

An assessment of the reproductive biology of Yellowstone bison (*Bison bison*) subpopulations using noncapture methods

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Abstract: Five parameters of reproductive biology (number of live calves, rates of tending lactating and nonlactating cows, and age-specific calving and pregnancy rates) were measured for the Mary Mountain (≈ 2500) and Northern Range (≈ 600) herds of bison (*Bison bison*) in Yellowstone National Park between 1990 and 1993. Three physiological events (ovulation, pregnancy, fetal loss) affecting reproductive success were measured using urinary or fecal steroid analysis. Adult Mary Mountain cows had significantly fewer pregnancies and calves than the Northern Range cows. Approximately 85% of cows tended by bulls, 76% of detected ovulations, and 78% of detected fall pregnancies were among nonlactating cows. Greater than 80% of all pregnancies occurred in cows ≥ 4 years old in both herds. However, 100% of all pregnancies among lactating cows occurred in cows ≥ 5 years old in both herds. In the Mary Mountain subpopulation, only 5% of all pregnancies were among cows < 4 years old, while 14.2% of all pregnancies in the Northern Range herd occurred in cows in the same age group. These data indicate that (i) the number of live calves and the pregnancy rate are significantly reduced among lactating cows, (ii) reproductive failure among lactating cows is primarily caused by ovulation failure, (iii) lactating cows that successfully reproduce are exclusively animals ≥ 5 years old, and (iv) the results of urinary or fecal steroid analysis are consistent with behavioral and demographic data and can be used to evaluate specific aspects of reproductive physiology among free-ranging ungulates.

Résumé : Cinq variables reliées à la biologie de la reproduction (nombre de petits vivants, fréquence de la surveillance exercée sur les femelles nourricières et sur les femelles non nourricières, taux de grossesse et de mise bas en fonction de l'âge, ont été mesurées chez deux sous-populations de Bisons (*Bison bison*) du parc national de Yellowstone, entre 1990 et 1993, la sous-population de Mary Mountain (≈ 2500) et la sous-population des montagnes du nord (≈ 600). Trois processus physiologiques (ovulation, grossesse, perte de fœtus) qui affectent le succès de la reproduction ont été mesurés par analyse des stéroïdes urinaires et fécaux. Les femelles adultes de Mary Mountain ont eu significativement moins de grossesses et de mises bas que les femelles des montagnes du nord. Environ 85% des femelles surveillées par des mâles étaient des femelles non nourricières; de plus, 76% des ovulations et 78% des grossesses à l'automne ont été enregistrées chez les femelles non nourricières. Plus de 80% de toutes les grossesses ont été enregistrées chez les femelles ≥ 4 ans, chez les deux sous-populations. Cependant, 100% de toutes les grossesses de femelles nourricières ont été enregistrées chez des femelles ≥ 5 ans, chez les deux sous-populations. Chez la sous-population de Mary Mountain, seulement 5% de toutes les grossesses concernaient des femelles < 4 ans, alors que 14,2% des femelles du même groupe d'âge se sont trouvées enceintes chez la sous-population des montagnes du nord. Les données indiquent (i) que le nombre de petits vivants et les taux de grossesse sont significativement réduits chez les femelles nourricières, (ii) que l'échec de la reproduction chez les femelles nourricières est dû surtout à l'absence d'ovulation, (iii) que les femelles nourricières qui réussissent à se reproduire sont exclusivement des animaux ≥ 5 ans et (iv) que les résultats des analyses des stéroïdes urinaires ou fécaux correspondent aux données comportementales et démographiques et peuvent être utilisés pour évaluer des aspects spécifiques de la physiologie de la reproduction chez les populations libres d'ongulés. [Traduit par la Rédaction]

Introduction

Reproductive success varies greatly between populations and is influenced by species-specific characteristics, including

nutrition (Abler et al. 1976; Verme 1969; White et al. 1989), population composition (age structure and sex ratio) (Verme 1983), disease (Thorne et al. 1989), genetic factors (Chandley et al. 1975), climate (Verme and Doepker 1988), and human harassment (Yarmoloy et al. 1988). Interaction between these factors and their effects on reproductive physiology are poorly defined for most mammalian species and what little we know has been derived from controlled studies of rodents (Chitty 1967; Christian 1950, 1970; Krebs 1978). Although the ways in which reproductive success may change in response to changes in population density differ between large free-roaming mammals and rodents, there is sufficient information to develop hypotheses that may apply to ungulates. In general terms, Chitty (1967), (Krebs 1978), Christian (1950,

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1970), Christian and Davis (1964), Christian et al. (1965), and Charnov and Finerty (1980); all hypothesize that selection for aggressiveness in populations with greater densities is advantageous because it enhances an individual's ability to compete for limited resources. Selection for aggressiveness may, however, also lead to endocrine-related processes related to stress, which may in turn increase disease and mortality and thereby result in reproductive failure.

More specifically, free-ranging bison (*Bison bison*) have been studied in several environments to provide a better understanding of self-regulation in large ungulates. Three of North America's 10 free-roaming bison herds (those in Wood Buffalo National Park and McKenzie Bison Sanctuary in Canada and Yellowstone National Park (YNP) in the U.S.A.) are still relatively unmanaged and responsive to environmental influences. Previous reports have demonstrated significant differences in reproductive success between these herds (Fuller 1962; Halloran 1968; Lott and Galland 1987; Van Camp and Clef 1987; McHugh 1958). At least one report has hypothesized ovulation failure (Lott and Galland 1985) as the proximate cause of lowered reproductive rates among some herds in harsh climates or on poor nutritional planes.

This study tested a model and methods for assessing fecundity by means of fecal and urinary hormone measurements. More specifically, the study sought to provide insights into the physiological mechanisms of reproductive self-regulation in a large free-roaming ungulate by assessing the reproductive responses of two herds with historically disparate population densities to changing environmental conditions. The study was undertaken after the extensive forest fires of 1988 in which approximately 30% of the wooded areas of YNP were cleared by fire. Two subpopulations, the Mary Mountain (MM) and Northern Range (NR) herds, that lived in two areas of YNP that were differently affected by the fires were selected for study. During the first two winters following the fires, large ungulates in YNP were severely stressed nutritionally, but NR animals inhabiting the Lamar Valley less than those inhabiting portions of the MM herd range in the central regions of the park (DelGiudice and Singer 1996). Since 1989, growth of grasses on the ranges of both subpopulations has increased. The sizes of these two groups of bison differed substantially; the NR herd has been consistently smaller than the MM herd since the onset of these studies, largely because of annual culling of NR animals during winter months, when they leave the park.

These populations were used as a model for understanding the physiological basis for demographic changes occurring in response to environmental changes, using actual reproductive potential rather than theorized reproductive potential to evaluate the regulation of population growth in these two herds. Actual fertility is a result of physiological processes but reproductive potential has heretofore been viewed only as a theoretical construct. Most studies of reproductive success in wildlife have drawn upon recruitment as the endpoint measurement, yet immigration, emigration, predation, and mortality all affect recruitment. The direct evaluation of fecundity, in terms of ovulation and conception, provides a better measurement of actual reproductive potential. The present study was performed by applying noncapture methods to evaluate the reproductive potential of individual cows.

Reproductive potential was used to determine the contribution of changes in individual fecundity to changes in the reproductive rate of the herd. The specific parameters that were measured and compared included (i) calf production, (ii) calf survival, (iii) tending and ovulation rates of cows during the breeding season, (iv) fall pregnancy rates, (v) age-specific recruitment, and (vi) estimated fetal loss and neonatal loss rates.

Methods

All fecal and urine samples and behavioral data were collected annually from the two subpopulations of bison between July 15 and September 1 from 1990 through 1993 and during November from 1990 through 1993. Data collection from the MM herd were confined to animals inhabiting the Hayden Valley and various locations along the Fire Hole River; collections from the NR animals were made between Soda Butte and Tower Junction. Because cows may group differentially according to whether they have calves, care was taken to include as many groups as possible within each subpopulation. Behavioral observations were carried out as previously described by Kirkpatrick et al. (1992) to determine tending rates or estrous behavior. Observations were carried out between sunrise and sunset; a discrete band would be observed for 1–12 h and cows would be classified as tended if they were separated from the band or herd by a mature bull and not permitted to return to other animals. Other behaviors used to identify tending included licking of the cow's genitalia by the bull and mounting. The total number of tended cows observed during the course of each season was broken down into numbers of lactating and nonlactating cows.

Counts were conducted between July 15 and September 1 each year and included total bison, lactating and nonlactating sexually mature cows (≥ 2 years old), calves, and yearlings. During 1992 and 1993, counts included age estimates for each animal. Age was estimated on the basis of horn angle and size (Fuller 1959; Rutberg 1984), facial hair patterns, and hump size (Rutberg 1984). Between July 15 and September 1 each year, the percentage of the total number of lactating and nonlactating cows seen to be tended by a bull was recorded.

After initiation of rutting activity each year (usually August 1–5), either urine or fresh fecal samples were collected from approximately equal numbers of lactating and nonlactating cows not being tended at the time of collection. Urine samples were collected by packing urine-soaked earth, obtained 5–60 min after witnessed eliminations, into the barrel of plastic 5-cc syringes. Urine samples were later separated from the soil while still in the syringes by means of a clinical centrifuge, then decanted and frozen without preservatives. Urine samples were analyzed for pregnanediol-3-glucuronide (PdG) using an enzyme immunoassay procedure that was previously described (Shideler et al. 1990) and validated for application to bison (Kirkpatrick et al. 1991).

Fecal samples were collected in plastic snap-top containers and placed on ice packs immediately after collection in the field. At the end of the day the samples were frozen until extraction and assay. Fecal samples were extracted using an aqueous buffer containing 0.1% bovine serum albumin and 20% methanol, as described by Shideler et al. (1993). Fecal samples were analyzed for free progesterone (P_4) with an enzyme immunoassay described by Munro and Stabenfeldt (1984). Concentrations of urinary PdG and fecal P_4 were used to determine if cows were in the luteal phase of their estrous cycle and, therefore, whether ovulation had occurred (Kirkpatrick et al. 1991, 1992, 1993). A 2-fold increase in P_4 values, which proved reliable in previous studies with ear-tagged commercial bison (Kirkpatrick et al. 1992; Larter et al. 1993; Komers et al. 1994), was used to signal that ovulation had occurred. The possibility of false negatives, caused by sampling cows that had

Table 1. Calving and yearling rates, 1990–1992.

	MM subpopulation			NR subpopulation		
	1990	1991	1992	1990	1991	1992
Total no. of cows	524	1037	978	55	207	262 ^a
No. of bands ^b	10	26	21	4	6	5
No. of cows with calves	241 (45.9)	422 (40.6)	419 (42.8)	30 (54.5)	118 (57.0)	128 (48.8) ^c
No. of yearlings	—	375 (36.1)	173 (17.6)	—	77 (37.1)	127 (48.4) ^d

Note: Numbers in parentheses are percentages.

^aIncludes 153 live cows plus 109 killed during the previous winter in a controlled hunt outside YNP.

^bNumber of discrete bands in which the total number of cows were observed.

^cIncludes 80 live calves plus 48 fetuses among cows killed the previous winter.

^dIncludes 111 live yearlings plus 16 calves killed the previous winter.

Table 2. Numbers of tended cows that were lactating and nonlactating in 1991 and 1992.

	MM subpopulation		NR subpopulation	
	1991	1992	1991	1992
No. of lactating cows	4 (12.9)	4 (17.3)	1 (1.8)	6 (13.3)
No. of nonlactating cows	27 (87.0)	19 (82.6)	53 (98.1)	39 (86.6)

Note: Numbers in parentheses are percentages.

ovulated, reached the end of their estrous cycle, or were exhibiting low P_4 concentrations, was not ruled out. This opportunity for error was minimized by concentrating sample collections for ovulation detection within a 21-day period following the third day after the onset of rutting activity. Despite these precautions, we present the data as *estimated* ovulation rates.

The approximately equal numbers of samples collected from lactating and nonlactating cows throughout November each year were analyzed for urinary PdG, fecal P_4 , and fecal total estrogens, as described by Kirkpatrick et al. (1992), to determine pregnancy rates. Pregnancy rates in November 1990 and 1991 were with calving rates in the summer of 1991 and 1992, respectively, to estimate fetal loss rates. Calf counts in August 1990 and 1991 were compared with yearling counts in August 1991 and 1992, respectively, to estimate calf loss.

Data collected by the National Park Service from 268 bison killed outside YNP, primarily from the NR herd, were made available for this study. These data included age-specific pregnancy rates and were compared with data collected from bison in the park by non-invasive methods. Differences in calving, tending, ovulation, and pregnancy rates between the two subpopulations and across years were tested for significance by χ^2 tests with Yates' continuity correction. Differences in fetal loss (fall pregnancy rates versus spring calving rates) were tested for significance by paired t tests.

Results

Recovery of ^3H -labeled P_4 from bison fecal samples was 61.8%. The intra- and inter-assay coefficients of variation were 8.9 and 14.7% for the urinary PdG assay, 7.1 and 13.8% for the P_4 assay, and 6.4 and 15.7% for the estrogen assay, respectively.

The numbers and percentages of adult cows with calves in the MM and NR herds for 1990, 1991, and 1992 and the numbers and percentages of yearlings for 1991 and 1992 are shown in Table 1. The percentages of mature cows producing calves in the MM herd for these 3 successive years were 45.9, 40.6, and 42.8%, with a mean of 42.6%. This com-

pared with 54.5, 57.0, and 48.8%, with a mean of 52.6%, for the NR herd for the same 3 years. The difference in calving rates for the two subpopulations for 1990–1992 was significant ($p < 0.001$). Calf loss, based on the previous year's calving rates and the following year's yearling rates, was 38.9% over 2 years among the MM animals and 24.0% for the NR herd. Despite these strong trends, differences in calf loss rates between herds were not statistically significant ($p = 0.511$) because of year-to-year variation.

Within both subpopulations, the proportion of tended cows that were lactating increased between 1991 and 1992 and there was a corresponding decrease in the proportion of tended cows that were not lactating during the same period (Table 2). The 2-year mean for all MM cows observed being tended (85.1%) was not significantly different from the mean for NR cows (92.3%; $p > 0.80$). The difference between tending rates among lactating cows across the two herds was not significant ($p > 0.9$). During August 1992, 21 of 23 (91.3%) cows observed to be tended in the MM herd for which age estimates were available were ≥ 4 years old, compared with 35 of 42 (88.3%) tended NR cows in the same age range.

The total number of sampled adult cows estimated to be ovulating between the onset of the rutting season and September 1 in 1991 and 1992 was 126 for the MM herd and 128 for the NR herd. Differences in estimated ovulation rates between the two herds (65.9% for the NR herd versus 48.8% for the MM herd) were statistically significant ($p < 0.005$) in 1991 but not significant ($p > 0.01$) in 1992 (54.6% for the NR herd versus 46.6% for the MM herd).

During the same 2 years, the ovulation rates among nonlactating animals for 1991 and 1992 were 77.1 and 75.8% in the MM herd and 73.1 and 68.1% among nonlactating cows in the NR herd, respectively. Fewer nonlactating cows ovulated in 1992 than 1991, but more lactating cows in both herds ovulated during the same years, making up the differ-

Table 3. Pregnancy rates in November 1990–1992.

	MM subpopulation			NR subpopulation		
	1990	1991	1992	1990	1991	1992
Total no. of cows tested	85	80	54	83	87	52
No. of pregnancies	32 (37.6)	36 (45)	20 (37)	41 (49.3)	45 (51.7)	28 (53.8)
No. of lactating cows	5 (15.6)	6 (16.6)	6 (30)	6 (14.6)	11 (24.4)	8 (28.5)
No. of nonlactating cows	27 (84.3)	30 (83.3)	14 (70.0)	35 (85.3)	34 (75.5)	20 (71.4)

Note: Numbers in parentheses are percentages.

Table 4. Age-specific calving rates in 1992.

	MM subpopulation	NR subpopulation
Total no. of lactating cows aged ≥ 5 years	115	114
Age of cows with calves		
2 years	0 (0)	0 (0)
3 years	3 (2.6)	2 (1.7)
4 years	11 (9.5)	16 (14.0)
≥ 5 years	101 (87.8)	96 (84.2)

Note: Number in parentheses are percentages.

ence, which is consistent with the corresponding increase in tending rates. The increase in estimated ovulation rate for lactating cows was 4.99% for the NR herd and 1.3% for the MM herd. Significantly more ($p < 0.001$) nonlactating than lactating cows ovulated in both subpopulations during the study. The probability that a lactating cow was more likely to ovulate in the NR population than in the MM population was not significant ($p > 0.1$).

The mean pregnancy rate for MM cows from 1990 to 1992 was 39.8%, with 79.1% of pregnancies among nonlactating animals (Table 3). Among NR cows, the mean pregnancy rate was 51.6% for the same period, with 77.7% of all pregnancies among nonlactating cows. The difference in total pregnancy rates between the two populations from 1990 through 1992 was significant ($p < 0.005$), but the difference in the numbers of pregnancies among nonlactating cows across the two subpopulations was not significant ($p > 0.9$). By comparing the previous year's fall pregnancy rates with the next year's calving rates, estimated fetal loss rates after November were 0 and 2.1% for the MM cows for 1990–1991 and 1991–1992, respectively, and 0 and 2.7% for the same 2 years for the NR cows, with no significant differences ($p > 0.5$) between the two subpopulations.

Within both subpopulations, the percentage of lactating cows that were pregnant increased between 1990 and 1992 (Table 3). In addition, the overall pregnancy rate for both lactating and nonlactating MM cows was 37.6% in 1990, increasing by an additional 7.4% in 1991 but returning to the 1990 rate in 1992, whereas in the NR herd the overall pregnancy rate climbed from 49.3% in 1990 to 51.7% in 1991 and 53.8% in 1992.

Approximately 85% of all calves were born to cows ≥ 5 years old (Table 4). Among MM cows, 70% of all diagnosed pregnancies were among animals ≥ 5 years old, and among the NR cows, 78.4% of all diagnosed pregnancies were among animals ≥ 5 years old (Table 5). There were no

Table 5. Age-specific pregnancy rates in November 1992.

	MM subpopulation	NR subpopulation
Total no. of cows tested	54	52
Total no. of cows pregnant	20 (37)	28 (53.8)
No. of pregnant cows aged:		
2 years	0 (0)	0 (0)
3 years	1 (5)	4 (14.2)
4 years	5 (25)	2 (7.1)
5–7 years	8 (40)	5 (17.8)
≥ 8 years	6 (30)	17 (60.7)

Note: Numbers in parentheses are percentages.

pregnancies among lactating cows that were < 5 years old in either population. Of 109 mature females from the NR herd killed outside YNP during the winter of 1991–1992, 48 (44.0%) were pregnant. Of these 109 females, 84 were of known age and of these, 48 were pregnant (57.1%); of these 48, 33 (80.5%) were cows ≥ 5 years old (Taylor 1992).

There were significant climatic differences between the two subpopulations during these studies (Table 6), with significantly less snowfall recorded at the Northeast Entrance of the park, closest to the NR herd. February and March are the peak months for accumulated snowfall. The 5-year mean temperatures for February and March did not differ significantly between the two study sites, but the 5-year mean snow depths were significantly greater in the Hayden Valley (closest to the MM herd) in both February ($p = 0.002$) and March ($p = 0.012$).

Discussion

Validation of the accuracy of remote detection of ovulation and pregnancy under field conditions is always difficult. In the case of bison, the methods were first validated with both captive commercial and free-roaming animals (Kirkpatrick et al. 1991, 1992, 1993). Nonetheless, in the current study it was encouraging to see the similarity in data between observed tending and calving rates for lactating and nonlactating cows and estimated ovulation and pregnancy rates for the same two groups. Accuracy was further confirmed by the strong similarity between the scarcity of calves among cows ≤ 4 years old, the scarcity of pregnancies among this group, and the correspondingly low pregnancy rates among animals of this age group that were killed and examined out-

Table 6. Mean temperatures and snowfall for Canyon (MM herd) and the Northeast Entrance (NR herd) in February and March 1989–1993.

Weather station	Year	February		March	
		Temp. (°C)	Snowfall (cm)	Temp. (°C)	Snowfall (cm)
Canyon	1989	−5	22.6	2	34.0
	1990	−3	27.0	2	30.0
	1991	2	19.4	1	27.0
	1992	2	20.5	6	24.6
	1993	−3	25.5	4	30.9
5-year mean ± SE		−1.4 ± 1.44	23.0 ± 1.43	3.4 ± 0.87	29.3 ± 1.61
Northeast Entrance	1989	−5	16.9	2	21.7
	1990	−1	17.8	5	20.2
	1991	4	11.8	3	16.7
	1992	4	17.6	8	19.9
	1993 ^a	−1	—	6	—
5-year mean ± SE		0.2 ± 1.71	16.1 ± 1.43	4.8 ± 1.07	19.7 ± 1.07

^aNo snowfall data are available for 1993.

side the park. Taken collectively, observed behaviors and calf counts, estimated ovulation and pregnancy rates, and data from killed animals all provide a consistent picture.

Reproductive success, defined earlier as the number of live calves divided by the number of sexually mature cows, was significantly greater in the smaller NR herd than in the MM herd over the 3 years of this study. While the difference was not statistically significant, the calf loss rate for the MM herd was 14% higher than that of the NR herd. Measuring the reproductive success of free-roaming populations as the number of live calves divided by the number of mature cows over so few years may be overly simplistic: neonatal loss may reduce the number of live calves observed and this in turn may obscure other important physiological mechanisms.

An obvious weakness of the remote pregnancy-testing approach is the inability to measure early pregnancies, at least among bison. Pregnancy determination based on urinary or fecal testing is not reliable until the third month of gestation (Kirkpatrick et al. 1992). Despite this shortcoming of the methodology, comparisons of witnessed tending rates, estimated ovulation rates during the August rutting season, and pregnancy rates later in fall can provide insights into early pregnancy losses.

The ability to measure pregnancy rates among cows in the two subpopulations permitted evaluation of both neonatal loss and fetal loss as a cause of differential calving rates. Firstly, a comparison of fall pregnancy rates with calving rates the following summer indicated that differential neonatal loss rates among calves were not a factor in the differential calving rates in these two YNP subpopulations. Secondly, a comparison of fall pregnancy rates during the winters of 1991–1992 and 1992–1993 with calving rates during the respective following summers supports the contention that fetal loss, after November, was not a significant factor in decreased calving rates among YNP bison.

In spite of the apparent increase in tending, ovulation, and pregnancy rates in lactating cows over the 3 years of the

study, field observations provided circumstantial evidence that relatively few lactating cows were experiencing estrus, which implied that few were ovulating, in contrast to nonlactating cows. Estimated ovulation rates, based on urinary PdG or fecal P₄ levels, confirmed that only a small number of lactating cows were ovulating. This conclusion was further supported by a similarly low fall pregnancy rate among lactating cows. Thus, data derived from remote determination and estimation of ovulation and pregnancy rates permitted construction of a pattern of reproduction based on physiological mechanisms. Overall, lactating bison cows reproduce at significantly lower rates than nonlactating cows; the proximate cause of this failure to reproduce is failure to display estrus and failure to ovulate; neither fetal loss after 3 months' gestation nor neonatal loss has a significant effect upon reproductive outcome for YNP bison.

While the focus of this study was development of a model for noncapture studies of reproduction in free-roaming ungulates in general, the findings are consistent with data from other bison herds living in environments with a harsh climate or suffering from poor nutrition. The survival rate of YNP bison calves is similar to the low survival rates previously reported for bison at YNP (Meagher 1973), Wood Buffalo National Park (Fuller 1962), Wichita Mountains Wildlife Refuge (Halloran 1968), Santa Catalina Island (Lott and Galland 1987), and Slave River, N.W.T., Canada (Van Camp and Calef 1987). In the latter case, calves made up 15% of the herd in May of each year but <2% by the following March. The poor survival rate of YNP calves provides a striking contrast to the high survival rates among bison of Badlands National Park, where the juvenile mortality rate over a 5-year period was <2% (Berger 1992).

The reproductive success of YNP bison is significantly lower than that of commercial bison herds and several free-roaming herds. Only 40–50% of the YNP cows that are ≥2 years old are successful in producing live calves annually, but calving rates for bison cows aged 2–12 years were 78–100% among bison on the National Bison Range, Montana

(McHugh 1958), approximately 75% in Theodore Roosevelt National Park (Roger Andrascik, National Park Service, personal communication), and 80–95% among commercial bison herds (McHugh 1958).

Two primary observations relate to this overall lower success among YNP bison. First, successful reproduction among young cows is delayed compared with other herds, and more than 85% of all calves are born to animals ≥ 5 years old. We found no 2-year-olds producing calves, while Shaw and Carter (1989) reported a 12% calving rate among 2-year-old bison from Wichita Mountains Wildlife Refuge. The latter reported calving rates for bison cows in the age-classes 3–7, 8–13, and 14–18 years, and it was not possible to compare 4- or 5-year-olds with those in YNP. Second, there could be an alternate-year reproductive pattern among YNP cows, with approximately 85% of lactating cows failing to reproduce during a given year. Meagher (1973) suggested a similar pattern of reproduction in YNP, and more recently the same pattern was observed among bison of Badlands National Park (Cunningham and Berger 1990).

We can attribute reproductive failure among the YNP lactating cows to failure of the ovaries to recrudescence in time for the rutting season. Soper (1941), Fuller (1961), and Halloran (1968) interpreted reduced fertility in some bison herds as the expression of a 3-year cycle in which cows calved for 2 successive years, the energy load of pregnancy and lactation progressively delaying the next year's ovulation. By the third year, the accumulated delay impaired successful breeding. Lott and Galland (1985) demonstrated that individual variation in calving rates between cows in the same environment was not consistent with such a simple sequence of events. The present study provides evidence for a unifying concept that includes consideration of age in addition to environmental influences as regulatory factors. The present data suggest that harsh environmental conditions contribute to prolonged lactation and delayed ovulation the following season, but this delay is more severe for younger than for older cows. The differential impact of a harsh environment on fully grown, lactating adult females and on still-developing females that are lactating may have contributed to the differences in reproductive success observed by Lott and Galland (1985).

The present study suggests that at least three variables act to influence the overall reproductive performance of YNP bison herds: environmental conditions, age, and lactational status. Environmental conditions appear to have the most profound and general impact, since, during the study period, the MM herd was less productive than the NR herd. Both herds, however, exhibited positive changes in reproductive performance in at least 1 year during the study, indicating that within each environmental setting or microhabitat, the resident herds are capable of an immediate reproductive response to more favorable conditions (by immediate we mean that it was manifested in the following year's count of live calves per sexually mature female). While it is not clear which conditions (amount of forage enhanced by the clearing effect of the fires, or increases in snowfall reducing access to forage in winter and increasing foraging time) affected the observed changes in reproductive performance, the environmental impact clearly operated at the level of ovarian func-

tion by delaying recrudescence and preventing ovulation. While the fires of 1988 may have provided the nutritional base for the overall increased performance of cows in both herds over the 3-year study period, the increase in the amount of forage was not sufficient to maintain the early positive trend seen in the MM herd. This trend may have been facilitated by reduced snowfall in combination with increased forage from the fires, but the increased snowfall at the end of these studies neutralized or eliminated this facilitative effect, resulting in the negative inflection in the MM herd pregnancy rate.

While comparisons with closely related domesticated, semidomesticated, or intensively managed animals of the same species may provide some useful clues to the physiological mechanisms underlying reproductive success, such observations might obscure the reproductive strategies that have made this species so successful. There are considerable differences between YNP bison, which, except for shooting of NR animals that leave the park in the winter, are relatively unmanaged, and other bison herds, which are intensively managed, with respect to nutrition, climate, genetic manipulation (culling of barren animals), and time of weaning. Ultimate explanations of the small difference in calf production between the two YNP populations must consider the synergistic effects of local (i) nutritional differences, (ii) climatic differences, and (iii) population density. Under natural conditions, without genetic manipulation, supplemental feeding, or regular culling of barren animals, the reproductive performance of the YNP bison may be "normal" or even good, given the climatic conditions under which these animals live.

More broadly, the methods described in this study help address the basic evolutionary concept of fitness, i.e., an animal is either capable or not capable of reproducing in a given environment. The ability to measure reproductive hormone levels allows evaluation of individual fecundity, or the capacity to reproduce, and realized fertility, or the actual number of conceptions. These evaluations can be compared with the number of live births attributable to an individual during its reproductive lifetime. Taken together, these assessments bring us closer to a practical, as opposed to theoretical, means of assessing the fitness of individuals in free-roaming populations and to relevant estimates of future expansion or contraction of their numbers.

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