
Reproductive Synchrony in Brucellosis-Exposed Bison in the Southern Greater Yellowstone Ecosystem and in Noninfected Populations

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Abstract: *Shooting of bison (Bison bison) in the Greater Yellowstone Ecosystem is a highly polarized, emotional issue because native ungulates exposed to brucellosis (Brucella abortus) may infect cattle when they disperse or migrate beyond protected reserves. Both bison and elk (Cervus elaphus) carry brucellosis, a disease that causes abortion in livestock and is often transmitted through contact with expelled fetuses or birth membranes and fluids. If Brucella-infected bison experience a prolonged period of birth, cattle in areas of sympatry will have increased susceptibility to disease. We tested the hypothesis that reproductive synchrony differs between Brucella-free and Brucella-infected bison by contrasting patterns between the Brucella-exposed bison population (in Jackson Hole, Wyoming) within the southern Greater Yellowstone Ecosystem with three non-exposed populations (National Bison Range in Montana, and Wind Cave and Badlands National Parks in South Dakota) that inhabit prairies. Populations averaged 42 births per site per year. Fifty percent of all the births occurred within 1 month, and 95% within 61 days at three sites. It took 89 days for 95% of the births to occur at the noninfected Badlands site. Multiple comparison of regression slopes of the relationship between birth synchrony and the cumulative proportion of total births revealed interpopulation differences ($p < 0.01$), but the brucellosis-exposed population did not exhibit a parturition period different from that of the nondiseased populations. These among-population similarities suggest that reproductive synchrony is not protracted in Brucella-infected bison. Although Brucella transmission from bison to cattle occurs experimentally, captive densities during testing exceeded the mean for the Greater Yellowstone Ecosystem by about 1500 times, and that in 10 noninfected populations by more than 100 times. Although mean density can be misleading as a surrogate for the potential transmission of disease from bison to cattle, bison densities have not approached those reported for disease transmission. Among the ecological factors that may affect the spread of brucellosis from bison to cattle in the southern Yellowstone region, two stand out: (1) access to high-quality food, perhaps because animals in superior physiological condition tend to exhibit tighter reproductive synchrony and (2) incidence of disease in elk. The timing of parturition in bison is neither a simple process nor is it likely to be based on responses to a single variable. A potentially fertile area for future investigation will concern relationships among food, reproductive synchrony, and spatial-temporal components of bison, elk, and cattle distribution.*

Sincrinización Reproductiva de Bisontes Expuestos a Brucelosis en el Ecosistema del Sur del Yellowston Mayor y en Poblaciones no Infeccadas

Resumen: *La caza de Bisontes (Bison bison) en el Ecosistema del Yellowston Mayor es un asunto muy polarizado y emocional debido a que los ungulados nativos expuestos a brucelosis (Brucella abortus) pueden infectar ganado bovino cuando se dispersan o migran más allá de los límites de las reservas protegidas. Tanto los*

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bisontes como los alces (*Cervus elaphus*) portan brucelosis, una enfermedad que ocasiona abortos en el ganado y que es frecuentemente transmitida mediante el contacto con fetos expulsados o con membranas y fluidos de parto. Si los bisontes infectados con *Brucella* experimentan un período de nacimiento prolongado, el ganado en las áreas simpátricas tendrá mayor susceptibilidad a la enfermedad. Evaluamos la hipótesis de que la sincronía reproductiva difiere entre bisontes libres de *Brucella* y bisontes infectados mediante el contraste de patrones entre la población expuesta a *Brucella* (en Jackson Hole, Wyoming) dentro del ecosistema sur del Yellowstone Mayor con tres poblaciones no expuestas y que habitan las praderas (National Bison Range en Montana, Wind Cave y parque nacional Badlands en Dakota del Sur). Las poblaciones promediaron 42 nacimientos/sitio/año. Cincuenta por ciento del total de los nacimientos ocurrieron dentro de un mes y 95% dentro de 61 días en los tres sitios. Tomó 89 Días para que el 95% de los nacimientos ocurriera en el sitio no infectado de Badland. Comparaciones múltiples de pendientes de regresiones (de la relación entre sincronización de nacimientos y la proporción acumulada del total de nacimientos) reveló diferencias inter-poblacionales ($p < 0.01$), pero la población expuesta a brucelosis no exhibió un período de parto diferente al de las poblaciones no expuestas. Estas similitudes entre poblaciones sugieren que la sincronización reproductiva no se prolonga en poblaciones de bisontes infectadas por *Brucella*. Aunque la transmisión de *Brucella* de los bisontes al ganado ocurre a nivel experimental, las densidades cautivas utilizadas durante el tiempo de prueba excedieron la media de las densidades del Ecosistema del Yellowstone Mayor por casi 1500 veces y en 10 de las poblaciones no infectadas por más de 100 veces. Aunque la densidad promedio puede erróneamente conducir hacia una transmisión potencial de la enfermedad de los bisontes hacia el ganado, las densidades de bisontes no se acercan a las reportadas para la transmisión de la enfermedad. Entre los factores ecológicos que podrían afectar la transmisión de brucelosis del bisonte al ganado en la region sur de Yellowstone sobresalen dos: (1) acceso a comida de alta calidad, quizá debido a que los animales en condiciones fisiológicas superiores tienden a exhibir sincronización reproductiva compacta; y (2) incidencia de la enfermedad en alces. El tiempo de partos en bisontes no es un proceso simple, ni está basado en respuestas a una sola variable. Un área potencial de investigación a futuro concierne a las relaciones entre alimento, sincronización reproductiva y componentes espacio-temporales de la distribución de bisontes, alces y ganado.

Introduction

One of the best-known examples of a mammal rescued from extinction is the North American bison (Berger & Cunningham 1994). Populations once numbered in the millions, but at the turn of the century fewer than 1000 individuals remained (Roe 1970). Currently, more than 150,000 bison exist, most in heavily managed reserves or on ranches. Within the contiguous United States, the least-restricted populations are one in the Henry Mountains of Utah (Van Vuren 1983; Van Vuren & Bray 1986) and two in the Greater Yellowstone Ecosystem (GYE)—one in Yellowstone Park itself and the other in Jackson Hole, Wyoming (Thorne et al. 1991; Meagher et al. 1997). Since 1988 almost 3000 bison have been shot as they left Yellowstone National Park and entered Montana. Both bison and elk in the GYE carry brucellosis (*Brucella abortus*), a bacterial disease that can cause abortion in both wildlife and livestock (Davis et al. 1990; Williams et al. 1997). A low but undetermined risk of infecting sympatric cattle exists, and some state officials have sanctioned the removal of all bison outside the park irrespective of disease status. No such policy exists for elk (Dobson & Meagher 1996). Nevertheless, if livestock are infected with brucellosis, a state's "brucellosis-free" status, which affords significant marketing advantages, can be revoked by the U.S. Department of Agriculture, resulting in substantial economic losses (Cheville & McCullough 1998).

Although much is known about the etiology of brucellosis (Crawford & Hildago 1977; Adams 1990), the risk of disease transmission from wild bison to cattle is poorly understood, partly because no cases have been documented (Meyer & Meagher 1995). In addition, there is a paucity of quantitative data concerning the interaction among ecological factors, disease, and the reproductive biology of bison. If sufficient data were available, conservation planning would be enhanced. For instance, where the timing of parturition is predictable, a desirable conservation tactic would be to minimize spatial overlap between bison and cattle during this period, particularly because brucellosis is most readily transmitted through contact with fetal and placental tissue and membranes (Blood et al. 1979). Nevertheless, the minimization of disease risk has been hampered due to a lack of data as rudimentary as the timing of births.

An understanding of factors that affect reproductive synchrony in bison is important for two reasons. First, at a descriptive level, because events associated with parturition and abortion are the major avenues through which disease is transmitted (Meyer & Meagher 1995), knowledge about ecological determinants of gestation and birth is critical. It has direct relevance for identifying periods in which cattle experience heightened susceptibility to disease. Second, from a scientific perspective, if interpopulation variation in the timing of births exists, investigations of the contribution of multiple factors to

such variation should be possible so that spatial and temporal overlap between bison and livestock could be minimized during periods of susceptibility. Although the acquisition of such data represents a critical first step toward solving problems, this process inevitably represents one small component needed for resolution of the brucellosis issue in the GYE. This, among other reasons, is because *Brucella*-infected elk also occur throughout the ecosystem, and their total population size exceeds that of bison by about 40 times (Boyce 1989; Cheville & McCullough 1998). Still, a mandatory first step is the assessment of what occurs in simple, single-species disease systems (like that with bison alone) prior to consideration of the potential interactive effects involving a more complex system with two or more species (Anderson & May 1985).

Reproductive synchrony, the birth of offspring in a short time frame, is a well-known characteristic of both invertebrate and vertebrate taxa (Ims 1990), including gregarious ungulates of tropical savannas and northern boreal and circumpolar environments. This phenomenon involves concentrated birth pulses in social species such as caribou (*Rangifer tarandus*) and wildebeest (*Connochaetes taurinus*; Lent 1966; Estes 1976) but also in asocial ones such as moose (*Alces alces*; Bowyer et al. 1998). Two nonexclusive hypotheses, predator-satiation and plant phenology (Rutberg 1984; Bowyer 1991; Rachlow & Bowyer 1991), have been invoked to explain birth pulses in ungulates. From a conservation perspective, what is relevant is the extent to which reproductive synchrony is affected by disease. If brucellosis prolongs the period in which bison fetal or birth membranes are available for disease transmission, then the time frame during which cattle are susceptible will expand. Alternatively, if brucellosis-infected bison do not experience a prolongation in the timing of births, then it may be more straightforward to devise strategies to reduce disease transmission.

Regrettably, little detailed information has been published on bison demography and life histories (Green & Rothstein 1991; Berger & Cunningham 1994), and virtually nothing exists about reproductive costs (Clutton-Brock et al. 1989) as they relate to disease. Thus, while much is known about how ecological variables such as food quality and population density interact to affect female physiological condition and subsequently rates of pregnancy (Fig. 1), few data are available to reveal the extent to which these factors affect reproductive synchrony. And although an inverse relationship exists between the length of parturition period and food quality (Berger 1992), there is a lack of understanding of how brucellosis affects reproductive synchrony (Fig. 1).

In other female ungulates, individuals not experiencing the energetic demands of gestation, either due to a lack of conception or because of recent abortion, tend to be in better physiological condition; they regularly re-

cycle and give birth earlier than the population mean (Clutton-Brock et al. 1982, 1989; Cameron et al. 1993) or experience estrus at other times when fetuses are lost (Berger 1986). Because abortion or premature birth may alter the timing of reproductive cycles, the period of births should differ between brucellosis-infected and brucellosis-free populations.

Fortunately, assessment of the potential effects of brucellosis on reproductive synchrony is possible in bison because population profiles exist. Data on the timing of estrus or subsequent birthdates of individual females are available from three northern prairie populations in the absence of disease (Berger 1992), and these can be compared with data in the brucellosis-exposed population in Jackson Hole (Wyoming), within the southern GYE. We tested the hypothesis that brucellosis-free and brucellosis-exposed bison differ in the timing of reproductive synchrony. Our appraisals are unlikely to assuage public, agricultural, and scientific concerns about the ecological antecedents of potential disease transmission. Thus, we

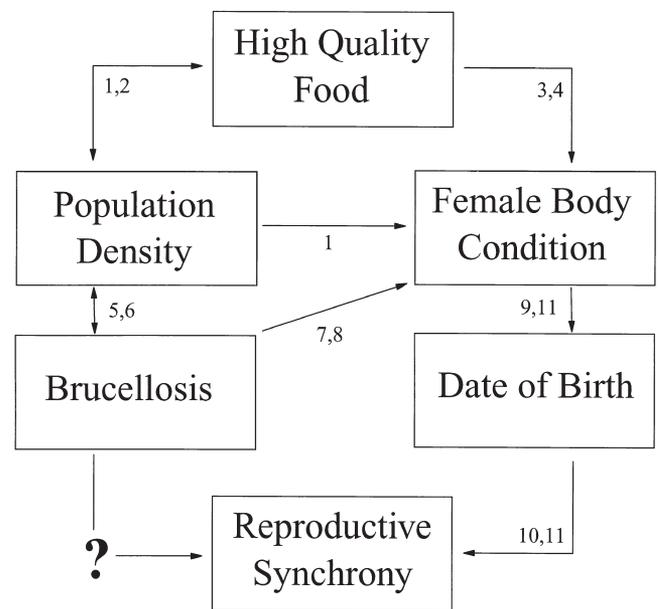


Figure 1. Flow diagram of substantiated relationships among ecological, population, and individual variables and the uncertain role of disease on reproductive synchrony in ungulates. Numbers refer to studies that provide empirical support of the depicted interactions (references 5 and 6 are nonspecific): 1, McCullough (1979) and Clutton-Brock et al. (1982); 2, Sinclair (1977); 3, Albon et al. (1983); 4, Fowler (1987); 5, Anderson and May (1985); 6, May and Anderson (1979); 7, Thorne et al. (1978); 8, Thorne et al. (1979); 9, Guinness et al. (1978); 10, Elias et al. (1991); 11, Berger (1992) and Berger and Cunningham (1994). The question mark designates uncertainty with respect to the effects of brucellosis.

also considered densities of disease-free and disease-exposed bison from 10 noncaptive bison populations to evaluate conditions under which it is known that live-stock contract brucellosis from bison. Finally, we considered how factors other than disease may affect the timing of reproduction.

Study Area and Methods

The Greater Yellowstone Ecosystem contains about 19 million acres and includes Yellowstone National Park, Grand Teton National Park, seven national forests, and three national wildlife refuges. Bison in both national parks have tested seropositive for brucellosis (Meagher 1973; Williams et al. 1993; Meyer & Meagher 1995). Unlike bison from Yellowstone National Park, which either occupy U.S. Park Service land or often are killed upon leaving the park, those in the Jackson population live in a jurisdictionally more complex environment. Lands inhabited by these bison are managed by the U.S. Forest Service, U.S. Fish and Wildlife Service, U.S. National Park Service, and the private sector (Meagher et al. 1997). We focused on bison using portions of Grand Teton National Park, the National Elk Refuge, and the Bridger-Teton National Forest of Wyoming, an area we collectively refer to the southern Greater Yellowstone Ecosystem (sGYE).

Bison in the sGYE population exhibited a high level of seasonal fidelity, using low-elevation summer ranges in Grand Teton National Park and wintering on the National Elk Refuge to the south, where they are fed supplementally along with 7,000–10,000 elk (*Cervus elaphus*) (Boyce 1989; Smith & Robbins 1994). Seasonal ranges had been delineated during a 1987–1990 radio-telemetry study, but during 1991–1992 additional regions also were searched to address the possibility that bison might have colonized new areas (S.L.C., unpublished data). We conducted bison calving surveys over an area comprising about 500 km² during the spring and summer of 1991 and 1992. These were conducted in a Maule M-235 fixed-wing aircraft flown about 170 m above ground level, lasted from 1.0 to 1.5 hours, and extended from mid-April through June. The entire seasonal range of bison was surveyed during each flight, and all bison observed were counted.

A major issue in all field studies is sampling intensity (Caughley 1977), and it requires some explanation. If we failed to detect some births in which calves subsequently died and these births occurred outside the primary parturition season, we would incorrectly conclude that the birth season was shorter than it really was. Unfortunately, there is no way to counter this possibility when dealing with populations of wild bison ranging over areas as large as 500 km² or more, other than to include sampling intervals in which periods of no births

were detected. Clearly, the smaller a study area, the easier it is to detect births.

Fortunately, we were afforded an unusual opportunity to estimate the number of calves potentially missed. First, we made the assumption that calf survival was 100%. This seems reasonable because calf survival in predator-free populations varies from 95% to 99% (Rutberg 1984; Green & Rothstein 1991; Berger & Cunningham 1994). Second, to evaluate the proportion of calves potentially missed during our spring and summer counts, we counted the total number of individual calves occurring at the National Elk Refuge during winter, an area where 95% of the bison during the time of our study concentrated. During spring and summer censuses we counted 24 calves in 1991 and 28 in 1992; in respective winters there were 24 and 31 calves. Hence, we detected a maximum of 52 of 55 (94.5%) that survived. In short, although our sampling scheme was imperfect and some neonates may have been missed, our methods were likely to have been rigorous enough to detect a high proportion of the births.

The data we report on the timing of births are from two sources: the aerial censuses described above for sGYE and detailed studies of the behavioral ecology of brucellosis-free bison at Badlands (Berger & Cunningham 1994) and Wind Cave National Parks (Green & Berger 1990) in South Dakota and the National Bison Range in Montana (Rutberg 1984). Thus, in addition to the sGYE bison, our analyses (Figs. 2–5) include the populations from Badlands National Park (BNP), Wind Cave National Park (WCNP), and the National Bison Range (NBR). We did not use information from Yellowstone National Park because statistical parameters associated

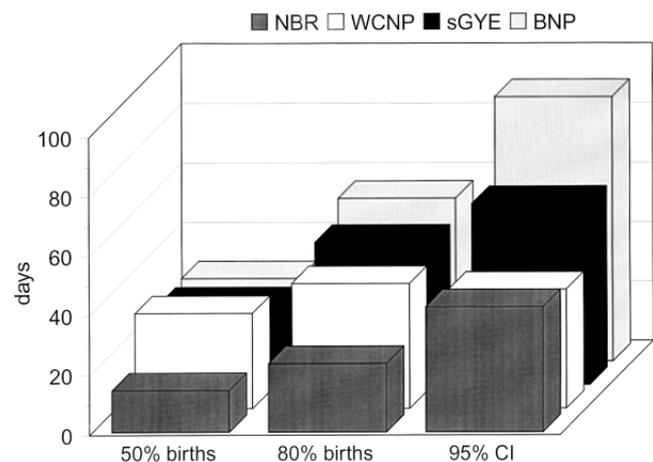


Figure 2. Descriptive summary of number of days since onset of first birth until 50% and 80% occur and 95% confidence intervals (NBR, National Bison Range; WCNP, Wind Cave National Park; sGYE, southern Greater Yellowstone Ecosystem; and BNP, Badlands National Park).

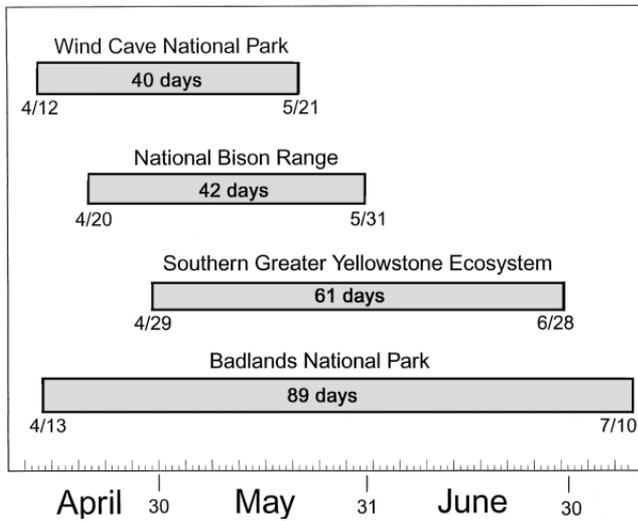


Figure 3. Number of days required to achieve the 95% confidence interval of the parturition period, beginning with the mean date of first birth in brucellosis-free bison populations (Wind Cave, Badlands, National Bison Range) and one brucellosis-exposed bison population (southern Greater Yellowstone Ecosystem).

with the temporal distribution of birthdates began only in 1996 (T. Roffe, personal communication). Our data are based on live births because we did not observe still births or abortions, although both occur in bison.

The presence of *Brucella* antibodies may be detected serologically in live animals, but tests are neither 100% accurate nor do they indicate whether the potential hosts actively carry the disease (Dobson & Meagher 1996). In the sGYE population, 77% of 35 animals harvested between 1989 and 1991 tested seropositive or suspect for *Brucella* antibodies, and 36% (4 of 11) were cultured positive (Williams et al. 1993). Thus, bison in this population were infected with brucellosis at the time of our surveys. The sGYE bison population may have first contracted brucellosis in 1980, the year they first concentrated on supplemental feedlines with brucellosis-infected elk on the National Elk Refuge (Peterson et al. 1991). Our other study populations were brucellosis-free.

Not all data sets on the timing of births used in our analyses are strictly comparable. Those from the National Bison Range are based on only 1 year (Rutberg 1984); data from Wind Cave and Badlands Park are for 3 and 5 years, respectively (Green & Berger 1990; Berger & Cunningham 1994). We used mean values with attendant measures of variation from these latter two populations and the sGYE population. Statistically, it is preferable to contrast multiple, nondiseased populations with more than the single *Brucella*-exposed population, but data of the resolution required (e.g., frequency of births at different periods) are currently unavailable from else-

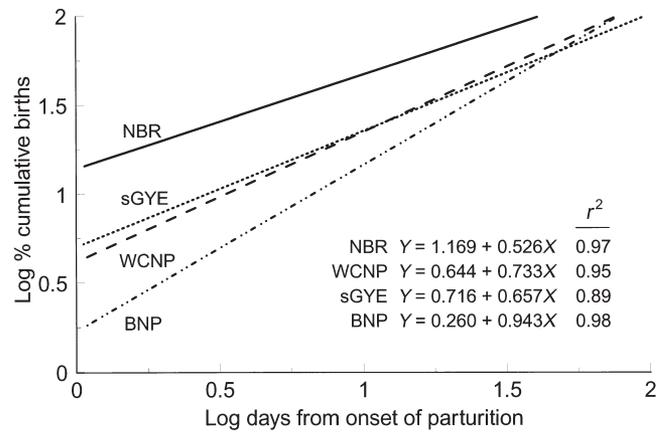


Figure 4. Synchrony of births in four bison populations, and the number of weeks upon which sampling periods were based are as follows: National Bison Range (NBR), 8; southern Greater Yellowstone Ecosystem (sGYE), 10; Wind Cave National Park (WCNP), 12; and Badlands National Park (BNP), 12. Regression equations in the figure are composites of all years per site; individual years are as follows: BNP: 1985, $Y = 0.234 + 0.957X$, $r^2 = 0.98$; 1986, $Y = 0.467 + 0.826X$, $r^2 = 0.97$; 1987, $Y = 0.213 + 0.944X$, $r^2 = 0.98$; 1988, $Y = 1.19 + 1.017X$, $r^2 = 0.94$; 1989, $Y = 0.293 + 0.939X$, $r^2 = 0.97$; sGYE: 1991, $Y = 0.317 + 0.868X$, $r^2 = 0.77$; 1992, $Y = 1.17 + 0.487X$, $r^2 = 0.97$.

where because brucellosis is not an issue in most bison populations (Berger & Cunningham 1994).

We standardized estimates of the birth progression by using the frequency of known births per 7-day interval. Subsequent analyses employed commonly accepted statistical protocols for within- and between-population contrasts (Caughley 1977; Rachlow & Bowyer 1991; Bowyer et al. 1998). These involve regression using log transformations of both x and y variables, which in our case are the number of days that births occurred, beginning with the day of first birth in a given year and the cumulative proportion of births, respectively. To test for homogeneity of multiple slopes, we used analysis of covariance, with the interaction between population and the covariate (x) examined separately (Wilkinson et al. 1992). Power analyses were conducted following procedures described by Cohen (1988). Briefly, these involved the transformation of product-moment correlation coefficients to Fisher's z and subsequently employed critical values of the t distribution.

Information on both crude (overall) and ecological densities (Eisenberg & Seidensticker 1976) were derived for 10 bison populations either by dividing the size of a refuge by the number of animals in a given year or, when available, from previously existing data. Where estimates of population size were available for more than

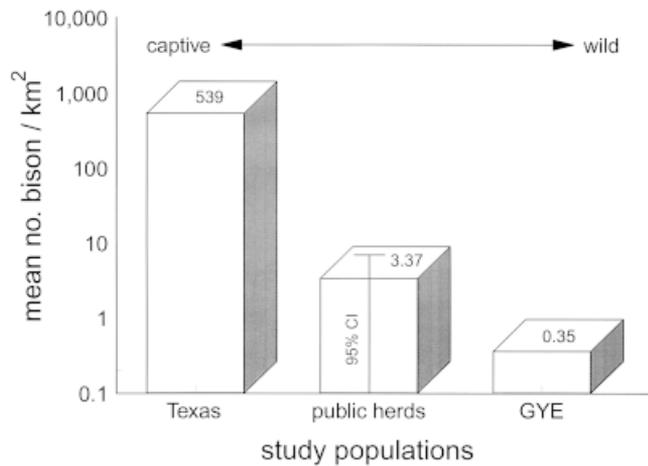


Figure 5. Mean annual densities from bison populations. Sites and sources as follows: Texas captive study (Davis et al. 1990); 10 populations: Wind Cave,* Theodore Roosevelt (North and South Units), Custer State Park,* National Bison Range, Henry Mountains, Yellowstone Park (Greater Yellowstone Coalition, unpublished data); Jackson Hole* (S.L.C., unpublished data); Badlands* (Berger & Cunningham 1994); Wichita Mountains* (Halloran 1968; Shaw & Carter 1989). For the GYE, the populations are Jackson Hole and Yellowstone Park (combined). Ecological densities denoted by asterisk.

1 year, we used the mean. For the sGYE population, we were deliberately conservative, using maximum densities during the time of study.

Results

Reproductive Synchrony

In the sGYE, 50% of the bison births were achieved 1 and 5 days earlier than in the Badlands or Wind Cave populations, respectively (Fig. 2). Births of bison from the National Bison Range were more tightly clumped, reaching 50% about 2 weeks earlier than in the sGYE. Similarly, the period during which 80% of the births (after first onset) occurred at the National Bison Range was 2 weeks shorter than in the other three populations. In the brucellosis-free populations, this 50% point was reached in 42–55 days. The range covered by 95% confidence intervals was from 40 (Wind Cave) to 89 (Badlands) days (Fig. 3). The brucellosis-exposed Jackson population was intermediate (Fig. 3).

Inter-population differences in the onset of parturition also existed. The two prairie populations (Badlands and Wind Cave) averaged about 16–17 days earlier than the sGYE bison (Fig. 3), events that are likely to be delayed because of the higher elevations and delayed plant phenology in Jackson Hole (elevation 2000 m) when com-

pared with the Badlands (<1000 m). Intrapopulation median birth dates did not vary annually at either Badlands (2 May 1985, 8 May 1986, 6 May 1987, 5 May 1988, 2 May 1989 over 5 years; median test $\chi^2 = 1.01$; $df = 4$; NS; Berger & Cunningham 1994) or in the sGYE (23 May 1991, 20 May 1992; $p = 0.561$).

If brucellosis affects the timing of parturition, then the temporal distribution of births should vary between populations with and without the disease, perhaps because infected females may abort or are likely to recycle at other times of the year. Comparisons of the slopes of regression of the onset of parturition and the cumulative proportion of births developed for each population (Fig. 4) substantiate the existence of interpopulation variation ($F_{3, 34} = 8.63$; $p < 0.0001$; one-tailed). Most notable, however, is that the brucellosis-infected bison from the sGYE did not vary from two of the noninfected populations and that the duration of parturition in the infected population was statistically less, not more, than that in the disease-free Badlands animals (Table 1). In other words, the sGYE bison exposed to brucellosis experienced neither longer nor more concentrated birth pulses than two of the three brucellosis-free populations and the sole population (Badlands) that they differed from ($F = 9.63$; $p < 0.006$; Table 1) experienced less reproductively synchrony—opposite the result we predicted.

Although variation among slopes was not detected between southern Greater Yellowstone bison and those from Wind Cave and the National Bison Range (Table 1), perhaps the degree of relationship between the two variables—days of onset of births and cumulative proportion of births—is more strongly associated in one population than another. We examined this possibility by contrasting the correlation between these variables in the two populations that were most different, Badlands and sGYE (Fig. 4), because we suspected that if differences were not evident in these, they would also be absent in comparisons involving the other populations. Because the null hypothesis of no differences cannot be rejected ($z = 1.111$; $0.20 < p < 0.50$), we determined the power of this test by estimating the one-tailed probability of the normal deviate (that is, the proportion of the normal curve that lies beyond the given normal deviate; Cohen 1988), which is 0.802. Power is $1 - 0.802$, or 0.198. Clearly, the degree of relationship involving onset of parturition and cumulative proportion of births,

Table 1. Matrix of population-by-covariate interaction of pair-wise contrasts for homogeneity of slopes (from Fig. 4) showing F ratio and p values (in parentheses).

| Site* | WCNP | NBR | sGYE |
|-------|--------------|---------------|--------------|
| NBR | 8.46 (0.010) | | |
| sGYE | 0.61 (0.445) | 1.68 (0.216) | |
| BNP | 9.11 (0.007) | 44.32 (0.000) | 9.63 (0.006) |

*Refer to Fig. 2 legend for definitions of site abbreviations.

irrespective of disease status, is similar at least in those temperate bison populations in the United States for which data are available.

In Situ and Ex Situ Estimates of Density

To what extent do captive and semi-free or unconfined bison occur at comparable densities? An at least approximate answer to this question is relevant for prudent conservation planning because experimental work substantiates that bison can transmit brucellosis to cattle (Davis et al. 1990). We addressed this issue by compiling data on mean bison densities representing three scenarios: (1) captive conditions in which experimental transmission of brucellosis was documented; (2) 10 free-ranging populations (and the associated 95% confidence intervals), and (3) the Greater Yellowstone Ecosystem (Fig. 5).

In the experimental setting in which brucellosis was transmitted to cattle, densities do not approximate those in wild or semiwild populations. In the former, densities were exceptional, more than 1000–1500 times greater than those that occur under field conditions (Fig. 5). The mean density of 10 bison populations is 3.37 animals/km², still about ten times greater than that of brucellosis-exposed bison in the Greater Yellowstone Ecosystem (both populations combined; Fig. 5).

Discussion

Our analyses fail to support the hypothesis that brucellosis-free and brucellosis-exposed bison differ in the timing of reproductive synchrony. The timing of births in *Brucella*-exposed animals differed in only one of three brucellosis-free populations (Table 1; Fig. 4); and not in the predicted direction. That is, *Brucella*-exposed bison from the sGYE were more, not less, synchronous than the nonexposed Badlands population. These data suggest that brucellosis must have had a relatively minor effect on the progression of births. To what extent might variables other than disease exert a stronger influence on reproductive synchrony?

Two prominent factors that have clear effects on demographic and reproductive dynamics are resource availability and population management, possibilities that are not necessarily unrelated. Where, for instance, the sex or age structure of a population is manipulated or food is restricted, numerous demographic processes are altered, including reproductive synchrony (Caughley 1977; Schwartz & Hundertmark 1993), and these have direct consequences for understanding potential relationships between bison reproduction and brucellosis.

Ecological components of management at the National Bison Range are illustrative of the potential interaction between food availability and the timing of birth. High-quality food is apparently abundant because bison are rotated

among enclosures and subjected to annual culls. If population size is maintained below carrying capacity, fecundity should be relatively high and individuals in good physiological condition, as is the case in organisms affected by density dependence (Franzmann & Schwartz 1985; Fowler 1987). At the National Bison Range, bison have the highest calf-cow ratios known (Rutberg 1984). In contrast, the *Brucella*-free population at Badlands had been unmanaged during 4 consecutive years when the reproductive synchrony data were gathered. The Badlands populations roamed freely in a 250-km² area, but fecundity rates there were lower than those at either of the more managed, *Brucella*-free Wind Cave or National Bison Range sites (Berger & Cunningham 1994). These disparate lines of evidence from populations free of disease suggest that the highly synchronous National Bison Range population (Fig. 4) was not limited by nutrition.

If food affects reproductive synchrony, then individuals in poor body condition should have longer gestation lengths, and populations lacking abundant, high-quality food should be less synchronous. Data on some mammals (Guinness et al. 1978; Bronson 1989) including bison (Berger & Cunningham 1994) support this prediction. Bison in good condition adjusted their gestation lengths an average of 6 days to calve closer to the birth peak, whereas those in poor condition did not (Berger 1992). Whether this was true of the National Bison Range population is not clear. Perhaps the greater compression of births at the National Bison Range relative to other populations (Table 1; Fig. 2) may result not from enhanced nutrition per se but rather because accuracy in sampling is improved because births in smaller areas are more detectable (enclosures there were approximately 9 km²) and animals may have been more habituated. Thus, variation among ecological, nutritional, and sampling conditions makes it difficult to judge why the National Bison Range population appeared more synchronous than others.

What is clear is that the birth period of the *Brucella*-exposed population in the southern Greater Yellowstone population is not substantially different from that of the two more managed, disease-free populations. Because bison from the southern Greater Yellowstone region are supplemented with alfalfa pellets during winter at the National Elk Refuge, females remain in relatively good physiological condition, and they experience rates of increase that are among the highest of any free-ranging bison population (Berger & Cunningham 1994; Grand Teton National Park and National Elk Refuge 1996). So nutrition may have a more profound effect on enhancing reproduction than the debits typically associated with brucellosis. Although abortions have occurred in Yellowstone Park bison since at least 1917 (Meagher 1973; Dobson & Meagher 1996) and they also occur in bison from the sGYE (B. Smith, personal communication), the high rate of growth of the Jackson Hole population is indicative of a population free from disease constraints.

Two factors, one biological and the other statistical, may affect our interpretations of birth synchrony. First, where human predation results in skewed adult sex ratios (favoring females over males), the parturition season may be extended because only a portion of the females conceive on first estrus (Ginsberg & Milner-Gulland 1994); the others may recycle and thus give birth later (Schwartz & Hundertmark 1993; Schwartz et al. 1994). Also, once sex ratios are highly skewed, younger or less fertile males may breed, resulting in lower or delayed conception rates (Noyes et al. 1996). Neither of these scenarios, however, is applicable to the four bison populations we sampled (Fig. 3). At the respective study areas, sex ratios were not dissimilar to that reported for unharvested polygynous ungulates (Ralls et al. 1980; Clutton-Brock et al. 1982; Berger 1986), and young males mated infrequently (see Lott 1979; Berger & Cunningham 1994). Thus, demographic parameters associated with human harvest and their coincident effects on reproduction (Ginsberg & Milner-Gulland 1994) do not seem to have been crucial in mediating bison reproductive synchrony at our sites. Second, the concordance between the number of calves enumerated in the spring and during the subsequent winter suggests that few were missed and that mortality was low.

Nevertheless, field investigations of live animals involving demographic, reproductive, and disease parameters rarely achieve perfection, and our results indicate little about the frequency of abortions. In fact, irrespective of disease status, few data exist on the proportion of pregnant females giving birth, and it remains unknown when females who have prematurely terminated pregnancies return to estrus. Without such comparative data it will never be possible to gauge disease-related effects on reproductive failure, but our results on reproductive synchrony are capable of offering conservation insights because they identify windows of opportunity in which cattle may be exposed to the birth membranes or fluids of bison.

Although both bison and elk pose undetermined levels of brucellosis threat, they have not produced obvious catastrophic effects on agriculture at a system-wide scale (Keiter & Froelicher 1993). Four outbreaks of brucellosis in cattle herds have occurred in northwestern Wyoming; three were attributed to elk and one to either elk or bison because a cattle source could not be identified (U.S. Department of Agriculture 1997). To eliminate risk, it would be ideal if bison could be rendered disease free. Currently, however, there is no technology available to accomplish this without decimating herds (Cheville & McCullough 1998). And because both sGYE bison and elk have been sympatric with cattle during calving seasons for about 30 and 100 years, respectively (Wilbrecht & Robbins 1979), without proving to be a significant source of brucellosis in cattle, a continued scientific focus on minimizing the risk of disease transmission appears warranted.

The ecological relationship between population density and disease transmission is not necessarily straightforward, although models and empirical study demonstrate that frequency-dependent transmission often occurs (Anderson & May 1985). Nevertheless, our measures of mean density may obscure locally clumped distributions or ecological and behavioral separation between bison and cattle, factors that may disproportionately affect the possibility of transmission. But in the absence of more exacting data, particularly the temporal partitioning of density, recognition of the use and limitations of density estimates helps to highlight rather than obscure issues involving disease transmission. Such estimates are also critically important to evaluating the extent to which the ex situ transmission of brucellosis from bison to cattle parallels that which occurs under in situ conditions.

How the risk of brucellosis transmission from bison to cattle in situ is affected by local population density in the wild is uncertain. The extreme densities (539 individuals/km²) of bison and cattle in which interspecies transfer of disease has been documented experimentally (Davis et al. 1990) probably never occur in the wild (Fig. 5), although additional examination of this issue is necessary.

Prudent conservation planning requires minimizing the risks of disease transmission. Our results indicate that bison and cattle in the sGYE should be separated during periods of potential abortion (e.g., late gestation, which corresponds to late winter), as is already done (Grand Teton National Park and National Elk Refuge 1996), and during May and June when 95% of bison births occur (Fig. 3). In most instances, avoidance of overlap during the calving period could easily be accomplished by delaying until 1 July the period during which cattle and native ungulates co-inhabit public lands. Such a preemptive tactic also would avoid overlap with elk during their parturition period (Smith & Robbins 1994).

In sum, although interpopulation variation in birth synchrony occurs, the evidence suggests that *Brucella*-exposed bison failed to deviate from two nondiseased populations. In contrast, disease-free Badlands bison experienced lower fecundity and a longer period of births. Our comparative data from four populations, coupled with literature on wild and domestic mammals (Fig. 1), suggest that food may play a greater role in the timing of bison reproduction than does brucellosis exposure alone. Thus, one side-effect of human manipulations of this system (e.g., food provisioning of bison and elk during winter on the National Elk Refuge) is that bison may be less likely to abort fetuses or transfer brucellosis to domestic stock than in areas where infected populations are in poorer physiological condition. Whether this prediction is true requires further study. What is clear is that rigorous investigation of this idea will yield critical ecological and reproductive data to facilitate conservation planning in the Greater Yellowstone Ecosystem.

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