevalent.

The fourth view is that population dynamics can be described as short-term noise imposed on longer term patterns, which are imposed on even longer and more significant trends. At Elk Island, short-term noise, patterns and long term trends are evident in several ungulate populations. The difference between this idea and the others is that it is an empirical description of population dynamics, while the others propose mechanisms.

The first two theories are supported by short-term studies while the latter only emerge from long-term studies like that of Elk Island. What is most important, is that the latter theories challenge much of the current ecological theory pinned on the underlying assumption of constancy or ecological balance. Alternate ecological theory has been developed which accepts long-term cycles, complex attractors and long-term trends as evidence of highly variable ecological equilibria. Such models predict that populations are preadapted to constantly varying ecological equilibrium. Because the aspen parkland is such a dynamic ecosystem, it is logical that ungulates populations exhibit such complex dynamics. Alternatively it can be argued that the complex dynamics are a consequence of the small size or incomplete nature of the park. To a limited extent this is supported by the differences observed between the Main Park and smaller Isolation Area, but both areas display complex dynamics consistent with that reported for the same species in other areas.

Intrinsic Rates of Increase.-- When resources are not limiting, ungulate populations with stable age distribution, grow at their intrinsic rate of increase r_m. They are constrained to an upper limit by their physiology interacting with those components of the environment that are not resources (Caughley and Sinclair 1994). The r_m can occur in established populations but is most often reported for recently introduced populations expanding in a new environment. Intrinsic rates of increase r_m tend to vary with body weight (W). The relationship was calculated by Caughley and Krebs (1983) as $r_m = 1.5W^{-0.36}$. Using the mean adult weights estimated by Blyth and Hudson (1987), the theoretical r_m would be 0.16 for bison, 0.19 for moose, 0.20 for elk, and 0.36 for deer.

Bison populations have been reported to have sustained mean r_m of $\underline{r} = 0.09 - 0.21$ for several years after being introduced to a new environment. Higher intrinsic rates of increase ($\underline{r} = 0.26$) were common for several populations after becoming well established. In 1963, a population of 18 wood bison was introduced to the MacKenzie Bison Sanctuary. This population grew at a mean $\underline{r}$ of 0.215 ($\lambda = 1.24$) and reached an $\underline{r}$ of 0.27 ($\lambda = 1.31$) in 1975 (Gates and Larter 1990). Roe (1970) described the former Buffalo National Park herd as having increased following introduction at $\lambda = 1.18$ ($\underline{r} = 0.17$). He also noted that the first year of increase was very low owing to stress from the reintroduction. Eliminating this first year and using the numbers provided, I calculated the rate of increase to be $\lambda = 1.22$ ($\underline{r} = 0.19$). The maximum rate of increase observed (r_{max}) $\lambda = 1.34$ occurred fourteen years after introduction in 1924, during a five year period with a mean $\lambda = 1.29$ ($\underline{r} = 0.25$). The early growth phase of the bison population of the National Bison Range (NBR) in Montana was analyzed in detail by several authors (Roelle 1977, Fredin 1984, Eberhardt 1987). During the first ten years the NBR population increased rapidly with a mean $\lambda = 1.25$ ($\underline{r} = 0.22$). The maximum rates of increase ($\lambda = 1.30$ a[illegible] population occurred during the first two years of population growth. Eberhardt (1987) de[illegible] growth phase as having an $\underline{r} = 0.20$ but fitted a model with $\lambda = 1.24$ ($\underline{r} = 0.22$) to the data [illegible] Mountains bison population in Utah grew at a much lower maximum $\underline{r} = 0.09$ from [illegible]uren and Bray 1986). A higher estimate of $\underline{r} = 0.18$ ($\lambda = 1.20$) was also derived by assuming hunting mortality to be additive.

By comparison, the $\underline{r}$ of the plains bison population at Elk Island following introduction and immediately after the first park expansion, was only 0.16 ($\lambda = 1.17$). It then increased at an exponential rate of 0.21 ($\lambda = 1.23$) until reaching peak numbers in 1936. The wood bison population at Elk Island increased at an $\underline{r}$ of 0.19 ($\lambda = 1.21$) during the initial period of introduction to the park. These initial periods of population eruption following introduction should suggest the r_m for bison at Elk Island but they do not represent significantly high rates of increase. They are however close to the r_m predicted by Caughley and Krebs (1983). At Elk Island, higher r was observed after the population was well established during periods where forage resources were not limited. During 1969-73, the plains bison population was free from forage resource limitation with a young even sex ratio population structure. The resulting elevated fecundity and low mortality resulted in a r_m of ($\lambda = 1.30$, $\underline{r} = 0.26$) and a r_{max} of ($\lambda = 1.47$, $\underline{r} = 0.38$). A similar r_{max} for plains bison was recorded in 1944 ($\lambda = 1.49$, $\underline{r} = 0.40$) These values are the highest r_{max} recorded in a wild bison population. The period from 1987-91, also exhibited a r_m of $\lambda = 1.30$ because of adequate forage resources and a young female dominated population structure. For the wood bison population, a r_{max} of $\lambda = 1.59$ ($\underline{r} = 0.46$) and $\lambda = 1.51$ ($\underline{r}$ 0.41) were realized. These rates of increase cannot be considered indicative of a r_m expected in a wild population because of the managed population structure and intense animal husbandry of this captive population during these early years. The $\lambda = 1.33$ and 1.36 in 1983 and 1988 are more realistic indicators of r_m for the wild wood bison population at Elk Island.

Like plains bison, elk populations in the Main Park and Isolation areas of Elk Island both sustained low mean r_m during the early years of population growth ($\underline{r} = 0.15$, $\lambda = 1.16$). In the Main Park there were individual years during which the elk population grew at rates indicative of the r_{max} ($\lambda = 1.50$, 1.42 and 1.40). Sustained r_m at high levels in the Main Park was not realized until 1931-35 (after park expansion) when the population increased at a mean $\underline{r} = 0.31$ ($\lambda = 1.36$). After this, high rates of increase again indicative of r_{max} ($\lambda = 1.51$ and 1.48) were observed during single years but another significant period of r_m was not observed until 1961-63 when the mean $\underline{r} = 0.35$ ($\lambda = 1.42$). In this period the elk population was again expanding following substantial population reductions by management. In the Isolation Area, the mean $\underline{r} = 0.31$ (1983-87) was identical to that of the Main Park from 1931-35.

The intrinsic rate of increase for elk has been reported for other areas. In RMNP the elk population increased from 500 in 1914 to 2,500 in 1925 (Rounds 1977). The r_m ($\underline{r} = 0.15$) observed here during the initial stages of population growth was identical to Elk Island and occurred during approximately the same years. Studies of elk in Missouri, California, and Washington reported intrinsic rates of increase from $\underline{r} = 0.29 - 0.31$ (Murphy 1963, Gogan and Barret 1987 and McCorquodale 1988). The r_m observed in these populations are similar to that of Elk Island during latter years. Burris and McKnight (1973) documented six years of population growth of an elk population introduced to Afognak Island, Alaska. The r_m (mean $\underline{r} = 0.37$) of this population is slightly higher than observed at Elk Island. Many of these r_m are higher than that predicted by Caughley and Krebs (1983). The reports of these populations and Elk Island suggest that sustained mean r_m of $\underline{r} = 0.31$ ($\lambda = 1.36$) can be expected. During situations where population structure and environmental conditions dictate, a r_{max} near 0.50 can be realized in a specific year.

VanBallenberghe (1983) reviewed rates of increase for moose populations. He noted that λ values exceeding 1.30 ($\underline{r} = 0.26$) had not been reported for moose populations in North America. Populations with adequate resources, little predation and/or hunting pressure, ranged from $\lambda = 1.15 - 1.30$ (mean $\lambda = 1.23$) (Spencer and Hakala 1964, Krefting 1974, Mercer and Manuel 1974, Roley and Keith 1980, and Gasaway et al. 1983). Few good examples of r_m derived from measures of moose populations during the early stages of population growth are available. Bergerud (1981) reported the r_m for moose in Ontario was at least $\underline{r} = 0.35$. This was considered by VanBallenberghe (1983) to be too optimistic however, I calculated the same r_m ($\underline{r} = 0.35$) for the moose population at RMNP, from 1953-57 when it increased from 250 to over one thousand. In the absence of data describing actual populations, the intrinsic rate of increase has been estimated from values of survival and fecundity. In Newfoundland, Pimlott (1959) calculated the rate of increase of the island's moose population as $\lambda = 1.33$ ($\underline{r} = 0.29$) which he compared to similar calculations for Sweden ($\lambda = 1.37$, $\underline{r} = 0.32$) by Skunche (1954) and ($\lambda = 1.36$, $\underline{r} = 0.30$) for British Columbia by Edwards and Ritcey (1958). Values of r_m for North American moose, estimated from reported values of survival and fecundity, fell within the range of $\underline{r} = 0.25 - 0.30$ (VanBallenberghe 1983). The observed r_m for moose at Elk Island exceeds the estimates for all these moose populations. In the Main Park, there were three periods (6-7 years in duration) where moose populations increased rapidly from low densities. The mean $\underline{r}$ of 0.32, 0.34 and 0.36 during these three periods and a similar six-year period in the Isolation Area $\underline{r} = 0.34$ (λ [illegible]) suggests the r_m for moose. This r_m [illegible] much higher than predicted by body weight however, it has been shown that a high percent of females first breed as yearlings and conceive twins as adults when moose are at low densities (Blood 1974, Simkin 1974). Geist (1974) theorized that this exceptional reproductive potential for moose is a function of the dynamic nature of the ecosystem to which they are adapted.

This ability to twin in combination with female-dominated population structures and excellent environmental conditions also allowed extremely high r_{max} during some years. VanBallenberghe (1983) proposed that the r_{max} for moose could approach $\underline{r} = 0.35$ ($\lambda = 1.49$) for populations where age distributions were not stable, dispersal was prevented, adult annual survival was about 0.95, calf survival approached 0.8, and fecundity was at a maximum. This estimate is well below that of the observed r_{max} for Elk Island. For example in 1944, (the same year as the bison population was reported to have expressed it's r_{max}), the moose population also increased at $\lambda = 1.84$ ($\underline{r} = 0.60$). A moose population of 75% females with more than 50% producing twins and nearly all yearlings producing a calf along with the same assumptions made by VanBallenberghe (1983) could produce this rate of increase. Calving rates of this magnitude have been documented at Elk Island (Blood 1974). Less extreme but nonetheless still very impressive population increases (r_{max}) of $\lambda = 1.50 - 1.75$ ($\underline{r} = 0.40 - 0.55$) also occurred in 12 other years during the history of Elk Island's two moose populations. This confirms that high r_{max} are not a rare occurrence in the moose population.

White-tailed deer populations exhibit very high intrinsic rates of increase. In the George Deer Reserve the first period of introduction and a subsequent experimental period, designed to determine r_m, resulted in $\underline{r}$ of 0.52 ($\lambda = 1.68$) and 0.49 ($\lambda = 1.63$) respectively (McCullough 1983). The largest r_{max} recorded ($\underline{r} = 0.91$) occurred in 1976 when the population grew from 21 to 52. Fuller (1990) reviewed the potential r_m for several other white-tailed deer populations. Using the data of Martin and Krefting (1953) he calculated the r_m in an unfenced refuge in Wisconsin as $\lambda = 1.58$ and using data provided by Ozoga and Verme (1982) a $\lambda = 1.40$ for a captive herd in northern Michigan. Fryxell et al. (1991) estimated the r_m to be $\underline{r} = 0.45$ ($\lambda = 1.56$) for the Canonto Study area in south eastern Ontario. Here he also observed a r_{max} of over $\lambda = 1.6$. Like moose, the ability of white-tailed deer to conceive twins at low population densities, allows for a r_m much higher than predicted by body weight.

By comparison, the r_m of deer populations at Elk Island following introduction, was very low. For example, the mule deer population over the ten-year period from 1908-18, increased from 35 to 111, which was an $\underline{r}$ of only 0.12. White-tailed deer in the Main Park increased from 30 - 110 over the six-year period from 1954-60 at an $\underline{r}$ of 0.22. Although almost double that of the preceding mule deer population, the r_m over this initial period is less than half that of the George Deer Reserve. Even the best period of population growth (1952-62 in the main park) with an $\underline{r} = 0.27$ ($\lambda = 1.31$) is well below that of other reported r_m for deer. By contrast, observed rates of increase for deer at Elk Island during some years are extremely high when compared to the previously mentioned populations but, probably do not represent a true r_{max}. Increases resulting in more than doubling of the population over one year ($\lambda = 2.89$ in 1959, 2.4 in 1970, and 2.5 in 1986), suggest that immigration contributes to the population. This probably obscures evidence of the r_m or r_{max} that may exist in this unmanaged population.

Trends in the Rates of Increase - The rate of increase of a population usually fluctuates around a mean of zero (Caughley and Sinclair 1994). If this were not true all unmanaged populations would eventually be either extinct or interminably large. Of course nothing in nature dictates that rates of increase should be symmetric at all temporal scales. At Elk Island, the ungulate populations have each maintained a similar positive mean rate of increase. In the Main Park before 1985, the mean rate of increase remained stationary for moose and bison at λ = 1.20. The mean rate of increase (λ = 1.21) for white-tailed deer was also stationary, but was significantly higher than the (λ = 1.04) for mule deer that had preceded them. The mean rate of increase for elk (λ = 1.19) was not stationary, due mainly to an abrupt and permanent increase after 1940. This trend was described by a fifth order polynomial.

Despite the trend in the elk population rate of increase prior to 1985, the mean for the entire period remained consistent for each species. In fact when one includes the data from the most recent period of adaptive experimental management, the mean rate of increase is exactly the same for all four ungulate populations in the Main Park (λ = 1.19). This resulted from somewhat reduced rates of increase in the moose, bison, and white-tailed deer populations and stationarity in the average rate of increase in the elk. This was consistent with the ARIMA models which had forecast slightly lower stationary mean rates of increase for bison and white-tailed deer. In particular the ARIMA model for elk had held that differencing was not required, predicting a stationary mean λ of 1.19.

The Isolation Area showed greater intra and interspecific differences in mean λ. Wood bison and moose were on average higher than the Main Park. However, given the shorter period of record and the greater observed variability about the observed rates of increase, there was no significant difference. The shorter record in the Isolation Area also does not allow for valid detection or analysis of long-term trends.

The positive mean λ for the entire history of the Main Park can be explained by ungulate populations that were, for much of their early history, increasing from low numbers following introduction to the park. After that they were usually kept at population numbers where animals were in good condition. When populations reached the point where declines occurred, management programs were invoked to reduce the populations. These actions in part caused the return to low densities where population increases would again occur. The mean positive λ that resulted is not surprising but the similarity of λ for each species is. Given the different biology, population dynamics, and management strategies of each species, the mean λ would be expected to be different. Perhaps this suggests that despite differing biology all the ungulate species may be able to obtain similar positive rates of productivity in this ecosystem. In the pristine system this increase, which at Elk Island has been removed by management, would be removed by other forces resulting in the expected stable population.

Periodicity in the Rates of Increase.-- Few ungulate populations have been studied by spectral analysis, leaving authors to speculate as to the prevalence of population cycles. At Elk Island, periodic oscillations in the rates of increase were found in each of the ungulate populations except deer. The existence of cycles at more than one frequency was also found for both bison and elk. Spectral analyses of moose, elk, bison and deer population dynamics are particularly rare, but those studies reveal surprisingly similar periodicity in different ecosystems.

The elk population in the Main Park was dominated by a periodic component of 10 years with a minor peak at 2.4 years. This is identical to the results of Sauer and Boyce (1979) who studied the temporal periodicity of annual winter counts of elk on the National Elk Refuge in Jackson Hole, Wyoming. They presented evidence suggesting this periodicity was not correlated with artificial feeding, harvest or climate. It was instead a function of vegetation-herbivore dynamics as proposed by Caughley (1976). At RMNP the elk population reached peak densities in 1990, 1980, 1969, 1959 and 1947. This also represents approximately 10 year intervals (Briscoe et al 1979, Tarlton 1992). Unfortunately these data are incomplete thus not allowing for spectral analysis.

The Elk Island moose populations showed periodicity of 15.6 - 18 years (main park) and 13 - 11 years (Isolation area). The frequency was lower than elk but the Main Park periodicity was the same as reported for moose in Isle Royale (McLaren and Peterson 1995). The similar dynamics of these moose populations is also evident upon visual inspection (Fig. 31). As in the case of elk, it is interesting that two populations of the same species inhabiting different ecosystems with different management histories, climate and rates of predation should exhibit such similar periodicity. At Isle Royale the common harmonic pattern of 16 - 18 years in both browsing suppressed tree-ring chronologies and moose was cited as evidence of top-down control in a trophic system.

The dominant low frequency periodicity of the Elk Island plains bison population (13 years) was intermediate to that of moose and elk. A review of the literature failed to find an example of spectral analysis of a bison population for comparison with Elk Island. The minor high frequency periodicity of two years in both the plains and wood bison at Elk Island was similar to that of Elk. Halloran (1968) concluded that calving rates of bison in Wichita Mountains Wildlife Refuge, were influenced by a tendency of individual females to produce calves in alternate years. He attributed this pattern to the superior condition of non-lactating females. Studies by Shaw and Carter (1989) of the same herd during a latter period of low densities failed to detect such a pattern. They suggested that the nutritional stress imposed at high population densities may explain the calving pattern that Halloran (1968) observed. At Elk Island the calving success of individual cows is not known but this may offer an explanation for the higher frequency periodicity in bison and elk.

The consistent periodicity displayed by the ungulate populations at Elk Island and the same species in other ecosystems may depend on how they respond to resource availability. A basic mechanism generating cycles can be a series of repeated time delays. If the cycle is characterized by a series of time delays all of approximately the same duration, then the total length of the cycle should be four times the length of the time delay (Begon et al. 1990). At Elk Island, time lags in the demographic response to density were found in each of populations where periodicity was detected, but the frequency of periodicity did not correspond in this manor to the length of the delay.

Logistic population models incorporating delayed density-dependence suggest that dynamic behaviour of populations depend on the r_{max} or 'resilience' and the lag time (T) of demographic response to resource availability (May 1973). If r_{max} T is >0 and r_{max} T is <0.37, then populations should monotonically approach a stable point. If r_{max} T is >0.37 and r_{max} T is <1.57, then populations should show damped oscillations as it approaches a stable point. If r_{max} T is >1.57, then the population should exhibit a stable limit cycle. On this basis the elk population (r_{max} T = 0.8-1.0) should display a clear cyclical pattern gradually decreasing in amplitude and frequency as it approaches a stable point The bison population (r_{max} T = 0.39) predicts that it should show damped fluctuations, but this value is very close to that of a monotonical approach to a stable point. For moose the r_{max} T = 1.5 - 1.67 predicts that the population dynamics should be characterized by a stable limit cycle. The actual periodicity displayed by the ungulate populations at Elk Island does not strictly follow the predicted patterns of periodicity but is not inconsistent with them. It is likely that this is due to a variety of density independent forces such as climate, plant production, and population management. The latter may be particularly important in its effect on population periodicity in that cycles may reflect the response time of managers to perceived overabundance.

The Relationship of Density and Rate of Increase

The ungulate populations of Elk Island provide evidence of both delayed and direct density-dependent population change. The form of the functional relationship between per capita and per unit area rates of increase and density provide empirical data for comparison with conceptual models of density-dependence.

It has been postulated that at very low densities, a positive relationship between per capita population growth rate and population size could occur; i.e., inverse density-dependence (Allee 1931). This could be caused by difficulties finding mates, difficulty fending off competition or predators, social/physiological facilitation, or low density consequent to habitat fragmentation resulting in high juvenile mortality during dispersal (Boyce 1992). It could also occur because a critical number may be required before a resource can be properly exploited (Begon et al. 1990). The consequences of Allee effects are important because they may create a threshold or critical density below which populations may grow very slowly or perhaps become extinct. The generality of this phenomenon are not well-known due to a lack of empirical evidence. As a result it is rarely incorporated in conceptual models of density-dependent population growth.

Data from Elk Island suggest that Allee effects commonly occur in moose, bison and elk and that this critical density is much higher than expected. Plains bison achieved a maximum per capita rate of increase at a population size of approximately 500 (0.05/ha). Throughout the record the highest calving rates were also displayed at the same population size or density (Fig. 32). This suggests that factors affecting fecundity or calf survival are largely responsible for reduced population growth at low numbers. Although the Elk Island plains bison population has a similar initial trajectory of population growth to that of others, a critical density has not been reported for other populations. If such a high critical number or density could be generalized for bison it would not be inconsistent with their social organization. It would also offer a factor contributing to the near extinction of this species in the late 1880's.

Compared to the bison population, the critical density for moose at Elk Island is much lower (0.01-

0.02/ha). At populations below this density the per capita rate of increase was quite low rapidly increasing when densities reached this critical density. This resulted in a very unusual functional relationship describing rate of increase per unit area versus density, below MSY (Fig. 8). Nygren's (1983) data for moose in Finland also showed nonlinearity in reproductive rates including a reduced rate at the lowest populatio [illegible] ities. It is perhaps this critical density [illegible] prevent many moose populations from obtaining the densities seen at Elk Island. Especially those reported to be predator limited at low densities (Gasaway et al. 1992). Similarly, elk populations also exhibited this relationship between per capita rate of increase and density. The wide variation in per capita rates of increase from 1960-84 resulted from population management that frequently reduced the population to numbers just below the critical density (Fig.25).

The Allee effect results in per capita population growth rates that strongly deviate from linearity at low densities. Per capita rates of population growth thus increase from the lowest density, but as density is further increased the per capita growth rate begins to decline. The rate of population change per unit area in relation to density is thus characterized by marginal production until the critical density is reached. After this, population growth per unit area increases at an increasing rate to the point of MSY. As the population density increases still further from MSY toward K, the rate of growth declines at an increasing rate until reaching K. It is this exponential increase in population growth between the critical density and MSY that contributes to the outstanding productivity Elk Islands ungulates are noted for.

Most species with low reproductive rates, long life-spans and populations limited by resources tend to be most productive (MSY) at densities close to ecological carrying capacity (K). These are known as K-selected species. In resource limited populations K-selection increases the efficiency of resource utilization. Those species with high reproductive rates, short life spans and populations held below the limits of resources are most productive at densities below 0.5 of K. These r-selected species maximize resource use to enhance fitness through increased reproduction or growth. Ungulates are generally believed to fall within the category of K-selected species (Fowler 1981). At Elk Island the ungulate populations have shown both types of density-dependent responses. The expected nonlinear density-dependent response was displayed by bison throughout the period. This is consistent with the life history of bison which have a large body size, relatively low rate of reproduction in that two-year olds do not frequently calve, twining is rare and that historically bison are reported to have been found in large numbers presumably close to K. In Elk Island the moose population displayed linear rates of density-dependent increase such that MSY was approximately 0.5 of K during two of the four periods of population increase. The ability of moose to twin and reproduce at a younger age than bison offer life history explanations for such a response. This ability to display an r-selected density-dependent response is also not inconsistent with the ecology of moose. Elk have also shown both types of density-dependent response however, unlike moose the nonlinear alteration of the rate of increase has increased through time. As a result MSY was close to 0.5 of K from 1906-22 whereas more recently MSY has increased to 0.7 of K. This change is consistent with the general trend in the rate of increase previously mentioned.

Like the form of the density-dependent response, the range of densities at which MSY and K occurred was different for bison, elk and moose at Elk Island. Plains bison MSY occurred at the highest densities (0.07 - 0.14/ha, 31.5 - 63 kg/ha) followed closely by Elk (0.06 - 0.08/ha, 14.5 - 19.4). Moose MSY density was much lower at (0.021 - 0.028/ha, 6.5 - 8.7 kg/ha). The range of K densities followed the same relative order with Bison K occurring at the highest density (0.10 - 0.18/ha, 45.0 - 81.0 kg/ha), followed by elk (0.085 - 0.15/ha, 20.6 - 36.3 kg/ha) and moose (0.033 - 0.053, 10.2 - 16.4 kg/ha). In the Isolation Area, the relative MSY and K densities for each species was similar but marginally lower than the Main Park. It is interesting that K for moose occurs at the same density as MSY for elk and the K for elk is similar to the MSY density for bison. Thus at a density of 0.05/ha the moose population would be expected to be stable or declining while at the same density elk would be increasing at the greatest rate per unit area. Similarly at a density of 0.14/ha the elk population would be expected to be stable or declining while at the same density bison would be increasing at its highest rate per unit area. These densities describe relative carrying capacities consistent with the observed biomass densities for Elk Island and proposed historic abundance mentioned previously.

Despite many studies of MSY and K for ungulates, comparisons with Elk Island must be viewed with caution because of differing assumptions or methods used for analysis, reliance upon extrapolations from limited data, or a failure to consider lagged density-dependence. For example, Fredin (1984) analyzed the NBR bison population by fitting a curve to moving averages. By this method he reported linear density-dependence with MSY of 0.5K. Also assuming a linear relationship, Eberhardt (1987) fit various models to these data and reported an MSY of 860 and K of 1720. Fowler (1981), using a different method, reported this population as an example of nonlinear density-dependence with MSY being greater than 0.5K. Assuming the area available for bison in the NBR as reported by Malcolm (1987) and estimates by Eberhardt (1987), one can derive an MSY density of 0.11/ha and K of 0.23/ha. The MSY value falls in the middle of the range of MSY densities for Elk Island. The K value of 0.23/ha is higher than Elk Island but this can be attributed to the extrapolation of K from an assumption of linear density-dependence. Custer State Park, S. Dakota, maintains a very productive bison population at densities of 0.09 - 0.14/ha (Walker 1987). However, most reported bison densities and carrying capacity estimates based on other criteria are much lower. For example, the population in Wind Cave N. P., South Dakota, is currently managed at a density of 0.04/ha with a carrying capacity (criteria unknown) of 0.098/ha (Bone, 1987). Similarly the National Refuge at Fort Niobrara, Nebraska maintains a bison herd at densities of 0.04/ha.

Several moose populations have been described with respect to MSY and K population densities (Crete et al. 1981, Messier and Crete 1984, Bergerud and Snider 1988, Crete 1989, and Gasaway et al. 1992). Unfortunately these well-understood populations are predator-limited. In eastern Quebec Crete (1989) concluded that K exceeded 0.02/ha with MSY approximately 0.5 of K. This linear density-dependence is consistent with that reported for Elk Island. Prior to this he modeled moose populations in southwestern Quebec describing a moose population that followed a logistic growth function with MSY density of approximately 0.6 K (Crete et al. 1981). Here K density was much lower ranging from 0.003 - 0.006 depending upon the method of statistical analysis. Other predator limited moose populations with similar low MSY and K densities have been described for Ontario and Alaska (Bergerud and Snider 1988, Gasaway et al. 1992). These MSY and K densities are more than tenfold lower than observed for Elk Island were wolves and bears are not present.

Many elk populations have been studied with respect to carrying capacity for the purposes of population management but only a few have been characterized in sufficient detail to provide comparison with Elk Island. The northern Yellowstone elk population has been studied by several authors and provides over 50 years of demographic records from which to assess K and MSY (Houston 1982, Eberhardt 1987, and Merrill et al. 1988). Despite this extensive record the form of density-dependent population growth described for this population depends largely upon analytical assumptions. Houston (1982) used the pattern of population growth from 1968-76, when hunter harvest was low, to project a K of approximately 15,000 (0.15/ha). Unfortunately heavy hunter harvest in 1976 obliterated the nature of the growth curve as K was approached. Eberhardt (1987) suggested that the logistic model was unrealistic and fit a strongly concave model which resulted in a lower K. In the years that followed, the elk population exceeded the value of K predicted by Houston (1982). Merrill et al. (1988) suggested that the population continued to grow because of mild winters, and overshot long-term average K. Because of this they argued that the population would oscillate with decreasing amplitude while converging toward K. They recommended a logistic model (K = 15,000) contrary to that expected by Fowler (1987) for large mammals. This K is the same as that shown by the Elk Island population from 1923-40 and the suggested logistic model is also similar to that describing Elk Island's population during this period.

Another elk population with sufficient data for comparison is that of the Jackson elk herd. Here Boyce (1989), using the Gilpin and Ayala (1973) model, assumed per capita population growth to be a concave function of population size. As a result he estimated MSY to be 0.65K for the Grand Teton National Park and 0.74K for the National Elk Refuge components of the population. In both instances he noted that there was perhaps inadequate empirical data describing the populations at K. The combined population was also described by the same model but did not provide a very convincing plot as significant variance was noted. Nevertheless, MSY was estimated as 0.71K with K being approximately 14,000(0.23/ha). The K value for this population was higher than Elk Island or the northern Yellowstone but the nonlinear alteration of MSY is similar to the present form of density-dependence at Elk Island. Again the comparison with Elk Island must be cautioned in that the density-dependent form of the rate of per capita growth of the Jackson herd is based on fitting a particular model.

Density-dependence was not detected in deer populations of Elk Island. Thus, MSY and K densities were not characterized. This is unfortunate in that density-dependent deer population dynamics are well understood in other areas and would have provided good comparisons (McCullough 1983). It is likely that deer in the park represent part of a greater regional population as deer can move freely in and out of the park. This is reflected in the general increase of deer numbers, in both the Main Park and the County of Strathcona, from 1983-93 (Rippen 1994). Given this, it is not surprising that density-dependence was not detected through an analysis of the Elk Island National park surveys.

The form of the curves describing Elk Island's ungulate populations are simple plots of empirical data after smoothing and compensation for delayed density-dependence. The Elk Island data are, thus, not subject to assumptions that force the fitting of the data to a predetermined functional relationship. This is true for all the populations including bison, moose and elk. As a result the data at Elk Island portray different density-dependent relationships for different periods and populations, each free from a priori assumptions. It suggests that MSY and K equilibria should not be considered as points defining a curve but rather a region of attraction capable of shifting in relation to other forces. This is consistent with chaos theory and the suggestions of authors like Merrill et al (1988) who necessarily invoke vegetation productivity and climate as important forces influencing the realized shape of a potential density-dependence curve. The lack of sufficient data for populations at K also hamper current methods of validating estimated K values for bison, elk and moose in most areas. All of this suggests the need for researchers to evaluate density-dependence by treating the time series data with appropriate filters and delays then producing a plot free of assumptions as has been done for Elk Island.

Interspecific Population Interactions

Intraspecific density-dependence is evident for the moose, elk and bison populations at Elk Island. The populations of each of these species do not function in isolation but as members of a grazing guild. As such, interspecific competition or facilitation could be expected with the results of such interactions being evident in the dynamics of each species or the entire guild. Caughley and Sinclair (1994) state that long-term studies are now showing that species densities vary in the same habitat and they also change over a longer time scale measured in years. Thus populations may go through periods when there are abundant resources and, although there is overlap with other species even at supposedly difficult times of year, the species coexist. Occasionally there are periods of resource restriction and it is only at these times that one sees competition (Weins 1977). This interspecific competition could, at these times, affect the numerical or spatial dynamics of a population. McCullough (1990), in describing the nature of interspecific competition and its effects on population dynamics, proposed that social dominance with environmental heterogeneity could influence the shape of the function of density-dependent rates of increase. Like Weins (1977), he concludes that apparent density independence would be seen up to the threshold of carrying capacity based upon the number of homogeneous habitats that could be fitted into an area. For the parkland grazing guild, this type of density-dependent response between species is suggested by the population dynamics described here and previous ecological studies conducted at Elk Island.

Studies suggest that at Elk Island, moose, elk, bison and deer overlapped significantly in habitat use and winter food habits (Telfer and Cairns 1979, Cairns and Telfer 1980, Telfer and Cairns 1983). These studies also showed that spatial partitioning of the fine grained highly interspersed habitat allowed for high densities of the 'sympatric' ungulate species to coexist in Elk Island. Given such spatial partitioning one would expect density-dependent interspecific population interactions to occur near K as suggested by Weins (1977) and McCollough (1992). Evidence for this was found in cross-correlation that failed to detect an ongoing relationship between population rates of increase and density of the combinations of species comprising the grazing guild. However, analysis of discrete periods (when populations were at or near K) revealed that the MSY and K densities changed for moose during periods of high elk numbers. Thus, high elk numbers can be correlated with linear alteration of moose density-dependence by their reduction of K to a density closer to MSY. The effects of this were evident in the magnitude of population change of the Isolation Area moose population when elk were virtually absent and the recent stability of the moose populations concurrent with high elk numbers. Blood (1974), investigating female moose slaughtered between 1959 and 1974, suggested that reproductive performance of moose decreased because of high combined moose and elk densities.

Although bison can obtain concurrently higher K densities than elk, the interspecific effect of bison upon elk K is less clear. During all but the most recent period, bison and elk numbers have approached K concurrently. Only during the most recent period have elk numbers increased toward K while bison populations have been held below K. Several more years of data must be collected before evidence of a higher elk K with lower bison numbers can be confirmed. If such an interspecific population interaction does occur between all the species of the grazing guild it would be expected that the K densities of each species would be influenced by their social dominance hierarchy. McHugh (1958) placed bison at the top of the interspecific dominance hierarchy followed by elk, deer, and moose. This is consistent with the relative K densities observed for these species at Elk Island.

Vegetation - Ungulate Interactions

At Elk Island high ungulate population densities, significant population reductions caused by management and vegetation community change are well documented suggesting the existence of multiple stable states in the aspen parkland ecosystem. The idea of equilibrium vegetation communities that progress steadily toward or away from a climax state depending on grazing pressure by ungulate populations seems not to apply in many ecosystems (Archer and Smeims 1991). Multiple stable states, thresholds, and discontinuous or sometimes irreversible transitions are more common than once thought. Often groups of plants or vegetation assemblages have been displaced by another because of altered climate-grazing-fire interactions that may then persist for long periods. Occasionally, increases in ungulate populations and associated elevated amounts of herbivory have caused abrupt, nonlinear development of woody plant communities in areas formerly dominated by grasses (Archer et al. 1988). Alternatively, elevated amounts of herbivory have changed woodland vegetation to tall grass (Field and Ross 1976). In other instances, reductions of ungulate populations to low numbers have resulted in replacement of grasslands with woody plant communities (Sinclair 1979). In many of these instances the new vegetation provides a different amount of available forage resources causing the ungulate population to function at a new density. Evidence of this latter case is presented for Elk Island. Here, reductions in ungulate numbers preceded replacement of grasslands with aspen forest that in turn altered ungulate population dynamics.

The changes in vegetation cover at Elk Island were documented by analysis of air photography by Blyth and Hudson (1987) (Fig. 3). They found that in 1923, the north end of the Main Park was 23% grassland while the south was 50% grassland. At the time of peak ungulate numbers in the mid 1930's, range condition was judged as heavily overgrazed (Strickland 1938). Browsing was reported to be preventing aspen regeneration from replacing older trees (Hadwen 1939). Ungulate population biomass was subsequently reduced by almost two-thirds (Fig. 29). Measurements of forest stand age show that, following this population reduction, much of the park grassland was replaced by aspen forest (Telfer 1974, Schultz 1992). As a result, much of today's aspen forest originates in the late 1930's and early 1940's immediately after these population reductions. It is likely that the heavy grazing of the late 1930's, preconditioned grasslands to allow the establishment of woody species. The major ungulate population reductions that followed then allowed young regeneration to grow to mature trees and allowed aspen groves in the grasslands to expand. This is confirmed by historical accounts of the range condition at the time (Banfield 1946). Blyth and Hudson (1987) record that by 1950, only 8% of the north and 21% of the south area of the Main Park now remained in grassland. They also noted that much of the park previously recorded as open aspen groveland was now covered by closed forest. By the late 1950's, the grasslands that were left were now reported as overgrazed despite the lower ungulate populations. A major population reduction program again followed. Flook (1970) described aspen regeneration previously suppressed by heavy use by elk and moose, as responding to the reduction in browsing pressure with a marked increase in height. He also noted that from 1960-66 aspen forest continued to encroach on grassland openings. This was confirmed by Blyth and Hudson (1987) who found less than 8% of the south area of the Main Park covered in grassland by 1972. Forest age measurements also show many forest stands also originated in this period. Today many grassland areas remaining are still recorded as only in fair condition (Stromsmoe 1993, Osco 1994). Exclosure plots of some areas suggest that despite exclusion from grazing for more than thirty years the grass composition has remained the same (Blyth et al. 1994). Browse surveys of the shrub layer conducted from 1983-94, indicated that the shrub layer has remained stable despite the increasing ungulate numbers. Encroachment of forest on the remaining grasslands since the late 1960's has been arrested. The current vegetation ungulate regime has again reached a new stable state.

Ungulate population dynamics have also been influenced by the changing vegetation assemblages. Analysis of bison carrying capacity has shown that K densities are related to the proportion of grasslands available in the park (Fig. 20). Holsworth (1959) noted that heavy moose and elk browsing on deciduous regeneration (Populus spp., Salix spp. and Corylus spp.) arrested forest succession and maintained grassy openings, which provided forage for bison. Elk productivity experienced a permanent and abrupt increase following the change in forest cover after the late 1930's. It is also possible that the general upward trend in elk r may also be associated with vegetation change. Concurrent with the reduction of grasslands in the late 1950's, white-tailed deer completely displaced mule deer from the park. It is not likely that this change in vegetation was solely responsible for this shift, as white-tailed deer were displacing mule deer throughout the region. It was probably a significant factor as mule deer are still found today in open grassland areas next to the park. Moose population dynamics do not appear to have been influenced by vegetation changes but, by other factors as previously discussed. It is likely that much of the important moose habitat has remained stable as many boreal wetland vegetation communities changed little because of ungulate population management.

It appears large artificial reductions of ungulate numbers by management rather than having the desired effect of reducing grazing pressure on grass species instead resulted in a new equilibrium condition. In this new condition, many grasslands are replaced by forest with those grasslands remaining still being grazed at intensities similar to that which occurred before the population reductions. It points towards the idea of multiple stable thresholds as a valid concept by which to evaluate ecological integrity of the ecosystem. The vegetation changes seen this century at Elk Island suggested that the reductions of bison, elk and deer populations in the 1800's may have caused the expansion of aspen groves in the aspen parkland. This may have resulted in the forests cleared and burned by settlement in the late 1800's. This correlation of bison extirpation with aspen expansion throughout western Canada was confirmed by analysis of pollen assemblages by (Campbell et al. 1994) At Elk Island, evidence of aspen dominance in the recent pollen record was also found (Vance 1979). Elk Island now carries out a prescribed fire program to restore much of the original vegetation and plant species diversity of the park. The resulting vegetation and ungulate numbers may present a remnant of the once vast ecosystem no longer in operation in any other area of Canada.

Grazing System

Grazing systems are management tools designed to influence ungulate production over time by changing the quality or quantity of forage produced and/or consumed. Vegetation production improves if the benefits of rest or deferment exceed the detrimental effects of grazing. Whatever the effects of a grazing system on the vegetation complex, its effects on ungulate production vary depending upon the direct effects on the ratio of forage demand/forage availability. A conceptual model of the theoretical ongoing effects of animal density on productivity in various year-long grazing systems was constructed by Heitschmidt and Taylor (1991). In this model the highest K density is realized by short duration grazing followed by continuous grazing (CG), deferred rotation (DR), rest rotation (RR) and finally high intensity low frequency grazing (HILF). The MSY density is approximately the same for SD and CG followed by DR, RR and HILF. The highest production per unit area theoretically occurs in the CG followed by DR, SD, RR and HILF. Although not strictly applicable to natural unmanaged ecosystems the principle that frequency and timing of vegetation removal influences ungulate carrying capacity is relevant to an understanding of density-dependent productivity. In the pristine ecosystem bison were observed in the summer in large herds moving over vast areas of the great plains. Their use pattern could be considered a high intensity-low frequency grazing system. In winter they returned to the aspen parkland where they remained relatively sedentary in herds of smaller size. This could be considered a seasonal rest rotation grazing system. The other ungulates in the aspen parkland namely moose, elk and deer were recorded as year-round residents with little evidence of seasonal migration. With this being the case, a continuous grazing systems model would perhaps best apply. It is possible however that although these ungulates had year-round access to grazing they may have or may still naturally use forage resources in another spatial temporal pattern. It is possible to imagine that bison during the winter, or elk on a year round basis, may use a particular grassland meadow for a short period then move on to another before returning, thus following an SD grazing system. This is unlikely given the importance of spatial partitioning previously discussed and high density of ungulates in the pristine aspen parkland or at Elk Island today. It is more likely that seasonal use of various forage communities, such as sedge meadows during the winter, could occur but this would still be a continuously grazed system.

The consideration of grazing system management is relevant for Elk Island in that the park is fenced and that bison are moved into winter pastures for handling purposes where they remain for the winter. They are essentially being managed in a seasonal, rest rotation grazing system. The other ungulates remain year-round in the park and without research showing otherwise must be considered as managed in a continuous grazing system. Contrary to the general model, the influences of an RR grazing system was not observed in the productivity of the ungulates at Elk Island. It is interesting that the productivity model for the SD grazing system is similar to that seen for moose and elk during some periods Instead it appears that the major benefit from the employment of the grazing system at Elk Island is related to the indirect moderation of stocking rates during the critical winter period. The ungulates in the Main Park benefit from the decreasing stocking rate of bison in the park during the winter while the bison benefit from the setting aside of a winter range with an abundant available forage. This is consistent with Heitschmidt and Taylor (1991) who note that the functional aspects of each grazing system centre around high production or high use tactics. The major factor influencing this is stocking rate in that high rates of stocking insure that high use grazing tactics are employed rather than high production grazing whatever the type of system. From this one can speculate that today's ungulate carrying capacity for the park would be different from the pristine grazing system. The current RR system at Elk Island is the reverse of the historic pattern where bison used the parkland in the winter. In this historic setting bison would have increased the stocking density during winter increasing the dormant season grazing pressure. During the summer, grazing pressure would have been reduced as they moved out to the great plains. In mild winters bison were also documented to have stayed out on the prairies to the south. This historic pattern would probably result in the effects of an RR system. Despite the alteration to the natural grazing system, relative benefits to ungulate production are likely to vary greatly over time and space thereby making it difficult to make conclusions regarding relative merits.

The influence of system size upon the dynamics of the Elk Island ungulate population is important. Because r at low densities is related to the physiological capability of the species, a population in a small system will reach the K density over a shorter period. The result is that plant species have a shorter period to adjust to increasing ungulate numbers. In addition delayed density-dependence could result in populations over K before population decline begins. This is seen in the moose population dynamics at Elk Island where the amplitude and frequency of the moose population cycle are increased in the smaller Isolation Area. The effect of system size is unclear for the other species.

The fence surrounding the two sections of the park is also an important influence on the population dynamics of the park ungulate populations. Deer populations, which freely move across the fence, exhibit complex apparently random population fluctuations around a trend similar to the populations of the greater region outside the park. Some moose and elk can breach the fence occasionally, whereas the bison populations are completely prevented from leaving the park. These park ungulate populations can thus be considered as distinct populations as would be seen in an Island setting such as Isle Royale. The similarities of the moose populations in Elk Island and Isle Royale attest to this. The degree to which this perimeter fence influences the population dynamics of moose and elk was tested for a limited period in the Isolation Area with the installation of jump ils in the fence. This allowed free passage by moose and elk into the Blackfoot grazing reserve. This gave the moose and elk populations of the Isolation Area access to a total area the size of the Main Park (the Blackfoot area itself being surrounded by a fence similar to Elk Island). During this time it appeared that the population dynamics of both moose and elk followed similar patterns to the Main Park that did not have jumprails. Unfortunately this test could not be conducted for a longer period to eliminate other factors as possible causes. The closure of the jumprails and resulting higher apparent K and MSY densities hints toward the effect of system size. It may also suggest that the general ungulate population densities are not as unnaturally high as one might expect given that the animals did not leave the park into the sparsely populated Blackfoot area at lower densities. The observations of the last five years suggest that further testing of this is now required to make firm conclusions.

Parasites and Diseases

The winter tick, has been associated with major die-offs of the moose population at Elk Island and other areas (Samuel 1978). This associated mortality suggests that the winter tick may, either by itself or in concert with other factors, exert a significant influence on moose population dynamics at Elk Island. From the anecdotal information reviewed in park files by Blyth and Hudson (1987), the population dynamics reported in this study and research by authors such as Samuel and Welch (1991), I propose the following interaction of the winter tick and the population dynamics of its primary host. At low densities, moose at Elk Island appear in good condition due to abundant resources with most individuals having low tick numbers. In this state, the moose population can increase rapidly. During this initial phase the numbers of ticks per moose remains low because the number of host moose the year before is much lower than the current year owing to rapid population increase from low densities. As the moose reach higher densities they now saturate the environment with ticks to be picked up the next year. The moose at these high densities also now experience a decline in condition due to both forage limitations and high tick numbers. The rate of population increase is now effected by the declining condition of the individuals comprising the population. At this point park managers observing the condition of the moose usually invoked slaughter operations to decrease their numbers. Besides this, many moose in poor condition, but not shot, also die. The ticks deposited in the environment the year before by the higher population continue to allow for significant infestation the next year. This period of declining moose numbers associated with tick related alopecia usually lasted two-three years. After this decline, the moose population now again consists of individuals in good condition due to abundant forage resource and low tick numbers due to low host moose density. This pattern can be fit to all the periods of moose population increase and decline seen at Elk Island. Recently, moose population slaughters have not been conducted so that moose population dynamics have been moderated. Tick associated alopecia and concurrent moose population declines have, however, continued albeit with decreased magnitude and higher frequency.

This relationship of moose and winter ticks has also been reported for Isle Royale (Peterson 1991). After reaching almost 1,700 moose in 1988 the population of Isle Royale decreased by some 25% because of high mortality, largely caused by winter ticks. Peterson (1991) speculated that the winter tick may compensate, in some respects at least, for the reduced presence of wolves during these years. This would be consistent with the close associations that moose numbers and ticks appear to exhibit at Elk Island. He also noted that winter ticks can be very influential, but their populations may be driven by weather patterns that are largely unpredictable. This effect of weather was documented by Drew and Samuel (1985) as an important factor influencing the success of tick infestation of moose. Despite this, it appears that at Elk Island, ticks have reached high densities on moose following all major periods of moose increase. This shows that, although important, weather conditions have not been capable of preventing large tick outbreaks. If the winter tick can influence moose condition and contribute to mortality then ticks should be considered as an important determinant of the form of density-dependence at Elk Island.

The effect of brucellosis on bison population productivity is not well documented. Fuller (1966) speculated that the low pregnancy rates in bison at Wood Buffalo National Park was related to the incidence of brucellosis. In Yellowstone National Park, Meagher (1973) found that pregnancy rates of bison were not influenced by the incidence of brucellosis. At Elk Island, I found lower cow calf ratios during the period when brucellosis was prevalent (1947-66) as compared to the period after elimination of the disease (Fig. 13). However, the female-dominated sex ratio during the brucellosis infection period and density-dependent productivity obscured any effect on herd productivity. It can also be argued that the improved cow/calf ratios observed after brucellosis elimination was a result of lowered bison density, and a younger age structure caused by the population reductions carried out to eliminate the disease. This disease, despite being known to affect reproduction in other species, does not appear to have had a significant effect on the bison population dynamics at Elk Island.

Climate and Weather

Noise or unpredictable variation in ungulate population dynamics has been attributed to various factors including, climate, management, and disease. Of these factors, climate or weather has long been considered one of the most obvious with ample data available to characterize it's influence. In particular, the general severities of winters or winter climate events have been associated with unusually high rates of mortality and occasionally subsequent low fecundity of ungulate populations in northern mid latitude continental climates. This association of severe winter weather and ungulate population declines has led to several studies designed to develop indices of winter severity to predict ungulate population declines (Verme 1968, Sauer and Boyce 1983 and Picton 1984). At Elk Island, following the much publicized winter weather related mortality of several elk in the early 1970's, similar research was also conducted (Cairns 1974, Van Camp 1975). The basic theory behind these studies suggested that winter severity had its greatest influence on a population when the population is at or near K (Picton 1984). It was also suggested that, in the environmental context at Elk Island, severe winters are primarily characterized by snow depth and density as they influence the availability of forage resources.

At Elk Island, single years of poor productivity causing noise in otherwise consistently productive periods were observed. Most notably, the years 1943, 1948, 1956 and 1974 displayed these unexpected low rates of population increase. In these years, warm winter weather and total snowfall over 180 cm showed that snow density and depth could have been responsible for limiting the availability of forage resources thus causing mortality and a decline in productivity. In 1965, snowfall over 220 cm was recorded. That year both elk and bison populations actually declined during a period of otherwise excellent ungulate population growth. Other winters with similar snow depth and temperatures (1907, 1920, 1935-36 and 1983 were also recorded as severe and caused significant mortality of ungulates, but failed to show a significant deviation from expected rates of increase as predicted by density-dependence. Excepting 1935-36, these were years of low population density. The correlation of winter severity and population dynamics at Elk Island appear to confirm the suggestion that winter severity can cause random short term deviation of ungulate population dynamics when populations are close to K. The rarity of these climatic conditions (approximately 13% of the years) and resulting population declines also supports the speculation that the aspen parkland and in particular the Beaver Hills was favored winter ungulate habitat.

MANAGEMENT IMPLICATIONS

In most Canadian national parks, ungulate populations are managed simply by protection from poaching or highway-related mortality. Since animals can disperse into the surrounding lands where populations are often hunted, most national parks are never forced to consider carrying capacity and regulate animal populations accordingly. This is not true at Elk Island. The absence of effective predators and dispersal mechanisms creates new challenges for park managers. As the only fenced National Park in Canada and a highly productive ecosystem capable of rapid vegetation succession, Elk Island demands careful consideration of the question of carrying capacity in management planning. This is a vital step that can be ignored neither politically nor ecologically. "Carrying Capacity" is a complex idea without a uniformly accepted definition. MacNab (1985) concluded that; "rarely in the field of resources management has a term been so frequently used to the confusion of so many. Close (and related) rivals in perplexity include overpopulation, overharvesting, and overgrazing." Nowhere is this statement more true than in the management of national parks largely because of the variety of prior notions held by park staff drawn from varied disciplines. Further difficulty results from choosing between ecological objectives such as 'preserving ecosystems or environments essentially unaltered by man' or 'ecological integrity' and more anthropogenic objectives such as 'low ungulate mortality', 'ecosystem health' or 'presence of indicator plant species'. Although the former probably should be the mandated goal of a national park, many people fail to appreciate that populations may naturally stabilize at densities accompanied by considerable winter mortality and successional changes in vegetation. Both conditions are perceived as indicators of overpopulation and, by implication, of mismanagement. The unfortunate result is public pressure to feed or harvest. Besides the importance of this concept for management, long-term records of vegetation succession and ungulate populations at Elk Island provide a rare opportunity to learn about this all but vanished ecosystem. Continually evolving park management should in some respects be regarded as scientific experimentation that probes the dynamics of the parkland grazing system and allows some expectation of the consequences of future management.

Concepts of Carrying Capacity

Carrying capacity has a variety of names and meanings. In population ecology, it is defined as the density at which a population will stabilize if left alone. Roughly equivalent terms are 'ecological carrying capacity' (Ferrar et al. 1983), 'subsistence density' (Dasmann 1981), 'environmental carrying capacity' (Clark 1976), 'potential carrying capacity' (Riney 1982) and 'K carrying capacity' (McCullough 1979). Often such natural equilibria are unsatisfactory for many reasons so carrying capacity is redefined in terms of an appropriate goal such as maximum sustained yield or a corresponding economic optimum. Criteria also can be aesthetic or ecological such as animal densities that freeze plant succession, allow expression of certain plant communities, maximize plant diversity, or prevent appreciable winter starvation. With specific reference to Elk Island, target animal densities might be those that maintain or increase floral and faunal diversity, or reflect the historical character of the parkland.

The basic distinction is whether carrying capacity is viewed as a threshold, equilibrium, or target. This traces to the faith that managers place on the ability of populations to stabilize. Traditionally, it was believed that if populations were allowed to exceed some threshold, vegetation would drastically decline and populations would crash to extinction. This view has been largely displaced and will not be discussed further. Today, those such as Caughley (1970), offer hope that plants and animals generally do stabilize following perturbation and that we should not be alarmed by initial oscillations in plant and animal numbers. Others argue that grazing systems are now so highly fragmented and natural controls so modified, that stable equilibria simply are no longer possible. Thus, carrying capacity should be considered from the perspective of target populations.

Ecological equilibria are reached when the average rate of increase for both plants and herbivores is zero. Stabilization in this sense does not necessarily equate with a steady population number. There is often yearly variability caused by factors such as winter severity as noted at Elk Island. Populations of large ungulates may also momentarily overshoot ecological carrying capacity (Caughley 1970). This typically follows a pattern of dampened oscillations converging towards a stable point or, alternately, a stable 'limit cycle' as seen in the dynamics of Elk Island's moose populations.

Three important factors are commonly responsible for regulating herbivore populations: depletion of food, dispersal, and predation. The depletion of food resources results in lower fecundity, and higher rates of mortality as populations increase to a point where they exceed the available food supply. Birthrate and juvenile survival both decline as populations increase and deplete resources. With increasing age of reproductive maturity these factors result in lowered productivity. On the other hand, adult mortality increases as populations increase. In most ungulate populations, density-dependent changes in adult survival occur close to carrying capacity, as does the previously mentioned rates of reproduction.

The exact role that dispersal played in the pristine parkland ecosystem may never be known. Most likely, ungulates dispersed from local areas but resources would still ultimately have become the limiting factor. Today, the role of dispersal is highly altered, influencing the population dynamics of most wild populations in the aspen parkland. This occurs in two main ways. The first is that most populations can now disperse into surrounding areas that have artificially low numbers due to man. This serves to continuously drain away individuals from populations and thus reduce the equilibrium density below that of a pristine setting. In other instances like Elk Island, fences or other barriers reduce dispersal.

Predation is the third factor regulating ungulate populations. The impact of predators on prey populations is largely dependent on the size of the prey populations and predator effectiveness. Models and studies of the role of predators suggest that the availability of prey has a significant impact on predator populations. If the predator is efficient and alternative prey sources are available prey and predator populations may stabilize at a point where prey populations are high having little impact on the prey population or at a low population where predators may severely deplete the prey population. If the predator is ineffective then a stable point is only reached with high prey populations. In the pristine parkland the wolf and bear as effective predators probably existed at the higher stable point where they did not affect the absolute levels of prey population change. Today, the coyote exists at higher population numbers but does not affect the ungulate populations.

At Elk Island, all these factors are important because fences restrict dispersal of large ungulates and large predators such as wolves and bears no longer reside in the area. Despite the lack of predators and insularization imposed by the surrounding fence and land uses, an equilibrium population density may still be possible. Many examples of large ungulate populations being introduced to Islands and theoretical population models where food availability is the only regulating factor suggest that if left alone the large ungulate populations can eventually reach an equilibrium density. However, we do not know the critical system size at which this would fail to occur. In addition we may not wish to accept the loss of vegetation and faun[illegible]ersity that might o[illegible] local scale.

Grazing systems ofte[illegible]aged as 'production ecosystems'. Therefore, carrying capacity is used in a totally different sense; nam[illegible] the stocking density at which maximum animal production is achieved. Occasionally, where production costs are inversely related to density, the economic maximum may occur at densities tha[illegible]higher than those that maximize yields. Either way, this optimum density is variously described as 'economic carrying capacity' (Ferrar et al. 1983), the point of 'maximum sustained yield' MSY (Riney 1982), 'optimum density' (Dasmann 1981) and 'I carrying capacity' (McCullough 1979). This population is maintained by harvesting because at MSY natural mortality is low and fecundity is high. Setting population limits at or below MSY may produce maximum numbers of animals but is not a target where plant succession/production reaches a balance with ungulates As a result, plant succession can go in a direction that changes the point at which MSY occurs. This can ultimately result in the manager having to change the management target. At Elk Island low animal mortality, large calf crops, and healthy individual animals have historically been used to set target population size. As a result, the park managed ungulate populations at or below 'economic carrying capacity'(MSY) rather than at ecological carrying capacity (K).

Ecological criteria can also become the basis for setting target population numbers. Managers are asked to decide whether a national park is overstocked or if certain populations of large ungulates are above carrying capacity. Vegetation consumption in relation to vegetation production is often considered as the key physical attribute on which to assess the overabundance of large ungulates. As a result, many different methods have been developed to determine range condition in relation to animal stocking rates. One traditional method is the 'climax' approach where the presumed climatic-climax vegetation is the standard by which all other conditions are compared and ranked (Dyksterhuis 1949, Stoddart et al. 1975). Unfortunately, most managers fail to recognize that this indication of excess animals was developed for the assessment of economic carrying capacity (MSY) not ecological carrying capacity (K). The popular usage of this idea soon resulted in lightly grazed climax vegetation as the objective or desired condition, although this was not the original intent. Despite the recognition that climax vegetation is likely not the most frequent condition of a naturally functioning aspen parkland ecosystem, the role of substantial long-term vegetation consumption by large herbivores and its effects on vegetation change is still a focus of debate. Controversy stems from differences in time scale and permissible limits to change. Recently retrogression and multiple stable states have been offered as valid alternatives by which to assess vegetation response to ungulate populations. At Elk Island the history of vegetation change and ungulate populations appears to fit these models. Although these ideas may be complex, definition of these terms can be stated to assess objectives such as carrying capacity and related assessments of overgrazing, overpopulation, or natural succession. This is especially true in Elk Island, where a spatially and temporally diverse ecotonal grazing system must be preserved in perpetuity in an area much smaller than it's pristine state.

Animal criteria also are used as indicators of appropriate stocking but in spite of the sophistication of techniques used to assess condition of populations or individual animals, their application to determining optimum populations is still highly subjective It is also not universally accepted that grazing systems should be managed for animal 'quality'. Another perennial point of confusion occurs when target populations limits are judged aesthetically rather than decided objectively. Often this feeling of what is best is nothing more than a visual impression obtained at a moment in time, which is usually associated with free ranging large ungulate populations sparsely distributed at well below ecological carrying capacity. It is not surprising that when a high population of animals is seen to apparently cause this attractive, stable state to change, it is considered undesirable and measures are taken to halt the process.

Alternately, our belief of what should be 'ecological integrity' or [illegible] was 'natural environment' has emerged as an important criterion. This 'naturalistic' perception of the aspen parkland is based on the few remaining areas which are not farmed or urbanized. Unfortunately, these areas lack pristine populations of bison, elk, moose and deer and also the natural process of fire. From this perspective, Elk Island may seem uncomfortably overpopulated leading to public pressure to feed or reduce populations. While the public may be excused, a more serious mistake was made by park planners who for similar reasons, believed that boreal mixedwood vegetation was the natural climax and inappropriately chose to manage for this vegetation.

Long term studies have now shown that seral or subclimax vegetation is often quite productive and stable (Noy-Meir 1981). This is the case at Elk Island. Models to test the concepts of production and stability have also pointed toward the substantially grazed subclimax vegetation as the point of equilibrium or ecological carrying capacity (Caughley 1970, May 1973). This leads to the assumption that the pristine condition of natural ecosystems with abundant large herbivore populations must have been some form of grazing disclimax. In the past, the large herds of bison and elk described by the early explorers probably resulted in such a condition. Redmann (1981) noted that the first photographs of the Canadian prairies, taken before the complete elimination of bison and introduction of cattle, show a vegetation dominated by increaser and invader plant species.

Whereas managers think of species-management, ungulates typically are members of grazing guilds and management of one influences others. It is hard enough to detect carrying capacity for a single species let alone optimum numbers and combinations for an ungulate grazing guild. The 'animal unit' concept was developed to accommodate differences in grazing pressure imposed by different classes of livestock or more generally herbivore species. The animal unit is defined as a mature 454-kg domestic cow with an associated forage demand of 12 kg dry matter/day. 'Animal unit equivalents' (AUE's) are used to approximate the numbers of a particular species that consume/require the same quantity of forage as does this single 'animal unit' cow. On this basis the average 450-kg bison, 245-kg elk, 310-kg moose, and 70-kg deer would equal 0.825, 0.45, 0.57, and 0.13 AUE's respectively based on relative metabolic $W^{0.75}$. The traditionally accepted AUE's are those first developed by Stoddard and Smith (1955); they described moose and elk as 0.75 AUE's, deer as 0.20 AUE's and bison as exactly equivalent to 1.0 animal unit. However, interspecific differences in food habits are not addressed. Consequently Hobbs and Carpenter (1986) urge that whenever animal unit equivalents are used to compare species, they should be weighted by dietary differences. Others, such as Scarnecchia (1986), argue that animal unit equivalents should express the demand, not consumption, of forage in animal units; they should not involve diet quality, diet selection, or other processes influencing consumption rates. In other words, animal unit equivalents are units of demand not substitution ratios for calculating possible combinations for a herbivore guild. The native herbivore guild at Elk Island supports 18% more grazing than the cattle-dominated grazing system of the Blackfoot grazing reserve located in the similar habitat immediately south of Elk Island (Telfer and Scotter 1975). The authors suggested that forage preferences and habitat interspersion were important factors. Studies suggested that at Elk Island's, moose, elk, bison and deer overlapped strongly in habitat use and to a lesser extent in winter food habits (Cairns and Telfer 1980). Spatial distribution was the resource where the least degree of overlap occurred (Telfer and Cairns 1983). In particular, deer did not occupy areas where high numbers of elk and moose occurred, perhaps because of competition for browse. The indices developed by Telfer and Cairns (1983) show the relative importance of habitat, diet, and space that can serve as a basis for finding possible alternative stocking combinations. Studies of African and South American savanna ecosystems by Fritz and Duncan (1994) suggest that herbivore species richness affects carrying capacity primarily during periods of low resource availability. They concluded that the important dichotomy in terms of ecosystem carrying capacity was between ecosystems with high herbivore biomasses and those where herbivores were absent or rare. Such a conclusion is consistent with the observed density-dependent carrying capacities for the native herbivore guild at Elk Island.

Linear programming can be used to calculate optimal stocking combinations in relation to any number of objectives (Hudson and Blyth 1986, Glover and Conner 1988, and Plumb 1991). In this approach several key pieces of information are evaluated and the optimum solution computed. The calculated optimal 'stocking strategies' are highly dependent upon the accuracy of the information used to construct the program. The considerations of aspen leaf litter as a forage type or the use of browse by bison are two examples of information that could highly alter the result of a linear program.

Population Management Strategies for Elk Island

Parks are often managed like museums to protect a maximum number of natural features and objects. Recently this has been expressed under the banner of maximization of biodiversity. The success of management is gauged with species lists and similar inventories of other natural features. The attractiveness of this goal is its simplicity and it fits well with communication programs that introduce the public to pieces of nature. The problem is that managing for the maximum number of features or natural objects do not necessarily maintain the character of natural landscapes which is a more valid but perhaps elusive goal. Optimal stocking patterns are not entirely at the discretion of park managers, because of the public's highly differentiated perceptions of what this means. As a result, objectives must compromise several sometimes inconsistent ecological, aesthetic and even economic goals. Everyone has their own idea of what constitutes good management and what represents 'ecological integrity'. In the national parks of Canada, the maintenance of ecological integrity was prescribed by legislation in 1988. Subsequently, several attempts were made to define this concept in practical terms to formulate management programs (Woodley 1993).

Given the national park's mandate in Canada, the prime concern of conservation should be to consider the amount of change that the grazing system can withstand, and still return to its original condition or in other words resilience. Resilient systems often are unstable in that they are highly dynamic but they usually manage to recover rapidly following severe disturbance. Diversity in the quality and physical structure of habitats and heterogeneity exhibited in the pattern or spatial distribution of parkland habitats also provides stability. In ecological theory and practical applications, evidence suggests that if a system is maintained at a particular state or condition (artificially stabilized), its resilience decreases through loss of diversity, heterogeneity and the processes of change that allow recovery from disturbance. The aspen parkland in its natural state is a prime example of a very resilient, highly dynamic system. As a system that exists both temporally and spatially between two very different vegetation conditions (Mixed-wood Boreal to Fescue grassland) fire, moisture regimes, beaver activities and large ungulate vegetation consumption are all forces or processes creating change, increasing diversity and over a large scale increasing heterogeneity. Paleoecological evidence provides ample indication of the ecosystem that existed throughout the period following the altithermal until the mid 1800's. Traditional preservation objectives aimed at preventing two of the most important natural forces of change, overgrazing and fire, have resulted in loss of diversity through a preponderance of forest unknown to the area in it's natural state. As a result, return to its natural state now requires active intervention. This should include the reintroduction of native plant and animal species, and the natural process of fire. This is not a unique situation faced by Elk Island. Many national parks in Africa are also fenced, and have also prevented fire and periodic overgrazing from causing changes to the system. Many of these parks now have reintroduced fire by prescription and allow natural periodic heavy grazing pressure (Ferrar 1983). It is widely recognized that long-term resilience in these highly productive African systems is more important than short-term stability in the preservation of the systems. This perspective is perhaps not inappropriate for Elk Island but several key differences require careful consideration. These include: the extremely small size of the park, and the absence of predators.

The importance of man's influence on the dynamics and character of pristine North American ecosystems has been largely ignored by parks managers. Authors such as Chase (1986) and Kaye (1991) have clearly illustrated that to consider man apart from the functions of a natural ecosystem can result in misinterpretations of the past and inappropriate directions for the future. In the pristine parkland of the Beaver Hills, we know that man caused fires were frequent, almost annual in occurrence and that they maintained open habitats. We have no way of knowing how heavily ungulates were harvested leaving one to speculate about what extent the seasonal or yearly population dynamics were effected. Nevertheless the effects of the native hunters and their use of fire had impacts on the parkland vegetation and herbivores. This must be considered as important to the evolution of the parkland grazing system and it's natural status.

Outside the realm of the actual national park mandate, several public agendas currently influence decisions. People eager to obtain breeding stock for game farms, other government agencies needing stock for hunted populations, or managers who might wish to maximize revenue through animals sales may see high densities and mortality as wasteful. Others argue that wildlife and vegetation in national parks are a national treasure and that it does not matter if disease, severe winters or starvation are natural ecological controls on population growth. American national parks have experienced this form of backlash to their policy of allowing the natural course of events to determine the state of their natural resources (Chase, 1986). This has resulted from adherence to such a policy even when the ecosystem is spatially incomplete, fragmented or lacking in natural controls such as predators. At Elk Island both sentiments will be felt.

In setting future stocking strategies for Elk Island, several factors that influence ungulate population dynamics must be considered. The form of the density-dependent curves that define the relationship between density and productivity at Elk Island is somewhat unique. Parasite infestations may in some aspects act like a predator influencing food-related density-dependence. Interspecific interactions at high densities must also be considered. The result in moose, is the reduction of MSY to a density closer to 0.5 K than predicted. Vegetation succession from grassland to forest appears to have lowered populations at MSY and K for bison, while increasing them for elk. Another factor, is that of system size that may change the magnitude and frequency of population cycles. Moose population dynamics clearly show that, in the smaller Isolation Area, the magnitude and frequency of population fluctuations are increased. Finally, management programs appear to affect the dynamics of carrying capacity. The impact of these programs is manifested primarily in yearly variability that occurs around the expected outcomes of density-dependence. Over the long-term, management does not appear to have the expected impact. In the 1940's and 1950's, populations were successfully managed at numbers near MSY. The density of MSY and rates of declining productivity toward K remained remarkably constant. Both elk and bison, populations were very resilient to management but moose K and MSY densities may be effected by management. The most recent period of moose decline, where the normal intervention by slaughter was foregone, proved the ability of the population to self regulate and correlated with a shift of MSY closer to K.

Elk Island has historically and should be in the future an ecosystem heavily influenced by abundant wildlife populations in balance with the naturally productive and resilient aspen parkland vegetation, fire, predators and man. Despite the major alterations to the grazing system by modern man over the last 200 years, it appears likely that density-dependent population regulation may still function leaving some potential for self-regulating ungulate populations. Natural equilibria between the vegetation and the ungulate populations should be the eventual endpoint, with management programs designed to restore the grazing system, predation, and native hunters. Episodic population decline due to severe winters or population declines resulting when the ungulate populations requirements exceed K are primary forces of natural population regulation and may eventually result in a more stable population. If suitable compensation for the other natural forces of control are undertaken then they should not be considered as a bad. Consequently, a clear informative interpretation and information program is necessary. These programs should not just follow textbook descriptions of parkland ecosystems but must highlight the subtle and acute differences that the past and present park environs represent. The management program that will be called for during these times must be designed to simulate or replace natural forces of ungulate population regulation, not reduce the population well below K or to prevent mortality unless the size of the natural decline is believed to be very large. All programs of population reduction should be based on a prediction of population instability, not a predetermined arbitrary number. Outside this general approach, limits of extreme over and under-abundance can be used as danger signs to signal the need for major intervention.

The assessment of under-abundance or minimum population size is more straight forward than [illegible]e. A comprehensive review of minimum viable population analysis was written by Boyce [illegible] general, two key criteria form the basis for such a decision. The first is maintenance of genetic [illegible] and the second is a stochastic lower limit at which there exists a high probability of extinction of the species within the park. It is generally accepted that loss of genetic diversity depends upon the size of a population. The smaller the population, the faster genetic diversity is lost. When populations quickly decline to minimum numbers, genetic variability can also be lost, especially those alleles of low frequency. The total amount of genetic variation lost is based on how fast the population recovers to a significant size. From a genetic perspective, the effective minimum population size is judged by the total number and sex ratio of reproductive individuals. An effective population of at least 50 was suggested by (Foose 1983). In terms of total population size this would probably represent 75 to 100 individuals depending on sex ratio. Artificial migration has become a routine method of preserving genetic diversity in zoo situations. At Elk Island the potential exists to exchange animals between the main and wood bison areas of the park. In the past elk have been moved from the Main Park to the wood bison area. This practice could be continued. In the smaller Isolation Area, this can be particularly beneficial for ensuring diversity especially during periods when moose or elk populations are at low numbers. These general rules and models that assess potential loss of genetic diversity are generic in nature. Loss of genetic variability that may have resulted from previous population bottlenecks or the small founding number of bison (approx. 40), elk (23), and moose (approx. 30) are not considered. Recombinant DNA technology offers the ability to map and discover genetic markers that can detail quantitative evidence of genetic diversity. At Elk Island, some of this work has been done for the plains bison, wood bison and elk populations (Bork et al. 1990). This type of research should be continued to provide a baseline upon which future genetic drift can be detected. If this type of research continues, minimum herd numbers of each ungulate species in the main and wood bison area may someday be more accurately accounted. This would also allow herd reduction programs to consider genetic criteria besides the current demographic criteria.

The assessment of a minimum lower number to avoid accidental extinction of an ungulate species from the park are usually determined using computer models which assess probability. Several different models have been developed for endangered species that can be easily adapted for bison, moose, or elk. The results of these modeling efforts usually show that 20-30 individuals would insure the survival of a species. This number is lower than that proposed to ensure genetic diversity that, in the Main Park, is also lower than the minimum viable density expressed by the density-dependent production curves. This suggests that in the Main Park the threshold limits of under-abundance should be based on the minimum viable density which being the largest of the three would naturally allay genetic and stochastic concerns. In the Main Park this would result in the limit of under-abundance being set at 130 moose, 165 bison and 165 elk. In the Isolation Area the genetic lower limit of 75 (50 founders) represents the highest of the three criteria and thus no less than 75 (effective population of 50) individuals of each species should be maintained. In assessing the likely success of these limits of under-abundance it is comforting to remember that populations were reduced to very low numbers in the past and successfully recovered. Past attempts to eliminate moose and elk populations in the Isolation Area failed after populations recovered from less than 10 individuals. In assessing this criterion the precision and accuracy of census data are very important. For example in the winter of 1990, moose were removed from the Isolation Area resulting in a population of only 77 individuals owing to an error in the survey that was not detected until after the management action was taken.

Overabundance should be defined as the point where animal numbers cause the system to become terminally unstable. MacNab (1985) stated that animals may also be considered overpopulated if human life or livelihood is threatened, they depress the densities of species favored by man, or they are 'too numerous for their own good'; i.e.,some animals are periodically in poor condition and undergo natural mortality. Unfortunately these situations when animals are considered overpopulated are often confused with each other, or both ecological and economic carrying capacities. This is especially true in national parks or other natural areas. In Alberta, the most frequent example of the first case is the reduction of park elk populations when they are causing crop damage in areas outside park lands. Beaver may be considered overpopulated when their flooding causes loss of habitat for species favored by man.

Of special note is the situation where large ungulates may be considered 'too numerous for their own good'. Here natural mortality of an ungulate population fluctuating around the stable natural ecological carrying capacity can be mistaken as 'overpopulation', especially in national parks. Whether the deaths are chronic mortality or conspicuous episodic mortality, they are often considered as wasteful or cruel. The ideas of waste and cruelty may be inappropriate biological perspectives from which to view and manage natural ecosystems, nevertheless they are important ethical considerations that influence park management.

The first is the public demand that if animals are going to die then they should be used for food or monetary gain rather than be left to decompose in a natural system. Most people realize that all animals eventually die but it is often hard to consider that natural mortality usually involves predation, disease and starvation. The latter may occur due to natural occurring environmental fluctuation such as snow depth or the inability to consume food because of physical infirmity resulting from old age. Affection for animals and the aversion to killing or allowing natural mortality in a fenced environment, is a deep-rooted sentiment. People who share it form a committed block of supporters for conservation, in financial, political and moral terms. Pragmatic conservationists must accept that these sentiments are the legitimate beliefs of potential allies and must be handled with sensitivity. Full and factual explanations of carrying capacity and assessment of overpopulation are invariably the best policy to follow. From this, positive public support should develop. Furthermore, clarification of political and ecological considerations will improve the logical basis for decision making by the park manager. At Elk Island, the information contained in this study will facilitate the communication program required.

For Elk Island, the suggested extreme limits of overabundance are based upon the population dynamics displayed by the historic data before 1985 and the recent period of management. In the Main Park plains bison should not exceed one thousand, unless the pristine grazing system is reestablished allowing the bison to migrate to a grassland area during the summer and inhabit the more forested parkland of the park during the winter. The wood bison population should not exceed 750 for similar reasons. In the short term however, this population should be maintained at approximately 300(0.06-0.07/ha) to maximize the number of individuals available for reestablishing populations in the wild. Moose should not exceed 900 in the Main Park or 450 in the Isolation Area. The response of the moose populations to the current management program shows that there is no danger of this upper limit being exceeded. For deer the concept has little utility. These numbers are based on evidence derived from the proceeding analysis, recognizing public sentiments for animals dieing in a naturally regulated grazing system.

Current logistical and political considerations make predator reintroduction unlikely. Should this change, a predator reintroduction program could be considered. It should be remembered that the predators may not exert the kind of control expected (Boutin 1992). Native man as one of the primary 'predators' must still be considered as an addition force which will require replacement by park's initiated population reductions. If predators are reintroduced, the knowledge gained by comparing the population dynamics before and after reintroduction would significantly contribute to our understanding of predation.

Technology and changing public sentiments may also someday allow the construction of gates in the main park's perimeter fence that will allow easy migration of the elk and moose to and from the park. Periodic closure of these gates could be considered to prevent the converse problem; that of unnaturally high rates of emigration due to the unnaturally low populations of the surrounding region. The preliminary testing in the Isolation Area gave favorable results.

Past fire prevention and control practices as well as excessively large population reductions have caused successional changes at a rate that may never have occurred in the natural environment. A bold and ambitious program of vegetation restoration will be required to ensure that future processes of herbivory and fire can appropriately influence the course and rate of ecosystem dynamics.

In the future lies the challenge to resurrect the native parkland that characterized the pristine setting of Elk Island. The planting of conifers, the brushing and forage crop planting, the cutting of fireguards, the slaughters and trapping of animals simply to prevent mortality, the artificial support of populations by feeding, and all the other management programs of the past should be pushed behind us, but not forgotten. For it is these past man-caused changes that leave us with what today is often mistaken as natural. In turn the ungulate population numbers, fire use/control, and park use decisions of today will decide what will appear, to future generations, as natural. At Elk Island the challenge will be not to eliminate the influence of man, but to decide the nature of man's role in the evolution of Elk Island's parkland ecosystem. To ignore man's role or to attempt to divorce man from the ecology of this ecosystem, would be both irresponsible and in a broad sense would be to deny the natural role that man has always played in the evolution of the parkland ecosystem.

CONCLUSIONS

1. The Elk Island ungulate population data appears consistent and accurate. The 87 years of record represents the longest time series analyzed for any North American herbivore guild.

2. A combination of time series analysis and adaptive experimental management was found to offer an excellent method of clarifying the complex population dynamics of an ungulate guild.

3. The aspen parkland is capable of large amounts of secondary productivity. Data from Elk Island suggest a maximum sustained yield of 10.6-18.3 kg/ha/yr with a standing stock or biomass of ≈50-90 kg/ha. In fact, the Main Park of Elk Island has supported an average of 56 kg/ha of ungulates from 1906-93.

4. The standing stock or live biomass of the ungulate guild at K was ≈76-134 kg/ha. The historic records describe ungulate biomass of 18.05-92.5 kg/ha. From the observed ecological carrying capacities at Elk Island it can be concluded that the upper estimates of historic descriptions are plausible.

5. The mean rate of increase ($\lambda = 1.19$) for the entire history of the Main Park was the same for each species, despite the inherent biological differences in each species and the different management regimes applied to each. This may imply a basic productivity for ungulates in this ecosystem.

6. The r_m for ungulate populations at Elk Island during the initial population growth phase following introduction was $\underline{r} = 0.16$ ($\lambda = 1.17$) for plains bison, $\underline{r} = 0.19$ ($\lambda = 1.21$) for wood bison, $\underline{r} = 0.15$ ($\lambda = 1.16$) for elk, $\underline{r} = 0.19$ ($\lambda = 1.20$) for moose and $\underline{r} = 0.27$ ($\lambda = 1.31$) for deer. This was at or below rates reported for other areas. The r_m realized during later periods of population growth of $\underline{r} = 0.21$ ($\lambda = 1.23$) for plains bison and $\underline{r} = 0.31$-0.35 ($\lambda = 1.36 - 1.42$) for elk, are among the most productive reported. The r_m reported for moose at Elk Island of $\underline{r} = 0.32 - 0.36$ ($\lambda = 1.37 - 1.42$) was higher than reported in most other moose populations.

7. The r_{max} of $\lambda = 1.49$ for plains bison, $\lambda = 1.51$ for elk and $\lambda = 1.84$ for moose at Elk Island exceed any other population reported. The r_{max} for deer was obscured due to immigration.

8. The ungulate populations are preadapted to constantly varying ecological conditions as evidenced by the complex population dynamics characterized by low and high frequency periodicity, complex attractors, long-term trends and short term noise.

9. Spectral analysis suggested that periodicity is common in the ungulate populations at Elk Island. The periodicity observed is consistent with populations in other areas suggesting that the biology of these species is an important determinant of periodic population dynamics.

10. Periodicity was predicted to be a consequence of delayed density-dependence and r_{max}. The periodicity displayed at Elk Island and other areas does not strictly follow the predicted pattern but is not entirely inconsistent.

11. The ungulate populations provide evidence of both delayed and direct density-dependent population dynamics. For bison this evidence includes reduced body weight and calving rates as density increases. For moose increased mortality and decreased fecundity was in evidence as densities increased.

12. Per capita population increases strongly deviate from linearity at low densities (inverse density-dependence). This suggests the Allee effect is an important determinant of population dynamics at low densities.

13. The ungulate populations displayed both r and K selected density-dependent responses. The type of response was consistent with the life histories of the species. Moose twin and reproduce at a younger age realizing MSY densities at 0.5 of K during two periods whereas bison consistently exhibit K-selected density-dependent population dynamics.

14. Density-dependence was not detected in the deer populations. Deer population dynamics are influenced by the greater regional population that can move freely in and out of the park as shown by a general increase in deer numbers, in both the Main Park and the County of Strathcona.

15. The K and MSY densities supported at Elk Island are higher than reported in studies of the same species in other ecosystems.

16. Plains bison MSY occurred at the highest densities (0.07 - 0.14/ha, 31.5 - 63 kg/ha) followed closely by Elk (0.06 - 0.08/ha, 14.5 - 19.4). Moose MSY density was much lower at (0.021 - 0.028/ha, 6.5 - 8.7 kg/ha). The range of K densities followed the same relative order with Bison K occurring at the highest density (0.10 - 0.18/ha, 45.0 - 81.0 kg/ha), followed by elk (0.085 - 0.15/ha, 20.6 - 36.3 kg/ha) and moose (0.033 - 0.053, 10.2 - 16.4 kg/ha). In the Isolation Area, the relative MSY and K densities for each species was similar but marginally lower than the Main Park. These relative carrying capacities are consistent with the observed relative abundance reported for the pristine aspen parkland.

17. Interspecific density-dependence only occurred at densities near K suggesting an important interaction of social dominance and spacial partitioning of resources. As a result the relative MSY and K densities were consistent with the interspecific dominance hierarchy proposed for these species. In particular, moose reproductive performance was shown to be influenced by combined moose and elk densities near K.

18. The ungulate and vegetation dynamics at Elk Island suggest the idea of multiple stable states as a valid construct for the aspen parkland. Man caused reductions in ungulate populations at K preceded replacement of grasslands with aspen forests that in turn resulted in new K densities. Plains bison K densities were seen to decrease with a reduction in the proportion of grassland habitat. The elk λ displayed an abrupt and permanent increase after 1940 correlated with a sudden increase in forest cover.

19. The current grazing system at Elk Island is the reverse of the historic pattern where bison used the parkland in the winter. In this historic setting bison would have increased the stocking density during winter increasing the dormant season grazing pressure. From this one can speculate that today's ungulate carrying capacity for the park would be different fr[illegible] pristine grazing system. The effects of this on the vegetation and the other ungulate population dynamics are likely to vary over space and time, making it difficult to conclude relative merits. However, the national park's mandate for the maintenance ecological intergity should dictate that the original grazing system be restored.

20. The amplitude and frequency of moose population cycles were increased in the smaller Isolation Area. This suggests that system size can influence the dynamics of a species with a high r_m.

22. The winter tick influences moose population dynamics similar to predation by the way that it contributes to mortality of moose at and following high moose densities.

23. The disease brucellosis, did not appear to have significantly influenced the bison population dynamics at Elk Island.

24. Climate causes short term noise in the population dynamics of the ungulate populations. Severe winters or specific winter climate events have caused declines or reduced the population rate of increase not predicted by ungulate population density.

TABLES

Table 1. Demographic summary of mean annual ungulate populations in the main park area, Elk Island National Park

MAIN PARK	Elk	Moose	Plains bison	Wt-tailed deer	All
# late fall before management	547 ± 41	283 ± 18	812 ± 59	83 ± 10	1725 ± 128
# early spring after management	475 ± 36	251 ± 17	690 ± 51	81 ± 10	1497 ± 114
#/ha late fall before management	0.053 ± 0.004	0.028 ± 0.001	0.076 ± 0.005	0.008 ± 0.001	0.165 ± 0.011
#/ha early spring after management	0.047 ± 0.003	0.025 ± 0.001	0.065 ± 0.004	0.007 ± 0.001	0.144 ± 0.009
kg/ha late fall before management	12.91 ± 0.	8.32 ± 0.48	34.40 ± 2.04	0.38 ± 0.04	56.01 ± 2.08
kg/ha early spring after management	11.35 ± 0.78	7.45 ± 0.45	29.36 ± 1.79	0.37 ± 0.05	48.53 ± 3.07
rate of increase $\lambda = 1 + r$	1.193 ± 0.019	1.191 ± 0.028*	1.192 ± 0.013*	1.197 ± 0.099*	
# increase	84 ± 13	36 ± 7*	125 ± 14*	9 ± 6	254 ± 40
kg/ha increase	1.98 ± 0.30	1.09 ± 0.22*	5.27 ± 0.50*	0.04 ± 0.03	8.38 ± 1.05
# removed by management	70 ± 11	31 ± 6	122 ± 20*	4 ± 2	227 ± 39
kg/ha/yr removed by management	1.53 ± 0.24	0.84 ± 0.16	4.64 ± 0.73*	0.02 ± 0.01	7.49± 1.14
kg increase/kg/ha	0.19 ± 0.02	0.19 ± 0.03*	0.19 ± 0.01*	0.24 ± 0.08	
kg removed/kg/ha	0.10 ± 0.01	0.09 ± 0.01	0.12 ± 0.01*	0.05 ± 0.03	
MSY #/ha	0.06 - 0.08	0.021 - 0.028	0.07 - 0.14		
K #/ha	0.085 - 0.15	0.033 - 0.053	0.10 - 0.18		
periodicity	10yr, 2.5yr	18yr	13yr, 2yr		
ARIMA	$(000)(011)_6$ SMA = 0.35 Mean = 19.18	$(000)(011)_{18}$ SMA = 0.515	$(000)(000)_{13}$ Mean = 18.39	$(000)(000)_2$ Mean = 19.92	
period of record	1906-93	1909-93 1911-93*	1907-93 1910-93*	1951-93 1960-92*	

Table 2. Demographic summary of mean annual ungulate populations in the Isolation Area, Elk Island National Park

ISOLATION AREA	Elk	Moose	Wood bison	White-tailed deer	All
# late fall before management	103 ± 23	130 ± 9	153 ± 20	131 ± 9	517 ± 62
# early spring after management	98 ± 22	114 ± 8	135 ± 17	123 ± 8	470 ± 55
#/ha late fall before management	0.022 ± 0.005	0.027 ± 0.002	0.033 ± 0.004	0.028 ± 0.002	0.11 ± 0.013
#/ha early spring after management	0.021 ± 0.005	0.024 ± 0.002	0.029 ± 0.004	0.026 ± 0.002	0.100 ± 0.013
kg/ha late fall before management	5.30 ± 1.20	8.31 ± 0.54	15.54 ± 2.03	1.39 ± 0.09	30.54 ± 3.86
kg/ha early spring after management	5.04 ± 1.16	7.30 ± 0.49	13.64 ± 1.74	1.31 ± 0.09	27.29 ± 3.48
rate of increase λ = 1 + r	1.168 ± 0.041	1.224 ± 0.057	1.247 ± 0.022	1.189 ± 0.098	
# increase	17 ± 5	18 ± 7	29 ± 4	8 ± 10	72 ± 26
kg/ha increase	0.85 ± 0.25	1.16 ± 0.43	2.95 ± 0.38	0.08 ± 0.11	5.04 ± 1.17
# removed by management	6 ± 3	16 ± 5	19 ± 5	7 ± 4	47 ± 17
kg/ha/yr removed by management	0.31 ± 0.13	1.02 ± 0.31	1.88 ± 0.49	0.07 ± 0.04	3.26 ± 0.97
kg increase/kg/ha	0.17 ± 0.04	0.23 ± 0.06	0.23 ± 0.01	[illegible] ± 0.10	
kg removed/kg/ha	0.06 ± 0.03	0.11 ± 0.03	0.10 ± 0.02	0.04 ± 0.02	
MSY #/ha	0.05 - 0.06	0.018 - 0.03	0.05		
K #/ha	0.08	0.03 - 0.05	0.06		
periodicity		11yr	2yr		
ARIMA		$(002)(011)_{18}$ SMA = 2.21 MA = -0.71	$(000)(000)_2$ Mean = 24.34		
period of record	1959-93	1[illegible]-93	1965-93	1959-93	

Table 3. Density (#/ha) and rates of increase (r) of elk,bison, moose, and deer in various ecosystems in North America.

Location	Ecological Setting	Citation	Elk #/ha	Elk (r)	Bison #/ha	Bison (r)	Moose #/ha	Moose (r)	WtDeer #/ha	WtDeer (r)
Blackfoot Grazing Res, Alberta	Aspen Parkland	Rippen 1994	0.016		0.0		0.007		0.025	
		Telfer & Scotter 1975	0.08				0.03		0.04	
County of Strathcona, Alberta	Aspen Parkland-Agricultural	Rippen 1994							0.008-0.018	
Buffalo N. P., Wainwright, Alberta	Aspen Parkland-Fescue Prairie	Harkin 1928	0.009		0.10	0.20	0.001		Mule deer 0.03	
		Harkin 1933 Roe 1970 1911-1927	0.020		0.15	0.18 0.20	0.002		Mule Deer 0.048	
Alberta	Aspen Parkland	Wishart 1984							0.024-0.12	
Riding Mntn. N. P., Manitoba	Aspen Parkland	Rounds 1977	0.017-0.056				0.008-0.005			
Rochester, Alberta	Boreal Forest	Rolley & Keith 1980					0.002-0.007	0.24 0.03		
Peace River, Alberta	Boreal Forest-Parkland	McFetridge 1984		0.45						
PrLocationince Albert N. P., Saskatchewan	Aspen Parkland-Boreal Forest	Tarlton 1988	0.015				0.005			
Saskatchewan	Aspen Parkland	Symington & Benson 1957							0.03	
Minesota	Boreal Forest	Peek 1974					0.009			
Eastern Quebec	Boreal Forest	Crete 1989					0.018-0.02			
Mackenzie Bison Sanctuary, N.W.T.	Boreal Forest	Gates & Larter 1990			0.005 0.002	0.27 0.10 0.215				
Newfoundland	Boreal Forest	Bergerud & Manuel 1968					0.047			
Isle Royale, Michigan	Boreal-Northern Hardwood	Peterson 1994					0.018-0.096			
Goerge Deer reserve, Michigan	Oak-Hickory Forest-Grassland	McCullough 1984							0.21-0.39	0.51
Southern Ontario, Michigan, Minesota	N.E. Harwood & Boreal	Blouch 1984							0.01-0.06-0.17	

Location	Ecological Setting	Citation	Elk #/ha	Elk (r)	Bison #/ha	Bison (r)	Moose #/ha	Moose (r)	WtDeer #/ha	WtDeer (r)
Gros Venture, Wyoming	Aspen ecosystem	DeByle 1979	0.06-0.26							
Northern Yellowstone	Mixed Grass Pondorosa Pine	Huston 1982 Eberhardt 1987	0.12-0.14	0.19	0.002		0.002		Mule Deer 0.13	
Cache, Northern Utah		Kimball & Wolfe 1979 Eberhardt 1987		0.15-0.17 0.20-0.22						
Henry Mountains, Utah	Pinyon Pine- Douglas Fir-Shrub Steppe	Van Vuren & Bray 1986			0.002-0.005 0.005-0.01	0.05 0.09				
Pennsylvania	Hardwood Agricultural	Eveland et al. 1979	0.001-0.003	0.18						
Peidmont Plateau, Georgia	Oak-Hickory Forest	Whittington 1984							0.15-0.20	
Nova Scotia	Eastern Hardwood	Telfer 1968					0.005			
Tyson Park, Missouri		Murphy 1963		0.29						
Wichita Mountains N.W.R.	Mixed-tall grass & Oak	Waldrip & Shaw 1979	0.023		0.025				0.021	
Point Reyes, California	Coastal Prairie Scrub	Gogan & Barret 1987	0.04	0.17 0.29	Cattle 0.4				Mule Deer 0.3	
Grizzly Isl. California	Tule marsh, Agricultural	Gogan & Barret 1987	0.023-0.03	0.31						
Prairie Cr. Redwood State Pk. California	Coastal Redwoods	Franklin & Lieb 1979	0.028-0.035							
Yosemite N. P. California		Moffit 1934		0.18						
Columbia White-tailed Deer Refuge, Washington	N.W. Forest	Gavin 1979							0.25-0.29	
Roseburg, Oregon		Smith 1982							0.22-0.27	
Southwest Oregon	Coastal Old Growth Douglas Fir	Smithy et al. 1984	0.085						0.07	
East Kootenay B.C.	Interior Douglas Fir	Schuerholz 1984	0.05							
Arid lands Ecology Res., Washington	Shrub-Steppe	McCorquodale et al. 1988	0.003	0.20-0.30						
Afognak Isl., Alaska		Burris & McKnight 1973		0.37						
East Central Alaska	Boreal	Gasaway et al. 1992					0.004-0.014	0.18		

Location	Ecological Setting	Citation	Elk #/ha	Elk (r)	Bison #/ha	Bison (r)	Moose #/ha	Moose (r)	WtDeer #/ha	WtDeer (r)
Nat. Bison Range, Montana	Mixed Grass Prairie	Fredin 1984 Eberhardt 1987 Malcolm 1987	0.017	0.188	0.05				Mule/ Wt-tailed 0.05	
Wind Cave N. P., South Dakota	Mixed Grass Prairie	Bone 1987	0.05		0.04					
Theodore Roosevelt N.P., North Dakota	Mixed Grass Prairie	Bradybbaugh 1987			0.01-0.026					
North Dakota	Shortgrass-Mixed Grass	Petersen 1984							0.01-0.10	
Fort Niobrara, Nebraska		Ellis & Sellers 1987			0.039				0.007 Mule/ Wt-tailed	
Custer State Park, South Dakota	Mixed grass	Walker 1987			0.14-0.09					
Llano Basin, Texas	Mesquite Prairie	Teer 1984							0.36	

FIGURES

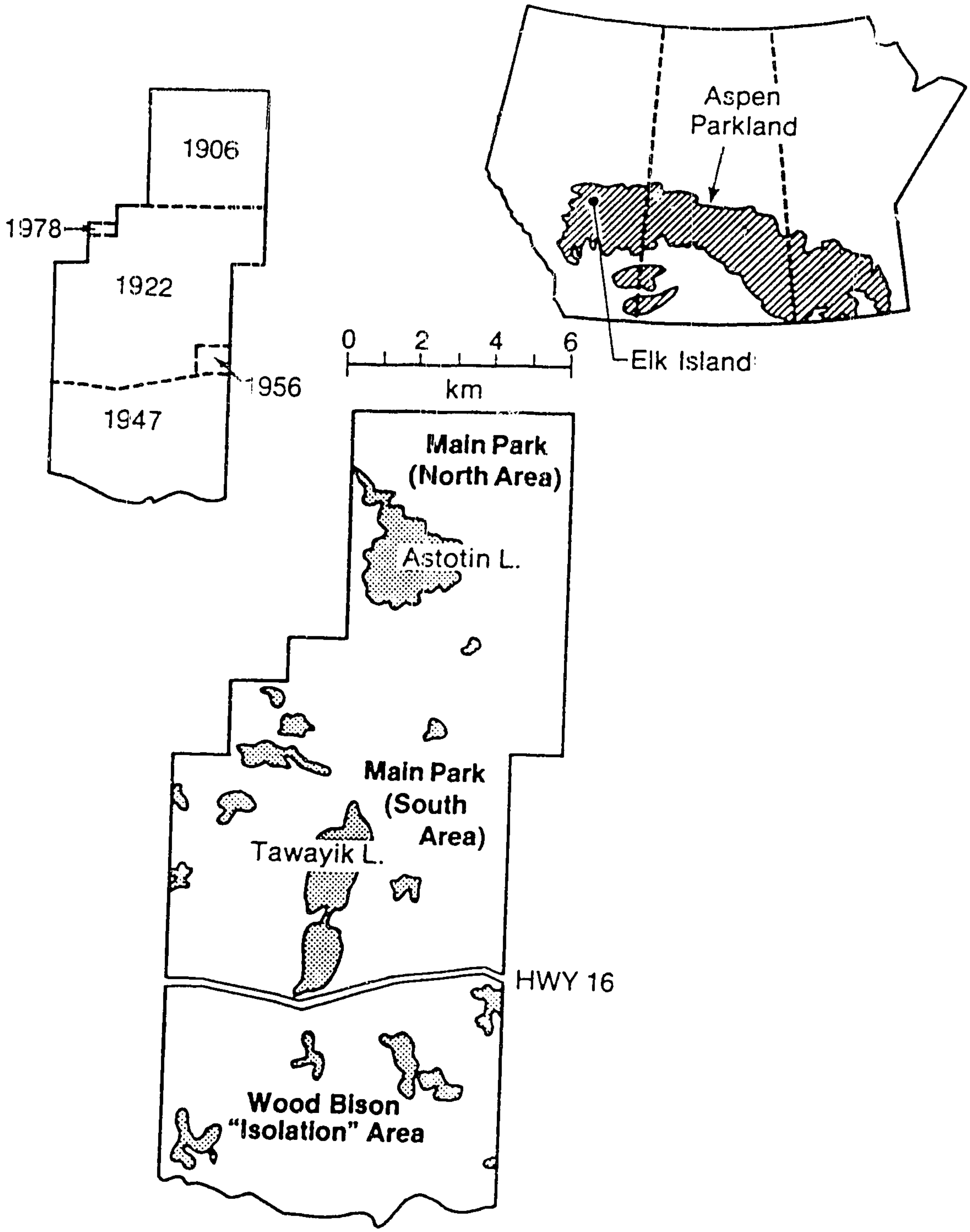

Fig. 1. Elk Island National Park, geographic location, dates of park expansion and boundaries.

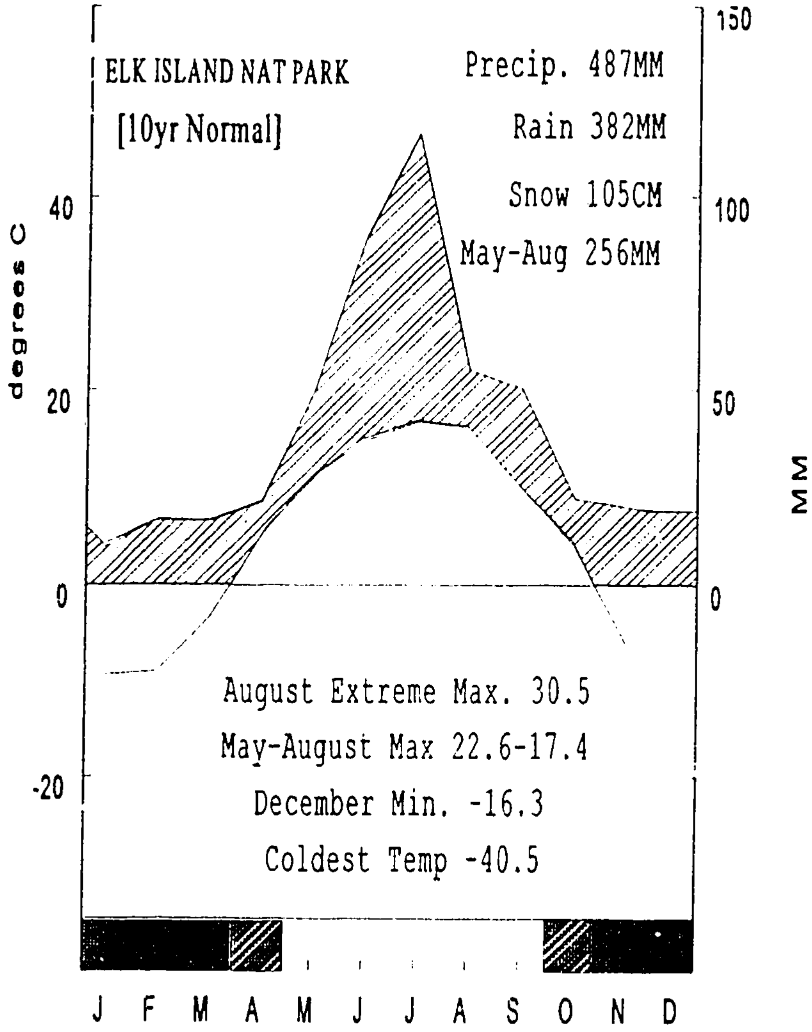

Fig. 2. Ecoclimatic diagram from data recorded at the Elk Island National Park climate station from 1983-92. Bar at the bottom of the chart indicates the summer months with mean daily temperatures above 0 degrees C, the winter with mean daily temperatures below 0 degrees C and the shoulder seasons with mean daily temperatures above 0 but mean minimum temperatures below 0 degrees C. Precipitation is graphed over temperature with area between indicating relatively humid climate.

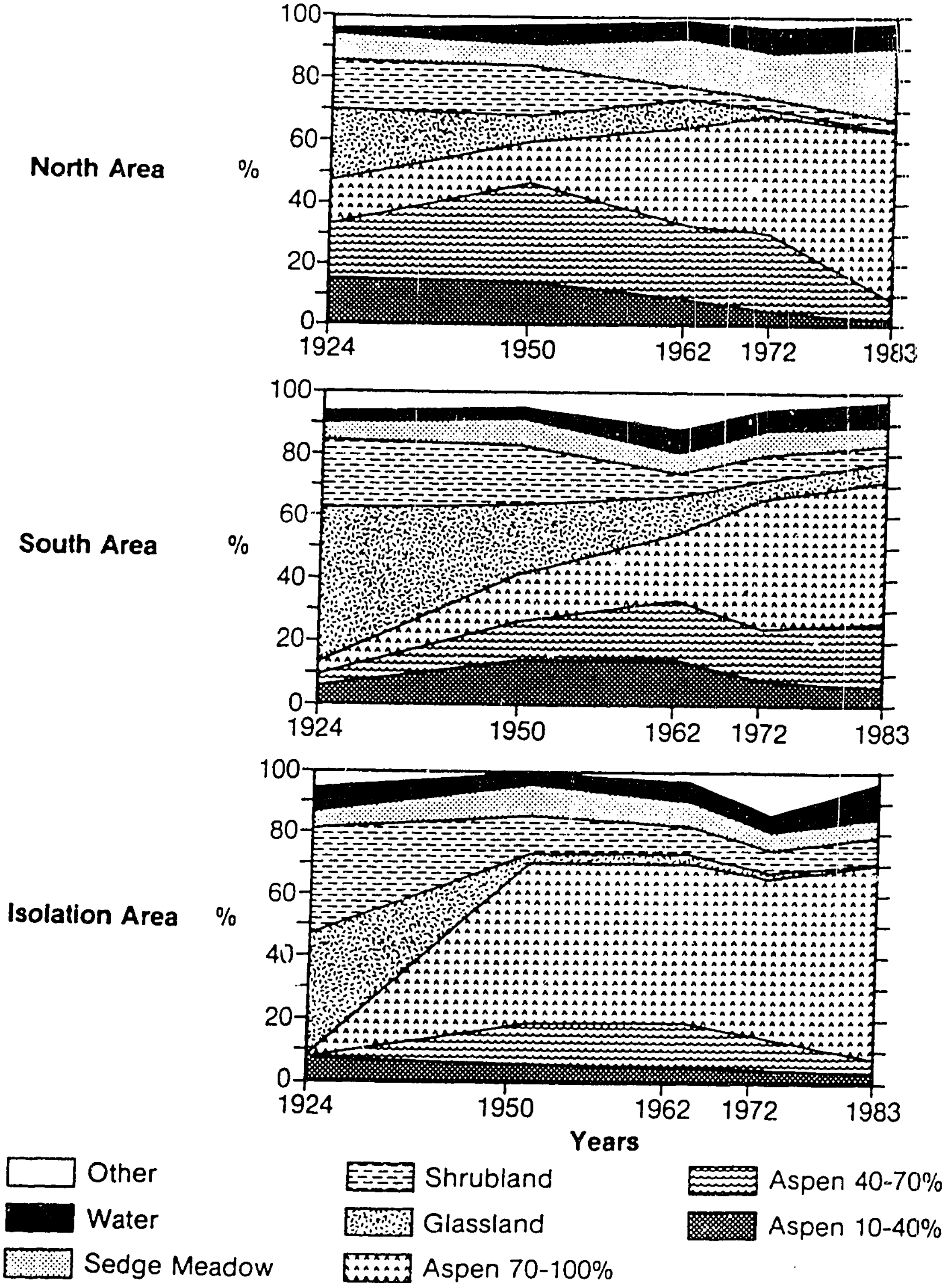

Fig. 3. Vegetation cover in the main park and isolation area from 1923-83. From Blyth and Hudson (1987).

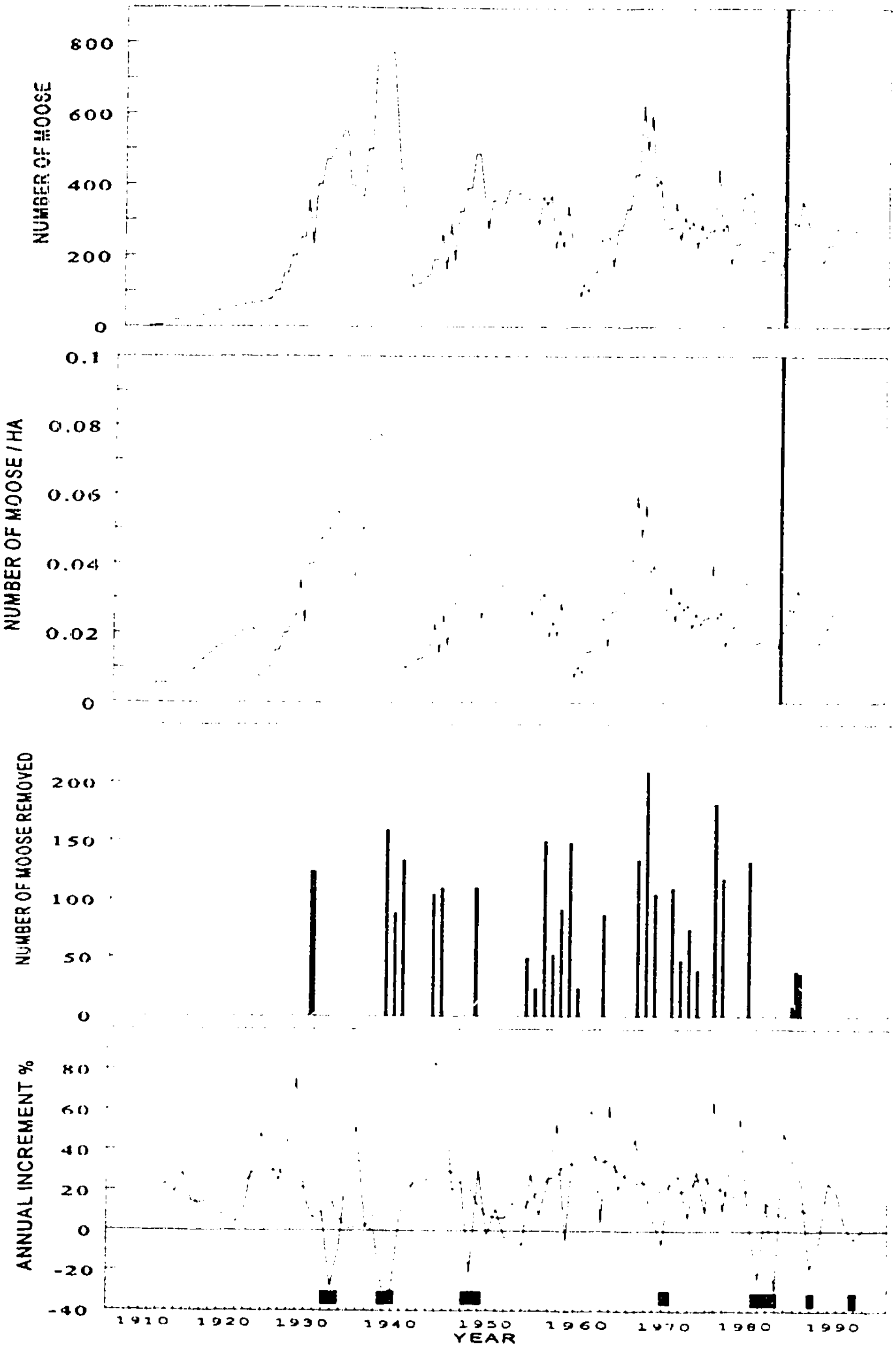

Fig. 4. Moose numbers, density, numbers removed and annual increment (r) expressed as a percent in the main park area from 1909-94. Annual increment is displayed as both a yearly and ten year moving average. Vertical bar devides time period of initial analysis and recent management. Dark horizontal bar indicates time periods when tick related alopecia was observed.

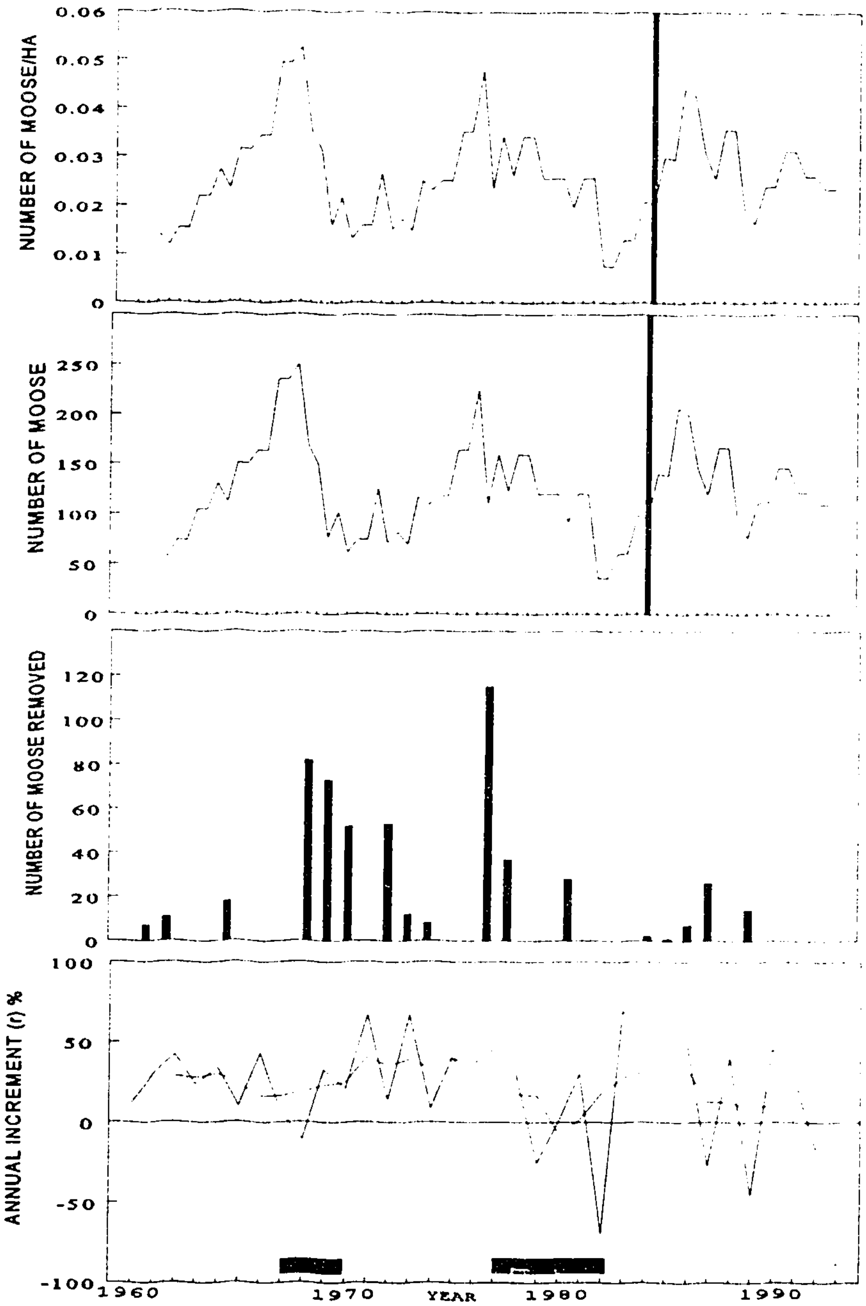

Fig. 5. Moose numbers, density, numbers removed and annual increment (r) expressed as a percent, with 5 year mean increment in the Isolation area 1960-93. Vertical bar divides time period of initial analysis and recent management. Dark horizontal bar indicates time periods when tick related alopecia was observed.

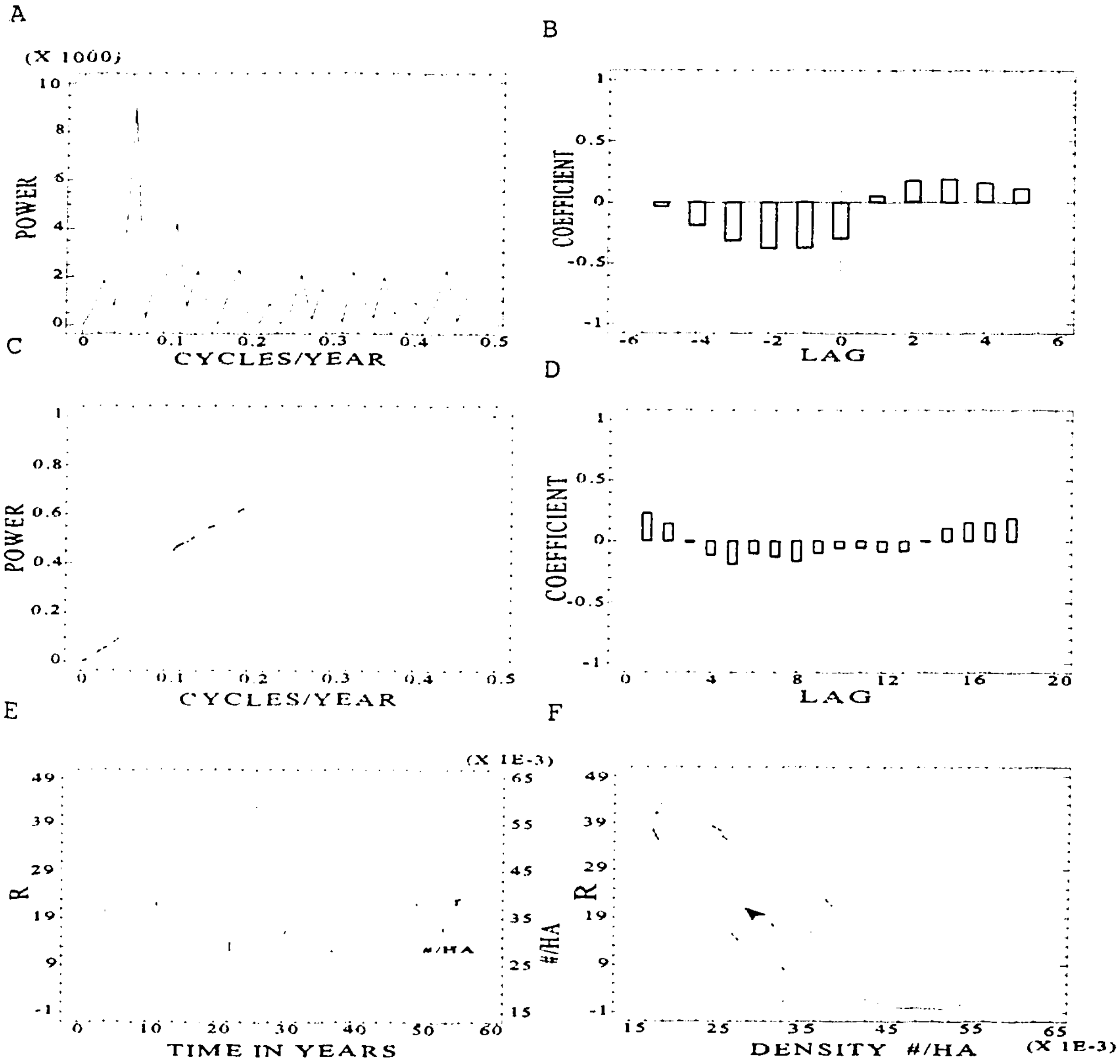

Fig. 6. Time series analysis of the main park moose population dynamics 1906-85. (A) Periodiogram of annual increment. (B) Crosscorrelation of annual increment and population density. (C) Integrated periodiogram of annual increment with 95% & 75% Kolmogorov-Smirnov bounds for uniform distribution of ordinates. (D) Autocorrelation of undifferenced annual increment with mean removed. (E) Plot of detrended and filtered (Spencers 21 term) patterns of density and annual increment. (F) Phase diagram of detrended and filtered (Spencers 21 term) patterns of density and annual increment.

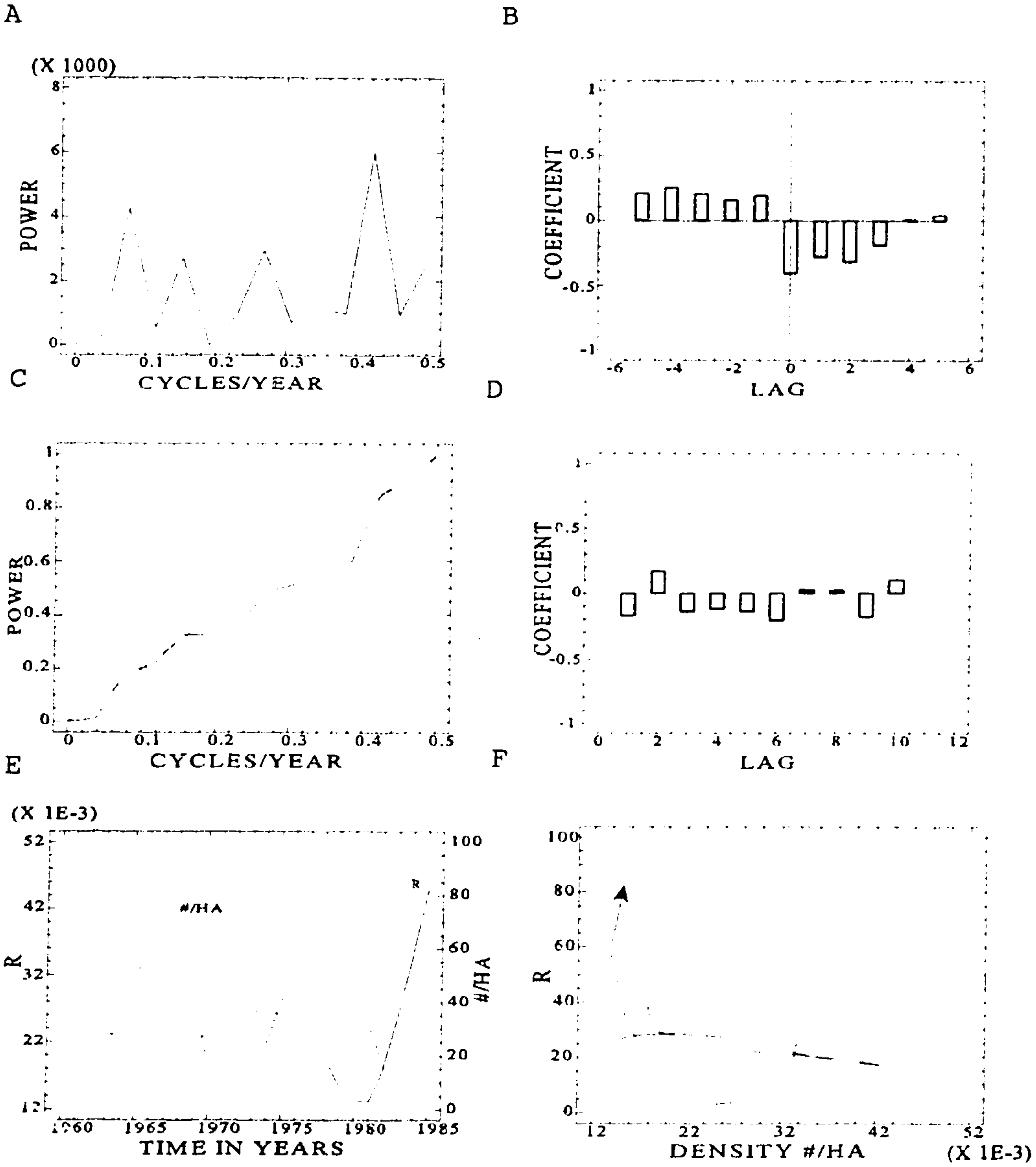

Fig. 7. Time series analysis of the Isolation area moose population dynamics, 1960-85 (A) Periodogram of annual increment, (B) Crosscorrelation of annual increment and population density, (C) Integrated periodogram of annual increment with 95% & 75% Kolmogrov-Smirnov bounds for uniform distribution of ordinates. (D) Autocorrelation of undifferenced annual increment with mean removed. (E) Plot of filtered (3 term) density and filtered (5 term then 3 term) annual increment. (F) Phase diagram of the same filtered density and annual increment.

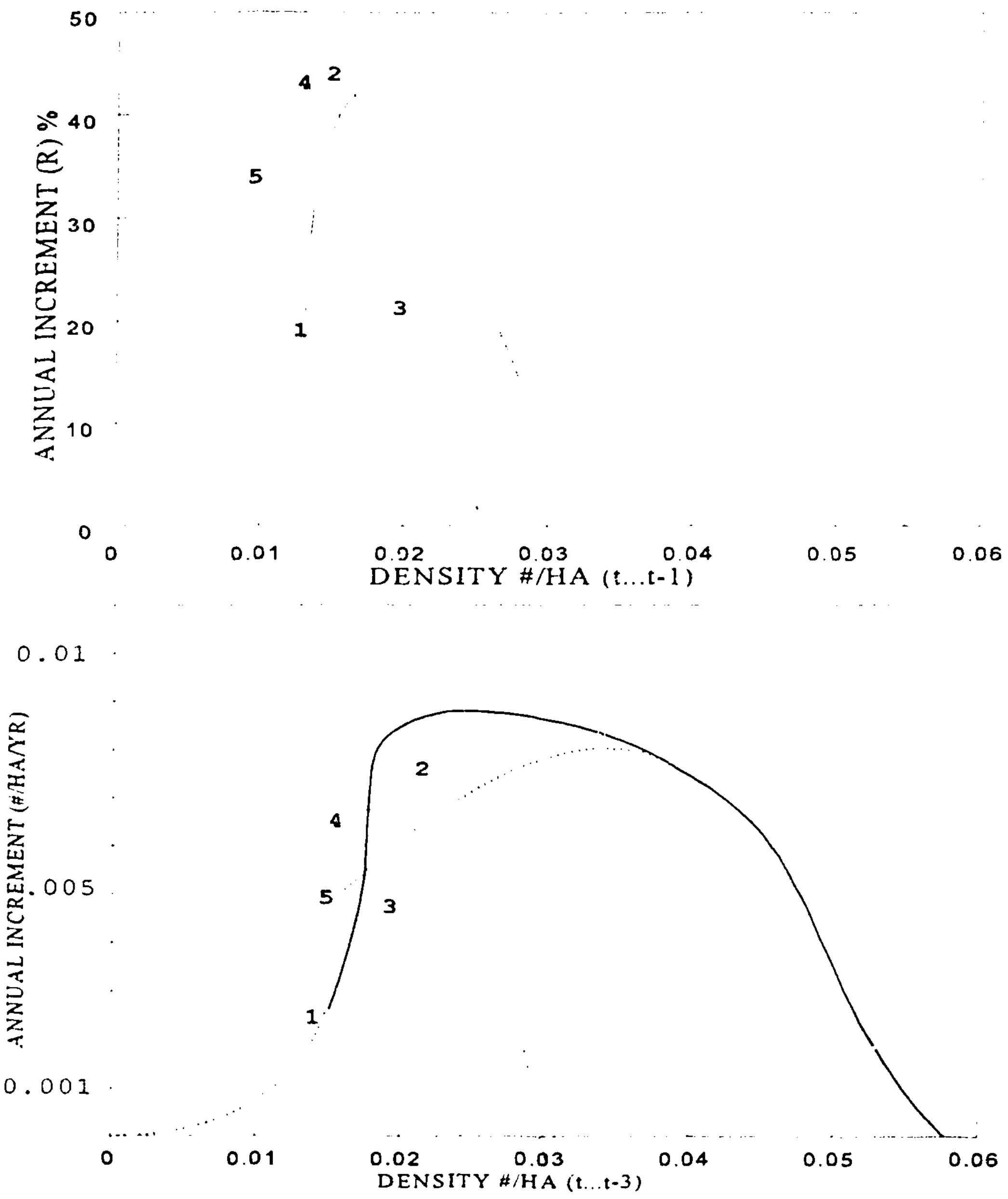

Fig. 8. Density-dependent annual population growth r (%) and r (per unit area) for moose at Elk Island, 1909-86. (1) Main park, 1909-40 & 1960-80. (2) Main park, 1941-60. (3) Main park, 1981-86. (4) Isolation, 1973-86. (5) Isolation area 1960-72.

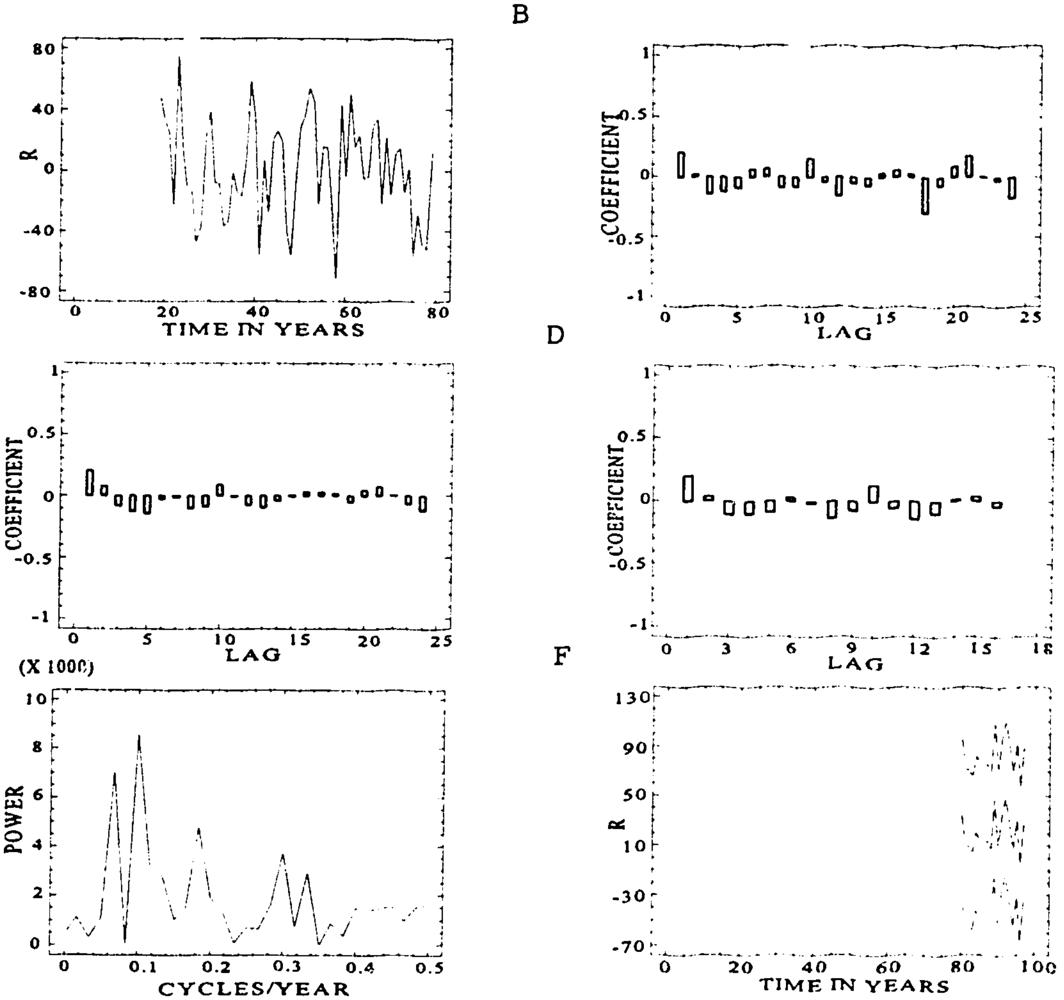

Fig. 9. ARIMA model (0,0,0)(0,1,1) 18 , of the main park moose population annual increment (r), 1906-85. (A) Single seasonally differenced annual increment. (B) Autocorrelation of one seasonal differenced annual increment. (C) Autocorrelation of residuals. (D) Partial autocorrelation of residuals. (E) Periodogram of residuals. (F) Plot of forcast of estimates from the model with 95% confidence intervals.

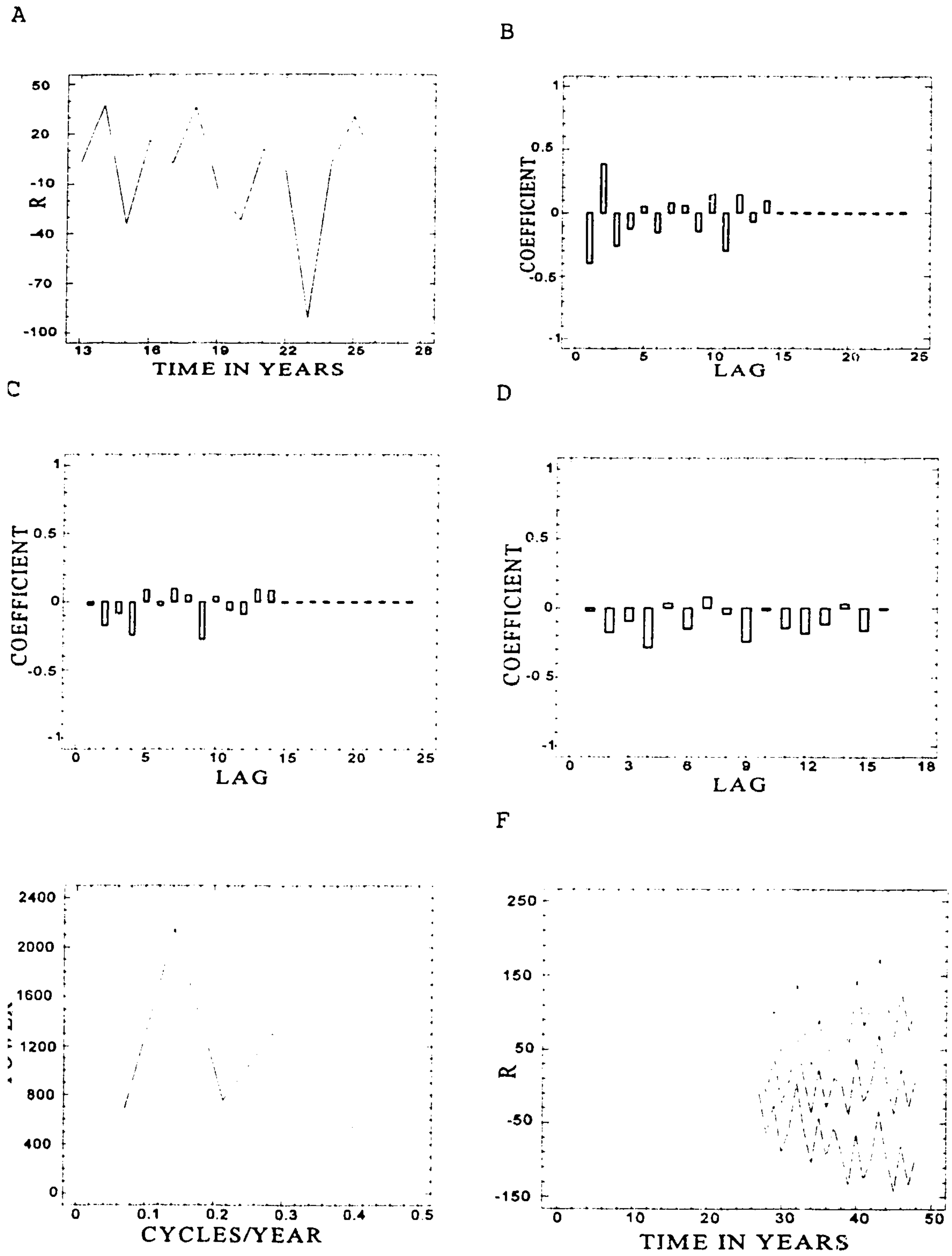

Fig. 10. ARIMA model (0,0,2)(0,1,1)11 for the Isolation area moose population annual increment (r), 1960-85. (A) Single seasonally differenced annual increment. (B) Autocorrelation of seasonally differenced annual increment. (C) Autocorrelation of residuals. (D) Partial autocorrelation of residuals. (E) Periodogram of residuals. (F) Plot of model estimates with 95% confidence intervals.

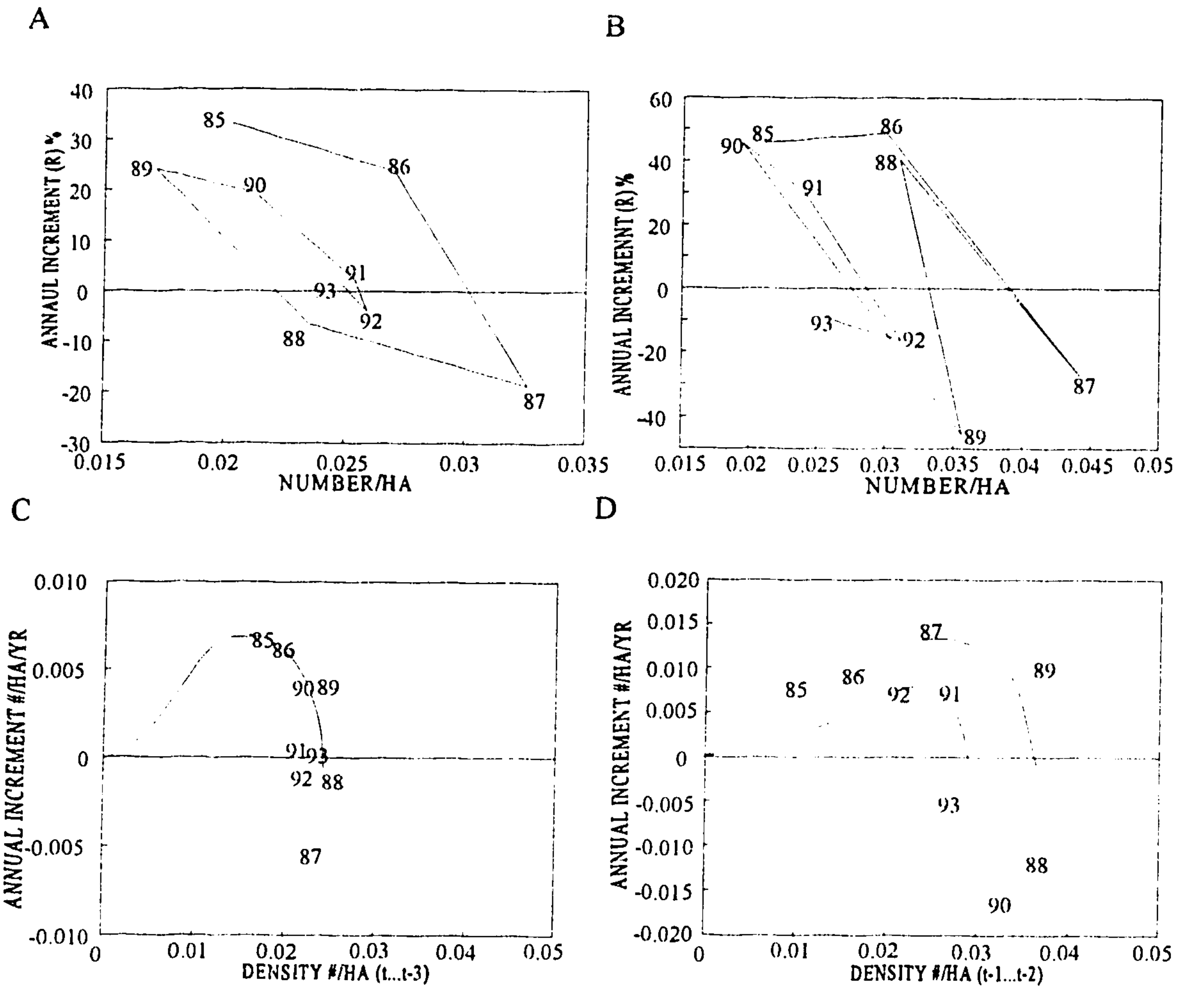

Fig. 11. Recent moose population response to management (1985-93). (A) Phase diagram of density vs annual increment (r) in the main park. (B) Phase diagram of density vs annual increment (r) in the Isolation area. (C) Annual increment (per unit area) density dependent carrying capacity for the main park area moose population. (D) Annual increment (per unit area) density dependent carrying capacities for the Isolation area moose population before and after fence closure.

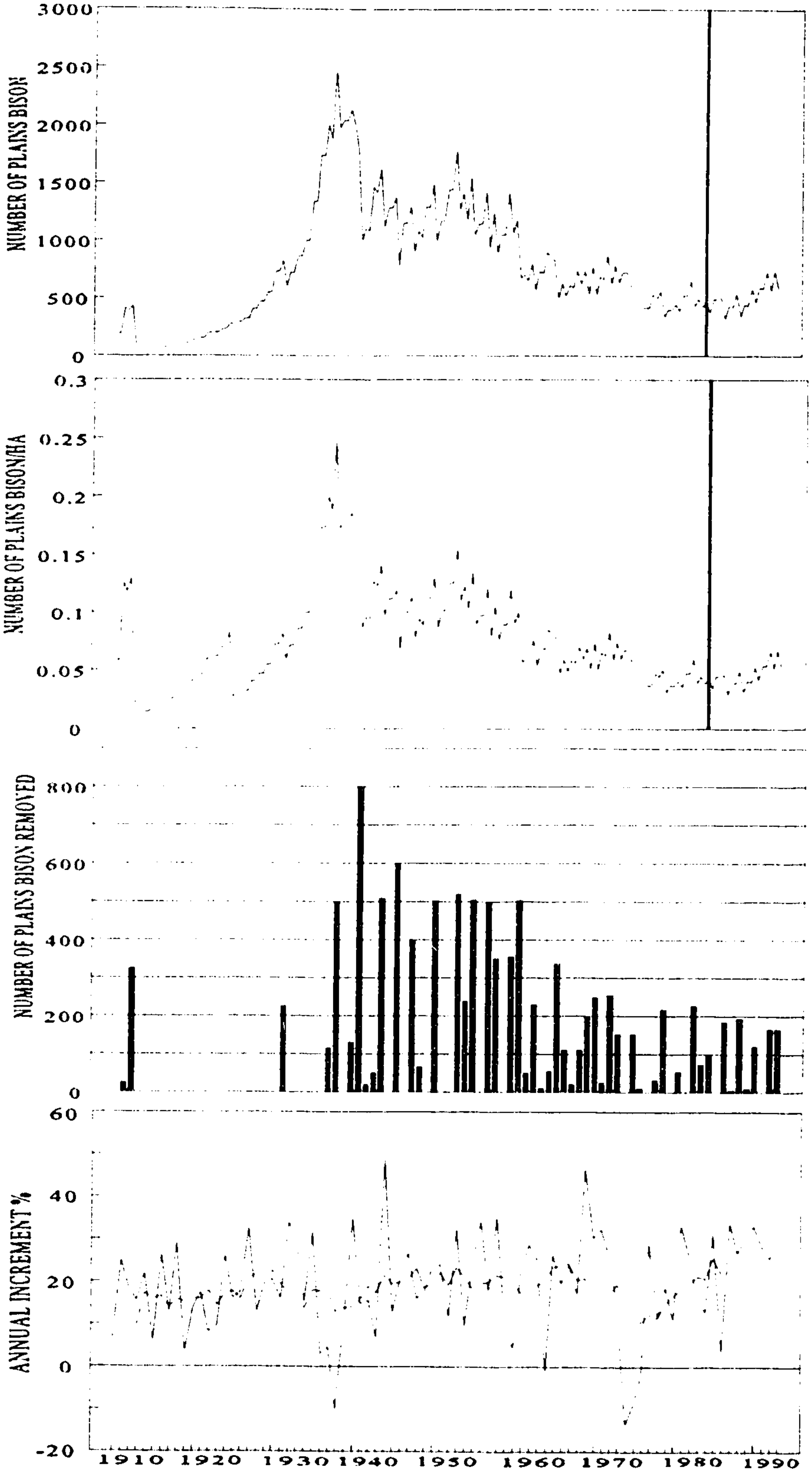

Fig. 12. Plains bison numbers, density, numbers removed by management and annual increment (r) expressed as a percent, 1907-93. Vertical bar devides the time period of initial analysis and recent management. Annual increment is displayed as yearly and ten year mean.

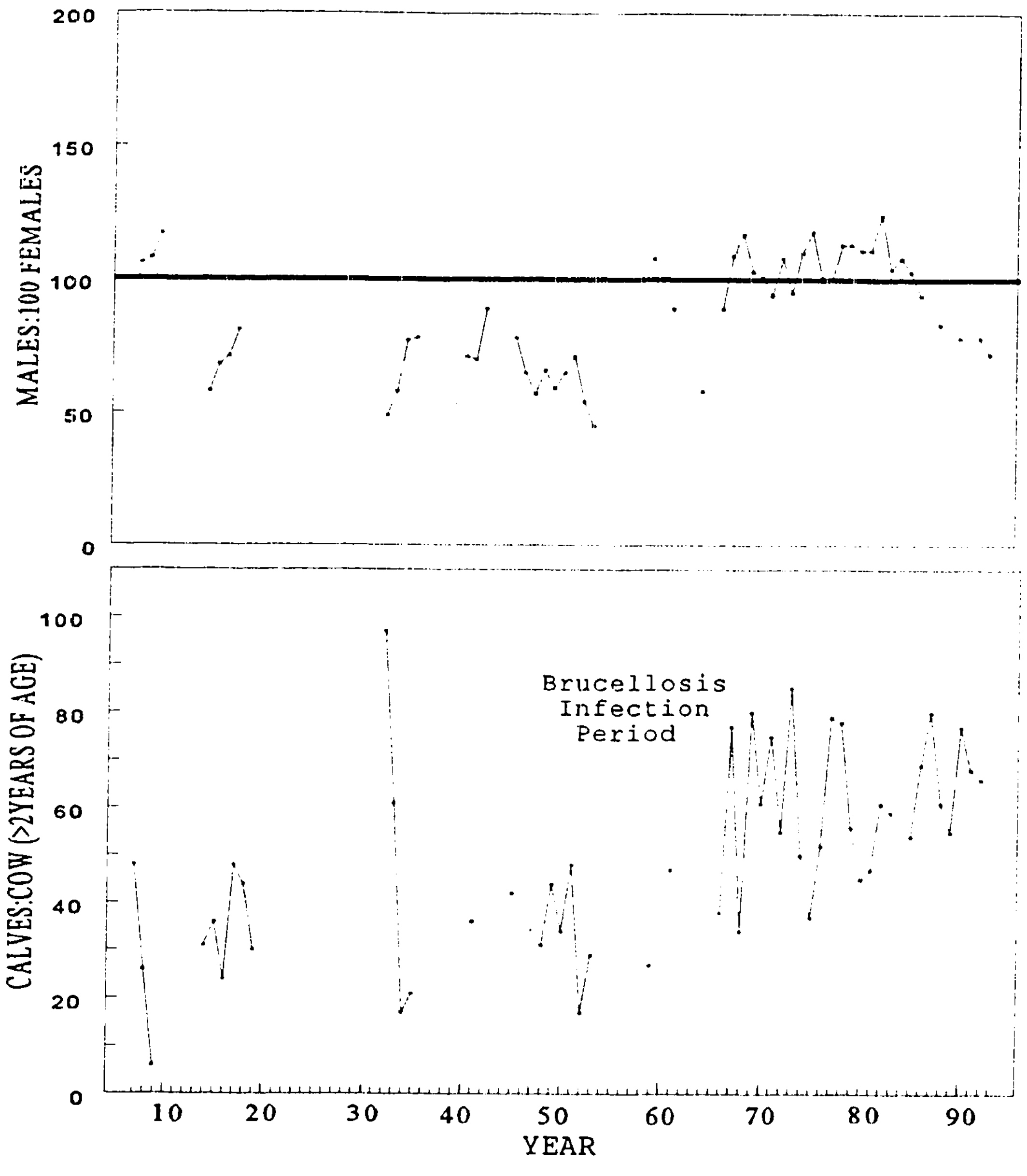

Fig. 13. Plains bison sex ratio (males:100 females) and calf cow ratio (calves:100 females two years of age and older), 1907-93. Period of brucellosis is indicated.

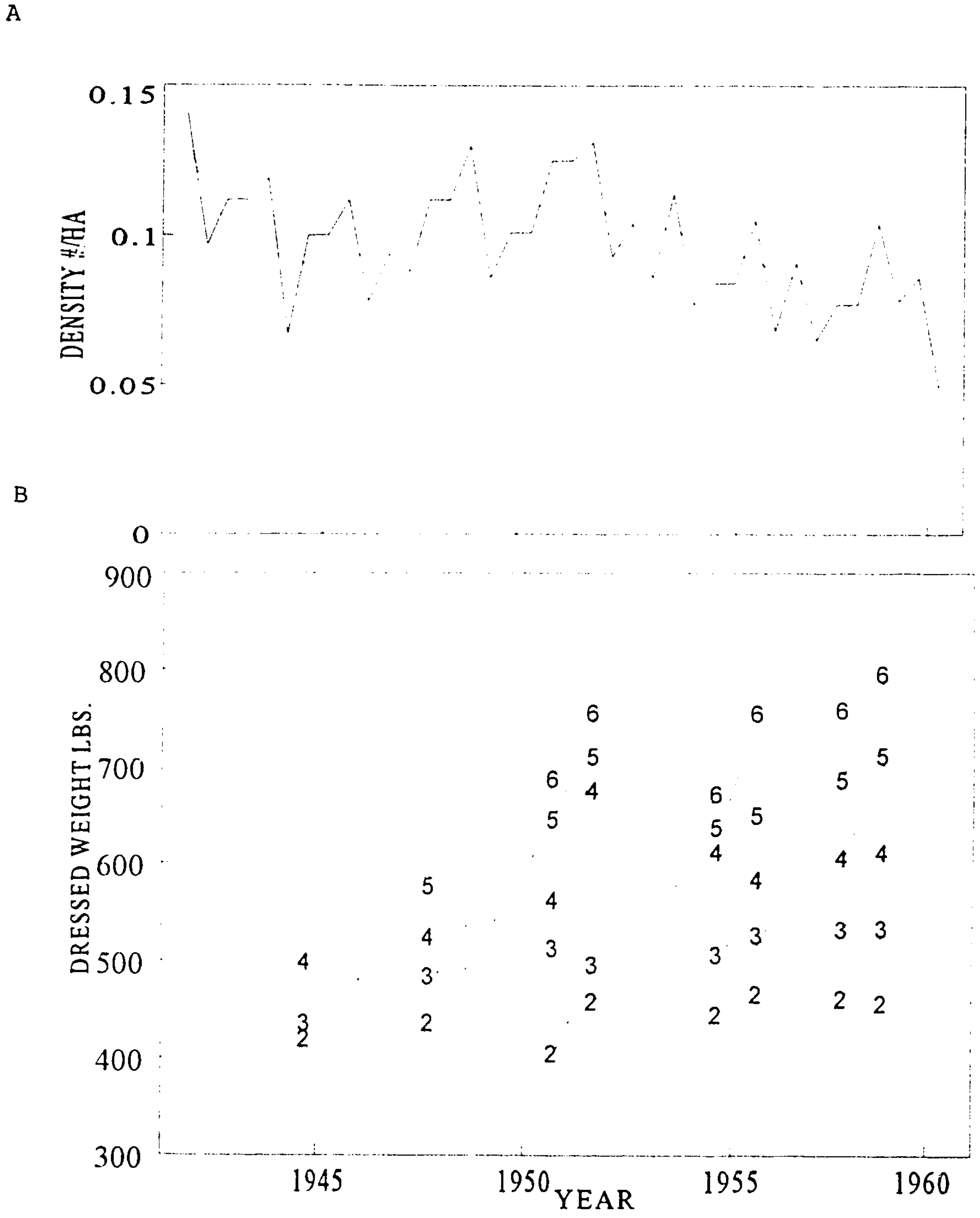

Fig. 14. Dressed weights of plains bison males (2-6 years of age) compared to population density during the period of 1945-60. (A) Density of plains bison in the main park. (B) Dressed weights of each cohort 2-6 years of age. Solid lines indicate the change in weight of a cohort through time. Dotted lines indicate the change in weights of each age class through time.

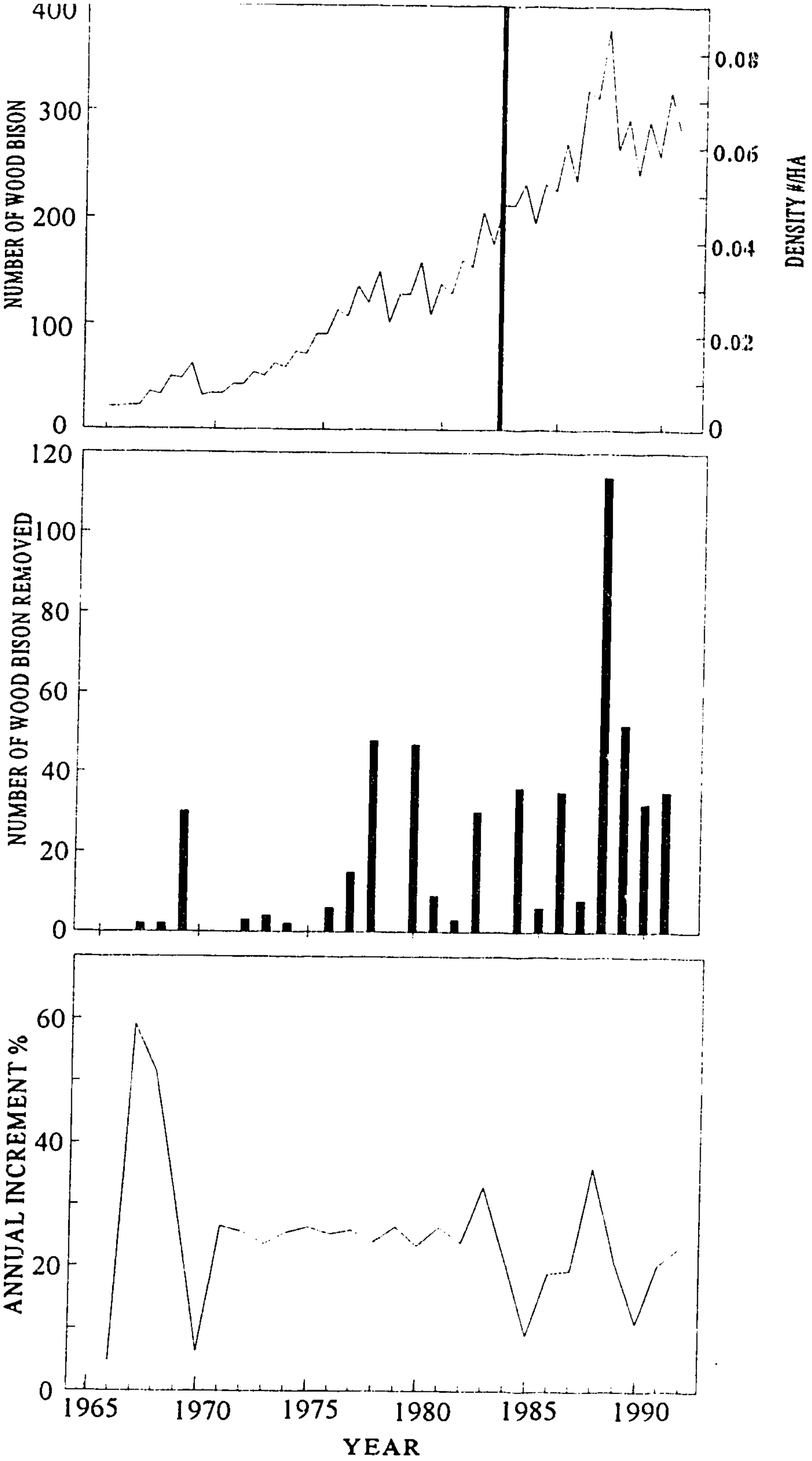

Fig. 15. Wood bison population numbers, density, numbers removed through management and annual incremental rate of population increase (r) expressed as a percent, 1965-92. Vertical bar divides the time of initial analysis from the recent period of management.

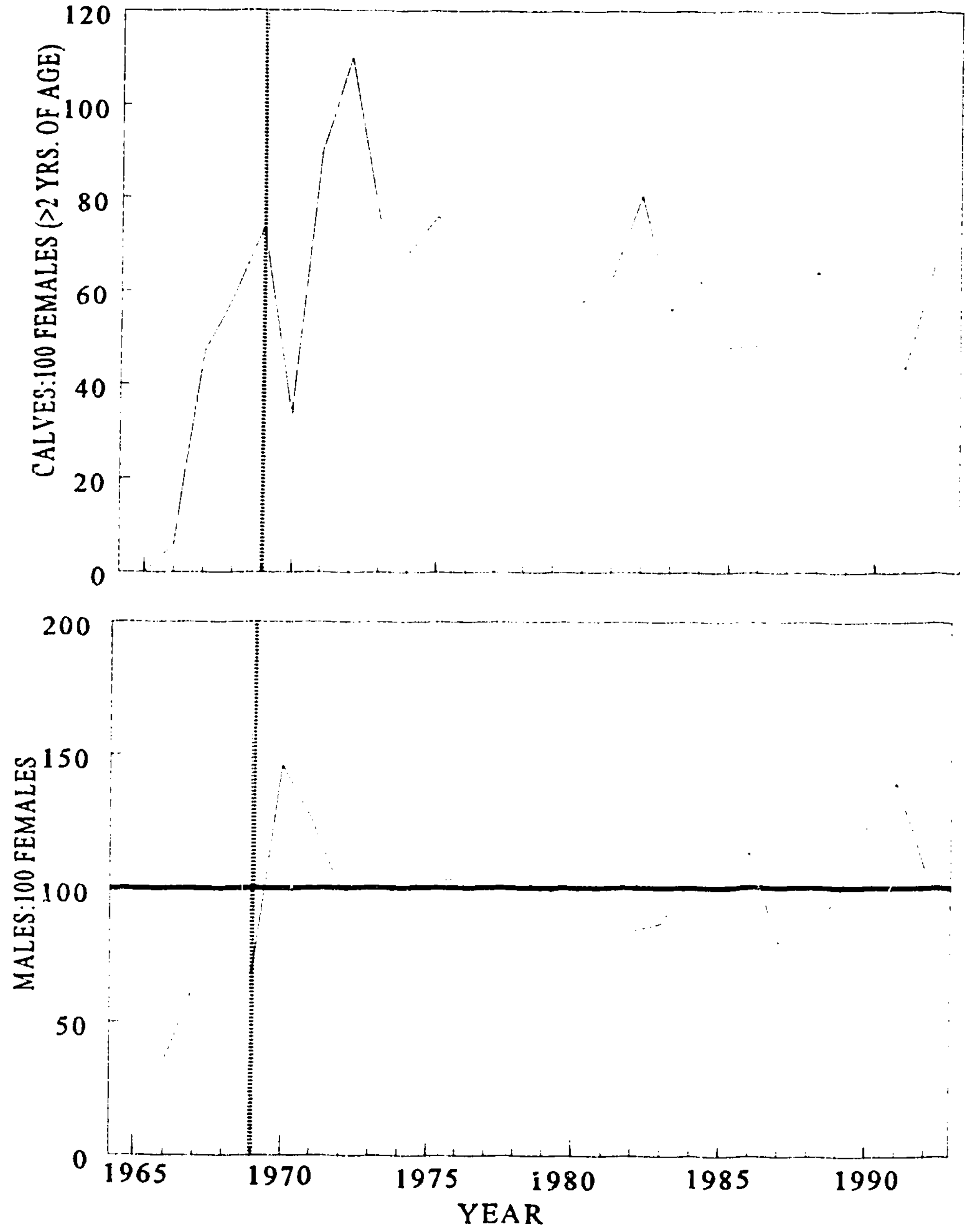

Fig. 16. Wood bison population structure. Sex ratio and number of calves:100 females 2 years of age and older. The 1969 slaughter of Brucellosis infected females is indicated by a dashed line.

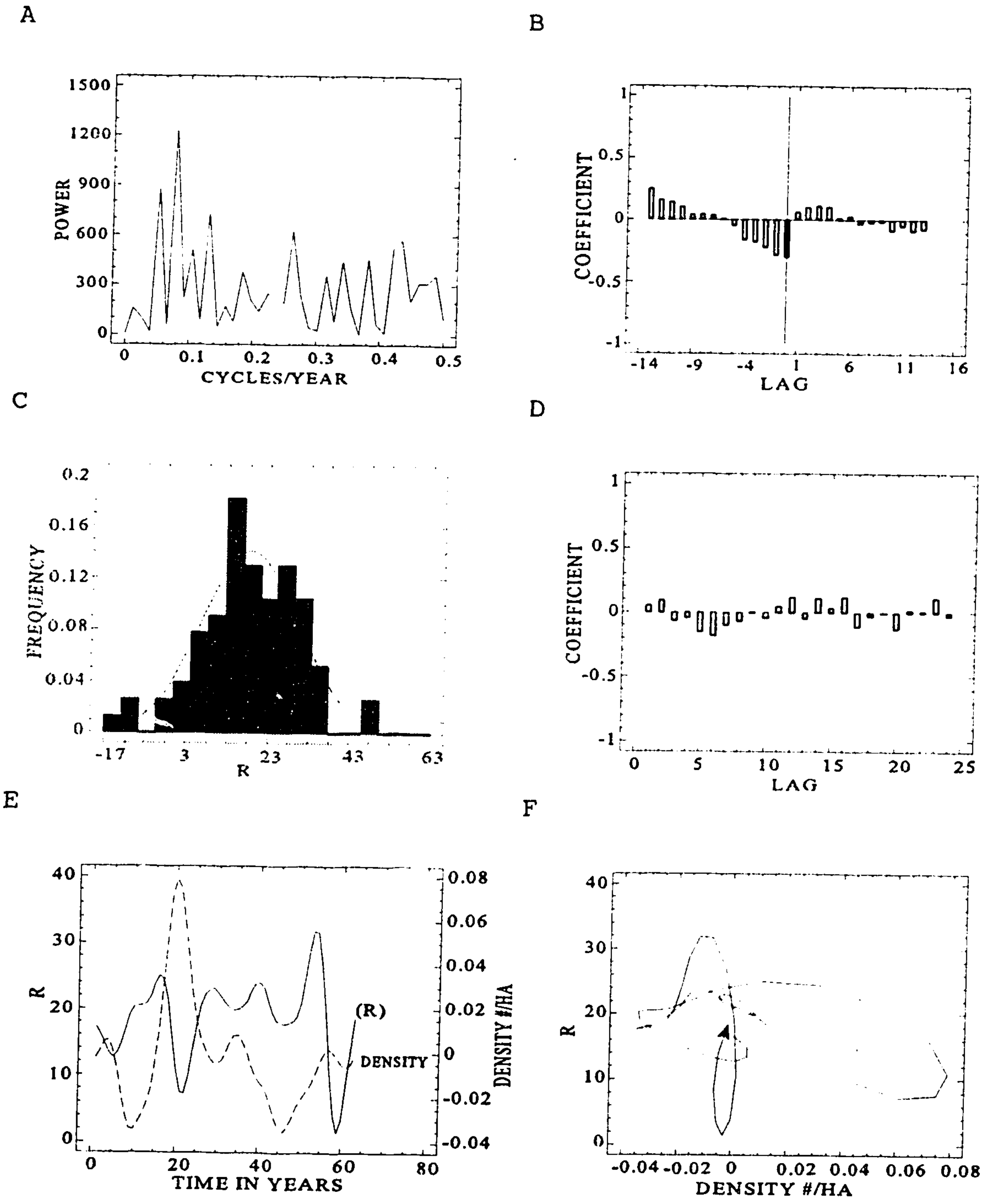

Fig. 17. Plains bison time series analysis. (A) Periodogram of annual increment(r) with mean removed. (B) Crosscorrelation of (r) and second order detrended density. (C) Distribution of (r) on the normal curve. (D) Autocorrelation of (r). (E) Filtered (Spencers 15 term) detrended density and (r). (F) Phase diagram of detrended filtered density vs. filtered (r).

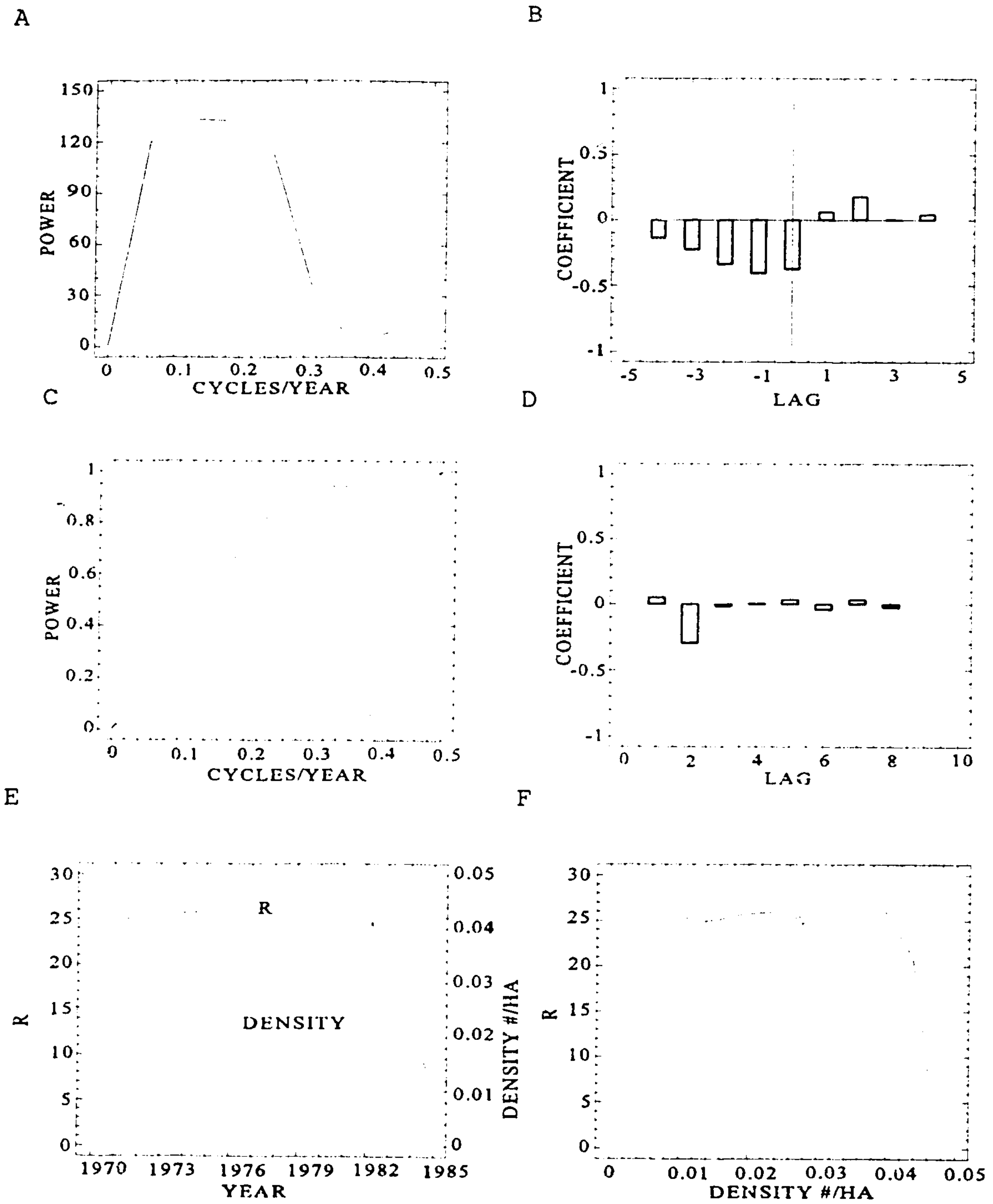

Fig. 18. Wood bison time series analysis for the period 1965-85. (A) Periodogram of annual increment (r). (B) Crosscorrelation of (r) and density. (C) Integrated periodogram with 95% and 75% Kolmogorov-Smirnov bounds of uniform distribution of ordinates. (D) Autocorrelation of (r). (E) Filtered (3-term unweighted) density and (r). (F) Phase diagram of filtered density vs (r).

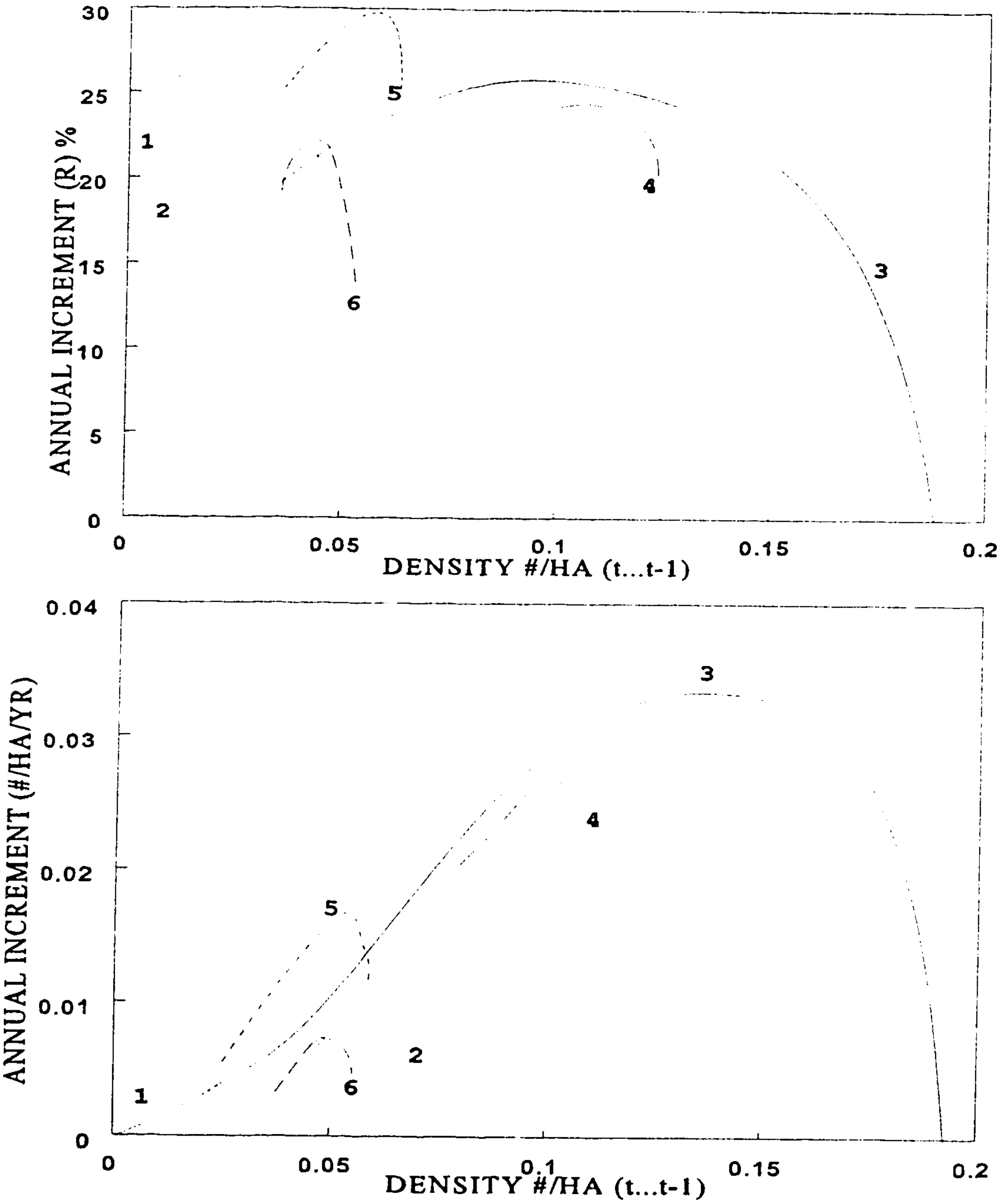

Fig. 19. Density-dependent percent annual incremental population growth (r) and annual increment (#/ha/yr) for bison at Elk Island, 1910-86. (1)Wood bison, 1970-86. (2)Plains bison, 1910-22. (3)Plains bison, 1923-40. (4)Plains bison, 1941-60. (5)Plains bison, 1961-75. (6)Plains bison, 1976-86.

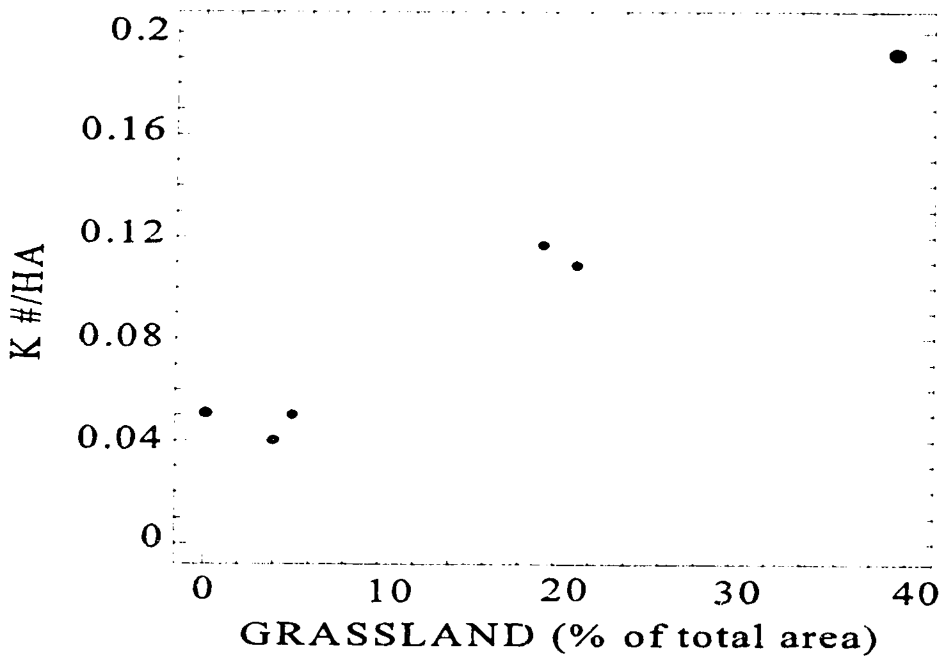

Fig. 20. Plains bison carrying capacity (K) density in numbers/ha compared to the percent of the main park covered in grassland habitat. Linear model: $Y = 0.035+0.0038X$, $SE = 0.01$, $R^2 = 0.97$

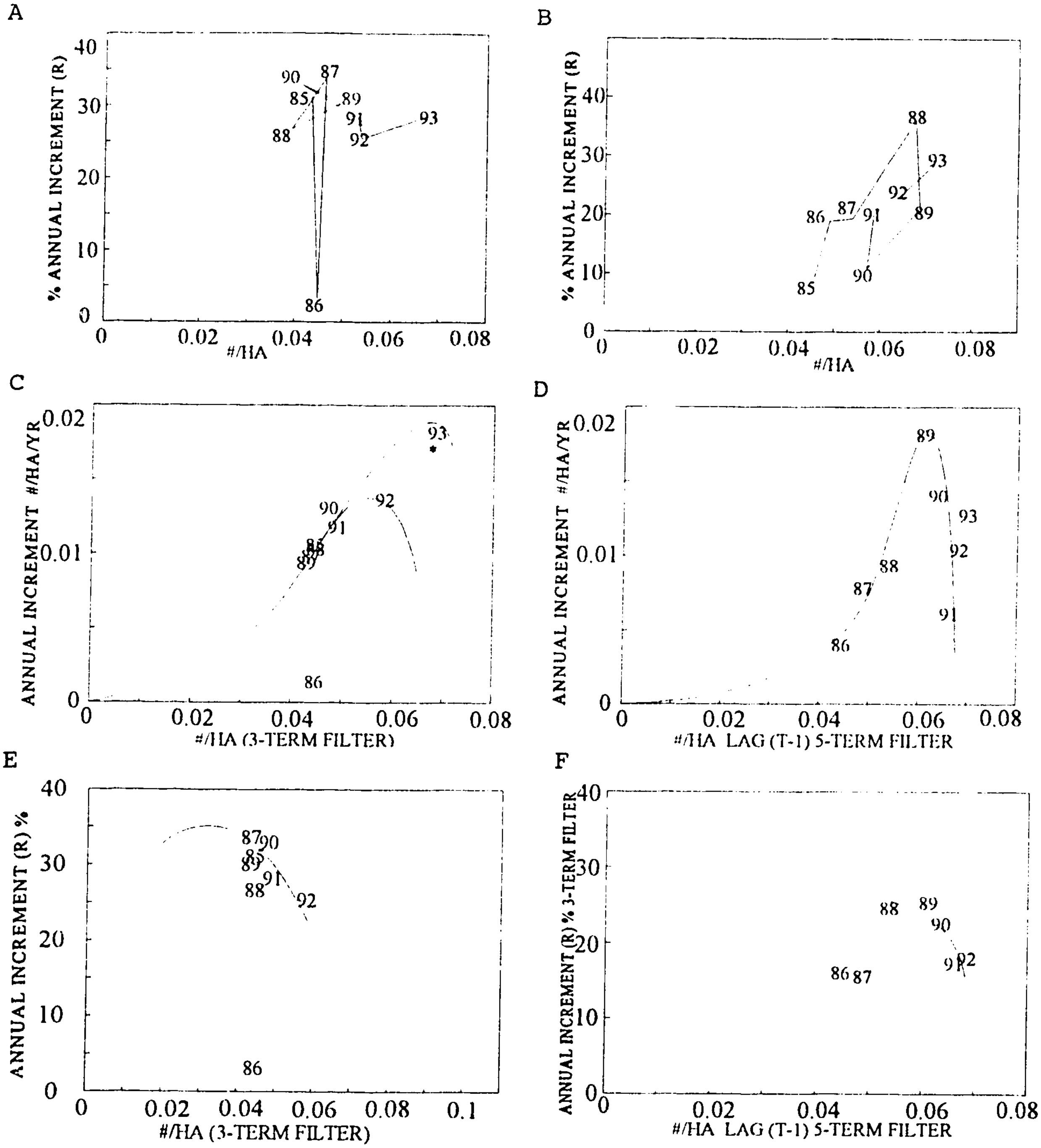

Fig. 21. Bison population dynamics,1986-93 . (A) Phase diagram of plains bison density vs (r). (B) Phase diagram of wood bison density vs (r). (C) Plains bison lagged and filtered density vs annual increment (#/ha/yr) with two alternative curves fit to the data. *The 1993 data point unlagged and unfiltered. (D) Wood bison annual increment (#/ha/yr) vs lagged and filtered density. (E) Plains bison % annual increment (r) vs lagged and filtered densiity. (F) Wood bison % annual increment (r) filtered vs lagged and filtered density.

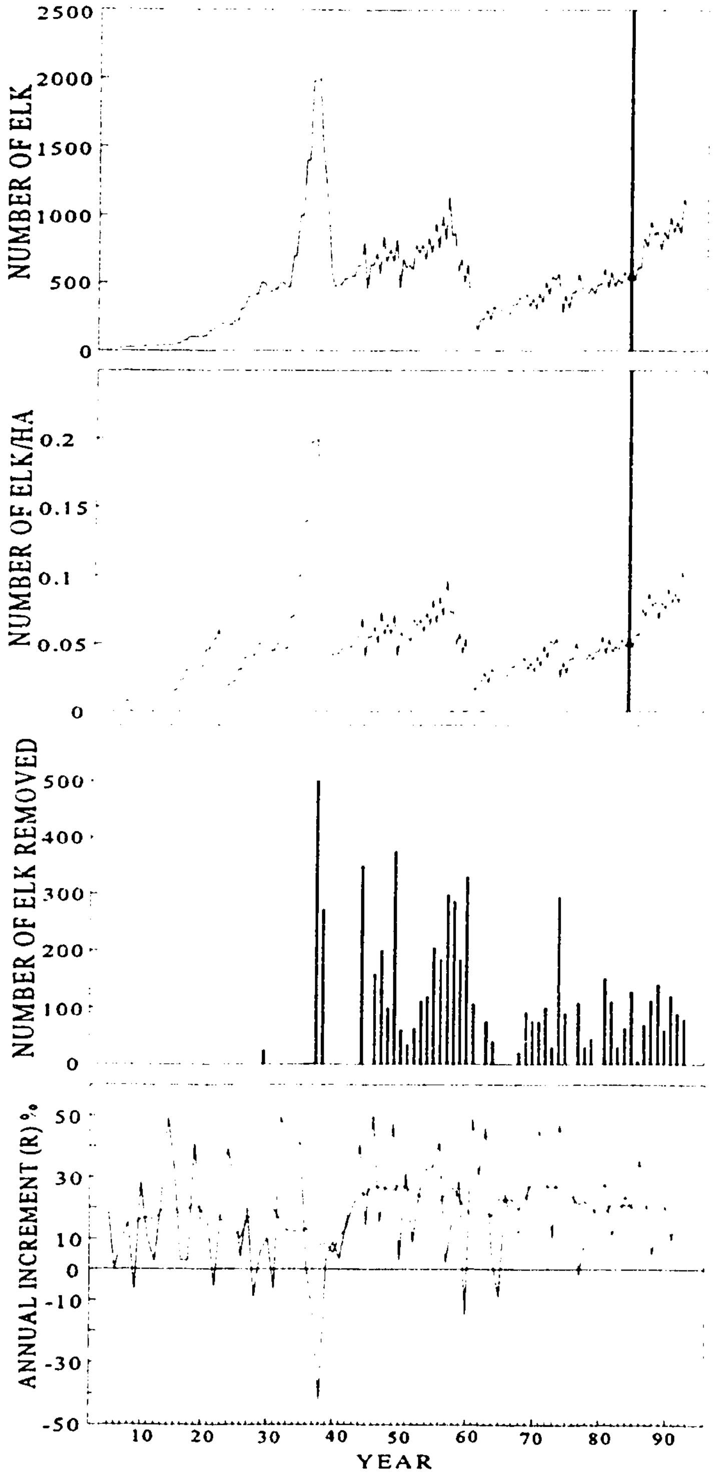

Fig. 22. Elk population dynamics, main park 1906-93. Includes total number, density, number removed by management and annual increment (r) expressed as a percent. Verticle bar indicates most recent period of analysis. Annual increment is displayed as yearly and ten year mean.

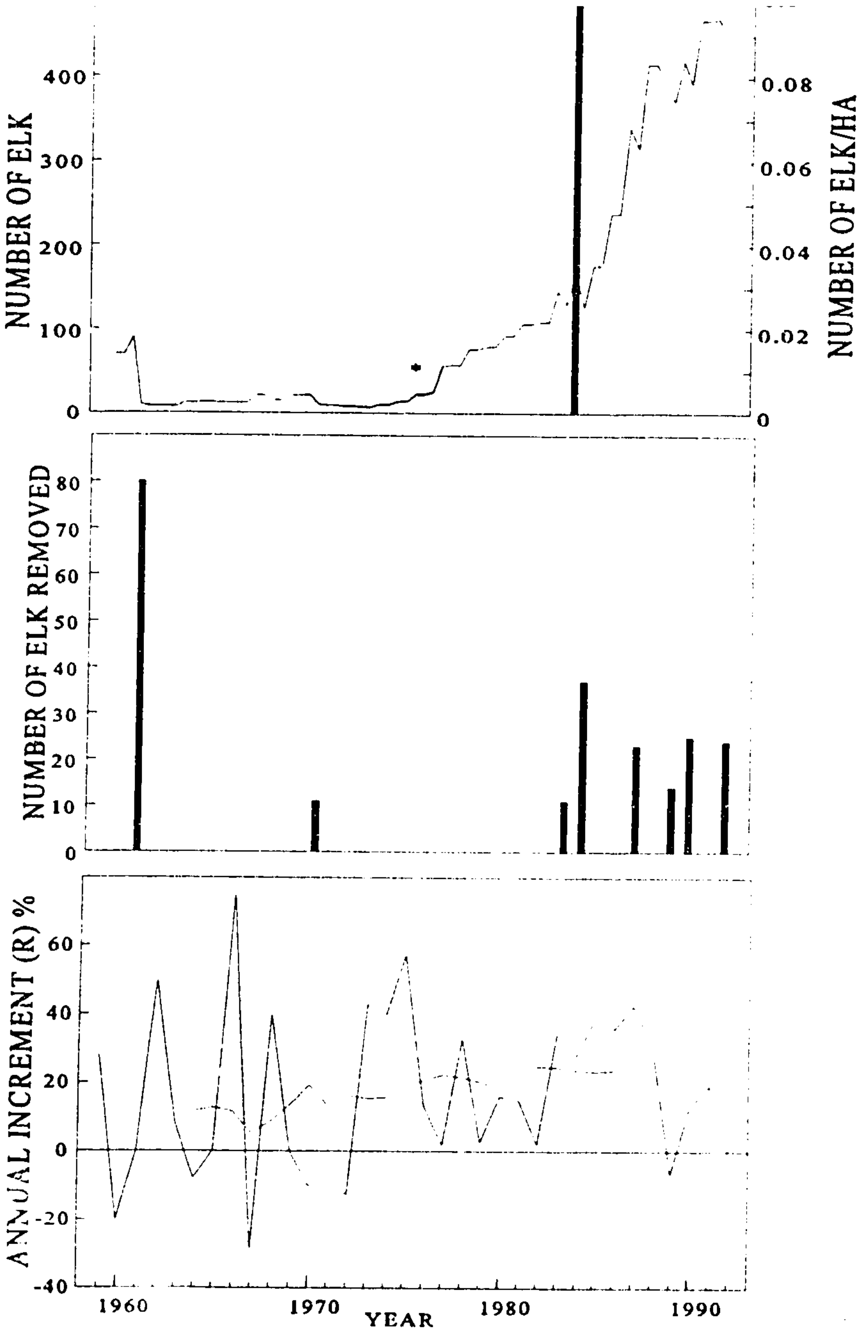

Fig. 23. Elk population numbers, density, number removed by management, and percent annual increment (r) in the Isolation area from 1959-92. Vertical bar devides time period of initial analysis and recent management. Annual increment is displayed as yearly (r) and ten year mean. * In 1977, 29 elk were added to the Isolation area from the main park.

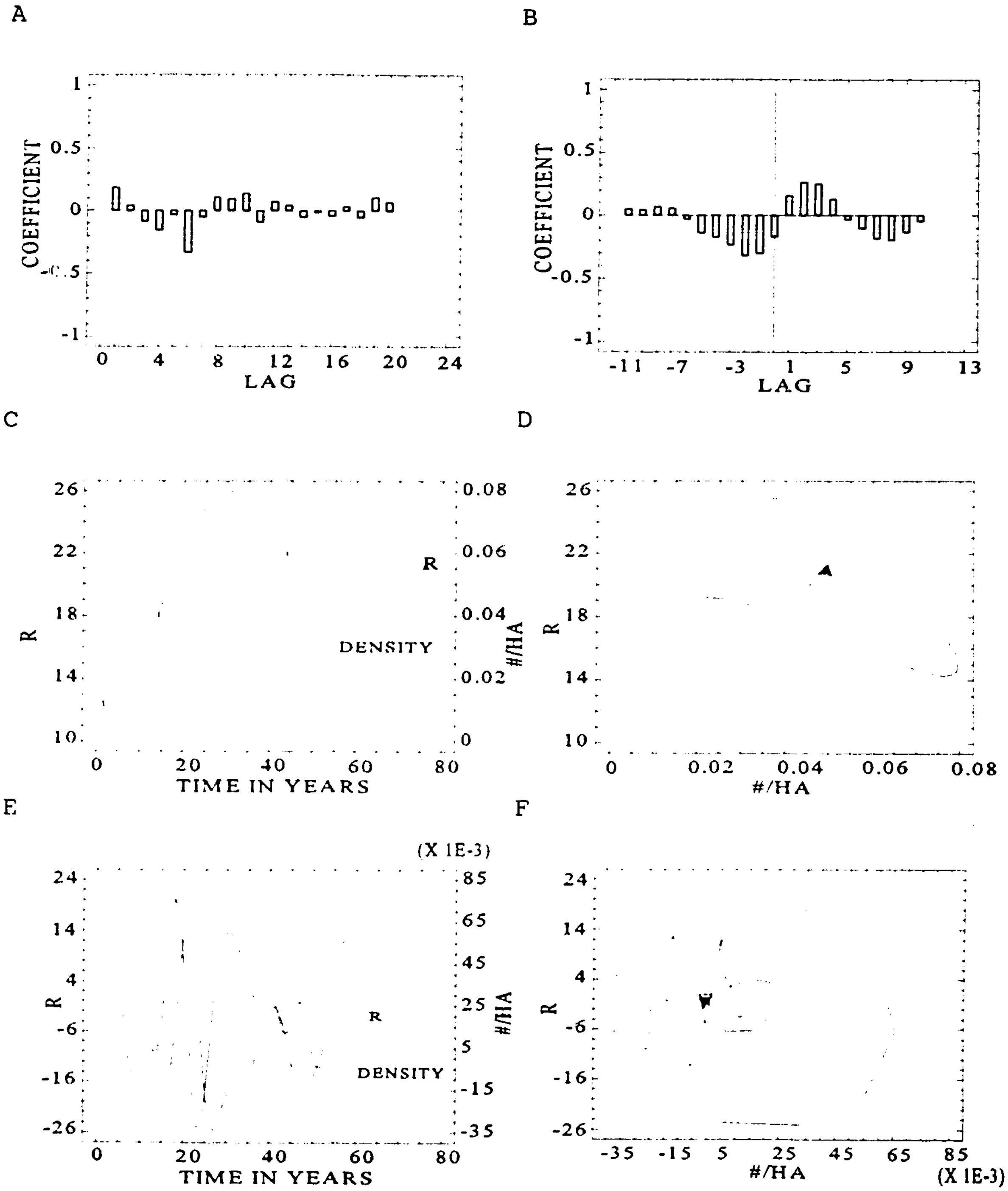

Fig. 24. Time series analysis of (r) and density for elk in the main park, 1906-85. (A) Autocorrelation of (r). (B) Crosscorrelation of (r) and density. (C) Plot of the fifth order polynomial trend of density and (r). (D) Phase diagram of the same trend of density vs (r). (E) Plot of density and (r) with the trend and noise removed by Spencers 15 term filter. (F) Phase diagram of density vs (r) with the trend and noise removed by Spencers 15 term filter.

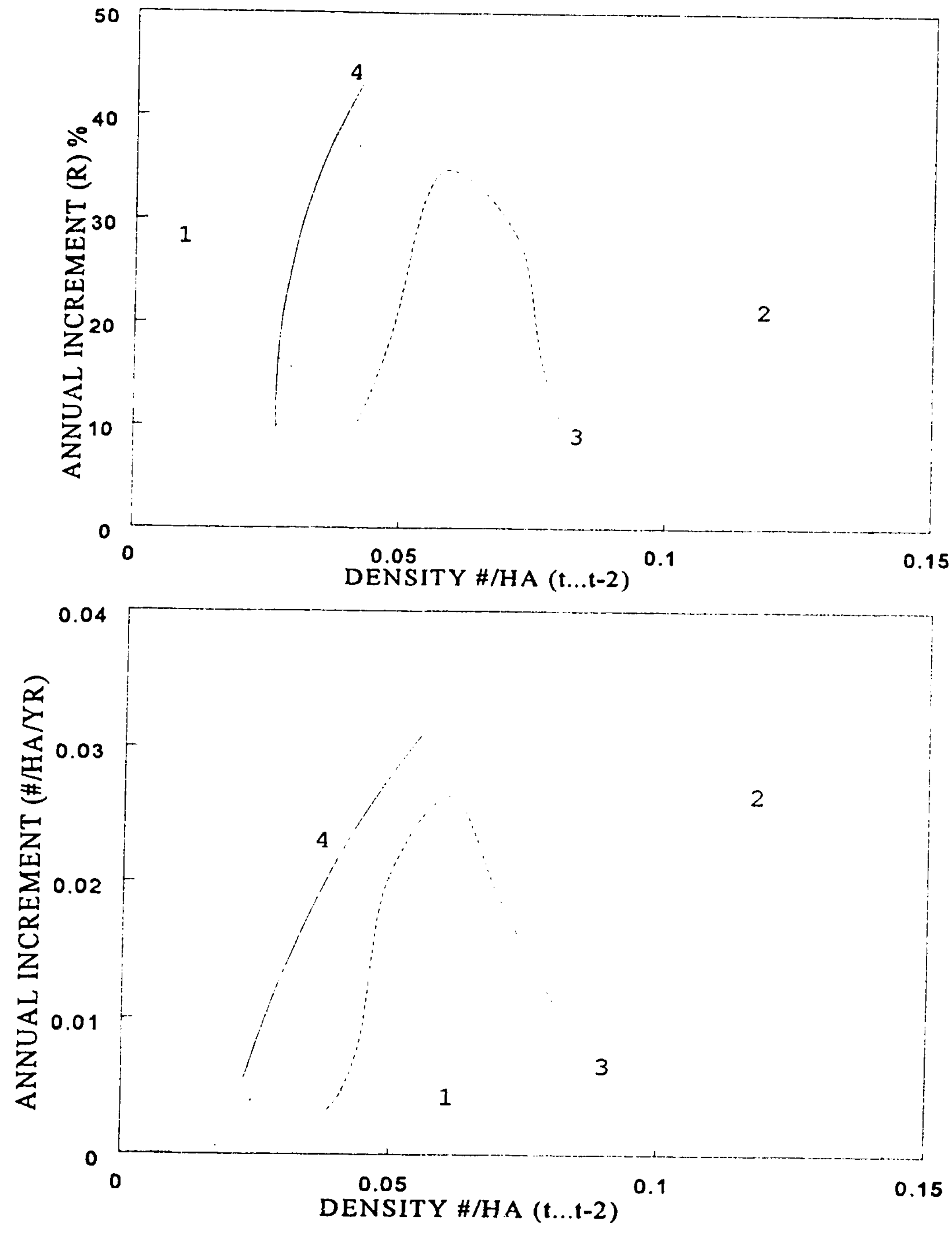

Fig. 25. Density-dependent percent annual incremental population growth (r) and annual increment (#/ha/yr) for elk in the main park area. (1)1906-22. (2)1923-40. (3)1941-60. (4)1960-84.

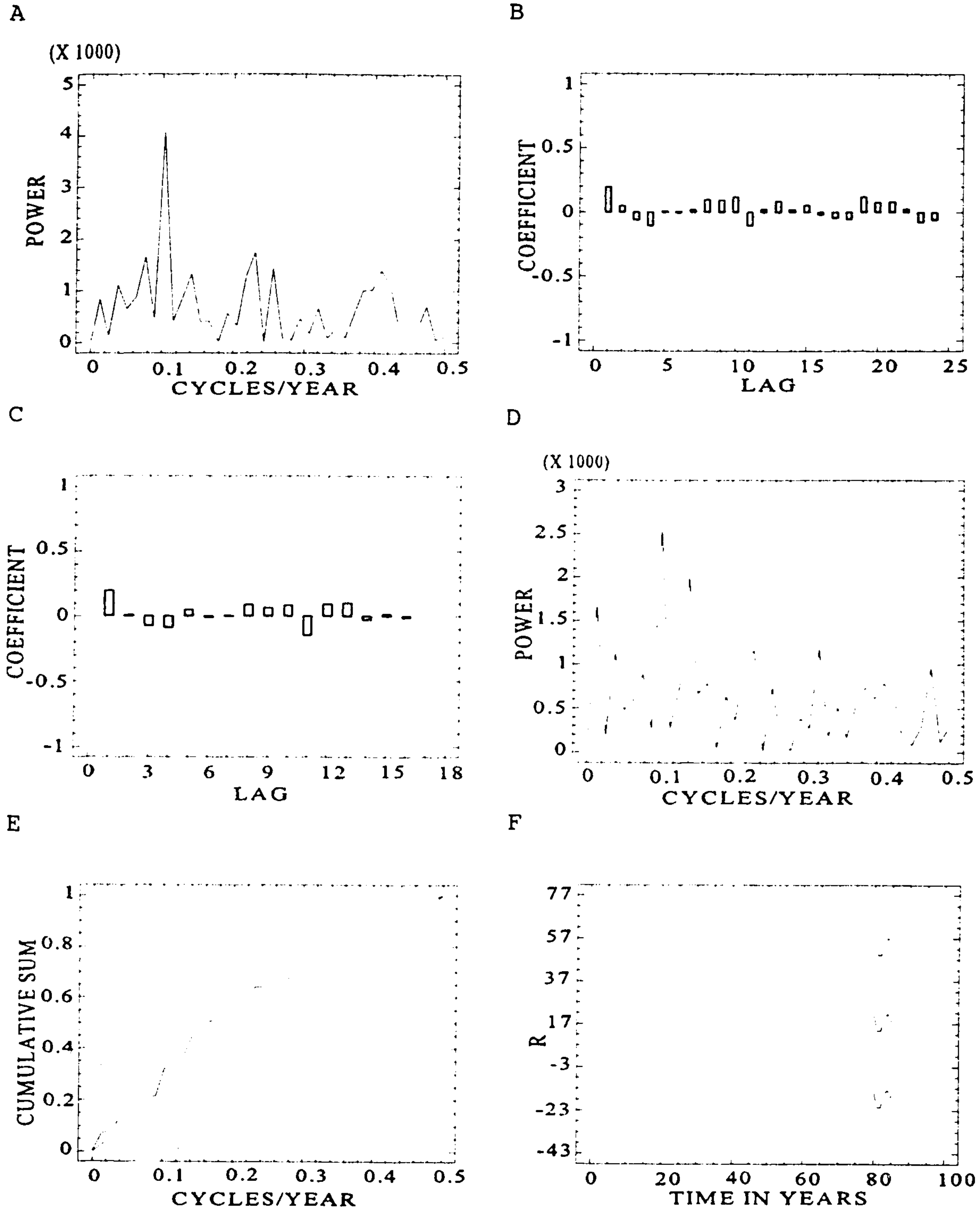

Fig. 26. ARIMA model of the main park elk population annual increment (r), 1906-85. (A) Periodogram of (r). (B) Autocorrelation of model residuals. (C) Partial autocorrelation of model residuals. (D) Periodogram of model residuals. (E) Integrated periodogram of model residuals. (F) ARIMA model forcast of six years.

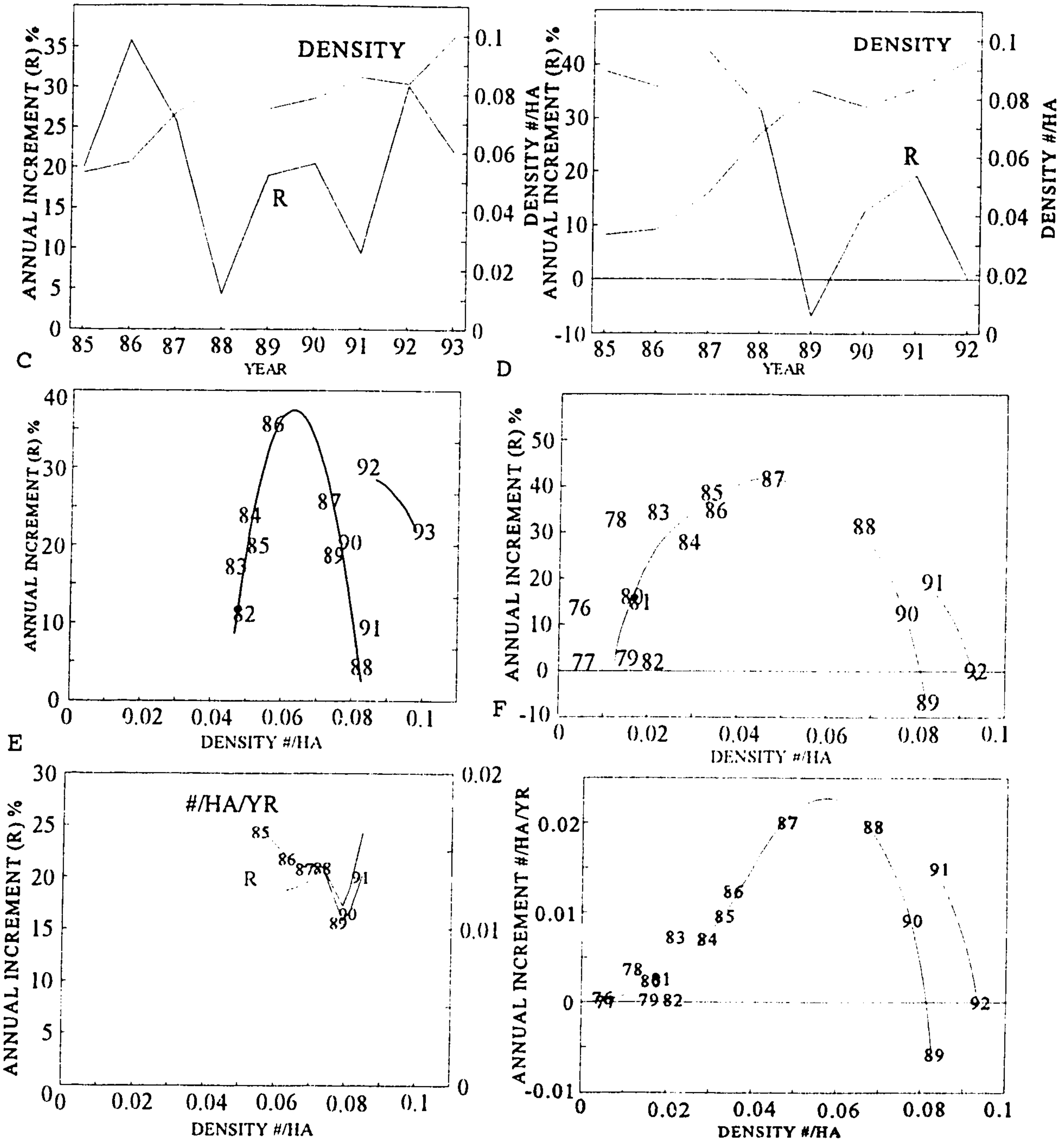

Fig. 27. Recent elk population response to management (1985-93). (A) Density and annual increment (r) expressed as a percent for the main park. (B) Density and annual increment (r) expressed as a percent for the Isolation area. (C) Percent annual increment (r) vs density in the main park. (D) Percent annual increment vs density in the Isolation area. (E) Filtered (5-term) annual increment (#/ha/yr) and percent annual increment vs density in the main park, 1985-91. (F) Annual increment (#/ha/yr) vs density in the Isolation area, 1976-92.

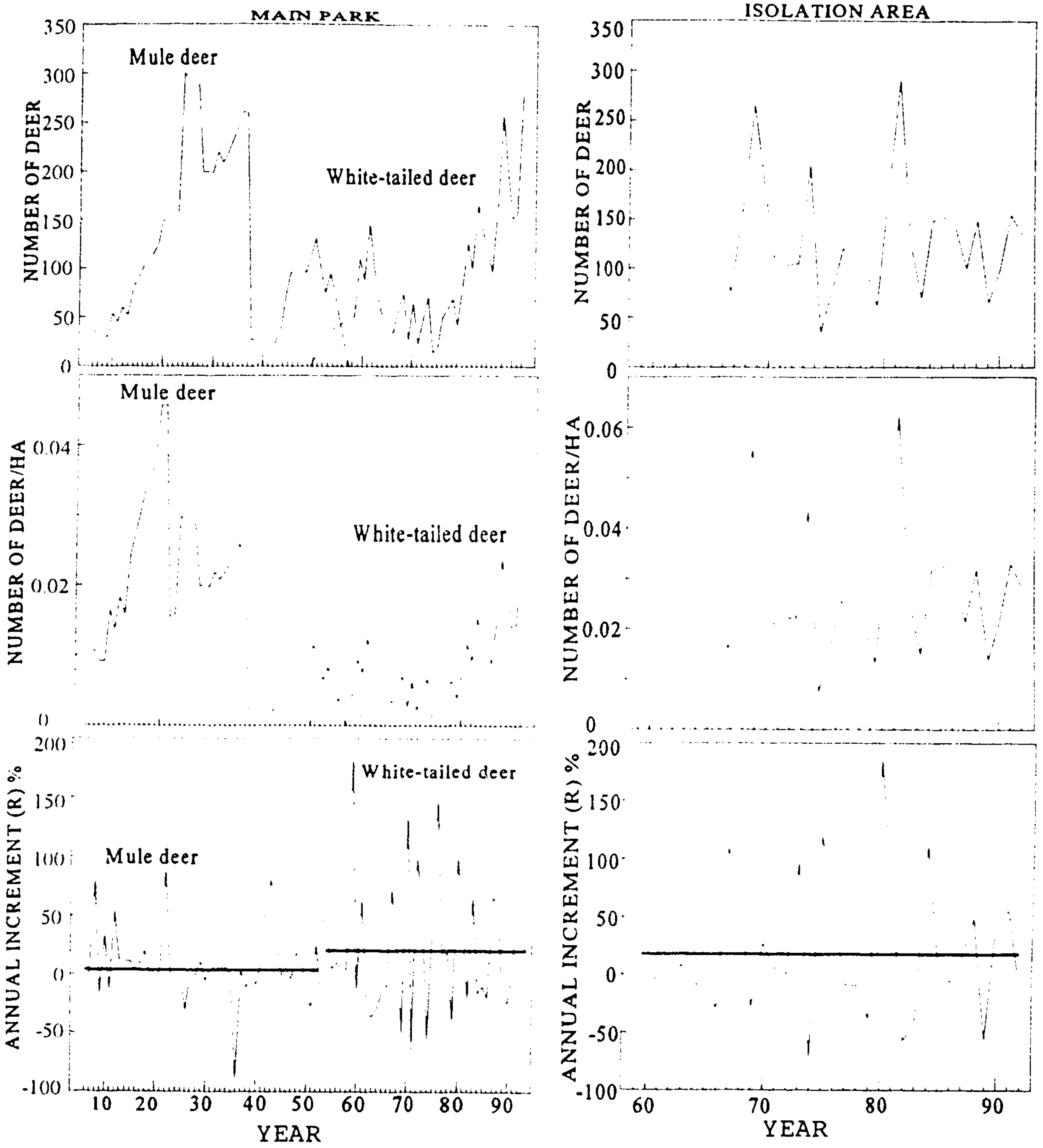

Fig. 28. White-tailed and mule deer population dynamics in the Main Park, 1906-93 and white-tailed deer population dynamics in the Isolation area from 1959-92. This includes deer numbers, density, and annual increment (r) expressed as a percent. Horizontal line indicates mean (r) for the period indicated.

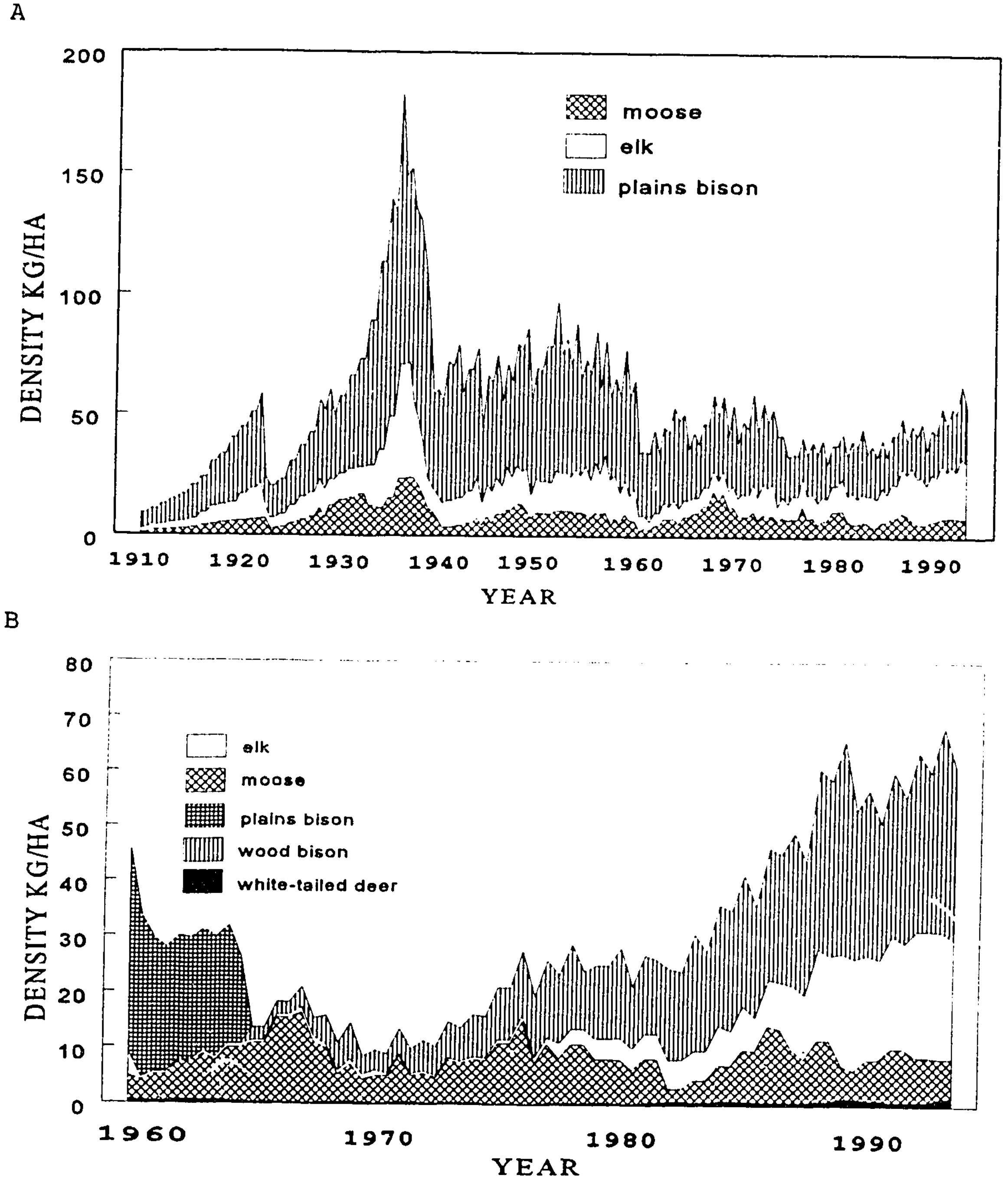

Fig. 29. Total standing stock biomass (kg/ha), of all ungulates in (A) the Main Park and (B) the Isolation Area, from 1910 to 1993. Note that the white-tailed deer density is not included in the main park as the biomass density is generally less than 1 kg/ha throughout the period of record and thus cannot be seen on a graph at this scale.

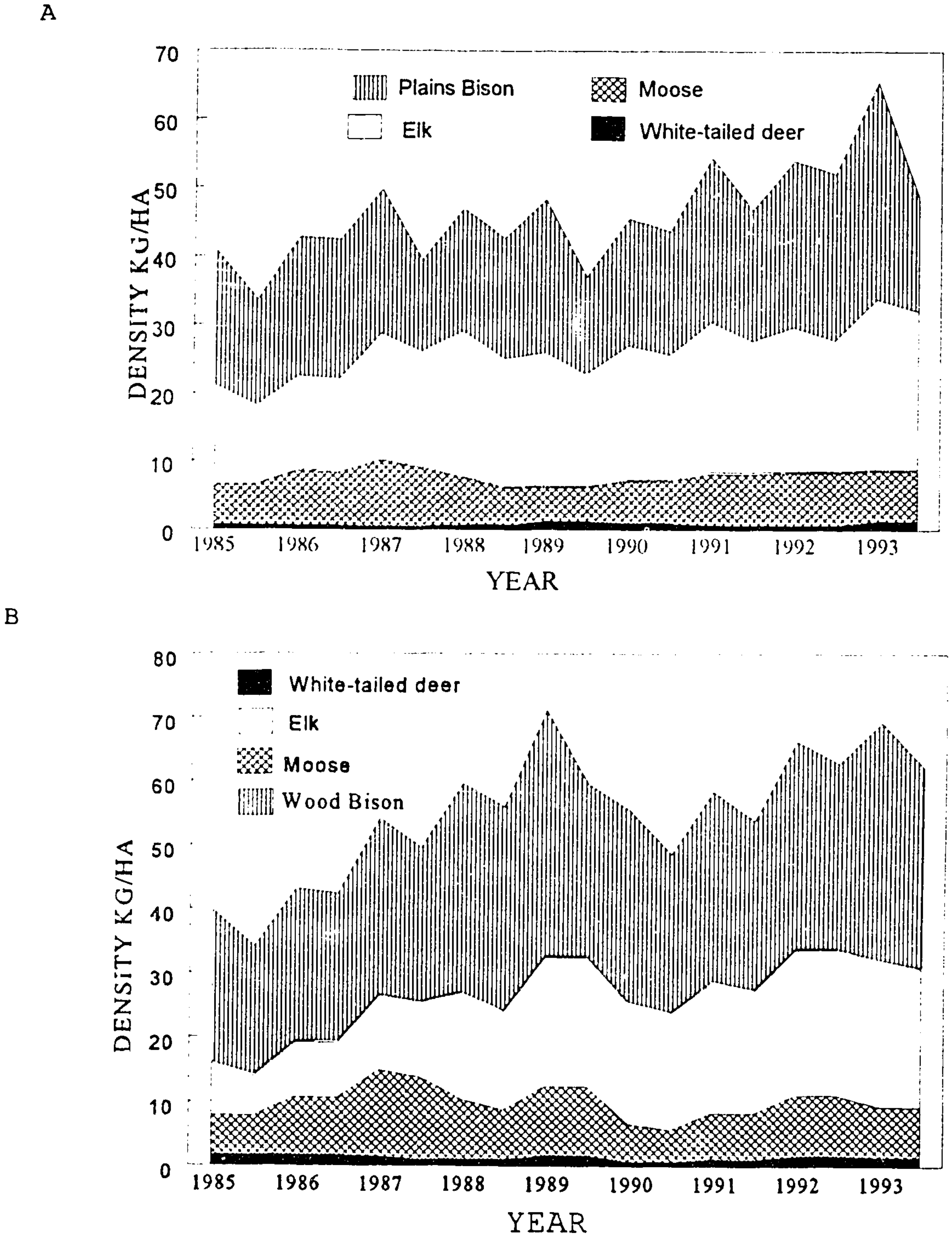

Fig. 30. Total standing stock (kg/ha) of moose, white-tailed deer, bison, and elk from 1985-93. (A) Main Park area. (B) Isolation area.

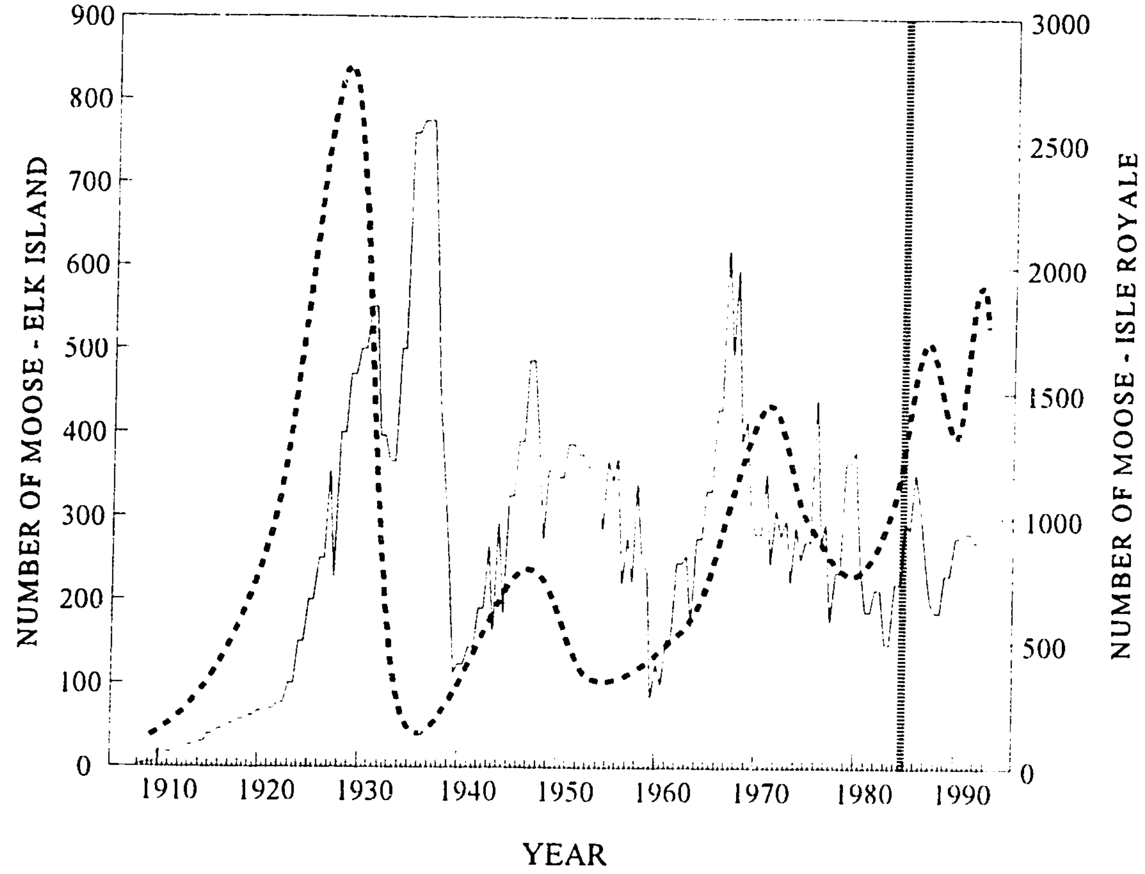

Fig. 31. A comparison of moose population dynamics at Elk Island (solid line) and Isle Royale (dashed line). Verticle line marks the beginning of the period of management at Elk Island where moose population reductions were ended and elk populations were allowed to increase. At Isle Royale this same period represents a time of very low wolf numbers with reduced predation. Isle Royale data from Peterson (1977) and Peterson (1994).

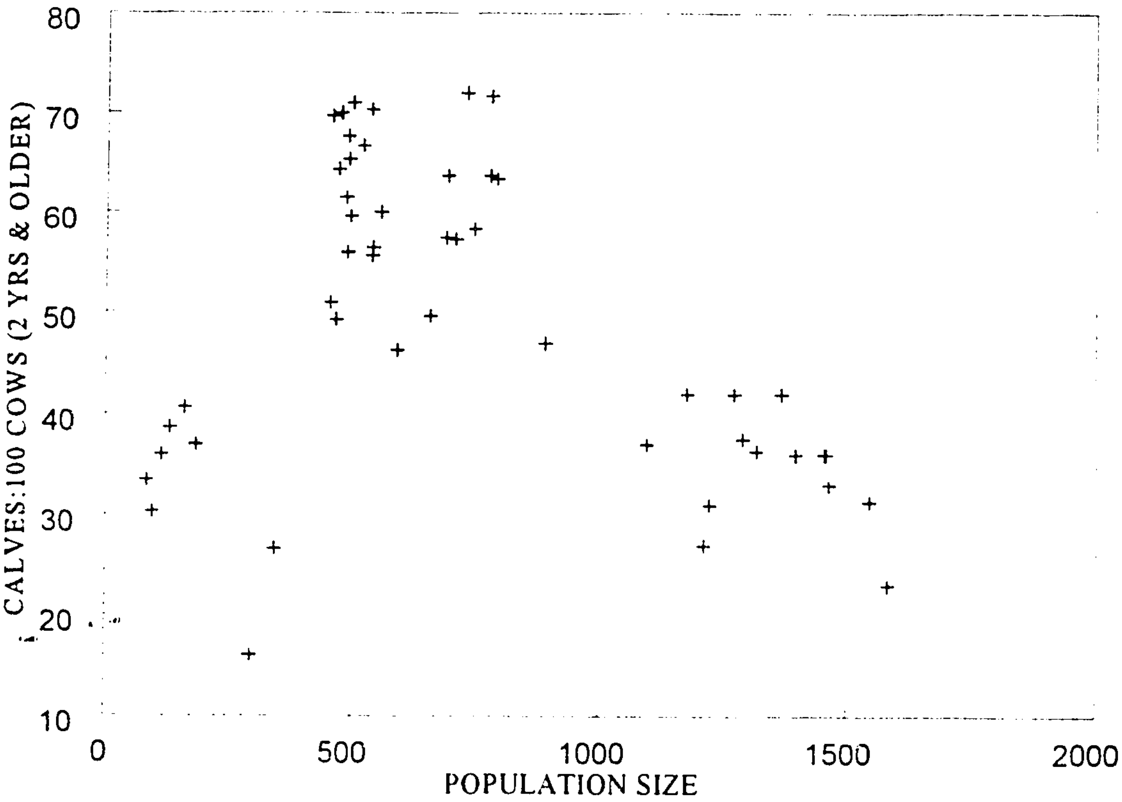

Fig. 32. Elk Island plains bison calf:cow ratio during fall or winter handling compared to population size, 1910-30 and 1940-92.

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APPENDICES

Appendix 1. Ungulate population data for the Main Park, 1906 – 93.

Year	Elk Before Mgmt	Elk After Mgmt	Moose Before Mgmt	Moose After Mgmt	Bison Before Mgmt	Bison After Mgmt	Mule Deer Before Mgmt	Mule Deer After Mgmt	White-tailed Before Mgmt	White-tailed After Mgmt	Area ha Elk, Moose and Deer	Area ha Bison
1906	20	20					35	35			3275	
1907	24	24			190	190	35	25			3275	3275
1908	24	24			411	386	30	30			3275	3275
1909	26	26	3	3	426	101	30	30			3275	3275
1910	30	30	5	5	45	45	54	54			3275	3275
1911	28	28	19	18	48	48	45	45			3275	3275
1912	36	36	18	18	60	60	60	60			3275	3275
1913	40	40	21	21	71	71	52	52			3275	3275
1914	41	41	26	26	82	82	80	80			3275	3275
1915	50	50	31	31	100	100	90	90			3275	3275
1916	75	75	40	40	106	106	100	100			3275	3275
1917	100	100	46	46	134	134	111	111			3275	3275
1918	103	103	52	52	151	151	115	115			3275	3275
1919	106	106	57	57	195	195	125	125			3275	3275
1920	150	150	62	62	202	202	150	150			3275	3275
1921	174	174	67	67	230	230	150	150			3275	3275
1922	200	200	70	70	270	270	155	155			3275	3275
1923	189	189	77	77	292	292	158	158			10020	11470
1924	223	223	101	101	320	320	300	300			10020	11470
1925	311	311	150	150	404	404	294	294			10020	11470
1926	400	400	200	200	469	469	292	292			10020	11470
1927	415	415	250	250	550	550	288	288			10020	11470
1928	500	500	357	227	729	729	200	200			10020	11470
1929	454	430	400	400	823	598	200	200			10020	11470
1930	453	453	470	470	716	716	199	199			10020	11470
1931	500	500	500	500	863	863	220	220			10020	11470
1932	467	467	550	550	1000	1000	209	209			10020	11470
1933	700	700	396	396	1340	1340	219	219			10020	11470
1934	1000	1000	366	366	1740	1740	232	232			10020	11470
1935	1400	1400	500	500	2000	1884	246	246			10020	11470
1936	1979	1979	760	760	2479	1979	261	261			10020	11470
1937	1997	1497	774	774	2039	2039	260	260			10020	11470
1938	1272	1000	775	615	2131	2000	27	27			11470	11470
1939	574	473	439	350	1795	995	28	28				
1940	488	488	247	113	1104	1084	25	25			11470	11470
1941	532	532	123	123	1464	1414	24	24			11470	11470
1942	550	550	144	144	1624	1114	22	22			11470	11470
1943	631	631	190	190	1286	1286	24	24			11470	11470
1944	800	450	265	160	1373	773	40	40			11470	11470
1945	635	635	294	184	1150	1150	72	72			11470	11470
1946	723	563	325	325	1296	895	96	96			11470	11470
1947	851	651	390	390	1085	1019	95	95			11470	11470
1948	751	651	487	487	1291	1291	100	100			11470	11470
1949	830	755	382	272	1496	993	96	96			11470	11470
1950	674	613	355	355	1167	1167	113	113			11470	11470
1951	630	596	348	348	1440	1440	131	131	1	1	11470	11470
1952	784	721	387	387	1785	1264	103	103	10	10	11470	13532
1953	782	671	375	375	1411	1173	75	75	20	20	11470	13532
1954	840	721	360	360	1552	1048	95	95	30	30	11470	13532
1955	955	750	335	285	1146	1146	73	73	40	40	11470	13532
1956	999	813	367	343	1426	926	47	47	42	42	11724	13532
1957	1149	851	370	220	1242	891	24	24	46	46	11724	13532
1958	865	578	275	222	1049	1049	0	0	48	48	11724	13532
1959	680	496	342	247	1417	1062			50	38	11724	13532
1960	640	310	234	83	1173	670			110	103	11724	13532
1961	260	154	123	99	700	650			88	88	11724	16686
1962	230	230	153	153	794	564			145	145	10469	15431
1963	300	225	245	245	725	714			100	100	10469	15431
1964	330	290	255	168	896	841			64	64	10469	10469
1965	302	302	275	275	830	493			45	45	10469	10469
1966	275	275	332	332	623	512			38	38	10469	10469
1967	343	343	429	429	612	591			34	34	10469	10469
1968	393	373	627	493	733	622			59	59	10469	10469
1969	418	326	600	391	728	528			74	54	10469	10469
1970	383	307	415	300	774	526			27	27	10469	10469

Year	Elk Before Mgmt	Elk After Mgmt	Moose Before Mgmt	Moose After Mgmt	Bison Before Mgmt	Bison After Mgmt	Mule Deer Before Mgmt	Mule Deer After Mgmt	White-tailed Before Mgmt	White-tailed After Mgmt	Area ha Elk, Moose and Deer	Area ha Bison
1971	426	351	280	280	685	659			65	65	10469	10469
1972	510	410	353	243	872	618			23	23	10469	10469
1973	552	522	310	278	780	627			46	46	10469	10469
1974	570	275	297	222	719	719			71	31	10469	10469
1975	406	316	289	249	622	469			14	14	11119	11119
1976	430	430	271	271	428	418			20	20	11119	11119
1977	568	460	449	267	410	410			50	50	11119	11119
1978	450	420	293	175	529	496			58	58	11119	11119
1979	464	419	234	20[illegible]	553	336			69	69	10871	10871
1980	486	486	366	366	399	399			42	42	10871	10871
1981	607	456	380	247	443	389			84	84	10871	10871
1982	584	474	187	[illegible]7	518	518			126	126	10871	10871
1983	527	497	214	214	652	425			100	100	10871	10871
1984	583	519	148	148	492	418			166	166	10871	10871
1985	643	515	221	221	472	372			139	135	10871	10871
1986	618	613	295	286	488	488			121	121	10871	10871
1987	832	763	354	315	504	320			97	97	10871	10871
1988	959	847	255	199	428	422			161	161	10871	10871
1989	884	743	186	186	535	341			258	256	10871	10871
1990	884	824	231	231	444	433			201	201	10871	10871
1991	992	872	276	276	576	456			153	153	10871	10871
1992	954	865	282	282	585	585			156	156	10871	10871
1993	1039	960	271	271	734	568			279	279	10871	10871

Appendix 2. Ungulate population data for the Isolation area, 1959–93.

Year	Elk	Elk	Moose	Moose	Wood Bison	Wood Bison	White-tailed		Area ha Available to Ungulates
	Before Mgmt.	After Mgmt.	Before Mgmt.	After Mgmt.	Before Mgmt.	After Mgmt.	Deer Before Mgmt.	Deer After Mgmt.	
1959	70	70					150	150	4962
1960	90	10	68	61			160	160	4763
1961	8	8	68	57			154	154	4763
1962	8	8	74	74			149	149	4763
1963	12	12	105	105			140	118	4763
1964	13	13	130	112			128	128	4763
1965	12	12	150	150	21	21	118	118	4763
1966	12	12	164	164	22	22	107	107	4763
1967	21	21	235	235	35	33	76	76	4763
1968	15	15	250	168	50	48	159	159	4763
1969	21	21	150	77	62	32	265	245	4763
1970	21	10	102	62	34	34	177	77	4688
1971	9	9	75	75	43	43	98	98	4688
1972	8	8	125	72	54	51	103	103	4688
1973	7	7	82	70	63	59	104	104	4688
1974	10	10	117	109	74	72	205	120	4688
1975	14	14	118	118	91	91	35	35	4688
1976	22	22	165	165	114	108	77	77	4688
1977	25	54	225	110	136	121	120	120	4688
1978	55	55	160	123	150	102	110	110	4688
1979	73	73	160	160	129	129	100	100	4688
1980	75	75	120	120	159	110	62	62	4688
1981	87	87	120	92	139	130	177	177	4688
1982	100	100	120	120	161	155	291	291	4688
1983	102	102	36	36	206	176	125	125	4688
1984	137	122	61	61	213	213	70	70	4688
1985	156	119	98	96	232	196	148	147	4688
1986	165	135	140	139	233	227	152	151	4688
1987	224	224	207	200	271	236	142	87	4688
1988	319	296	145	119	321	313	100	100	4688
1989	389	389	167	167	379	265	149	149	4688
1990	363	349	91	77	294	242	65	65	4688
1991	393	368	112	112	291	259	99	99	4688
1992	439	439	146	146	319	293	154	154	4688
1993	440	306	122	306	372	298	134	134	4688