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Month/Year: 2009Pages: 217-235

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## Partial Migration in Central Yellowstone Bison

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### Theme

The conservation of bison (*Bison bison*) in Yellowstone National Park from near extinction to a high of 5000 animals has led to societal conflict regarding overabundance and potential transmission of brucellosis to cattle with widespread economic consequences. As abundance increased during 1971–1996, more bison migrated from the Hayden and Pelican valleys to the lower-elevation Madison headwaters area and, eventually, outside the park (Meagher 1998, Fuller *et al.* 2007). Meagher (1998) and others (Taper *et al.* 2000, Gates *et al.* 2005) concluded these migratory movements were stress-related responses to decreased food availability as bison fully occupied habitat in the Pelican and Hayden valleys and, subsequently, the Firehole and Madison river drainages. This hypothesis implies that these areas have a relatively fixed capacity for wintering bison and, as a



result, a larger proportion of bison migrate to the Madison headwaters and elsewhere as bison numbers increase beyond this capacity. However, density-independent factors such as genetic predisposition, individual asymmetries (*e.g.*, age, sex), and stochastic variations in climate that influence food availability may also affect migration (Lundberg 1987). We used data collected during 1970–1971 through 2005–2006 to quantify annual variations in the magnitude and timing of migration by central herd bison, identify potential factors driving this variation, and evaluate if the proportion of migrants increased with abundance.

## I. INTRODUCTION

On large spatial scales, migration serves to reduce the environmental heterogeneity experienced by an organism and place it under favorable conditions for survival (Dingle 1996). Migratory movements are often predicated on the need for resources, especially food, which may be affected by biotic and abiotic factors (*e.g.*, Whitehead 1996, Knight *et al.* 1999). A density-related reduction in per capita resources may lead to the establishment of migratory behavior for a population or affect the magnitude and timing of migration (Mahoney and Schaefer 2002, Whalen and Watts 2002, Marra *et al.* 2005). The effects of seasonality and climate on migratory patterns have also been documented in various studies (Kaňuščák *et al.* 2004), including effects of air temperature on birds (Gordo *et al.* 2005) and precipitation on insects (Dingle *et al.* 2000). These factors may modify the availability and quality of suitable habitat and forage. They can interact to influence an animal's choice of migratory decisions and destinations, as well as the rate of movement during migration (Ahola *et al.* 2004, Hulbert *et al.* 2005). Thus, quantifying the effects of density-dependent and independent mechanisms on migratory behavior is essential for comprehending population processes, evaluating habitat requirements, and designing management strategies for migratory species.

Variability in individual migratory behavior has been documented in various ungulate populations (Talbot and Talbot 1963, Morgantini and Hudson 1988, Bergerud *et al.* 1990, Nelson *et al.* 2004). White *et al.* (2007) suggested pronghorn (*Antilocapra americana*) assessed individual asymmetries, behaviors, and environmental conditions when deciding whether to migrate. Also, Ball *et al.* (2001) suggested differences in snow attributes between ranges of migrant and resident moose (*Alces alces*) may be a factor that influences behavior. Migrations in response to density and climate, which may ultimately affect population dynamics (Langvatn *et al.* 1996, Forchhammer *et al.* 1998, Post and Stenseth 1998, Jacobson *et al.* 2004), have been documented for assorted ungulates (Bergerud 1988, Fryxell and Sinclair 1988, Pettorelli *et al.* 2005). While wildebeest (*Connochaetes taurinus*) migration in response to rainfall (Maddock 1979) is a classic example, many other large herbivores follow forage productivity gradients and migrate in response to climate variation (Leimgruber *et al.* 2001, Myserud *et al.* 2001). Mule deer (*Odocoileus hemionus*) migration between summer and winter ranges in response to snow has been detailed (Gilbert *et al.* 1970, D'Eon and Serrouya 2005). Further, sika deer (*Cervus nippon*) and elk (*Cervus elaphus*) have been found to migrate to areas of lesser snow pack in winter (Igota *et al.* 2004, White and Garrott 2005). Therefore, migratory movements may be influenced by weather conditions that affect vegetation quality and quantity, as well as forage availability.

After near extirpation in the early twentieth century, bison in the Lamar and Pelican valleys of Yellowstone National Park were subject to intense animal husbandry during 1902–1938 and reintroduced into the Hayden and Firehole Valleys of Yellowstone in 1936 (Meagher 1973). As numbers increased, movements between the Hayden and Firehole valleys were observed during all seasons and bison began using areas beyond the Firehole Valley and throughout the Madison headwaters area (Meagher 1973, Gates *et al.* 2005, Figure 12.1). Seasonal migrations are now the norm, with migration into the Madison headwaters area from the higher-elevation summer range in the Hayden and Pelican Valleys beginning in autumn and continuing through winter along the Mary Mountain trail until bison return to the summer range in June (Bjornlie and Garrott 2001, Chapter 27 by Bruggeman *et al.*, this volume). Increased use of areas beyond the Madison headwaters area has been occurring since the





**FIGURE 12.1** After near extirpation a century ago Yellowstone's bison population has been fully restored and has reestablished migratory movements throughout the park and across its boundaries. These animals are crossing the Yellowstone River in the Hayden Valley where they summer, with many of the central herd animals migrating westward into the Madison headwater drainages to winter (Photo by Jeff Henry).

1990s. Meagher (1993, 1998) attributed these changes in distribution to stress-related dispersal in response to food limitations as bison fully occupied wintering areas and compensated for decreasing per capita resources by moving to additional areas. She concluded that movements by bison in the Pelican Valley westward had a domino effect on bison wintering in the Hayden Valley, resulting in larger movements of more bison earlier to the Madison headwaters area (Meagher 1998). This "domino effect" hypothesis, whereby increased abundance was coupled with cascading increases in distribution, was adopted by other scientists as a mechanism by which bison could maintain a relatively stable winter density. For example, Gates *et al.* (2005:115) referred to this hypothesized gradual and linear range expansion as "the density-equalization effect," whereby the area occupied by bison during winter expanded within available grassland and meadow habitats as the central and northern herds increased in abundance. Also, Taper *et al.* (2000) proposed range expansion as a mechanism explaining stable population growth in Yellowstone bison.

Our goals were to (1) test the predictions that significant migration by the central herd did not occur until bison had fully occupied the Hayden and Pelican valleys, and more animals migrated earlier as numbers increasingly exceeded this limit, and (2) assess the influence of biotic and abiotic mechanisms on the magnitude and timing of the annual migration to winter range in the Madison headwaters area. We analyzed one recent (1996–1997 through 2005–2006) data set from winter ground surveys and one historic (1970–1971 through 2005–2006) data set from winter aerial surveys using an information-theoretic approach to evaluate competing hypotheses regarding the relative influence of snow pack, forage productivity, and population size on the timing and magnitude of bison migration patterns.

## II. METHODS

### A. Development of Migration Response Variables

The number and distribution of bison wintering in the Madison headwaters area were determined by conducting comprehensive ground-based surveys every 10–14 days during November–May, 1996–1997 through 2005–2006 (Bjornlie and Garrott 2001, Bruggeman *et al.* 2006). Seventy-four sampling units



were surveyed over two days using six distinct routes (Ferrari 1999, Bjornlie 2000) that afforded a nearly complete enumeration of bison in this area as determined from an aerial-ground double-sampling study (Hess 2002). A small portion of migratory bison remained uncouned because we did not survey winter range areas along the Mary Mountain trail and western park boundary. Observers using snowmobiles, trucks, or snowshoes started each route simultaneously to minimize missing or double counting bison (Bjornlie and Garrott 2001). We defined 2-week time intervals,  $i$  ( $1 \leq i \leq 14$ ), from November–May for each winter,  $j$  ( $1 \leq j \leq 10$ ), centered on the bimonthly ground surveys. To investigate the magnitude of migration, we defined a response variable, MAXIMUM, as the highest number of bison counted in the Madison headwaters area each winter during ground surveys. To investigate the timing of migration, we defined a response variable, TIMING, as the number of bison in the Madison headwaters area for the  $ij$ th period as determined from ground surveys.

We also obtained aerial estimates of abundance and distribution for central herd bison during winters 1970–1971 through 2005–2006, as well as removal data from the western boundary of the park, to investigate “historic” patterns in the magnitude of migration (Dobson and Meagher 1996, Hess 2002). We defined a response variable, HISTORIC<sub>max</sub>, as the highest number of bison counted on the west-side winter range (Firehole, Gibbon, and Madison river drainages) during flights conducted between January and mid-April each year, plus removals that occurred before the flights. This definition of “west-side” winter range differs from Meagher (1993) who considered the west-side to be from Madison Junction along the Madison River to Hebgen Lake, excluding the Firehole drainage.

## B. Development of Covariates

We anticipated snow would affect migration behavior by bison because it affects their foraging, movements, and distributions (Bruggeman 2006, Figure 12.2). We used a validated snow pack simulation model (Watson *et al.* 2006, Chapter 6 by Watson *et al.*, this volume) to compute daily estimates of average snow water equivalent (SWE; *i.e.*, amount of water in the snow) on the bison



**FIGURE 12.2** Bison travelling and feeding at the mouth of Trout Creek in the Hayden Valley. As snow pack increases on the summer range of the central bison herd foraging and movement becomes difficult and provides an impetus for animals to migrate to the lower elevation winter range in the Madison headwater drainages (Photo by Jeff Henry).



summer range, encompassing all  $28.5 \times 28.5$  m pixels within the Hayden and Pelican valleys. We defined a covariate,  $\text{SWES}_{ij}$ , as the average SWE on the bison summer range for each  $ij$ th period between November–May for each year to be used in the timing of migration analysis. We added daily SWE values from October 1–April 30 to calculate a covariate,  $\text{SWE}_{\text{acc}}$ , and obtain a measure of annual winter severity (Garrott *et al.* 2003) for use in both the recent and historic magnitude of migration analyses. We also calculated a covariate,  $\text{SWE}_{\text{acc},ij}$ , as the sum of daily SWE estimates from October 1 through the  $ij$ th period for a temporal measure of winter severity for the timing of migration analysis.

Warm season climate variation, particularly with regard to precipitation, temperature, and the rate of evapotranspiration, influences plant growing conditions and, in turn, the quantity and quality of grasses available for bison (McNaughton 1985, Sala *et al.* 1988, Stephenson 1990). As a result, vegetation productivity may affect ungulate distribution, breeding phenology, and reproductive success (McNaughton 1985, Pettorelli *et al.* 2006, Wittemyer *et al.* 2007). Recent analyses of bison demographic rates and migration patterns in Yellowstone (*e.g.*, Bruggeman 2006, Fuller *et al.* 2007) have reported significant relationships with the Palmer Drought Severity Index (Palmer 1965), which was used as a single integrator of annual variability in regional warm season climate. Northwestern Wyoming experienced severe, sustained drought conditions during 1995–2006, with the mean Palmer Drought Severity Index during May–July decreasing from 0.9 to  $-9.0$  compared to a mean index of  $-1.0$  during 1969–1994 (range =  $-6.4$  to  $2.9$ ). This index is cumulative, so the intensity of drought during a given month is derived from the current weather patterns plus the cumulative patterns of previous months. Certainly, food limitations during periods of drought are known to affect population dynamics (Sinclair *et al.* 1985, Mduma *et al.* 1999) and provide additional stimuli for animals to migrate (Polovina *et al.* 2001, Burtenshaw *et al.* 2004, Varpe *et al.* 2005). However, we did not use the Palmer Drought Severity Index in our current analyses because it was significantly and negatively correlated with summer counts of bison in the central herd during 1998–2006 ( $R^2 = 0.80$ ,  $F_{1,7} = 27.5$ ,  $P = 0.001$ ). Also, we were unable to detect any correlation between this drought index and growing season precipitation in the Madison headwaters area during 1989–2005 ( $R^2 = 0.03$ ,  $F_{1,15} = 0.5$ ,  $P = 0.51$ ).

Instead, we used remotely sensed, normalized differential vegetation index (NDVI) data from summers 1989–2005 for the Hayden and Pelican valleys as a measure of forage production. The NDVI is correlated with green biomass and serves as a measure of temporal and spatial variability in vegetation growth (Wittemyer *et al.* 2007). Specifically, we used the L-integral, which is the integral of the seasonal NDVI curve over the growing season (Garel *et al.* 2006), to calculate a covariate,  $\text{NDVI}_{\text{int}}$ , to index summer range forage productivity prior to winter. We also calculated a covariate,  $\text{NDVI}_{\text{len}}$ , as the length of the growing season as determined from NDVI data. Because NDVI data were available only from 1989–2005, we did not have complete data for the historic migration analysis. Therefore, we developed an index for the L-integral from 1971–1988 using L-integral data from 1989–2005 and assorted precipitation, temperature, and snow data obtained from the Canyon SNOTEL site (National Resource Conservation Service 2007). We conducted an all-subsets regression using PROC REG in SAS version 9.1.3 (SAS 2004) using the L-integral response variable and 78 climate covariates, and selected the model with the highest adjusted  $R^2$  value (Neter *et al.* 1996). We then used data from the Yellowstone Lake CLIM site from 1970–1980 and Canyon SNOTEL site from 1981–1988 to estimate the  $\text{NDVI}_{\text{int}}$  covariate for 1970–1988 for use in the historic migration analysis.

Aerial population estimates for the central herd were obtained during late July or August each year, prior to the migration (Dobson and Meagher 1996, Hess 2002). We used these annual estimates to define a covariate, BISON, which provided a measure of the effect of bison density on migration. We also defined a covariate, DATE, as the Julian date of the January–April winter survey used to calculate  $\text{HISTORIC}_{\text{max}}$  because, in general, more migratory bison should be counted as winter progresses (*i.e.*, later survey dates; Bjørnlie and Garrott 2001, Bruggeman *et al.* 2006).

### C. 1996–1997 Through 2005–2006 Migration Patterns: Model Development and Statistical Analyses

We developed and compared *a priori* hypotheses, expressed as multiple regression models, in two modeling exercises to estimate the relative contributions of snow pack, forage productivity, and density on variations in the magnitude and timing of migration from 1996–1997 through 2005–2006 (Appendix 12A.1). We calculated variance inflation factors (VIFs; Neter *et al.* 1996) while forming our model list to quantify multicollinearity between model predictors, including interactions. Models containing predictors having a  $VIF > 5$  were removed from our *a priori* list. Hypotheses for the timing of migration analysis were expressed as 11 regression equations consisting of additive main effects (SWES, BISON,  $NDVI_{int}$ ) and interactions (SWES\*BISON, BISON\* $NDVI_{int}$ ) of covariates, while those for the magnitude of migration analysis were expressed as 11 equations of main effects (SWE<sub>acc</sub>, BISON,  $NDVI_{int}$ ) and interactions (SWE<sub>acc</sub>\*BISON, BISON\* $NDVI_{int}$ ). In exploratory analyses, we systematically substituted covariates SWE<sub>acc,ij</sub> for SWES and  $NDVI_{len}$  for  $NDVI_{int}$ .

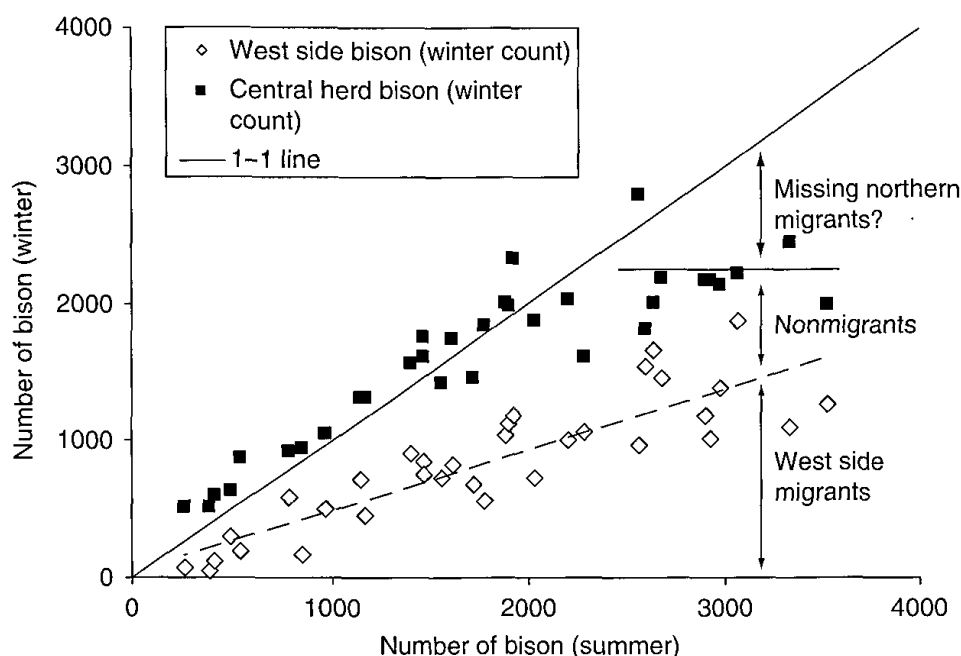
For each covariate and interaction, we made a hypothesis about the sign of the effect on each response variable. We predicted the magnitude of migration (MAXIMUM) would be positively correlated with BISON because increasing population size would lead to a decrease in per capita resources on the summer range and result in more bison migrating to the winter range to find forage. Second, we hypothesized that MAXIMUM would be negatively correlated with  $NDVI_{int}$  (or  $NDVI_{len}$ ) since decreased primary productivity would decrease the quality and quantity of forage and bison would need to migrate to obtain adequate food resources. Third, we predicted increasing SWE<sub>acc</sub> would result in increased bison migration (MAXIMUM) because greater snow pack on the summer range would provide more impetus for bison to migrate to lower elevations to find more accessible forage during winter. Fourth, we anticipated the influence of bison density would vary with snow pack in the form of a positive BISON\*SWE<sub>acc</sub> interaction effect because high population sizes at high SWE<sub>acc</sub> would result in further increases in bison migration (MAXIMUM). Finally, we hypothesized that density would interact with primary productivity (BISON\* $NDVI_{int}$ ) because the influence of population size would be accentuated during years of reduced productivity (negative sign), leading to increased bison migration (MAXIMUM).

We used similar rationale for the timing of migration analysis to hypothesize that TIMING would be positively correlated with BISON and negatively correlated with  $NDVI_{int}$  (or  $NDVI_{len}$ ). Second, we predicted that TIMING would be positively correlated with SWES (or SWE<sub>acc,ij</sub>) because increasing snow pack on the summer range would provide an impetus for more bison to migrate to the lower-elevation, geothermally influenced winter range with easier access to forage. We anticipated the effect of population size would vary with climate and plant productivity in the form of BISON\*SWES and BISON\* $NDVI_{int}$  interactions because combinations of high population sizes and high snow levels, or high population sizes and reduced plant productivity, could further accelerate the timing of migration (TIMING).

We used regression techniques in R version 2.3.1 (R Development Core Team 2006) to fit models and estimate parameter coefficients. To facilitate comparisons of parameter coefficients, each continuous predictor was centered and scaled prior to analysis by subtracting the midpoint and dividing by half of the range, resulting in values between –1 and 1. We calculated a corrected Akaike's Information Criterion ( $AIC_c$ ) value for each model, ranked and selected the best approximating models for the timing and magnitude analyses using  $\Delta AIC_c$  values, and calculated Akaike weights ( $w_i$ ) to obtain a measure of model selection uncertainty (Burnham and Anderson 2002).

### D. 1970–1971 Through 2005–2006 Migration Patterns: Model Development and Statistical Analyses

Examination of central herd summer and winter count data from 1970–1971 through 2005–2006 revealed an unexpected relationship between the total number of bison enumerated from the July–August summer flight and the total count during the January to mid-April winter flight (Figure 12.3).



**FIGURE 12.3** Relationships between the number of west-side migratory bison from the winter flight and central herd population size from the summer flight, and the central herd population size from the winter flight and central herd population size from the summer flight (1970–1971 through 2005–2006). The line depicting a 1–1 relationship is denoted for reference. Note the break point around 2350 bison for the central herd population size count comparisons.

We noted a change from an approximately 1–1 correlation, with fewer bison counted during winter compared to summer surveys as population size exceeded 2000 bison. We used piecewise regression methods (Neter *et al.* 1996) using PROC NLIN in SAS version 9.1.3 (SAS 2004) to determine this break point occurred at a count of approximately 2350 bison. Fuller *et al.* (2007) suggested a change in bison spatial dynamics, with increased emigration from the central herd and immigration into the northern herd, resulted in changes in herd dynamics beginning in 1981–1982. We suspected these movements onto the northern range caused this break point, but the data did not exist to further investigate the timing and magnitude of these movements. Thus, we censored summer counts when the central herd population was >2350 from the data set (1993–1997, 2002–2006) before beginning the analysis, and only examined migration to the west-side winter range.

We developed and compared *a priori* hypotheses to estimate the relative contributions of snow pack, forage productivity, density, and winter survey date on variations in the magnitude of migration for years when the central herd population size was <2350 bison during summer (*i.e.*, 1971–1992, 1998–2001; Appendix 12A.1). During 1982, 1983, and 1988, there was either no July–August flight or the count was deemed poor. Thus, no population size data were available to apply for the subsequent winters. We had 22 observations for the analysis after removing these years and a data point from 1987 owing to a high leverage NDVI<sub>int</sub> value. We calculated VIFs (Neter *et al.* 1996) while forming the model list and removed any predictors with VIF > 5. Hypotheses were expressed as 20 regression equations consisting of additive main effects (SWE<sub>acc</sub>, BISON, NDVI<sub>int</sub>, DATE) and interactions (SWE<sub>acc</sub>\*BISON, BISON\*NDVI<sub>int</sub>) of covariates. Our predictions were similar to the extent of migration analyses during 1996–1997 through 2005–2006. We used regression techniques in R version 2.3.1 (R Development Core Team 2006) to fit models and estimate parameter coefficients using centered and scaled continuous covariates as described above. We calculated AIC<sub>c</sub> for each model, ranked and selected the best approximating models using AIC<sub>c</sub>, and calculated  $w_i$  (Burnham and Anderson 2002).

## E. Estimates of Nutritional Intake

To explore differences in nutrition of bison, which we hypothesize may be a primary driver of migration, we estimated metabolizable energy intake (nutrition) by bison in the Hayden Valley and Madison headwaters area during the winter of 2005–2006 using molar ratios of allantoin:creatinine (A:C) obtained from fresh urine deposited in snow. We opportunistically collected samples from mixed groups of adult and calf bison using the collection, storage, and assay procedures described by Pils *et al.* (1999) during eight 14-day intervals between December 18 and April 8. Frozen snow-urine samples were then thawed at room temperature and extraneous debris was eliminated by filtration from the snow-urine mixture. The filtrate was refrozen at 20°C until assayed. Creatinine concentrations in filtered samples were assayed at the Department of Animal and Range Sciences, Montana State University, Bozeman, using a modification of the kinetic Jaffé reaction (Larsen 1972). Creatinine is a compound produced and excreted in relatively constant proportion to muscle mass, allowing comparisons to be made among animals of different body size and hydration and among samples of different snow dilution (Coles 1980). Allantoin concentrations were determined using a microplate modification of the colorimetric procedures described by Young and Conway (1942). Allantoin is a metabolite that reliably indexes rumen microbial flow in domestic ruminants and free-ranging elk during a several-day period prior to the time urine was voided (Chen *et al.* 1992a,b; Vagnoni *et al.* 1996, Garrett *et al.* 1997). Allantoin and creatinine were assayed from the same sample at the same time to avoid additional freeze-thaw cycles that tend to degrade allantoin. Sensitivities of allantoin and creatinine assays were 0.027 and 0.079  $\mu\text{mol}$ , respectively. Coefficients of variation for high and low snow-urine pools of allantoin and creatinine were less than 15%. The relationship between digestible dry matter intake and urinary A:C ratios has not been tested for bison during captive feeding trials.

Pils *et al.* (1999) reported that mean A:C ratios of samples collected from mixed groups of adult female and calf elk were highly variable and consistently overestimated the true mean A:C ratio of adult females. These problems were alleviated by trimming 15% off the right tail of the ordered sample distribution and 20% off the left tail and calculating the mean of the remaining samples. Trimmed estimates of mean A:C ratios were consistently less biased, with lower variability of sample means and smaller confidence intervals than untrimmed means (Pils *et al.* 1999). We calculated trimmed A:C ratios for bison in the Hayden Valley and Madison headwaters area during each collection period and used a one-tailed t-test to compare paired sample means. We predicted nutritional estimates for bison wintering in the Hayden Valley would be significantly lower than those of bison wintering in the lower-elevation and more heterogeneous Madison headwaters area.

## III. RESULTS

### A. Temporal Variation in Migratory Behavior (1996–1997 Through 2005–2006)

The number of bison observed in the Madison headwaters area (TIMING) increased with time each winter, usually peaking in late March or early April (see Figure 27.1a in Chapter 27 by Bruggeman *et al.*, this volume). During 109 ground distribution surveys, the number of bison counted in the Madison headwaters area ranged from 205–1538 bison (mean  $\pm$  SE;  $775 \pm 30$ ). The highest number of bison counted in the Madison headwaters area each year (MAXIMUM) varied between 888–1538 bison ( $1174 \pm 64$ ). The central herd population grew from 1473–3441 bison ( $2556 \pm 250$ ) during 1997–1998 through 2005–2006, after decreasing from 2928 bison in 1996–1997 owing to management-based removals at the park boundary and mortality during a severe winter. Snow accumulation in the Hayden and Pelican valleys began in October and built through the winter before generally peaking in early April, with annual peak SWES,  $\text{SWE}_{\text{acc},ij}$ , and  $\text{SWE}_{\text{acc}}$  ranging from 18.0–44.1 cm ( $26.1 \pm 0.2$ ), 66–5236

cm days ( $1367 \pm 102$ ), and 1750–5236 cm days ( $2843 \pm 309$ ), respectively. Covariates NDVI<sub>int</sub> and NDVI<sub>len</sub> ranged between 2071–2688 ( $2376 \pm 56$ ) and 12.7–17.1 weeks ( $14.6 \pm 0.4$ ), respectively.

One best approximating model structure was supported by the data for the magnitude of bison migration (Tables 12.1 and 12.2). This model ( $AIC_c = 135.1$ ,  $K = 2$ ,  $w_i = 0.593$ , adjusted  $R^2 = 0.40$ ) contained a significant BISON effect (estimate: 190.5; 95% CI: 29.7, 351.3) and had a relative likelihood of 3.9 compared to the second best model ( $\Delta AIC_c = 2.74$ ,  $K = 3$ ,  $w_i = 0.150$ , adjusted  $R^2 = 0.41$ ), which included BISON (estimate: 194.7; 95% CI: 35.3, 354.0) and SWE<sub>acc</sub> (estimate: –100.6; 95% CI: –307.9, 106.8). There was no improvement in the top model when NDVI<sub>len</sub> was substituted for NDVI<sub>int</sub> in the exploratory analysis.

Three best approximating models were supported by the data for the timing of bison migration (Tables 12.1 and 12.3). The top model ( $AIC_c = 1,518.2$ ,  $K = 4$ ,  $w_i = 0.426$ , adjusted  $R^2 = 0.35$ ) consisted of BISON (estimate: 208.0; 95% CI: 129.1, 286.9), SWES (estimate: 367.4; 95% CI: 243.3, 491.6; Figure 12.4), and NDVI<sub>int</sub> (estimate: 142.5; 95% CI: 27.6, 257.3) covariates. The second best model ( $\Delta AIC_c = 0.94$ ,  $K = 5$ ,  $w_i = 0.266$ , adjusted  $R^2 = 0.35$ ) included a SWES\*BISON interaction (estimate: –101.4; 95% CI: –284.3, 81.5) with the confidence interval overlapping zero, in addition to

**TABLE 12.1** AIC model selection results for the best supported *a priori* models in the magnitude and timing of migration analyses

Model structure	k	$\Delta AIC_c$	$w_i$
Magnitude of migration, 1996–1997 through 2005–2006			
$\beta_0 + \beta_1(\text{BISON})$	2	0	0.59
$\beta_0 + \beta_1(\text{SWE}_{acc}) + \beta_2(\text{BISON})$	3	2.74	0.15
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{int})$	3	2.77	0.15
$\beta_0 + \beta_1(\text{SWE}_{acc})$	2	5.68	0.03
$\beta_0 + \beta_1(\text{NDVI}_{int})$	2	6.19	0.03
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{int}) + \beta_3(\text{BISON} * \text{NDVI}_{int})$	4	6.79	0.02
$\beta_0 + \beta_1(\text{SWE}_{acc}) + \beta_2(\text{BISON}) + \beta_3(\text{SWE}_{acc} * \text{BISON})$	4	7.87	0.01
$\beta_0 + \beta_1(\text{SWE}_{acc}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int})$	4	8.41	0.01
$\beta_0 + \beta_1(\text{SWE}_{acc}) + \beta_2(\text{NDVI}_{int})$	3	9.03	0.01
Timing of migration, 1996–1997 through 2005–2006			
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int})$	4	0	0.43
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int}) + \beta_4(\text{SWES} * \text{BISON})$	5	0.94	0.27
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int}) + \beta_4(\text{BISON} * \text{NDVI}_{int})$	5	1.61	0.19
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON})$	3	3.93	0.06
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{SWES} * \text{BISON})$	4	4.00	0.06
Historic magnitude of migration, 1970–1971 through 2005–2006			
$\beta_0 + \beta_1(\text{BISON})$	2	0	0.33
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{SWE}_{acc})$	3	0.49	0.26
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{int})$	3	2.69	0.08
$\beta_0 + \beta_1(\text{SWE}_{acc}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int})$	4	3.04	0.07
$\beta_0 + \beta_1(\text{SWE}_{acc}) + \beta_2(\text{BISON}) + \beta_3(\text{SWE}_{acc} * \text{BISON})$	4	3.34	0.06
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{acc}) + \beta_3(\text{BISON})$	4	3.46	0.06
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{int}) + \beta_3(\text{BISON} * \text{NDVI}_{int})$	4	3.78	0.05
$\beta_0 + \beta_1(\text{SWE}_{acc}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int}) + \beta_4(\text{BISON} * \text{NDVI}_{int})$	5	5.28	0.02
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int})$	4	5.71	0.02
$\beta_0 + \beta_1(\text{SWE}_{acc}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int}) + \beta_4(\text{SWE}_{acc} * \text{BISON})$	5	6.07	0.02
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{acc}) + \beta_3(\text{BISON}) + \beta_4(\text{NDVI}_{int})$	5	6.43	0.01
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{acc}) + \beta_3(\text{BISON}) + \beta_4(\text{SWE}_{acc} * \text{BISON})$	5	6.72	0.01
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{int}) + \beta_4(\text{BISON} * \text{NDVI}_{int})$	5	7.10	0.01

All models are ranked according to  $AIC_c$  and presented along with the number of parameters (k), the  $\Delta AIC_c$  value (i.e., change in  $AIC_c$  relative to the best model), and the Akaike weight ( $w_i$ ). The  $AIC_c$  values for the top models for the magnitude and timing of migration analyses during 1997–2006 were 135.1 and 1518.17, respectively. The  $AIC_c$  value for the top model for the historic magnitude of migration analyses during 1971–2006 was 289.18.



**TABLE 12.2** Coefficient values ( $\beta_i$ ) and 95% confidence limits for covariates from the best approximating models for the magnitude of migration analyses during 1996–1997 through 2005–2006 (recent) and 1970–1971 through 2005–2006 (historic)

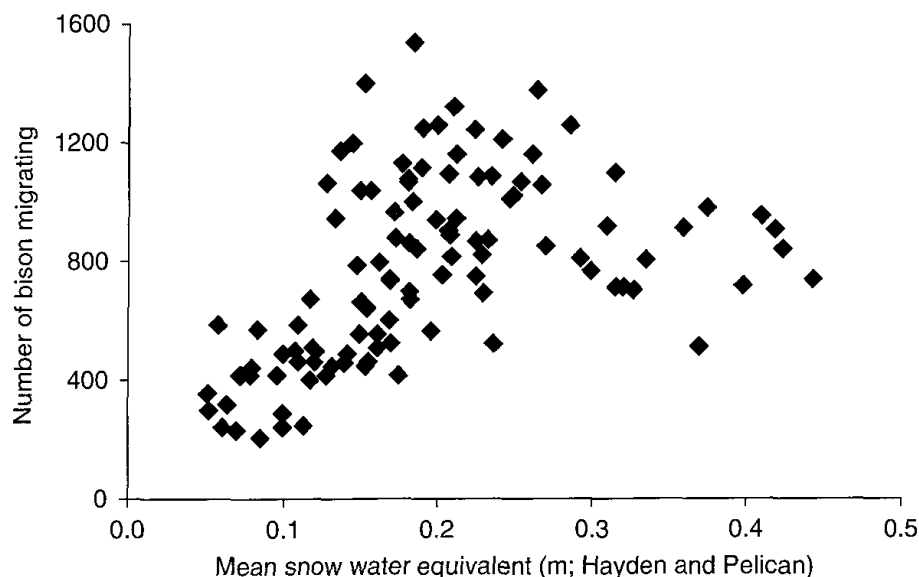
Covariate	$\beta_0 + \beta_1(\text{BISON})$	$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON})$	$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{\text{int}})$
1996–1997 through 2005–2006 (Recent)			
BISON	<b>190.5 (29.7, 351.3)</b>	<b>194.7 (35.3, 354.0)</b>	<b>232.4 (50.8, 414.0)</b>
SWE <sub>acc</sub>		–100.6 (–307.9, 106.8)	
NDVI <sub>int</sub>			111.2 (–120.1, 342.5)
1970–1971 through 2005–2006 (Historic)			
BISON	<b>536.4 (417.1, 655.6)</b>	<b>554.3 (434.9, 673.8)</b>	<b>537.7 (410.5, 664.9)</b>
SWE <sub>acc</sub>		95.0 (–48.0, 238.0)	
NDVI <sub>int</sub>			5.07 (–130.3, 140.5)

Values in bold denotes significant coefficients at  $\alpha = 0.05$ .

**TABLE 12.3** Coefficient values ( $\beta_i$ ) and 95% confidence limits for covariates from the best approximating models for the timing of migration analyses during 1996–1997 through 2005–2006

Covariate	$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}})$	$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{SWES} * \text{BISON})$	$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{BISON} * \text{NDVI}_{\text{int}})$
SWES	<b>367.4 (243.3, 491.5)</b>	<b>371.2 (247.0, 495.3)</b>	<b>366.2 (241.7, 490.6)</b>
BISON	<b>208.0 (129.1, 286.9)</b>	<b>169.7 (64.9, 274.5)</b>	<b>208.8 (129.8, 287.9)</b>
NDVI <sub>int</sub>	<b>142.5 (27.6, 257.3)</b>	<b>132.8 (16.8, 248.8)</b>	<b>125.8 (2.6, 249.0)</b>
SWES*		–101.4 (–284.3, 81.5)	
BISON			
BISON*			119.6 (–196.3, 435.5)
NDVI <sub>int</sub>			

Values in bold denotes significant coefficients at  $\alpha = 0.05$ .



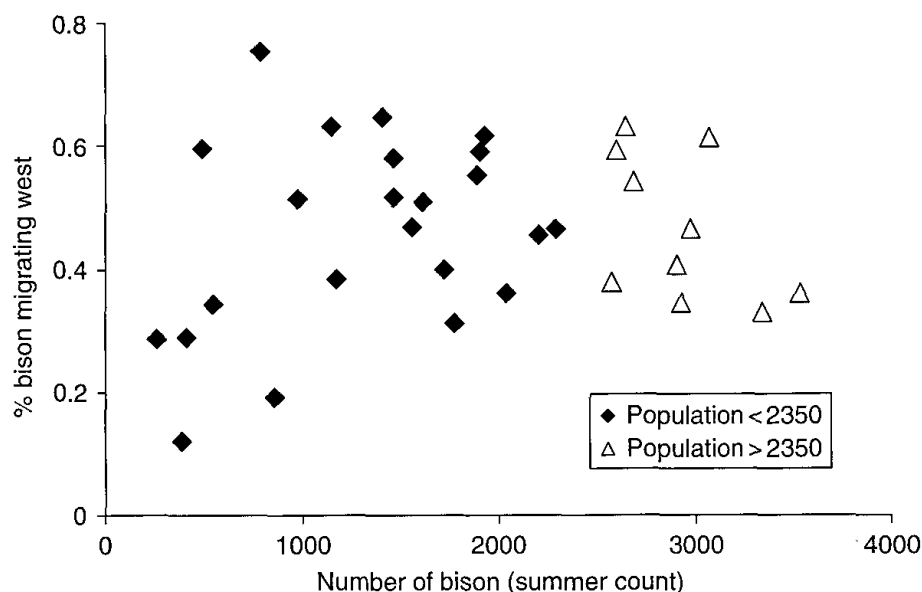
**FIGURE 12.4** Data depicting the positive correlation between the number of bison in the Madison headwaters area for each two-week period (1996–1997 through 2005–2006) and the average summer range snow water equivalent covariate (SWES; in meters) for the timing of migration analysis in Yellowstone National Park, Wyoming, USA.

BISON (estimate: 169.7; 95% CI: 64.9, 274.5), SWES (estimate: 371.2; 95% CI: 247.0, 495.3), and NDVI<sub>int</sub> (estimate: 132.8; 95% CI: 16.8, 248.8). The third best model ( $\Delta AIC_c = 1.61$ ,  $K = 5$ ,  $w_i = 0.190$ , adjusted  $R^2 = 0.35$ ) included a BISON\* NDVI<sub>int</sub> interaction (estimate: 119.6; 95% CI: -196.3, 435.5), along with BISON (estimate: 208.8; 95% CI: 129.8, 287.9), SWES (estimate: 366.2; 95% CI: 241.8, 490.6), and NDVI<sub>int</sub> (estimate: 125.8; 95% CI: 2.6, 249.0). There was no improvement in the top models when substituting either SWE<sub>acc,ij</sub> for SWES or NDVI<sub>len</sub> for NDVI<sub>int</sub> in the exploratory analysis.

## B. Historic Migration Patterns (1970–1971 Through 2005–2006)

Summer counts of the central herd increased from 261 to 3531 bison ( $1801 \pm 161$ ) during 1970–2005 with the maximum number of bison migrating westward to the Madison headwaters area (HISTORIC<sub>max</sub>) ranging from 47 bison in winter 1971–1972 to 1877 in winter 1995–1996 ( $843 \pm 75$ ). There were no presurvey winter removals at the west boundary during 1970–1971 through 1984–1985 and removals thereafter were negligible ( $\leq 2\%$  of migrating bison), except during winters 1992–1993 (78 bison removed), 1994–1995 (48 bison), and 1996–1997 (293 bison).

Summer and winter counts of the entire central herd were highly and positively correlated when counts were  $< 2350$  bison (slope of line = 0.81; 95% CI = 0.66, 0.95;  $R^2 = 0.87$ ,  $df = 22$ ). However, this relationship completely disappeared at higher counts (slope of line = -0.05; 95% CI = -0.72, 0.62;  $R^2 = 0.003$ ,  $df = 9$ ), with fewer bison counted during winter compared to summer surveys (Figure 12.3). Though the number of bison migrating west to the Madison headwaters area consistently increased with population size across the entire range of summer counts (slope of line = 0.44; 95% CI = 0.35, 0.53;  $R^2 = 0.76$ ,  $df = 32$ ; Figure 12.3), the proportion of migrants remained approximately constant though highly variable (slope of line = 0.002; 95% CI = -0.004, 0.008;  $R^2 = 0.02$ ,  $df = 32$ ). The maximum proportion of bison on the Madison headwaters range (*i.e.*, HISTORIC<sub>max</sub>/BISON) varied between 0.12 in winter 1970–1971 and 0.75 in winter 1975–1976 ( $0.46 \pm 0.03$ ), but was relatively consistent after winter 1977–1978 with variation between 0.31–0.65 ( $0.49 \pm 0.02$ ; Figure 12.5). When summer population counts exceeded 2350, the total number of bison counted in the



**FIGURE 12.5** The proportion of bison migrating to the west-side winter range versus the total central herd population size as determined from the July–August summer count during 1970–1971 through 2005–2006 in Yellowstone National Park, Wyoming, USA.

west-central portion of the park (*i.e.*, Hayden and Pelican valleys, Madison headwaters area) during winter remained approximately constant (slope of line =  $-0.049$ ; 95% CI =  $-0.721, 0.662$ ;  $R^2 = 0.004$ ,  $df = 9$ ; Figure 12.3), even though summer counts of central bison continued to increase to  $>3500$  bison by 2006.

During winters 1970–1971 through 2005–2006,  $SWE_{acc}$  in the Hayden and Pelican valleys ranged from 849–5236 cm days ( $2651 \pm 155$ ). The L-integral NDVI index developed for the  $NDVI_{int}$  covariate had an  $R^2 = 0.79$  and consisted of an intercept of 6116.6 and four covariates and their interactions: (1) average daily precipitation (inches) for April–August (coefficient =  $-59363.5$ ), (2) average daily maximum temperature ( $^{\circ}C$ ) for April–May (coefficient =  $-4.53$ ), (3) mean daily average temperature ( $^{\circ}C$ ) for May (coefficient =  $113.64$ ), (4) average daily maximum temperature ( $^{\circ}C$ ) for July (coefficient =  $-149.83$ ), (5) interaction between average daily precipitation for April–August and the average daily maximum temperature for July (coefficient =  $2265.97$ ), (6) interaction between the average daily maximum temperature for April–May and the mean daily average temperature for May (coefficient =  $24.45$ ), and (7) interaction between the mean daily average temperature for May and the average daily maximum temperature for July (coefficient =  $12.40$ ). Predicted  $NDVI_{int}$  for summers during 1970–1988 from this model varied between 2184.9 and 3610.2 ( $2486.0 \pm 73.7$ ), while  $NDVI_{int}$  for 1989–2005 (obtained from actual NDVI data) varied between 2070.5 and 2687.5 ( $2341.6 \pm 40.9$ ).

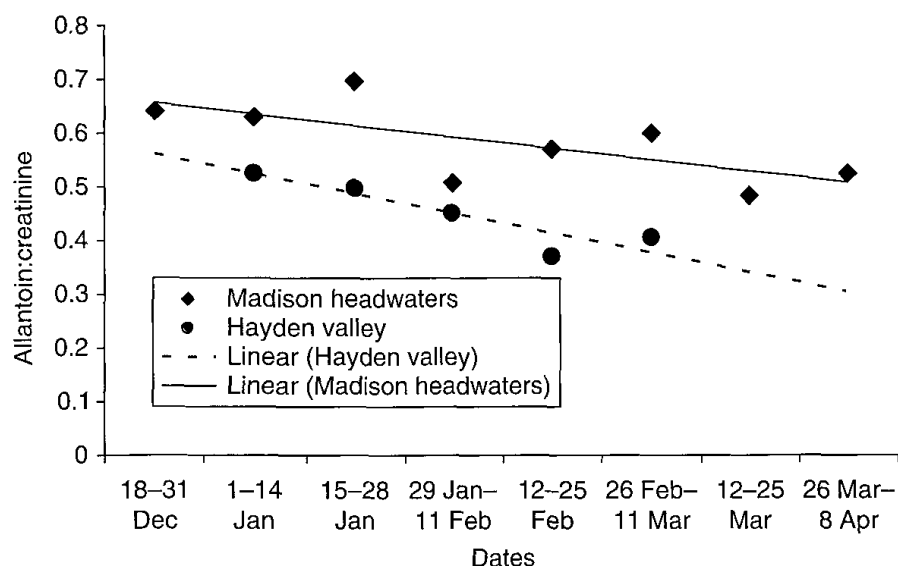
Two top approximating models were supported by the data for the historic migration analysis when counts of the central herd were  $<2350$  (Tables 12.1 and 12.2). The top model ( $AIC_c = 289.2$ ,  $K = 2$ ,  $w_i = 0.325$ , adjusted  $R^2 = 0.81$ ) contained BISON (estimate: 536.4; 95% CI: 417.1, 655.6) and had a relative likelihood of 1.3 compared to the second best model ( $\Delta AIC_c = 0.48$ ,  $K = 3$ ,  $w_i = 0.255$ , adjusted  $R^2 = 0.82$ ) that included BISON (estimate: 554.3; 95% CI: 434.9, 673.8) and  $SWE_{acc}$  (estimate: 95.0; 95% CI:  $-48.0, 238.0$ ).

### C. Estimates of Nutritional Intake

We collected 426 samples of urine-soaked snow from bison in the Hayden Valley ( $n = 170$ ) and Madison headwaters area ( $n = 256$ ; Table 12.4). Mean A:C ratios during five 14-day collection periods between January 1 and March 11 for which we had sufficient samples ( $n > 20$ ) in each wintering area were consistently and significantly lower ( $t = 5.12$ ,  $df = 4$ ,  $P = 0.003$ ) for bison in the Hayden Valley than bison in the Madison headwaters area (Figure 12.6).

**TABLE 12.4** Allantoin:creatinine ratios from urine-soaked snow samples deposited by groups of adult and calf bison during 2005–2006 in the Madison headwaters area and the Hayden Valley of Yellowstone National Park, Wyoming, USA

Period	Start	End	Madison headwaters			Hayden Valley		
			n	Mean	Trimmed mean	n	Mean	Trimmed mean
1	18-Dec	31-Dec	17	0.623	0.641	0		
2	1-Jan	14-Jan	49	0.629	0.629	54	0.512	0.523
3	15-Jan	28-Jan	35	0.710	0.697	25	0.477	0.498
4	29-Jan	11-Feb	39	0.533	0.508	35	0.447	0.451
5	12-Feb	25-Feb	41	0.557	0.571	29	0.343	0.371
6	26-Feb	11-Mar	22	0.898	0.599	26	0.408	0.404
7	12-Mar	25-Mar	28	0.445	0.484	0		
8	26-Mar	8-Apr	25	0.530	0.524	1		



**FIGURE 12.6** Allantoin:creatinine ratios from urine-soaked snow samples deposited by groups of adult and calf bison during 2005–2006 in the Madison headwaters area and Hayden Valley of Yellowstone National Park, Wyoming, USA.

#### IV. DISCUSSION

This study provided unequivocal evidence that bison from the central herd in Yellowstone National Park were partially migratory at least two decades before their abundance approached the estimated food-limiting carrying capacity of their range (Coughenour 2005). We detected substantial migration by central bison to the Madison headwaters area before the Hayden and Pelican valleys were fully occupied, as evidenced by 12–75% of the herd migrating each winter before counts reached 2000 bison. This partial migration was initially detected when bison abundance was low (<300 bison) and the Hayden and Pelican valleys should have provided ample resources for bison year-round. The number of bison migrating to, and remaining in, the Madison headwaters area increased consistently with abundance, but there was no evidence the proportion of migrants increased with population size—though there was substantial variability among years. As a result, the number of animals wintering in the Hayden and Pelican valleys (*i.e.*, nonmigrants) also increased with abundance. Thus, these findings do not support the “domino effect” hypothesis (Meagher 1993, 1998; Gates *et al.* 2005), whereby bison should have fully occupied the Pelican and Hayden valley wintering areas before compensating for decreasing per capita resources by moving westward over the Mary Mountain trail to the Madison headwaters area.

However, after the central herd exceeded 2350 animals the number of bison wintering in the Hayden and Pelican valleys appeared to stabilize, while bison continued to migrate to the Madison headwaters area along the west side of the park (Figure 12.3). These findings provide support for the “density-equalization effect,” whereby the area occupied by bison during winter expanded as the central herd increased in abundance (Meagher 1998, Taper *et al.* 2000, Coughenour 2005, Gates *et al.* 2005). Also, the total number of wintering bison counted in the west-central portion of the park (*i.e.*, Hayden and Pelican valleys, Madison headwaters area) remained approximately constant, even though summer counts of central bison continued to increase. Given the high sightability of bison during aerial surveys in this system (Hess 2002), these results suggest some bison migrated outside the west-central portion of the park between the summer and winter counts, perhaps relocating to northern range as hypothesized by Meagher (1998) and Fuller *et al.* (2007). Thus, there may have been an increase in the proportion of migrants as habitat in the central and west-side ranges was occupied during winter and bison began migrating elsewhere. This speculation is supported by ground survey data dating back to winter 1996–1997 that indicate a relatively consistent maximum number of bison occupying the Madison headwaters area each winter,

despite an increase in the central herd size by nearly 1000 bison during 1997–2006. Central herd bison have been detected making pre- or early-winter movements to the northern range through the Washburn Range, across the Solfatara Plateau, over the Mirror Plateau, and along the Norris to Mammoth road corridor before significant snow accumulates on the landscape (Meagher 1973, 1993; Bruggeman *et al.* 2007; Olexa and Gogan 2007; R. Wallen, National Park Service, unpublished data).

Population size had a significant, positive effect on the magnitude and timing of migration, with more bison migrating earlier to winter in the Madison headwaters area as density increased (as hypothesized by Meagher 1998). Decreased per capita resources due to increased abundance likely provided an impetus for bison to migrate. Coughenour (2005) reasoned that as the central bison herd grew following the cessation of management removals, they eventually reached a density where nutritional stress was high enough to elicit increased competition for key resources and subsequent behavioral responses to search for additional range. In turn, once new ranges were found, carrying capacity was increased in a positive feedback cycle. Estimates of metabolizable energy intake during the winter of 2005–2006 suggested bison in the Hayden Valley had consistently lower nutrition than bison in the Madison headwaters area, thereby providing an impetus for migration. Density-related movement responses, spurred by limitations in high quality resources, have been documented for bison in other regions (Gates and Larter 1990, Larter *et al.* 2000) and other ungulate populations (Heard and Calef 1986, Messier *et al.* 1988, Reynolds 1998, Ferguson and Messier 2000, Mahoney and Schaefer 2002).

Some of the annual variability in the proportion of bison migrating each winter was explained by density-independent climate covariates. Snow accumulation in the Hayden and Pelican valleys had a positive effect on the timing of migration with more bison moving to the lower-elevation Madison headwaters area as winter progressed and snow pack deepened. Also, the second best model in the historic magnitude of migration analysis included a positive annual winter severity ( $SWE_{acc}$ ) effect, though its coefficient had confidence intervals slightly spanning zero. Ungulate migrations are affected by snow in many ecosystems owing to the need for easier access to forage (Sweeney and Sweeney 1984, Sabine *et al.* 2002, Doerr *et al.* 2005). Limitations on access to forage by deep or wet snow is the major factor influencing bison foraging behavior across the central winter range in Yellowstone (Bruggeman 2006), and migrations to lower elevations are likely a landscape-scale behavioral response to reduced forage availability caused by increasing snow pack. Also, during winter bison spend the majority of their time foraging, and displacing snow to access forage is a prominent energetic cost (Bjornlie and Garrott 2001, Bruggeman *et al.* 2006, Chapter 27 by Bruggeman *et al.*, this volume). The Madison headwaters area affords easier access to vegetation in winter because geothermally-warmed basins reduce snow accumulation, thereby providing a refuge for bison from nearby areas of deep snow (Figure 12.7). The influence of snow on the number of migrants suggests bison may employ a conditional migration strategy based on climate variability (Hazel *et al.* 2004).

Our findings are certainly not conclusive because analyses were performed on “snap-shots” of distributional patterns for the central bison herd obtained a few times per year. Only recently has intensive monitoring of movements by individual animals been initiated and, to date, sample sizes have been limited (Bruggeman *et al.* 2007, Olexa and Gogan 2007). There is much to be learned about the spatial dynamics of Yellowstone bison from continuing this work, including whether the central and northern herds are becoming more integrated, the differential effects of management removals on each herd given their respective movement dynamics, if individuals have strong fidelity to particular seasonal movement strategies and destinations, and factors influencing specific bison movement patterns and distributions. Also, limited assessments of the central herd from radio-collared animals suggest that the vast majority of bison have vacated the Hayden and Pelican valleys by the end of the winter in recent years—something not evident in the aerial survey data used in our analyses. In addition, we detected a significant influence of forage biomass (*i.e.*,  $NDVI_{int}$ ) on the timing of migration, but the effect was the opposite (*i.e.*, earlier migration with higher forage) of what we predicted. Thus, monitoring and research of montane grasslands to link measurements of forage biomass and phenology with remote sensing indices is needed. The management of bison in and near





**FIGURE 12.7** Adult bull bison foraging in reduced snow pack amidst steam in a geothermal area near Midway Geyser Basin in Yellowstone National Park, Wyoming, USA (Photo by Jason Bruggeman).

Yellowstone National Park is one of the most contentious and high-profile issues facing park managers. Thus, we encourage the continuation of research and monitoring efforts to gain insights into these key uncertainties and improve the knowledge base for making effective management decisions.

## V. SUMMARY

1. We used aerial and ground data collected during 1970–1971 through 2005–2006 to quantify annual variations in the magnitude and timing of migration by central herd bison, identify potential factors driving this variation, and evaluate the “domino effect” hypothesis (Meagher 1998) that (a) significant migration to the Madison headwaters area did not occur until bison had fully occupied the Hayden and Pelican valleys, and (b) more animals migrated earlier as numbers increasingly exceeded this limit.
2. Bison from the central herd in Yellowstone National Park were partially migratory, with a portion of the animals migrating to the lower-elevation Madison headwaters area during winter while some remained year-round in or near the Hayden and Pelican valleys.
3. Contrary to the “domino effect” hypothesis, there was significant bison migration to the Madison headwaters area before the Hayden and Pelican valleys were fully occupied and abundance approached the food-limiting carrying capacity of these valleys.
4. However, after the central herd exceeded 2350 animals the number of bison wintering in the Hayden and Pelican valleys appeared to stabilize, while bison continued to migrate to the Madison headwaters area. Also, more bison migrated earlier as density increased (as hypothesized by Meagher 1998).
5. Our results suggest some bison migrated outside the west-central portion of the park between the summer and winter counts each year when the central herd exceeded 2350 bison, perhaps relocating to northern range as hypothesized by Meagher (1998) and Fuller *et al.* (2007).
6. Some of the annual variability in the proportion of bison migrating each winter was explained by density-independent climate covariates. The timing and magnitude of bison migration were accentuated during years of severe snow pack that limited access to food.



## VI. REFERENCES

- Ahola, M., T. Laaksonen, K. Sippola, T. Eeva, K. Rainio, and E. Lehtikainen. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology* 10:1610–1617.
- Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: Characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology* 7:39–47.
- Bergerud, A. T. 1988. Caribou, wolves and man. *Trends in Ecology and Evolution* 3:68–72.
- Bergerud, A. T., R. Ferguson, and H. E. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. *Animal Behavior* 39:360–368.
- Bjornlie, D. D. 2000. Ecological effects of winter road grooming on bison in Yellowstone National Park. Thesis. Montana State University, Bozeman, MT.
- 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.
- Bruggeman, J. E. 2006. Spatio-temporal dynamics of the central bison herd in Yellowstone National Park. Dissertation. Montana State University, Bozeman, MT.
- Bruggeman, J. E., R. A. Garrott, D. D. Bjornlie, P. J. White, F. G. R. Watson, and J. J. Borkowski. 2006. Temporal variability in winter travel patterns of Yellowstone bison: The effects of road grooming. *Ecological Applications* 16:1539–1554.
- Bruggeman, J. E., R. A. Garrott, P. J. White, F. G. R. Watson, and R. W. Wallen. 2007. Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. *Ecological Applications* 17:1411–1423.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multi-Model Inference*. Springer, New York, NY.
- Burtenshaw, J. C., E. M. Oleson, J. A. Hildebrand, M. A. McDonald, R. K. Andrew, B. M. Howe, and J. A. Mercer. 2004. Acoustic and satellite remote sensing of blue whale seasonality and habitat in the Northeast Pacific. *Deep-Sea Research II* 51:967–986.
- Chen, X. B., Y. K. Chen, M. F. Franklin, E. R. Orskov, and W. J. Shand. 1992a. The effect of feed intake and body weight on purine derivative excretion and microbial protein supply in sheep. *Journal of Animal Science* 70:1534–1542.
- Chen, X. B., G. Grubic, E. R. Ørskov, and P. Osuji. 1992b. Effect of feeding frequency on diurnal variation in plasma and urinary purine derivatives in steers. *Animal Production* 55:185–191.
- Coles, E. H. 1980. *Veterinary Clinical Pathology*. W. B. Saunders, Philadelphia, PA.
- Coughenour, M. B. 2005. *Spatial-Dynamic Modeling of Bison Carrying Capacity in the Greater Yellowstone Ecosystem: A Synthesis of Bison Movements, Population Dynamics, and Interactions with Vegetation*. Final report to U.S. Geological Survey Biological Resources Division, Bozeman, MT.
- D'Eon, R. G., and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using Global Positioning System radiotelemetry. *Journal of Mammalogy* 86:736–744.
- Dingle, H. 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, New York, NY.
- Dingle, H., W. A. Rochester, and M. P. Zalucki. 2000. Relationships among climate, latitude and migration: Australian butterflies are not temperate-zone birds. *Oecologia* 124:196–207.
- Dobson, A., and M. Meagher. 1996. The population dynamics of brucellosis in the Yellowstone National Park. *Ecology* 77:1026–1036.
- Doerr, J. G., E. J. DeGayner, and G. Ith. 2005. Winter habitat selection by Sitka black-tailed deer. *Journal of Wildlife Management* 69:322–331.
- Ferguson, M. A. D., and F. Messier. 2000. Mass emigration of arctic tundra caribou from a traditional winter range: Population dynamics and physical condition. *Journal of Wildlife Management* 64:168–178.
- Ferrari, M. J. 1999. An assessment of the risk of inter-specific transmission of *Brucella abortus* from bison to elk on the Madison-Firehole winter range. Thesis. Montana State University, Bozeman, MT.
- Forchhammer, M. C., N. C. Stenseth, E. Post, and R. Langvatn. 1998. Population dynamics of Norwegian red deer: Density-dependence and climatic variation. *Proceedings of the Royal Society of London B* 265:341–350.
- Fryxell, J. M., and A. R. E. Sinclair. 1988. Seasonal migration by white-eared kob in relation to resources. *African Journal of Ecology* 26:17–31.
- Fuller, J. A., R. A. Garrott, and P. J. White. 2007. Emigration and density dependence in Yellowstone bison. *Journal of Wildlife Management* 71:1924–1933.
- Garel, M., E. J. Solberg, B. Saether, I. Herfindal, and K. Hogda. 2006. The length of growing season and adult sex ratio affect sexual size dimorphism in moose. *Ecology* 87:745–758.
- Garrott, R. A., J. G. Cook, J. G. Berardinelli, P. J. White, S. Cherry, and D. B. Vagnoni. 1997. Evaluation of the urinary allantoin: creatinine ratio as a nutritional index for elk. *Canadian Journal of Zoology* 75:1519–1525.
- Garrott, R. A., L. L. Eberhardt, P. J. White, and J. 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., and N. C. Larter. 1990. Growth and dispersal of an erupting large herbivore population in northern Canada: The Mackenzie wood bison (*Bison bison athabasca*). *Arctic* 43:231–238.

- Gates, C. C., B. Stelfox, T. Muhly, 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.
- Gilbert, P. F., O. C. Wallmo, and R. B. Gill. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. *Journal of Wildlife Management* **34**:15–23.
- Gordo, O., L. Brotons, X. Ferrer, and P. Comas. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biology* **11**:12–21.
- Hazel, W., R. Smock, and C. M. Lively. 2004. The ecological genetics of conditional strategies. *American Naturalist* **163**:888–900.
- Heard, D. C., and G. W. Calef. 1986. Population dynamics of the Kaminuriak caribou herd, 1968–1985. *Rangifer Special Issue* **1**:159–166.
- Hess, S. C. 2002. Aerial survey methodology for bison population estimation in Yellowstone National Park. Dissertation. Montana State University, Bozeman, MT.
- Hulbert, L. B., A. M. Aires-da-Silva, V. F. Gallucci, and J. M. Rice. 2005. Seasonal foraging movements and migratory patterns of female *Lamna ditropis* tagged in Prince William Sound, Alaska. *Journal of Fish Biology* **67**:490–509.
- Igota, H., M. Sakuragi, H. Uno, K. Kaji, M. Kaneko, R. Akamatsu, and K. Maekawa. 2004. Seasonal migration patterns of female sika deer in eastern Hokkaido, Japan. *Ecological Research* **19**:169–178.
- Jacobson, A. R., A. Provenza, A. von Hardenberg, B. Bassano, and M. Festa-Bianchet. 2004. Climate forcing and density dependence in a mountain ungulate population. *Ecology* **85**:1598–1610.
- Kaňuščák, P., M. Hromada, P. Tryjanowski, and T. Sparks. 2004. Does climate at different scales influence the phenology and phenotype of the River Warbler *Locustella fluviatilis*? *Oecologia* **141**:158–163.
- Knight, A., L. P. Brower, and E. H. Williams. 1999. Spring remigration of the monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae) in north-central Florida: Estimating population parameters using mark-recapture. *Biological Journal of the Linnean Society* **68**:531–556.
- Langvatn, R., S. D. Albon, T. Burke, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology* **65**:653–670.
- Larsen, K. 1972. Creatinine assay by a reaction-kinetic approach. *Clinical Chemistry Acta* **41**:209–217.
- Larter, N. C., A. R. E. Sinclair, T. Ellsworth, J. Nishi, and C. C. Gates. 2000. Dynamics of reintroduction in an indigenous large ungulate: The wood bison of northern Canada. *Animal Conservation* **4**:299–309.
- Leimgruber, P., W. J. McShea, C. J. Brookes, L. Bolor-Erdene, C. Wemmer, and C. Larson. 2001. Spatial patterns in relative primary productivity and gazelle migration in the eastern steppes of Mongolia. *Biological Conservation* **102**:205–212.
- Lundberg, P. 1987. Partial bird migration and evolutionarily stable strategies. *Journal of Theoretical Biology* **125**:351–360.
- Maddock, L. 1979. The “migration” and grazing succession. Pages 104–129 in A. R. E. Sinclair and M. Norton-Griffiths (Eds.) *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press, Chicago, IL.
- Mahoney, S. P., and J. A. Schaefer. 2002. Long-term changes in demography and migration of Newfoundland caribou. *Journal of Mammalogy* **83**:957–963.
- Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* **142**:307–315.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs* **55**:259–294.
- Mduma, S. A. R., A. R. E. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: A 40-year record. *Journal of Animal Ecology* **68**:1101–1122.
- Meagher, M. 1973. *The Bison of Yellowstone National Park*. National Park Service Scientific Monograph Series No. 1, National Park Service. US Government Printing, Office, Washington, DC.
- Meagher, M. 1993. *Winter Recreation-Induced Changes in Bison Numbers and Distribution in Yellowstone National Park*. Yellowstone National Park, WY.
- Meagher, M. 1998. Recent changes in Yellowstone bison numbers and distribution. Pages 107–112 in L. Irby and J. Knight (Eds.) *International Symposium on Bison Ecology and Management in North America*. Montana State University, Bozeman, MT.
- Messier, F., J. Huot, D. LeHenaff, and S. Lettich. 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. *Arctic* **41**:279–287.
- Morgantini, L. E., and R. J. Hudson. 1988. Migratory patterns of the wapiti, *Cervus elaphus*, in Banff National Park, Alberta. *Canadian Field-Naturalist* **102**:12–19.
- Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001. Plant phenology, migration and geographic variation in body weight of a large herbivore: The effect of a variable topography. *Journal of Animal Ecology* **70**:915–923.
- National Resource Conservation Service. 2007. Canyon SNOTEL data. <http://www.wcc.nrcs.usda.gov/snotel/snotel.pl?sitenum=384&state=wy>. Accessed April 1, 2007.
- Nelson, M. E., L. D. Mech, and P. F. Frame. 2004. Tracking of white-tailed deer migration by Global Positioning System. *Journal of Mammalogy* **85**:505–510.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied Linear Statistical Models*. McGraw-Hill, New York, NY.
- Olexa, E. M., and P. J. P. Gogan. 2007. Spatial population structure of Yellowstone bison. *Journal of Wildlife Management* **71**:1531–1538.



- Palmer, W. C. 1965. Meteorological Drought. Office of Climatology Research Paper 45, Weather Bureau, Washington, DC.
- Pettorelli, N., J. Gaillard, A. Mysterud, P. Duncan, N. C. Stenseth, D. Delorme, G. Van Laere, C. Toigo, and F. Klein. 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: The case of roe deer. *Oikos* **112**:565–572.
- Pettorelli, N., A. Mysterud, N. G. Yoccoz, R. Langvatn, and N. C. Stenseth. 2005. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proceedings of the Royal Society B* **272**:2357–2364.
- Pils, A. C., R. A. Garrott, and J. J. Borkowski. 1999. Sampling and statistical analysis of snow-urine allantoin:creatinine ratios. *Journal of Wildlife Management* **63**:1118–1132.
- Polovina, J. J., E. Howell, D. R. Kobayashi, and M. P. Seki. 2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography* **49**:469–483.
- Post, E., and N. C. Stenseth. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. *Journal of Animal Ecology* **67**:537–543.
- R Development Core Team. 2006. R: A language and environment for statistical computing. <http://www.R-project.org>. Accessed September 12, 2006.
- Reynolds, P. E. 1998. Dynamics and range expansion of a reestablished muskox population. *Journal of Wildlife Management* **62**:734–744.
- Sabine, D. L., S. F. Morrison, H. A. Whitlaw, W. B. Ballard, G. J. Forbes, and J. Bowman. 2002. Migration behavior of white-tailed deer under varying climate regimes in New Brunswick. *Journal of Wildlife Management* **66**:718–728.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* **69**:40–45.
- SAS. 2004. SAS/STAT 9.1 User's Guide. Cary, NC.
- Sinclair, A. R. E., H. Dublin, and M. Borner. 1985. Population regulation of Serengeti wildebeest: A test of the food hypothesis. *Oecologia* **65**:266–268.
- Stephenson, N. L. 1990. Climatic control of vegetation distribution: The role of the water balance. *American Naturalist* **135**:649–670.
- Sweeney, J. M., and J. R. Sweeney. 1984. Snow depths influencing winter movements of elk. *Journal of Mammalogy* **65**:524–526.
- Talbot, L. M., and M. H. Talbot. 1963. The wildebeest in western Masailand, East Africa. *Wildlife Monographs* **12**:1–88.
- Taper, M. L., M. Meagher, and C. L. Jerde. 2000. *The Phenology of Space: Spatial Aspects of Bison Density Dependence in Yellowstone National Park*. U.S. Geological Service, Biological Resources Division, Bozeman, MT.
- Vagnoni, D. B., R. A. Garrott, J. G. Cook, P. J. White, and M. K. Clayton. 1996. Urinary allantoin:creatinine ratios as a dietary index for elk. *Journal of Wildlife Management* **60**:728–734.
- Varpe, Ø., Ø. Fiksen, and A. Slotte. 2005. Meta-ecosystems and biological energy transport from ocean to coast: The ecological importance of herring migration. *Oecologia* **146**:443–451.
- Watson, F. G. R., W. B. Newman, J. C. Coughlan, and R. A. Garrott. 2006. Testing a distributed snowpack simulation model against spatial observations. *Journal of Hydrology* **328**:453–466.
- Whalen, D. M., and B. D. Watts. 2002. Annual migration density and stopover patterns of Northern Saw-whet Owls (*Aegolius acadicus*). *Auk* **119**:1154–1161.
- White, P. J., T. L. Davis, K. K. Barnowe-Meyer, R. L. Crabtree, and R. A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation* **135**:518–526.
- White, P. J., and R. A. Garrott. 2005. Northern Yellowstone elk after wolf restoration. *Wildlife Society Bulletin* **33**:942–955.
- Whitehead, H. 1996. Variation in the feeding success of sperm whales: Temporal scale, spatial scale and the relationship to migrations. *Journal of Animal Ecology* **65**:429–438.
- Wittemyer, G., H. B. Rasmussen, and I. Douglas-Hamilton. 2007. Breeding phenology in relation to NDVI variability in free-ranging African elephant. *Ecography* **30**:42–50.
- Young, E. G., and C. F. Conway. 1942. On the estimation of allantoin by the Rimini-Schryver reaction. *Journal of Biological Chemistry* **142**:839–853.

## APPENDIX

## APPENDIX 12A-1

AIC model selection results for the *a priori* models in the magnitudes and timing of migration analyses. All models are ranked according to AIC<sub>c</sub> and presented along with the number of parameters (*k*), the  $\Delta\text{AIC}_c$  value (*i.e.*, the change in  $\Delta\text{AIC}_c$  value relative to the best model), and the Akaike weight ( $w_i$ )

Model structure	<i>k</i>	$\Delta\text{AIC}_c$	$w_i$
Magnitude of migration, 1996–1997 through 2005–2006			
$\beta_0 + \beta_1(\text{BISON})$	2	0	0.59
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON})$	3	2.74	0.15
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{\text{int}})$	3	2.77	0.15
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}})$	2	5.68	0.03
$\beta_0 + \beta_1(\text{NDVI}_{\text{int}})$	2	6.19	0.03
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{\text{int}}) + \beta_3(\text{BISON} * \text{NDVI}_{\text{int}})$	4	6.79	0.02
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON}) + \beta_3(\text{SWE}_{\text{acc}} * \text{BISON})$	4	7.87	0.01
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}})$	4	8.41	0.01
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{NDVI}_{\text{int}})$	3	9.03	0.01
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{BISON} * \text{NDVI}_{\text{int}})$	5	15.30	0.00
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{SWE}_{\text{acc}} * \text{BISON})$	5	16.37	0.00
Timing of migration, 1996–1997 through 2005–2006			
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}})$	4	0	0.43
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{SWES} * \text{BISON})$	5	0.94	0.27
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{BISON} * \text{NDVI}_{\text{int}})$	5	1.61	0.19
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON})$	3	3.93	0.06
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{BISON}) + \beta_3(\text{SWES} * \text{BISON})$	4	4.00	0.06
$\beta_0 + \beta_1(\text{SWES})$	2	20.89	0.00
$\beta_0 + \beta_1(\text{SWES}) + \beta_2(\text{NDVI}_{\text{int}})$	3	22.99	0.00
$\beta_0 + \beta_1(\text{BISON})$	2	27.05	0.00
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{\text{int}})$	3	28.69	0.00
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{\text{int}}) + \beta_3(\text{BISON} * \text{NDVI}_{\text{int}})$	4	30.21	0.00
$\beta_0 + \beta_1(\text{NDVI}_{\text{int}})$	2	39.31	0.00
Historic magnitude of migration, 1970–1971 through 2005–2006			
$\beta_0 + \beta_1(\text{BISON})$	2	0	0.33
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON})$	3	0.49	0.26
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{\text{int}})$	3	2.69	0.08
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}})$	4	3.04	0.07
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON}) + \beta_3(\text{SWE}_{\text{acc}} * \text{BISON})$	4	3.34	0.06
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{\text{acc}}) + \beta_3(\text{BISON})$	4	3.46	0.06
$\beta_0 + \beta_1(\text{BISON}) + \beta_2(\text{NDVI}_{\text{int}}) + \beta_3(\text{BISON} * \text{NDVI}_{\text{int}})$	4	3.78	0.05
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{BISON} * \text{NDVI}_{\text{int}})$	5	5.28	0.02
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}})$	4	5.71	0.02
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{SWE}_{\text{acc}} * \text{BISON})$	5	6.07	0.02
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{\text{acc}}) + \beta_3(\text{BISON}) + \beta_4(\text{NDVI}_{\text{int}})$	5	6.43	0.01
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{\text{acc}}) + \beta_3(\text{BISON}) + \beta_4(\text{SWE}_{\text{acc}} * \text{BISON})$	5	6.72	0.01
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{BISON}) + \beta_3(\text{NDVI}_{\text{int}}) + \beta_4(\text{BISON} * \text{NDVI}_{\text{int}})$	5	7.10	0.01
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{\text{acc}}) + \beta_3(\text{BISON}) + \beta_4(\text{NDVI}_{\text{int}}) + \beta_5(\text{BISON} * \text{NDVI}_{\text{int}})$	6	9.05	0.00
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{\text{acc}}) + \beta_3(\text{BISON}) + \beta_4(\text{NDVI}_{\text{int}}) + \beta_5(\text{SWE}_{\text{acc}} * \text{BISON})$	6	9.90	0.00
$\beta_0 + \beta_1(\text{DATE})$	2	36.61	0.00
$\beta_0 + \beta_1(\text{NDVI}_{\text{int}})$	2	36.65	0.00
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}})$	2	37.83	0.00
$\beta_0 + \beta_1(\text{SWE}_{\text{acc}}) + \beta_2(\text{NDVI}_{\text{int}})$	3	38.83	0.00
$\beta_0 + \beta_1(\text{DATE}) + \beta_2(\text{SWE}_{\text{acc}}) + \beta_3(\text{NDVI}_{\text{int}})$	4	41.14	0.00

The AIC<sub>c</sub> values for the top models of the magnitude and timing of migration analyses during 1996–1997 through 2005–2006 were 135.1 and 1518.17, respectively. The AIC<sub>c</sub> value for the top model of the historic magnitude of migration analyses during 1970–1971 through 2005–2006 was 289.18.