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RH: Emigration and Density Dependence in Yellowstone Bison · *Fuller et al*.

EMIGRATION AND DENSITY DEPENDENCE IN YELLOWSTONE BISON

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Abstract: Understanding the relative importance of density-dependent and density-independent feedback on population growth is essential for developing management strategies to conserve wildlife. We examined a 99-year time series of annual counts and removals for 2 bison (*Bison bison*) herds occupying northern and central Yellowstone National Park in the western United States. Yellowstone's aggressive management intervention effectively recovered bison from 46 animals in 1902 to >1,500 animals in 1954. Supplemental feeding of the northern herd facilitated rapid growth ($r = 0.16$) during 1902 to 1952. Augmentation of the central herd with 71 animals also led to rapid growth over 1936 to 1954 ($r = 0.10$). In 1969, manipulative management ceased in the park, and we detected evidence of density-dependent changes in population growth rates for both herds during 1970 to 2000 as numbers increased to >3,000 animals. The central herd showed evidence of a constant density-dependent response over 1970 to 2000. In contrast, density dependence had a stronger effect on the northern herd's growth rate during 1970 to 1981 than during 1982 to 2000. We found evidence to suggest that these trends resulted from pulses of emigration from the central herd to the northern range beginning in 1982 in response to resource limitation generated by an interaction between density and severe snow pack. Corroborative evidence supporting this interpretation included: 1) the annual growth of the central herd was negatively correlated with snow pack but that of the northern herd was not; 2) growth rates of the central and northern herds were uncorrelated during 1970 to 1981 but significantly and negatively correlated during 1982 to 2000; and 3) the northern herd could not have sustained the high removals experienced during 1984 to 2000 without immigration. Density-related emigration from the central herd to the northern range may be fueling bison emigration onto private and public lands where large-scale removals occur, exacerbating the brucellosis controversy for natural resource managers.

Key words: Bison, density dependence, emigration, irruption, time series, Yellowstone

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A dominant paradigm in managing large herbivores is that populations increase to peak abundance following introduction to a new range, crash to a lower abundance, and then increase to a carrying capacity lower than peak abundance (Forsyth and Caley 2006). Increasing density regulates ungulate populations through declining forage quality and quantity, negatively influencing nutrition and body condition, and decreasing survival and reproductive rates (Sinclair 1975, Caughley 1976, Eberhardt 2002). Stochastic effects of climate (e.g., droughts, snows) can exacerbate these effects by further reducing the availability of forage and increasing energetic costs of foraging and locomotion (Clutton-Brock et al. 1985, Sæther 1997, Gaillard et al. 2000). Several recent reviews of large herbivore dynamics focused on density-related effects to survival and reproduction (Gaillard et al. 1998, Gaillard et al. 2000, Eberhardt 2002, Festa-Bianchet et al. 2003), but few studies considered the equally plausible possibility of spatial responses to increasing density (Sæther et al. 1999, Amarasekare 2004). Emigration and range expansion have been documented in several large ungulate populations when forage quantity or quality decreased due to density-dependent resource consumption (Lemke et al. 1998, Aanes et al. 2000, Larter et al. 2000, Ferguson et al. 2001).

The mechanisms underlying density-dependent feedbacks on population growth of bison (*Bison bison*) in Yellowstone National Park (YNP) are of special interest to ecologists and park managers. As bison numbers increased from 46 animals in 1902 to nearly 5,000 animals in 2005, bison expanded their range and began crossing the park boundary into adjacent areas of Montana (Gates et al. 2005). Range expansion was likely a natural response to increasing population density (Bjornlie and Garrott 2001, Gates et al. 2005), but may have been facilitated by the presence of mechanically snow-packed roads for snowmobiles in the central and western areas of YNP that provided energy-efficient travel routes to lower-elevation areas where forage was more readily available; thereby lessening winter mortality and resulting in increased population growth (Meagher 1993). Regardless, range expansion is of great interest because bison may be vectors of brucellosis (*Brucella abortus*) to cattle and a perceived threat to the brucellosis-free status of Montana (Cheville et al. 1998, National Park Service 2000).

Understanding the demography of YNP bison is essential for developing feasible conservation strategies and addressing controversies over how and why bison leave YNP. We analyzed multiple competing model formulations of population dynamics using a 99-year time series of bison count and removal data that spanned periods of intensive husbandry, protection, and management culls. Our objective was to evaluate the extent to which bison spatially and numerically respond to increasing density (Cole 1971, Meagher 1973, Dobson and Meagher 1996, Hess 2002). We expected population growth rates during intensive husbandry (1902 to

1954) would approximate the maximum because bison were not food-limited. We expected bison would respond spatially, rather than numerically, to increasing density during the period of protection within the park (1968 to 2000). As a result, we did not expect population growth rates to decrease with increasing population size.

Study Area

Yellowstone National Park encompasses 9,018 km^2 in the western United States, including portions of Wyoming, Montana, and Idaho. The bison population exists almost entirely within the boundaries of the Park and consists of the central and northern herds. These herds were spatially distinct before the 1980s, but recent information suggests interchange may be occurring (Hess 2002, Gates et al. 2005). Present-day ranges of the central and northern herds are comparable in size (1,200 km^2; Hess 2002); but the herds exist in areas with different plant communities, different precipitation patterns, and different numbers of wintering elk (*Cervus elaphus*), potential competitors for forage. The range of the northern herd encompasses a decreasing elevation gradient extending approximately 90 km between Cooke City and Gardiner, Montana (Houston 1982, Barmore 2003). The northern range is drier and warmer than the rest of the park, with mean annual precipitation decreasing from 35 to 25 cm along the elevation gradient (Houston 1982, Farnes et al. 1999, Barmore 2003). Average snow-water equivalents range from 29.5 cm to 2.0 cm in the higher- and lower-elevation portions of the range, respectively (Farnes et al. 1999). Upland grasses comprise the majority of forage in the northern range, followed by sedges (*Carex spp.*) and rushes (*Juncus spp.*; Barmore 2003). Bison share this range with a large elk herd, which increased from 3,200 to >19,000 individuals during 1968 to 1994, and then decreased to approximately 12,000 individuals by 2002 (White and Garrott 2005).

The range of the central herd extends from the Hayden and Pelican Valleys in the east to the lower-elevation Madison-Firehole Valley in the west (Hess 2002). Winter conditions are severe, with snow-water equivalents averaging 35.1 cm and temperatures reaching -42 C (Meagher 1973, Farnes et al. 1999). Windswept areas in the upper portions of the Hayden Valley and snow-free geothermal areas throughout the range provide some relief from deep snows and facilitated access to forage (Kittams 1949, Craighead et al. 1973). The central range includes a higher proportion of mesic meadows than the northern range, which contain grasses, sedges, and willows (*Salix* spp.), with upland grasses in the drier areas (Craighead et al. 1973). The central herd coexists with an average of 400 to 800 elk during winter (1965 to 1998; Craighead et al. 1973, Aune 1981, Garrott et al. 2003).

Management actions to conserve YNP bison changed as their abundance increased. The northern herd was subject to intense animal husbandry during 1902 to 1938 to increase their remnant numbers. Park managers rounded up northern herd bison from their summer ranges, confined them, and fed them hay throughout winter in the Lamar Valley (Cahalane 1944). Roundups and confinement ceased in 1938, but managers continued to feed bison on the northern range through winter until 1952 (Meagher 1973). Park managers implemented periodic removals during 1925 to 1968 to limit the growth of the northern herd bison population (Meagher 1973). Without such intense husbandry, the central herd remained <100 bison through the mid-1930's. To stimulate population growth, park managers augmented the central herd with 71 bison from the northern herd in 1936 (Cahalane 1944). Park managers periodically culled the central herd during 1954 to 1968 to limit bison numbers (Meagher 1973).

Park managers instituted the natural regulation policy in 1969, which ceased culling, augmentation, and feeding of wildlife inside Yellowstone (Cole 1971). Without human interference, weather, predators, and resource limitation influenced bison populations inside the park. Between 1984 and 2000, however, the State of Montana culled more than 3,000 bison that left the park to prevent the possible transmission of brucellosis from bison to cattle (National Park Service 2000). A cooperative Bison Management Plan between the State of Montana and YNP (National Park Service 2000) allowed continued culling of bison leaving the park.

Methods

Data

The count and removal data for YNP bison consisted of 2 time series when bison counts regularly occurred: 1902 to 1954 and 1970 to 2000 (Fig. 1 and 2; Appendix A). Park managers made counts during 1902 to 1954 predominantly from horseback, foot, or skis, although managers also used airplanes after 1949 (Meagher 1973). Park managers used the 1902 to 1954 counts on the northern herd as population censuses, because managers held bison captive in pens through winter until 1938, and supplemental feeding encouraged bison to stay centrally located during the winter until 1952. Little information regarding survey methods for the central herd over 1902 to 1969 existed, so we could not determine the quality of these data. We did not consider the data from 1954 to 1969 because only 9 counts occurred for each herd, park managers did not document counting methods, and the 1965 to 1969 counts suggested that counting methods or areas surveyed were too different for sensible comparison. Biologists used consistent counting methods throughout 1970 to 2000, when aerial counts of all bison (calves and adults) occurred 2 to 18 times per year (Dobson and Meagher 1996, Hess 2002). However, biologists did not record survey effort until 1997, precluding the use of some methods for population estimation. For each year during 1970 to 2000, we used the bison count taken during summer months (June through August), a time when bison were highly detectable due to gregarious behavior during the rut (Hess 2002). If multiple counts occurred during a given summer, we used the single highest count during June through August. These counts occurred after the birth pulse in each year, but before any management removals. We analyzed data from the central and northern herds separately because of differing habitat factors, environmental conditions, and management actions (Meagher 1973, Gates et al. 2005). We also analyzed the years 1902 to 1954 separately from 1970 to 2000 because of the different management paradigms and because herd sizes were large enough to expect to detect density dependence in 1970 to 2000.

Population Models – 1902 to 1954

We did not evaluate density-dependent models for this period because density-related suppression of growth was highly unlikely for either herd. The northern herd received supplemental feeding throughout winter and park managers periodically culled it to keep it at low abundance (Meagher 1973). The central herd began this period at 25 bison and only increased to 61 bison by 1928. There was an 8-year gap in the time series from 1928 to 1936, when park managers augmented the herd with 71 bison. After augmentation, the herd grew rapidly, but densities remained much lower than eventually reached in the 1990's when the population exceeded 3,000. Thus, we assumed bison were not resource limited during 1902 to 1954 and used exponential growth models to estimate the growth rates for each herd before and after significant management actions: before and after the augmentation of the central herd, and before and after the culling on the northern herd (Table 1). We calculated the annual, relative change in the total size of each herd (r_t) as

$$r_t = \log_e(n_t) - \log_e(n_{t-1}) \qquad (1)$$

where n refers to the number of counted individuals and the annual index $t = (1, 2, \ldots, N–1)$ (Eberhardt 1987). Frequent and substantial removals in the northern herd during the 1926 to 1950 complicated the data. We accounted for removals with the modification:

$$r_t = \log_e(n_t) - \log_e(n_{t-1} - RM_{t-1}) \qquad (2)$$

where RM_{t-1} represents removals taken after the count at n_{t-1} (Eberhardt 1987). We estimated growth rate and 95% confidence intervals using an equation describing perturbed exponential growth

$$r_t = a + \varepsilon \qquad (3)$$

where a represents the growth rate in the absence of density dependence and ε represents the stochastic contribution from noise and un-modeled processes (Zeng et al. 1998, Jacobson et al. 2004). For the northern herd, we compared the simple model estimating a single growth rate from the entire time series of r_t values (1902 to 1952) with a 2-period model that estimated a separate growth rate for the pre-culling (1902 to 1925) and culling (1926 to 1952) periods by including an indicator variable in equation 3 to designate the 2 periods ($r_t = a_1 + a_2 P + \varepsilon$). We then compared 1- and 2-period models using corrected Akaike's Information Criterion (AIC$_c$) for model selection (Burnham and Anderson 2002).

We conducted the analysis for the central herd differently. Removals over 1902 to 1954 did not complicate count data for the central herd. We expected differing population sizes and growth rates between the 1902 to 1928 and 1936 to 1954 periods, so we tested for differences between these periods using a piecewise log$_e$-linear regression (Eberhardt 1987, Morris and Doak 2000) and AIC$_c$ for model selection (Burnham and Anderson 2002). We evaluated 3 models: 1) a 1-intercept, 1-growth rate model (all 1902 to 1954); 2) a 2-intercept, 1-growth rate model (1902 to 1928 and 1936 to 1954); and 3) a 2-intercept, 2-growth rate model (1902 to 1928 and 1936 to 1954; Fig. 3).

Population models – 1970 to 2000

We ran preliminary analyses of all count data for the years before removals (1970 to 1984 for the northern herd and 1970 to 1994 for the central herd) using $\log_e$-linear regression. This model regressed the $\log_e$ of count data against time, allowed inspection of residuals, and we used it to detect abrupt changes in population growth rates (Piepho and Ogutu 2003). The time series of counts for the central herd during 1970 to 1994 revealed a significant breakpoint at 1982, with the 2-intercept, 2-slope piecewise regression model being more supported than a continuous model or a 2- intercept model ($w_i = 1.0$; Fig. 3). Based on this finding, we developed a suite of density-dependent and density-independent models for the entire time series (1970 to 2000) and for 2-period models allowing different density-dependent or density-independent dynamics during 1970 to 1981 and 1982 to 2000.

We considered 2 density-dependent model formations to evaluate the relative annual change in total size for each herd throughout 1970 to 2000. We calculated r_t using equation 2, which accounted for time periods with removals and reduced to equation 1 for periods without removals. The Ricker model assumed linear density dependence,

$$r_t = a + bn_{t-1} + \varepsilon \quad \text{(1 period)} \tag{4}$$

$$r_t = a_1 + b_1 n_{t-1} + a_2 P + b_2 P n_{t-1} + \varepsilon \quad \text{(2 periods)} \tag{5}$$

while the Gompertz model assumed a decrease in growth rates with $\log_e$ counts.

$$r_t = a + b(\log_e(n_{t-1})) + \varepsilon \quad \text{(1 period)} \tag{6}$$

$$r_t = a_1 + b_1(\log_e(n_{t-1})) + a_2 P + b_2 P(\log_e(n_{t-1})) + \varepsilon \quad \text{(2 periods)} \tag{7}$$

In both of these models, *b* represents the strength of density dependence and a population is said to exhibit a density-dependent response if *b* differs significantly from 0 (Zeng et al. 1998, Jacobson et al. 2004). We also considered 2 density-independent models, including the stochastic growth equation describing perturbed exponential growth (equation 3) and a random-walk model where population growth rate is uncorrelated with population size (Zeng et al. 1998, Jacobson et al. 2004):

$$r_t = \varepsilon \tag{8}$$

We explored the possibility that population changes depended on time-delayed dynamics using partial rate correlation functions (PRCF) for all periods without removals (Berryman and Turchin 2001). The results suggested we did not need to consider time lags (i.e., delayed density dependence) >1 yr in our analysis. Therefore, our final *a priori* model suite included Gompertz, Ricker, and exponential growth models calculated with and without the estimation of the first-order (AR1) autocorrelation parameter.

We used program R 2.0.0 to fit models and estimate parameter coefficients. We calculated AIC_c values for each model and then ranked and selected the best models using ΔAIC_c values (Burnham and Anderson 2002). Finally, we calculated Akaike weights (w_i) to obtain a measure of model selection uncertainty (Burnham and Anderson 2002). In an analysis such as this, measurement error inflates the variance around the estimated population growth parameter because counts are estimates and may not accurately reflect the true population size. In the case of density-dependent models, this type of variance may result in over-estimation of the strength of density dependence (Shenk et al. 1998, Viljugrein et al. 2005). We did not expect this would be problematic because bison in YNP are large, gregarious, and inhabit open landscapes, making count accuracy high relative to other herbivores (Hess 2002). To evaluate the level of sampling error, we used an approach recently developed by Staples et al. (2004), which uses a mixed-models approach to separating process and sampling error. This method was only available for the exponential model, so we used it for the time periods when we thought exponential growth was possible. Results indicated that sampling error only slightly inflated growth rate estimates and variances, suggesting the influences of sampling variance on the interpretation of results were slight.

To explore the potential influence of annual climate variation on bison population dynamics, we evaluated 1 warm-season and 1 cold-season climate covariate. We used the Palmer Drought Severity Index (PDSI; Palmer 1968) from the National Climatic Data Center as our warm-season climate covariate because it incorporates multiple environmental factors and gauges growing conditions across the USA (Alley 1985). We averaged PDSI over the growing season (May 1 through July 31) across region 1 of Wyoming. We predicted a positive correlation between PDSI and relative population change because dry years (i.e., low PDSI) would decrease plant production, thereby decreasing fat reserves for bison entering winter and resulting in lower calf survival. We lagged PDSI 1 year such that the drought index in $t-1$ affected the annual growth rate for year t (Appendix B). We used the accumulated daily value of snow water equivalent (SWE_{acc}) during October 1 to April 30 as our cold-season climate covariate because it integrates the depth, density, and duration of the snow pack (Garrott et al. 2003). We used SWE_{acc} data from the Tower Falls CLIM site from 1949 to 2000 for the northern range, and from the Canyon SNOTEL site from 1981 to 2000 for the central range (Farnes et al. 1999; Appendix B). We re-scaled the PDSI covariate by adding 7 to each value to remove negative figures and allow a square-root transform, because we expected population growth rates to increase with increasing PDSI, but that growth rates could potentially plateau at higher values of PDSI. We re-scaled

SWE_{acc} by dividing it by 1000 to enhance interpretability of coefficients and allow a quadratic transform, because we expected population growth rates to decrease with increasing SWE_{acc}, and that the higher values of SWE_{acc} could have stronger negative effects. We added combinations of our warm- and cold-season covariates to the top ranked models (e.g., $r_t = a + ... + c(PDSI) + d(SWE_{acc}) + e(SWE_{acc} x PDSI) + \varepsilon$) based on the AIC_c model selection results from the density-dependent and density-independent model suite. We used AIC_c to rank models and followed a stepwise model selection procedure to determine if the data supported the nonlinear forms of the covariates more than the linear forms (Borkowski et al. 2006).

Results

Population Models – 1902 to 1954

The piecewise $\log_e$-linear regression model allowing 2 intercepts and the estimation of 2 growth rates (1902 to 1928 and 1936 to 1950) was the most supported model for the central herd during 1902 to 1954, receiving 98% of the Akaike model weight (Fig. 3, Table 2). This model estimated the growth rate of the central herd at $\hat{r}$ = 0.06 (95% C.I. = 0.05, 0.07; $P < 0.01$) during 1902 to 1928 and $\hat{r}$ = 0.10 (95% C.I. = 0.08, 0.13; $P < 0.01$) after the herd was augmented with 71 bison in 1936 ($R^2 = 0.97$, $F_{1,36} = 339.2$; $P < 0.01$).

The northern herd 1-period (1902 to 1950) and 2-period (1902 to 1925, 1926 to 1950) models received similar support from the data (1-period: $\Delta AIC_c = 0.0$, $w_i = 0.55$; 2-period: $\Delta AIC_c = 0.39$, $w_i = 0.45$). The population growth rate estimate for the 1-period model (1902 to 1950) was $\hat{r}$ = 0.16 (95% C.I. = 0.13, 0.20; $P < 0.01$). The population growth rate estimates for the 2-period model were $\hat{r}$ = 0.19 (95% C.I. = 0.14, 0.23; $P < 0.01$) for 1902 to 1925 and $\hat{r}$ = 0.14 (95% C.I. = 0.08, 0.21; $P = 0.18$) for 1926 to 1954 ($R^2 = 0.04$, $F_{1,46} = 1.75$).

Population models – 1970 to 2000

The central herd showed evidence of a density-dependent response, with the 1-period Gompertz and 1-period Ricker models receiving high weights (w_i = 0.40 and 0.30, respectively). All other models had weights ≤8% (Table 3). The addition of autocorrelation parameters did not improve the fits of any of the top models. We also found evidence of density dependence in the northern herd during 1970 to 2000, with the 2-period Ricker and 2-period Gompertz models receiving nearly equal model weight (Table 4, w_i = 0.45 and 0.37). Residual analysis identified 1 influential point from the northern herd (r_{1997} = 2.44), which we censored because it was biologically infeasible.

For the northern herd, parameter estimates from the 2-period Ricker equation were $\hat{a}_1$ = 1.16 (95% C.I. = 0.63, 1.68), $\hat{a}_2$ = -0.48 (95% C.I. = -0.77, -0.19), $\hat{b}_1$ = -0.004 (95% C.I. = -0.006, -0.002), and $\hat{b}_2$ = 0.003 (95% C.I. = 0.001, 0.005). The first period demonstrated rapid decreases in growth rates with increasing density, as indicated by the negative value of $\hat{b}_1$ and 95% CI that did not encompass 0. There was a lessening of density dependence in the second period, as indicated by the positive value of $\hat{b}_2$. The density dependence term for the second period ($\hat{b}_1 + \hat{b}_2$) was -0.001 (95% C.I. = -0.002, -0.000), indicating that density dependence had a stronger effect during 1970 to 1981 when population counts were lower (182 to 457), compared to 1982 to 2000 when population counts were higher (405 to 756; Fig. 4).

Growth rates for the central and northern herds were not significantly correlated during 1970 to 1981 (P = 0.17, $F_{1,9}$ = 2.3, R^2 = 0.20, slope = -1.09, 95% C.I. = -2.50, 0.32; Fig. 5), but there was a strong negative correlation during 1982 to 2000 (P < 0.01, $F_{1,16}$ = 10.5, R^2 = 0.40, slope = -1.13, 95% C.I. = -1.81, -0.45; Fig. 6). We added climate covariates to the best models for the central and northern herds based on the availability of climate data (Appendix B). In both herds, transforming SWE_{acc} to SWE_{acc}^2 resulted in a decrease in 1 to 2 AIC points per model. The square-root transformation was not supported for PDSI. For the central herd, the Gompertz 1-period model received most of the model weight (79%), but the SWE_{acc}^2 coefficient indicated a negative correlation with growth rate (c = -0.007; 95% C.I. = -0.013, -0.002; Table 5). For the northern herd, the 2-period Ricker model without climate covariates was the top model, receiving 68% of the model weight. All 4 models containing climate covariates received 32% of total model weight (Table 5) and all climate covariates had coefficients overlapping 0, thus providing minimal support for effect of climate on population growth rates in the northern herd.

Discussion

We detected evidence of density-dependent changes in population growth rates for bison during 1970 to 2000 as numbers increased to >3,000 animals. The central herd showed evidence of a constant response, while density dependence had a stronger effect on the northern herd's growth rate during 1970 to 1981 than during 1982 to 2000. These trends apparently resulted from pulses of emigration from the central herd to the northern range beginning in 1982 in response to resource limitation generated by an interaction between density and severe snow pack. Evidence supporting this interpretation included: 1) growth rates of the central and northern herds were uncorrelated during 1970 to 1981 but significantly and negatively correlated during 1982 to 2000; 2) the northern herd could not have sustained the high removals experienced during 1984 to 2000 without immigration; and 3) the annual growth of the central herd was negatively correlated with snow pack, but that of the northern herd was not.

The changes in population growth rates of central and northern bison during 1970 to 2000 did not appear to be due to differential survival and reproduction. The only available herdspecific survival and reproductive rates for radio-marked cows during 1995 to 2001 did not differ significantly (Fuller 2006). Also, recruitment as indexed by calf-adult ratios during 1970 to 1997 did not significantly differ between herds or pre- and post-1981 periods (Fuller 2006). Rather, the divergent dynamics in these herds separated by only 30 km and at similar densities (0.2 bison/km^2) at the start of the 1970-2000 period were likely due to a change in movement patterns, with bison from the central herd emigrating to the northern range. This emigration would have inflated population counts and growth rates of the northern herd, while resulting in opposite effects for the central herd. Winter conditions are known to cause large ungulates to disperse or migrate to find more accessible forage (Aanes et al. 2000). Winters are more severe in the central regions of YNP and the drier northern range would be a logical option for dispersing central herd bison. Range expansion in the central herd occurred in the 1980's as the central herd moved westward into areas that it previously used rarely, if at all (Taper et al. 2000 in Gates et al. 2005). Central herd bison could also move to the northern range because no ecological barriers existed to the north, while high-elevation ridges and lack of foraging meadows likely blocked dispersal to the east and south. An influx of central herd bison onto the northern range would not have been easily detected because no individual bison in YNP were marked until 1995.

Increased emigration from the central herd to the northern range is also supported by removal data, which indicate the northern herd sustained the removal of >2,000 bison during 1982 to 2000 even though counts never exceeded 900 bison. In contrast, the central herd sustained only half as many removals (1,111 bison) even though it was 3 times larger (>3,000 bison. The northern herd could not have sustained this high removal rate without immigrants from the central herd. For example, managers counted 877 bison on the northern range during 1996 and removed 725 bison that winter. Next year, managers counted 354 bison, an increase of 230%. This increase could not have been realized solely from intrinsic productivity. Hence, substantial immigration must have occurred. Differential removals by sex could influence population growth rates, but the composition of 1,809 bison removed at the park boundaries during the winters of 1988 to 1989 and 1996 to 1997 indicated approximately equal proportions of males and females. If YNP bison herds have approximately equal sex ratios, as suggested in Shaw and Meagher (2000), then there was no overt bias in removals that would influence population growth rates.

Ungulate populations generally become more sensitive to density-independent factors that affect resource availability as they approach high densities (Sæther 1997, Gaillard et al. 1998, Gaillard et al. 2000). Therefore, we expected exogenous, density-independent processes such as drought and snow pack to have a major influence on the dynamics of both bison herds during 1970 to 2002. As predicted, the population growth rate of the central herd was negatively correlated with snow pack (SWE_{acc}), similar to the findings of numerous studies of large ungulates in relation to winter severity (Gaillard et al. 2000, Clutton-Brock and Coulson 2002, Garrott et al. 2003, Jacobson et al. 2004, Wang et al. 2006). We did not observe a negative effect of snow pack on the northern herd, possibly due to influx from central herd bison during or immediately after severe winters. Spring precipitation positively affects elk calf recruitment in YNP and surrounding areas (Merrill and Boyce 1991, Coughenour and Singer 1996, Taper and Gogan 2002, Lubow and Smith 2004), as well as ungulate population growth in other biomes (Sinclair 1975, Van Vuren and Bray 1986, Mduma et al. 1999, Gaillard et al. 2000). However, we found no strong evidence of warm-season drought effect on population growth rates of either the central or northern bison herds. It is possible that the effect of spring and summer precipitation on bison calf survival exists, but the overall population effect was too small for detection. Further research into these effects would be useful.

Management Implications

Our findings suggest that pulses of climate-induced dispersal of bison from the central herd to the northern range during winter could create a source-sink dynamic that exacerbates the current controversy about management of bison when they leave the protection of the park and are culled to reduce the potential of brucellosis transmission to cattle. These movements will also complicate future analyses of bison time series because removals at the northwestern boundary can no longer be reliably assigned to the northern herd. Long-term studies of marked animals from both herds should be initiated to elucidate the extent and factors influencing these movements.

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Literature Cited

Aanes, R., B. E. Sæther, and N. A. Ǿritsland. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. Ecography 23:437-443.

Alley, W. M. 1985. The Palmer Drought Severity Index as a measure of hydrologic drought. Water Resources Bulletin 21:105-114.

Amarasekare, P. 2004. The role of density-dependent dispersal in source-sink dynamics. Journal of Theoretical Biology 226:159-168.

Barmore, W. J. 1968. Bison and brucellosis in Yellowstone National Park. July 1968, Yellowstone Archives, Yellowstone National Park, Wyoming, USA.

Barmore, W. J., Jr. 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park: research and synthesis, 1962-1970. National Park Service, Mammoth Hot Springs, Wyoming, USA.

Berryman, A., and P. Turchin. 2001. Identifying the density-dependent structure underlying ecological time series. Oikos 92:265-270.

Bjornlie, D. D., and R. A. Garrott. 2001. Effects of winter road grooming on bison in Yellowstone National Park. Journal of Wildlife Management 65:560-572.

Borkowski, J. J., P. J. White, R. A. Garrott, T. Davis, A. R. Hardy, and D. J. Reinhart. 2006. Wildlife responses to motorized winter recreation in Yellowstone National Park. Ecological Applications 16:1911-1925.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cahalane, V. H. 1944. Restoration of wild bison. Transactions of the North American Wildlife Conference 9:135-143.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183-246 *in* T.H. Coaker, editor. Applied Biology 1. Academic Press, London, UK.

Cheville, N. F., D. R. McCullough, and L. R. Paulson. 1998. Brucellosis in the Greater Yellowstone Area. National Research Council, Washington D.C., USA.

Clutton-Brock, T. H., and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society of London Series B 357:1285-1298.

Clutton-Brock, T. H., M. Major, and F. E. Guinness. 1985. Population regulation in male and female red deer. Journal of Animal Ecology 54:831-846.

Cole, G. F. 1971. An ecological rationale for the natural or artificial regulation of ungulates in parks. Transactions of the North American Wildlife Conference 36:417-425.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6:573-583.

Craighead, J. J., F. C. Craighead Jr., R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison drainage herd as determined by biotelemetry. Wildlife Monographs 33.

Dobson, A., and M. Meagher. 1996. The population dynamics of brucellosis in the Yellowstone National Park. Ecology 77:1026-1036.

Eberhardt, L. L. 1987. Population projections from simple models. Journal of Applied Ecology 24:103-118.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841-2854.

Farnes, P., C. Heydon, and K. Hansen. 1999. Snowpack distribution across Yellowstone National Park. Department of Earth Sciences, Montana State University, Bozeman, Montana, USA.

Ferguson, M. A., D., L. Gauthier, and F. Messier. 2001. Range shift and winter foraging ecology of a population of Arctic tundra caribou. Canadian Journal of Zoology 79:746-758.

Festa-Bianchet, M., J. M. Gaillard, and S. D. Côté. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. Journal of Animal Ecology 72:640-649.

Forsyth, D. M., and P. Caley. 2006. Testing the irruptive paradigm of large-herbivore dynamics. Ecology 87:297-303.

Fuller, J. A. 2006. Population demography of the Yellowstone National Park bison herds. M.S. Thesis, Montana State University, Bozeman, Montana, USA.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81:33-45.

Gates, C. C., B. Stelfox, T. Muhley, T. Chowns, and R. J. Hudson. 2005. The ecology of bison movements and distribution in and beyond Yellowstone National Park. University of Calgary, Alberta, Canada.

Hess, S. C. 2002. Aerial survey methodology for bison population estimation in Yellowstone National Park. Ph.D. Dissertation, Montana State University, Bozeman, Montana, USA.

Houston, D.B. 1982. The northern Yellowstone elk. MacMillan Publishing Company, New York, New York, USA.

Jacobson, A. R., A. P. Provenzale, A. von Hardenberg, B. Bassano, and M. Festa- Bianchet. 2004. Climate forcing and density dependence in a mountain ungulate population. Ecology 85:1598-1610.

Kittams, W. H. 1949. Preliminary report on Hayden Valley bison range. Document 720.04.1, July 1949, Yellowstone Archives, Yellowstone National Park, Wyoming, USA.

Larter, N. C., A. R. E. Sinclair, T. Ellsworth, J. Nishi, and C. C. Gates. 2000. Dynamics of reintroduction in an indigenous larger ungulate: the wood bison of northern Canada. Animal Conservation 4:299-309.

Lemke, T. O., J. A. Mack, and D. B. Houston. 1998. Winter range expansion by the northern Yellowstone elk herd. Intermountain Journal of Sciences 4:1-9.

Lubow, B. C., and B. L. Smith. 2004. Population dynamics of the Jackson elk herd. Journal of Wildlife Management 68: 810-829.

Mduma, S. A. R., A. R. E. Sinclair, and R. Hillborn. 1999. Food regulates the Serengeti wildebeest: a 40-year record. Journal of Animal Ecology 68:1101-1122.

Meagher, M. M. 1973. The bison of Yellowstone National Park. National Park Service Scientific Monograph Series Number 1, National Park Service, Washington, D.C., USA.

Meagher, M. M. 1993. Winter recreation-induced changes in bison numbers and distribution in Yellowstone National Park. National Park Service, Yellowstone National Park, Wyoming, USA.

Merrill, E. H., and M. S. Boyce. 1991. Summer range and elk population dynamics in Yellowstone National Park. Pages 263-273 *in* R. B. Keiter and M. S. Boyce, editors. The greater Yellowstone ecosystem. Yale University Press, New Haven, Connecticut, USA.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer Press, Sunderland, Massachusetts, USA.

National Park Service, U.S. Department of the Interior. 2000. Winter Use Plans Final Environmental Impact Statement, Volume I, for the Yellowstone and Grand Teton National Parks and John D. Rockefeller, Jr., Memorial Parkway. National Park Service Intermountain Regional Office, Lakewood, Colorado, USA.

Palmer, W. C. 1968. Keeping track of crop moisture conditions, nationwide: the new crop moisture index. Weatherwise 21:156-161.

Piepho, H. P., and J. O. Ogutu. 2003. Inference for the break point in segmented regression with application to longitudinal data. Biometrical Journal 45:591-601.

Sæther, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143-149.

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Sæther, B. E., S. Engen, and R. Lande. 1999. Finite metapopulation models with density-dependent migration and stochastic local dynamics. Proceedings of the Royal Society of London, Series B 266:113-118.

Shaw, J. H., and M. M. Meagher. 2000. Bison. Pages 447-464 *in*: S. Demarais and P.R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall Press, New Jersey, USA.

Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. Ecological Monographs 68:445-463.

Sinclair, A. R. E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. Journal of Animal Ecology 44:497-520.

Staples, D. F., M. L. Taper, and B. Dennis. 2004. Estimating population trend and process variation for PVA in the presence of sampling error. Ecology 85:923-929.

Taper, M. L., and P. J. P. Gogan. 2002. The northern Yellowstone elk: density dependence and climatic conditions. Journal of Wildlife Management 66:106-122.

Van Vuren, D., and M. P. Bray. 1986. Population dynamics of bison in the Henry Mountains, Utah. Journal of Mammalogy 67:503-511.

Viljugrein, H., N. C. Stenseth, G. W. Smith, and G. H. Steinbakk. 2005. Density dependence in North American ducks. Ecology 86:245-254.

Formatted: German (Germany)

Wang, G., N. T. Hobbs, R. B. Boone, A. W. Illius, I. J. Gordon, J. E. Gross, and K. L. Hamlin. 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. Ecology 87:95-102.

White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves – expectations, realizations and predictions. Biological Conservation 125:141-152.

Zeng, Z., R. M. Nowierski, M. L. Taper, B. Dennis, and W. P. Kemp. 1998. Complex population dynamics in the real world: modeling the influence of time-varying parameters and time lags. Ecology 79:2193-2209