YELLOWSTONE BISON FETAL DEVELOPMENT AND PHENOLOGY OF PARTURITION

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Abstract: Knowledge of Yellowstone bison (*Bison bison*) parturition patterns allows managers to refine risk assessments and manage to reduce the potential for transmission of brucellosis between bison and cattle. We used historical (1941) and contemporary (1989–2002) weights and morphometric measurements of Yellowstone bison fetuses to describe fetal growth and to predict timing and synchrony of parturition. Our method was supported by agreement between our predicted parturition pattern and observed birth dates for bison that were taken in to captivity while pregnant. The distribution of parturition dates in Yellowstone bison is generally right-skewed with a majority of births in April and May and few births in the following months. Predicted timing of parturition was consistently earlier for bison of Yellowstone's northern herd than central herd. The predicted median parturition date for northern herd bison in the historical period was 3 to 12 days earlier than for 2 years in the contemporary period, respectively. Median predicted birth dates and birthing synchrony differed within herds and years in the contemporary period. For a single year of paired data, the predicted median birth date for northern herd bison was 14 days earlier than for central herd bison. This difference is coincident with an earlier onset of spring plant growth on the northern range. Our findings permit refinement of the timing of separation between Yellowstone bison and cattle intended to reduce the probability of transmission of brucellosis from bison to cattle.

Among ungulates, timing and synchrony of parturition may enhance offspring survival, maternal survival, and future reproductive success. Rutberg (1987) hypothesized that timing and synchrony of births served as adaptations to weather, resource availability, or predation (predator saturation, confusion, and group defense). Parturition may occur when food resources are plentiful or of high quality (Bunnell 1980, 1982; Bowyer et al. 1998; Linnell and Anderson 1998; Sinclair et al. 2000), coincident with the high energetic demands of lactation (Millar 1977, Loudon 1985). Parturition and lactation at a period of high nutrient quality or availability may enhance the female's responses to the energetic demands of lactation and improve her physiological condition when she enters the next period of resource limitation or breeding season (Murray 1982). Thus, selection of parturition timing may act against birthing when the probability of high nutrient forage for the postpartum period is low (Ozoga and Verme 1982). Similarly, offspring born at the onset of a period of high nutrient abundance or quality may enter the next period of resource limitation with a larger body size and consequently greater probability of survival as calves and yearlings (Clutton-Brock et al. 1987) compared to late-born calves that are unable to gain sufficient body mass to survive the following period of nutritional deprivation (Thorne et al. 1976, Guinness et al. 1978, Clutton-Brock et al. 1987, Festa-Bianchet 1988, Rachlow and Bowyer 1991, Smith and Anderson 1998).

Ungulate species in seasonal environments commonly exhibit pulse or restricted birthing seasons (Bunnell 1982, Rutberg 1987, Sinclair et al. 2000). Such synchronized parturition may be achieved by reduced variability in timing of conception and length of gestation. The nutritional plane of breeding females as determined by weather conditions or population density may affect timing of conception and gestation length (Parr et al. 1982, Clutton-Brock et al. 1988, Schwartz and Hundertmark 1993), thereby affecting the level of birthing synchrony as well (Adams and Dale 1998). Synchronous parturition in some ungulate populations may be an antipredator strategy enhancing neonate survival by predator swamping (Watson 1969, Estes 1976, Estes and Estes 1979). Other ungulate popula-

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tions may exhibit asynchronous birthing as a means of avoiding predation on neonates (Sinclair et al. 2000).

High and low levels of parturition synchrony have been reported in North American bison. Highly synchronized parturition is characterized by 50% of births occurring within 13 to 27 days and 80% of cumulative births within 23 to 60 days (Rutberg 1984, Green and Berger 1990, Berger 1992, Berger and Cunningham 1994, Berger and Cain 1999). Low parturition synchrony is characterized by 50% of births occurring within >90 days (Wolfe and Kimball 1989, Wolfe et al. 1999) and 80% of cumulative births within 60 to 70 days (Berger 1992, Green and Rothstein 1993*a*). Bison at Badlands National Park (BNP), South Dakota, achieved high synchrony in calving by synchronizing conception or a post-conception shortening of the gestation period by late-breeding females in adequate nutritional condition (Berger 1992). In contrast, bison in poor nutritional condition showed low synchrony in birthing (Berger 1992). However, no relationship was found between parturition date and maternal condition in bison at Wind Cave National Park (WCNP), South Dakota, except that the oldest females gave birth to their last calves "unusually late" (Green and Rothstein 1993*b*). Late birth dates for female calves increased the probability of reproductive failure as an adult; females born early in the calving season were more fecund than those born later for up to 9 years of life (Green and Rothstein 1993*b*). In addition, synchrony and timing of births in bison may be impacted by the presence of diseases (Berger and Cain 1999).

The patterns of inter-annual variation in timing and synchrony of calving in Yellowstone bison have not been reported. Knowledge of variations in these patterns provides insight in to the species population ecology and has management implications. Yellowstone bison are infected with brucellosis, an exotic disease caused by the bacterium *Brucella abortus* (Mohler 1917, Rush 1932). Concerns that range overlap between Yellowstone bison and domestic cattle may lead to infection of brucellosis-free cattle prompted the development and implementation of an interagency federal-state bison management plan (U.S. Department of the Interior and U.S. Department of Agriculture 2000). The plan limits the spatial and temporal distribution of bison and cattle beyond the boundaries of Yellowstone National Park (YNP), particularly during the last trimester of bison pregnancy (U.S. Department of the Interior and U.S. Department of Agriculture 2000). An understanding of the variability in timing and synchrony of birth in Yellowstone bison could allow refinement of the current management plan.

We investigated timing and synchrony of parturition in Yellowstone bison through fetal development. Fetal growth rates have been used to predict fetal ages and thereby timing and synchrony of conception and parturition for a variety of free-ranging ungulate populations (Morrison et al. 1959, Grimsdell 1973, Sinclair 1977, Salwasser and Holl 1979, Schwartz and Hundertmark 1993). We investigated patterns of fetal development by quantifying weight and linear growth relationships to develop fetal growth curves for Yellowstone bison. We evaluated the appropriateness of assumptions necessary to develop the growth curves by comparing parturition dates calculated from fetal growth data with known parturition dates for Yellowstone bison taken in to captivity during pregnancy. We then used fetal growth to predict timing and synchrony of parturition when bison were under different management and nutritional regimes in historic and contemporary periods. For the contemporary period, we investigated differences in timing of parturition for 2 Yellowstone bison herds occupying ranges with seasonal differences in plant phenology.

STUDY AREA

The 8,987-km^2 YNP lies within 73,000 km^2 of public and private lands of the Greater Yellowstone Area (GYA) in Wyoming, Montana and Idaho (Keiter 1991). Yellowstone bison occurred in 2 distinct herds within YNP (Fig. 1). Some 75% to 85% occurred in a central herd, comprised of the previously designated Mary Mountain and Pelican herds (Meagher 1973, Thorne et al. 1991), while the remaining 15% to 25% were found in a northern herd. Previous observations (Meagher 1971, 1973, 1989) suggested, and tracking of instrumented bison from November 1997 to April 2000 (E. M. Olexa, U.S. Geological Survey, unpublished data) confirmed, very little interchange of animals between the 2 herds.

Bison Herds

Central Herd.—The central bison herd wintered primarily at elevations of 2,000–2,250 m in the major geyser basins within YNP and toward Hebgen Lake, Montana (Fig. 1). In winter, bison moved between areas that remained snow-free or
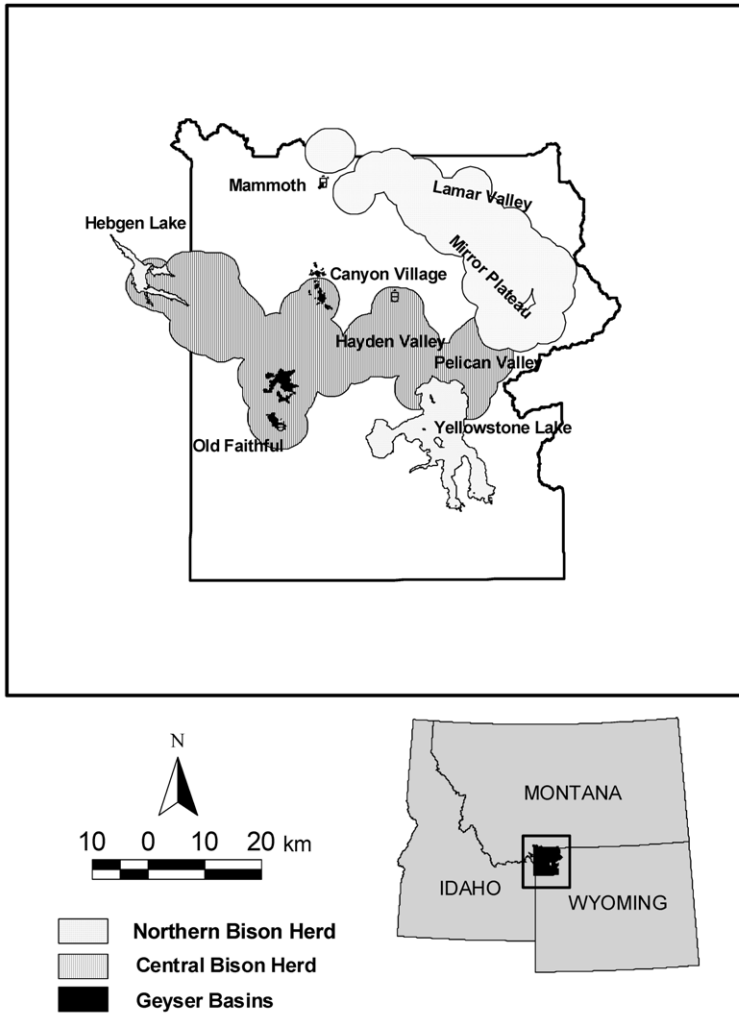
Fig. 1. Spatial distribution of the northern and central bison herds, Yellowstone National Park, Wyoming, USA, 1997–2000.

Douglas fir (*Pseudotsuga menziesii*), and mesic grasslands on sedimentary deposits. Extensive areas of conifer forest, swept by crown fires in 1988, were characterized by dense stands of regenerating lodgepole pine and sparse herbaceous ground cover. Mesic grasslands along the Madison, Firehole, and Gibbon (MFG) river valleys were characterized by a mixture of grasses, sedges (*Carex spp.*), and reedgrass (*Calamagrostis* spp.). Thermally influenced soils supported Nuttall's alkaligrass (*Puccinellia nuttalliana*) and thermal western witchgrass (*Panicum capillare*) with an intermixed herbaceous cover of hairy golden-aster (*Heterotheca villosa*) and sheep sorrel (*Rumex acetosella*; Despain 1987). The Hayden and Pelican valleys supported a predominantly big sagebrush (*Artemisia tridentata*), Idaho fescue (*Festuca idahoensis*) steppe. More mesic sites supported silver sage (*A. cana*) with tufted hairgrass (*Deschampsia cespitosa*) and sedges limited to drainages and adjacent areas (Despain 1987).

Snow accumulations at Canyon Village, comparable in elevation to the Hayden Valley, began on average by 25 October, reached a maximum snow water equivalency (SWE) of 37.8 cm by 8 April, and remained on the ground through 26 May (Farnes et al. 1999). On average, snow began accumulating within geyser basins at the 2,285 m Old Faithful area on 7 November, and snow remained on the ground through 11 May with a maximum SWE of 29.7 cm on 1 April (Farnes et al. 1999). The estimated onset of annual growth for graminoids and forbs was 1 June at Canyon Village and 18 May at Old Faithful (Farnes et al. 1999).

with reduced snow cover within the major geyser basins to other geothermally influenced areas in the approximately 2,500 m elevation Hayden and Pelican valleys (Meagher 1973). The bulk of the herd summered in the Hayden and Pelican Valleys and intermingled with bison of the northern herd in the latter area.

Most of the central herd's range was within the Yellowstone caldera (Pierce and Morgan 1992, Good and Pierce 1996). Soils of the region were derived from rhyolitic rock or sedimentary deposits (Good and Pierce 1996). Vegetation within the central herd's range was a conifer forest of lodgepole pine (*Pinus contorta*) interspersed with Engelmann spruce (*Picea engelmannii*) and

Northern Herd.—The northern bison herd wintered on rolling terrain on the northwestern half of its annual range at elevations of approximately 1,500 to 2,000 m near YNP's northern boundary (Fig. 1). In summer, most of these bison shifted their distribution to the upper Lamar Valley and adjacent Mirror Plateau at approximately 2,745 m, while some ranged southward in to Pelican Valley. With the exception of Pelican Valley, this herd's range was beyond the boundaries of the Yellowstone caldera, and geothermally influenced areas were uncommon. Valley bottoms were filled with glacial debris of andesitic, volcanic, and sedimentary composition (Despain 1987). Vegetation of the area was primarily grassland or big sagebrush steppe characterized by Idaho fescue, bluebunch wheatgrass (*Elymus spicata*), and bearded wheatgrass (*E. trachycaulus*; Houston 1982, Turner et al. 1994). Coniferous forest of Douglas-fir, Engelmann spruce, and lodgepole pine occurred at higher elevations and on north-facing slopes at the periphery of the grassland and sagebrush steppe (Houston 1982). The sagebrush steppe at lower elevations was interspersed with stands of conifers and aspen (*Populus tremuloides*). Approximately 35% of the northern herd's range burned in the 1988 fires (Despain et al. 1989).

Mean annual precipitation ranged from 35 cm in the upper Lamar Valley to 24 cm at Mammoth (Coughenour and Singer 1996). Snow accumulations in the upper Lamar Valley began on average by 21 November, reached a maximum SWE of 8.4 cm by 17 March, and remained on the ground through 13 April (Farnes et al. 1999). On average, snow began accumulating at Mammoth on 27 November and remained on the ground through 23 March, with a maximum SWE of 7.6 cm on 26 February (Farnes et al. 1999). The estimated onset of annual growth for graminoids and forbs ranged from 17 April at Mammoth to 30 April in the upper Lamar Valley (Farnes et al. 1999).

Management History

Management of YNP bison has varied considerably in the last century. Successful protection and recovery of a remnant population in the early 1900s was followed by a period of intensive management from the 1920s until the late 1960s that included provision of supplemental feed, roundups, and selective culling (Meagher 1973). Northern herd bison were provided hay as supplemental feed from 1939 through 1952, and management reductions limited numbers through 1968 (Meagher 1973). Intrusive management of bison within YNP ended in 1968 with National Park Service adoption of a policy of natural regulation of free-ranging ungulates (Cole 1971, National Park Service 1988, Wagner et al. 1995). Increasing numbers of Yellowstone bison from <700 in winter 1970–1971 to >3,800 in 1996–1997 resulted in range expansion and movement of free-ranging bison beyond the boundaries of YNP in some winters since 1984 (Taper, M. L., M. Meagher and C. L. Jerde. 2000. The phenology of space: spatial aspects of bison density dependence in Yellowstone National Park. Department of Ecology, Montana State University. Typewritten report.). Bison adjacent to park boundaries have been subjected to intensive management, including lethal removal.

Wolves (*Canis lupus*), a major potential predator of bison (Lopez 1978), were largely eliminated from YNP by 1880, extirpated by 1930 (Schullery 1997), and restored in 1996 (Bangs and Fritts 1996). While present in the GYA, grizzly bear (*Ursus arctos*) were not considered a common predator of bison (Meagher 1973, Craighead et al. 1995).

METHODS

We used weights and morphometric measurements of Yellowstone bison fetuses to assess fetal development and predict timing and synchrony of parturition. Weight and crown-rump (CR) length have commonly been used to estimate fetal ages in ungulates (Huggett and Widdas 1951, Hamilton et al. 1985, Schwartz and Hundertmark 1993) since degree of development is indicative of age in days for mammalian fetuses (Evans and Sack 1973). We weighed and measured fetuses during the winters of 1988–1989, 1996–1997, 1998–1999, and 2001–2002, and we supplemented our data with similar measurements from fetuses collected in the winters of 1940–1941 (Skinner 1941), 1994–1995, 1995–1996, and 1996–1997 (K. Aune, Montana Department of Fish, Wildlife and Parks, unpublished data).

We classified samples by location relative to YNP's northern or western boundaries and winter of collection. We classified fetuses from the winter of 1940–1941 as a historic sample and fetuses from the winters of 1988–1989 through 2001–2002 as contemporary samples. Although Yellowstone bison typically occur in 2 distinct herds, some bison of the central herd have been observed moving to the range of the northern

herd in some winters (Meagher 1971, 1993; J. A. Mack, YNP, personal communication), most recently in 2001–2002 (R. L. Wallen, YNP, personal communication). In contrast, northern herd bison have not been observed making reciprocal winter movements to the range of the central herd. Thus, we treated bison sampled along YNP's western boundary as exclusively members of the central herd and bison sampled along YNP's northern boundary as representative of the northern herd but possibly including central herd bison. The historic sample was limited to the northern herd, while contemporary samples were obtained for both.

Contemporary period fetuses were sampled opportunistically as bison were killed adjacent to YNP's boundaries. These bison may have differed to an unknown degree in terms of nutritional plane, age, or stress due to hazing from those remaining within YNP. Furthermore, criteria used to determine whether bison were slaughtered, varied by herd as well as within and between years. Yet, age structures of central herd bison killed at the YNP boundary and dying of natural causes during the winter of 1996–1997 differed little among >4-year-olds, where pregnancy and serological rates for brucellosis were highest (P. J. P. Gogan, U.S. Geological Survey, unpublished data). Also, we obtained samples from the northern herd during winters where >50% of the herd was removed (National Park Service 2000). We therefore treated our samples as representative of each herd.

Fetal Development

We removed uteri in toto from slaughtered bison and maintained them at temperatures ≤4°C. Within 24–48 hrs of maternal death, we removed the fetus from the uterus and measured CR length (mm) and fetal weight (g). We measured CR length as the straight length from the apex of the crown of the head at the forehead to the tuberosity of the ischium. We examined relationships of CR length vs. weight to assess differences among samples. We linearized the CR length to weight relationship via log-log transformation. Log-log transformation changes a curvilinear relationship of the form $y = ax^b$ to the linear form $\ln(y) = \ln(a) + b*\ln(x)$ such that the slope equates to the exponent, b, and intercept equates to the constant, a, of the original raw form. We tested the assumption that slopes (i.e., exponents) were not significantly different and then tested for differences among the intercepts

(i.e., constants) using analysis of covariance (ANCOVA; Zar 1984).

Timing of Parturition

We used fetal weight (the parameter common to most samples) to estimate gestational age, and we combined gestational age with collection date to calculate conception and parturition dates. Because no published data existed for bison fetus weights of known gestational ages, we developed growth functions using data from cattle fetuses and birth parameters assumed for bison. To determine an appropriate fetal growth function, we first fit a curve through pooled weights of known-aged fetuses of several diverse breeds of domestic cattle (Winters et al. 1942, Swett et al. 1948, Ellenberger et al. 1950, Lyne 1960, Eley et al. 1978). Birth weights for the various cattle breeds represented ranged from ~25 kg to ~42 kg (Andersen and Plum 1965). Regardless of ultimate birth weights, cattle fetuses developed similarly up to approximately 75 days. We assumed that bison fetuses grew similarly during this initial stage of growth and that most differences between cattle and bison occurred after the first 75 days of gestation, when cattle fetal development diverged by breed. We developed bison fetal growth curves by using the growth function identified for cattle fetuses, forcing the curves to maintain similar growth to cattle fetuses ≤75 days, but we allowed them to deviate after 75 days to different assumed sex-specific birth parameters of gestation length and birth weight for Yellowstone bison in historic and contemporary periods. To reduce the magnitude of spread in weights, we used the cube-root of weight (Lyne 1960) when developing fetal growth curves.

We made 3 basic assumptions when constructing the predictive fetal growth curves for bison. First, that fetuses collected during periods of higher nutrition had shorter gestation lengths than those collected during periods of lower nutrition. Good maternal physical condition and higher nutrition are known to shorten the gestation period in bison (Berger 1992), moose (*Alces alces*; Saether and Heim 1993, Schwartz and Hundertmark 1993, Keech et al. 2000), red deer (*Cervus elaphus*; Hamilton and Blaxter 1980), white-tailed deer (*Odocoileus virginianus*; Verme 1965), and cattle (Hutchinson and MacFarlane 1956). Second, we assumed that fetuses collected during periods of higher nutrition had greater birth weights than those collected during periods of lower nutrition. Nutritional experiments on

domestic livestock have shown that higher planes of nutrition resulted in heavier birth weights in cattle (Hight 1966, Tudor 1972, Corah et al. 1975, Bellows and Short 1978) and sheep (Khalaf et al. 1979). Third, we assumed that birth weight of males was greater than that of females, as previously shown in bison (Agabriel and Petit 1996, Rutley et al. 1997, Agabriel et al. 1998), wisent (*Bison bonasus*; Krasinska and Krasinski 2002), elk (Hudson et al. 1991), white-tailed deer (Robbins and Moen 1975), and many breeds of cattle (Roy 1980).

We assumed separate common gestation lengths for bison in the historic and contemporary periods. The gestation period is nearly constant for ungulates (CV ≤ 4%; Kiltie 1982). We calculated a CV of 2.6% for captive bison (Agabriel et al. 1998). We used a 265-day gestation length for dietary supplemented Yellowstone bison in the historic period. This was based on mean gestation lengths of 264 to 267 days reported for ranched bison managed for high nutritional levels by supplemental feeding, movement among pastures, and/or maintenance at low densities (Rutberg 1986; Agabriel and Petit 1996; Agabriel et al. 1998; Staudinger 2001; D. L. Staudinger, MFL Ranches, unpublished data). Gestation lengths of intensively managed bison were consistent, and no reported gestation length was ≥276 days. Similarly, wisent receiving dietary supplements in winter had a mean gestation length of 264 with all gestation lengths ≤272 days (Krasinski and Raczynski 1967). We utilized a 272-day gestation length for Yellowstone bison receiving no dietary supplements in the contemporary period. This 7-day-longer gestation length for the contemporary period was based upon observed peaks in breeding and births of Yellowstone bison. Peaks in rutting activity occurred in early August (1 Aug to 15 Sep, McHugh 1958; mid-Jul to mid-Aug, Meagher 1973; 15 Jul to 31 Aug, Kirkpatrick et al. 1993) as did timing of ovulations detected via fecal steroids (1 Aug to 15 Aug, Kirkpatrick et al. 1993). Subsequent births occurred in early May (first 2 weeks of May, McHugh 1958; early May, Meagher 1973; 9 May, E. M. Olexa, U.S. Geological Survey, unpublished data). Reported gestation lengths of ≥285 days (Haugen 1974) do not fit observations in Yellowstone bison.

We used a birth weight of 25 kg for females and 30 kg for males in the historic period based upon mean birth weights of intensively managed bison (Agabriel and Petit 1996, Rutley et al. 1997, Agabriel et al. 1998) and wisent provided dietary supplements in winter (Krasinska and Krasinski 2002). Birth weights of free-ranging bison have not been directly measured but have been estimated from 14–32 kg for both sexes (McHugh 1958, Park 1969, Meagher 1986). We used contemporary period birth weights that were 10% lighter than managed bison (22.5 kg for females and 27.0 kg for males), since these weights were consistent with our recorded maximum weights of near-term fetuses in the contemporary period. Birth weights 7–22% lighter have been observed for cattle maintained at low nutritional planes (Hight 1966, Tudor 1972, Corah et al. 1975, Bellows and Short 1978).

We assessed the validity of our methods by comparing the predicted birth dates of our 1996–1997 northern Yellowstone sample to observed parturition dates of seronegative bison transferred from the Yellowstone northern range to captive facilities in January 1997 (D. L. Hunter, Idaho Fish and Game, unpublished data; K. Aune, Montana Department of Fish, Wildlife and Parks, unpublished data). We used median tests to identify differences among the calculated parturition dates of Yellowstone bison by location and year, and we evaluated synchrony with the Fligner-Killeen test for homogeneity of variance (Conover et al. 1981). Small samples ($n \leq 10$) were omitted from statistical comparisons. We used Table Curve 2D version 4.07 to fit curves describing fetal growth gestation stage. Statistical analyses were conducted in SYSTAT version 10, SAS version 8.02, and R version 1.2.1.

RESULTS

Fetal Development

We obtained 74 fetal weights and CR lengths from historic period and 223 fetal weights and 98 CR lengths from contemporary period Yellowstone bison. Sampling dates ranged from 20 January to 6 February and 14 November to 30 April in the historic and contemporary years, respectively. All fetuses were singletons.

The CR length to weight relationship was nonlinear for all samples (Fig. 2). Log-log transformation and subsequent ANCOVA indicated that differences existed among samples in the relationship of length to weight ($F_{4, 162} = 37.13$, df = 4, $P < 0.001$). Bonferroni adjustment for multiple comparisons indicated that the historic sample was different from all contemporary samples and that there was a high degree of overlap among contemporary samples. Fetuses were heavier at given body lengths in the historic sample than in contemporary samples. There was no interaction
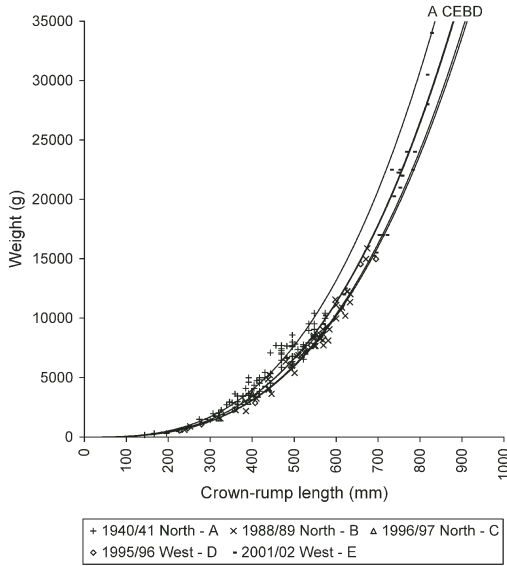
Fig. 2. Relationship between weight and crown-rump length of bison fetuses sampled adjacent to the north and west boundaries of Yellowstone National Park, Wyoming, USA, winters 1940–1941, 1988–1989, 1995–1996, 1996–1997, and 2001–2002.

Fig. 4. A generalized fetal growth curve for cattle compared to growth curves for Yellowstone bison fetuses by sex for the historic and contemporary periods.

between ln(CR) and sample ($F_{4, 158} = 0.230$, $P = 0.922$). Therefore, even though the samples differed in magnitude, the exponential nature of the relationship was similar among samples.
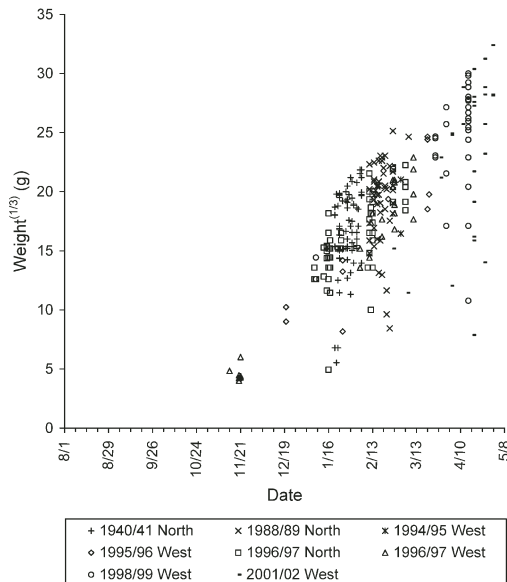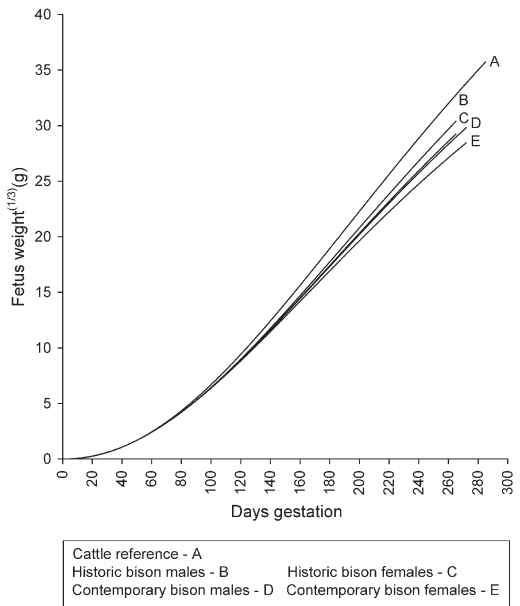

Fig. 3. Distribution of the cube root of weight by collection date of bison fetuses sampled adjacent to the north and west boundaries of Yellowstone National Park, Wyoming, USA, winters 1940–1941, 1988–1989, 1994–1995 to 1998–1999, and 2001–2002.

Timing of Parturition

Examination of a plot of the cube root of fetal weights by dates of collection (Fig. 3) showed a marked spread in weights on given dates with no visual evidence of separated birth pulses (see Schwartz and Hundertmark 1993). We input the recorded weights into a growth curve based on sex and date of collection (Fig. 4) to calculate the stage of gestation in days. Calculated gestation stage was then used to determine conception and parturition dates from the collection date. The growth curve for cattle is $weight^{1/3} = 79.94/(1 + [days\ gestation/315.71] - 2.08)$; the growth curve for historic males is $weight^{1/3} = 80.82/(1 + [days\ gestation/334.26] - 2.03)$; the growth curve for historic females is $weight^{1/3} = 67.54/(1 + [days\ gestation/302.53] - 2.04)$; the growth curve for contemporary males is $weight^{1/3} = 66.79/(1 + [days\ gestation/300.66] - 2.04)$; and the growth curve for contemporary females is $weight^{1/3} = 57.26/(1 + [days\ gestation/275.71] - 2.05)$.

The median parturition date predicted by our fetal growth calculations for the north 1996–1997 sample (6 May) was not different from the median observed parturition date of 1997 captive northern Yellowstone bison (5 May; $\chi^2 = 1.131$, df $= 1$, $P = 0.288$; Fig. 5). Similarly, synchrony did not differ between the predicted and observed births
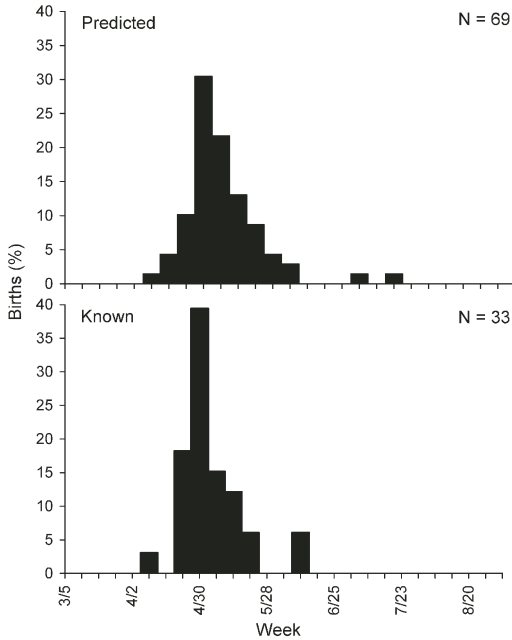
Fig. 5. Predicted dates of parturition based on fetal growth rates of free-ranging bison (upper panel), and the observed birthing pattern for captive bison (lower panel), northern herd, Yellowstone National Park, Wyoming, USA, 1997.

(χ^2 = 0.4349, df = 1, P = 0.510). Because our method adequately predicted timing and synchrony of births for this validation pair, we calculated estimated birth dates of all samples.

The earliest and latest births predicted from fetal weights ranged from 25 March in northern Yellowstone bison in 1988–1989 to 24 September in central Yellowstone bison in 2001–2002 (Fig. 6). Median predicted birth dates ranged from 25 April for the historical northern Yellowstone bison to 22 May for the contemporary central Yellowstone bison (Table 1) and varied among years and locations (χ^2 = 30.739, df = 5, $P < 0.001$), as did synchrony (χ^2 = 24.884, df = 5, $P < 0.001$). In the contemporary period, median birth dates differed (χ^2 = 18.135, df = 4, P = 0.001), as did synchrony of births (χ^2 = 19.426, df = 4, $P < 0.001$). However, the predicted median birth dates for northern Yellowstone bison in the 2 contemporary years did not differ (χ^2 = 2.803, df = 1, P = 0.094); although, synchrony of births did (χ^2 = 10.042, df = 1, P = 0.002). The contemporary central Yellowstone bison varied in predicted median birth dates (χ^2 = 12.021, df = 2, P = 0.003) and synchrony (χ^2 = 7.526, df = 2, P = 0.023). In 1997, the single year with predicted parturition patterns for both the northern and central herds, the median birth date for the north-
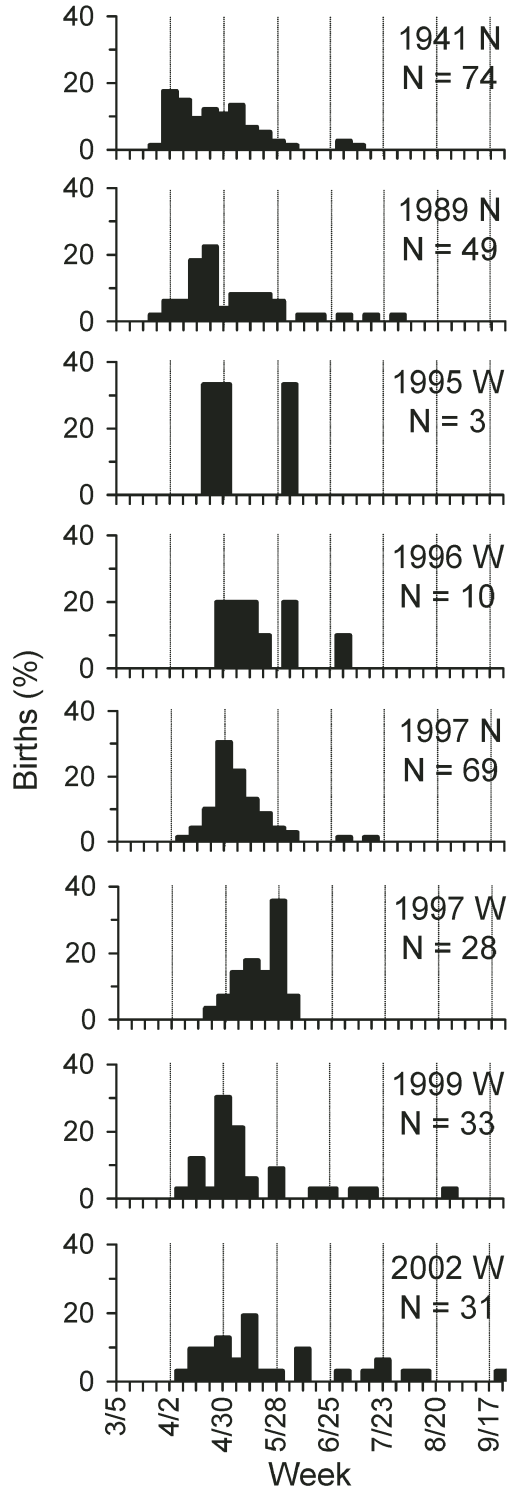

Fig. 6. Predicted weekly parturition patterns of bison adjacent to the north and west boundaries of Yellowstone National Park, Wyoming, USA, 1941, 1989, 1995 to 1997, 1999, and 2002.

Table 1. Annual parturition characteristics of northern and central bison herds, Yellowstone National Park, Wyoming, USA, 1941, 1989, 1997, 1999, and 2002.

Herd	Year	No.	Onset of parturition	Median birth date	Days in interquartile range	Days for 80% of cumulative births
Northern	1941	74	31 Mar	25 Apr	29	43
	1989	49	10 Apr	28 Apr	30	59
	1997	69	12 Apr	6 May	13	37
Central	1997	28	27 Apr	22 May	18	33
	1999	33	10 Apr	7 May	19	46
	2002	31	18 Apr	14 May	43	82

ern herd was 16 days earlier than for the central herd (22 May; Table 1; χ^2 = 10.146, df = 1, P = 0.001), but synchrony did not differ between the 2 herds (χ^2 = 2.075, df = 1, P = 0.649).

The distribution of parturition dates in Yellowstone bison is generally right-skewed with a majority of births in April and May and a small percentage occurring throughout the summer (Fig. 6). The most compressed 50% of births occurred within 29 days in the historic period and 13 to 43 days in the contemporary period (Table 1). Eighty percent of predicted cumulative births occurred within 43 days in the historic period and 33 to 82 days in the contemporary period (Table 1).

DISCUSSION

Fetal Development

Relationships between CR length and weight in Yellowstone bison were similar to those seen in other ungulate species. Weight was related to CR length[2.95] in our bison samples. Associations between weight and length that were described, or that we calculated from reported data for cattle (Winters et al. 1942, Lyne 1960) and white-tailed deer (Armstrong 1950), showed weight to be approximately related to length[3] or length to be related to weight[1/3]. Although all Yellowstone bison samples had a similar overall relationship, the magnitude of the relationships varied. Fetuses were heavier at given CR lengths in the historic period than in the contemporary period. Better maternal nutrition and body condition in the historic period explains the heavier fetuses for given CR lengths compared with the contemporary period. Historically, bison were baited into the Lamar Valley, artificially fed in the winter, and maintained at ≤700 animals through active culling for the 5 years prior to the sample year (Meagher 1973). Differences in fetal development between the historic and contemporary period justified our use of different assumed fetal development parameters for the 2 periods.

Timing of Parturition

Our growth curves fairly represented fetal growth of bison because (1) an initial growth function derived from cattle was reasonable given similarities in biology and size to adult bison; (2) birth weights for captive bison were similar to some of the smaller cattle breeds (e.g., Jersey); and (3) the calculated range of birth dates, median parturition date, and birthing synchrony for northern 1996–1997 herd fetuses agreed closely with the observed 1997 pattern of birth dates for captive northern herd bison (Fig. 5).

While there is a possibility that our 1996–1997 northern sample was obtained from bison that differed from captive animals in nutritional status and/or serological status for brucellosis, we suggest that these differences were minimal. The captive females remained in poor nutritional condition throughout the remainder of their pregnancies in spite of supplemental feeding (D. L. Hunter, Idaho Fish and Game, personal communication). We obtained our 1996–1997 northern Yellowstone sample from female bison that tested either seropositive or seronegative for brucellosis and that showed no signs of abortion. Seroprevalence does not equate to an active infection of the female reproductive tract that impairs fetal development (Cheville et al. 1998). Other than females actively or recently aborting, the reproductive tracts of a sample of pregnant, seropositive Yellowstone bison were negative to culture for *B. abortus* (Rhyan et al. 2001). Thus we interpret the observed birth dates of captive bison as representative of free-ranging northern Yellowstone bison.

The predicted onset of calving 10–12 days earlier in historic than contemporary northern Yellowstone bison (Table 1) is consistent with field observations, "From 1937 to about 1950, the first calves were regularly reported in the Lamar before mid-April. Since 1950, first calves have all been reported later" (Meagher 1973:75). We attribute this difference to northern Yellowstone bison being on a higher nutritional plane throughout much of pregnancy in the historic period due to active management (Skinner and Alcorn 1951). This pattern is consistent with observations of other ungulate species where birth dates at high population densities, and presumed lower nutritional levels, are

later than those at lower densities and presumed higher nutritional levels (Clutton-Brock et al. 1987, McCullough 1999, Forchhammer et al. 2001). However, differences in predicted median birth dates between the historical and contemporary periods were less clear and differed by only 3 days in 1 instance and 11 days in the other (Table 1).

Although our samples include only 1 winter (1996–1997) from both herds, median birth dates for contemporary Yellowstone bison were consistently earlier in northern range animals (Table 1). The 16-day earlier predicted median birth date for northern than central herd Yellowstone bison in 1997 (Table 1) was consistent with an average 24-day earlier onset of plant growth on the lower elevations of each herd's winter range (northern herd [Mammoth, Wyoming], 17 Apr; central herd [West Yellowstone, Montana], 12 May; [Farnes et al. 1999]). This delayed plant growth in the central range shortens the growing season of forage available to central herd bison to improve body condition prior to conception. Similarly, mule deer occupying high elevation areas characterized by a delayed growing season conceived approximately 60 days later than those at near sea level (Bowyer 1991).

Differences in parturition dates between the 2 Yellowstone herds may be greater than our calculations indicated. Bison of the central herd declined to a lower nutritional plane in winter than did bison of the northern herd (DelGuidice et al. 1994, 2001). If a lower maternal nutritional plane extends the gestation period (Berger 1992), our assumption of common gestation length for both Yellowstone bison herds may be incorrect. A lengthened gestation time for central herd bison could further increase differences in median parturition dates between the 2 Yellowstone herds. Also, inclusion of any central herd bison in our northern boundary sample could contribute to a later calculated median birth date for the northern herd. Records show that some central herd bison were removed at the northern boundary during the winter of 1996–1997. However, radiotelemetry data for bison of both herds demonstrated that there was virtually no interchange of adult bison between the 2 herds from October 1997 through May 2000 (E. M. Olexa, U.S. Geological Survey, unpublished data). Also, with herd mixing, variance in parturition dates should be greater for bison from northern samples, but we detected no evidence of this. Thus, contamination of samples between locations is likely not an issue in most years.

Both the predicted median birth dates for contemporary northern Yellowstone bison of 28 April and 6 May and the earliest predicted median birth date for contemporary central herd bison of 7 May 1999 (Table 1) overlap the range of 2 May to 8 May for 5 consecutive years of observations at BNP (Berger and Cunningham 1994). The other 2 predicted contemporary median birth dates for the central Yellowstone herd (Table 1) were 7–15 days later than the predicted median date for 1999 and later than the range of dates reported for BNP (Berger and Cunningham 1994). However, they approximate the median birth dates for Jackson Valley, Wyoming bison for 2 years (20 May and 23 May; Berger and Cain 1999). Bison of the central Yellowstone and Jackson Valley herds winter at higher elevations where spring green-up is likely delayed. The Yellowstone central herd has access to snow-free thermal features, while the Jackson Valley herd has access to supplemental feed in winter.

The predicted median parturition dates in the contemporary period covered 9 days for northern Yellowstone bison and 16 days for Yellowstone's central herd (Table 1). Median parturition dates for bison at BNP spanned 8 days (Berger 1992), and median parturition dates of bison in the Jackson Valley differed by only 4 days (Berger and Cain 1999).

Fifty percent of all births occurred within 13–43 days for contemporary period Yellowstone bison, which embraces the 29 days calculated for our historic period. With the exception of the central bison herd in 2002, all of our estimated interquartile ranges (Table 1) were consistent with a calculated 13 days at the NBR (interpolated from Rutberg 1984 by Berger 1992), 21 days at WCNP (Green and Berger 1990), 20–27 days at BNP (Berger 1992), and approximately 25 days for the Jackson bison herd (interpolated from Berger and Cain 1999). The narrowest interquartile range in our study (13 days) in northern Yellowstone bison in 1997 was identical to the 13 days reported for bison at the NBR (Rutberg 1984). In contrast, bison at Antelope Island (AI), Utah, have a prolonged calving season from March through October with 40% of the calves born from August through October (Wolfe and Kimball 1989, Wolfe et al. 1999).

Although synchrony of parturition differed between the 2 Yellowstone bison herds in the contemporary period and among contemporary years within herds, we were unable to statistically determine which years were more synchronous than

others. The complementary log-log analysis used by others (Rachlow and Bowyer 1991, Berger and Cain 1999) to compare synchrony between years and locations was inappropriate for our data because the underlying cumulative distributions could not be linearized (Caughley and Caughley 1974). However, the interquartile ranges of 13–29 days for Yellowstone bison, excluding the central herd in 2002 (Table 1), were virtually identical to ranges reported for the NBR, WCNP, and BNP (Berger 1992). The extended parturition period for the central Yellowstone herd in 2002 (Table 1) may be classified as synchronous or asynchronous: synchrony is indicated by 50% of births occurring within <90 days (Wolfe and Kimball 1989, Wolfe et al. 1999) while asynchrony is suggested by 80% of cumulative births occurring >70 days (Green and Rothstein 1993*a*, Berger 1992). Possible explanations for the extended birthing period in 2002 and for between year and herd differences in birthing periods in general include differences in nutrition (Berger 1992; DelGiudice et al. 1994, 2001) as influenced by snowpack conditions (Farnes et al. 1999) and population densities (Kirkpatrick et al. 1996).

Our prediction of parturition in Yellowstone bison typically extending in to July and August is consistent with previous reports of late calving in Yellowstone bison (Meagher 1973). Such late-born calves may not achieve an adequate body size needed to survive the harsh Yellowstone winter. Calving in August and September has been reported for other bison herds (Haugen 1974, Rutberg 1984, Wolfe and Kimball 1989, Van Vuren and Bray 1986, Green and Rothstein 1993*a*).

Wolves were restored to the GYA in the winters of 1995 and 1996 (Bangs and Fritts 1996) and have preyed largely on elk since their reintroduction (Douglas Smith, YNP, personal communication). Documented wolf-killed Yellowstone bison numbered <10 from 1997 to 1999 (Smith et al. 2000). Thus, our assessment of timing and synchrony of births in Yellowstone bison was undertaken during a period of little exposure to wolf predation. Extensive wolf predation on bison calves from May through October has been observed in Wood Buffalo National Park (WBNP), northern Alberta, Canada (Carbyn et al. 1993), and bison calves were ≥80% of the wolf-predated bison in winter at the Mackenzie Bison Sanctuary, Northwest Territories, Canada (Gates and Larter 1990). However, observations of bison herds in the absence of wolves suggest that such bison have no tradition of behavioral responses

to potential wolf predation such as predator swamping through increased group size (McHugh 1958, Rutberg 1984). Therefore, we conclude that potential wolf predation was not a factor likely to have influenced synchrony of birth during the historical or contemporary periods. As wolf numbers increase, there may be a greater impact on bison calves, thereby influencing future birthing synchrony.

Brucellosis-infected, primiparous bison typically lose their first conceptus via abortion in the third trimester (Cheville et al. 1998), and they thereby reduce maternal exposure to the energetic demands of late pregnancy and lactation. These females may be poised to improve in nutritional condition from the onset of spring plant growth to the August rut, resulting in early conception and parturition the subsequent spring. Although, the presence of brucellosis in Yellowstone bison could enhance breeding synchrony, we found levels of synchrony comparable to brucellosis-free herds. The comparable levels of synchrony also do not support the suggestion of Berger and Cain (1999) that brucellosis-infected females might abort early in pregnancy and conceive again late in the same breeding season, thereby extending the calving season by birthing later than nonaborting bison.

Our findings are consistent with the hypothesis that availability of spring forage is a major factor in the timing of parturition in temperate climate ungulates (Bunnell 1982, Rutberg 1987, Bowyer et al. 1998). The documented timing and synchrony of parturition is similar for a number of isolated bison herds (Rutberg 1984, Green and Berger 1990, Berger 1992, Berger and Cain 1999). However, all these herds occur in interior North America within a narrow latitudinal band relative to the historical range of bison. A strong correlation has been demonstrated between latitude and timing and synchrony of parturition in bighorn sheep (Bunnell 1982). Such a pattern may also be characteristic of bison. In northern Canada, the onset of parturition in bison does not begin until 10 May, and parturition is more synchronous than that of bison to the south (Soper 1941). However, the higher level of birth synchrony in northern bison populations may be influenced by wolf predation on calves (Gates and Larter 1990, Carbyn et al. 1993).

Although timing and synchrony of parturition varied from year to year within northern and central herd bison, calculated differences in timing (especially in the 1 year when both herds were sampled) suggest real differences between herds.

Opportunistic sampling during management removals precluded a more rigorous assessment of herd differences in parturition patterns. Herd differences in timing of parturition are consistent with investigations showing little interchange of animals between the 2 herds between 1997 and 2000 (E. M. Olexa, U.S. Geological Survey, unpublished data) and differences in dental wear patterns between the 2 herds (Christianson et al. 2005).

MANAGEMENT IMPLICATIONS

Current management of Yellowstone bison focuses on herd distributions during the third trimester of pregnancy and calving. Managers seeking temporal and spatial separation between bison and cattle during this period can use our documentation of timing and parturition in Yellowstone bison to confidently set a benchmark date. Identification of differences in the onset of birthing and median birth dates between herds permits the development of alternative management scenarios to account for differences. A benchmark date based on the first birthing event is 10 April for both herds, and a benchmark date set on the median birth date is about 28 April for the northern Yellowstone herd and 7 May for the central Yellowstone herd.

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