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EFFECTS OF EXOTIC SPECIES ON YELLOWSTONE'S GRIZZLY BEARS

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ABSTRACT.—Humans have affected grizzly bears (*Ursus arctos horribilis*) by direct mortality, competition for space and resources, and introduction of exotic species. Exotic organisms that have affected grizzly bears in the Greater Yellowstone Area include common dandelion (*Taraxacum officinale*), nonnative clovers (*Trifolium* spp.), domesticated livestock, bovine brucellosis (*Brucella abortus*), lake trout (*Salvelinus namaycush*), and white pine blister rust (*Cronartium ribicola*). Some bears consume substantial amounts of dandelion and clover. However, these exotic foods provide little digested energy compared to higher-quality bear foods. Domestic livestock are of greater energetic value, but use of this food by bears often leads to conflicts with humans and subsequent increases in bear mortality. Lake trout, blister rust, and brucellosis diminish grizzly bears foods. Lake trout prey on native cutthroat trout (*Oncorhynchus clarkii*) in Yellowstone Lake; white pine blister rust has the potential to destroy native whitebark pine (*Pinus albicaulis*) stands; and management response to bovine brucellosis, a disease found in the Yellowstone bison (*Bison bison*) and elk (*Cervus elaphus*), could reduce populations of these 2 species. Exotic species will likely cause more harm than good for Yellowstone grizzly bears. Managers have few options to mitigate or contain the impacts of exotics on Yellowstone's grizzly bears. Moreover, their potential negative impacts have only begun to unfold. Exotic species may lead to the loss of substantial high-quality grizzly bear foods, including much of the bison, trout, and pine seeds that Yellowstone grizzly bears currently depend upon.

Key words: exotic species, grizzly bears, Yellowstone, Ursus arctos, *white pine blister rust, brucellosis, lake trout, clover, dandelion.*

Grizzly bears (*Ursus arctos horribilis*) in the contiguous United States were extirpated from 98% of their historical range between 1850 and 1950 by human-caused mortality, often precipitated by competition for space and resources (U.S. Fish and Wildlife Service 1993). The Greater Yellowstone Area (GYA) contains 1 of the 2 largest remaining grizzly bear populations in the contiguous United States, in an area of about 23,000 km^2. Grizzly bears in this region were listed as threatened under the U.S. Endangered Species Act in 1975 for several reasons, including "the present or threatened destruction, modification, or curtailment of habitat or range" (U.S. Fish and Wildlife Service 1993). In the GYA, deleterious human influences persist in the form of human developments, roads and trails, direct mortality, loss of secure habitat, and availability of human foods. Humans also have affected grizzly bears by introducing exotic or nonnative species.

Yellowstone's grizzly bears have coexisted with exotic species for decades. However, the spread of exotics and their effects on Yellowstone's bears have escalated in recent years. Of all the exotics potentially influencing grizzly bears in the GYA, a select group is notable as being of either the greatest benefit or the greatest harm. This group includes lake trout (*Salvelinus namaycush*), white pine blister rust (*Cronartium ribicola*), domesticated livestock such as cattle and sheep, bovine brucellosis (*Brucella abortus*), common dandelion (*Taraxacum officinale*), and nonnative clovers (*Trifolium* spp.).

In this paper we present an overview of these nonnatives and their current and potential future effects on Yellowstone's grizzly bears. We review and interpret existing relevant information, including published scientific studies and data recently collected by management agencies in the Yellowstone region. We first address nonnatives that are potentially

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important sources of nutrition and then nonnatives that are, directly or indirectly, potentially important threats to bears.

SITE

The Yellowstone grizzly bear population currently occupies over 6 million acres (Fig. 1) in Montana, Idaho, and Wyoming (U.S. Fish and Wildlife Service 1993). This encompasses lands managed by Yellowstone (YNP) and Grand Teton national parks (including the John D. Rockefeller Memorial Parkway) and the Gallatin, Shoshone, Bridger-Teton, Targhee, and Beaverhead national forests as well as some state and private lands (Gunther et al. 1999). Detailed descriptions of the recovery area can be found in U.S. Fish and Wildlife Service (1993, 1994) and Mattson et al. (1991, 1992).

EXOTIC FOODS

Nonnative Clovers and Dandelion

Nonnative clovers and dandelion are widespread in the Yellowstone region. Red and alsike clovers (*Trifolium repens* and *T. hybridum,* respectively) and dandelion arrived in the New World probably along with the first livestock from Europe. Their spread to the GYA was inevitable and was abetted by cultivation of hay in and around YNP, as well as transport of feed into backcountry areas for horses and cattle. There were a surprising number of livestock and haying operations in YNP itself dating back to the late 1800s (Haines 1996, Meagher and Houston 1998). The spread of nonnative clovers and dandelions probably proceeded apace with the well-documented invasion of common timothy (*Phleum pratense*) between the 1880s and 1950s (Houston 1982, Meagher and Houston 1998). More recently, these weedy species have continued to spread on their own along roads and trails aided, in the case of clovers, by the seeding of roadbeds by managers on non-park lands. Even more dramatically, red and alsike clover were broadcast-seeded on U.S. Forest Service lands in the wake of extensive fires during 1988 to stabilize denuded steep slopes and valley bottoms.

Grizzly bears eat dandelion and nonnative clovers wherever these plants are common in grizzly bear range (Mattson 1990). In Yellowstone most consumption of dandelions and clovers by bears occurs between May and August, with use of dandelion peaking earlier (May and June) and use of clover peaking later (July and August). Heaviest grazing of nonnative clovers by bears occurs on dense patches found in low-elevation meadows (Graham 1978, Gunther 1991). Grazing by bears at these sites can be intense enough to maintain a grazing lawn typified by persistent regrowth of succulent foliage stimulated by the heavy cropping. It is not uncommon to find 5 to as many as 50 bear feces at such sites during July. Sites where bears graze dandelions are less well defined, but they are typified by an abundance of dandelions and other forbs (Mattson 2000).

There is no evidence that use of nonnative clovers and dandelion has a population-level effect on either birth or death rates of grizzly bears (Mattson 1998, 2000, Pease and Mattson 1999). As with many other lower-quality foods, however, clover and dandelions can be a substantial source of energy for individual bears for abbreviated periods of time (Graham 1978, Gunther 1991). Overall, the low return of net digested energy obtained from clover and dandelions compared to trout, ungulates, and pine seeds (Mattson et al. 1999) and the generally small fraction of time devoted to grazing these foods (Mattson et al. 1991, Mattson 2000) suggest that population-wide effects on fecundity would be minor.

There is evidence that use of clover, in particular, can lead to elevated conflicts between grizzly bears and humans (unpublished data, Bear Management Office, YNP). This occurs when clover along roads, backcountry trails, or near human developments attracts bears to these areas where they are more likely to encounter humans. Increased exposure to humans can lead bears to lose their fear of man, resulting in an increase of bear-human conflicts and human-caused grizzly bear mortalities (Gunther 1994, Gunther et al. 2000).

To date, there has been little control of nonnative clovers or dandelions by managers of public lands. Managers have often been responsible for the propagation of clover. Compared to other invasive exotic plants that are the focus of management, clovers and dandelions are quite benign. It is unlikely that resources will be allocated for the control of nonnative clovers and dandelion in the near future. Thus, these beneficial exotic foods will likely

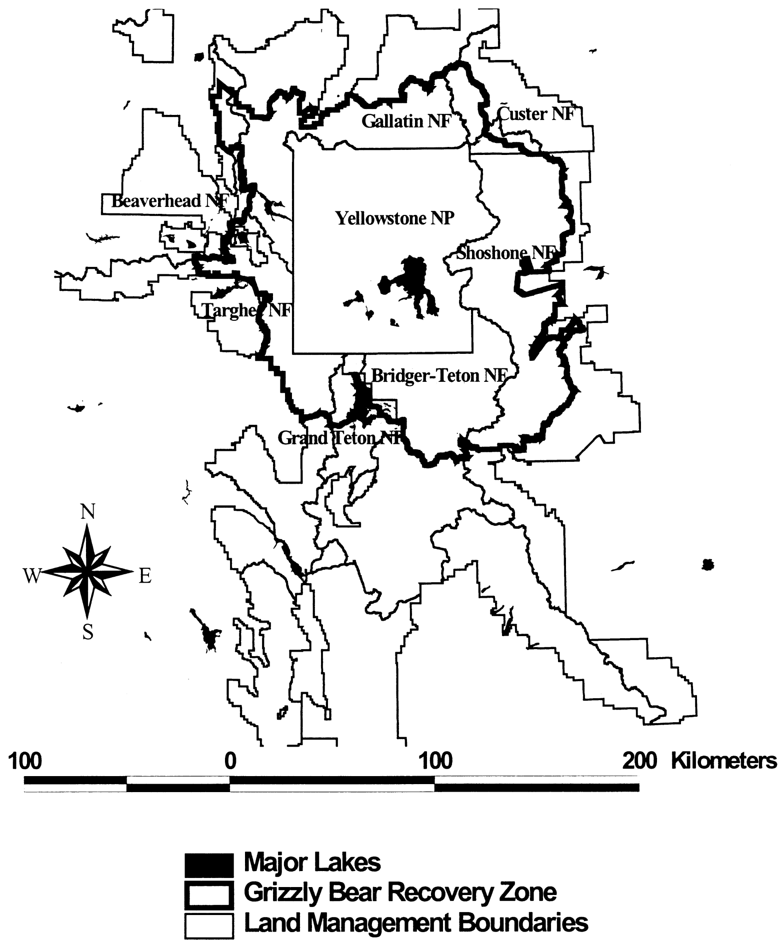

Fig. 1. The Yellowstone Grizzly Bear Recovery Zone on federal lands in the Greater Yellowstone Area.

remain available to bears. However, given local problems with roadside or trailside conflicts arising from grizzly bear use of clover, control of clover in these locations might be considered when secondary negative effects are mitigated and such control is within the scope of governing policies.

Livestock

Grizzly bears prey on domestic cattle, sheep, and occasionally horses in areas where these nonnatives have been introduced into grizzly bear range. Livestock are potentially a high-quality, abundant food source for bears in the GYA. However, livestock also compete with bears for some vegetal foods (Jorgensen 1983, Stivers and Irby 1997), and bears that persistently prey on livestock are usually killed in control actions. Historically, predator control of livestock-depredating carnivores was widespread (Anderson et al. 1997) and contributed significantly to the grizzly bear's decline throughout the western United States (Storer and Tevis 1955, Brown 1985).

In the Yellowstone region most livestock producers winter their livestock on private land, and they then pay a fee to the federal government to graze their livestock on public land (grazing allotment) during the summer season (Mack et al. 1992). There are approximately 392 active grazing allotments encompassing 16,642 km^2 (35%) of public land in the GYA (Mack et al. 1992). Approximately 105,000 sheep, 77,000 cattle, and 1,000 horses (Mack et al. 1992) seasonally occupy these allotments. In comparison, there are an estimated 56,000 elk (*Cervus elaphus*), 6,000 moose (*Alces alces*), and 4,000 bison (*Bison bison*) in the GYA (U.S.

Fish and Wildlife Service 1994). Thus, livestock are potentially both a significant source of nutrition for bears and competitors for vegetal bear foods.

Most grizzly bears will opportunistically prey on livestock (Knight and Judd 1983, Mattson 1990). The majority of grizzly bear depredations on livestock occur from mid- to late June through September while livestock are being grazed on public land (Murie 1948, Jorgensen 1983, Anderson et al. 1997). From 1992 to 1998, of the 301 reported incidents of grizzly bear depredations in the Yellowstone ecosystem, 84% occurred on federal grazing allotments, 15% on private lands, and 1% on state lands (Gunther et al. 1993, 1994, 1995, 1996, 1997, 1998, 1999). Old-age male bears are most likely to become chronic depredators of cattle (Mattson 1990, Anderson et al. 1997).

Livestock are potentially an important source of energy for Yellowstone's grizzly bears. At approximately 4.0–5.5 kcal $\cdot$ g^{-1}, meat from native ungulates and domestic livestock is one of the most concentrated sources of net digestible energy available to bears in the GYA (Mattson et al. 1999). Individual bears can consume numerous cattle or sheep (Anderson et al. 1997). In addition to predation, grizzly bears also scavenge livestock that die from other causes. Even though individual bears may obtain considerable energy from livestock, there is no clear evidence that use of domestic livestock translates into a significant population-level increase in female fecundity (Mattson 2000). Moreover, given that males depredate on livestock more often than females (Anderson et al. 1997), such a population-level effect would be unexpected.

Any positive population-level effect on grizzly bear birth rates is likely negated by the higher death rate of bears that repeatedly kill livestock. Between 1996 and 1999, four grizzly bears involved in livestock depredations were captured and euthanized in control actions. An additional 19 grizzly bears were captured and relocated to areas away from livestock grazing allotments (Gunther et al. 2000); relocated bears typically exhibit higher mortality (Blanchard and Knight 1996). Total livestock-related grizzly bear mortality may be underestimated as some incidents are not reported (Jorgensen 1983).

The number of livestock depredations by grizzly bears in the GYA is increasing (Gunther et al. 2000). Between 1996 and 1999, we documented 265 livestock depredations in the GYA; during 1992–1995 there were 120 depredations (Gunther et al. 2000). Most of the increase in incidents during 1996–1999 occurred outside the designated grizzly bear recovery zone (U.S. Fish and Wildlife Service 1993, Gunther et al. 2000). At present, highly selective control of livestock-depredating grizzly bears has resulted in removal of only the most chronic depredators. Depredation on livestock will likely continue to increase as grizzly bear activity outside the designated recovery zone increases. At some point the level of public tolerance of grizzly bear depredations on livestock will likely be exceeded, especially in areas far from the recovery zone boundary. Predator control actions against depredating grizzly bears will likely increase as well. The interface areas between occupied grizzly bear habitat and livestock-producing agricultural areas are likely to be a continual challenge to grizzly bear managers in the Yellowstone region.

EXOTIC THREATS

Bovine Brucellosis

Bovine brucellosis is a nonnative bacterial disease of ungulates, causing placentitis, metritis, and abortion in newly infected individuals. The precise origin of this disease in North America is not known, but domestic cattle imported from Europe were the likely vector (Meagher and Meyer 1994). Transmission of brucellosis occurs through contact with infected tissue such as aborted fetuses, birth membranes, or vaginal discharges from infectious animals (U.S. National Park Service 2000). Although the disease affects reproduction in wild ungulates, the primary management concern in the GYA is potential transmission from wild ungulates—primarily bison and elk—to domestic cattle. The first known case of brucellosis in Yellowstone bison occurred in 1917 (Meagher and Meyer 1994, U.S. National Park Service 2000). Currently, both bison and elk in the GYA maintain endemic brucellosis.

Carnivores are exposed to brucellosis when preying on infected ungulates or feeding on infected carrion. Blood samples from grizzly bears in the GYA exhibited a 17% (n = 69) seroprevalence to brucellosis, suggesting bears are exposed to the disease through contact with infected ungulates (K. Aune, Montana

Department of Fish, Wildlife and Parks, personal communication). However, there is no evidence the disease negatively impacts reproductive performance in any carnivore. Although the direct effect of brucellosis on grizzly bears is unknown, it is probably negligible. Brucellosis is likely to impact the Yellowstone grizzly bear population indirectly, if reductions in ungulate populations are instituted for disease management.

Until 1968 bison and elk were maintained at low numbers within YNP by direct reductions (Houston 1982). Following termination of this program, numbers of elk and bison and amount of biomass associated with bison and elk increased significantly (Fig. 2; Singer and Mack 1993). Changes in climate during the early 1980s, to drier winters and wetter summers, also may have contributed to this increase (Despain et al. 1986, Engstrom et al. 1991, Balling et al. 1992). For almost 30 years, the YNP bison herd grew steadily, increasing 10-fold by 1996 (U.S. National Park Service 1997). Within the last 2 decades, changes in movements led to increased wintertime use of areas outside YNP by bison (Meagher 1989). These changes in distribution increased the potential for transmission of brucellosis to domestic cattle and brought this issue to the forefront of public and scientific debate.

Planning for control of brucellosis in or near YNP is currently underway (U.S. National Park Service 2000). Interestingly, brucellosis itself is not expected to have an effect on ungulate populations in the Yellowstone region (Meagher and Meyer 1994, U.S. National Park Service 2000). Rather, management of native ungulates to reduce exposure of cattle to the disease may have a greater impact on numbers and distributions of bison. Over 2000 bison were killed between 1994 and 1999 in attempts to limit their movement into agricultural areas (U.S. National Park Service 2000; G. Kurz, YNP, personal communication). Current management plans include the possibility of maintaining bison herds at substantially lower levels than those of the late 1980s. Thus, this disease stands to affect the GYA grizzly population mostly through a management response to the real, or perceived, threat of bovine brucellosis to domestic cattle.

Currently, the GYA supports some of the highest native ungulate densities in North America (Mattson 1997). There was a strong positive relationship between estimated annual standing biomass of ungulates and minimum grizzly bear population estimates (Fig. 2). Although this correlation does not prove cause and effect, it adds further supportive evidence that the availability of ungulates may have a positive influence on the Yellowstone grizzly bear population.

Grizzly bears in the GYA are unique among interior North American populations in their substantial consumption of ungulates (Craighead and Mitchell 1982, Mattson et al. 1991, Mattson 1997). Recently, N_{15} isotopes in grizzly bear hair were used to index the proportion of meat in grizzly bear diets in the GYA (Hildebrand et al. 1999). Findings indicate that ungulate meat comprises almost half of the annual energy intake of adult females and over half for adult males (Hildebrand et al. 1999). Of all ungulate species consumed by grizzly bears, bison are used with disproportionately greatest frequency and intensity, contributing 24% of total ungulate biomass consumed (Green et al. 1997, Mattson 1997). Because ungulates are one of the most concentrated sources of net digestible energy available to Yellowstone's grizzly bears (Mealey 1975, Pritchard and Robbins 1990, Craighead et al. 1995, Mattson et al. 1999), availability of ungulates—especially bison—potentially affects fecundity of the grizzly bear population.

Availability of ungulate meat may influence levels of human-caused grizzly bear mortality. Numbers of bear-human conflicts and human-caused bear mortalities are negatively correlated with availability of high-quality natural foods (Mattson et al. 1992, Gunther et al. 2000). Any significant reduction in ungulate numbers to control the spread of brucellosis may contribute to increases in bear-human conflicts and human-caused grizzly bear mortalities, especially during shortages of other natural foods.

Lake Trout

Yellowstone Lake is home to the largest inland population of native cutthroat trout (*Oncorhynchus clarkii*) in the world. Lake trout were discovered in Yellowstone Lake in 1994. Since then, Yellowstone anglers have caught thousands of lake trout, and tens of thousands have been caught in gill nets set by YNP Aquatic Resources staff (Mahony et al. in preparation). Lake trout are not native to the

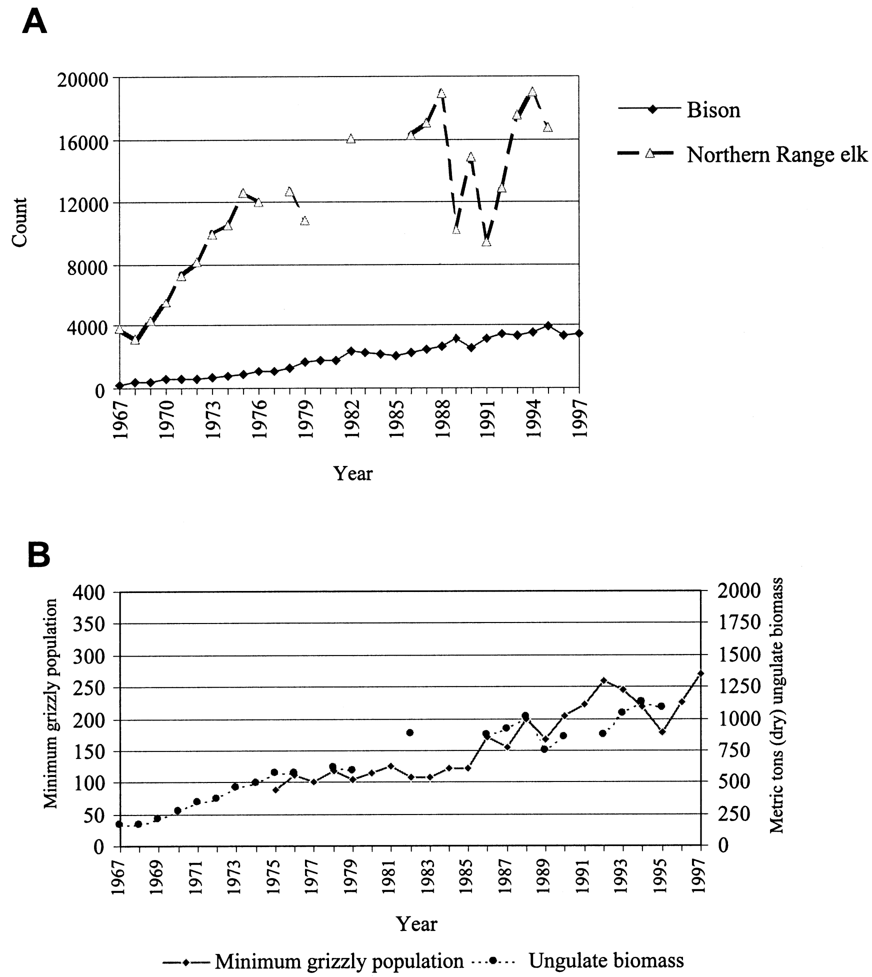

Fig. 2. A, Numbers of bison and northern range elk in YNP, 1967–1997; B, estimated metric tons of standing ungulate (bison and northern range elk) biomass from 1967 to 1997 in Yellowstone National Park. Annual counts of the northern range elk and YNP bison populations are from NPS (1997). Estimates of standing biomass of elk and bison in the Yellowstone ecosystem were calculated using annual ungulate counts, estimated sex and age composition of ungulate populations, and estimates of edible dry weight biomass available from different sex and age classes of elk and bison. Estimates of average sex and age composition for the northern range elk were calculated from Houston (1982). Average sex and age composition estimates for YNP bison were from J. Mack (National Park Service, personal communication) and K. Frey (Montana Fish, Wildlife, and Parks, personal communication). Estimates for dry weight of edible meat available from different sex and age classes of elk and bison were from Mattson (1997). Grizzly bear minimum population estimates and ungulate biomass were positively correlated (r = 0.74) between 1975 and 1996 before reductions in bison and wolf reintroduction occurred.

GYA; they were stocked in historically barren Lewis Lake, approximately 7 miles from Yellowstone Lake in 1896. Although the exact origin of lake trout in Yellowstone Lake is not known, they likely came from Lewis Lake. Recent catches of lake trout from Yellowstone Lake revealed a reproducing population, with some 25+-year-old individuals, indicating lake trout have existed in Yellowstone Lake for some time (Mahony et al. in preparation).

Lake trout are major piscivorous predators that threaten to reduce Yellowstone Lake's native cutthroat trout population and adversely affect numerous wildlife species that depend on the cutthroat (Kaeding et al. 1996). The long-term impact of the illegally introduced lake trout on cutthroat trout is potentially substantial (McIntyre 1995, Kaeding et al. 1996, Ruzycki and Beauchamp 1997). Lake trout have reduced native cutthroat trout populations in western North American lakes including Bear Lake, Utah; Lake Tahoe, Nevada; Jackson Lake, Wyoming; and Heart Lake, Yellowstone National Park (Ruzycki and Beauchamp 1997).

Significant reduction of cutthroat trout populations in Yellowstone Lake will alter ecosystem processes, including energy flow to consumers at higher trophic levels. These consumers include 28 known terrestrial and avian species, including grizzly bears (Schullery and Varley 1995). Cutthroat trout are vulnerable to terrestrial and avian predators because they spawn in tributaries and use shallow water within Yellowstone Lake. By contrast, because lake trout primarily use deep waters, they are unavailable to this same suite of predators (Schullery and Varley 1995, Kaeding et al. 1996).

Because of their current abundance, high digestibility, and energy content (Pritchard and Robbins 1990), cutthroat trout are an important part of the diet for numerous grizzly bears (Reinhart and Mattson 1990, Mattson and Reinhart 1995). Despite the limited distribution of fishable cutthroat trout spawning streams, bears from a large portion of the ecosystem likely consume cutthroat trout at some point in their lives (Mattson and Reinhart 1995).

A substantial number of grizzly bears in the GYA are known to use spawning cutthroat trout. Results from a lake-wide survey of all Yellowstone Lake spawning streams during 1987 estimated a minimum of 44 autonomous bears using these streams (Reinhart and Mattson 1990). Analysis of DNA from hair samples collected on selected spawning streams between 1997 and 1999 identified 85 individual grizzly bears (including dependent young) on these streams (Haroldson et al. 2000). This corresponds to approximately 10–30% of the GYA bear population past the age of weaning (Eberhardt and Knight 1996).

Lake trout may already be affecting Yellowstone Lake cutthroat trout abundance. Continued monitoring of front-country cutthroat trout spawning streams near Lake and Grant villages showed a decline in the relative abundance of cutthroat trout from the late 1980s through the mid-1990s. However, in recent years spawning runs have increased to earlier levels on most streams around Yellowstone Lake, but have continued to decline in West Thumb streams (Fig. 3; Haroldson et al. 2000). The decline of spawning cutthroat trout in West Thumb streams may be an early indication of impacts from lake trout. Most lake trout currently occur in the West Thumb area of Yellowstone Lake, despite the removal of thousands by anglers and park managers (Mahony et al. in preparation).

The prognosis for Yellowstone Lake's cutthroat trout is potentially grim. Fisheries biologists have concluded that there is only a slight chance of eliminating lake trout from Yellowstone Lake (McIntyre 1995). They also predict the native cutthroat trout population could be reduced by ≥70% if nothing is done to suppress lake trout. However, there is at least a 50% chance that effective control measures could be instituted (McIntyre 1995). Mechanical measures used by YNP managers to control lake trout include lake-wide gillnetting, capture on spawning grounds, and directed angling. During 1995–2000, catches of lake trout in Yellowstone Lake increased from 200 · year^{-1} to over 13,000 · year^{-1} (Mahony et al. in preparation). Yellowstone National Park intends to continue efforts to reduce lake trout numbers and maintain native cutthroat trout populations at levels sufficient to ensure viability and their role as an important ecological component in the GYA.

White Pine Blister Rust

White pine blister rust arrived from Eurasia in North America near Vancouver, British Columbia, in 1910. This fungus infects 5-needled pines and was first noticed in western white pine (*Pinus monticola*) and whitebark pine (*P. albicaulis*) in 1921 and 1926, respectively (Hoff et al. 1994). Of all pines affected by blister rust, whitebark pine is among the least resistant. Over 99% of all trees are susceptible to infection, and of those that become infected, virtually none survive (Hoff et al. 1994). Thus, in areas where blister rust has long been established, almost all whitebark pine are either infected or dead (Kendall 1995). Blister rust spread rapidly south and east and was known from the GYA as early as the 1940s. Following the initial spread, progressive, dramatic losses of whitebark pine to blister rust were documented between the 1960s and the present, especially in areas subject to maritime climatic influences (Keane and Arno 1993, Keane and Morgan 1994, Keane et al. 1994). In the Yellowstone ecosystem, rates of

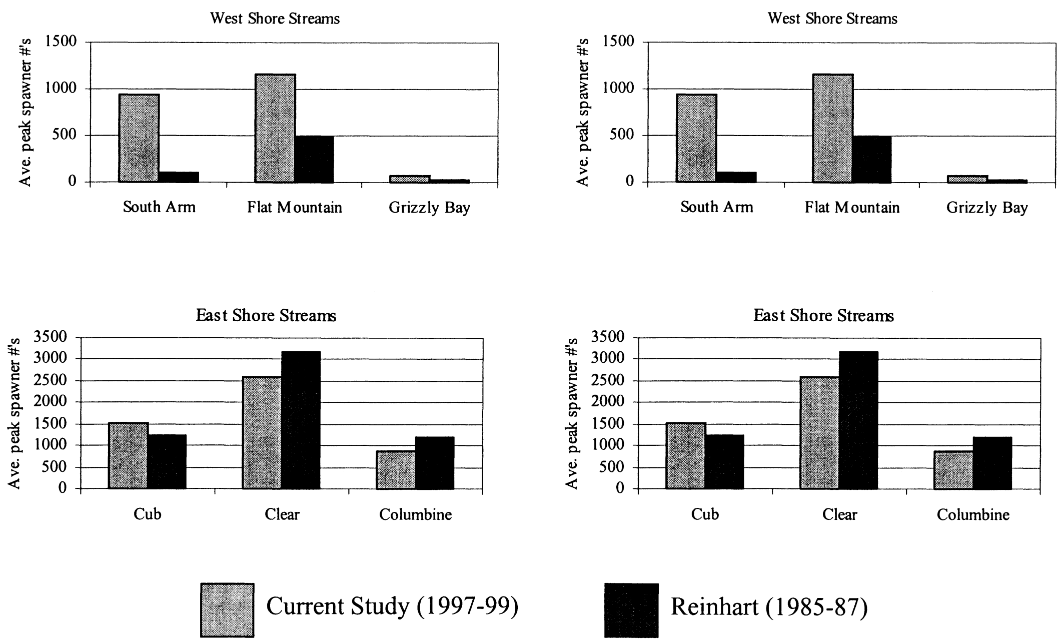

Fig. 3. Comparisons of average peak numbers of spawning cutthroat trout between study periods for 4 different areas of Yellowstone Lake (from Haroldson et al. 2000).

infection have increased from 0–7% in the 1960s to 9–54% in the 1990s, depending on the location (Smith and Hoffman 1998). The prognosis for the future in Yellowstone is inevitable spread of the disease and, along with it, eventual loss of most whitebark pine (Smith and Hoffman 1998, Koteen 1999).

Currently, whitebark pine is abundant in the Yellowstone area. Forests containing mature whitebark pine cover 26% of the landscape (Mattson 2000). Whitebark pine grows to maturity at elevations >2400–2600 m (Mattson and Reinhart 1990). Because of this high-elevation distribution, stands of mature whitebark pine are typically far from most human facilities or places where humans are otherwise active.

Yellowstone's grizzly bears make frequent and substantial use of the large, fatty seeds of whitebark pine (Mattson and Reinhart 1994). During some years pine seeds can comprise the majority of food consumed by bears ecosystem-wide. Consumption peaks during August–October, concurrent with maturation of cones and their harvest by red squirrels (*Tamiasciurus hudsonicus*). This late growing-season period corresponds with hyperphagia—a time of intensive feeding among bears prior to hibernation. Use of whitebark pine seeds by Yellowstone's grizzly bears has substantial effects on their birth and death rates. These benefits result from the energy and nutrients obtained from pine seeds, as well as from the behaviors associated with foraging on this food. Whitebark pine seeds provide substantial concentrations of fat and energy (Mattson et al. 1999) and are used twice as often by female grizzly bears as by males (Mattson 2000). Compared to females that consume few pine seeds, females that use whitebark pine seeds extensively reproduce at an earlier age, produce litters more frequently, and produce more 3-cub litters (Mattson 2000). Death rates of mature grizzly bears also nearly double during years when pine seed crops are small compared to years when they are large (Pease and Mattson 1999). Grizzly bears tend to spend most of their time in remote whitebark pine forests during years when seed crops are large. By contrast, during years when seed crops are small, bears spend much more time at lower elevations, which tend to be nearer human facilities, and consequently experience much more contact and conflict with humans (Mattson et al. 2001) Thus, high-elevation whitebark pine stands act as a refuge where grizzly bears have little contact or conflict with humans (Mattson et al. 1992).

Blister rust is poised to take a major toll on whitebark pine in the GYA. If it does, grizzly bears in the GYA will be negatively affected. With the loss of most whitebark pine, birth rates of grizzly bears will likely decline as death rates increase. Unfortunately, there are no strategies by which the short-term effects of blister rust on whitebark pine can be forestalled. Deliberate or natural selection of blister rust–resistant genomes will be beneficial only over the very long term (Hoff et al. 1994), with success contingent on reestablishment of whitebark pine in areas where it was eliminated. Of all the exotics affecting Yellowstone's grizzly bears, white pine blister rust threatens to be the most damaging.

CONCLUSIONS

Among the exotic species present in the GYA are those of potential benefit and those of potential harm to Yellowstone grizzly bears. However, when viewed in their totality, exotic species have caused or are likely to cause more harm than good. Although important to some bears, clover and dandelion provide little net digested energy compared with bison, trout, and whitebark pine seeds. Clover and dandelion provide about 1.5–2.0 kcal $\cdot$ g^{-1} in contrast to 4.0–5.5 kcal $\cdot$ g^{-1} for bison, 4.5 kcal $\cdot$ g^{-1} for trout, and 2.5 kcal $\cdot$ g^{-1} for pine seeds (Mattson et al. 1999). By contrast, livestock are a concentrated source of energy, similar to bison, and are used by a small proportion of grizzly bears living on the periphery of the GYA and provide a small part of the total meat ingested by Yellowstone's grizzly bears (Mattson et al. 1991, Mattson 1997). Livestock depredations can also lead to removal of bears from the ecosystem and erode public support for grizzly bear conservation. Because of their association with humans or human facilities, exotic foods can increase the frequency of conflicts between grizzly bears and humans, thus leading to deleterious outcomes that likely outweigh energetic benefits to the bear population.

Unfortunately, managers typically have few options to mitigate or contain the impacts of exotics on Yellowstone's grizzly bears. The U.S. National Park Service (NPS) is mandated to prevent the spread and establishment of nonnative species (U.S. National Park Service 1988). Currently, YNP administers programs to monitor and aggressively control lake trout in Yellowstone Lake and noxious weeds throughout the park at a cost of hundreds of thousands of dollars annually (Olliff et al. 2001, Mahony et al. in preparation). There is ongoing research on the use of fire and other silvicultural tools to limit the effects of blister rust in whitebark pine ecosystems (Keane and Arno 2001). However, management strategies focused on nonnative species are costly and of unknown efficacy. Further complications arise in the case of white pine blister rust because management options have been limited by loss to wildfires in 1988 of about 25% of forest stands containing mature whitebark pine in YNP (Renkin and Despain 1992, Mattson et al. 2000).

Ungulate meat may become even more important to the nutritional well being of Yellowstone's grizzly bears if whitebark pine seeds and cutthroat trout are reduced by introduced exotics. The NPS is developing plans to manage brucellosis (U.S. National Park Service 2000). Unfortunately, the effects on grizzly bears of various proposals to control brucellosis have not yet been rigorously examined. Any programs that reduce ungulate numbers will likely exacerbate the effects of whitebark pine and cutthroat trout declines. Short-term bear-human conflicts and related human-caused grizzly bear mortalities will likely increase, especially during years when natural bear foods are in short supply. Long-term reproductive success will be reduced because of older age of first reproduction, longer between-litter intervals, decreased litter size, and lower cub survival (Boyce et al. 2000, Mattson 2000). In essence, the grizzly bear population will likely exhibit characteristics of a nutritionally stressed population similar to those observed a decade following the closure of the open pit garbage dumps in 1972 (Craighead et al. 1995).

We have focused on a few exotic organisms, but others could affect Yellowstone grizzly bear habitat and foraging opportunities. Noxious weeds can impact ecosystem processes, leading to changes in native plant community structure and distribution as well as foraging and abundance of ungulate and small mammal populations (Kurz 1995, Trammel and Butler 1995, Thompson 1996). In aquatic systems recent findings of New Zealand mudsnails (*Potamopyrgus antipodarum*) and whirling disease (*Myxobolus cerebralis*) in the Yellowstone drainage (Mahony et al. in preparation) may further reduce native cutthroat trout abundance. Additional exotics with the potential to affect bears may be present in the GYA, or they could arrive in the near future and have not yet been identified.

The most troubling aspect of exotic species, especially with respect to bears, is that their potential negative impacts have only begun to unfold. At best, exotic organisms increase the uncertainty of any projection for Yellowstone's grizzly bear population. At worst, exotics could lead to declines in carrying capacity, fecundity, and overall resilience to long-term stressors. Certainly, the potential effects of exotics need to be considered in long-term planning for conservation of the Yellowstone grizzly bear population.

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