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FORUM

Wolves trigger a trophic cascade to berries as alternative food for grizzly bears

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Introduction

Trophic cascades involving large carnivores have generated much recent interest and scientific research which has illustrated new and sometimes surprising linkages involving predators and food webs (Estes *et al*. 2011; Ripple *et al*. 2014). We recently wrote an article (Ripple *et al*. 2013) on potential trophic cascades involving two large carnivores, ungulates and plants. In our article, we explored potential connections among grey wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), Rocky Mountain elk (*Cervus elaphus*) and berry-producing shrubs in Yellowstone National Park. We hypothesized competition between elk and grizzly bears whereby changes in the abundance of elk would change the amount of browsing on shrubs, thus affecting the available fruit to grizzly bears. The commentary by Barber-Meyer (in press) addresses three main concerns with our article including the following: (i) the use of serviceberry (*Amelanchier alnifolia*) as a focal species in our field study, (ii) selection of study areas in Yellowstone National Park and (iii) an alternative foods hypothesis for grizzly bears. Below we reply to each of these three points. We show a rationale for both the selection of serviceberry and our study areas. We also provide evidence that the alternative foods hypothesis as described by Barber-Meyer (in press) would likely be part of a trophic cascade from reintroduced wolves, to decreases in elk, to increases in berry production and finally to the ability of bears to switch from other foods to consuming more berries.

Serviceberry as a focal species

Barber-Meyer (in press) questions the selection of serviceberry as a focal species for our fieldwork. She suggested that serviceberry is not an appropriate plant species because it has not been a major food for Yellowstone's grizzlies and that the serviceberry field study site is not near Yellowstone Lake where previous scat data were collected for a recent grizzly bear diet study. We reject the Barber-Meyer (in press) claim that this berry-producing shrub is an inappropriate species because: (i) serviceberry has been shown to be a major food source for grizzly bears in northern ecosystems (Interagency Grizzly Bear Committee 1987), (ii) there is great potential for increased serviceberry production in the Greater Yellowstone Area in that berry production inside ungulate exclosures was, on average, over 100 times greater compared to areas outside exclosures (Fig. 2 in Ripple *et al*. 2013), (iii) the northern range has productive soils and little conifer cover which makes it an area of high potential for berry production in the future and (iv) to obtain spatial control regarding a trophic cascade, we needed a species that was growing inside an existing ungulate exclosure and the Yellowstone Lake region has no ungulate exclosures. Finally, the serviceberry field data should be viewed as a separate data set from the grizzly bear scat data sets; thus, there is no strong reason that our shrub field study needed to be in the same area as the retrospective scat project.

The Study areas

Barber-Meyer (in press) indicated concern that the pre-wolf reintroduction grizzly scat study area was larger than the post-wolf reintroduction scat study area. Ideally, both grizzly bear scat collection areas would be the same but, as with most retrospective studies, we were constrained by available data. Moreover, in our text, we clearly state the limitations of these scat data (Ripple *et al*. 2013, p. 7): 'Because some of the area burned in the 1988 fires, this increase [fruit consumption] 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'. Regardless of these limitations, it is noteworthy that we documented very high levels of August fruit consump-

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tion by grizzly bears in recent years and that these recent grizzly bear food habits appear to be at biologically significant levels (e.g. for females, 39% fruit in August diet in 2008).

Alternative foods hypothesis

Barber-Meyer (in press) suggested that the post-wolf reintroduction increase in fruit consumption by grizzly bears could be the result of decreases in other foods such as whitebark pine (*Pinus albicaulis*) nuts rather than a trophic cascade. We agree that the availability of other foods can influence the level of fruit consumption by grizzly bears especially in the post-wolf reintroduction period and indicated that perspective in our article. We clearly describe in Ripple *et al.* (2013, p. 9) evidence of how alternative foods, such as whitebark pine nuts, might be inversely related to fruit consumption, stating: ‘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 per tree respectively), but lowest when whitebark pine nuts were abundant (46 cones per tree in 2009) (Haroldson & Prodruzny 2012).

At first glance, the alternative food hypothesis seems plausible to at least partially explain the increase in fruit consumption by grizzly bears. But, it is important to put this issue in an historical context because it is not the first time that Yellowstone grizzlies have lost a major source of food. Park officials closed all garbage dumps by 1971 which ended a significant food subsidy for the grizzly bears. Even with the extreme food stress, human conflicts and a rapidly declining bear population after the dump closures (Craighead, Sumner & Mitchell 1995), fruit consumption by grizzlies generally decreased rather than increased during the 1970s and 1980s (Ripple *et al.* 2013). Furthermore, it was during this same period that elk populations were increasing, and we found that fruit consumption by grizzly bears was strongly and inversely correlated with the number of elk ($r^2 = 0{\cdot}73$, $P < 0{\cdot}001$, Figure 1b in Ripple *et al.* 2013). These results strongly suggest that it was not possible for grizzly bears to increase their consumption of fruit after the dump closures because fruit production was rapidly decreasing due to intense browsing by a rising elk population. Given such strong evidence that the bears did not increase fruit consumption following dump closures, our conclusion regarding the role of alternative food sources during that period in time appears valid (Ripple *et al.* 2013).

If Barber-Meyer’s alternative food hypothesis is correct, there should be an inverse relationship between grizzly bear consumption of pine nuts vs. consumption of fruit during the period before wolf reintroduction in the 1990s. We tested this with 20 years of grizzly scat data (1968–1987 a period without wolves) and found no correlation ($r^2 = 0{\cdot}00$, $P = 0{\cdot}99$) between consumption of pine nuts and fruit on an annual basis (Fig. 1). However, now that woody plants are growing taller and berry production may be higher since wolf reintroduction, we would hypothesize, at least sometimes, an inverse correlation between consumption of pine nuts and fruit because of the increased availability of fruit as an alternative to pine nuts during years of low pine nut production. If the ongoing changes in elk behaviour or density are sufficient to allow increasing berry production to occur, as appears to be underway, then, the Barber-Meyer (in press) alternative food hypothesis may now apply. Ironically, any increases in availability of fruit as an alternative to pine nuts for grizzly bears would likely be part of a trophic cascade involving wolves, elk and increased berry production which would now make this type of food switching an option available to bears.

CONCLUSIONS

We appreciate Barber-Meyer’s (in press) interest and comments regarding our paper and hope that it leads to a continuing discussion and additional research regarding the ecological effects of wolf reintroduction to Yellowstone. As far as we know, our article is the first to show evidence of a trophic cascade from wolves to grizzly bears via plant foods. Our approach clearly utilized multiple data sets and study areas as well as several lines of evidence to investigate potential trophic linkages in Yellowstone National Park. In our article (Ripple *et al.* 2013), we also documented:

1 Historical accounts before the loss of wolves in Yellowstone described abundant berries which were being consumed by grizzly bears (Table 1 in Ripple *et al.* 2013).

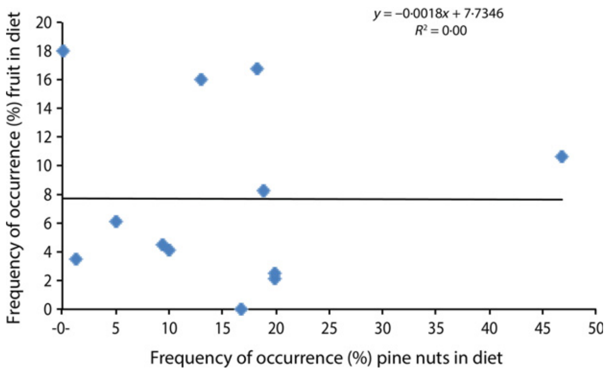

Fig. 1. Relationship between pine nuts and fruit (per cent frequency of occurrence on annual basis) found in Yellowstone grizzly bear scat between 1968 and 1987. The relationship was not statistically significant ($P = 0{\cdot}99$). Grizzly bear scat data were collected during a 20-year time span from 1968 through 1987 (6231 scats). During this period, there was some variation on the locations of scat which was collected during the warm season of each year beginning as early as April and concluding as late as October. 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).

2 Great potential for increased berry production (including serviceberry) in the future in the Greater Yellowstone Area based on comparisons inside and outside ungulate exclosures (Kay 1995; Fig. 2 and Fig. 5b in Ripple *et al.* 2013).
3 Ungulate herbivory caused a significant long-term decline in northern range berry production. Contemporary levels of production per plant outside exclosures were, on average, two orders of magnitude less compared to that for plants inside ungulate exclosures (Fig. 2 and Fig. 5b in Ripple *et al.* 2013) and, when we consider the potential area historically occupied by berry-producing shrubs, the decrease in total berry production was likely much >2 orders of magnitude.
4 There was a strong inverse relationship between the number of elk and the frequency of fruit in the grizzly bear diet (Fig. 3 in Ripple *et al.* 2013).
5 Serviceberry established both before and after wolf reintroduction when protected from ungulate browsing (i.e. inside exclosure) and only after wolf reintroduction in areas outside the exclosure (Fig. 5 in Ripple *et al.* 2013). This spatial control (inside and outside of exclosures) and short-term temporal control (pre- and post-wolf reintroduction) reduces long-term climate change as a dominant confounding factor. We recognize that climate change is occurring, but our analysis focuses largely on the decade prior to wolf reintroduction and the ˜15 years afterwards.
6 After wolf reintroduction, there have been dramatic decreases in local elk numbers, decreases in browsing and corresponding increases in the heights of: (i) serviceberry (Fig. 5c and Fig. 6 in Ripple *et al.* 2013), (ii) five other species of berry-producing shrubs (Beschta & Ripple 2012), (iii) willow (Beyer *et al.* 2007), (iv) aspen (Painter *et al.* 2015) and (v) cottonwood (Beschta & Ripple 2015).

Collectively, these multiple lines of evidence along with the recent high levels of fruit in grizzly bear diets suggest that our trophic cascade hypothesis is plausible and probable. Continued increases in Yellowstone's berry production appear to have occurred in recent years. French (2014) reported on recent high berry production and low bear mortality in Yellowstone with a quote from Kerry Gunther, the Yellowstone National Park bear biologist, about the bears being 'fat and happy…It was a really good food year for bears,…in the 31 years I've been there [Yellowstone], the last two have been the best for berries'. Our research results and this statement by Gunther make us wonder if a major trophic cascade from wolves to elk to berry production to berry consumption by grizzly bears is now well underway. This trophic cascade and any increases in fruit production might thus allow grizzly bears to switch from pine nuts to fruit during years of low pine nut availability. Such food switching by grizzly bears was apparently not possible during the period without wolves and intense elk browsing (Fig. 1).

We intended for our article to stimulate interest, additional research and hopefully periodic monitoring of vegetal grizzly bear foods. We recognize that more long-term data are needed to better understand how and to what extent food webs have been changing since the return of wolves and to help clarify the relative merits of alternative hypotheses. We thus continue to recommend that the Interagency Grizzly Bear Study Team establish permanent berry-producing shrub and tall forb transects and conduct scat surveys on an annual basis to more fully understand the current food habits of grizzly bears in the grizzly bear recovery area both inside and outside Yellowstone National Park.

References

Barber-Meyer, S.M. (in press) Trophic cascades from wolves to grizzly bears or changing abundance of bears and alternate foods? *Journal of Animal Ecology* (in press).
Beschta, R.L. & Ripple, W.J. (2012) Restoring berry-producing shrubs with wolves in Yellowstone National Park. *Forest Ecology and Management*, **276**, 132–138.
Beschta, R.L. & Ripple, W.J. (2015) Divergent patterns of riparian cottonwood recovery after the return of wolves in Yellowstone, USA. *Ecohydrology*, **8**, 58–66.
Beyer, H.L., Merrill, E.H., Varley, N. & Boyce, M.S. (2007) Willow on Yellowstone's northern range: evidence for a trophic cascade? *Ecological Applications*, **17**, 1563–1571.
Craighead, J.J., Sumner, J.S. & Mitchell, J.A. (1995) *The Grizzly Bears of Yellowstone*. Island Press, Washington, DC, 535 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.
French, B. (2014) *More Grizzlies Eating Moths in Region South of Yellowstone*. Billings Gazette, Billings, MT. 13 November 2015.
Haroldson, M.A. & Prodruzny, 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.
Interagency Grizzly Bear Committee (1987) *Grizzly Bear Compendium*. The National Wildlife Federation, Washington, DC, 540 p.
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), pp. 310–320. US Forest Service, INT-GTR-315, Ogden, UT.
Mealey, S.P. (1975) The natural food habits of free-ranging grizzly bears in Yellowstone National Park, 1973–74. MS thesis. Montana State University, Bozeman, MT, 158 pp.
Painter, L.E., Beschta, R.L., Larsen, E.J. & Ripple, W.J. (2015) Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? *Ecology*, **96**, 252–263.
Ripple, W.J., Beschta, R.L., Fortin, J.K. & Robbins, C.T. (2013) Trophic cascades from wolves to grizzly bears in Yellowstone. *Journal of Animal Ecology*, **83**, 223–233.
Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M. *et al.* (2014) Status and ecological effects of the World's largest carnivores. *Science*, **343**, 1241484, doi: 10.1126/science.1241484.

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