On the Origin of Brucellosis in Bison of Yellowstone National Park: A Review

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Abstract: *Brucellosis caused by* Brucella abortus *occurs in the free-ranging bison (*Bison bison*) of Yellowstone and Wood Buffalo National Parks and in elk (*Cervus elaphus*) of the Greater Yellowstone Area. As a result of nationwide bovine brucellosis eradication programs, states and provinces proximate to the national parks are considered free of bovine brucellosis. Thus, increased attention has been focused on the wildlife within these areas as potential reservoirs for transmission to cattle. Because the national parks are mandated as natural areas, the question has been raised as to whether* Brucella abortus *is endogenous or exogenous to bison, particularly for Yellowstone National Park. We synthesized diverse lines of inquiry, including the evolutionary history of both bison and* Brucella, *wild animals as* Brucella *hosts, biochemical and genetic information, behavioral characteristics of host and organism, and area history to develop an evaluation of the question for the National Park Service. All lines of inquiry indicated that the organism was introduced to North America with cattle, and that the introduction into the Yellowstone bison probably was directly from cattle shortly before 1917. Fistulous withers of horses was a less likely possibility. Elk on winter feedgrounds south of Yellowstone National Park apparently acquired the disease directly from cattle. Bison presently using Grand Teton National Park probably acquired brucellosis from feedground elk.*

Paper submitted September 1, 1993; revised manuscript accepted April 5, 1994.

Sobre el origen de la brucelosis en el bisonte del Parque Nacional Yellowstone: Una revisión

Resumen: *La brucelosis causada por* Brucella abortus *afecta al bisonte (*Bison bison*) de los Parques Nacionales Yellowstone y "Wood Buffalo" y al alce (*Cervus elaphus*) de la Gran Area del Yellowstone. Como resultado de programas de erradicación de la brucelosis a lo largo de toda la Nación, los estados y provincias próximos a los parques nacionales son considerados como libres de brucelosis bovina. Como concecuencia de esto, se ha prestado más atención a la vida silvestre dentro de estas áreas como posibles reservorios para la transmisión de brucelosis al ganado. Dado que los parques nacionales son asignados por mandatos como áreas naturales, ha surgido el interés en determinar si* Brucella abortus *es endógena o exógena al bisonte, en particular en lo que respecta al Parque Nacional Yellowstone. Nosotros sintetizamos varias líneas de investigación, que incluyen la historia evolutiva tanto del bisonte como de* Brucella, *el estudio de animales salvajes como portadores de* Brucella, *la información bioquímica y genética, las características de comportamiento del portador y del organismo, y la historia del área a los efectos de desarrollar una evaluación del problema para el Servicio de Parques Nacionales. Todas las líneas de investigación indicaron que el organismo fue introducido en América del Norte con el ganado, y que la transmisión al bisonte americano ocurrió directamente a partir del ganado poco despues de 1917. La transmisión a partir de cruzeras fistulosas de caballos fue una posibilidad menos probable. Los alces que habitan las áreas de pastoreo invernales al sur del Parque Nacional Yellowstone aparentemente adquirieron la enfermedad directamente del ganado. Los bisontes que usan en la actualidad el Parque Nacional "Grand Teton" probablemente adquirireron la brucelosis a partir de alces de las áreas de pastoreo.*

Conservation Biology, Pages 645–653
Volume 8, No. 3, September 1994

Introduction

Brucellosis is primarily a reproductive disease caused by bacteria of the genus *Brucella*. It occurs mainly in domestic animals world-wide and secondarily as undulant fever in humans (Young & Corbel 1989; Nielsen & Duncan 1990). Abortion by females is considered the hallmark of the disease, but host-organism relationships demonstrate great variation on this basic theme. Transmission is mainly a function of abortions; other herd members ingest the organism with contaminated feed or by licking aborted tissues. Serology is commonly used to detect exposure, but culture of the organism provides the only definitive diagnosis. In cattle the correlation between serology and culture may be as high as 95% (Manthei & Deyoe 1970).

Numerous serological surveys of bison (*Bison bison*) and elk (*Cervus elaphus*) of the Greater Yellowstone Area show widespread exposure to brucellosis caused by the bacterium *Brucella abortus*. (Thorne et al. 1991). The bacteria have been cultured from members of both species. According to serological standards for cattle, the prevalence of brucellosis in the Yellowstone bison has been approximately 40%, but correlation with culture results was approximately 25% (Meyer & Meagher 1995). According to these data the true prevalence would be closer to 10%. Effects on the bison population appear to be minimal (Meagher 1973*a*; Meyer & Meagher 1994).

During the last decade, as a nationwide effort progressed to eradicate the disease from livestock, controversy increased and lawsuits developed over the question of possible transmission of infection from wildlife to cattle and the management measures necessary to prevent this. Attention has focused particularly on the Yellowstone bison as the presumptive source for the *Brucella* organism in other wildlife throughout the area. Brucellosis also occurs in the free-ranging bison of Wood Buffalo National Park (WBNP), Canada, where a complex of disease and bison subspeciation concerns resulted in a recommendation for depopulation of bison (Federal Environmental Assessment Panel 1990). Similar, less formal proposals have been made for the Yellowstone bison during the past 30 years (Meagher 1973*b*).

Brucellosis was first identified serologically in bison in the YNP population in 1917 (Mohler 1917). Because later investigators suggested that brucellosis might have existed in these bison for a long time and appeared to have little population effect (Rush 1932*b*; Tunnicliff & Marsh 1935; Meagher 1973*a*, 1973*b*; Meyer 1992; Meyer & Meagher 1995), the National Park Service questioned the origin of the *Brucella* organism as a native or exotic entity. Reynolds et al. (1982) suggested that brucellosis was present in North American wildlife prior to the arrival of modern man. The question of exotic versus endogenous origins persists because of diverse public opinions about proposed removals of wildlife to protect livestock.

Yellowstone National Park (YNP) is managed as a natural area to the maximum extent allowed by accommodation of human recreational use. Ecological processes generally are allowed to function as they would without the presence of modern man. Native biota are protected; exotic species would be eradicated where technologically and ecologically feasible.

The question of origin cannot be answered directly, but the general consensus of experts on brucellosis is the *B. abortus* was introduced by cattle. Cooperative interagency management planning efforts now underway for the Yellowstone bison, with attendant preparation of an Environmental Impact Statement and public review, generated a need for an evaluation of the origin question for the National Park Service. To do this we synthesized diverse lines of inquiry about the origin of brucellosis in North American bison in general and in Yellowstone bison in particular. We also examined the possible origin of brucellosis in several other North American wildlife hosts.

Origin in North America

An Evolutionary Perspective on Bison

Because cattle are the preferential host of *B. abortus* (Meyer 1964*a*) and because cattle and bison are Bovidae and relatively closely related (McDonald 1981), we reviewed the evolution of North American bison. Bison and cattle apparently diverged from a common ancestor in Asia in the late Pliocene Age (McDonald 1981), some 2 million years ago. Bison evolution remains controversial (Meagher 1986). *B. priscus*, the so-called steppe bison, may have reached North America after the middle Pleistocene Age and may be ancestral to the modern North American bison. Alternatively, Wilson (1988) proposed that a post-glacial influx about 10,000 years ago might have led to the modern form. A later influx would seem more likely to have facilitated the mutual arrival of host and organism with a relationship that persisted to the present but resembled Old World bovid host-organism relationships.

A consensus does not exist at present for modern bison subspeciation. Because of gradation in size and form, modern bison were dated arbitrarily by McDonald (1981) to 5000 years ago. Two subspecies commonly were recognized (Reynolds et al. 1982; Meagher 1986). Genetically the two appeared to be very closely related. Ying and Peden (1977) could not distinguish chromosomal differences. Peden and Kraay (1979) argued that the subspecific distinction perhaps was not valid; they found that blood types and carbonic anhydrase polymorphisms were similar. Geist and Karsten (1977) described phenotypic differences, and Van Zyll de Jong

(1986) endorsed the subspecific designations using morphometric analyses. More recently, Geist (1991) concluded that phenotypic differences were widely distributed historically and appeared to reflect a major environmental component, and that available information no longer warranted subspecific designations. Recent mtDNA analyses suggested geographic isolation only (Bork et al. 1990). Strobeck (1991, 1992, 1993) determined that genetically distinct subspecies were not supported. The foregoing suggests a very recent divergence. Accordingly, associated disease organisms likely would have been found throughout the distribution of modern bison if those organisms arrived when bison colonized North America.

An Evolutionary Perspective on *Brucella*

Compared with vertebrates, organisms such as *Brucella* provide scant evidence of their possible origin in time. Bovine brucellosis was "known in ancient times" (Stableforth 1959:53); presumably, the term ancient refers to Biblical or other early written accounts. Pavolovskii et al. (1987:25) stated that "We consider brucellae an independent taxonomic group of pathogenic microorganisms—the constituents of specific biocenoses, which existed long before wild animals were exploited by man." Others (discussed by Pavolovskii et al. 1987) proposed a Mediterranean origin during early domestication of sheep and goats.

Taxonomic affinities within the genus *Brucella* and with other microorganisms may provide insight. Meyer (1990*a*, 1990*b*) presented an evolutionary model for *Brucella* with *B. abortus* biovar 2 as ancestral to the presently extant species and possibly as ancestral to all other species and biovars. Prior to 1966 three classical species were recognized (*B. abortus*, *B. melitensis*, *B. suis*); subsequently, three new species were added to the genus (*B. neotomae*, *B. canis*, *B. ovis*). These latter species appeared to be of recent origin, perhaps in the last 50 years. Meyer (1990*a*, 1990*b*) observed that this was a genetically labile organism; most changes among species biovars could be explained by one-step sequential mutations. She reviewed recent DNA work and concluded that, by all available molecular genetic techniques at the genome level, all *Brucella* appeared to be very closely related. Hoyer and McCullough (1968), Verger et al. 1985, and Ficht et al. (1991) agree that all *Brucella* share more than 90% homology in DNA sequences. Current technological methods for identifying evolutionary relationships indicate that the genus *Brucella* is unrelated to other pathogens but is closely related to the agrobacterium-rhizobium complex and perhaps shared a common ancestor (De Ley et al. 1987). Given the generation time of microorganisms, divergence might have occurred more recently than for vertebrates.

Meyer (1964*a*, 1981) evaluated the species identity of 550 strains of *Brucella* by the combined use of conventional determinative bacteriological methods, bacteriophage typing, oxidative metabolic patterns, and correlations with data on host and tissue of origin. All forms of *B. abortus* obtained worldwide could be grouped into the currently recognized biovars regardless of host or geographic loci, including the strain obtained from Yellowstone bison by Tunnicliff and Marsh (1935). Each of the recognized species of Brucella have a decided host preference, and the organisms are not readily transmitted to a dissimilar host. Tessaro (1987) found no differences in *B. abortus* taken from bison of WBNP and cattle. Assuming *B. abortus* biovar 2 is the progenitor, with cattle as the preferential host, it seems probable that strains of *B. abortus* with different characteristics would have evolved if there had been a long association with bison.

The foregoing lines of evidence (evolutionary model, new forms, mutability, close genetic relationship, possible common ancestry with plant pathogens) suggest a relatively recent origin for the organism. Otherwise, we would expect more distinct forms with additional preferential hosts. The spectrum of the host-organism relationships indicated that this is mainly an organism of aggregation. Cattle were first domesticated about 8000 years ago in Greece and western Asia (Clutton-Brock 1989). With bovine brucellosis *B. abortus* biovar 2 as the apparent progenitor of the other forms (directly or indirectly), *Brucella* appeared to be of more recent origin than are bison and to have arisen in a geographic locale at a time that precluded long association with North American bison.

Wild Animals as Hosts

Wildlife appear to be widely exposed to members of the genus *Brucella*, including North America (Moore & Schnurrenberger 1981; McCorquodale & DiGiacomo 1985; Tessaro 1986; Davis 1990). But with the demonstrated preferential host relationships of the various *Brucella* species, most are considered end hosts. This does not exclude wild animal hosts from a potential transmission role in some instances, nor does this preclude the enzootic presence of *Brucella* in some wildlife populations. Rementsova (1987) surveyed more than 18,000 wild animals from five orders of mammals and a variety of nonmammals. Seventy *Brucella* cultures were obtained and compared with 768 serological reactors. Rementsova focused primarily on ticks and rodents as reservoirs of infection in domestic animals and humans. Infected wild animals appeared to be mostly associated with foci of infection in domestic animals, although hares (*Lepus* sp.) in some areas of Europe maintained *B. suis* independently. Meyer (1964*a*) identified this as *B. suis* biovar 2. While infectious for swine, the geographic distribution of this biovar reflects that of hares rather than swine (Meyer 1990*a*, 1990*b*).

Meyer (1976) discussed the subject of rodents as a natural reservoir. With the exception of *B. neotomae*, she found all supposedly unique rodent strains worldwide to be similar to existing strains of *B. suis*. She concluded that *Brucella* were transmitted to rodents from other animals, especially livestock, and not vice versa, and *Brucella* were not native to rodents. While the desert woodrat (*Neotoma lepida*) of the Great Salt Lake area, Utah, is enzootically infected with *B. neotomae* (Stoenner & Lackman 1957), this rodent does not serve as a source of infection for other animals. This species of *Brucella* has not been found to cause either experimental or natural infections in any other animal.

Caribou (*Rangifer tarandus*) and reindeer (semidomestic caribou) are preferential hosts for *B. suis* biovar 4 (Meyer 1964*b*, 1965). Because the identical organism was found to be circumpolar, Reynolds et al. (1982) suggested that it was native to caribou. Given the close relationship of all forms of *Brucella* and the mutability of the organism, however, it seemed all but impossible that identical biovars might have evolved simultaneously and independently on both sides of the Bering Sea. Meyer (1965) was able to trace the introduction of *B. suis* biovar 4 to Alaska with reindeer imported from Siberia early in the twentieth century. Except for the woodrat mentioned previously, no other instances of wildlife serving as a preferential host have been demonstrated in North America. (Insofar as feral swine in the United States serve as a preferential host for *B. suis* biovars 1 and 3, the origin for these organisms is domesticated swine.)

Population densities and natural or induced aggregations of a host species would facilitate transmission of many infectious organisms. Serologic surveys for *Brucella* antibodies have shown seroreactors among many ungulate species worldwide (Davis 1990), some of which are highly gregarious. In North America, both cattle and bison are gregarious; size of aggregations vary with husbandry practices (cattle) or habitat (wild bison). Historical accounts indicate that free-ranging bison congregated in large numbers on the Great Plains of North America (see Roe 1970; Dary 1974). But in order to forage adequately, large aggregations would have developed nomadic behavior. Bison are almost constantly on the move, with shifting and melding of groups (Van Vuren 1979, 1983; Lott & Minta 1983; Rutberg 1984; Meagher & Wallace 1993). In contrast, cattle are much more sedentary (Van Vuren 1981).

Although there are many other behavioral and ecological differences between the two animal species, the presumptive role of bison as a host and reservoir for bovine brucellosis has been extrapolated entirely from the host-organism relationship as it is understood for cattle. This appeared to have happened because of the relatively close taxonomic relationship between the two bovids and because most bison now are maintained as fenced herds and consequently are classified as livestock (Tessaro 1989). Recent work suggests, however, that the host-organism relationship in bison differs markedly from that of cattle, that abortions are relatively rare, and that bison do not function as a preferential host and a reservoir for transmission, particularly in the wild (Meyer 1992; Meyer & Meagher 1995).

Domestication likely ensured that more animals remained in relatively close contact for longer periods of time and in more restrictive loci than occurs among naturally gregarious wild ancestors. There seems little reason to doubt the influence of man in domesticating livestock and thereby ensuring that most brucellosis foci would be called anthropogenic. *Brucella* appear primarily to be organisms of animal husbandry that have adapted to and exist secondarily in some wildlife hosts.

Historical Perspective

Historical and ethnological accounts provide a final area of inquiry into the origin of *B. abortus* in North America. The scholarly and popular literature is vast, but Roe (1970) was exhaustive in his examination of available source material. Apparently, nowhere did he find accounts that suggest the presence of brucellosis in wild bison prior to near-extermination (prior to about 1900). The many popular accounts (see McHugh 1972; Dary 1974) likewise make no such mention. Careful review of the establishment of the earliest domesticated herds founded by capturing wild calves and of the exchange of animals among these founding herds turned up no evidence (Coder 1975). Archeological and ethnological literature (see Speth 1983) indicated quantities of bison butchered and the use of all body parts. Given the consumption of raw organ meat by both Native Americans and newcomers, documented by Ewers (1958:13), it appears impossible that bison could have been infected with brucellosis without transmitting it to humans. This would have undoubtedly appeared in the literature, as would anecdotal if not historical documentation of the disease in bison in the form of abortion. In contrast, northern native peoples are well aware that the caribou are the source of their illness, as are people of Middle East populations who acquire *B. melitensis* from goats and sheep (Mediterranean Fever Commission 1905; Meyer 1964*b*). Contrary to recurring and understandable assumptions (see Flores 1991), brucellosis apparently did not exist in wild bison prior to the near-extermination of them in the last century, nor was it introduced to the free-ranging herds from cattle.

Origin in Yellowstone National Park

Introduced Bison

Bison calves captured from wild herds commonly were mothered by domestic bovine cows, and semidomestic bison and cattle were often pastured together (Haley 1936). Bison were brought to YNP in 1902 from two semidomestic herds (Meagher 1973*a*). Of these, the 18 pregnant cow bison from the Pablo-Allard herd of Montana would appear to offer the most likely source. But this captive herd was free of brucellosis when purchased by the Canadian government in 1907 (Bison Disease Task Force 1988:4). Their descendants apparently acquired brucellosis later, probably at Buffalo National Park, Wainwright, Alberta, and introduced the disease to WBNP in the 1920s (Tessaro 1987). Three Goodnight bison bulls were shipped to YNP, but the history of the ranch (Haley 1936) does not suggest the presence of brucellosis. Also, for anatomical reasons, infected bovine bulls used for natural breeding apparently are a negligible agent in the transmission of the disease (Manthei & Deyoe 1970). Comparable bovid anatomy suggests the same would be true for bison bulls. Thus, bison introduced into YNP do not appear to be a possible source of brucellosis.

Horses

While horses with fistulous withers may have been a source of brucellosis for cattle (White & Swett 1935; Fitch & Dodge 1939), transmission of the disease by them is considered a rare event (Nicoletti 1980). Prior to 1917, however, with the advent of mechanized transportation for tourists, large numbers of horses were used in the Park (Haines 1977). For example, 800 were pastured at times at just one location (Houston 1982). After automobiles were permitted, horses continued to be used for some purposes, including the Buffalo Ranch and ranger patrol, where they are still used. Because bison are observed to dominate horses, mingling between the two would have been rare. Accordingly, horses would have posed a minimal risk for transmission of infection to wild bison. Thus, the captive herd maintained at the Buffalo Ranch after 1907 appeared to be the only Park bison that might have had sufficient proximity to and association with horses to be exposed to an infective Brucella dose.

Cattle

The history of cattle in the YNP area begin about the time bison were extirpated outside the Park. The beginnings of small ranches near the Park were established by the late 1860s (Haines 1977); bison calves were raised on some of these (Garretson 1938), but there was no indication that any of these bison became part of the Park population (Meagher 1973*a*; Coder 1975). Cattle were also maintained at various times and places within the park. Five illegal small cattle ranches existed from 1882 to 1884 in the northern part of the park (A. L. Haines, letter to M. Meagher, May 30, 1990). Cattle were pastured for milk and beef production, especially during the short tourist season, roughly mid-June to late August. Most of this occurred prior to 1915 and the general admission of automobiles (Haines 1977). Dairy herds for hotel supply were maintained on several extensive meadows, Fountain Flats on the Firehole, Hayden Valley near Canyon, and Swan Lake Flats near headquarters in the north. Beef cattle were pastured and slaughtered at the south edge of Swan Lake Flats (Haines 1977). Some milk cows often were maintained at outposts and tourist developments for the use of both employees and for small commercial purposes. With the exception of the Buffalo Ranch, none of these enterprises appeared to offer much potential as a source of brucellosis in the bison.

Timing, distance, geography, decline of native bison numbers, and behavioral differences made transmission of brucellosis highly unlikely from most of the cattle kept in the Park. Bison had disappeared from the northern winter range in the 1880s and from Firehole-Hayden Valley by 1900 (Meagher 1973*a*). The remnant wild bison in the remote Pelican area would have had no contact with any of the cattle because of seasonal migrations and winter range-use patterns (Meagher 1973*a*). Bison dominate cattle; while they displace them from food sources (Van Vuren 1981) they would not mix socially, further ensuring separation. Once effectively protected from poaching around 1900, the remaining wild bison increased steadily from the official low of 23 to more than 50 by 1913 (Meagher 1973*a*), arguing against acquisition of a reproductive disease.

The ability of the *Brucella* organism to survive outside the host in numbers sufficient for infection also precluded most cattle sources. *Brucella* do not form spores but may persist in the environment for variable periods of time (Crawford et al. 1990). They are readily killed by heat, sun, and dryness. Continuous freezing temperatures could ensure viability of the organism for a period of years, but seasonal fluctuations of temperature would preclude longevity. The presence of bison at the Buffalo Ranch for 10 years prior to occurrence of abortion in 1917 appeared to obviate infection from the environment.

The introduced herd was maintained in an enclosure at headquarters from 1902 to 1907. Undoubtedly, some milk cows were kept in the general area. While mechanical transfer of infected material by coyotes or other scavengers may have been possible, it would seem unlikely, particularly considering the numbers of organisms sufficient for infection. The four calves captured from the wild population between 1903 and 1909 (Meagher 1973*a*) were mothered by domestic cows (Holte 1910); only the calf captured in 1904 was female. In the fenced herd it appeared highly improbable that 13 years would elapse before detection of brucellosis in 1917.

The Buffalo Ranch

The Buffalo Ranch was established in 1907 on the northern range 60 kilometers east of headquarters. A few milk cows were kept there until about 1919 (Rush 1932*a*, 1932*b*). The vague term "buffalo range" appeared in Rush (1932*a*), but he specifically identified the "Buffalo ranch" in Rush (1932*b*:108).

This bison herd history provided an additional insight into disease presence. Army records maintained at YNP indicated that bison were viewed as accountable property, so good records were kept. Disease with attendant mortality (such as hemorrhagic septicemia) received particular attention, but abortions were not mentioned. This suggested that few if any were observed, although the herd was maintained in a fenced pasture and closely monitored until about 1915. Calf numbers recorded for the introduced herd from 1903 through 1917 did not indicate a reproductive problem. Low numbers in 1907 may have been related to a two-day trail drive to the Buffalo Ranch. There was no suggestion of a spate of abortions comparable to those recorded for cattle (up to 90% of susceptible pregnant bovine cows; Roberts 1956), although the bison would have been immunologically naive compared to present herds (Meyer 1992).

After about 1915 the bison were pastured loosely in the valley near the ranch. This would have made contact with infections material from cattle or horses more likely and would appear to coincide with the 1917 date for observing two abortions (Mohler 1917). A herd size of 200–300 animals appears to be necessary for *B. abortus* to become enzootic in bison (Dobson 1993); the Buffalo Ranch herd numbered 193 in 1914 (Meagher 1973*a*).

Elk

Some northern-range Yellowstone elk undoubtedly wintered on the Buffalo Ranch feedground with the introduced bison, where they probably acquired brucellosis as a result of mingling (Rush 1932*a*, 1932*b*). They might have been exposed to the same source that infected the bison, but it is more likely that bison on the feedground were the source. It appeared probable, however, that elk on the National Elk Refuge in Jackson Hole south of YNP acquired the organism independently of Yellowstone bison or elk and directly from cattle after ranches were established on elk winter range. The resulting depredations of hay by hungry elk led to establishment of winter feedgrounds by 1909; elk and cattle probably mingled prior to that date. Jackson Hole elk were tested serologically and showed brucellosis exposure by 1930 (Thorne et al. 1978). In 1930 some of the elk of the National Elk Refuge summered in the southern part of YNP, as they do now (Cole 1969; Boyce 1989), but the likelihood of contact with bison and exposure to infective numbers of the organism would have been remote. Bison had not been reestablished yet in the Firehole-Hayden Valley areas of YNP. The Pelican bison numbered less than 100 from 1900 to about 1930 and would have moved northeastward in spring (Meagher 1973*a*). Elk concentrate naturally during winter in suitable mountain valleys of the area; resident cattle and feedgrounds would have increased the likelihood of transmission of organisms from cattle to elk and from elk to elk (Thorne et al. 1991). In turn, bison of the Grand Teton National Park probably acquired brucellosis from elk of the National Elk Refuge on the feedgrounds after 1978 (Williams et al. 1993).

Conclusions

We conclude that *B. abortus* was introduced to North America with cattle. The timing and source of introduction of brucellosis into YNP bison are not entirely clear. It probably occurred in the first decade of operation of the Buffalo Ranch shortly before 1917. The most likely source was cows maintained for Park employees. Horses with fistulous withers present a less likely source. Infected domestic bovine cows nursing captured wild bison calves appear to be a remote source. Northern Yellowstone elk probably acquired brucellosis from the bison, but National Elk Refuge elk probably acquired the disease directly from cattle.

Acknowledgments

We thank T. Carter, D. Houston, and J. Shaw for their comments on an early draft. Thanks to T. Thorne for many conversations. L. G. Adams recommended the initial contact between us that led to a rewarding collaboration on several publications. A. L. Haines has been unfailingly generous with his unpublished historic files. P. Dratch and an anonymous reviewer improved the final manuscript with their careful reviews.

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