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Potential for recreational restrictions to reduce grizzly bear–caused human injuries

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Abstract: In 2011, 2 hikers were killed by grizzly bears (*Ursus arctos*) in separate incidents on backcountry trails in Hayden Valley, Yellowstone National Park, USA (YNP). Hayden Valley provides prime habitat for grizzly bears and is known to have high densities of bears. During 1970–2017, 23% (10 of 44) of all backcountry grizzly bear–inflicted human injuries and fatalities in YNP occurred in the valley even though it comprises only 1% of the park. In addition, 3 of the last 5 fatal bear attacks in the park occurred in the valley. We evaluated retrospectively whether restrictions and closures on visitor recreational activity would have prevented many of these injuries. We considered prohibitions on recreational activity during seasons when bears forage for specific high-quality foods; potential closures that coincided with the times of day and year bears were most active in the valley; and visitor use restrictions that would have prevented the most common human behaviors associated with grizzly bear–caused human injuries. The food-based closure that may have prevented the most human injuries occurred during middle to late summer when bears scavenge bison (*Bison bison*) carcasses that result from annual rutting behavior of bison in the valley. However, safety precautions such as hiking in groups of ≥3, remaining on maintained trails, and carrying bear spray would likely reduce the frequency of bear-inflicted human injuries more than most food-based seasonal closures. Our analyses provide broadly applicable findings regarding use of visitor behavior restrictions and seasonal closures to reduce the risk of bear-inflicted human injuries.

Key words: backcountry, bear-inflicted human injury, bear safety regulations, bear spray, grizzly bear, group size, hiking, off-trail travel, seasonal recreational closures, *Ursus arctos,* Yellowstone National Park

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In 2011, 2 hikers were killed by grizzly bears (*Ursus arctos*) in separate encounters on backcountry trails in Hayden Valley in Yellowstone National Park, USA (YNP; Frey et al. 2011, 2012). Hayden Valley is optimum summer grizzly bear habitat (Hornocker 1962) and is known to have a high grizzly bear density (Knight 1975). During 1970–2017, 23% (10 of 44) of all grizzly bear–inflicted human injuries and fatalities in backcountry areas of YNP occurred in Hayden Valley (Fig. 1), even though the valley comprises only 1% (11,000 ha) of the 899,139-ha park. In addition, 3 of the last 5 grizzly bear–caused human fatalities in YNP occurred in Hayden Valley (Gunther 2015).

Park managers attempt to lessen the risk of bear-inflicted human injuries by providing extensive bear safety information to visitors during face-to-face interactions and through media such as the internet, videos, handouts, posters, press releases, and trailhead signs. However, compliance with safety recommendations for hiking and camping in bear country is poor (Gunther 1990). For example, YNP recommends people hiking into the backcountry travel in groups of ≥3 people, yet most visitors hike alone or with just one partner (Gunther 1990, Coleman et al. 2013, Gunther et al. 2015). The park also recommends all backcountry recreationalists carry bear spray, but only 52% of overnight backpackers and 13% of day hikers comply with these recommendations (Gunther et al. 2015). In addition, in an effort to reduce bear-inflicted injuries, park managers designated Bear Management Areas in 1983 with restrictions and closures on recreational activity in areas with seasonally high densities of grizzly bears (National Park Service 1983, Gunther 1990, Coleman et al. 2013). However, in 1983 when

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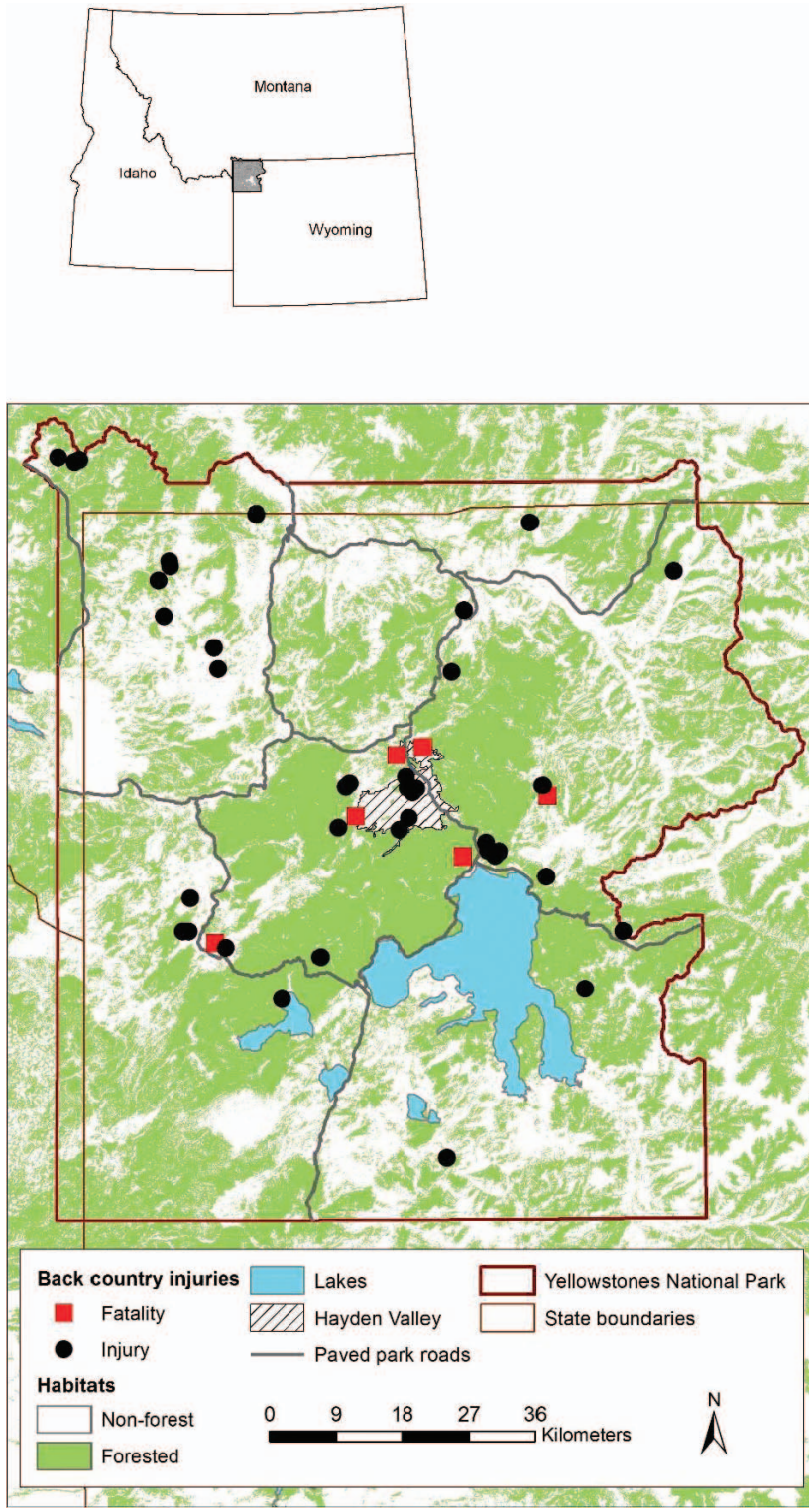

Fig. 1. Map of Yellowstone National Park, USA, displaying Hayden Valley and all bear-caused human injuries and fatalities that occurred in backcountry areas of the park, 1970–2017.

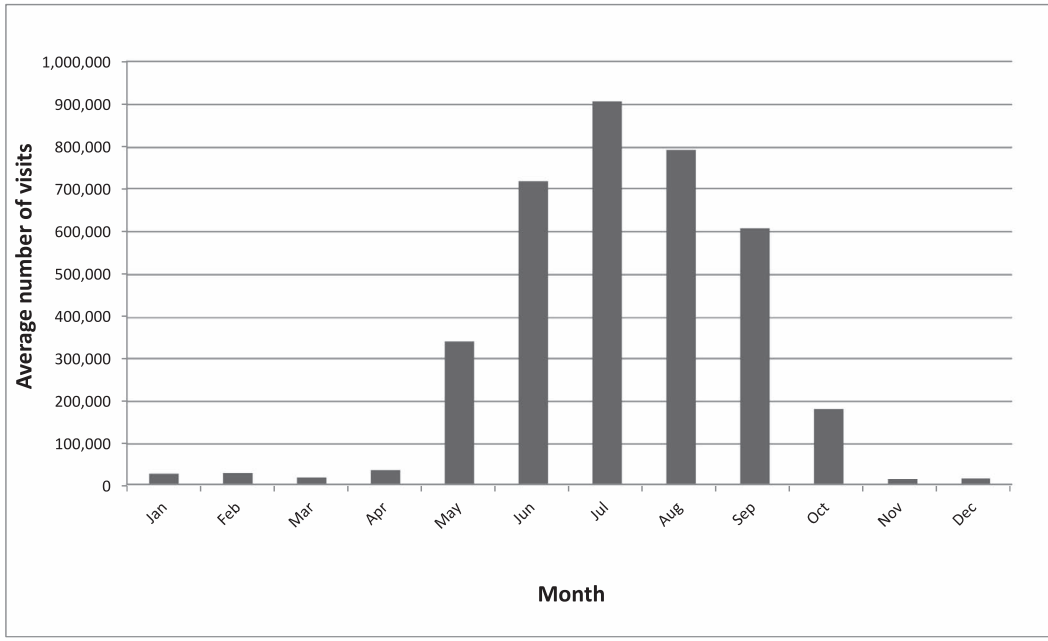

Fig. 2. Average number of recreational visits per month in Yellowstone National Park, Wyoming, USA, 2012–2017.

Bear Management Areas were created, only one bear-inflicted human injury had occurred in Hayden Valley in the previous 12 years. Therefore YNP did not designate Hayden Valley as a Bear Management Area in 1983.

Given the relatively large number of bear-caused human injuries in Hayden Valley compared with other areas of the park since 1983, we evaluated whether visitor use restrictions and seasonal closures could be implemented to reduce the risk of attack while still allowing for reasonable recreational opportunities. We investigated annual, seasonal, and diel activity patterns of grizzly bears and considered a suite of seasonal closures during time periods when grizzlies are most active and when bears feed on specific high-calorie foods in the valley. In addition, we evaluated the potential efficacy of requiring minimum group sizes, hiking on maintained trails, and carrying bear spray to lower the risk of attack and injury. Our analysis will help managers make quantitatively based decisions on the merits of using visitor use closures and/or restrictions on hiker behavior to reduce the frequency of bear-inflicted human injuries on recreationalists in Hayden valley. The methods used in this analysis may also be useful to other managers that are responsible for human recreational activities on lands occupied by grizzly bears. We believe that it is important to reduce the frequency of bear-inflicted human injuries not only for the safety of park visitors and to reduce the number of bears that are captured and killed in subsequent management actions, but also to maintain societal support for grizzly bear conservation.

Study area

Hayden Valley is located in the approximate center of YNP, which was established in 1872 and encompasses approximately 8,991 km^2 in the states of Wyoming (96%), Montana (3%), and Idaho (1%), USA. Most (~98%) of the habitat in YNP is relatively pristine, undeveloped land; 92% of the park has been recommended for wilderness designation and, by National Park Service policy, is managed so as not to preclude that designation in the future (National Park Service 2006). Only approximately 2% of the park's habitat has been significantly altered through construction of roads and developments (Gunther et al. 2017). During the study period (1970–2017), visitation to the park gradually increased from an average of 2.2 million visits/year in the 1970s, to 4.2 million visits/year after 2015 (Gunther 2018). The majority (>96%) of visitation occurs from May through October (Fig. 2; Gunther 2018), the same period when most

grizzly bears of all sex and age classes are out of winter dens and active on the landscape (Haroldson et al. 2002). Yellowstone National Park does not keep records of backcountry recreational day-use for Hayden Valley or anywhere in the park. However, from our experience conducting grizzly bear field research and management activities in YNP's backcountry over the past 30 years, we believe that trends in backcountry day-use mirrored trends in total park visitation, and therefore have increased significantly since 1970. Our experience also indicates that most backcountry day-use recreational activities occur within 5 km of trailheads and road-based access points. Therefore, areas >3 miles from roads are still very wild and pristine.

Hayden Valley (Fig. 1) is a relatively large, nearly treeless area surrounded by a forested plateau (Graham 1978). Flora consists of sagebrush (*Artemisia* spp.) and a variety of forbs, grasses, and sedges (Meagher 1973). Lodgepole pine (*Pinus contorta*) dominates the plateau, with spruce (*Picea engelmannii*) and fir (*Abies lasiocarpa*) interspersed (Graham 1978, Despain 1990). Grizzly bears den in the area and are active in the valley from March through November. Hayden Valley has one of the highest densities of grizzly bears in the Greater Yellowstone Ecosystem (GYE). We evaluated grizzly bear density in Hayden Valley relative to other portions of YNP and the GYE using a density index developed by Bjornlie et al. (2014) for the period 1983–2012. Average index values for 2 14 × 14-km cells containing Hayden Valley (index values of 21 and 19) exceeded the 99th percentile for the GYE (Text S1, Supplemental Material). In comparison, the Lamar Valley, another large non-forested valley inhabited by bears in YNP, had an average grizzly bear density index value of 11 during the same time period (Text S1).

Calorie-rich food resources that attract grizzly bears to Hayden Valley during spring include wolf (*Canis lupus*)–killed bison (*Bison bison*) and elk (*Cervus canadensis*) carcasses in March, winter-killed bison carcasses from March through mid-May (Mealey 1975), bison calves from late April through June (Varley and Gunther 2002), and newborn elk calves from mid-May through mid-June. Important summer and autumn grizzly bear foods in Hayden Valley include dense patches of clover (*Trifolium* spp.) from July through August (Mealey 1975, Graham 1978), carcasses of bison injured during their breeding season from mid-July through mid-September, and predation on adult male elk preoccupied with breeding behavior during their autumn rut from September through mid-October (Mealey 1975). Bears in the valley also feed on adult northern pocket gophers (*Thomomys talpoides*) and their food caches (Apr–Jun), meadow voles (*Microtus* spp.; Apr–May), biscuit root (*Lomatium* spp.; mid-Jun–Jul), elk thistle (*Cirsium* spp.; Jul), neonate pocket gophers (Jul), strawberry (*Fragaria virginiana;* Aug), whortleberry (*Vaccinium scoparium;* Aug–Sep), and yampa roots (*Perideridia gairdneri;* Sep–Oct [Mealey 1975, Graham 1978]). In addition, grizzly bears have been documented eating grasses (*Agropyron* spp., *Bromus* spp., *Deschampsia* spp., *Melica* spp., *Phleum* spp.; Apr–Jun), sedges (*Carex* spp.; Apr–Jun), horsetail (*Equisetum* spp.; Jun–Jul), ants (*Formicidae;* Jul–Aug), buttercup (*Ranunculus* spp.; Aug), Solomon's seal rhizomes (*Maianthemum* spp.; Sep–Oct), and mushrooms (*Russula* spp.; Sep–Oct) in the valley (Mealey 1975, Graham 1978).

Methods

Yellowstone National Park law enforcement and bear management staff collected data on bear-inflicted human injuries during interviews with injured hikers and via incident field investigations. These records were entered into a database and stored in the Bear Management Office. We analyzed all grizzly bear–inflicted human injuries that occurred in Hayden Valley from 1970 to 2017 including the date, time of day, party size, whether the hiker(s) were traveling on maintained trails or hiking off-trail, and whether or not the hiker(s) were carrying bear deterrent spray. We conducted a retrospective analysis considering a suite of potential seasonal and diel recreational closures, as well as restrictions on the behaviors of hikers, to evaluate which actions might have prevented the most bear-inflicted human injuries had the closures and restrictions been in place during the years the incidents occurred (Text S2, Supplemental Material).

Seasonal recreational closures based on bear foods

Habitat quality can influence the distribution of bears on the landscape and, therefore, the chances of bear–human encounters and the frequency of bear-caused human injuries (Herrero 2002). Grizzly bears select foods that are relatively high in nutrients, are easily digested, and are concentrated spatially on the landscape to make for efficient foraging (Gunther et al. 2014a). We identified 22 seasonal bear foods present in Hayden Valley and the average peak periods of their use from literature reviews and field experience. We then compared the average peak period of use for each food to the dates of past grizzly bear–inflicted human injuries that occurred in Hayden Valley from 1970 to 2017, to estimate how many

Table 1. Common grizzly bear (*Ursus arctos*) foods and peak season of their use in Hayden Valley, Yellowstone National Park, Wyoming, USA, 1970–2017.

Documented grizzly bear food in Hayden Valley	Source	Peak period of consumption	Source
Wolf-killed non-neonate elk (usurping or scavenging)	D. Stahler, YNP, pers. comm.	~1 Mar–31 Mar	Metz et al. 2012
Wolf-killed non-neonate bison (usurping or scavenging)	D. Stahler, YNP, pers. comm.	~1 Mar–15 Apr	Smith et al. 2000
Winter-killed bison (scavenging)	Mealey 1975	~15 Mar–15 Apr	Meagher 1973, Green et al. 1997
Meadow voles (predation at nests)	Mealey 1975	~1 Apr–31 May	Mattson et al. 1991, Craighead et al. 1995, Mattson 2004a
Pocket gopher (predation on adults & kleptoparasitism of root food caches)	Mealey 1975, Graham 1978	~1 Apr–31 May	Mattson 2004b
Graminoid foliage (grazing)	Graham 1978	~1 Apr–30 Jun	Mattson et al. 1991
Bison calves (predation)	Varley and Gunther 2002	~21 Apr–30 Jun	Varley and Gunther 2002, Geremia et al. 2015
Elk calves (predation)	Direct observations by authors	~15 May–15 Jun	Gunther and Renkin 1990, Barber-Meyer et al. 2008
Horsetail (grazing)	Mealey 1975, Graham 1978	~1 Jun–31 Jul	Mattson et al. 1991
Biscuitroot root (digging roots)	Direct observations by authors	~15 Jun–31 Jul	Mattson et al. 1991, Craighead et al. 1995
Ants (predation)	Mealey 1975, Graham 1978	~21 Jun–31 Jul	Craighead et al. 1995
Pocket gopher (neonate predation)	Mealey 1975, Graham 1978	~1 Jul–31 Jul	Mattson 2004b
Elk thistle (grazing)	Mealey 1975, Graham 1978	~1 Jul–31 Jul	Mattson et al. 1991
Rut-killed bison (scavenging)	Direct observations by authors	~15 Jul–15 Sep	Direct observations by authors
Strawberry (consuming berries & leaves)	Mealey 1975, Graham 1978	~1 Aug–31 Aug	Mealey 1975
Buttercup (grazing)	Mealey 1975, Graham 1978	~1 Aug–31 Aug	Mealey 1975
Whortleberry (consuming berries & leaves)	Mealey 1975, Graham 1978	~1 Aug–31 Aug	Mattson et al. 1991
Clover (grazing)	Mealey 1975, Graham 1978	~1 Aug–7 Sep	Gunther 1991, Mattson et al. 1991
Rutting adult male elk (predation)	Mealey 1975, Mattson et al. 1991	~1 Sep–15 Oct	Mealey 1975
Yampa (digging roots)	Mealey 1975, Graham 1978	~1 Sep–31 Oct	Mattson et al. 1991
False Solomon's seal (digging rhizomes)	Mealey 1975	~1 Sep–31 Oct	Mealey 1975
Mushrooms (consuming caps and stems)	Mealey 1975	~1 Sep–31 Oct	Mealey 1975, Mattson et al. 1991

incidents may have been prevented if seasonal recreational closures had been in place during the peak period each food is consumed by bears (Table 1; Text S2).

Recreational closures and restrictions based on bear activity

Recreational closures based on seasonal activity. In addition to seasonal foods, the presence of rub trees, scent-marking areas, ponds for thermoregulation, estrous females, day-bedding sites, denning sites, mineral feeding sites, travel routes, and other factors also influence the distribution of grizzly bears on the landscape, and therefore, the probability of encounters with backcountry recreationalists. We analyzed 163 very high frequency (VHF) telemetry locations from 7 male and 267 locations from 7 female radiocollared grizzly bears that frequented Hayden Valley during spring, summer, and autumn of 1986–2017, to determine the peak periods during which male and female grizzly bears were active in the valley. We obtained these VHF locations via fixed-wing aircraft approximately once per week during early to mid-morning hours. We calculated the proportion of these locations that occurred in Hayden Valley each week from den emergence through den entry.

We compared the peak period of activity for male, female, and male and female grizzlies combined in Hayden Valley with the dates of all bear-inflicted human injuries in the valley during 1970–2017. From this comparison, we estimated how many bear attacks may have been prevented if seasonal recreational-activity closures corresponding to the peak periods during which male and female grizzly bears were active in the valley had been in place the years the incidents occurred.

No grizzly bears were captured or radiocollared specifically for this study. All radiotelemetry data used for this study were collected by the Interagency Grizzly Bear Study Team as part of other research projects. Grizzly bear capture and handling procedures were reviewed and approved by the Animal Care and Use Committee of the U.S. Geological Survey (IACUC #2018-1); procedures conformed to the Animal Welfare Act, and to the U.S. government principles for use and care of vertebrate animals in testing, research, and training. Captures were conducted under U.S. Fish and Wildlife Service Endangered Species Permit [Section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40 (b)], with additional state research permits for Wyoming, Montana, and Idaho, and National Park Service research permits for Yellowstone and Grand Teton National Parks.

Time-of-day recreational restriction based on grizzly bear diel activity. Grizzly bear diel-behavior patterns may also influence the frequency of human–bear encounters (Penteriani et al. 2017). Grizzly bears in YNP are most active during crepuscular and nocturnal time periods (Schleyer 1983, Harting 1985, Gunther 1990). A time-of-day restriction (e.g., recreational activity allowed only from 0900 to 1900 hours that prohibits recreational activity during nocturnal and crepuscular periods when grizzly bears are most active) could potentially reduce the temporal overlap between human recreational activities and bear foraging and traveling activity, thereby reducing the chances of surprise encounters and subsequent defensive bear aggression. A time-of-day restriction would also contribute toward making human activity in Hayden Valley more predictable to bears, thereby potentially reducing the chances bears would react defensively during surprise encounters. We investigated the potential impact that prohibiting recreational activity in Hayden Valley during crepuscular or nocturnal hours (1900 to 0900 hr) would have had on the frequency of bear-caused human injuries. We analyzed timing of bear attacks in the valley from 1970 to 2017 to determine how many occurred during nocturnal and crepuscular periods versus diurnal periods. We then calculated the proportion of bear-inflicted human injuries that may have been prevented by prohibiting hiking during nocturnal and crepuscular time periods.

Recreational restrictions based on human behavior

Certain human behaviors may influence the probability of encountering bears, as well as outcomes of those encounters (Herrero 2002, Penteriani et al. 2017). Herrero (2002) analyzed grizzly bear–inflicted human injuries from throughout North America and identified many similarities between the circumstances of, and human behavior in, human–grizzly bear encounters in backcountry areas. Herrero (1985, 2002) and Gunther and Hoekstra (1998) reported that party size and whether or not the hiker(s) were traveling on maintained trails or hiking cross-country off-trail both appeared to influence the frequency of encounters and bears reactions to them. Physical contact by bears was more likely to occur during encounters with small party sizes ($\leq$3 people) and during off-trail encounters (Herrero 1985, 2002; Gunther and Hoekstra 1998). In addition, bear spray has proven effective at stopping aggressive behavior in bears during encounters and reducing the length and severity of bear attacks when they occur (Herrero and Higgins 1998, Smith et al. 2008). However, many backcountry hikers in YNP choose not to carry bear spray (Gunther et al. 2015). We developed visitor use restrictions that potentially would prevent the most common situations where human behaviors result in injuries by grizzly bears, including 1) requiring a minimum party size of $\geq$3 people for hiking in Hayden Valley, 2) prohibiting off-trail travel in the valley, and 3) requiring all hikers in the valley to carry bear spray. We then retrospectively applied these restrictions to Hayden Valley for the 1970–2017 time period to determine how many past injuries might have been prevented had these restrictions been in place. We calculated estimates of the potential effectiveness of the human-behavior-based recreational restrictions as follows:

Group size restriction. We assumed the proportion of bear-caused human injuries involving groups of $\geq$3 people in Hayden Valley would be approximately equal to the proportion of all hikers injured by bears in YNP during 1970–2017 that were traveling in groups of $\geq$3 people. Over the past 48 years, only 4% ($n = 2$) of the backcountry recreationalists injured by grizzlies in YNP were traveling in groups of $\geq$3 people when attacked. Most ($n = 42$, 95%) bear-inflicted human injures involved people hiking alone ($n = 21$, 48%) or with just 1 ($n = 21$, 48%) partner. Therefore, we assumed only 4% of those people hiking in groups of $\geq$3 people in Hayden Valley would be injured by grizzly bears.

Off-trail travel restriction. To estimate the efficacy of requiring hikers in Hayden Valley to stay on designated trails, we assumed that prohibiting off-trail travel would have prevented all of the past grizzly bear–caused human injuries in Hayden Valley that occurred while people were traveling cross country off-trail.

Requirement to carry bear spray. When deployed, bear spray is about 92% effective at stopping aggressive behavior in bears (Smith et al. 2008). However, not all people carrying bear spray are able to successfully deploy it during close-range aggressive encounters with grizzly bears. During 1970–2017, 30% of the people injured by bears in backcountry areas of YNP were carrying bear spray but were not able to deploy it, either because they did not have time to retrieve it, or they failed to get the safety tab off in time. To estimate the efficacy of implementing a requirement to carry bear spray, we assumed that the proportion of bear attacks stopped or defused by bear spray in Hayden Valley would be similar to the proportion of all hikers injured by bears in YNP for the years 1970–2017 that were carrying bear spray and had time to deploy it when attacked by a bear (70%), multiplied by the known proportion of bear spray deployments that are successful at stopping aggressive behavior in bears (92%; Smith et al. 2008). Therefore, we estimated bear spray would be effective at stopping or reducing the severity of attacks 64% of the time (0.70 proportion able to deploy bear spray $\times$ 0.92 proportion effective when deployed $=$ 0.64 efficacy in stopping or reducing severity of attacks).

Results and discussion

Characteristics of grizzly bear attacks in Hayden Valley, 1970–2017

Ten people were injured by grizzly bears in backcountry areas of Hayden Valley during 1970–2017, with 3 dying from their injuries (Table 2). The bodies of 2 of the 3 fatalities were partially consumed by bears. All 10 injuries occurred from late May through early October and between 1030 and 2100 hours. Eight of the injured people were day-hiking, 1 was backpacking, and 1 was day-riding but was on foot leading a mule at the time of attack. Four of the people were traveling alone and 6 were traveling with 1 other person. None of the injured people were in a group of $\geq$3. Seven of the injured people were traveling cross-country off of the designated trail and 3 were traveling on the designated trail. Eight of the 10 incidents, including 1 fatality, involved defensive aggression by grizzlies following surprise encounters. In 2 incidents (both fatalities with bear consumption of the body) the cause of attack was not known. In 1 of these 2 incidents, evidence suggests a photographer likely approached the grizzly bear for a picture prior to the attack. The circumstances surrounding another fatality are not known; however, there was evidence of a bison carcass nearby. Female grizzly bears (4 accompanied by young) were known to be involved in 8 of the10 incidents. Three of the 10 incidents were known to have occurred near bison carcasses. However, the presence of cubs and ungulate carcasses may have been underreported because cubs and bear-cached carcasses near encounter sites may not always have been visible to the injured hikers.

Efficacy of seasonal recreational closures based on bear foods

We analyzed the efficacy of closing Hayden Valley to recreational use during 22 different time periods that coincided with the peak seasons during which grizzlies consume a variety of foods found in the valley (Text S1). Applying seasonal closures that coincided with the peak period during which grizzlies consume specific foods in Hayden Valley potentially would have prevented from as many as 6 (60%) to as few as none (0%) of the bear-caused human injuries that occurred in the valley during 1970–2017 (Table 3). The food-based closure that potentially would have prevented the most bear-caused injuries occurred during mid to late summer and coincided with the peak season during which bears scavenge bison carcasses that died from injuries sustained during the bison breeding season. Hayden Valley and Lamar Valley are the 2 primary bison breeding areas in YNP (White et al. 2015). However, Hayden Valley has much higher grizzly bear density index values (values of 19 and 21) than does the Lamar Valley (11), and more bear activity is generally observed on bison carcasses in Hayden Valley. Although the bison rut occurs from mid-July through mid-August (Meagher 1973, White et al. 2015), some adult males do not die from rut-related injuries and/or infection until early to mid-September. Bison carcasses can attract and hold large numbers grizzly bears for several days to several weeks. Telemetry data from radio-instrumented grizzly bears have shown direct straight-line movements toward carcasses from as far as 15 km away (van Manen et al. 2017). Twenty grizzly bears were observed in the immediate vicinity of a bison carcass in Hayden Valley during an aerial telemetry flight on 3 August 2007 (Fig. 3), and Craighead et al. (1995) reported a ground observation of 23 grizzly bears congregating around a single bison carcass in YNP. The number and concentration of bears attracted to bison carcasses increases the likelihood of surprise encounters between hikers and bears

Table 2. Characteristics of grizzly bear (*Ursus arctos*) –inflicted human injuries in Hayden Valley, Yellowstone National Park, USA, 1970–2017.

Date	Time (hr)	Sex and age class of attacking bear	Human activity	Party size	No. injured	Trail use	Cause of attack	Person's reaction to encounter	Severity of injury—time in hospital
25 Aug 2011	1100[a]	Adult F	Day-hiker	1	1	On-trail	Unknown; Bison carcass nearby	Unknown	Fatality
6 Jul 2011	1050	Adult F + Cub	Day-hikers	2	1	On-trail	Surprise encounter	Run	Fatality
23 May 2007	1100	Adult F + Cub	Day-hiker	1	1	Off-trail	Surprise encounter	Play dead	Severe—several weeks in hospital
18 Jun 2004	2045	Adults—mating pair	Day-hiker	1	1	Off-trail	Surprise encounter	Play dead	Minor—1 day in hospital
17 Jul 1994	1430	Adult, sex unknown	Day-riders	2	1	Off-trail	Surprise encounter	Play dead; Bear driven off by partner on mule	2 days in hospital
4 Oct 1986	1100–1200[a]	Adult F	Day-hiker–Photographer	1	1	Off-trail	Unknown: Approach for Picture? Blow elk bugle?	Unknown	Fatality
20 Aug 1984	1600	Adult F + 2 cubs	Day-hikers	2	2	Off-trail	Surprise encounter at bison carcass	Yell–Play dead; Stand ground–Play dead	1 person, 1 day in hospital (minor); 1 person, 3 days in hospital
20 Jul 1984	1415	Adult M	Backpacker–Researchers	2	1	Off-trail	Surprise encounter	Spray bear with bear spray	Minor—<1 day in hospital
3 Sep 1970	1100	Adult F + Yearling	Day-hikers	2	1	On-trail	Surprise encounter	Run	Minor—<1 day in hospital

[a]Estimated time of day based on available evidence.

in the vicinity of carcasses. In addition, bison have large body size and, thus, their carcasses generally have edible biomass that attracts and holds bears for approximately 2 weeks before complete depletion by scavengers (Green 1994), further increasing the probability of human–bear encounters. Bears will often defend bison carcasses from conspecifics, wolves, and humans because of the high caloric value of the carcasses. Closing Hayden Valley during the peak period of rut-related bison mortality could reduce the chances of hikers encountering bears at bison carcasses. Had a seasonal closure been in effect in the Hayden Valley during the peak period of rut-related bison mortality (15 Jul–15 Sep), it may have prevented 6 of the 10 (60%) grizzly bear–inflicted human injuries that occurred in Hayden Valley during 1970–2017.

Although bears consume several foods during spring and early summer that are concentrated sources of calories and are known to attract and hold bears at specific locations (e.g., wolf-killed and winter-killed non-neonate bison and elk), none of the spring closures (Mar–May) would have been very effective at preventing the bear encounters that resulted in human injuries because few people hike in Hayden Valley during that time of year. The road through Hayden Valley does not open to the public until early May. Even after the road opens, the depth of accumulated snow and wet muddy conditions associated with spring snow melt limit visitor activity until later in June.

Closure of Hayden Valley during early summer (Jun–mid-Jul) would also be relatively ineffective at preventing encounters with grizzly bears that result in human injury. Except for elk calves, most foods consumed by bears in the valley during early summer are of lower caloric value, generally more dispersed across the landscape, and, therefore, not subject to directed grizzly feeding activity and less likely to be defended by bears. Although elk calves are a concentrated source of calories, they are generally consumed in just 1 or 2 feeding bouts immediately after predation (Gunther and Renkin 1990). Predation by grizzly bears on neonate elk does not attract and hold multiple bears for long periods of time; therefore, it is less likely to lead to human–bear encounters than larger carcasses such as bison.

Closures coinciding with the peak periods during which bears eat autumn foods would also not be very

Table 3. Potential reduction in grizzly bear (*Ursus arctos*) –inflicted human injuries in the Hayden Valley area of Yellowstone National Park, USA, 1970–2017, based on a retrospective evaluation of different types of grizzly food-based and activity-based seasonal recreational closures and human behavior-based recreational restrictions.

Type of regulation	No. of days closed to recreational activity	Potential reduction in grizzly bear attacks in Hayden Valley
Bear-food-based seasonal recreational closures		
Rut-killed bison scavenging season, ~15 Jul–15 Sep	63	60%
Clover grazing season, ~1 Aug–7 Sep	38	40%
Biscuitroot root-digging season, ~15 Jun–31 Jul	47	40%
Horsetail grazing season, ~1 Jun–31 Jul	61	40%
Strawberry consumption season, ~1 Aug–31 Aug	31	30%
Whortleberry consumption season, ~1 Aug–31 Aug	31	30%
Pocket gopher neonate predation season, ~1 Jul–31 Jul	31	30%
Elk thistle grazing season, ~1 Jul–31 Jul	31	30%
Ant predation season, ~21 Jun–31 Jul	41	30%
Buttercup grazing season, ~1 Aug–31 Aug	31	30%
Rutting adult male elk predation season, ~1 Sep–15 Oct	45	20%
Yampa root digging season, ~1 Sep–31 Oct	61	20%
Mushroom consumption season, ~1 Sep–31 Oct	61	20%
False Solomon's seal rhizome digging season, ~1 Sep–31 Oct	61	20%
Graminoid foliage grazing season, ~1 Apr–30 Jun	91	20%
Bison calf predation season, ~21 Apr–30 Jun	71	20%
Elk calf predation season, ~15 May–15 Jun	32	10%
Meadow vole neonate predation season, ~1 Apr–31 May	61	10%
Pocket gopher food cache kleptoparasitism season, ~1 Apr–31 May	61	10%
Wolf-killed non-neonate bison carcass scavenging season, ~1 Mar–15 Apr	56	0%
Wolf-killed non-neonate elk carcass scavenging season, ~1 Mar–31 Mar	31	0%
Winter-killed bison carcass scavenging season, ~15 Mar–15 Apr	32	0%
Grizzly bear activity-based seasonal recreational closures		
Closure during peak period of female grizzly bear activity in Hayden Valley, ~15 Jun–15 Aug	62	40%
Closure during peak period of male grizzly bear activity in Hayden Valley, ~1 Jul–31 Aug	62	50%
Closure during peak period of male and female grizzly bear activity in Hayden Valley, ~15 Jun–31 Aug	78	70%
Grizzly bear activity-based time of day restriction		
Restrict hiking in Hayden Valley to diurnal time periods (0900–1900 hr)	0	10%
Human-behavior-based recreational restrictions		
Group size restriction (require parties of ≥3 people to hike in Hayden Valley)	0	95%
Prohibition of off-trail travel in Hayden Valley	0	70%
Requirement to carry bear spray while hiking in Hayden Valley	0	64%

effective at preventing grizzly attacks. By late September and October, visitation to YNP (Fig. 2) and the number of people hiking in Hayden Valley decreases substantially, reducing the odds of bear–human encounters and, therefore, bear-inflicted human injuries.

Most of the food-based seasonal closures would have been ineffective at preventing bear-caused human injuries. The dates of our food-based closures were based on the average peak period during which bears consume different foods. However, ungulate migrations in spring and plant phenological development can vary by several weeks to a month or more depending on winter snow accumulation, spring snow melt, and spring and summer temperatures and precipitation. Therefore, the average dates of our food-based closures may not have aligned well with the actual periods during which bears sought specific foods during any given year.

Efficacy of recreational closures based on bear activity

Recreational closure based on seasonal activity. For the 7 radiocollared male grizzly bears that frequented Hayden Valley, 43 of 163 (26%) telemetry locations recorded were inside and 120 outside of the valley.

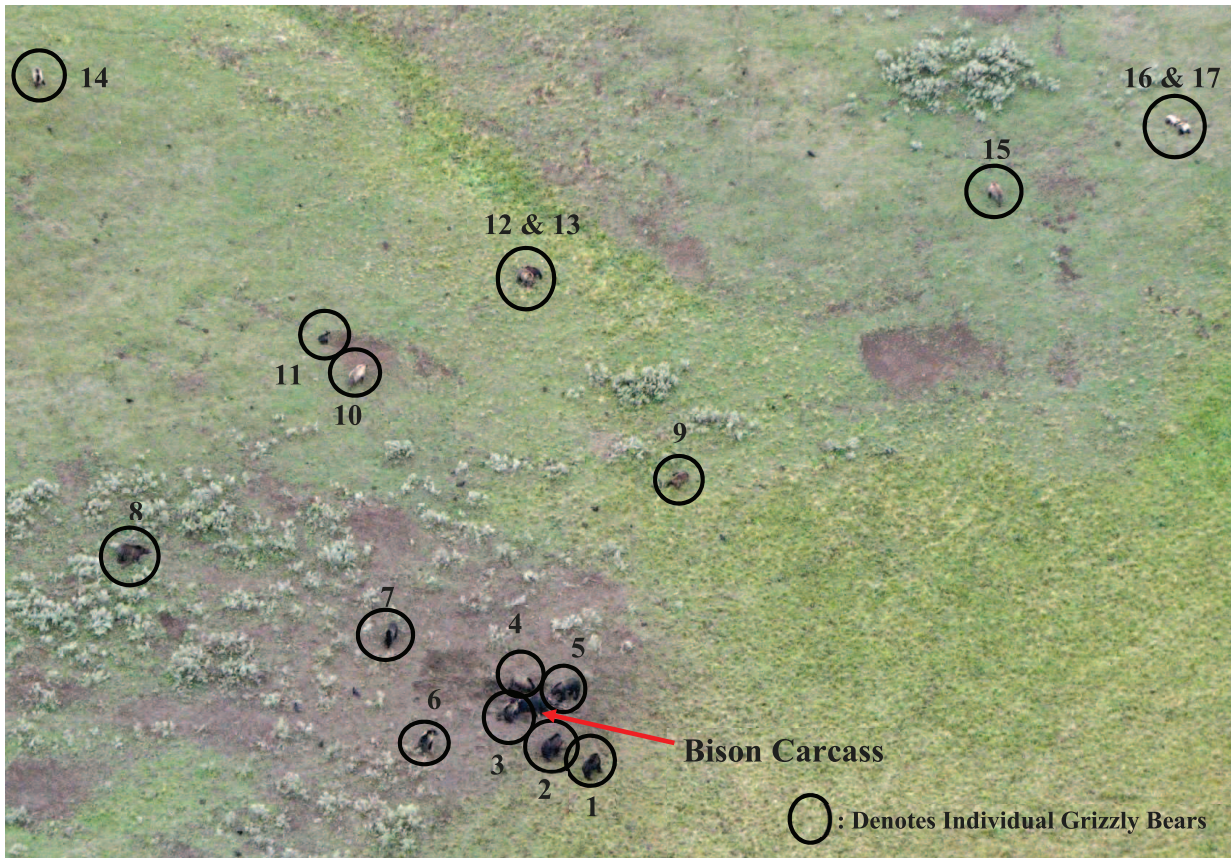

Fig. 3. Photo of 17 of 20 grizzly bears (*Ursus arctos*) counted congregating around a bison (*Bison bison*) carcass in Hayden Valley, Yellowstone National Park, USA, on 3 August 2007. Three additional grizzly bears were observed just outside of the photo frame. (Photo by Interagency Grizzly Bear Study Team).

Of the 43 telemetry locations inside Hayden Valley, over half (56%, $n = 24$) occurred during the 62-day period between 1 July and 31 August. For the 7 radiocollared female grizzly bears that frequented Hayden Valley, 90 of 267 (34%) telemetry locations recorded were in the valley. Of these 90 locations, over half (58%, $n = 52$) occurred during the 62-day period between 15 June and 15 August. Applying a seasonal closure during the period in which male grizzly bears are most active in Hayden Valley (1 Jul–31 Aug) may have prevented 5 of the 10 (50%) human injuries that occurred during 1970–2017 (Table 3). Had a seasonal closure been in effect in Hayden Valley from 1970 to 2017 during the peak period of female grizzly bear activity in the valley (15 Jun–15 Aug), 4 of the 10 (40%) grizzly bear–caused human injuries that occurred in the valley may have been prevented. Applying a seasonal closure that combines the peak period during which both male and female bears are active (15 Jun–31 Aug) may have prevented 7 of the 10 (70%) human injuries.

Time-of-day recreational restriction based on diel activity. Only 1 of 10 people injured by grizzlies in Hayden Valley from 1970 to 2017 was injured during nocturnal or crepuscular time periods. Nine of the 10 (90%) people were injured during diurnal time periods. Therefore, time-of-day restrictions closing Hayden Valley to recreational activity during nocturnal or crepuscular periods and allowing recreational use only during diurnal periods (0900–1900 hr) may have prevented only 1 (10%) of the bear-caused injuries in Hayden Valley (Table 3). The ineffectiveness of a time-of-day restriction in reducing bear attacks is likely due to 2 factors. First, most bear-inflicted human injuries in YNP occur during the time periods when people are most active (1000–1700 hr) and, thus, have the greatest chance of surprising bears. Few backcountry recreationalists are active during

nocturnal and crepuscular time periods; therefore, there is little chance of hikers being injured during nocturnal and crepuscular time periods. In addition, female grizzly bears with cubs are more diurnal than other grizzly bears (Gunther 1990). Therefore, prohibiting recreational activity during nocturnal and crepuscular time periods would be most effective at reducing the chances of surprising adult male grizzly bears and female bears during years when they do not have cubs, but would be less effective at reducing the chances of encounters with females accompanied by cubs. Female grizzly bears with cubs are responsible for most human injuries involving defensive reactions during surprise encounters (Herrero 1970, Gunther and Hoekstra 1998). The presence of cubs may increase a bear's individual space requirements and the likelihood the bear will elect to fight if other bears or hikers enter that space (Craighead et al. 1995, Smith 2006). In addition, overnight camping is prohibited in Hayden Valley (National Park Service 1983), so there is very little chance of bear attacks during nocturnal and crepuscular time periods. A regulation limiting hiking in Hayden Valley to diurnal time periods would not be very effective at reducing the frequency of grizzly bear–caused human injuries in Hayden Valley.

Potential efficacy of recreational restrictions based on human behavior

Group size restriction. There is evidence that hiking in large groups reduces the risks of bear attack (Herrero 1985, Gunther and Hoekstra 1998). Large groups tend to make more noise that alerts bears to the group's presence at a distance, and large parties are also more intimidating to grizzly bears than smaller groups (McClung 2001, Herrero 2002). In addition, larger groups generally have better vigilance (the 'many eyes' effect) than smaller groups (Penteriani et al. 2017), thereby reducing the chances of surprise encounters. Herrero (2002) analyzed 165 grizzly bear–inflicted human injuries from North America and found no encounters involving parties of ≥6 people that resulted in human injuries. In YNP, groups of ≥3 people are rarely injured by grizzly bears (Gunther and Hoekstra 1998), and nobody in a group of ≥5 people has been injured in the past 47 years (1970–2017, YNP Bear Management Office records). Park-wide, solo hikers account for 48% of all bear-inflicted human injuries, hiking parties of 2 people account for 48% of all injuries, and groups of ≥3 people account for only 4% of all injuries (YNP Bear Management Office records).

All 10 people injured by bears in Hayden Valley from 1970 to 2017 were traveling alone or with just one partner. Therefore, retroactively applying a party size restriction requiring groups of ≥3 people to hike in Hayden Valley, and assuming 4% of those people would still be injured during encounters with bears (10 people × 0.04 = ∼1 person injured), the party size restriction may have prevented approximately 9.5 of the 10 (95%) bear-caused human injuries that occurred in Hayden Valley during 1970–2017 (Table 3).

Prohibition of off-trail travel. The danger of surprise encounters with grizzly bears decreases if people are alert and bears know where to expect people (Herrero 2002). With the current popularity of wildlife photography and advances in ultra-light backcountry gear, cross-country travel is becoming increasingly popular, making human activities less predictable to grizzlies and surprise encounters more probable. A restriction prohibiting off-trail travel would make human activity in Hayden Valley more spatially predictable to bears, possibly reducing the chances that bears will react defensively during surprise encounters. Bears may associate trails with people and react less aggressively toward people on trails where they expect to encounter them (Gunther and Hoekstra 1998). Bears appear to react more aggressively to encounters with people in off-trail areas where they are not expecting people (Gunther and Hoekstra 1998). Herrero and Fleck (1990) reported an increasing trend for grizzly bear–inflicted human injuries in North America to occur in off-trail areas. Gunther and Hoekstra (1998) reported that approximately half of the grizzly bear–inflicted human injuries in backcountry areas of YNP occurred while people were hiking off-trail. Yellowstone National Park has >1,600 km of maintained designated hiking trails. It is difficult to accurately compare the proportion of injuries that occur while people are travelling on trails versus off of trails because YNP does not keep records of how many recreationists travel on-trail versus off-trail. Maintained trails make travel and navigation easier and more efficient, so most backcountry recreationists in YNP likely spend the majority of their time on the designated trail system. Coleman (2012) reported that 67% of the backcountry recreationalists he surveyed in YNP remained on designated trails for the entirety of their hikes. In YNP during 1970–2017, 21 of the 44 (48%) people injured by grizzly bears in backcountry areas were traveling off-trail and 21 (48%) were traveling on designated trails (YNP Bear Management Office records). Two incidents (4%) occurred in backcountry campsites.

Seven of the 10 people injured by grizzly bears in Hayden Valley during 1970–2017 were traveling cross-country off-trail when the incidents occurred. Therefore, retroactively applying a prohibition of off-trail travel may

have prevented 7 of the 10 (70%) bear-caused human injuries that occurred in Hayden Valley (Table 3).

Requirement to carry bear spray. Bear spray has proven effective at stopping aggressive behavior by bears during surprise encounters (Herrero and Higgins 1998, Smith et al. 2008) and is often recommended as a defensive tool to stop or defuse bear attacks (Brown 1996, Lapinski 1998, Herrero 2002, Rubbert 2006, Smith 2006, McCloskey 2009, Snow 2016). Although the first documented use of bear spray in YNP occurred in 1984, bear spray was not readily used by employees or recreationists in the park until the early 1990s. In the early to mid-1980s, bear spray was still primarily in the test phase (Hunt 1984, Rogers 1984), and in the late 1980s many people were still skeptical of its efficacy. Only 10 of the 46 (22%) people attacked by bears in backcountry areas of YNP during 1970–2017 were carrying bear spray. Seven of the 10 (70%) people had time to deploy it and all received only minor injuries. Five of these 7 did not deploy their bear spray until after the bear had already made contact. Hypothetically, if all 10 people injured by grizzly bears in Hayden Valley over the past 48 years (1970–2017) had been carrying bear spray, approximately 70% of them would likely have been able to deploy it. With a 92% efficacy rate (Smith et al. 2008), approximately 6–7 of them would likely have been able to stop or reduce the duration and severity of the interaction (10 previous injuries $\times$ 0.70 able to deploy bear spray $\times$ 0.92 success at stopping attack when bear spray deployed $=$ 6.4 attacks stopped or of reduced severity; Table 3). Under the current paradigm, where more effort is being made to teach visitors about the importance of bear spray and how to use it effectively (Gunther et al. 2014b), we might expect that an even greater proportion of backcountry recreationists would be able to successfully deploy their bear spray to stop aggressive interactions with bears. A regulation requiring backcountry recreationists to carry bear spray has the potential to significantly reduce the number and severity of human injuries from grizzly bears in Hayden Valley.

Management considerations

Our sample sizes of backcountry bear attacks are admittedly small (i.e., 10 bear-inflicted human injuries in Hayden Valley and 44 park-wide), making them inherently difficult to analyze. However, our conclusion that simple changes in human behavior are likely the most efficient way to reduce the risk of bear attack are also supported by results from other studies in North America and the world (Herrero 1970, 1985, 2002; Herrero and Fleck 1990; Gunther and Hoekstra 1998; Herrero and Higgins 1998; Smith et al. 2008; Penteriani et al. 2017). Our analysis suggests that human behavior–based recreational restrictions that mandate people take certain safety precautions (i.e., requiring min. party sizes $\geq$3 people, prohibiting off-trail travel, requiring carry of bear spray) may have substantially more potential to prevent bear-inflicted human injuries than most food-based seasonal closures that correspond to the time periods grizzlies consume specific foods. The following management options provide potentially effective methods to reduce the number and severity of bear attacks in Hayden Valley and/or YNP, while still providing for reasonable recreational opportunities and minimizing restrictions placed on the public that may negatively affect their experience (Table 4).

Management options include:

1) *Require a group size of $\geq$3 people for hiking in Hayden Valley*. A regulation requiring $\geq$3 people for parties entering Hayden Valley has the greatest potential to reduce grizzly bear–caused human injuries (potential 95% reduction in grizzly-inflicted human injuries). All human injuries caused by grizzly bears in Hayden Valley since 1970 have involved parties with <3 people. However, most people in YNP hike alone or with one partner (Gunther et al. 2015), so a group size requirement of $\geq$3 would likely be difficult for many visitors to comply with, and therefore would likely have some negative impact on visitor experience. In addition, implementing bear safety through federal regulations may conflict with wilderness values and detract from the wilderness character of Hayden Valley, which has been recommended for wilderness designation. A group size requirement would be difficult for YNP to enforce, so would rely primarily on voluntary compliance.
2) *Prohibit off-trail hiking in Hayden Valley*. A regulation prohibiting off-trail travel would also be effective at substantially reducing the frequency of grizzly-caused human injuries in Hayden Valley (70% reduction in grizzly-inflicted human injuries). Seventy percent of the people injured by grizzly bears in Hayden Valley since 1970 were traveling off-trail. Coleman (2012) found that 67% of the parties of backcountry recreationalists he surveyed in YNP never left designated trails, 27% spent some time traveling both on and off-trails, and 6% traveled completely off-trail.

Table 4. Positive and negative aspects of the management options with the most potential to reduce grizzly bear (*Ursus arctos*) –inflicted human injuries in Hayden Valley, Yellowstone National Park, USA, 1970–2017.

Management option	No. of days valley closed to recreation	Potential efficacy	Positive aspects	Negative aspects
Group size of ≥3 required for hiking	0	95%	No impact to visitor access	Difficult for average visitor to comply with; Impact to wilderness values; Difficult to enforce
No off-trail travel allowed	0	70%	No impact to trail use	Impact to wilderness values; Difficult to enforce
Closure during peak periods of activity of male and female grizzly bears combined in Hayden Valley	78	70%	Unrestricted visitor access during spring and autumn	Long period of closure to public; Impact to wilderness values; Difficult to enforce
Bear spray required if party size <3	0	64%	No impact to visitor access; Easy for many visitors to comply	Impact to wilderness values; Financial burden for visitors; Difficult to enforce
Bear spray required for all hikers in Hayden Valley	0	64%	No impact to visitor access; Easy for many visitors to comply	Impact to wilderness values; Financial burden for visitors; Difficult to enforce
Bison rut closure	63	60%	Unrestricted visitor access during spring, early summer, and autumn	Moderate period of closure to public; Impact to wilderness values; Difficult to enforce
Closure during peak period male grizzlies are active in Hayden Valley	62	50%	Unrestricted visitor access during spring and autumn	Moderate period of closure to public; Impact to wilderness values; Difficult to enforce
Closure during peak period female grizzlies are active in Hayden Valley	62	40%	Unrestricted visitor access during spring, late summer, and autumn	Moderate period of closure to public; Impact to wilderness values; Difficult to enforce
Horsetail grazing season closure	61	40%	Unrestricted visitor access during spring, late summer, and autumn	Moderate period of closure to public; Impact to wilderness values; Difficult to enforce
Clover grazing season closure	38	40%	Relatively short closure period	Impact to wilderness values; Difficult to enforce
Biscuitroot root digging season closure	47	40%	Relatively short closure period	Impact to wilderness values; Difficult to enforce
Improved bear safety messaging	0	Unknown	No impact to visitor access; No impact to wilderness values; No enforcement necessary	High cost to implement effectively; Unknown efficacy
Status quo	0	1 attack ~every 5 yr	No impact to visitor access; No impact to wilderness values; No enforcement necessary	1 human injury ~every 5 yr; 1 human fatality ~every 16 yr; Removal of 1 grizzly every 12 yr[a]

[a]Four grizzly bears involved in bear-caused human injuries were removed (lethally or sent to zoos) from Hayden Valley during the 48-yr period from 1970 to 2017.

Although most (67%) backcountry recreationalists never leave designated trails in YNP, almost half (48%) of the people injured by bears in YNP after 1969 were traveling off-trail when they encountered the bear that attacked them. This supports the conclusion by Herrero (2002) that off-trail travel increases the risk of surprise encounters and bear attacks. A prohibition on off-trail travel would likely have some negative impact on the wilderness experiences of the more adventuresome backcountry recreationalists that prefer to hike off-trail. A prohibition on off-trail travel would be difficult to enforce, and so would rely primarily on voluntary compliance.

3) *Close Hayden Valley during the period that male and female grizzlies are most active*. A seasonal closure of Hayden Valley during the time of the year (15 Jun–31 Aug) that male and female

grizzly bears spend the most time in the valley also has the potential to significantly reduce grizzly bear encounters that result in human injury (70% potential reduction in grizzly-inflicted human injuries). However, a closure during the peak period that male and female grizzlies are present in the valley would prevent recreational hiking for approximately 78 days during the peak season of park visitation, and therefore would not meet our criterion of allowing reasonable recreational opportunities.

4) *Require hikers in Hayden Valley to carry bear spray*. A regulation that required all hikers entering Hayden Valley to carry bear spray has the potential to reduce the chances of bears making physical contact with hikers when charging while reacting with defensive aggression to surprise encounters (64% reduction in grizzly-inflicted human injuries), and if contact is made, lessening the severity of human injuries that occur. However, such a regulation could be a financial burden to some hikers (bear spray costs ~US$50/can, although rentals at a rate of $9.25/day or $28/week, are also available), would be difficult to enforce, and would likely be opposed by many wilderness proponents that want the freedom of making their own safety choices when hiking in recommended or designated wilderness. A requirement to carry bear spray would be difficult to enforce, and so would rely primarily on voluntary compliance.

5) *Require hikers in Hayden Valley with <3 people in their group to carry bear spray*. A regulation that requires hikers that enter Hayden Valley in parties of <3 people to carry bear spray, while allowing those in groups of ≥3 people to hike without bear spray if they choose, has significant potential to improve visitor safety while also being relatively easy for most visitors to comply with. In addition, such a regulation would not require any closures of the area to visitors. Any backcountry recreationalists that arrive in YNP with <3 people could purchase bear-deterrent spray from many locations in and near the park. Bear spray rentals are also available in the park, making compliance relatively affordable for most visitors. No restrictions on visitors riding stock or hiking in groups ≥3 people are warranted because stock users and hiking parties of ≥3 are rarely injured by bears during surprise encounters. However, such a regulation could be a financial burden to some hikers, would be difficult to enforce, and would likely be opposed by some recreationalists that want the freedom of making their own safety choices when hiking in recommended or designated wilderness.

6) *Close Hayden Valley during the bison rutting season*. A seasonal closure of Hayden Valley during the period (15 Jul–15 Sep) that grizzly bears typically scavenge adult male bison that die of rut-related injuries also has the potential to significantly reduce grizzly bear encounters that result in human injury (60% reduction in grizzly-inflicted human injuries). A bison rut closure would prevent recreational hiking for approximately 60 days during the peak season of park visitation, but would still provide reasonable opportunity (~90 days) for recreational activity in the valley during spring, early summer, and autumn. A seasonal closure during the bison rut would also reduce human disturbance of bears foraging on bison carcasses, thereby increasing habitat effectiveness of the area.

7) *Expand public outreach*. An effective information and education campaign designed to improve backcountry recreationalists' awareness of how human behavior, party size, bear spray, off-trail travel, and seasonal timing of hikes can influence the frequency of human–bear encounters and the outcomes of those encounters also has the potential to significantly reduce the frequency of bear-inflicted human injuries in Hayden Valley and YNP. An educational campaign was successfully used to induce park visitors in YNP to stop a nearly century-old practice of hand-feeding bears along park roads (Wondrak Biel 2006, Garshelis et al. 2017). Educational safety campaigns have also been used successfully to increase seatbelt use (Vasudevan et al. 2009) and reduce tobacco use (McAfee et al. 2013, Xu et al. 2015) in the United States. Voluntary behavior changes are also generally better accepted by the public than are those required by federal regulation. However, recent surveys indicate very low compliance with hiking group size and bear spray carry recommendations in YNP (Gunther et al. 2015), despite significant messaging efforts (Gunther et al. 2014b, Gunther 2015). If managers choose a public outreach strategy, new innovative messaging campaigns will be needed to improve visitor compliance with bear safety recommendations. It is also important to understand the efficacy of educational campaigns. Therefore, implementation

of any new educational campaign designed to improve visitor safety in bear country should be accompanied by an evaluation program to measure its effectiveness.

8) *Retain status quo.* Many wilderness recreationists want the freedom to make their own safety choices and do not want to be burdened with governmental regulations, even if those regulations are for their own safety. For some, the risks associated with wilderness recreation are a desired factor when selecting areas in which to pursue their outdoor activities. For these types of recreationists, YNP's existing bear safety regulations may already be considered adequate or even burdensome. Indeed, National Park Service management guidance recommends a minimalist approach to safety in designated or proposed wilderness, although it does not completely rule out regulatory mechanisms, stating: "The National Park Service will not modify the wilderness area to eliminate risks that are normally associated with wilderness, but it will strive to provide users with general information concerning possible risks, any recommended precautions, related user responsibilities, and applicable restrictions and regulations, …" (National Park Service 2006: General Policy, Chapter 6.4.1:86).

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Supplemental material

Text S1, Table S1, Fig. S1, and Text S2