Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2013 doi: 10.1111/1365-2656.12123

Trophic cascades from wolves to grizzly bears in Yellowstone

William J. Ripple[1]*, Robert L. Beschta[1], Jennifer K. Fortin[2] and Charles T. Robbins[3]

[1]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA; [2]School of Biological Sciences, Washington State University, Pullman, WA, USA; and [3]School of the Environment and School of Biological Sciences, Washington State University, Pullman, WA, USA

Summary

1. We explored multiple linkages among grey wolves (*Canis lupus*), elk (*Cervus elaphus*), berry-producing shrubs and grizzly bears (*Ursus arctos*) in Yellowstone National Park.

2. We hypothesized competition between elk and grizzly bears whereby, in the absence of wolves, increases in elk numbers would increase browsing on berry-producing shrubs and decrease fruit availability to grizzly bears. After wolves were reintroduced and with a reduced elk population, we hypothesized there would be an increase in the establishment of berry-producing shrubs, such as serviceberry (*Amelanchier alnifolia*), which is a major berry-producing plant. We also hypothesized that the percentage fruit in the grizzly bear diet would be greater after than before wolf reintroduction.

3. We compared the frequency of fruit in grizzly bear scats to elk densities prior to wolf reintroduction during a time of increasing elk densities (1968–1987). For a period after wolf reintroduction, we calculated the percentage fruit in grizzly bear scat by month based on scats collected in 2007–2009 ($n = 778$ scats) and compared these results to scat data collected before wolf reintroduction. Additionally, we developed an age structure for serviceberry showing the origination year of stems in a northern range study area.

4. We found that over a 19-year period, the percentage frequency of fruit in the grizzly diet (6231 scats) was inversely correlated ($P < 0{\cdot}001$) with elk population size. The average percentage fruit in grizzly bear scats was higher after wolf reintroduction in July (0·3% vs. 5·9%) and August (7·8% vs. 14·6%) than before. All measured serviceberry stems accessible to ungulates originated since wolf reintroduction, while protected serviceberry growing in a nearby ungulate exclosure originated both before and after wolf reintroduction. Moreover, in recent years, browsing of serviceberry outside of the exclosure decreased while their heights increased.

5. Overall, these results are consistent with a trophic cascade involving increased predation by wolves and other large carnivores on elk, a reduced and redistributed elk population, decreased herbivory and increased production of plant-based foods that may aid threatened grizzly bears.

Key-words: bears, berry-producing shrubs, competition, endangered species, forbs, predators, trophic interactions, ungulates

Introduction

The removal of apex predators from much of the world has had diverse direct and indirect effects, oftentimes revealed through unexpected and complex interactions (Estes *et al*. 2011). For many predators, knowledge of the details of these indirect effects is still poorly known. Growth ring analysis of deciduous tree and willow (*Salix* spp.) recruitment (i.e. growth of seedlings/sprouts into tall saplings, shrubs or trees) has revealed trophic cascades occurred regularly in the northern and Gallatin ungulate winter ranges of Yellowstone National Park (YNP) when grey wolves (*Canis lupus*) were present but declined and eventually became rare after wolf elimination in the early

*Correspondence author. E-mail: bill.ripple@oregonstate.edu

20th century (Ripple & Larsen 2000; Beschta 2005; Wolf, Cooper & Hobbs 2007; Halofsky & Ripple 2008).

With these trophic cascades in mind, we considered if the loss of wolves in Yellowstone during the early 1900s may have also allowed elk (*Cervus elaphus*) to affect plant foods and cover used by grizzly bears (*Ursus arctos*). In contrast to recent information on the tri-trophic cascades of wolves–elk–woody plants, there is little work identifying potential effects of the presence or absence of wolves (carnivorous apex predators) on grizzly bears (omnivorous apex predators). Flourishing aspen (*Populus tremuloides*), cottonwood (*Populus* spp.) and willow stands are important to many grizzly bears because they are typically high in plant species diversity with understories rich in berry-producing shrubs and forbs, important bear foods (Aune & Kasworm 1989; Stivers & Irby 1997). Additionally, at high stem densities, these stands can provide hiding cover that create secure places for bears to rest and forage (Stivers & Irby 1997).

Although descriptions of trophic linkages involving ungulates and bears are rare, foraging by domestic or wild ungulates can contribute to declines in bear populations. For example, before going extinct in the American southwest during the late 1800s and early 1900s, grizzly bear diets shifted towards livestock depredation because of a lack of plant-based foods due to extensive overgrazing by livestock (Brown 1996). More recently, cattle grazing adjacent to Glacier National Park depleted important grizzly bear plant foods, particularly in aspen understories (Jonkel 1985). In a wild ungulate example, abundant white-tailed deer (*Odocoileus virgininianus*) caused an indirect extirpation of a once abundant American black bear (*Ursus americanus*) population on Anticosti Island in eastern Canada by over-browsing berry-producing shrubs (Côté 2005). In this study, we investigate whether a process similar to the above examples may have taken place with Yellowstone's bears.

The Greater Yellowstone Area has a history of one of the highest ungulate densities [primarily elk, bison (*Bison bison*), and domestic livestock] in North America as well as bears with some of the lowest berry consumption in interior North America (Mattson, Blanchard & Knight 1991; Reinhart *et al.* 2001). We hypothesized this was not a coincidence as the low availability of berries was at least partially caused by excessive ungulate browsing. For example, in recent decades, the annual average percentage dry matter of fruit in the Yellowstone's bears' diet (2·4%) was much lower than that found from studies in British Columbia (28·1%) and Alberta (18·3%) (Fig. S1, Supporting information). These differences in fruit utilization were greatest during the late summer hyperphagia period.

The hyperphagia period (July–October) is a time of the year that is most critical to the survival and reproduction of bears (Nelson *et al.* 1983). Grizzly bears have low reproductive rates compared with other terrestrial mammals and, because they give birth during hibernation, they must secure enough energy stores to sustain themselves and their offspring during hibernation (Hilderbrand *et al.* 1999; Robbins *et al.* 2012). Interior bears typically get much of their needed energy from fleshy fruits during hyperphagia because they contain large amounts of digestible carbohydrates, which are efficiently converted to fat (McDonald, Edwards & Greenhalgh 1981). However, the hyperphagia diet of Yellowstone's grizzlies differs from those of virtually all other interior bear populations by the paucity of fleshly fruits (Mattson, Blanchard & Knight 1991). Interestingly, the average percentage volume of fruit in bear scat during hyperphagia from 35 different studies in interior regions of North America, Asia and Europe was more than eight times greater than that of Yellowstone (Mattson, Blanchard & Knight 1991; Mattson 1998). In most places, fleshy fruits are a reliable source of food. In any given year, bears can often compensate for a crop failure of one berry species using other berry species when there are multiple species of shrubs producing fruit.

Our overall goal was to identify potential trophic effects of wolves and elk on plants that grizzly bears utilize (Fig. 1). To do so, we analysed historical data on elk numbers and grizzly bear diets as well as collected new data on grizzly bear fruit consumption and the establishment dates for stems of berry-producing shrubs. Specifically, we hypothesized the amount of fruit consumed by grizzly bears would (i) decline during a period of

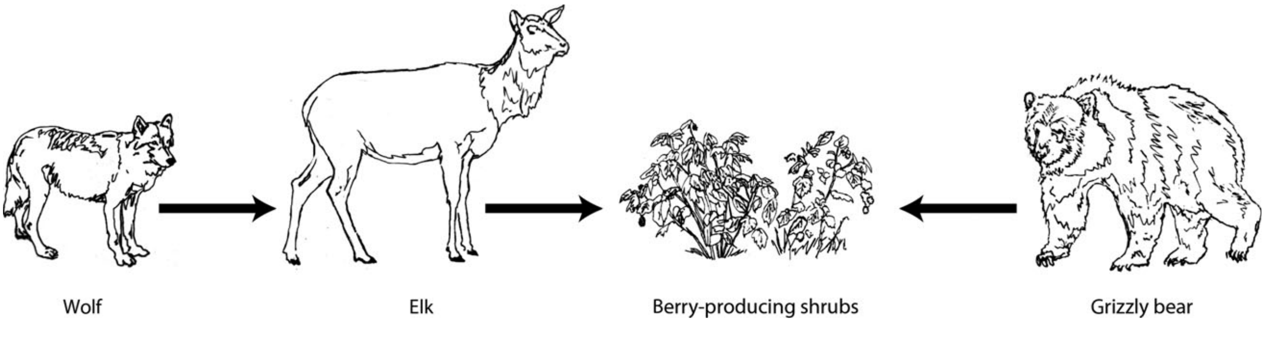

Fig. 1. Conceptual diagram showing a potential trophic cascade linking wolves to grizzly bears. The presence of wolves could reduce elk browsing, via reduced elk densities or altered elk foraging behaviour, on berry-producing shrubs allowing for increased berry production and a corresponding increase in the quantity of berries consumed by grizzly bears. This is a simplified diagram and other food web linkages are not shown.

increasing elk numbers when wolves were absent and (ii) increase following wolf reintroduction. We additionally hypothesized an increase in the establishment of berry-producing shrub stems after wolf reintroduction. The latter two processes might aid grizzly bears as other important foods, such as whitebark pine (*Pinus albicaulis*) nuts, cutthroat trout (*Oncorhynchus clarki*) and elk decline (Fortin *et al.* 2013).

HISTORICAL CONTEXT OF STUDY AREA

Early historical accounts indicate that wolves, bears and berries were once common in the Yellowstone area (Table 1, also see the early history in supporting online material and Schullery & Whittlesey 1992). However, predators other than bears were typically killed, and the last Yellowstone wolf was eliminated in 1926. Following wolf extirpation, park biologists soon became concerned about the impacts of elk browsing on vegetation and soils in the northern winter range (Skinner 1928; Rush 1932; Wright, Dixon & Thompson 1933; YNP 1958). Consequently, the Park undertook a programme of elk reductions that lasted from the mid-1930s until 1968. After the Park stopped culling elk, the population increased rapidly from an estimated low of just over 3000 in 1968 to a high of *c.* 19 000 by 1994 (Fig. S2, Supporting information). During the seven decades of wolf absence, from the 1920s to the mid-1990s, the recruitment of woody browse species on the northern range (e.g. aspen, willow and cottonwood) declined and eventually nearly halted (Ripple & Larsen 2000; NRC 2002; Beschta 2005; Wolf, Cooper & Hobbs 2007). Yellowstone National Park closed all garbage dumps by 1971, which ended this major food subsidy and grizzly bears previously dependent on garbage dispersed widely in search of alternate foods (Meagher & Phillips 1983). The subsequent increase in grizzly bear conflicts resulted in a substantial number of removed or killed bears and their numbers dramatically declined (NRC 1975; Craighead, Sumner & Mitchell 1995). Shortly thereafter, in 1975, the grizzly bear was listed as a threatened species by the U.S. Fish and Wildlife Service.

Table 1. Historical observations regarding berry-producing shrubs in the Yellowstone area

1869 *(September 12) —Cook, Folsom, Peterson Expedition—Tom Miner Creek, Northern Range near the northern boundary of Yellowstone National Park*

'… two old squaws who were engaged in gathering and drying choke-cherries… they had two or three bushels drying in the sun… so far as we could discover the cherries were their only means of subsistence' (Haines 1965, p. 12–13)

1870 *(August 24) – Washburn Expedition – near Yellowstone National Park*

'… we crossed a small stream bordered with black cherry trees [chokecherry], many of the smaller ones broken down by bears, of which animal we found many signs' (Langford 1972, p. 13)

1870 *(August 28) – Washburn Expedition – view of Hayden Valley from near Inspiration Point, Yellowstone National Park*

'Meadows verdant with grasses and shrubbery stretch away to the base of the distant mountains…' (Langford 1972, p. 33)

1915 *Northern Range, Yellowstone National Park*

'…mountain maple, service berry, wild rose, snow-berry, fly honey suckle, and many other shrubs are eaten [by elk] during the winter' (Smith 1915, p. 21)

Early 1900s *Yellowstone National Park*

'Towards the close of summer when the berries begin to ripen, bears may desert other banquets to luxuriate in the numerous beds of fragrant, juicy, toothsome berries' (Skinner 1925, p. 54).

Early 1900s *Yellowstone National Park*

'… They [grizzlies] feed largely on green plants during the summer months, especially juicy vegetation as thistles, cow parsnips, flower stems of bear grass, wild onions, lily bulbs, roots and tubers. As soon as berries begin to ripen they are eager for strawberries, blueberries, serviceberries, elderberries, currants, gooseberries and even fly honeysuckle' (Bailey 1930, p. 171).

1993 *Exclosures: Northern Range and Greater Yellowstone Area*

'Repeatedly browsed shrubs produced practically no berries whereas inside Yellowstone exclosures, there was a positive correlation between the size of the individual plants and the number of berries' (Kay 1995, p. 312).

By the early 1990s, ungulate browsing was implicated as a cause for the low level of berry production in the Greater Yellowstone Area (Kay 1995). Buffaloberry (*Shepherdia Canadensis*), serviceberry (*Amelanchier alnifolia*) and chokecherry (*Prunus virginiana*) production was over two orders of magnitude higher inside exclosures compared with adjacent areas outside of exclosures (Fig. 2). Berry production tended to increase exponentially with increased shrub height (Fig. S3, Supporting information).

Wolves were reintroduced into Yellowstone National Park in 1995–1997 after a 70-year absence (Fig. S2, Supporting information). Elk have been the primary prey of these wolves, and grizzly bears commonly kill elk calves and scavenge on carcasses of elk and other ungulates killed by wolves (Wilmers *et al.* 2003; Barber-Meyer, Mech & White 2008; Fortin *et al.* 2013). Studies of tri-trophic cascades involving wolves, elk and plants, such as aspen, cottonwoods and willows, generally indicate that the reintroduction of wolves restored a trophic cascade with young woody browse species growing taller and

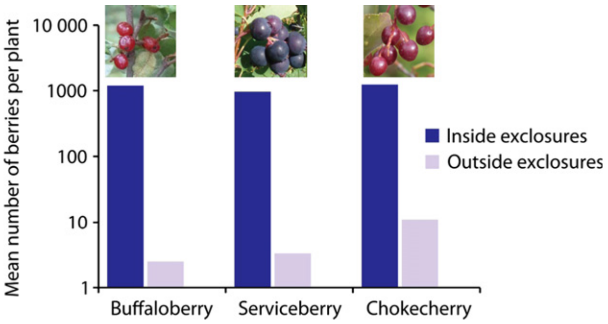

Fig. 2. Comparison of berry production inside and outside five ungulate exclosures in the Greater Yellowstone Area (log scale). On average, berry production was at least two orders of magnitude lower outside compared with inside the exclosures. Exclosures were built between 1932 and 1963. Number of enclosures per species include buffaloberry = 1, serviceberry = 4 and chokecherry = 3. Source: Kay (1995).

canopy cover increasing in some, but not all portions of the northern range (see review by Ripple & Beschta 2012). Elk browsing decreased and young aspen heights increased the most on the eastern portion of the northern winter range, likely due to a redistribution of elk caused by a combination of factors, including mortality due to predation and/or elk behavioural responses to the changing balance of predation risk on the northern range (White, Proffitt & Lemke 2012; Painter 2013).

After wolf reintroduction and decreases in the elk population on the northern range, both beaver (*Caster canadensis*) and bison (*Bison bison*) numbers increased, possibly due, in part, to the increase in available woody plants and herbaceous forage resulting from less competition with elk (Ripple & Beschta 2012; Smith & Tyers 2012). Because of the large body size of bison, their populations have been little affected by wolf predation in the park.

In 2011, wolves were removed from the endangered species list, and wolf harvesting was initiated in the northern Rocky Mountains, including the Greater Yellowstone Area in areas adjacent to Yellowstone and Grand Teton National Parks. Also in 2011, a ruling by the U.S. 9th Circuit Court of Appeals struck down the U.S. Fish and Wildlife Service's decision to remove Yellowstone's grizzlies from the endangered species list. The court indicated the U.S. Fish and Wildlife Service had failed to adequately demonstrate that whitebark pine decline and the lower availability of pine nuts would not impact grizzly bears (9th circuit court 2011, no. 09-36100). The court ruling did not discuss the issue of low berry production. This may have been because there has been little scientific research focusing on the specific topic of grizzly bear consumption of fruit in Yellowstone, which, in turn, is likely related to the lesser importance of fruits in the diet of Yellowstone grizzly bears in recent times. However, availability of grizzly bear food resources in the Greater Yellowstone Ecosystem is dynamic, and while some foods, such as whitebark pine nuts and cutthroat trout, are in decline, other resources, such as fruits, may increase in importance. Therefore, the impetus for this article was in large part due to this lack of research on Yellowstone fruit production, the recent court ruling and the future potential to include trophic interactions and berry production in grizzly bear monitoring protocols and management.

Materials and methods

To examine a possible link between elk densities and fruit consumption by Yellowstone's grizzly bears, we obtained data from grizzly bear diet studies that occurred between 1968 and 1987, which was a period before the 1988 fires, without wolves, and a rapidly rising elk population following the elimination of elk culling in 1968 (Fig. S2, Supporting information). We hypothesized an inverse relationship between fruit consumption by grizzly bears and elk population size because higher elk numbers would result in more elk browsing on fruit-producing plants used by bears. An alternative hypothesis, not involving elk, included an increase in fruit consumption by grizzly bears after the closing of the garbage dumps in 1971 because the bears would be more intensively searching for alternative food sources to replace garbage. For the period 1968–1987, we compared the percentage frequency of occurrence of fruit found in grizzly bear scats [Mealey 1975; Craighead, Sumner & Mitchell 1995; annual reports of the Interagency Grizzly Bear Study Team (IGBST)] against annual elk population counts (unpublished minimum elk counts, Yellowstone National Park). We used interpolation between years with successful elk counts to estimate the number of elk for years without counts. In cases when grizzly bear scat data collection spanned 2 or 3 years, we calculated a mean number of counted elk for the years involved.

For a period after wolf reintroduction, we calculated the percentage fruit in grizzly bear scat by month based on scats collected in 2007–2009 ($n = 778$ scats) as part of a larger study of bears by Fortin *et al.* (2013). Additionally, we compared these post-wolf reintroduction data to the percentage fruit found in grizzly bear scat published by Mattson, Blanchard & Knight (1991) for Yellowstone before wolf reintroduction in 1977–1987 ($n = 3423$ scats). Both sets of fecal data were adjusted for differential disappearance according to correction factors published by Hewitt & Robbins (1996).

In late August 2012, we searched for and collected data from all serviceberry patches that we found with dimensions of at least 10 m × 10 m within a 1200-hectare study area on the east portion of the northern range (Fig. S4, Supporting information). This study area was bounded between the Lamar Canyon on the east and the Yellowstone River on the west. The study area was selected because of a known occurrence of berry-producing shrubs from a previous study (Beschta & Ripple 2012). We chose serviceberry as a focal species for our plant measurements, because it was present in an ungulate exclosure located near our study area and is representative of other species of fruit producers on the northern range (Beschta & Ripple 2012). Within each serviceberry patch, we located the centroid of the patch and then placed four 5-m transects in each of the four cardinal directions radiating out from this centroid. At 1-m intervals along each transect, we measured the total height of the nearest serviceberry plant and determined the age of the plant based on architecture of the plant as shown by annual terminal bud scars and browse marks using methods similar to Ripple & Beschta (2012). Percentage browsing by year was determined by dividing the number of browsed stems for a given year by the total number of plants sampled. Adjacent to each sampled serviceberry patch, we enumerated ungulate scat by species in four 2 × 50 m belt transects. These belt transects were spaced 5 m apart and were parallel. All scat were counted regardless of age.

Because our serviceberry study area was located in the upper elevation sector of the northern range (White, Proffitt & Lemke 2012), we analysed trends in elk densities for this sector (472 km^2). We summed the number of elk counted in census units 26–52 for the years 1987 through 2012 and converted these raw counts to densities per km^2 by year. We used a Student's *t*-test (unequal variances) to check for significant differences ($P < 0{\cdot}05$) in elk density for this sector for the period before wolf reintroduction compared with after wolf reintroduction.

All serviceberry patches found in the study area were growing on mesic sites. To establish information on reference conditions for serviceberry, we searched for and selected all serviceberry patches growing on mesic sites in the nearby Lamar West ungulate exclosure, which was built in 1962. Within each selected serviceberry patch inside the exclosure, we measured heights of all stems, and for those <100-cm tall, we also measured plant architecture (height at terminal bud scar by year, $n = 38$). Because some serviceberry plants within the exclosure were too large to determine ages with plant architecture methods, we sectioned 14 stems at ground level that were taller than 100 cm (height range 105–230 cm). We sanded each section and counted annual rings to determine plant age. We conducted a regression ($n = 52$) between height and age [based on plant architecture ($n = 38$) and sections ($n = 14$)] of plants to predict ages based on height.

We considered other factors that could potentially affect serviceberry height growth including site productivity and snowpack depths. We determined the 2012 current annual growth (CAG, an index of site productivity) of unbrowsed serviceberry stems by subtracting leader heights in the spring of 2012 from those in September of 2012. To test for a relationship between plant height and productivity, we compared serviceberry height against annual leader growth of unbrowsed stems. Because snowpack accumulations can influence patterns of predation, ungulate foraging and plant-available soil moisture each spring, we indexed annual snowpack amounts. An average annual cumulative daily snowpack water equivalent (SWE_{acc}) for the period 1 October–30 April was calculated from SNOTEL data for the Northeast Entrance (Station MT10d07s) and Canyon (Station WY10e0s) sites [see Garrott, Eberhardt & White (2003) for methods]. We used a *t*-test (unequal variances) to test for difference between the SWE_{acc} during the period before wolf reintroduction (1981–1996) compared with after wolf reintroduction (1997–2012).

Results

Percentage frequency of occurrence of fruit in grizzly bear scat generally decreased from 1968 to 1987 and was inversely related to elk population size ($r^2 = 0{\cdot}73$, $P < 0{\cdot}001$, Fig. 3). The percentage fruit in the grizzly bear diet was variable (Fig. 4), but higher during the post-wolf reintroduction period (2007–2009) than during the pre-wolf reintroduction period (1977–1987). In July and August, consumption of fruit by grizzly bears averaged 0·3% and 7·8%, respectively, before wolf reintroduction (Mattson *et al.* 1991) compared with 5·9% and 14·6%, respectively, after wolf reintroduction. Additionally, we found that grizzly bear fruit consumption in August, depending on year, was as high as 29% for male and 39% for female grizzly bears during the post-wolf period (Fig. 4).

Age and height (HT) of serviceberry plants were closely related ($r^2 = 0{\cdot}92$), and establishment year (EY) for individual stems was estimated as follows: $\mathrm{EY} = 2012-(0{\cdot}0004*\mathrm{HT}^2 + 0{\cdot}039*\mathrm{HT})$. Serviceberry stems inside the Lamar West exclosure ($n = 247$) established both before and after wolf reintroduction with dates ranging from 1982 to 2011. The age structure (frequency distribution of number of stems by year) generally followed an expected exponential relationship with fewer old stems than young stems (Fig. 5a).

Mean elk densities in the upper elevation sector of the northern range decreased between 1987 and 2012 (Fig. 5b). For the period before wolves (1987–1994), elk densities averaged 12·1 per km^2 ($n = 7$ years), which was an order of magnitude greater ($P < 0{\cdot}001$) than the 1·2 per km^2 for the recent post-wolf period of 2006–2012 ($n = 7$ years).

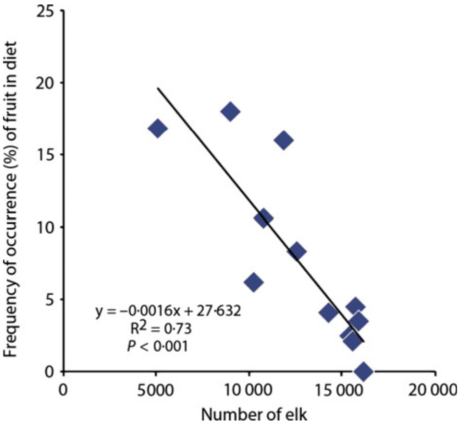

Fig. 3. Relationships between number of elk counted on the northern range and the amount of fruit (percentage frequency of occurrence) found in Yellowstone grizzly bear scat between 1968 and 1987, a period when elk numbers increased from <5000 to >16 000. Grizzly bear scat data were collected during a 20 year time span from 1968 through 1987 (6231 scats). The bear scat was collected during the warm season of each year beginning as early as April and concluding as late as October. During this 20 year period, there was some variation on the locations of collected scat. Sources: Craighead, Sumner & Mitchell (1995); Mealey (1975) and annual reports of the interagency study team Yellowstone Grizzly Bear Investigations 1977–1981 and 1983–1987 (1982 was not included due to low sample size and lack of springtime scats).

We found 12 serviceberry patches of at least 10 m × 10 m in size within the study area and measured 20 plants per patch for a total of 240 serviceberry plants. Because these serviceberry stems were young, we used plant architecture to determine ages and years of establishment. All 240 serviceberry plants established after wolf reintroductions of 1995–1996 during the period of 2003 through 2011 (Fig. 5b), a time of dramatically decreasing elk numbers for this portion of the northern range (Fig. 5c). The mean ungulate scat counts per 100 m^2 for the 12 sites included bison = 6·26, elk = 0·16, pronghorn (*Antilocarpa americana*) = 0·05 and deer (*Odocoileus* spp.) = 0·02.

Heights of serviceberry plants accessible to ungulates were inversely correlated with percentage browsing (Fig. 6). Between 2008 and 2012, the mean percentage browsing on serviceberry decreased from a high of 81% in 2008 to a low of 28% in 2012. Concurrently, mean spring heights of serviceberry plants increased from 38 to 65 cm between 2008 and 2012.

We found no correlation between the index of site productivity and serviceberry height ($r^2 = 0{\cdot}03$, $P = 0{\cdot}61$). We also found no difference in snow pack amounts (Fig. 7) between the period before (1981–1996) vs. after (1997–2012) wolf reintroduction (mean = 31·4 m vs. 31·5 m,

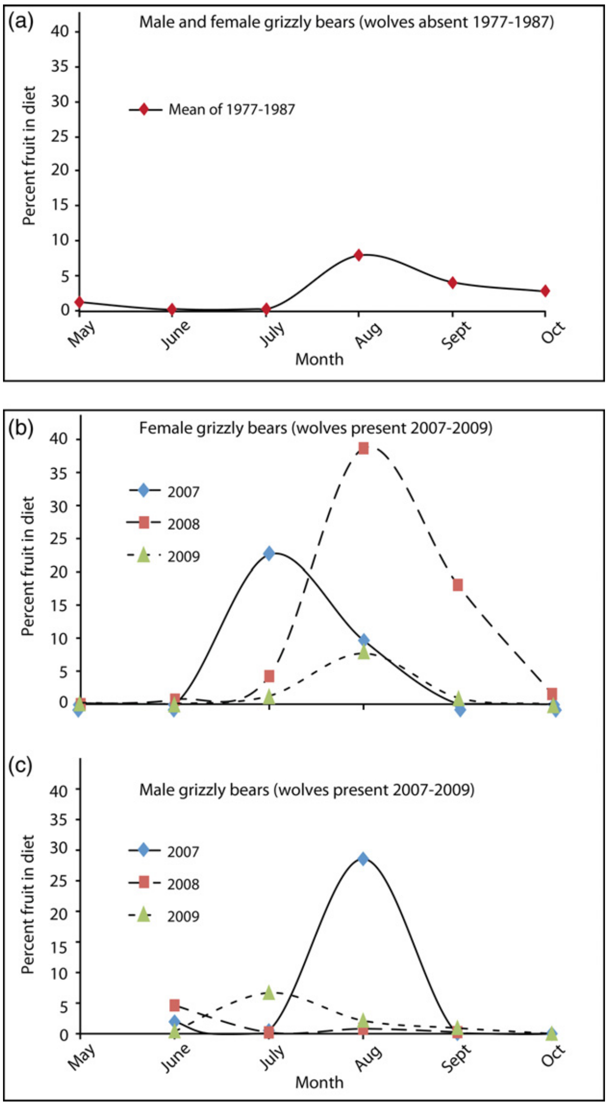

Fig. 4. Percentage fruit in grizzly bear scat (a) before wolf reintroduction showing monthly means for the period 1977–1987 in the Yellowstone area, and after wolf reintroduction (2007–2009) in the southern and eastern Yellowstone National Park for females (b) and males (c). Lines were plotted using a cubic smoothing spline. The line in (a) is not directly comparable with lines in (b) and (c). Year to year variability and data by sex are not shown in (a) because monthly data by year and sexual identities of grizzly bears were not available. See more details in text. Source for (a) Mattson, Blanchard & Knight (1991).

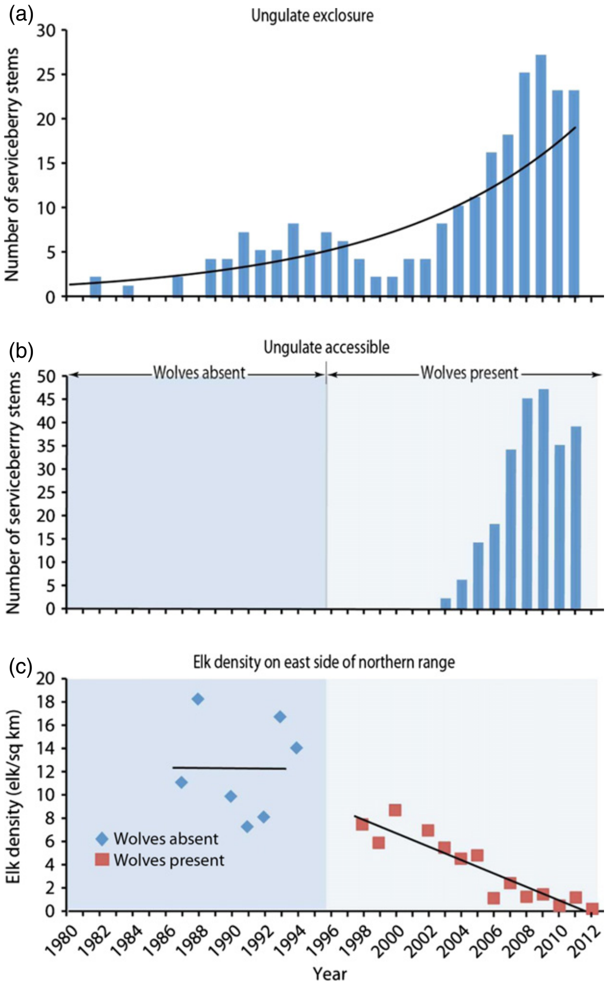

Fig. 5. (a) Histogram of serviceberry stem ages vs. year of establishment (i.e. age structure) within the Lamar West ungulate exclosure, (b) histogram of serviceberry stem ages vs. year of establishment in our study area, which was accessible to ungulates, and (c) density of elk per km^2 (uncorrected counts) in upper elevation sector on the eastern portion of the northern range. Source for (c): Yellowstone National Park.

respectively, $P = 0{\cdot}98$) or for the period before wolf reintroduction (1981–1996) vs. after the first serviceberry stems originated in 2003 (2003–2012) (mean = 31·4 m vs. 29·7 m, $P = 0{\cdot}59$).

Discussion

Our findings are consistent with the trophic cascade hypothesis that decreased elk densities following the reintroduction of wolves contributed to increased fruit production and fruit consumption by grizzly bears. The results provide rare evidence of the potential link between elk abundance and the diet of grizzly bears and are consistent with both Craighead, Sumner & Mitchell (1995) and Kay (1995) who argued that abundant elk in Yellowstone impacted the growth and production of fruit-producing shrubs. Our findings are also consistent with Mattson (2000, p. 129), who suggested the abundance of exotic plants and lower quality grizzly bear foods were directly correlated with elk population levels, stating: ‘The likelihoods that dandelions, elk thistles, and graminoids were grazed by bears increased with numbers of elk’.

We found support for our first hypothesis in that we discovered a significant inverse correlation between elk population size and fruit consumption by grizzly bears during the period 1968–1987 when elk numbers were generally increasing (Fig. 3). The alternative hypothesis of increased fruit consumption by grizzly bears after the closing of the garbage dumps was not supported because fruit consumption exhibited a decreasing trend after these closures.

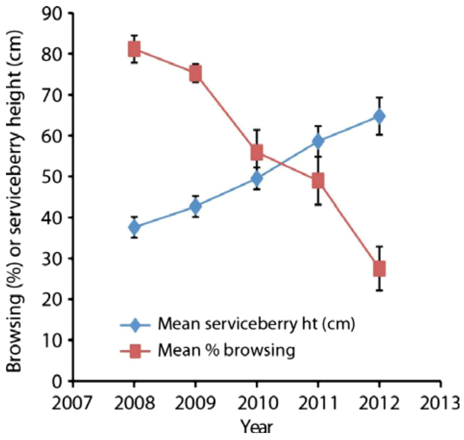

Fig. 6. Mean values and standard errors for percentage browsing and stem height based on plant architecture measurements for serviceberry during 2008–2012 showing trends and the inverse relationship between browsing levels and plant height [$n = 12$ patches (20 plants/patch or 240 total plants)].

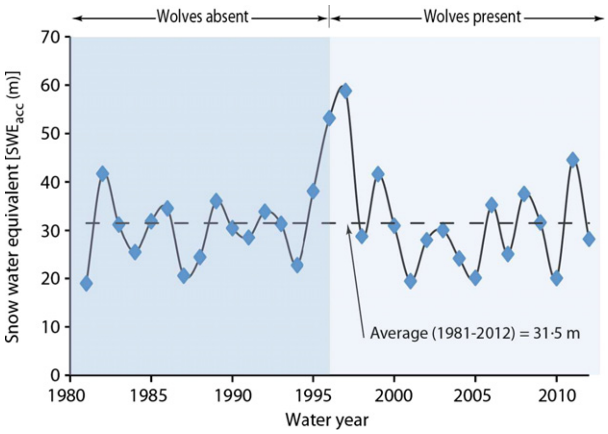

Fig. 7. Average annual snowpack water equivalent accumulation (SWE$_{acc}$) by year (October through April) for the Canyon (elev. = 2400 m) and Northeast Entrance (elev. = 2240 m) SNOTEL sites. Annual values of *SWE* were compiled from daily data over their concurrent 32-year period of record (1981–2012); *SWE* data were obtained from the USDA National Resource Conservation Service. Line was plotted using a cubic smoothing spline.

We found support for our second hypothesis when we compared the percentage fruit in the grizzly bear diet before and after wolf reintroduction. Percentage fruit in the bear's diet during July and August was, on average, 20 times higher and nearly twice as much, respectively, after wolf reintroduction compared with the period before wolf reintroduction. We suggest that this change in the amount of fruit consumed between the two periods may, at times, be biologically significant to the grizzly bears (e.g. for females, 39% fruit in August diet in 2008). Because some of the area burned in the 1988 fires, this increase may have been partly due to the effects of the fire or other factors. For example, there were also differences in the geographic extent of the scat collections with the scat from the early period from the larger Yellowstone ecosystem vs. from the south and central part of Yellowstone National Park for the later period.

We also uncovered support for our third hypothesis of an increase in berry-producing shrubs after wolf reintroduction. While serviceberry stems ($n = 247$) inside a nearby ungulate exclosure had established both before and after wolf reintroduction, we found that all sampled serviceberry stems ($n = 240$) in our study area (outside of enclosures) established after wolf reintroduction (Fig. 5). During recent years, we found a dramatic decrease in local elk densities, decreases in browsing and a corresponding increase in serviceberry stem heights. These results are consistent with other studies that show other woody browses growing taller in some, but not all, places since wolf reintroduction and inverse relationships between percentage browsing and woody plant height (see review by Ripple & Beschta 2012). We found no support for site productivity or snowpack depth to be associated with the increase in serviceberry stem establishment or an increase in stem heights.

During the seven decades without wolves in Yellowstone, the spatial extent of aspen appears to have decreased dramatically with most aspen stands on the northern range having died out (Renkin & Despain 1996). We expect that a similar decline happened to the number and size of berry-producing shrubs. With diminished plant communities, seed production and dispersal capabilities may have lessened during those seven decades.

Although wolves are now again in the park, we suggest that more significant increases in the number of berry-producing shrubs, shrub height and fruit production may take many years. Nevertheless, a recent study found that several species of berry-producing shrubs are growing taller on the eastern portion of the northern range (Beschta & Ripple 2012), which has lower elk densities than the western side of the northern range (White, Proffitt & Lemke 2012; Painter 2013). These species include twinberry (*Lonicera involucrata*), serviceberry, gooseberry (*Ribes* spp.), rose (*Rosa* spp.) and snowberry (*Symphoricarpos* spp.). Furthermore, in a 2012 random sample of 87 aspen stands across the northern range, we found gooseberry in 31%, serviceberry in 22%, buffaloberry in 17% and chokecherry in 15% of the stands (W. J. Ripple, unpublished data). At least one of these four species was present in 56% of the surveyed stands. Although occurrences are relatively low for each of these four species of berries, they have not been extirpated. Thus, it is likely they can provide sources for seed dispersal in the future. These berry-producing shrubs are highly palatable to elk (and likely bison), ranking very high in terms of year-round browsing preferences (Nelson & Leege 1982). In addition to benefits for bears, berry-producing shrubs are important for overall biodiversity by providing cover and food web support for a wide variety of other taxa including invertebrates, canids, lagomorphs, rodents, birds, ungulates and others (Beschta & Ripple 2012).

We found bison density, as indexed by scat, to be much greater than that of elk or other ungulates within the shrub study area. We have repeatedly seen and documented bison browsing of shrubs (Ripple *et al.* 2010; Painter & Ripple 2012). An increasing bison population on the northern range may impede increased fruit production on these plants.

The long period of open-pit garbage dumps from the 1890s to the 1970s may have buffered grizzly bears from major food shortages, possibly masking any cascading effects on berry production due to the extirpation of wolves. Food availability is a major determinant of grizzly bear productivity in Yellowstone. For example, nearly all cub and yearling deaths within the park between 1983 and 2001 were due to starvation and predation, and grizzly bear survival declined during years of low whitebark pine nut production (Schwartz *et al.* 2006). These findings are consistent with density-dependent mechanisms, suggesting that Yellowstone's bears have been at or near carrying capacity, but at the same time have been at relatively low densities compared with grizzly bear populations in several other interior regions (Schwartz, Miller & Haroldson 2003; Schwartz *et al.* 2006).

Our findings of low berry production before wolf reintroduction may be indicative of the status of other important plant-based foods for grizzly bears in Yellowstone. For example, key forbs have also been lacking in the Yellowstone grizzly bear diet, especially tall umbels such as cow parsnip (*Heracleum lanatum*; Mealy 1975; Knight, Blanchard & Kendall 1982; Mattson, Blanchard & Knight 1991). Cow parsnip is highly favoured by both ungulates and grizzly bears, and it is high in digestible energy and protein (McLellan & Hovey1995). These tall umbels are highly sensitive to ungulate grazing and declined significantly after just 6–9 weeks of cattle grazing (Stivers & Irby 1997). High levels of ungulate herbivory can eliminate cow parsnip from the landscape (Daubenmire 1970). In the early 1900s, Yellowstone elk regularly foraged on cow parsnip during July–November (Skinner 1928). Furthermore, cow parsnip can be an important tall forb in the early summer diet of interior grizzlies, but in recent times has been extremely low in Yellowstone grizzly bear scats (Fig. S5, Supporting information). This paucity of cow parsnip in the Yellowstone grizzly diet contrasts sharply with what was found in grizzly bear scats in both British Columbia (McLellan & Hovey 1995) and Alberta (Munro *et al.* 2006), where it was ranked as the number one diet item consumed in early summer (Fig. S5, Supporting information). As with fruits, the near elimination of cow parsnip as an important food for Yellowstone grizzly bears may have been partially caused by competition with ungulates for these forbs. Alternatively, historical cow parsnip production in Yellowstone may have been less than found in these other areas because of soils, moisture or other climatic factors.

Currently, the IGBST monitors 'key grizzly foods' in the Yellowstone area including: (i) the availability or use of ungulates, (ii) spawning cutthroat trout (*Oncorhynchus clarkii*), (iii) cutworm moths (*Euxoa auxiliaris*) at insect aggregation sites and (iv) whitebark pines. We recommend the IGBST also establish permanent berry-producing shrub transects both inside and outside the park that could be monitored on an annual basis. Three variables of interest would include shrub height, browsing levels and fruit production by species. Although not a shrub, strawberry (*Fragaria* spp.) production could also be included in these surveys because it is common in many forest understories (Craighead, Sumner & Mitchell 1995). Monitoring key tall forbs or at least umbels such as cow parsnip, angelica (*Angelica* spp.) and fern-leaved lovage (*Ligusticum filicinum*) would also be useful, particularly in areas with and without livestock outside the park boundary. Furthermore, grizzly bear scat surveys should be periodically conducted for comparing historical to contemporary fruit and forb consumption by bears.

ALTERNATIVE HYPOTHESES

An alternative to the trophic cascades explanation as to why Yellowstone has had such a scarcity of berries and other important fruit was offered by the U.S. Fish and Wildlife Service suggesting that the climate is not conducive to higher production of these grizzly bear foods: 'Although several berry-producing shrubs occur in the area [Yellowstone], these are relatively limited by climatic factors' (Federal Register 72 FR 14866, March 29, 2007).

This alternative explanation is contradicted by five lines of evidence: (i) historically, berries appear to have been common in Yellowstone, (ii) high levels of berry production occurred inside ungulate exclosures, with low production outside of exclosures, (iii) an inverse relationship between elk population size and amount of fruit in grizzly bear scat during a period of increasing elk numbers, (iv) an increase in the percentage fruit in grizzly diets after wolf reintroduction and (v) an increase in serviceberry stem establishment after wolf reintroduction. Taken collectively, these lines of evidence support the hypothesis that trophic interactions rather than climate represents the more important factor affecting fruit production dynamics.

We considered if fruit production might be affected by the unproductive rhyolite-derived soils on major parts of Yellowstone's central plateau. We conclude that these rhyolite areas likely have some effect on fruit production, but suggest the effects are not massive because spatially, rhyolite only covers 16% of Yellowstone National Park and only 7% of the larger grizzly bear recovery zone (Christiansen 2001). We also wondered if the low level of berry consumption by grizzly bears might be attributed to a high abundance of alternative bear foods (e.g. trout, elk) in Yellowstone. We suggest that the availability of alternative foods may have been an influence, but was likely not the main factor here because grizzly bears in many other interior regions of the world have high-quality alternative foods, but fruit is typically still the dominate grizzly bear food in late summer (McLellan & Hovey 1995; Mattson 1998).

The 9th Circuit Court of Appeals based their 2011 ruling primarily on inadequate documentation of the potential impacts of declining whitebark pine nut crops on grizzly bears. Based on the multiple lines of evidence, we suggest there is also a need to consider trophic interactions involving wolves and competition between ungulates and bears for berry-producing shrubs and forbs. It is plausible that competition for food between elk and bears in Yellowstone was significantly affected by intense elk browsing following the extirpation of wolves in the 1920s. Livestock grazing in grizzly bear habitat adjacent to the national park and bison herbivory in the park likely also contribute to increased foraging pressure on shrubs and forbs. Active livestock grazing allotments occurred across some 32% of the grizzly bear recovery zone outside the park in 1998, decreasing to 19% by 2011 (IGBST, unpublished data). This decrease in livestock use is likely to improve plant communities for bears, ungulates and other wildlife in addition to reducing grizzly-livestock conflicts and wolf-livestock conflicts.

The reintroduction of wolves may be helping buffer grizzly bears from climate change effects on whitebark pine nut production. For example, grizzly bear use of wolf-killed ungulate carcasses increased sharply during years with poor whitebark pine nut production ($r = -0{\cdot}81$, $n = 9$ years, Hebblewhite & Smith 2010). Likewise, in our diet study, fruit consumption by grizzly bears was highest in 2007 and 2008 when whitebark pine nuts were uncommon (15 and 9 cones/tree, respectively), but lowest when whitebark pine nuts were abundant (46 cones/tree) in 2009 (Haroldson & Podruzny 2012). Additional evidence for this potential buffering effect is derived from work by McLellan & Hovey (1995), who found that the grizzly bears in an area with high berry production in the Flathead drainage of British Columbia selected berries rather than whitebark pine nuts when both were available to them. McLellan & Hovey (1995, p. 710) stated 'Although white-bark pine are common in the Flathead study area, we have only once found evidence of bears eating their seeds, and none have been found in the scats'.

Conclusions

In ecosystems where wolves have been displaced or locally extirpated, their reintroduction may represent a particularly effective approach for passive restoration of berry-producing shrubs and important forbs for grizzly bears and a host of other mammals, birds and pollinators. Nevertheless, this is one of the first studies on this topic, and much more research is needed on the trophic cascades hypothesized herein. Specifically, more studies are needed on the effects of wolves and ungulates on berry production and how any effects vary in space and time.

Managing for 'ecologically effective' wolf populations (e.g. eliminating wolf harvesting) where they are sympatric with grizzly bears could be a management option for potentially improving the availability of plant-based foods for the bears. Likewise, reductions in livestock numbers or bison densities may similarly affect plant-based foods available to grizzly bears because these ungulates, just as elk, can browse on berry-producing shrubs and graze on forbs, which creates additional competition for bears. Thus, retiring livestock allotments in the Yellowstone grizzly bear recovery zone could benefit bears through increases in vegetal foods. We suggest researchers and policy makers consider wolves, trophic interactions and competition from wild and domestic ungulates when addressing research and management of grizzly bears.

Acknowledgements

This research was funded in part by the L.L. Stewart Faculty Scholars award for 2011 to W.J.R. by the Oregon State University Foundation and to C.T.R. by United States Geological Survey (USGS), Biological Resources Division Natural Resources Preservation Program, Interagency Grizzly Bear Study Team of the USGS Northern Rocky Mountain Science Center, Washington State University Bear Center and Bear Management Office of the Yellowstone Center for Resources in Yellowstone National Park. Personnel support was provided by Bear Management Office, the Interagency Grizzly Bear Study Team and Washington State University. J. Batchelor and L. Painter assisted in plant field data collection, while S. Arbogast and R. Comforto assisted in manuscript preparation. We thank C. Whitman, C. Dickinsen, J. Ball, G. Rasmussen and S. Thompson for their trapping effort and T. Coleman, S. Ard, K. West, S. Podruzny, G. Monroe, T. Rosen, J. Erlenbach, K. Quinton, C. Rumble, G. Wilson, R. Mowry, C. Wickhem, B. Fitzpatrick, S. McKenzie, P. Cross, N. Counsell, K. Miller, S. Hobbs, B. Harlow, S. McGeehan for help with sample collection or analyses. We also thank the many national park rangers who assisted us in many ways, from occasional transportation to monitoring our safety. We thank D. Mattson for enlightening conversations and sharing ideas as well as D. Smith and F. van Manen for conducting helpful reviews of an early version of this manuscript. Finally, we much appreciate comments and suggestions by two journal reviewers.

References

Aune, K. & Kasworm, W. (1989) *Final Report: East Front Grizzly Studies*, 332 p. Montana Department of Fish, Wildlife, and Parks, Helena, MT, USA.

Barber-Meyer, S.M., Mech, L.D. & White, P.J. (2008) Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs*, **169**, 1–30.

Beschta, R.L. (2005) Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. *Ecology*, **86**, 391–403.

Beschta, R.L. & Ripple, W.J. (2012) Restoring berry-producing shrubs with wolves in Yellowstone National Park. *Forest Ecology and Management*, **276**, 132–138.

Brown, D.E. (1996) *The Grizzly in the Southwest*, 304 p. University of Oklahoma Press, Norman, OK, USA.

Christiansen, R.L. (2001) Geology of Yellowstone National Park – the Quaternary and Pliocene Yellowstone Plateau Volcanic Field of Wyoming, Idaho, and Montana. U.S. Geological Survey Professional Paper, 729–G.

Côté, S.D. (2005) Extirpation of a large black bear population by introduced white-tailed deer. *Conservation Biology*, **19**, 1668–1671.

Craighead, J.J., Sumner, J.S. & Mitchell, J.A. (1995) *The Grizzly Bears of Yellowstone*. Island Press, Washington D.C., USA.

Daubenmire, R. (1970) Steppe vegetation of Washington. Technical Bulletin, Washington Agricultural Experiment Station, no. 62, 131 p.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.

Fortin, J.K., Schwartz, C.C., Gunther, K.A., Teisberg, J.E., Haroldson, M.A., Evans, M.A. *et al.* (2013) Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *The Journal of Wildlife Management*, **77**, 270–281.

Garrott, R.A., Eberhardt, L.L. & White, P.J. (2003) Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology*, **81**, 33–45.

Halofsky, J. & Ripple, W.J. (2008) Linkages between wolf presence and aspen recruitment in the Gallatin elk winter range of southwestern Montana, USA. *Forestry*, **81**, 195–207.

Haroldson, M.A. & Podruzny, S. (2012) Whitebark pine cone production. *Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2011* (eds F.T. van Manen, M.A. Haroldson & K. West), pp. 39–40. U.S. Geological Survey, Bozeman, MT, USA.

Hebblewhite, M. & Smith, D. (2010) Wolf community ecology: ecosystem effects of recovering wolves in Banff and Yellowstone National Park. *The Wolves of the world: New Perspectives on Ecology, Behavior, and Policy* (eds M.P.C. Musiani & P.C. Paquet), pp. 69–120. University of Calgary Press, Calgary, AB, Canada.

Hewitt, D.G. & Robbins, C.T. (1996) Estimating grizzly bear food habits from fecal analysis. *Wildlife Society Bulletin*, **24**, 547–550.

Hilderbrand, G.V., Schwartz, C.C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S.M. *et al.* (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology*, **77**, 132–138.

Jonkel, D.J. (1985) The Blackfeet Reservation: dilemmas in range and grizzly bear management. *Western Wildlands*, Spring, **11**, 25–27.

Kay, C.E. (1995) Browsing by native ungulates: effects on shrub and seed production in the Greater Yellowstone Ecosystem. *Proceedings: Wildland Shrub and Arid Land Restoration Symposium* (eds B.A. Roundy, E.D. McArthur, J.S. Haley & D.K. Mann, compilers), pp. 310–320. US Forest Service, INT-GTR-315, Ogden, UT, USA.

Knight, R.R., Blanchard, B.M. & Kendall, K.C. (1982) *Yellowstone Grizzly Bear Investigations: Report of the Interagency Study Team 1981*. National Park Service, USA.

Mattson, D.J. (1998) Diet and morphology of extant and recently extinct northern bears. *Ursus*, **10**, 479–496.

Mattson, D.J. (2000) *Causes and consequences of dietary differences among Yellowstone grizzly bears* (Ursus arctos). PhD dissertation, University of Idaho, Moscow, ID, USA.

Mattson, D.J., Blanchard, B.M. & Knight, R.R. (1991) Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology*, **69**, 1619–1629.

McDonald, P., Edwards, R.A. & Greenhalgh, J.F.D. (1981) *Animal Nutrition*, 3rd edn. Longman, New York, NY, USA.

McLellan, B.N. & Hovey, F.W. (1995) The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. *Canadian Journal of Zoology*, **73**, 704–712.

Meagher, M.M. & Phillips, J.R. (1983) Restoration of natural populations of grizzly and black bears in Yellowstone National Park. *International Conference on Bear Research and Management*, **5**, 152–158.

Mealey, S.P. (1975) *The Natural Food Habits of Free-Ranging Grizzly Bears in Yellowstone National Park, 1973–74*. MS Thesis, 158 pp. Montana State University, Bozeman, MT, USA.

Munro, R.H.M., Nielsen, S.E., Price, M.H., Stenhouse, G.B. & Boyce, M.S. (2006) Seasonal and diet patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy*, **87**, 1112–1121.

National Research council (NRC) (1975) *Report of Committee on the Yellowstone Grizzlies*. National Academy Press, Washington, DC, USA.

National Research Council (NRC) (2002) *Ecological Dynamics on Yellowstone's Northern Range*. National Academy Press, Washington, DC, USA.

Nelson, J.R. & Leege, T.A. (1982) Nutritional requirements and food habits. *Elk of North America: Ecology and Management* (eds J.W. Thomas & D. E Toweill), pp. 323–367. Stackpile books, Harrisburg, PA, USA.

Nelson, R.A., Folk, G.E. Jr, Pfeiffer, E.W., Craighead, J.J., Jonkel, C.J. & Steiger, D.L. (1983) Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *International Conference on Bear Research and Management*, **5**, 284–290.

Painter, L.E. (2013) *Trophic cascades and large mammals in the Yellowstone ecosystem*. PhD thesis, Oregon State University, Corvallis, OR.

Painter, L.E. & Ripple, W.J. (2012) Effects of bison on willow and cottonwood in northern Yellowstone National Park. *Forest Ecology and Management*, **264**, 150–158.

Reinhart, D.P., Haroldson, M.A., Mattson, D.J. & Gunther, K.A. (2001) Effects of exotic species on Yellowstone's grizzly bears. *Western North American Naturalist*, **61**, 277–288.

Renkin, R. & Despain, D. (1996) Notes on postfire aspen seedling establishment. *Ecological Implications of Fire in Greater Yellowstone* (ed. J.M. Greenlee), pp. 95–103, 105–106. International Association of Wildland Fire, Fairfield, WA, USA.

Ripple, W.J. & Beschta, R.L. (2012) Trophic cascades in Yellowstone: the first fifteen years after wolf reintroduction. *Biological Conservation*, **145**, 205–213.

Ripple, W.J. & Larsen, E.J. (2000) Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation*, **95**, 361–370.

Ripple, W.J., Painter, L.E., Beschta, R.L. & Gates, C.C. (2010) Wolves, elk, bison, and secondary trophic cascades in Yellowstone National Park. *Open Ecology Journal*, **3**, 31–37.

Robbins, C.T., Ben-David, M., Fortin, J.K. & Nelson, O.L. (2012) Maternal condition determines birth date and growth of newborn bear cubs. *Journal of Mammalogy*, **93**, 540–546.

Rush, W.M. (1932) *Northern Yellowstone Elk Study*. Montana Fish and Game Commission, Helena, MT, USA.

Schullery, P. & Whittlesey, L. (1992) The documentary record of wolves and related wildlife species in the Yellowstone National Park area prior to 1882. *Wolves for Yellowstone? A Report to the United States Congress* (eds J.D. Varley & W.G. Brewster), Vol. 4 Research and Analysis, pp. 750. National Park Service, Yellowstone National Park, WY, USA.

Schwartz, C.C., Miller, S.D. & Haroldson, M.A. (2003) Grizzly bear. *Wild Mammals of North America: Biology, Management, and Conservation*, 2nd edn (eds G.A. Feldhamer, B.C. Thompson & J.A. Chapman), pp. 556–586. The Johns Hopkins University Press, Baltimore, MD, USA.

Schwartz, C.C., Haroldson, M.A., White, G.C., Harris, R.B., Cherry, S., Keating, K.A. *et al.* (2006) Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs*, **161**, 68 pp.

Skinner, M.P. (1928) The elk situation. *Journal of Mammalogy*, **9**, 309–317.

Smith, D. & Tyers, D. (2012) The history and current status and distribution of beavers in Yellowstone National Park. *Northwest Science*, **86**, 276–288.

Stivers, T.S. & Irby, L.R. (1997) Impacts of cattle grazing on mesic grizzly bear habitat along the east front of the Rocky Mountain, Montana. *Intermountain Journal of Sciences*, **3**, 17–36.

White, P.J., Proffitt, K.M. & Lemke, T.O. (2012) Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist*, **167**, 174–187.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M. & Getz, W.M. (2003) Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology*, **72**, 909–916.

Wolf, E.C., Cooper, D.J. & Hobbs, N.T. (2007) Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications*, **17**, 1572–1587.

Wright, G.M., Dixon, J.S. & Thompson, B.H. (1933) A preliminary survey of faunal relations in national parks. USDI National Park Service Fauna Series No. 1, 157 pp. A preliminary survey of faunal relations in National Parks. U.S. National Park Service, Fauna Series 1. U.S. Government Printing Office, Washington, D.C., USA.

Yellowstone National Park (YNP) (1958) *Management Plan for Northern Elk Herd, Yellowstone National Park*. National Park Service, Mammoth Hot Springs, WY, USA.

Received 11 April 2013; accepted 16 July 2013
Handling Editor: Tim Coulson

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1. Early history of the study area.

Fig. S1. Comparison of fruit in the scat of grizzly bears in Alberta, British Columbia and Yellowstone.

Fig. S2. Wolf population levels and elk counts for the northern winter range of Yellowstone National Park.

Fig. S3. Scatter diagram showing the relationship between serviceberry plant height and the number of berries produced.

Fig. S4. Photo of serviceberry patch within NE Yellowstone study area.

Fig. S5. Comparison of cow parsnip in the scat of grizzly bears in Alberta, British Columbia and Yellowstone.

Supporting online material-Ripple et al. for "Trophic cascades from wolves to grizzly bears in Yellowstone", Journal of Animal Ecology.

Early history of the study area

The Yellowstone area was visited by Lewis and Clark in 1806, followed by a number of explorers during the early to mid-1800s. According to early historical accounts during this period, both wolves and grizzly bears were common and widely distributed throughout the present Park and Greater Yellowstone Ecosystem (Schullery & Whittlesey 1992). An examination of the writings and photographs from the early explorers to the Yellowstone area also provide evidence of abundant berry-producing shrubs before Euro-American settlement and park establishment (Kay 1995). For example, the journals of both the 1869 Cook-Folsom-Peterson and the 1870 Washburn expeditions indicated abundant berries in the Yellowstone area (Table 1 in the main text).

Yellowstone was established as the world's first national park in 1872, but uncontrolled hunting had significant effects on both carnivore and ungulate populations in the early years after park establishment. In 1886, the US Army assumed responsibility for protecting resources and successfully reduced the poaching of ungulates and bears in the park. Between late 1886 and 1907, the ban on hunting and increases in the amount of garbage in the park likely contributed to an increase in bears. Estimates of the numbers of grizzly bears in YNP were typically reported as "numerous" during this period (Skinner 1928; Craighead 1995). Starting in 1907, grizzly bears were commonly killed or shipped to zoos because they were considered to be "overabundant" (Craighead et al. 1995). Wolves were present in the park and woody species such as aspen and cottonwood were still recruiting into the overstory at this time (Ripple & Larsen 2000; Beschta 2005). Likewise, berries were still common in Yellowstone during these early years of the 20th century, apparently providing grizzly bears with copious feasts in late summer and early fall (Table 1 in the main text). From 1920 to 1933, it was estimated that the YNP grizzly bear population increased from approximately 40 to 260 bears possibly because of the increase in the number of tourists and correspondingly, an increase in the amount of garbage as a food subsidy (Craighead et al. 1995).

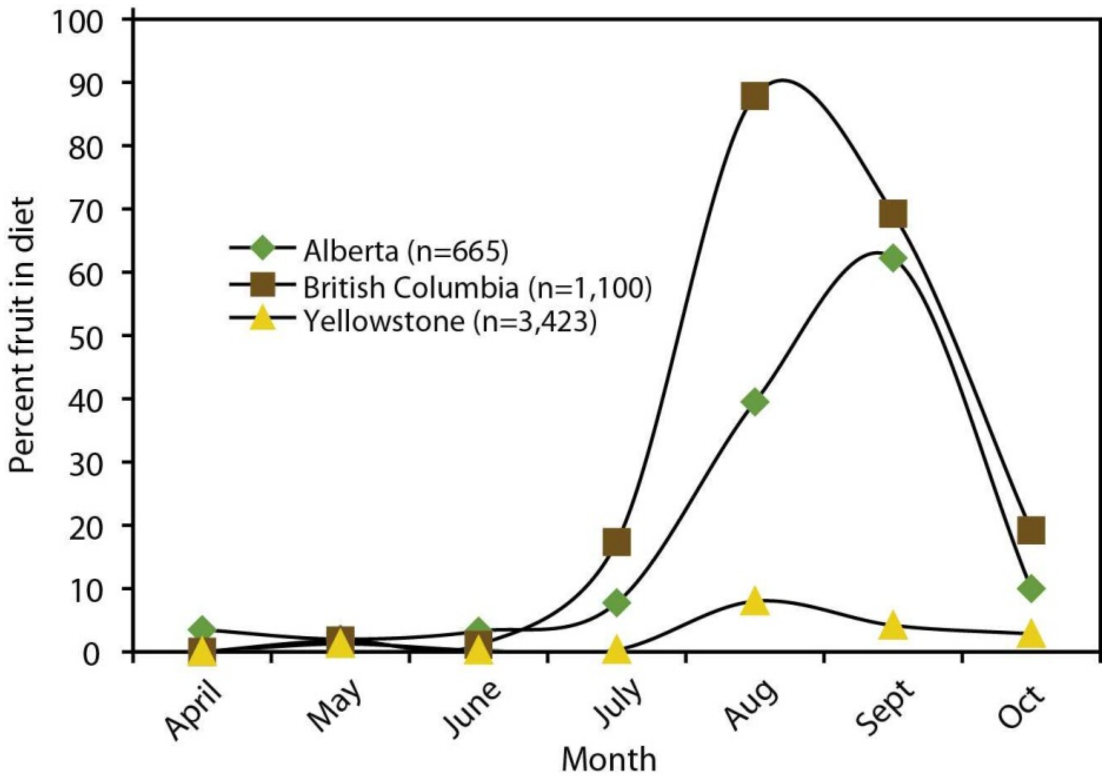

Figure S1. Comparison of fruit in the scat of grizzly bears in three study areas: 1) west central Alberta, 2001-2003 (Munro et al. 2006), 2) Flathead River, British Columbia, 1979-1991 (McLellan and Hovey 1995), and 3) Yellowstone, 1977-1987 (Mattson et al. 1991). All data were corrected for differential disappearance according to Hewitt and Robbins (1996).

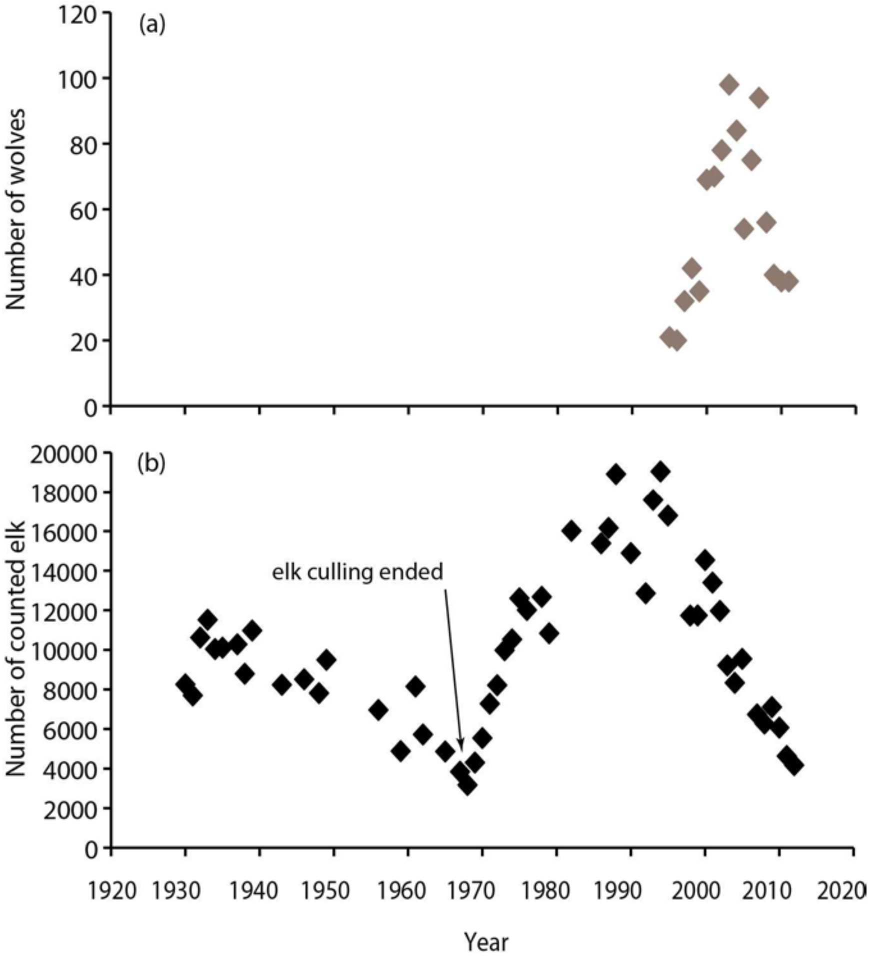

Figure S2. (a) Wolf population levels Yellowstone's the northern range between 1995 and 2011 and (b) elk counts for the northern winter range between the late 1920s and 2012. The period 1968 through 1987 represents the years for our analysis of the grizzly diet, a time of increasing elk populations after cessation of elk culling by park officials in 1968. Poor count years of 1977, 1989, 1991, and 2006 not shown.

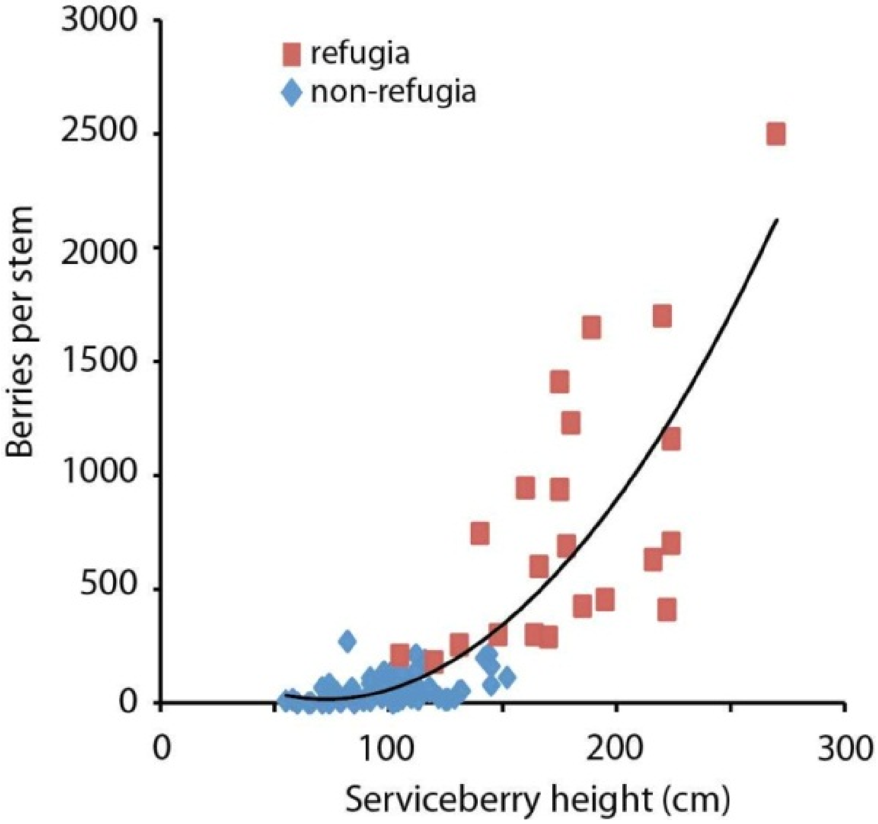

Figure S3. Scatter diagram showing the relationship between serviceberry plant height and the number of berries produced in 2011 on the northern range of Yellowstone National Park for plants accessible to ungulate browsing (diamonds) and plants in refugia (squares). Refugia included both plants in the exclosure and in a canyon protected from ungulate browsing.

We collected data on plant height and berries produced in September of 2011 (n = 83 plants) to help understand the relationship between serviceberry height and berry production per plant. We measured the heights of serviceberry plants and counted the corresponding number of berries per plants sampled in the Lamar West ungulate exclosure (n = 17), in a canyon refugia (n = 5), and at sites accessible to ungulates (n = 61) within the study area.

In 2011, berry production was positively related to serviceberry height ($r^2 = 0.71$). Serviceberry stem height ranged from 55 to 270 cm and the corresponding number of berries produced per stem ranged from 0 to 2,500. This relationship was curvilinear with taller plants producing more berries (Figure 10). As of September 1, 2011, 96% of the serviceberries from the shrubs sampled outside the exclosure had been removed by vertebrates as shown by residual pedicels. At this same time, four large and fresh bear scats (likely grizzly bears) were found within the study area. Three of the four scats were comprised entirely of serviceberries, in sharp contrast to serviceberries found in only 2 of 5,129 Yellowstone grizzly bear scats collected between 1977 and 1987 [annual reports of the Interagency Grizzly Bear Study Team (IGBST)]. In addition to bear utilization of serviceberries, cedar waxwings (*Bombycilla cedrorum*) and American robins (*Turdus migratorius*) were observed harvesting the berries.

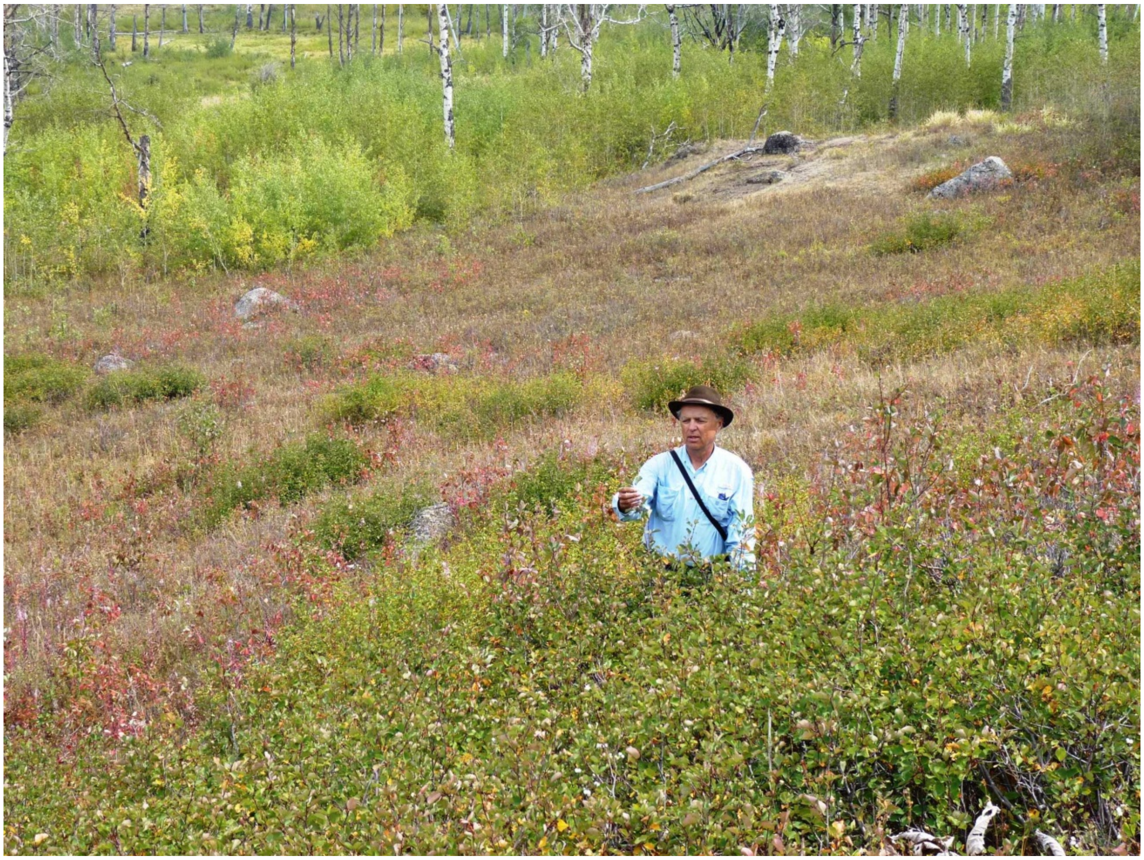

Figure S4. Photo of serviceberry patch within NE Yellowstone study area (outside exclosure) with serviceberry in front of subject approximately 150 cm tall, and aspen recruitment in the background.

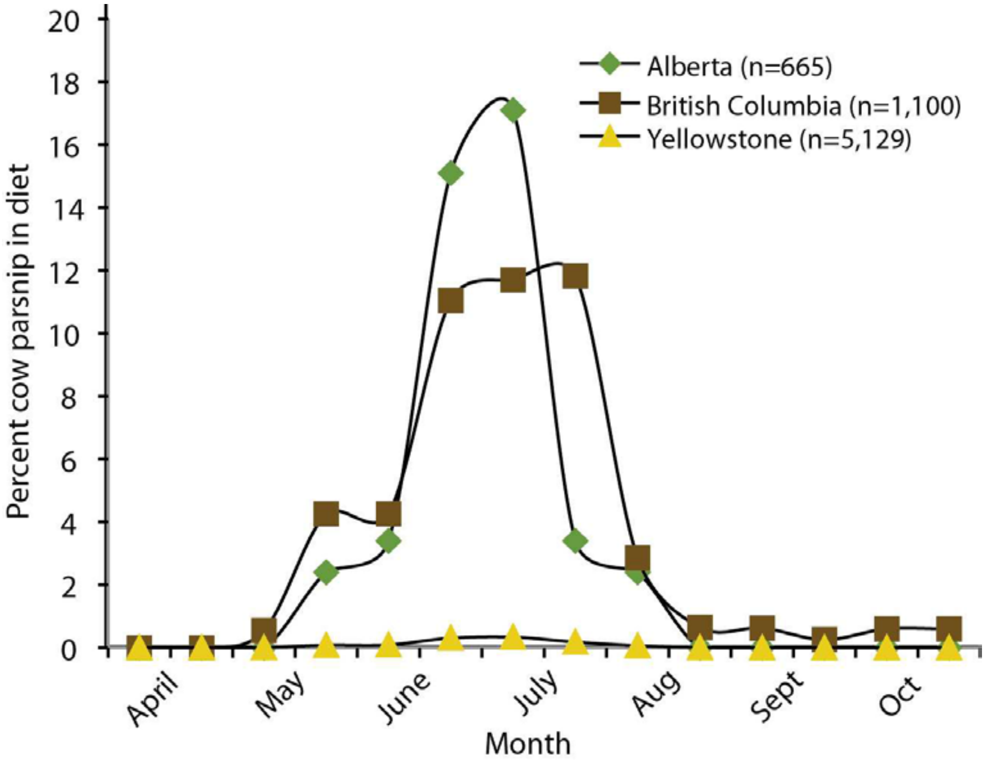

Figure S5. Comparison of cow parsnip in the scat of grizzly bears in three study areas: 1) west central Alberta, 2001–2003 (Munro et al. 2006), 2) Flathead River, British Columbia, 1979–1991 (McLellan and Hovey 1995), and 3) Yellowstone, 1977–1987, excluding 1982 (annual reports of the Interagency Grizzly Bear Team). All data were corrected for differential disappearance according to Hewitt and Robbins (1996). Cow parsnip was found in a total of only 43 out of 5,129 Yellowstone scats obtained between 1977 and 1987. Only yearly values were available for Yellowstone, so we modeled monthly values for Yellowstone based on the monthly distributions in British Columbia and Alberta.