Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada

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Abstract

We document the recolonization of an indigenous large herbivore into its historic range. Eighteen wood bison (*Bison bison athabascae*) were reintroduced into the Mackenzie Bison Sanctuary of the Northwest Territories, Canada, in 1963. The population subsequently increased in number and range, peaking at about 2400 in 1989; numbers were estimated at about 1900 in 1998. Recolonization occurred through a series of increases in local areas followed by pulses of dispersal and range expansion. This pattern was originally described for exotic species' introductions. Differences in diet and overwinter survival of calves over the bison's range suggest that intraspecific competition for food provided the stimulus for range expansion. For a conservation strategy, the reintroduction of animals into several independent sites in their historic range would facilitate recolonization and achieve a faster spread than a reintroduction into one site followed by waiting for the population to spread as a result of its own density dependent responses.

INTRODUCTION

Much has been written about the population dynamics of exotic ungulates introduced both to islands (Scheffer, 1951; Klein, 1968; Caughley, 1970*a*,*b*; Grenfell *et al.*, 1992) and continents (Tulloch, 1970; Choquenot, 1991, 1998; Hone, 1994). Such populations are characterized by over-compensatory density dependence and marked fluctuations of population (Caughley, 1970*a*; Tulloch, 1970; Clutton-Brock *et al.*, 1991, 1997; Grenfell *et al.*, 1992). In contrast, at least some well-established indigenous ungulates experience compensatory density dependence and less fluctuation in population size (Sinclair, 1977; Clutton-Brock, Guinness & Albon, 1982; Houston, 1982; Sinclair, Dublin & Borner, 1985; Skogland, 1985; Coughenour & Singer, 1996; Mduma, Sinclair & Hilborn, 1999). Where the same mammal species have been compared as indigenous and exotic populations, the variability of the populations is significantly higher in the exotic environment (Sinclair, 1997).

In other words, the amplitude of fluctuation is greater when a species becomes an exotic. Much less has been reported about the dynamics of reintroduced indigenous or endemic large mammals, the studies of Arabian oryx (*Oryx leucoryx*) (Stanley-Price, 1989) and muskox (*Ovibos moschatus*) (Le Henaff & Crete, 1989; Oleson, 1993; Reynolds, 1998) being exceptions. First, are such reintroductions prone to large amplitude oscillations or do they resemble established indigenous populations? Second, how do these results determine the strategy of reintroductions for conservation? In particular, the spatial dynamics of introductions has not been examined in any detail. Do populations expand gradually from a focal point or do colonizers breakaway from the founding population and start new foci of colonizers? Do such populations experience the characteristic negative feedbacks from density dependent processes described for the indigenous species referenced above? To address these questions, we report here the dynamics of a reintroduced population of the endemic wood bison subspecies (*Bison bison athabascae*) in the Northwest Territories (NWT), Canada.

The wood bison originally inhabited the Great Slave Lake region, NWT, up to the 1700s. Wood bison were nearly eliminated from their original range during the late 1800s, coinciding with the rapid decline in plains bison between 1840 and 1900 (Raup, 1933). By 1891, only 300 wood bison remained in the wilderness

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between Great Slave Lake and the Peace-Athabasca delta (Ogilvie, 1893), with numbers reaching an estimated low of 250 during 1896–1900 (Soper, 1941). After 1900, numbers were insignificant except in the Slave River lowlands and the area later designated as Wood Buffalo National Park (Gates, Chowns & Reynolds, 1992). In 1957 a very small group of wood bison was rediscovered in a remote northern part of Wood Buffalo National Park to the south of the lake (Banfield & Novakowski, 1960). In 1963 a group (*n* = 77) was captured to establish a captive breeding herd and, after testing for disease, 19 animals were transported to an area near Ft. Smith from which 18 animals were reintroduced into the wild that year; two did not survive their first winter. This area is the Mackenzie Bison Sanctuary on the north shore of Great Slave Lake north-east of the entrance to the Mackenzie River (61° 20′ N, 117° 20′ W).

METHODS

Study area

The Mackenzie wood bison inhabit an area exceeding 11 000 km^2, which includes the Mackenzie Bison Sanctuary (MBS) and adjacent areas located on the western side of Great Slave Lake (61° 30′ N, 117° 00′ W) in the Northwest Territories (Fig. 1). The study area is located in the Upper Mackenzie Section of the Boreal Forest Region (Rowe, 1972) in the emerged bed of a once vast glacial lake. The MBS proper represents the core area of the bisons' range, to the south-east of the Mackenzie Highway. This is where the newly introduced population resided, initially concentrating in the Falaise Lake area and later expanding their range to include the other lakebeds in the MBS. The area to the north-west of the Mackenzie Highway is the Mink Lake (ML) area, approximately 70 km north-west of the core of the MBS. Bison were first observed in this area in 1980. Because of the heavily forested south-eastern part of the area most bison are found in areas around Mink Lake, the lakes to the north and, more recently, towards the Horn Plateau to the east. The Mills Lake area is found at the junction of the Horn and Mackenzie Rivers, approximately 75km west of the core of the MBS. This area is flat lowland and major portions of it flood annually.

The undulating topography supports largely forested habitats, which include coniferous forest, dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and larch (*Larix laricina*), and mixed deciduous-coniferous forest, dominated by white spruce, aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Birch bog dominated by shrub birch (*Betula glandulosa*) is found in open, poorly drained areas of the forest. Shallow lakebeds originating from the scouring action of glaciers are widely dispersed throughout the area. These lakes are gradually filling in with sedges and grasses, while woody plants, notably willows (*Salix* spp.), are invading the lake margins. Wet sedge meadows (WM) and more mesic willow savannas (dry meadows, DM) associated with these lakebeds provide most of the forage used by bison, but represent <6% of the study area (Larter & Gates, 1991*a*; Matthews, 1992). The WM are found where there is year-round standing water. They contain high biomass stands of sedge, dominated by *Carex atherodes* and *Carex aquatilis*. The DM are located in more mesic areas often bordering WM. Grass–sedge associations of *Calamagrostis* spp., *Agropyron trachycaulum*, and *Carex atherodes* dominate the willow savanna plant community. *Hordeum jubatum*, *Phalaris arundinacea*, *Agrostis scabra*, and *Carex aquatilis* are also present. Willow represents only a minor portion of the ground cover.

Population estimates

Censuses were conducted on an approximately biannual basis from 1964 to 1998. They were conducted in March or April, a time when bison congregate in open habitats and fresh tracks in the snow are easy to distinguish. Estimates prior to 1989 were from total count aerial censuses. Aerial reconnaissance was conducted over all open habitats associated with the major lakebeds (Fig. 1) and the travel corridors between these lakebeds. The 1987 total count was conducted over both open and forested habitats. Open habitats were surveyed as above. Parallel transects 3 km apart were flown over all forested habitats in the study area. All fresh tracks were followed until animals were sighted. The plane then returned to the transect.

During the 1987 census we determined a sightability correction factor (as described by Steinhorst & Samuel, 1989) for animals in forested habitats, which was used for subsequent censuses. We compared the number of radio-collared females in forests sighted by the observers flying over the forests with the number of radio-collared females known to be in forests by radio transmissions. Marked animals were identified by their bright yellow collars. Forest counts were multiplied by a factor of 1.33 as a correction factor. Similar correction factors have been found for other large ungulates in forested habitats (Bear *et al.*, 1989; J. Woods, pers. comm.)

Population estimates for 1989, 1992, 1994, 1996 and 1998 were carried out using a stratified sampling design (Norton-Griffiths, 1978). The study area was divided into high, medium and low strata based upon population density estimates from reconnaissance flights prior to the census. In the high density stratum (all open habitat and major travel corridors), a total count was employed, with photographs used to verify counts. Two observers, one on either side of a Cessna 185, were responsible for counting groups, while one person recorded the information directly onto a 1:250 000 map of the area. Strut markers were positioned on the aircraft wings, which permitted observers to monitor a transect width of 500 m on either side of the aircraft (Norton-Griffiths, 1978). Parallel transects were flown, 1 km apart, at a constant altitude of 150 m above ground level (agl) so that the whole stratum was surveyed.
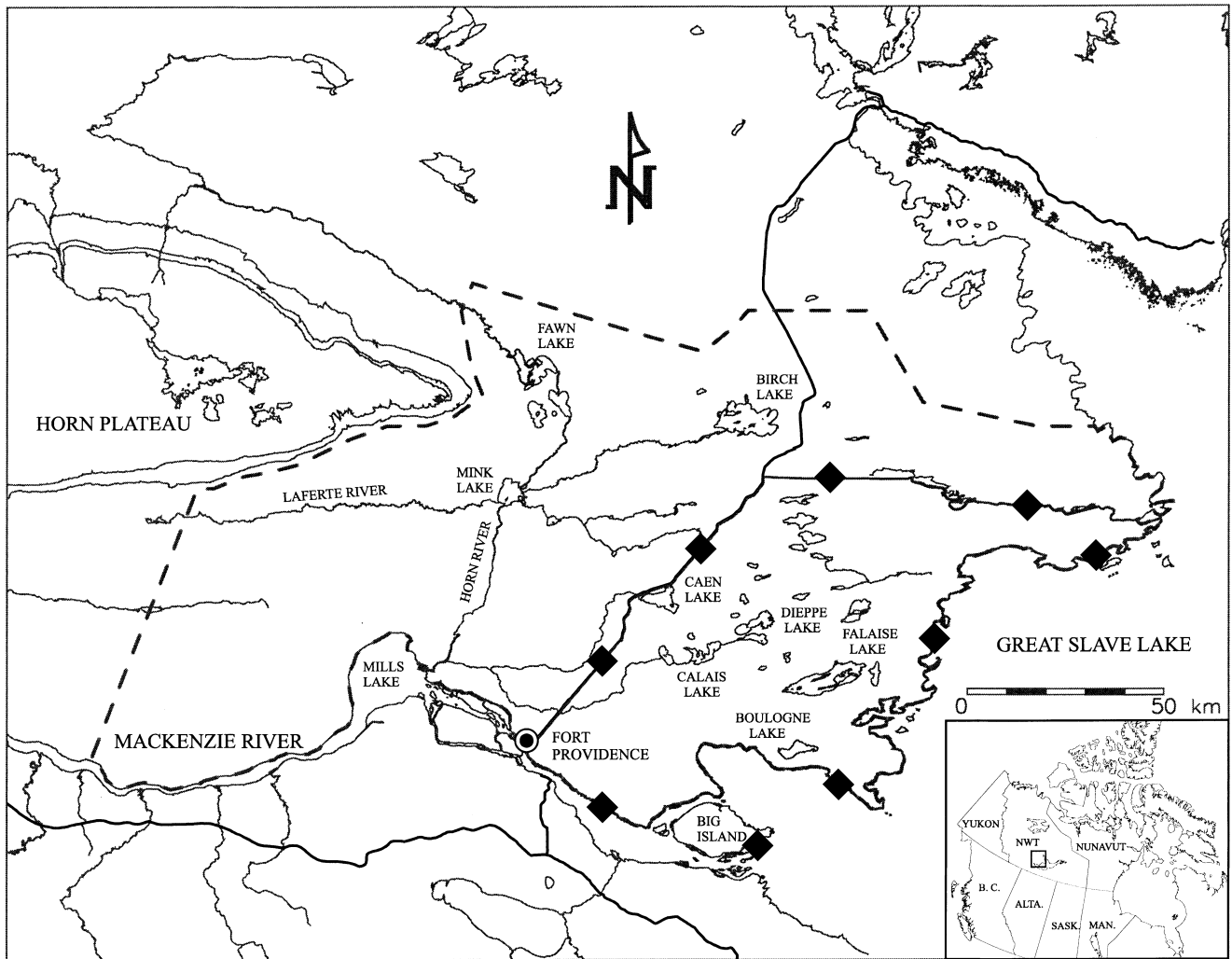
Fig. 1. The study area, Northwest Territories, Canada. The range of the bison population is indicated by the dashed line. The area marked with solid diamonds is the Mackenzie Bison Sanctuary.

In medium and low density strata (forest), parallel transects were flown at 150 m agl at varying distances apart providing coverage ranging from 4–25%. Transects ran across the shorter dimension of each stratum to increase the number of sampling units and reduce sampling error. Stratum area was determined using a polar planimeter and/or quickmap. Estimated population size and sample variance of the estimate were calculated for each stratum following Jolly's (1969) method for unequal sized sampling units (Norton-Griffiths, 1978). The population estimates and sample variances for each individual stratum were summed to obtain the total population estimate. We used the correction factor for animals counted on transects in forested habitats. We tested for differences in estimates between years using the formula given in Norton-Griffiths (1978) adapted from Cochran (1954).

The instantaneous rate of growth per year (r) was determined for each interval between censuses. We calculated population density by dividing the estimated population number by the census area. Prior to 1969 the census area was 76 km². From 1969 to 1983 the census

area was increased to 4667 km². The census area was expanded to 8175 km² for censuses in 1987, 1989 and 1992, and further increased to 10 912 km² and 11 849 km² for the 1996 and 1998 censuses, respectively. The census area for the three total counts conducted between 1969 and 1983 could not be accurately determined, and so these densities were not included in the analysis.

Calf production and overwinter survival

Aerial sex/age class counts were conducted in MBS once during summer from 1984 to 1988 and from 1992 to 1994. From 1989 to 1991, counts were conducted in early (mid-late June) summer and late (mid-late July) summer in both MBS and ML. From 1995–1998, counts were conducted once during summer in both MBS and ML. At least 80% of all calves are born by 1 July (Komers, 1992). Observers in helicopters were positioned near groups of bison, and the bison were encouraged to walk past the observers so that all animals could be classified into different sex/age categories. Animals were classified into calves, yearlings, adult ($\geq$ 2 year-

old) females, immature males and two classes of adult males (young and old). Body size, pelage, horn shape/wear and size were the characters used to separate animals into the six categories. Counts were conducted in 1 day so that the probability of recounting individuals in the different areas was negligible.

Ground-based sex/age counts were also conducted between 1986 and 1991. Observers used all-terrain vehicles to position themselves near groups. Aerial and ground count data were lumped only when ground count data were collected within a 10 day period encompassing the aerial count. Samples obtained between November and April were summed to give winter ratios.

We used the ratio of calves/100 adult ($\geq$ 2 year-old) females to estimate calf production. The standard error of the ratios was computed as described by Cochran (1977) and Sinclair & Grimsdell (1978). Ratios were compared between areas and between different sampling times using the proportions test (Zar, 1984), and over all sampling times using the sign test (Conover, 1980).

We estimated overwinter survival of calves by dividing the ratio of yearlings/100 adult females determined in July by the ratio of calves/100 adult females determined in July of the previous year. June data were used if July data were unavailable. We used the Mann–Whitney U test (Zar, 1984) to compare overwinter survival of calves between areas for those years when estimates were available for both areas.

Adult survival

Adult survival was estimated from radio telemetry data. Between 1986 and 1991, 53 adults (17 females and 36 males) were equipped with radio collars. We calculated adult survival (S) from the binomial distribution as described by White & Garrott (1990: pp. 208). Because the number of animals with radio collars varied greatly between years and data were lost by limiting them to year-long periods, we calculated a second estimate based upon radio collar-months. This was the ratio of radio-collared adults that died to radio-collared adults alive during the 5-year study period.

Bison diet

Fresh faecal samples (30 g wet weight) were collected during the summer (June to August) of 1989 and 1990, and in the winter (March) of 1990. Samples were grouped by month (range 18–62 samples/month). Samples were kept frozen until they were oven-dried at 60 °C for 48 h. Diet composition was determined by analyzing faecal plant fragments (Sparkes & Malechek, 1968) following the method outlined by R.M. Hansen (pers. comm.). Briefly, samples were ground in a centrifugal mill through a 1 mm screen, washed with Hertwig's clearing solution, mounted on microscope slides and cellular plant fragments were identified. Because diet components were only identified to genus, they were placed into five major forage groups: grass, sedge, shrub, forb and lichen. Shrub material was rep-

resented almost exclusively by willow. Trace quantities of *Equisetum* spp., moss, pine and spruce needles were discarded from the analyses.

Because of the lack of independence between forage class proportions, parametric tests were conducted only on the sedge class, which we considered to be the most important bison forage from previous data (Larter, 1988; Larter & Gates, 1991a,b). Sedge proportions were arc-sine transformed. We used a three-way ANOVA on the transformed summer dietary sedge proportions to determine whether there were year, month, or area (MBS and ML) effects. Because there were no year effects ($P > 0.2$), we pooled the data across years and used a two-way ANOVA with month and area as the factors. We used a one-way ANOVA to test for differences between areas in the winter dietary sedge proportions (Zar, 1984).

Diet quality

Composite samples of *Carex atherodes*, grass and willow were collected in willow savannas from MBS and ML during June, July and August. For sedge and grass samples, numerous individual plants (minimum 35 g ground dry weight sample), were clipped at random from areas directly adjacent to permanently marked line transects. Current year's growth was clipped at 3 cm above ground level to represent forage available to grazing bison (Larter, 1988). For willow samples, current annual growth of twigs and their leaves were clipped. During February and April, *C. atherodes* samples were collected from both willow savannas and wet sedge meadows. Samples were dried at approximately 60 °C in a propane oven for 12 h, and ground in a cyclone mill through a 1 mm screen. A $\geq$ 1 g subsample of ground forage was used for each quality analysis. Nitrogen content was determined using the micro-Kjeldahl technique (Nelson & Sommers, 1973). Crude protein was estimated as 6.25 $\times$ % nitrogen. Digestibility was determined using the acid–pepsin technique (Tilley & Terry, 1963; Larter, 1992).

We calculated an index of diet quality (I) for each forage type FT (Larter, 1988). The index (I) was determined for each month and area combination by the following formula:

$$I = \Sigma \, (CP_{(FT)} * DG_{(FT)} * DC_{(FT)}).$$

Where CP is the mean percentage of crude protein, FT is the forage type (sedge, grass, willow); DG is the mean percentage digested and DC is the percent composition in the diet.

The index of summer diet quality is based upon the sedge *C. atherodes*, grass and willow. The winter (March) index is based solely upon sedge because during winter, sedge meadows are frozen making sedges in both wet sedge meadows and drier willow savannas available to bison. Because forage samples were collected during mid-February and early April and diet data were collected during March we used the mean quality measures for sedges collected from both habitats during

both times to determine the March diet quality index. Because percentage crude protein and percentage digested had no significant year effects, we calculated the index for all month and area combinations and then averaged the month and area data across years. We compared relative differences between areas using log (*I*).

Faecal nitrogen condition index

We used faecal nitrogen as another measure of diet quality. Faecal samples were collected from ML and the MBS during summer, early winter (November), mid-winter (February) and late-winter (March–April). Scoops of 30 g (wet weight) from a minimum of five separate faecal pats were lumped together to form one sample, and 7–14 samples were collected from each area during each time period. Samples were stored frozen, dried for 48 h at 60 °C, and ground in a centrifugal mill through a 1.0 mm screen. We used the macro-Kjeldahl procedure (Parkinson & Allen, 1975) to determine faecal nitrogen content (p.p.m.). The data were corrected for dry matter weight and are expressed as total percentage nitrogen. Animals with high faecal nitrogen content have a better quality of diet and, therefore, were in areas of better food. We used a two-way ANOVA to determine if sampling time and/or location explained significant variation in faecal nitrogen content, and the Student's *t*-test to compare means between areas for a given sampling time.

Dispersal

Between 1986 and 1991, 93 animals were marked, either with brands, radio collars, or both. The majority (85) of these animals were initially marked in MBS. Movements were monitored by relocation of marked individuals during aerial relocation flights and during ground studies. Animals that moved from MBS to ML, ML to MBS, or into the Mills Lake area, and remained in that new area for all subsequent relocation surveys were considered to have dispersed.

RESULTS

Population estimates

The total bison population (MBS and ML subpopulations combined) has exhibited a classic pattern of eruptive oscillation (Fig. 2). It increased sigmoidally after 1964 reaching a peak of about 2400 in 1989 subsequently declining to near 1900 in 1998. The total estimated population size of 1857 in 1996 is the result of a post-survey recalculation. The original survey estimate of 1313 was clearly an underestimate; the population could not have increased to 1908 in the 2 years to 1998. There is some indication that a proportion of the population had moved out of the survey area during the census of 1996 (T. Ellsworth, pers. obs.). We used juvenile survivorship and yearling recruitment data from 1996–98 for the recalculation. During 1996–98 observed
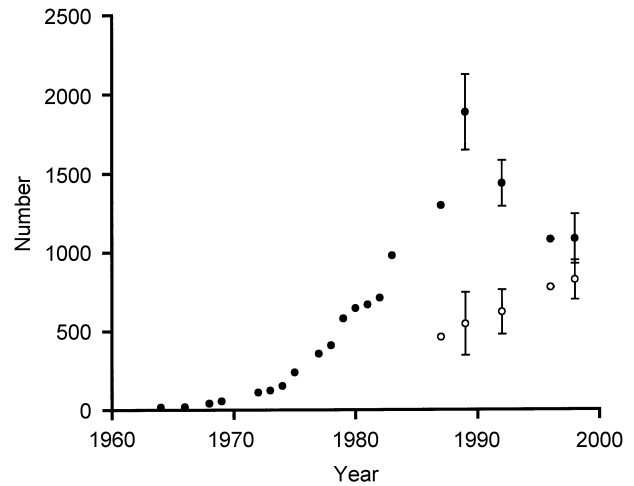
Fig. 2. Growth of the Mackenzie wood bison population since its introduction to the core area of the Mackenzie Bison Sanctuary (filled circles), and the expansion population at Mink Lake (open circles) since 1987. Bars represent 95% confidence intervals.

juvenile survivorship in the core area (Table 1) gave a yearling recruitment into the adult population of 7.16% while that on the expansion area was 10.0%. From adult survivorship (see below) mean annual adult mortality was 7.0% indicating that the population was effectively stationary in the core but increasing at 3% per year in the expansion area. Therefore, we calculated the 1996 population to be 1857 partitioned into 1080 for MBS and 777 for ML. The total population, therefore, was relatively stable over the period 1992 to 1998.

Population estimates of the two subpopulations have been conducted since 1987. The MBS subpopulation peaked at an estimated 1885 animals in 1989 then declined to an estimated 1084 animals in 1998 (Fig. 2). The ML subpopulation has exhibited a slow increase from an estimated 461 animals in 1987 to an estimated 824 animals in 1998. The difference in estimates between 1987 and 1998 is probably significant, but because the 1987 estimate represents a total count there is no associated variance to test for differences. The difference between the 1989 estimate (546 animals) and the 1998 estimate of 824 animals is not significant ($P = 0.09$) (Fig 2.).

When total population density is plotted against the instantaneous rate of growth a cyclical pattern appears during the eruptive increasing phase of the population dynamic (Fig. 3). Both population growth rate and density increased until population density exceeded approximately 0.55 animals/km². Once this point was reached both rate of growth and density decreased and the cycle began again. The decrease in density occurred even though the population was increasing because animals had dispersed into previously unoccupied areas. Hence, animals were distributed over an enlarged area. The cycle has been completed twice since the population was introduced with the two dispersal episodes occurring in 1969 and 1980, the years following peak population den-

Table 1. The ratios of the number of calves (Ca) and yearlings (Yr) per 100 adult (≥ 2 year-old) females (Cow) from 1984–1991

Year	Time	MBS Ca/100 Cow	Yr/100 Cow	ML Ca/100 Cow	Yr/100 Cow
1984	July	48	22	- - - - - -	- - - - - -
1985	July	53	38	- - - - - -	- - - - - -
1986	July	45	42	- - - - - -	- - - - - -
1987	July	41	14	- - - - - -	- - - - - -
1988	July	32	23	- - - - - -	- - - - - -
1989	June	46.4(±12.5)	26.1(±11.0)	48.0(±25.0)	32.0(±23.3)
	July	43.1(±9.5)	22.5(±8.0)	56.3(±18.7)	35.3(±18.1)
	August	37.6(±10.6)	23.4(±9.2)	61.9(±21.7)	28.6(±20.2)
	Winter	35.9(±11.6)	15.7(±8.8)	45.8(±28.8)	18.8(±22.5)
1990	June	32.3(±5.8)	37.3(±6.2)	11.4(±10.1)	36.8(±15.3)
	July	33.7(±6.5)	30.6(±6.9)	34.2(±11.5)	34.9(±11.6)
	August	34.9(±6.3)	26.3(±6.6)	- - - - - -	- - - - - -
1991	June	47.6(±6.7)	20.8(±5.4)	55.6(±24.8)	25.4(±21.8)
	July	39.2(±10.2)	24.1(±8.9)	46.7(±35.3)	33.3(±33.3)
	August	36.8(±11.7)	25.7(±10.6)	- - - - - -	- - - - - -
1992	June	30.2(±9.6)	20.9(±12.2)	- - - - - -	- - - - - -
1993	July	34.1(±4.1)	12.3(±1.8)	- - - - - -	- - - - - -
1994	June	42.9(±6.6)	27.1(±5.7)	- - - - - -	- - - - - -
1995	June	23.5(±3.7)	11.3(±2.4)	41.4(±14.9)	17.1(±8.7)
1996	July	30.5(±13.5)	9.2(±3.0)	49.6(±22.8)	16.3(±4.8)
1997	July	45.7(±11.5)	7.3(±1.8)	60.9(±7.8)	25.9(±9.2)
1998	July	44.0(±3.0)	17.9(±1.7)	58.2(±5.5)	33.3(±12.4)

Means (± SE) are presented for each subpopulation (MBS and ML) and for multiple times per year where available.

sity. Bison expanded their range from Falaise Lake into the surrounding lakes in the MBS during 1969, and expanded from the MBS proper into the ML area during 1980. Another episode of expansion began during winter 1992–93 when adult female and juvenile bison were observed occupying the Mills Lake area for the first time (T. Chowns, pers. comm.). During this time density was decreased because of a combination of range expansion and population stability. More recently (1998), the growth rate has increased as the density has decreased and another cycle may be underway (Fig. 3) because bison have begun to occupy areas near the Horn Plateau to the north-west of ML.

Recruitment and juvenile survival

Both calf/adult female and yearling/adult female ratios showed considerable yearly variation (Table 1). In the 7 years with data from both areas, June or July estimates for both calf/adult female and yearling/adult female ratios were significantly higher in ML ($P < 0.008$, $n = 7$ for both ratios, sign test).

Overwinter survival of calves also showed considerable yearly variation (Table 2). In years with data from both areas, overwinter survival was higher in the ML subpopulation, except 1989–90, but these differences were not significant ($P > 0.05$). Survival rates in the MBS during the 5 years prior to peak population averaged 63%; in the subsequent 9 years average overwinter survival was 49%. The average overwinter survival in ML, where the population has been slowly increasing, was 61%. Since 1989, both calf production and overwinter survival have been consistently higher in ML than MBS.

Adult survival

Eight adults (four out of 17 females and four out of 36 males) died during 1362 radio collar-months, seven of natural causes; one male was killed illegally. The estimates of annual survival (S) (as described by White & Garrott, 1990) ranged from a low of 75% (variance (var.) = 4.7%) to a high of 100% (var. = 0%) for adult females, with equivalent figures of 67% (var. = 3.7%) to 100% (var. = 0%) for adult males. However, because sample sizes were very small we have combined annual estimates for all adults with the lowest survival being 75% (var. = 4.7%) and the highest 96% (var. = 0.1%). Using radio collar information lumped over the entire study period, the probability of annual adult survival was 92.9%.

Demographic changes with population

Figure 4(a) shows the relationship of calf production, defined as the number of calves/100 females, to population size in the core site (MBS) and the expansion area (ML). On the core site calf production remained constant while the population declined. In contrast, calf production increased on the expansion site as the population increased.

Overwinter mortality of calves (from Table 2) in the core site increased as the population declined (Fig. 4(b)) suggesting an inverse density dependent mortality. Conversely, the increasing population on the expansion site exhibited increasing winter calf mortality suggesting a density dependent relationship.
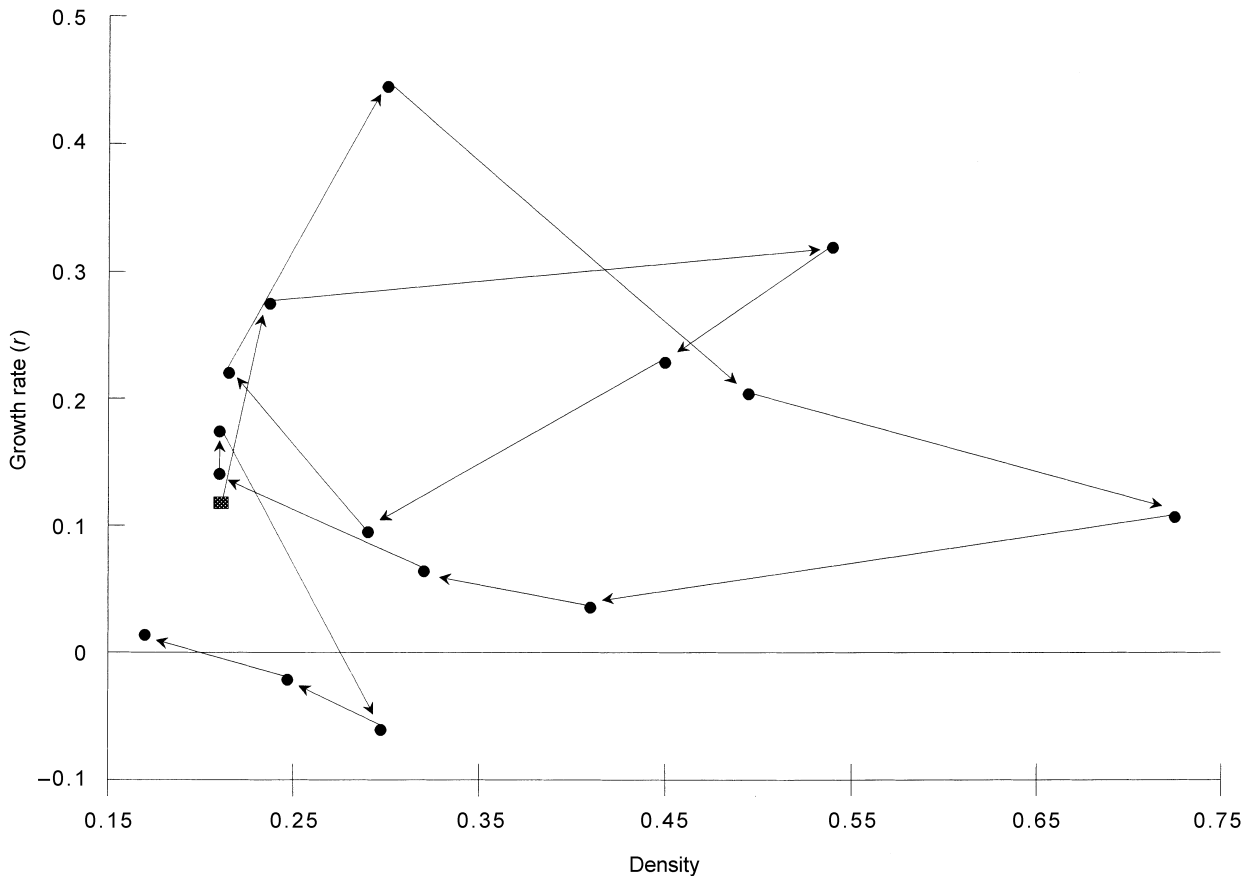
Fig. 3. The relationship between instantaneous growth rate per year (*r*) and total population density over time. Each point represents the population density of a given year, starting with 1964 (the shaded square), and the corresponding *r* of the population from that given year to the next year the population was estimated.

Table 2. Estimates of overwinter survival of bison calves from MBS and the expansion range, ML

| Time	MBS	ML
1984–85	79.2	
1985–86	79.2	
1986–87	31.1	
1987–88	56.1	
1988–89	70.3	
1989–90	71.0	62.0
1990–91	71.5	97.4
1991–92	53.3	
1992–93	40.7	
1993–94	79.5	
1994–95	26.3	
1995–96	39.1	39.4
1996–97	23.9	52.2
1997–98	39.2	54.7

Bison diet

There were significant area ($F_{(1, 499)}$, $P < 0.001$) and month ($F_{(2, 499)}$, $P < 0.001$) effects on the proportion of sedge in the summer (June–August) diet. Bison inhabiting the MBS had a higher dietary sedge component (Table 3), and the proportion of dietary sedge was highest in June. During late winter (March) bison inhabiting ML had a significantly higher proportion of sedge in the diet ($F_{(1, 48)}$, $P < 0.001$) as well as willow (Table 3).

Diet quality

Bison inhabiting MBS had a consistently higher index of diet quality than bison at ML during summer, regardless of year (Table 4). In contrast, during winter bison inhabiting ML had a higher index of diet quality than bison at MBS. Although the difference in winter diet quality was not great in absolute terms, in relative terms the index was 1.47 times higher than that for animals inhabiting ML. The relative differences during summer were much less, with values differing by a factor of 1.17 in July and 1.06 in August. Therefore, during late winter months bison in ML had a relatively superior diet to bison in MBS.

Faecal nitrogen condition index

There were significant location ($F_{(1, 83)}$, $P < 0.001$) and sampling time ($F_{(4, 83)}$, $P < 0.0001$) effects on nitrogen content of faeces. Faecal nitrogen concentrations were higher in summer than winter. They also declined as the winter progressed (Table 5). Regardless of sampling time, faecal nitrogen concentrations were significantly higher in animals from ML, indicating a better quality of diet for ML animals (range $P < 0.003$, $t = 3.59$, $n = 8$ for February to $P < 0.0003$, $t = 5.7$, $n = 8$ for November).
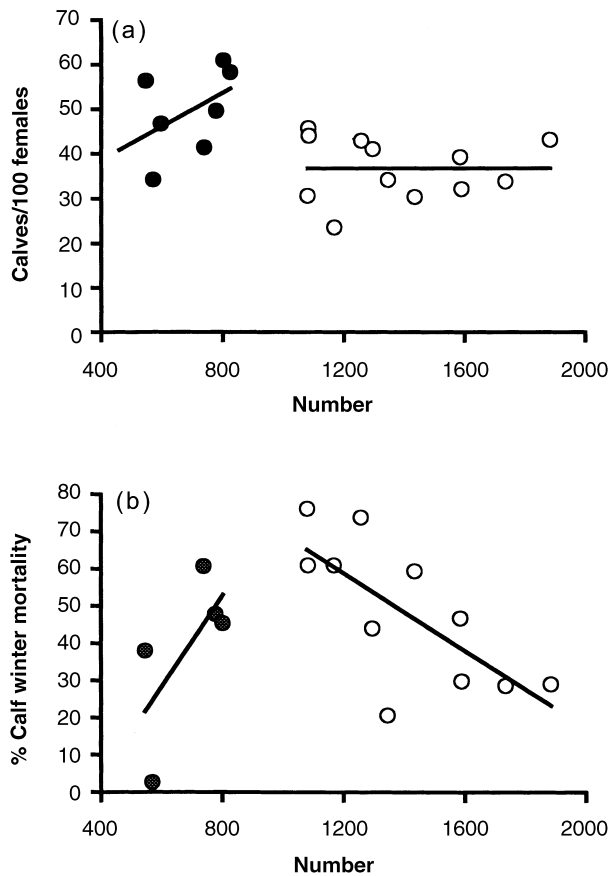
Fig. 4. The relationships between (a) calf production (calves/100 females) and (b) overwinter calf mortality (%) with population size in the Mackenzie Bison Sanctuary (open circles) and the expansion range, Mink Lake (filled circles).

Dispersal

The majority of animals remained in the area where they were originally collared. There were more radio-collared animals at MBS and also more males (Table 6). No animals moved from either MBS or ML to the Mills Lake

area (Fig. 1). Small numbers of adult males were the only residents of Mills Lake prior to winter 1992–93. They spent autumn and winter at Mills Lake, but moved into both ML and MBS during summer and throughout the rut (mid-July to late August). Three of the five males collared in Mills Lake lost their collars in fights during the first rut after they were radio-collared. The remaining two of these animals with collars returned to Mills Lake for the subsequent winter. The remaining male with a functioning radio collar in 1992 returned for a fourth consecutive winter to Mills Lake.

Two adult females moved from MBS to ML and remained there for as long as their radio collars functioned: one female moved 8 months after being radio-collared in 1986 and remained at ML for at least 46 months. No adult females collared in ML moved to MBS and remained there. One adult female spent 3 weeks of one summer in MBS, but returned to ML. One adult female and one adult male from MBS did the opposite, briefly moving to ML from MBS. This occurred during a few weeks in mid-summer.

DISCUSSION

Mechanism of range expansion

The population trajectory of the bison released at the core site in the Mackenzie Bison Sanctuary (MBS) exhibited an increase over 25 years, followed by a gradual decline. After about 20 years the population expanded into new range, the Mink Lake (ML) area, and that segment of the population has continued to increase. In the early 1990s a new phase of expansion was initiated into the Mills Lake region, and more recently another has been initiated into the Horn Plateau region, north-west of ML.

The instantaneous rate of increase appears to exhibit repeated phases of high rates followed by declines at high population density (Fig. 3). Expansion of the population then reduces the average density and population

Table 3. Diet composition of animals inhabiting the MBS and ML during summer (June–August) and winter (March)

Month	MBS					ML				
	Sedge	Grass	Shrub	Forb	Lichen	Sedge	Grass	Shrub	Forb	Lichen
June	34.8	53.8	10.4	1.0	0.0	28.1	53.4	16.9	1.6	0.0
July	27.8	57.8	12.4	1.7	0.3	18.1	62.2	18.8	0.9	0.0
August	31.4	49.6	13.3	1.5	4.2	13.4	40.8	44.3	1.2	0.3
March	40.7	57.2	1.0	1.1	0.0	54.9	41.3	0.1	3.7	0.0

Summer data are lumped over 2 years (1989 and 1990).

Table 4. Index of diet quality for the MBS and ML at different times of the year

Month	MBS	ML
June	9.76	7.49
July	4.75	3.78
August	3.75	3.47
March	0.33	0.47

See the text for calculation of index.

Table 5. Mean faecal nitrogen concentrations (%) for animals from MBS and ML at different times of the year

Month	MBS	ML
July	2.15	2.51
August	2.18	3.10
November	1.12	1.33
February	1.02	1.18
April	0.92	1.04

All concentrations are significantly ($P<0.01$) higher for ML.

Table 6. The numbers of male and female bison radio-collared at each location (Mackenzie Bison Sanctuary, Mink Lake, and Mills Lake)

	MBS	ML	Mills
Males	31	0	5
Females	14	3	0
Total	45	3	5

increase resumes. Numbers on the original range at MBS reached a peak and, although declining slightly, remained relatively high at over 1500 animals. This pattern of increase to high density followed by expansion into new range is similar to that described for exotic ungulates in New Zealand (Caughley, 1970*a,b*) and for muskox reinvading their historic native range (Reynolds, 1998).

On the core bison range (MBS) the level-out and decline of that segment of the population was not related to calf production since this remained constant (Fig. 4(a)). The smaller population in the expansion area showed increased calf production as the population increased, a feature that would accelerate the rate of population growth. An expanding population is likely to have higher recruitment due to a younger age-structure.

The overwinter mortality rate of calves on the original range increased as the population declined (Fig. 4(b)). Such a relationship would result in an accelerating decrease in the population if there was no compensatory effect. Since calf recruitment was constant there was no compensation in fertility or newborn survival. Although we had only small samples of adults ($n = 5–10$ / year) with which to calculate annual mortality over the period 1986–92, the estimate of adult mortality remained relatively constant and showed no trend with population change. In short, we have not yet detected any compensatory effects in the declining MBS population. In contrast, there does appear to be compensatory winter calf mortality in the smaller and increasing expansion population (ML), which could eventually regulate that population (Fig. 4(b)).

Causes of population regulation and range expansion

We can only speculate at this stage on the causes of these demographic changes. Wolf (*Canis lupus*) predation on bison became more evident in the MBS at approximately the time when the population levelled out, and when calf mortality became inversely density dependent (Larter, Sinclair & Gates, 1994). Since predation often has a delayed impact on prey populations, this may have been the cause for the trend in calf mortality.

However, the evidence from diet (Tables 3–5) suggests that the expansion population (ML) in winter ate a higher proportion of the nutritious sedge, *C. atherodes,* than did the core population (MBS). The index of diet quality also supports this evidence with the expansion area animals having an index that was much higher than those from the core area in winter. Faecal nitrogen is

also an indicator of nitrogen in the diet of grazing bovids (Sinclair, 1977). Again ML animals showed higher faecal nitrogen in winter than did MBS animals. Thus, all the indicators suggest that animals in the expansion area were obtaining better quality food at the potentially limiting time of year. Therefore, the growing food shortage in the MBS as the population reached a peak would produce density dependent mortalities in both calves and adults. We have not yet detected such mortality at MBS but we have seen it in calves at ML. Regulation by food remains an hypothesis to be tested.

Movements of animals suggested that dispersal was out of the core range and into the expansion range. There appeared to be no reversal of such movements. Therefore, it appears that the wood bison population increased after the initial release and then expanded its range through the following process. First, the population increased within its core range, MBS. As the density increased the rate of increase slowed. The lower quality of diet at the end of this process in the 1986–92 period suggests that food quality was falling and food could have been limiting. The population responded to these dietary pressures by a proportion moving into a new area, ML. There the dispersers found higher quality food and calf and yearling survival improved relative to the original range. That segment of the population then continued to increase while those on the original range began to decrease. In particular, the survival of calves over winter showed an accelerating decline in the MBS, suggesting a delayed effect of poor nutrition with the higher population numbers.

Conservation and reintroduction strategy

In general, therefore, the recolonization by a native species such as the wood bison into its historic range, appears to occur through a series of increases in local areas followed by pulses of dispersal and range expansion. This is then followed by a new phase of population increase in the new range before the pattern repeats itself. This pattern of pulsed expansion, originally described for exotic species (Caughley, 1970*a*), now appears in other indigenous recolonizing species. Apart from this example of bison, pulsed expansion is also demonstrated by elk (*Cervus elaphus*) in Yellowstone National Park, USA (Lemke, Mack & Houston, 1998), and by muskox in Alaska (Reynolds, 1998) and Greenland (Oleson, 1993), and it may have occurred on Banks Island in the 1970s and 1980s (J. Nagy & N. Larter, unpubl. results). Such a pattern would suggest that density dependent processes such as intraspecific competition for food provide the stimulus for animals to find new range.

For conservation strategy reintroductions would be facilitated if animals were released into several independent sites since all would first increase in their new sites before natural range expansion took place. In essence, we can facilitate recolonization and achieve a faster spread by several releases rather than waiting for a population to spread by its own density dependent

responses. Of course there are several additional considerations in implementing such a multiple release strategy. As with reintroductions in the face of predators (Sinclair *et al*., 1998), the larger the founding population the more likely it is to establish and so avoid random extinction. Thus, a multiple site release strategy would require that the number of animals at each release site be of a certain minimum population size. The cost of these multiple releases would be higher than that of a single release, but the former strategy may be more cost effective if the population establishes without failure or if it reaches self-sufficiency earlier (i.e. the point where protective conservation is no longer needed). A cost analysis is clearly required before releases are conducted.

Acknowledgements

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