

Timing of parturition events in Yellowstone bison *Bison bison*: implications for bison conservation and brucellosis transmission risk to cattle

Jennifer D. Jones, John J. Treanor, Rick L. Wallen & Patrick J. White

Yellowstone bison *Bison bison* are chronically infected with brucellosis (caused by the bacterium *Brucella abortus*), which raises concerns about possible transmission to cattle when they migrate to winter ranges outside the Yellowstone National Park. We monitored bison from April to mid-June during 2004-2007 to estimate the timing and location of parturition events that may shed tissues infected by *B. abortus*. Observed abortions (N = 29) occurred from January through 19 May, while peak calving (80% of births) occurred from 25 April to 26 May, and calving was finished by 5 June. Observed parturition events (N = 115) occurred in the Park and on the Horse Butte peninsula in Montana, USA, where cattle were not present at any time of the year. Allowing bison to occupy public lands outside the Park where cattle are never present (e.g. Horse Butte peninsula) until most bison calving is completed (late May or early June) is not expected to significantly increase the risk of brucellosis transmission from bison to cattle because: 1) bison parturition is essentially completed weeks before cattle occupy nearby ranges, 2) female bison meticulously consume birthing tissues, 3) ultraviolet light and heat degrade *B. abortus* on tissues, vegetation and soil, 4) scavengers remove fetuses and remaining birth tissues and 5) management maintains separation between bison and cattle on nearby ranges. Allowing bison to occupy public lands outside the Park through their calving season will help conserve bison migratory behaviour and reduce stress on pregnant females and their newborn calves, while still minimizing the risk of brucellosis transmission to cattle.

Key words: birth, bison, brucellosis, cattle, disease, transmission, Yellowstone

Jennifer D. Jones, John J. Treanor, Rick L. Wallen & Patrick J. White, National Park Service, Yellowstone National Park, P.O. Box 168, Mammoth, Wyoming 82190, USA - e-mail addresses: jjones60@uwyo.edu (Jennifer D. Jones); john_treanor@nps.gov (John J. Treanor); rick_wallen@nps.gov (Rick L. Wallen); pj-white@nps.gov (Patrick J. White)

Corresponding author: John J. Treanor

Received 21 September 2009, accepted 29 March 2010

Associate Editor: Marc Cattet

The increase of Yellowstone bison *Bison bison* from 23 animals in 1901 to 5,000 animals in 2005 is a prominent example of conservation success (Plumb et al. 2009). However, 40-60% of Yellowstone bison have been exposed to the bacterium *Brucella abortus* (Treanor et al. 2007), which was likely transmitted from European cattle before 1917 (Mohler 1917). Yellowstone bison exhibit seasonal migrations along altitudinal gradients with some bison moving from higher-elevation summer ranges inside Yellowstone National Park to lower-elevations in and

outside the northern and western boundaries of the Park during winter and spring (Meagher 1989, Bruggeman et al. 2009). Bison migration outside the Park into Montana, USA, has led to an enduring series of conflicts among various public and management entities regarding the transmission risk of *B. abortus* from bison to cattle.

Brucellosis infection in cattle results in direct economic loss for ranchers (e.g. slaughter of cattle) and indirect economic loss for Montana's cattle industry due to additional testing requirements and

transport restrictions (i.e. trade) to other states (Godfroid 2002). Management agencies have attempted to conserve the migration of Yellowstone bison to lower-elevation winter ranges in Montana, while maintaining separation from cattle (U.S. Department of the Interior (USDI) & U.S. Department of Agriculture (USDA) 2000, Plumb et al. 2009). To prevent the movement of bison outside established conservation zones in Montana, management agencies attempt to haze bison back into Yellowstone National Park by 1 May along the north boundary and 15 May along the western boundary using helicopters, all-terrain vehicles, snowmobiles and horses (USDI et al. 2008).

Hazing operations occur 2-4 weeks before bison and other ungulates typically begin to migrate to higher-elevation summer ranges in the Park (Frank & McNaughton 1992, Gates et al. 2005, White et al. 2007). These forced movements place additional stress on bison that are undernourished at the end of winter and vulnerable newborn calves; especially when conditions are not yet suitable on Park summer ranges due to deep snow persistently delaying vegetation green-up. The emergence of spring vegetation in the Park coincides with the receding snowpack, which can vary annually by a few weeks (Thein et al. 2009, Watson et al. 2009). Bison migration from summer range to winter range is positively related to snow build-up on the summer range, while return migration from lower elevation winter ranges aligns with temporal and spatial patterns of plant phenology (Bjornlie & Garrott 2001, Bruggeman et al. 2006). Management agencies may be able to conserve the migratory behaviour of Yellowstone bison and reduce hazing stress by extending bison access to low elevation ranges outside the Park for a few additional weeks. During years when green-up is delayed, grazing opportunities outside the Park will allow bison to begin replenishing body reserves and produce high quality milk for newborn survival, while probably having little effect on the risk of brucellosis transmission to cattle.

Brucellosis is a reproductive disease in bison and transmission concerns to cattle involve the shedding of *B. abortus* infected birth tissues onto the landscape where livestock can contact the bacteria. A symptom of *Brucella* infection is the induction of late-term abortions (Williams et al. 1997) with the highly infectious fetus serving as an important source of transmission (Thorne 2001). Additionally, the placental tissues and birth fluids associated with

newborn calves can be infectious, making live births a potentially important transmission source (Cheville et al. 1998, Rhyan et al. 2009). The timing and location of bison parturition events, defined here to include reproductive failures (e.g. abortions) and live births, directly affect the risk of brucellosis transmission to cattle. The purpose of our study is to identify the timing and location of bison parturition events and integrate these data with existing information on *B. abortus* persistence in the environment, to help management agencies conserve bison migratory behaviour and reduce hazing stress while minimizing the risk of brucellosis transmission from bison to cattle.

Material and methods

Yellowstone National Park encompasses 8,987 km² in northwestern Wyoming, USA (44°38' N, 110°51' W), and adjacent parts of Montana and Idaho (Fig. 1), with elevations between 1,500 and 2,600 m a.s.l. We monitored 121 radio-collared adult female bison and non-collared adult females within the same social groups through calving seasons from April to mid-June during 2004-2007. Visual cues (i.e. belly size, distended udders, swollen vulva, contractions, behaviour demonstrating discomfort and tissues or fluids exuding from the vulva) were used to record pregnancy status and schedule return observations to identify parturition locations and dates. Opportunistic observations and employee and visitor reports of parturition events were also investigated within and outside the calving period.

We divided observed parturition events into three categories: 1) reproductive failures, 2) live births and 3) radio-collared females with newborn calves. Observed reproductive failures included abortions (fetal stage), stillborn calves (near term) and females that died from complications during the birthing process. Retained placentas were used as an indicator of a reproductive failure if a calf was not observed with the female or as a live birth if a newborn calf was present. Parturition events were recorded as live births if the birth was directly observed or if the newborn calf, still wet from birth fluids, was observed being cleaned by the birthing female. The locations of the observed parturition events and dates of occurrence were recorded. Birth dates of radio-collared bison that were not directly observed were estimated based on previous observations of the pregnant female (i.e. female was

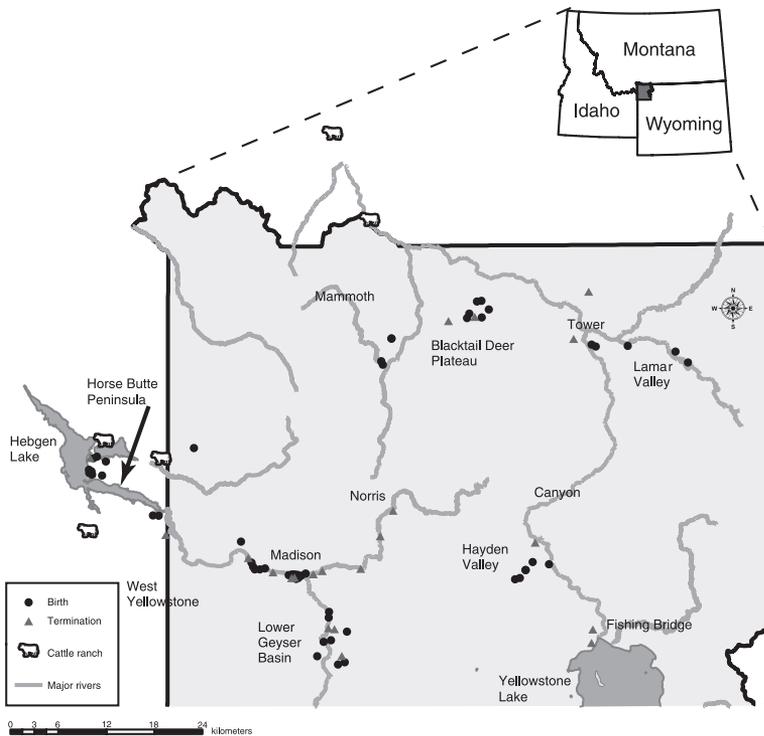


Figure 1. Locations of observed reproductive failures (terminations) and live bison births in the Yellowstone National Park and nearby areas of southwestern Montana during 2004-2007 in relation to cattle operations during winter and spring.

pregnant within four days of being observed with a calf).

Results

We observed 115 bison parturition events including 54 live births (49 direct observations and five placenta retentions with a calf present), 29 reproductive failures (13 stillborn calves, 11 placenta retentions with no calves present and five deaths of females during parturition) and 32 radio-collared females with newborn calves. Parturition events were primarily concentrated inside the Park but 12 events occurred outside the western boundary on the Horse Butte peninsula in Montana (see Fig. 1). Reproductive failures occurred primarily from Jan-

uary through April with 76% of observations occurring by the end of April and the latest reproductive failure observed on 19 May (Table 1). The earliest newborn calf was seen in late March or early April each year and the last observed birth typically occurred in late May or early June. Approximately 50% of births occurred by 6 May (\approx 40-day period), 80% by 16 May (\approx 50-day period) and 95% by 27 May (\approx 61-day period). Of the calvings, 80% occurred during the 32 days from 25 April to 26 May (Fig. 2).

Discussion

The observed parturition events were concentrated in April and May and occurred primarily within the

Table 1. Chronology of observed reproductive failures (e.g. abortions and still births), live births and radio-collared bison observed with a calf in Yellowstone National Park and nearby areas of southwestern Montana during 2004-2007.

Parturition event	January	February	March	April		May		June	Event, total
				(1-15)	(16-30)	(1-15)	(16-31)		
Reproductive failure	1	3	2	7	9	6	1	0	29
Live birth	0	0	1	2	13	30	7	1	54
Radio-collared bison observed with a calf	0	0	0	0	8	14	10	0	32
Total	1	3	3	9	30	50	18	1	115

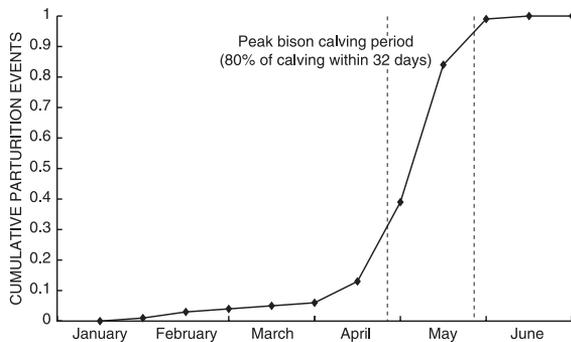


Figure 2. Cumulative proportion of observed bison parturition events (live births and reproductive failures) in Yellowstone National Park and the nearby areas of southwestern Montana during 2004-2007.

Yellowstone National Park. Parturition events outside the Park were located on public land (i.e. Horse Butte peninsula) where cattle are not present at any time of the year. Reproductive failures were observed from January to mid-May, covering the third trimester of pregnancy when *B. abortus*-induced abortions typically occur. Our observations of bison live births were highly synchronous with 50% of births occurring in 15 days and 80% of cumulative births occurring in 32 days. These observations are in agreement with previous findings of high calving synchrony in Yellowstone bison with > 50% of births occurring within 13-27 days and > 80% of cumulative births occurring within 23-60 days (Gogan et al. 2005). The phenomenon of reproductive synchrony, where birthing occurs in a short time frame or pulse, has been documented in a number of ungulates, including wildebeest *Connochaetes taurinus* (Estes 1976), roe deer *Capreolus capreolus* (Gaillard et al. 1993), moose *Alces alces* (Bowyer et al. 1998), caribou *Rangifer tarandus* (Adams & Dale 1998) and bison (McHugh 1958, Meagher 1973, Berger & Cain 1999). The synchrony of bison parturition events might be useful for managing bison near the boundaries of Yellowstone National Park. Brucellosis transmission from bison to cattle requires infectious birth products (e.g. birth fluids, tissues and aborted fetuses) to be shed onto the landscape where cattle can contact them. Thus, the relative risk of transmission is the product of the number of cattle in the exposure area, the number of infectious parturition events that occur in the exposure area and the persistence of bacteria shed by infectious events (Kilpatrick et al. 2009).

If bison and cattle do not share the same lands (i.e. exposure area) at any time, then the possibilities for

brucellosis transmission are limited. Allowing bison to occupy public lands on the Horse Butte peninsula until most calving is completed (i.e. late May or early June) is not expected to increase transmission potential because cattle are not present at any time of year and agency management prevents bison from accessing nearby cattle summer ranges. The number of cattle near the Horse Butte peninsula is low during winter and spring with no cattle in the management zone west of the Park (Kilpatrick et al. 2009, White et al. 2009). During mid-June and July, about 1,800 cattle are released onto public and private lands north and west of Yellowstone National Park (White et al. 2009) and the agencies have successfully maintained spatial and temporal separation between bison and cattle. During this period, maintaining successful separation benefits from the tendency of bison to follow the progressive green-up of grasses back into the Park interior as snow melts at higher elevations (Gates et al. 2005). The few bison that do remain on boundary ranges outside the Park are hazed back into the Park or lethally removed (USDI et al. 2008).

During our study, observed parturition events occurred weeks before the arrival of cattle on the summer ranges and did not occur in areas occupied by cattle year-round, or later used by cattle during summer. All observed reproductive failures, indicating the potential for highly infectious aborted pregnancies, occurred 2-6 weeks before cattle were released onto ranges near the Park's western boundary. Although newborn bison calves have been observed in Yellowstone in late summer, live births late in the summer are rare (Taper et al. 2000, Gates et al. 2005) and generally occur when bison have returned to the Park. These observations indicate that the main reproductive events (i.e. abortions and live births), which present the highest potential for brucellosis transmission, do not overlap with cattle occupancy at a large spatial scale. To date, there have not been any documented cases of brucellosis transmission from bison to cattle, and this success may be related to the absence of cattle on bison winter and spring ranges, the timing of parturition events prior to cattle arrival on nearby ranges and active prevention of bison co-mingling with cattle.

Brucella has the capacity to survive and persist in the environment under suitable conditions (Corbel 1989) and prevention of brucellosis transmission from bison to cattle should consider *B. abortus* persistence in the environment even if bison and cattle are spatially separated. Studies indicate that

B. abortus persistence decreases rapidly with increased ultraviolet exposure, heat and dry conditions (Cook et al. 2004). In Laramie, Wyoming, USA, Cook et al. (2002) found that *B. abortus* survived on the protected underside of a fetus for an average of 60.5 days in February, but only 2.8-4.7 days in May and June. Similarly, Aune et al. (2007) found that *B. abortus* survived on fetal tissue placed near Yellowstone National Park for a maximum of 77 days in February and 24 days in mid-May. These studies suggest that *B. abortus* persistence during summer near the western boundary of Yellowstone National Park is probably limited to a few weeks and allowing bison to occupy public land on the Horse Butte peninsula, where cattle are never present, is not expected to increase the potential for brucellosis transmission.

Infected birth tissues will most likely be removed from the environment long before *Brucella* bacteria die due to the cleaning behaviour of bison (Meagher 1973, Jones et al. 2009) and high scavenging rates of birth tissues and bacterial degradation (Cook et al. 2004, Aune et al. 2007, Maichak et al. 2009). During our study, observed bison birth sites covered small areas (e.g. 3 × 3 m) and female bison meticulously cleaned birth sites by consuming all birth tissues, eating the vegetation and licking the soil (Jones et al. 2009). This behaviour reduces the quantity of viable bacteria and transmission potential, because cattle, not being present at bison birth sites, would not have the opportunity to contact infectious tissues later. However, the 16 observations of retained placentas underscore the need to prevent bison from occupying lands used by cattle. Infectious tissues and fluids are not confined to parturition sites. Following parturition, discharges of vaginal exudates and placental retention can allow a *postpartum* bison female to contaminate a larger spatial area. The continued success of preventing brucellosis transmission from bison to cattle will require agency management to maintain separation of bison and cattle.

Scavengers also limit how long *B. abortus* will persist in tissues shed onto the landscape. The greater Yellowstone ecosystem has a diverse scavenger guild including bears *Ursus americanus* and *U. arctos*, coyotes *Canis latrans*, eagles *Aquila chrysaetos* and *Haliaeetus leucocephalus*, red foxes *Vulpes vulpes*, ground squirrels *Spermophilus armatus* and *S. lateralis*, magpies *Pica hudsonia*, ravens *Corvus corax* and wolves *Canis lupus*. These scavengers quickly and reliably remove fetuses and

birthing material from the landscape that may be infected with *B. abortus*, and their protection on feed grounds in Wyoming has been suggested as a means to reduce brucellosis transmissions in elk (Maichak et al. 2009). Two studies specific to the greater Yellowstone area examined the length of time a fetus would remain on the landscape before being scavenged. Cook et al. (2004) observed 16 different scavengers consuming 100% (N = 89) of bovine fetuses in an average of 26.8 hours from the National Elk Refuge in Wyoming, 40.7 hours from the state-operated elk feed grounds in Wyoming and 57.5 hours from Grand Teton National Park. Aune et al. (2007) found that bovine fetuses were scavenged and disappeared in an average of 7.5 days inside the Yellowstone National Park and 13.0 days outside the Park during 2001. They also reported that fetuses placed outside the northern and western boundaries of the Park on average disappeared in 18.2 days (range: 1-78; SD = 20.1) during 2002 and 2003. Month had no effect on the length of time for fetus disappearance. Thus, we concur with Aune et al. (2007:11) that "natural environmental conditions leading to bacterial degradation and animal scavenging, conspire to kill *Brucella* and remove potentially infected fetal tissue from the environment by 15 June."

Yellowstone bison that migrate beyond the Park's boundaries, present a challenge to management agencies that are attempting to conserve bison migratory behaviour while preventing brucellosis transmission to cattle near the Park boundaries. We propose that allowing bison to remain on specified public lands outside the Park where cattle are never present (e.g. Horse Butte peninsula) until late-May or early June, when most calving is completed and bison typically begin migrating back onto Park summer ranges, is unlikely to significantly increase the risk of brucellosis transmission to cattle. Brucellosis transmission from bison to cattle has not occurred and may be due to the cumulative effects of management to maintain separation between cattle and bison, synchrony of bison parturition events (i.e. parturition concentrated in a short period with abortion cycle earlier than the live birth cycle), bison parturition locations (i.e. spatial separation from cattle summer ranges), bison behaviour (i.e. thorough cleaning of birth sites), environmental degradation of *Brucella* (i.e. short persistence period in late spring weather conditions) and scavenger removal of potentially infectious birth tissues.

In the Greater Yellowstone Area, bison and elk are infected with *B. abortus* and there can be no guarantee that cattle near the boundaries of Yellowstone will not be exposed. Allowing bison to occupy public lands outside the Park for an additional few weeks will help conserve bison migratory behaviour and reduce stress on pregnant females and their newborn calves, but this will require active management to minimize the brucellosis transmission risk to cattle. Bison that do not move back into the Park following the calving season in early June should be hazed back inside. At this time, bison should be easier to move and more likely to remain within Yellowstone than in the preceding weeks due to receding snow and vegetation green-up at increasingly higher elevations. Yellowstone bison represent the last wild and free-ranging bison population and their ecological, genetic and cultural value to facilitate long-term conservation for the species cannot be overstated. We encourage management agencies to consider the information presented here to balance Yellowstone bison conservation with acceptable risk of brucellosis transmission.

Acknowledgements - our research was funded by the National Park Service. We thank Doug Blanton, Carrie Byron, Chris Geremia, Scott Laursen, Jeremiah Smith, Thomas Thein and Mary Kay Woodin for dedicated field work. We also thank the Ahrweiler family, Kurt and Beth Engstrom, Bonnie Gaffney, Craig Whitman, agents from the Montana Department of Livestock and various rangers in Yellowstone National Park for birth site information. Glenn Plumb provided helpful comments on an earlier version of this communication. The views and opinions in this article are those of the authors and should not be construed to represent any views, determinations or policies of the National Park Service.

References

Adams, L.G. & Dale, B.W. 1998: Timing and synchrony of parturition in Alaskan caribou. - *Journal of Mammalogy* 79: 287-294.

Aune, K., Rhyan, J., Corso, B. & Roffe, T. 2007: Environmental persistence of *Brucella* organisms in natural environments of the greater Yellowstone area - a preliminary analysis. - *United States Animal Health Association* 110: 205-212.

Berger, J. & Cain, S.L. 1999: Reproductive synchrony in brucellosis-exposed bison in the southern greater Yellowstone ecosystem and in noninfected populations. - *Conservation Biology* 13: 357-366.

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

Bowyer, R.T., Van Ballenberghe, V. & Kie, J.G. 1998: Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. - *Journal of Mammalogy* 79: 1332-1344.

Bruggeman, J.E., Garrott, R.A., Bjornlie, D.D., White, P.J., Watson, F.G.R. & Borkowski, J.J. 2006: Temporal variability in winter travel patterns of Yellowstone bison: the effects of road grooming. - *Ecological Applications* 16: 1539-1554.

Bruggeman, J.E., White, P.J., Garrott, R.A. & Watson, F.G.R. 2009: Partial migration in central Yellowstone bison. - In: Garrott, R.A., White, P.J. & Watson, F.G.R. (Eds.); *The Ecology of Large Mammals in Central Yellowstone*. Elsevier, San Diego, California, USA, pp. 217-235.

Cheville, N.F., McCullough, D.R. & Paulson, L.R. 1998: Brucellosis in the greater Yellowstone area. - *National Academy of Sciences, Washington D.C., USA*, 186 pp.

Cook, W.E., Mills, K.W., Williams, E.S., Bardsley, K.D. & Boerger-Fields, A. 2002: Survival of *Brucella abortus* strain RB51 on fetuses in the Wyoming environment. - *Progress Report UW#5-34204*, University of Wyoming, Laramie, Wyoming, USA, 19 pp.

Cook, W.E., Williams, E.S. & Dubay, S.A. 2004: Disappearance of bovine fetuses in northwestern Wyoming. - *Wildlife Society Bulletin* 32: 254-259.

Corbel, M.J. 1989: Microbiology of the genus *Brucella*. - In: Young, E.J. & Corbel, M.J. (Eds.); *Brucellosis: Clinical and Laboratory Aspects*. CRC Press, Boca Rotan, Florida, USA, 187 pp.

Estes, R.D. 1976: The significance of breeding synchrony in the wildebeest. - *East African Wildlife Journal* 14: 135-152.

Frank, D. & McNaughton, S. 1992: The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. - *Ecology* 73: 2043-2058.

Gaillard, J.-M., Delorme, D., Jullien, J.M. & Tatin, D. 1993: Timing and synchrony of births in roe deer. - *Journal of Mammalogy* 74: 738-744.

Gates, C., Stelfox, B., Muhly, T., Chowns, T. & Hudson, R. 2005: The ecology of bison movements and distribution in and beyond Yellowstone National Park. - *University of Calgary, Calgary, Alberta, Canada*, 313 pp. Available at: <http://www.nps.gov/yell/naturescience/gatesbison.htm>

Godfroid, J. 2002: Brucellosis in wildlife. - *Revue Scientifique et Technique Office International des Epizooties* 21: 277-286.

Gogan, P.J.P., Podruzny, K.M., Olexa, E.M., Pac, H.I. & Frey, K.L. 2005: Yellowstone bison fetal development and phenology of parturition. - *Journal of Wildlife Management* 69: 1716-1730.

Jones, J.D., Treanor, J.J. & Wallen, R.L. 2009: Parturition

- in Yellowstone bison. - National Park Service, Yellowstone National Park, Wyoming, USA, 15 pp. Available at: <http://www.greateryellowstonescience.org/topics/biological/mammals/bison/projects/popdynamics>
- Kilpatrick, A.M., Gillin, C.M. & Daszak, P. 2009: Wildlife-livestock conflict: the risk of pathogen transmission from bison to cattle outside Yellowstone National Park. - *Journal of Applied Ecology* 46: 476-485.
- Maichak, E.J., Scurlock, B.M., Rogerson, J.D., Meadows, L.L., Barbknecht, A.E., Edwards, W.H. & Cross, P.C. 2009: Effects of management, behavior, and scavenging on risk of brucellosis transmission in elk of western Wyoming. - *Journal of Wildlife Diseases* 45: 398-410.
- McHugh, T. 1958. Social behavior of the American Buffalo (*Bison bison*). - *Zoologica* 43: 1-40.
- Meagher, M. 1973: The bison of Yellowstone National Park. - National Park Service, Scientific Monograph Series 1: 1-161.
- Meagher, M. 1989: Range expansion by bison of Yellowstone National Park. - *Journal of Mammalogy* 70: 670-675.
- Mohler, J.R. 1917: Report of the Chief of the Bureau of Animal Industry, Pathologic Division. - Annual Reports of the Department of Agriculture, Washington, D.C., USA, 106 pp.
- Plumb, G.E., White, P.J., Coughenour, M.B. & Wallen, R.L. 2009: Carrying capacity, migration, and dispersal in Yellowstone bison. - *Biological Conservation* 142: 2377-2387.
- Rhyan, J.C., Aune, K., Roffe, T., Ewalt, D., Hennager, S., Gidlewski, T., Olsen, S. & Clarke, R. 2009: Pathogenesis and epidemiology of brucellosis in Yellowstone: serologic and culture results from adult females and their progeny. - *Journal of Wildlife Diseases* 45: 729-739.
- Taper, M.L., Meagher, M. & Jerde, C.L. 2000: The phenology of space: spatial aspects of bison density dependence in Yellowstone National Park. - U.S. Geological Survey, Biological Resources Division, Bozeman, Montana, USA, 263 pp.
- Thein, T.R., Watson, F.G.R., Cornish, S.S., Anderson, T.N., Newman, W.B. & Lockwood, R.E. 2009: Vegetation dynamics of Yellowstone's grazing system. - In: Garrott, R.A., White, P.J. & Watson, F.G.R. (Eds.); *The Ecology of Large Mammals in Central Yellowstone*. Elsevier, San Diego, California, USA, pp. 113-133.
- Thorne, E.T. 2001: Brucellosis. - In: Williams, E.S. & Baker, I.K. (Eds.); *Infectious Diseases of Wild Mammals*. Iowa State University Press, Ames, Iowa, USA, pp. 372-375.
- Treanor, J.J., Wallen, R.L., Maehr, D.S. & Crowley, P.H. 2007: Brucellosis in Yellowstone bison: implications for conservation management. - *Yellowstone Science* 15: 20-24.
- U.S. Department of the Interior, National Park Service and U.S. Department of Agriculture, Forest Service, Animal and Plant Health Inspection Service 2000: Record of decision for final environmental impact statement and bison management plan for the State of Montana and Yellowstone National Park. - Washington, D.C., USA, 869 pp.
- U.S. Department of the Interior, National Park Service and U.S. Department of Agriculture, Forest Service, Animal and Plant Health Inspection Service, and the State of Montana, Department of Fish, Wildlife, and Parks, Department of Livestock 2008: Adaptive adjustments to the interagency bison management plan. - Yellowstone National Park, Mammoth, Wyoming, USA, 8 pp. Available at: <http://ibmp.info/Library/2008%20IBMP%20Adaptive%20Management%20Plan.pdf>
- Watson, F.G.R., Anderson, T.N., Newman, W.B., Cornish, S.S. & Thein, T.R. 2009: Modeling spatial snow pack dynamics. - In: Garrott, R.A., White, P.J. & Watson, F.G.R. (Eds.); *The Ecology of Large Mammals in Central Yellowstone*. Elsevier, San Diego, California, USA, pp. 85-112.
- White, P.J., Cunningham, J., Frey, B., Lemke, T., Stoeffler, L. & Zaluski, M. 2009: Annual Report, Interagency Bison Management Plan, July 1, 2008 to June 30, 2009. - National Park Service, Yellowstone National Park, Mammoth Hot Springs, Wyoming, USA, 36 pp.
- White, P.J., Davis, T.L., Barnowe-Meyer, K.K., Crabtree, R.L. & Garrott, R.A. 2007: Partial migration and philopatry of Yellowstone pronghorn. - *Biological Conservation* 135: 518-526.
- Williams, E.S., Cain, S.L. & Davis, D.S. 1997: Brucellosis: the disease in bison. - In: Thorne, E.T., Boyce, M.S., Nicoletti, P. & Kreeger, T.J. (Eds.); *Brucellosis, Bison, Elk, and Cattle in the Greater Yellowstone Area: defining the problem, exploring solutions*. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA, pp. 7-19.