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WOLF–BISON INTERACTIONS IN YELLOWSTONE NATIONAL PARK

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We studied interactions of reintroduced wolves (*Canis lupus*) with bison (*Bison bison*) in Yellowstone National Park. Only 2 of 41 wolves in this study had been exposed to bison before their translocation. Wolves were more successful killing elk (*Cervus elaphus*) than bison, and elk were more abundant than bison, so elk were the primary prey of wolves. Except for a lone emaciated bison calf killed by 8 1-year-old wolves 21 days after their release, the 1st documented kill occurred 25 months after wolves were released. Fourteen bison kills were documented from April 1995 through March 1999. All kills were made in late winter when bison were vulnerable because of poor condition or of bison that were injured or young. Wolves learned to kill bison and killed more bison where elk were absent or scarce. We predict that wolves that have learned to kill bison will kill them more regularly, at least in spring. The results of this study indicate how adaptable wolves are at killing prey species new to them.

Key words: *Bison bison*, *Canis lupus*, *Cervus elaphus*, mortality, predation, restoration, wolf, Yellowstone National Park

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The question of how readily wolves (*Canis lupus*) learn to kill species of prey new to them has generated considerable discussion but limited testing. Certain wolf packs in northwestern Minnesota killed white-tailed deer (*Odocoileus virginianus*) routinely without taking domestic livestock in or near their territories (Fritts and Mech 1981). Reintroduced wolves in Montana denned in a livestock pasture (Diamond 1994) for about a year before they killed the surrounding cattle (E. E. Bangs, pers. comm.). Some wolf packs in northeastern Minnesota kill deer but rarely take moose (*Alces alces*—Mech 1966, 1977; Mech and Frenzel 1971). Thus, the predatory behavior of wolves reintroduced to Yellowstone National Park (YNP—Fritts et al. 1997), where a wide variety of prey exists, will shed light on wolf adaptation to novel prey. Of particular interest is the question of how soon after reintroduction YNP wolves, including inexperienced individuals, will kill bison (*Bison bison*), their largest and most formidable prey (Carbyn et al. 1993).

Historically, wolves and bison coexisted over vast areas of North America, but populations of both were drastically reduced because of predator control and market

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hunting (Lopez 1978). Wood Buffalo National Park and the adjacent Slave River Lowlands in Canada is 1 of the few areas where a wolf–bison system has been preserved and where wolves regularly prey on bison (Carbyn et al. 1993; Van Camp 1987). Bison there are the main prey of wolves, so questions of learning and selectivity are not pertinent. In the Mackenzie Bison Sanctuary in Canada, wolves avoid bison and kill moose, even though bison are more abundant (Larter et al. 1994).

We expected wolves reintroduced to YNP to avoid or rarely kill bison, instead preferring the familiar, more abundant, and more easily killed elk (*Cervus elaphus*—Carbyn 1983; Mech 1970). We predicted that wolves would have to learn to kill bison, and time to 1st bison kill would be longer than time to 1st elk kill. We also expected that when wolves did kill bison, they would take the most vulnerable animals, e.g., calves or animals weakened by harsh winters. Our wolf–bison study is ongoing, but we report here on initial circumstances of wolves interacting with and learning to kill their most formidable prey when prey that would be easier to kill were available.

Materials and Methods

Yellowstone National Park is a 891,000-ha protected area primarily in northwestern Wyoming, with a variety of habitats from high alpine to lower elevation sagebrush grasslands (Despain 1990). YNP and the surrounding area (Greater Yellowstone area) support an estimated 120,000 elk, 87,000 mule deer (*Odocoileus hemionus*), an unknown but low number of white-tailed deer, 5,800 moose, 3,900 bighorn sheep (*Ovis canadensis*), 2,000–4,000 bison, 800–1,000 mountain goats (*Oreamnus americanus*), and 400 pronghorn (*Antilocapra americanus*—Bangs and Fritts 1996; Varley and Brewster 1992).

Ungulate behavior and migration in winter are variable depending on species and winter severity (Houston 1982; Meagher 1973; Merrill and Boyce 1991). Distribution and abundance by season for any species are too complex to report individually for any given year, but for areas in question, wintering populations of ungulates do exist each year.

In March 1995, 14 wolves in 3 packs and in April 1996, 17 wolves in 4 packs were reintroduced into YNP (Bangs and Fritts 1996; Fritts et al. 1997; Phillips and Smith 1996). Wolves released in 1995 were captured just east of Jasper National Park, Alberta, Canada, where elk, deer, and moose were their main prey. The nearest bison were >600 km away. Because wolves sometimes disperse distances of >886 km (Fritts 1983), some donor wolves might have has some experience killing bison. Wolves reintroduced in 1996 came from an area where they preyed on bison (Weaver and Haas 1998). In addition to the 31 Canadian wolves, 10 bison-naive wolves were brought to YNP in September 1996 from northwestern Montana. Those 5-month-old pups were placed in a pen with other adult wolves for acclimation over the winter and were later released as yearlings in March or April 1997.

All wolves released into YNP were radiocollared (Bangs and Fritts 1996), and subsequently 30–50% of the pups born were collared. Wolves were acclimated for 10 weeks inside pens, which allowed us to identify individuals from the air by their markings. They were located aerially at least weekly for 10 months of the year and daily (weather permitting) from mid-November through mid-December and in March. We also located and observed wolves from the ground throughout the year, except for 3 remotely located packs of 6–33 wolves. Wolves in the Madison-Firehole area were radiotracked and then back-tracked from the ground from December 1997 through March 1999. In summer, wolf observations were made opportunistically and less frequently.

When wolves were sighted aerially, we noted time of day, location, habitat type, group size, age, activity, and sex (for collared wolves). We circled for several minutes if wolves were involved in an activity such as attacking prey; otherwise, we left the area. Any interactions with prey observed from the ground were monitored with spotting scopes and recorded onto data forms in the field or into a dictaphone and later transferred to data forms. Ground observers recorded the same data as did aerial observers but also recorded sequence of events: which species approached (wolf or prey), numbers of wolves or prey involved, response of wolves and prey

(stand, walk away, flee, or attack), duration of encounter, outcome, and distance over which the encounter took place. Observations reported here are limited to wolf–bison interactions. Bison numbers and distribution were recorded during aerial surveys as part of long-term research (Meagher 1998).

Wolf-killed prey were defined as prey observed being killed or prey determined as killed by wolves by observing wolves feeding on a carcass and then finding other sign that indicated that the prey had been killed by wolves (Peterson 1977). For example, we looked for blood in the snow along with signs of a struggle or searched for tracks indicative of a chase (Carbyn 1983; Peterson 1977). Condition of wolf-killed bison was assessed either by marrow fat from a leg bone (Cheatum 1949) or observation of the bison before it was killed by wolves.

Wolf selectivity and success rate in killing prey (elk or bison) were analyzed using a chi-square test with Yates' correction for continuity (Sokal and Rohlf 1981). Results were considered significant at $P < 0.05$.

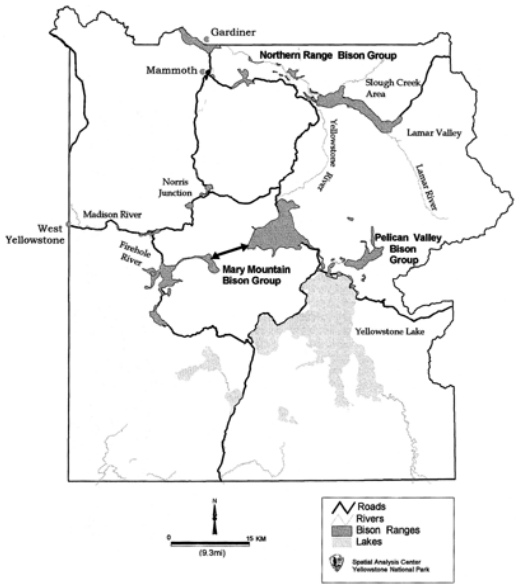

FIG. 1.—Winter ranges of bison in Yellowstone National Park when wolves were reintroduced in 1995.

RESULTS

Bison abundance and distribution.—Bison in YNP that historically have winter ranges restricted to Lamar (northern range), Mary Mountain (Hayden Valley-Firehole), and Pelican Valley (Meagher 1973; Fig. 1) have undergone major changes in numbers and distribution during the past 15 years (Meagher 1989; Meagher et al. 1997). Geographic designations no longer represent distinct wintering subpopulations because numbers occupying those locales change throughout winter. Lamar and Hayden valleys presently function as major summer range; summer use is limited on traditional winter ranges.

When wolves were reintroduced to YNP in March 1995, bison numbered about 4,000, with about 200 left in Pelican Valley in April. The herd decreased to about 3,500 in winter 1995–1996, with the majority in the Mary Mountain herd. A small number of bison again spent the entire winter in Pelican Valley. The population comprised about 3,400 bison in early winter 1996–1997. That winter was exceptionally severe, and with the ongoing changes in bison distribution (Meagher 1998), large numbers of bison moved out of YNP. Management actions outside YNP removed 1,084 bison, and about 400 died naturally within the park.

About 2,100 bison were counted in early winter 1997–1998 (Table 1). Within the Mary Mountain segment, 523 bison lived in Hayden Valley, 472 in the Nez Perce–Firehole River area, and 352 along the Madison River or in the western boundary area. By late winter–early spring, when counts are less accurate because bison are scattered, 1,769 bison were counted on 30 April 1998. Of those, 333 were on the Northern Range, 80 were in Pelican Valley, and 1,356 were in the Mary Mountain area. In December 1998, 2,203 bison were counted in YNP (Table 1). A March survey yielded 1,683 bison, with 349 on the northern range, 192 in Pelican Valley, and 1,142 in the Mary Mountain herd.

Wolf distribution.—All wolf packs in YNP (3–11 packs in 1995–1999) were exposed to bison, and all but 2 packs regularly

TABLE 1.—Distribution and abundance of bison and elk in Yellowstone National Park, December 1994–1999.

Winter season	Bison				Elk			
	Pelican Valley	Mary Mountain	Northern Range	Total	Pelican Valley	Mary Mountain	Northern Range	Total
1994–1995	1,123	2,156	694	3,973	0	651[a]	16,500	17,151
1995–1996	469	2,277	742	3,488	0	537[a]	16,000[b]	16,537
1996–1997	719[a]	1,874[c]	775[c]	3,368	0	438[a]	14,000[b]	14,438
1997–1998	365	1,347	393	2,105	9	594[a]	11,692	12,286
1998–1999	366	1,418	419	2,203	0	545[d]	11,742	12,287

[a] Eberhardt et al. (1998).
[b] No survey; number represents an estimate.
[c] Survey conducted October 1996.
[d] From R. A. Garrott and L. L. Eberhardt, pers. comm.

encountered them. In Pelican Valley, where the Crystal Creek pack wintered, we saw only 9 elk while aerially tracking wolves over 4 winters (1995–1999; Table 1).

Five other wolf packs coexisted with bison, but all packs also had access to elk. In 1995–1999, 4 wolf packs occupied the Northern Range of YNP. The Crystal Creek, Leopold, Rose Creek, and Druid Peak packs all shared winter and summer ranges with bison but also shared range with the Northern Yellowstone elk herd, consisting of 11,692–16,500 animals (Lemke et al. 1998). In winter 1998–1999, the Nez Perce pack occupied the Madison-Firehole area of YNP, part of the overwintering area of the Mary Mountain bison herd, and an area occupied by 537–651 nonmigratory elk and 1,347–2,277 bison (Table 1; Eberhardt et al. 1998).

Wolf–bison interactions.—From April 1995 through March 1999, field personnel observed 44 independent wolf–bison encounters, resulting in 57 total interactions (13 interactions involved the same bison and wolves), and saw 4 bison (7%) being killed; remains of 10 other wolf-killed bison were found (Table 2). During that same period, we observed 372 separate wolf–elk

TABLE 2.—Sex, age, and condition and date of kill for wolf-killed bison in Yellowstone National Park, 1997–1999.

Date killed	Sex	Age	Condition[a]	Location	Pack size	Wolf pack
8 April 1997	Unknown	Calf	Poor	Norris Junction	5	Sawtooth
12 April 1997	Female	Adult	Unknown	Pelican Valley	2	Crystal
30 March 1998	Unknown	Adult	Unknown	Pelican Valley	8	Crystal
10 December 1998	Male	Adult	Broken leg	Lamar Valley	7	Druid
30 December 1998	Unknown	Calf	Unknown	Firehole River	7	Nez Perce
8 January 1999	Unknown	Calf	Poor	Firehole River	7	Nez Perce
13 February 1999	Female	Calf	Poor	Firehole River	7	Nez Perce
10 March 1999	Unknown	Calf	Poor	Firehole River	7	Nez Perce
12–13 March 1999	Female	Adult	Fair	Slough Creek	18	Rose
17 March 1999	Female	Adult	Unknown	Pelican Valley	14	Crystal
23 March 1999	Unknown	Calf	Unknown	Nez Perce Creek	7	Nez Perce
24 March 1999	Unknown	Calf	Probably poor	Gibbon Meadows	1	1 wolf[b]
28 March 1999	Unknown	Yearling	Probably poor	Pelican Valley	14	Crystal
28 March 1999	Unknown	Calf	Probably poor	Firehole River	7	Nez Perce

[a] Condition was determined either by inspection of carcass or by observation of individual before death.
[b] Attack on bison calf also involved 4 coyotes.

interactions, during which wolves killed 77 elk (21%). Hence, wolves were more successful killing elk than killing bison when they encountered them ($\chi^2 = 5.18$, *d.f.* = 1, $P = 0.03$). We documented 589 other wolf-killed elk during that period. Although there were more elk in YNP than bison (Table 1; elk outnumbered bison 5.6:1), the ratio of elk : bison killed by wolves was much higher (47.6:1).

The 5-year average for the elk and bison population over the study period showed that elk comprised 83% (14,540) and bison 17% (3,027) of the available prey base. Based on our wolf–prey encounter rates of 372 (87%) for elk and 57 (13%) for bison, we found that wolves did not approach elk more often than they approached bison ($\chi^2 = 2.08$, *d.f.* = 1, $P = 0.15$).

One to 15 wolves (4.1 ± 0.5 *SE*) approached 1–55 bison (10.9 ± 1.5). Encounters lasted from 24 s to 9.5 h (17.5 ± 10.0 min, median = 3.0 min). Approach of wolves toward bison was direct, with no attempt at concealment. At least 17 (30%) of the encounters involved pups and adults, and 5 (9%) involved only pups. Forty-three (75%) bison approached by wolves stood their ground and did not flee; 12 (21%) of those animals were lone bison. Of the 45 encounters of multiple bison, 38 (84%) involved the bison grouping tightly, and in 32 (84%) of those cases, bison stood and faced the wolves.

When wolves attempted to attack bison they did so from the rear, when bison were running away (25%; $n = 14$). If bison did not run, wolves quickly lost interest. Hence, whether or not an attack occurred, duration of encounter, chase distance, and ultimate outcome of the encounter (failed attempt or successful kill) were determined by behavior of the bison. The conclusions of 2 attacks were observed, and wolves were attacking the neck of the bison, but we do not know if the wolves attacked the rear first.

Wolves killed primarily calves and cows. Ten (71%) of the 14 bison kills were made in March or April (Table 2). A calf and a bull with a broken leg were killed in December 1998, and lone calves were killed in January and February 1999. We detected only 2 kills in 1997, 3 in 1998, and 9 in 1999.

Six different wolf packs killed bison, but 10 of 14 kills were made by 2 packs. The Crystal Creek pack made 4 kills, the Nez Perce pack made 6, and the Druid Peak pack, Rose Creek pack, Montana pups, and a lone uncollared wolf made 1 kill each. Those kills involved 58–60 different wolves. None of those wolves had experience with bison prior to reintroduction in YNP, except for possibly the Druid Peak pack, which contained 2 members that as pups may have been exposed to bison in British Columbia.

Accounts of wolf-killed bison.—Only 4 bison were observed being killed by wolves; the other bison were determined after the fact to have been killed by wolves (Table 2). Of those 4 bison, only 1 kill sequence was observed from start to finish. On 17 March 1999, 14 wolves from the Crystal Creek pack, which resided in Pelican Valley, attacked a group of about 55 bison. The attack lasted 9.5 h. Wolves chased bison from areas of no snow to deep (1–2 m) snow, attacking them while they were in the deep snow with all members of the pack. A maximum of 14 wolves were observed biting bison simultaneously. After testing and attacking bison like this all day, wolves killed an adult female.

Another yearling bison was observed being killed by the same wolves at the same location on 28 March 1999. The entire kill was not observed. Fourteen wolves had 2 bison, a cow and a yearling, separated from a herd of 60–70 animals. The bison cow stood while wolves attacked the yearling. Ten wolves attacked the yearling simultaneously, with most of the attack focused on the neck. The yearling was killed while the cow remained motionless 5 m away, but she was never approached by the wolves.

The other 2 bison observed being killed by wolves were both calves in late winter.

One kill involved 5 yearling wolves that attacked a malnourished lone bison calf on 8 April 1997 (Table 2). That group, referred to as the Sawtooth wolves, was not a pack but was a temporary affiliation of young wolves released together. Another kill involved a lone wolf and 4 coyotes (*Canis latrans*) simultaneously attacking a malnourished lone bison calf on 24 March 1999. The wolf attacked the neck of the bison and the coyotes attacked a hind leg. Bites to the neck eventually killed the calf. The wolf then chased the coyotes away, but they remained 50 m away while the wolf fed on the calf.

Discussion

Our observations indicate that inexperienced wolves can learn to kill even the largest animals that the species preys on given the opportunity to do so. Yearling wolves that had been in captivity since 5 months of age killed a dying bison calf within 3 weeks of their release. Other packs killed adult bison within ≤25 months of release where no other prey were available (4 of 14 kills), where bison predominated (9 of 14 kills), or when bison were especially vulnerable (3 of these 14 kills; categories are not mutually exclusive).

These observations are contrary to our prediction that it would take several years for wolves to learn to kill bison, but they support our prediction that any bison that wolves did kill would be especially vulnerable ones. As with other large prey, wolves killed primarily calves and older adults in poor condition (Mech 1970; Mech et al. 1998). The 1 bull they killed had a broken leg. We also found that bison kills increased from 1997 through 1999, indicating that with experience wolves were more successful killing bison.

Wolves succeeded more often with attacks on elk than attacks on bison. The combination of elk being more numerous and easier to kill explains why elk are the primary prey of wolves in YNP. Selection for elk by wolves when moose and deer were available was documented in Riding Mountain National Park, Manitoba (Carbyn 1983), suggesting that elk are the preferred prey of wolves when multiple prey are available. Nevertheless, some reintroduced wolves settled where bison were their only possible prey in winter. Clearly, under some conditions, wolves will prey on whatever animals are available, not just the easiest or safest prey species, thereby avoiding the need to migrate to follow prey (elk migrate from Pelican Valley in winter where the Crystal Creek pack resides all year). This finding is not consistent with observations that wolves in Alaska do not prey on bison (Miquelle 1985; S. DuBois and R. Toby, pers. comm.). Perhaps those situations have not been studied closely enough to detect such kills, or the wolf population has been artificially reduced below the level where they need to prey on bison. In YNP, we predict that bison will become a regular prey item for some wolves, at least in spring.

Our findings lend some insight into wolf predation on livestock. For example, the wolf population in Minnesota expanded from its wilderness reservoir where deer and moose were the primary prey into semiagricultural land and at first rarely attacked livestock (Fritts and Mech 1981). Eventually, the population spread to agricultural land, and wolves learned to kill livestock, which became included regularly in their diet (Fritts et al. 1992). A similar situtation occurred with wolves in Montana (Diamond 1994) after they had been closely exposed to livestock for a year (E. E. Bangs, pers. comm.). However, because livestock are often kept near human habitations in open areas away from cover and are only seasonally available, it may take wolves longer to learn to include them regularly as prey. Our study suggests that wolves can adapt quickly to killing novel prey if the need arises or if an individual is physically vulnerable.

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