

- quality of elk (*Cervus elaphus*) and bison (*Bison bison*). *Wildlife Ecology* 11:215–220.
- Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742–2755.
- Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters* 10:690–700.
- Keigley, R. B., and M. R. Frisina. 1998. Browse evaluation by analysis of growth form. Montana Fish, Wildlife, and Parks, Bozeman, Montana, USA.
- Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* 3:1–7.
- Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation. *Canadian Journal of Zoology* 68:619–640.
- Lovaas, A. L. 1970. People and the Gallatin elk herd. Montana Fish and Game Department, Helena, Montana, USA.
- Miller, B., B. Dugelby, D. Foreman, C. Martinez del Rio, R. Noss, M. Phillips, R. Reading, M. E. Soulé, J. Terborgh, and L. Willcox. 2001. The importance of large carnivores to healthy ecosystems. *Endangered Species Update* 18:202–210.
- NRC [National Research Council]. 2002. Ecological dynamics on Yellowstone's northern range. National Academy Press, Washington, D.C., USA.
- Peek, J. M., A. L. Lovaas, and R. A. Rouse. 1967. Population changes within the Gallatin elk herd, 1932–65. *Journal of Wildlife Management* 31:304–316.
- Peterson, R. O., J. A. Vucetich, R. E. Page, and A. Chouinard. 2003. Temporal and spatial dynamics of predator–prey dynamics. *Alces* 39:215–232.
- Ray, J. C., K. H. Redford, R. S. Steneck, and J. Berger. 2005. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C., USA.
- Ripple, W. J., and R. L. Beschta. 2004a. Wolves and the ecology of fear: can predation risk restructure ecosystems? *BioScience* 54:755–766.
- Ripple, W. J., and R. L. Beschta. 2004b. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest Ecology and Management* 200:161–181.
- Ripple, W. J., and R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* 230:96–106.
- Ripple, W. J., and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138:514–519.
- Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* 95:361–370.
- Ripple, W. J., L. E. Painter, R. L. Beschta, and C. C. Gates. 2010. Wolves, elk, bison, and secondary trophic cascades in Yellowstone National Park. *Open Ecology Journal* 3:31–37.
- Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk and fire on the northern range of Yellowstone National Park. *Ecology* 76:2097–2106.
- Rush, W. M. 1932. Northern Yellowstone elk study. Montana Fish and Game Commission, Helena, Montana, USA.
- Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. *BioScience* 53:330–340.
- Smith, D. W., and D. B. Tyers. 2008. The beavers of Yellowstone. *Yellowstone Science* 16:4–14.
- Soulé, M. E., J. E. Estes, J. Berger, and C. M. del Rio. 2003. Ecological effectiveness: Conservation goals for interactive species. *Conservation Biology* 17:1238–1250.
- Terborgh, J., and J. A. Estes, editors. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, D.C., USA.
- White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves—expectation, realizations, and predictions. *Biological Conservation* 125:141–152.
- Wolf, E. C., D. J. Cooper, and N. T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications* 17:1572–1587.
- Wolff, J. O., and T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology* 81:266–271.
- Yellowstone National Park. 1961. Management of Yellowstone's northern elk herd, 15 December 1961. National Park Service, Mammoth Hot Springs, Wyoming, USA.

Ecology, 94(6), 2013, pp. 1425–1431
 © 2013 by the Ecological Society of America

Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: reply

MATTHEW J. KAUFFMAN,^{1,4} JEDEDIAH F. BRODIE,² AND ERIK S. JULES³

When wolves were returned to Yellowstone National Park (YNP) in 1995 after a 70-year absence, a grand natural experiment was initiated. This experiment has the potential to help ecologists learn whether a wide-ranging predator can initiate cascading indirect effects on an ecosystem, either through direct consumption of prey or through modifications of their behavior (i.e., behaviorally mediated trophic cascades, or BMTCs). But this experiment has no replication and no controls, and the lack of adequate methods to account for these shortcomings has strongly hindered the ability of ecologists to understand the wolf's ecological role in YNP.

Manuscript received 8 August 2011; revised 23 November 2011; accepted 1 December 2011. Corresponding Editor: C. C. Wilmers.

¹ U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Zoology and Physiology Department, University of Wyoming, Laramie, Wyoming 82071 USA.

² Wildlife Biology Program, University of Montana, Missoula, Montana 59812 USA.

³ Department of Biological Sciences, Humboldt State University, Arcata, California 95521 USA.

⁴ E-mail: mkauffm1@uwyo.edu

In their Comment, Beschta and Ripple (2013) seek to clarify how we ought to evaluate the occurrence of BMTCs involving Yellowstone's wolves. We appreciate their call for increased rigor, because we believe that many impressions about the cascading effects of wolves in YNP have been formed without sufficient critical evaluation of research methods, existing data, or alternative hypotheses. We initiated our work after reading the first study suggesting that a BMTC was occurring among wolves, elk, and aspen (Ripple et al. 2001). But when we started exploring field sites in YNP in 2004 (nine years after wolf reintroduction), we saw that aspen were heavily browsed everywhere we looked. We noted that elk foraging behavior did not seem to match assumptions about patterns of predation risk that had been previously published (Ripple et al. 2001, Ripple and Beschta 2003, 2004). And we witnessed long-term responses of aspen within large exclosures established in the 1950s. Two of these exclosures were in the heart of the famed Lamar Valley, which was a stronghold of the original Druid wolf pack and is where thousands of park visitors have now seen wolves. But here too, where risk of predation by wolves must be high, there was evidence of heavy browsing: aspen were thriving inside the exclosures but the vegetative shoots they sent out beyond the protection of the fence were eaten down to our knees.

At that time, a fundamental hindrance was our limited knowledge about spatial patterns of wolf predation risk. Prior investigators had characterized risk based largely on assumptions, without empirical support. For example, the first study by Ripple et al. (2001) claimed that predation risk varied between the core vs. periphery of wolf territories, a gradient that does not describe patterns of wolf predation (Kauffman et al. 2007). Later studies (e.g., Ripple and Beschta 2004, 2007) characterized riparian aspen sites as riskier than upland sites and claimed that the presence of aspen thickets and downed logs increased elk predation risk. Yet these assumptions about risk were untested, making it impossible to rigorously evaluate (1) if these sites were indeed more risky for elk, (2) whether increased risk altered elk foraging in these sites, and (3) whether altered foraging behavior translated into differences in aspen recruitment. A fundamental contribution of our study is that we estimated predation risk from the distribution of 774 wolf-killed elk over 10 years (Kauffman et al. 2007) and used this predation risk map as an a priori predictor of risk with which to test the BMTC hypothesis.

History of aspen recruitment failure

Beschta and Ripple (2013) make several comments relative to our dendrochronological analysis of aspen recruitment failure (illustrated in Fig. 2 of Kauffman et al. [2010]). Our results differed from those found in

previous studies completed in the same area (e.g., Romme et al. 1995, Ripple and Larsen 2000, Beschta and Ripple 2013). In response to this inquiry, we revisited our dendrochronological data set and discovered an important error in our own age data. We have now corrected that error (see Erratum below), which has reduced the number of core samples we were able to use. The corrected stand-specific recruitment dates have changed somewhat, and our historical data now appear to be more consistent with previous studies. Nevertheless, we believe these corrected data still support inferences we made in our original paper. Our responses to the questions Beschta and Ripple (2013) pose regarding our analysis of historical aspen recruitment failure (described below) reflect the corrected dates as described in the Erratum.

In their Comment, Beschta and Ripple (2013) take issue with the statement in our *Abstract*, "This pattern of recruitment failure appears more consistent with a gradual increase in elk numbers rather than a rapid behavioral shift in elk foraging following wolf extirpation." These comments refer to our findings presented in Fig. 2 of Kauffman et al. (2010); now corrected in Fig. 2B(rev) of the Erratum (below). Beschta and Ripple (2013) suggest that we are in error because elk were actually decreasing toward the end of the recruitment cessation period we recorded (Eberhardt et al. 2007). It is true that elk were declining when the last of our study stands stopped recruiting (~1930s), but that is not the time window to which we referred. The first of our 16 aspen stands to cease regenerating did so in 1883, and the last ~1938. There is no ambiguity in the historical record that elk abundance *increased* soon after the time of establishment of Yellowstone in 1872 up through the 1920s and 1930s when the National Park Service began culling elk (Romme et al. 1995, Schullery 2004). Thus, we stand by our statement that aspen regeneration began to fail during the buildup of elk numbers resulting from the end of market hunting and the loss of wolf predation.

Beschta and Ripple (2013) also suggest that an elk reduction "experiment" was conducted during the 1960s, at the tail end of elk culling, and aspen did not recover. Why culling of elk by the Park Service did not allow aspen recruitment at that time remains a mystery. We presume that browsing pressure *was* reduced during the period of intense culling, but that time period was not long enough to allow aspen to recruit. But the loss of wolves and the growth, and then culling, of elk were not the only changes to YNP during this time period. Elk browse aspen primarily during winter (Romme et al. 1995), and there is evidence that elk shifted their winter range from the lower elevation valleys (where they competed with cattle and were intensely hunted) to the suboptimal Northern Range inside the park (Skinner 1925, 1928). The timing of such migration loss fits well

with the timing of aspen recruitment failure, and if profound, would strongly alter how we understand elk–aspen relationships today. We simply do not know how few wintering elk on the Northern Range are required to allow aspen to recruit. It is notable that the elk culling “experiment” was only allowed to run for a few years (Beschta and Ripple 2013: Fig. 1). With wolves back in YNP, elk numbers may remain low for an ecologically meaningful time period (i.e., more than a few years), and sustained low levels of browsing could yet yield new aspen growth.

Beschta and Ripple (2013: Fig. 1) suggest that our dendrochronological data is consistent with their prior work. We agree that our corrected estimates (Erratum: Fig. 2B(rev) [below]) are not remarkably different from previous work, but we see notable differences that have bearing on the question of whether wolves caused a BMTC prior to their extirpation in the 1920s. Most importantly, we did not find an abrupt cessation of aspen recruitment noted by previous authors (e.g., Romme et al. 1995, Ripple and Larsen 2000, Beschta and Ripple 2013). We maintain that the decades-long duration of the regeneration failure we found using stand-specific data; see Erratum: Fig. 2B(rev) [below], helps correct an important misinterpretation regarding the historical influence of wolves on elk browsing behavior. Ripple and Beschta (2004) interpreted the abrupt decline in historical aspen recruitment as resulting from the loss of predation risk on the landscape as wolves were extirpated in the 1920s, making elk free to forage in places that had formerly been too risky. In contrast to Ripple and Larsen (2000), who only sampled one or two of the largest adults per stand from 92 stands, we randomly sampled ~10 aspen trees within each of 16 randomly located stands, leading to a more representative sample of the timing of regeneration failure (1883–1938). Thus, as a likely estimate, these changes took 55 years to come about on the landscape. If changes to elk behavior were responsible for the increased browsing and cessation of recruitment, one would expect such changes to occur rather rapidly on the landscape (i.e., within about one elk generation; Berger et al. 2001). Given the fitness costs of antipredator behavior for elk that risk starvation each winter (Parker et al. 2009), we fully expect that any profound antipredator behaviors would have been quickly lost following wolf extirpation. Thus, we maintain that one cannot logically infer the loss of a BMTC operating in the years before wolf extirpation.

Contemporary aspen recruitment

One of the unique findings of our study was a near total lack of recruitment of young aspen. We reported this particular result in our *Abstract*, where we wrote, “... aspen are not recovering in Yellowstone...,” a statement that Beschta and Ripple (2013) claim is

“factually incorrect.” The statement we made is, in fact, correct and is more readily understood when taken in context of our full statement: “In addition, our estimates of relative survivorship of young browsable aspen indicate that aspen are not currently recovering in Yellowstone, even in the presence of a large wolf population.” We define “recruitment” as achieving heights taller than 200 cm, since this is an approximate threshold above which aspens may escape elk browsing. Our finding was based on 16 randomly sampled aspen stands, including the measured heights of 3845 individual plants. Clearly, we were reporting on our own findings here. With 16 out of our 16 stands showing a complete failure of any sampled plants to exceed the browsing height threshold, such a conclusion seems well supported by our data.

At issue here is the scale and extent of any purported aspen recovery. We acknowledged that some local release of riparian aspen had been reported by Ripple and Beschta (2007), but we maintain that scattered aspen patches showing recruitment in a few areas can hardly be construed as a “recovery.” To us, a recovery of aspen would be indicated by a reasonably widespread and consistent level of aspen recruitment across northern Yellowstone. To fully understand the differences in findings between early studies and our own, it is critical to assess differences in sampling designs. First, our sites were randomly located, whereas it is unclear what criteria previous YNP aspen studies (i.e., Ripple et al. 2001, Ripple and Beschta 2004, 2007) used for site selection. Second, within a stand, the aspen we sampled were randomly selected, whereas Ripple and Beschta (2007:515) targeted the “5 tallest aspen.” While they suggest that such a sampling design provides them an “early view” of any release, choosing the five tallest individuals for an evaluation of stand-level height and growth is also inherently biased. We believe that researchers seeking to evaluate the recovery of an ecosystem ought to use random and representative sampling. It is unfortunate that Beschta and Ripple (2013) did not report in their Comment the simple proportion of their 98 monitored stands that showed height releases: this would have been a straightforward way to gauge the extent of any purported recovery. One of us (J. F. Brodie) has continued to monitor aspen on the Northern Range in the years since our original 2004 sampling. That work indicates that only one out of 104 aspen stands (<1% of total) have average sucker heights >200 cm (Brodie et al. 2012). Importantly, those sites were chosen with a stratified random design, and are thus representative of aspen across the Northern Range with respect to all ecological gradients (including riparian vs. upland).

We wish to stress an additional point here, which has largely been overlooked in the study of putative Yellowstone trophic cascades. All of the above mea-

surements of aspen height are difficult to interpret in light of BMTCs, because there are no comparable measurements from before wolf reintroduction (i.e., pre-1995). The case for growth release in Yellowstone shrubs following wolf reintroduction has often rested on a handful of photographs showing low shrub stature at some time in the past and taller stature recently (Ripple and Beschta 2004, 2006). Yet such “experimental design” is nonrandom, and such “analyses” suffer from exceedingly small sample sizes and potential bias (see Bilyeu et al. [2008] for an illustrative comparison of photographic evidence).

Even if we assume that aspen are recruiting in a few isolated stands across the Northern Range, what should we make of these observations? The main finding from Kauffman et al. (2010) is that such growth is probably not because elk fear to forage in riparian stands. We found no evidence for such a behavioral mechanism, despite the fact that eight out of the 21 total sites we used (four sites were used twice) were in riparian or wet areas (the rest were in upland). We still do not understand why Ripple and Beschta (2007) need to invoke complex effects of predation risk to explain why aspen grow taller and faster in wet areas (Frey et al. 2003) compared to dry areas (as we showed in Kauffman et al. [2010: Fig 5B]). We also find it unsurprising that a few aspen growing in moist, productive sites might show modest height increases when exposed to browsing from 10 000 fewer elk since wolf reintroduction.

A major assumption that underpins the Comment by Beschta and Ripple (2013) is that the only factor to have changed in YNP since the mid 1990s is the return of wolves. Yet, since that time, YNP has experienced many important ecological changes. Moose abundance has declined markedly following habitat changes caused by the massive 1988 fires (Tyers 2006). Grizzly bear abundance has increased at a rate of 4–7% from 1983–2002 (Schwartz et al. 2006), with a corresponding threefold increase in rates of elk calf predation between pre- and post-wolf time periods (Barber-Meyer et al. 2008). Finally, the drought that began in the mid- to late-1990s may also have influenced aspen. The three winters of 1995–1997 had the heaviest accumulation of snow among the previous 28 years (Creel and Christianson 2009). Because elk consume more browse and less grass and forbs when snow is deep (Christianson and Creel 2007), the drier winters after 1997 could explain the patchy recruitment observed by Beschta and Ripple (2013). Our point here is simply that “natural experiments” such as this one are fraught with confounding factors that need to be openly discussed and rejected before assigning all causation to wolves.

Aspen recruitment and predation risk

Beschta and Ripple (2013) are concerned that our use of kill sites does not fully represent the “landscape of

fear” that wolves create and foraging elk perceive. A key issue is that wolves typically pursue prey a fair distance prior to making a kill (Kauffman et al. 2007). To address this, we evaluated differences in our habitat variables between paired encounter and kill sites over the same 10-year period (we found none; $n = 46$ pairs; D. R. MacNulty, *unpublished data*). Thus, the habitats these kills identify—and that are described in our predation risk map—are largely representative of the habitats in which wolves encounter their prey. Behavioral studies also indicate that elk perception of risk is in line with our predation risk map. For example, elk are more vigilant (Liley and Creel 2008) and more likely to be killed in open grassland habitats (Creel et al. 2005), one of the riskiest habitats we modeled. Furthermore, elk tend to move out of these risky areas when wolves are present (Creel et al. 2005, Gude et al. 2006).

A dynamic whereby elk make preemptive movements to safer habitats, where they are then killed, could lend credence to Beschta and Ripple’s (2013) concerns. There are several reasons why this is unlikely to occur. First, preemptive movements were not detected following wolf reintroduction. Mao et al. (2005) conducted a detailed assessment of elk habitat selection on the Northern Range before and after wolf reintroduction and found essentially no differences: by and large, wintering elk use the same habitats now as they did before wolves. Second, even in the presence of wolves, mature male elk do not adjust their foraging effort (Winnie and Creel 2007). Third, strong preemptive antipredator behavior would impose severe fitness costs in elk by increasing the very real likelihood of winter starvation (Parker et al. 2009). In addition, the inconsistent predation cues that wide-ranging wolves provide (Kauffman et al. 2010) makes preemptive behavior of their prey of questionable value (*sensu* Schmitz 2008). Thus, the existing evidence, along with wolf and elk natural history, provide little support for the notion of strongly preemptive antipredator behavior in elk. Moreover, we suggest that our use of a priori predictions from an empirically derived predation risk map constitutes a vast improvement over prior risk characterizations (e.g., Ripple and Beschta 2003, 2004, 2007), most of which were subjectively determined in the absence of data on elk and wolves.

In their Comment, Beschta and Ripple (2013) state, “[t]o determine if a trophic cascade is behaviorally or density mediated, we suggest it is necessary to first confirm the occurrence of a response in the lowermost trophic level . . .” Here, they are suggesting that because none of our sites met the 200-cm browsing threshold, a test of the BMTC hypothesis is precluded. We are quite puzzled by this statement. If true, their contention would mean that hundreds of ecological studies seeking to evaluate the cascading effects of predators on plants would suffer from the same shortcoming. To our knowledge, the magnitude of predator effects on plants

has never been a prerequisite for the testing of BMTCs. Despite the fact that we did not find an aspen height release, aspen recovery via a wolf-initiated BMTC had been previously claimed (Ripple et al. 2001, Ripple and Beschta 2004, 2007) and widely reported in the press (e.g., Conway 2007, Morell 2007). Thus, a rigorous test of this hypothesis seemed warranted.

We took a hypothetico-deductive approach in our study. If the Yellowstone BMTC hypothesis is true, the foremost prediction that must hold is that variation in aspen demography is explained by variation in predation risk. We showed, across our 16 randomly located stands and our nine experimental exclosures, that there was ample landscape-level variation in aspen browsing, growth, heights, and survival (Kauffman et al. 2010: Figs. 3–6). We sampled aspen stands in some of the riskiest and safest habitats on the Northern Range. Despite this variation in aspen demography and predation risk, the prediction stemming from the BMTC hypothesis did not hold: none of the variation in aspen demography was attributable to variation in predation risk. If a BMTC were occurring, it is difficult to imagine that we would not find at least some empirical evidence for this straightforward prediction.

In their Comment, Beschta and Ripple (2013) suggest that measurements of plant height and browsing are the most appropriate plant response metrics to evaluate the strength and existence of a trophic cascade among wolves, elk, and woody plants. Certainly, if a BMTC was occurring, we should expect to see a reduction in browsing and an increase in plant height. We did not (Kauffman et al. 2010: Fig. 6), but we note that plant height and browsing are both strongly influenced by a variety of environmental forces wholly unrelated to wolves. For instance, numerous Northern Range studies demonstrate conclusively that soil moisture and access to the water table strongly influence willow growth and recruitment (Johnston et al. 2007, Bilyeu et al. 2008, Tercek et al. 2010), and our own work found a strong influence of abiotic conditions on aspen survivorship (Kauffman et al. 2010: Fig. 5A). Snow also strongly influences elk habitat selection (Mao et al. 2005), visitation to aspen sites (Brodie et al. 2012), and intensity of browsing vs. grazing (Creel and Christianson 2009). Thus, assuming that all variance in plant performance is due solely to predation risk—as Beschta and Ripple (2013) propose, and much of their previous work assumes—seems oversimplified at best. We accounted for strong abiotic gradients by pairing fenced and control plots within aspen stands that varied in their level of predation risk; we then used within-stand differences (between protected and unprotected suckers) in growth and survival as our response variables (Kauffman et al. 2010: Fig. 6). Studies that do not account for these strong abiotic gradients—especially when they also lack an empiri-

cally based assessment of predation risk—are, in effect, testing for a BMTC with unreliable treatment variables and no controls. Unfortunately, this situation characterizes many of the studies that have claimed the existence of wolf–elk–plant BMTCs in Yellowstone, including those focused on aspen (Ripple et al. 2001, Ripple and Beschta 2004, 2007), willow (Ripple and Beschta 2006, Beyer et al. 2007), and cottonwood (Ripple and Beschta 2003).

Conclusions

We welcome the suggestion made by Beschta and Ripple (2013) to carefully examine our methods and interpretation, and we suggest that such scrutiny be applied to all the research on wolf-mediated trophic cascades in YNP. We leave it to the ecological community to decide the extent to which randomized experimental design, unbiased sampling, *a priori* metrics of predation risk, and explicit accounting for abiotic gradients matter for how we understand the ecological role of wolves in YNP and elsewhere. We suspect that a careful re-reading of the mammal food web literature from YNP will show that there is substantially less evidence for a wolf–elk–aspen BMTC than is generally believed (e.g., Kimble et al. 2011). Studies in YNP have also cast substantial doubt on the cascading effects of wolves on willows (e.g., Bilyeu et al. 2007, 2008, Johnston et al. 2007, 2011, Wolf et al. 2007, Creel and Christianson 2009, Tercek et al. 2010).

A key point that has been largely overlooked in the body of work from YNP is that, while ecological consequences following the elimination of wolves can provide evidence for the importance of apex predators, the failure to detect such effects following reintroduction does not provide evidence against the value of predators. Rather, it may mean that the absence of wolves for seven decades in YNP caused fundamental changes in ecosystem states and processes that could not be quickly reversed by their restoration (e.g., Wolf et al. 2007). There is little doubt that the Yellowstone Ecosystem will function (is functioning) differently now that the original faunal assemblage has been restored. Our work simply suggests that the manner in which it is different does not conform to simple notions of fear-mediated trophic cascades as the textbooks (e.g., Cain et al. 2008) and the popular media (e.g., Chadwick 2010) now describe. Nutritional constraints of large herbivore prey, predator hunting mode, spatial and temporal heterogeneity in antipredator behavior, the attenuation of risk effects, interactions between prey density and behavior, and strong bottom-up controls are some of the factors that might mediate the influence of carnivores on woody plants in Yellowstone and elsewhere, and they deserve further attention (Lima and Dill 1990, Schmitz et al. 2004, Heithaus et al. 2009, Kauffman et al. 2010).

Acknowledgments

We thank S. Buskirk, J. Goheen, N. T. Hobbs, J. Maron, and A. Middleton for comments.

Literature cited

- Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* 169:1–30.
- Berger, J., J. E. Swenson, and I.-L. Persson. 2001. Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039.
- Beschta, R. L., and W. J. Ripple. 2013. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: comment. *Ecology* 93:1420–1425.
- Beyer, H. L., E. H. Merrill, N. Varley, and M. S. Boyce. 2007. Willow on Yellowstone's Northern Range: evidence for a trophic cascade? *Ecological Applications* 17:1563–1571.
- Bilyeu, D. M., D. J. Cooper, and N. T. Hobbs. 2007. Assessing impacts of large herbivores on shrubs: tests of scaling factors for utilization rates from shoot-level measurements. *Journal of Applied Ecology* 44:168–175.
- Bilyeu, D. M., D. J. Cooper, and N. T. Hobbs. 2008. Water tables constrain height recovery of willow on Yellowstone's northern range. *Ecological Applications* 18:80–92.
- Brodie, J. F., E. Post, F. Watson, and J. Berger. 2012. Climate intensification of a trophic interaction: snow, herbivory, and aspen recruitment. *Proceedings of the Royal Society B* 279:1366–1370.
- Cain, M. L., W. D. Bowman, and S. D. Hacker. 2008. *Ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Chadwick, D. H. 2010. Wolf wars. *National Geographic* March 2010:34–43.
- Christianson, D., and S. Creel. 2007. A review of environmental factors affecting elk winter diets. *Journal of Wildlife Management* 71:164–176.
- Conway, C. 2007. Yellowstone's wolves save its aspens. *The New York Times* (5 August 2007), New York, USA.
- Creel, S., and D. Christianson. 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. *Ecology* 90:2454–2466.
- Creel, S., and J. A. Winnie, Jr. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69:1181–1189.
- Creel, S., J. A. J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397.
- Eberhardt, L. L., P. J. White, R. A. Garrott, and D. B. Houston. 2007. A seventy-year history of trends in Yellowstone's northern elk herd. *Journal of Wildlife Management* 71:594–602.
- Frey, B. R., V. J. Lieffers, S. M. Landhausser, P. G. Comeau, and K. J. Greenway. 2003. An analysis of sucker regeneration of trembling aspen. *Canadian Journal of Forest Research* 33:1169–1179.
- Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing ecosystem. *Ecological Applications* 16:285–298.
- Heithaus, M. R., A. J. Wirsing, D. Burkolder, J. Thomson, and L. M. Dill. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* 78:556–562.
- Johnston, D. B., D. J. Cooper, and N. T. Hobbs. 2007. Elk browsing increases aboveground growth of water-stressed willows by modifying plant architecture. *Oecologia* 154:467–478.
- Johnston, D. B., D. J. Cooper, and N. T. Hobbs. 2011. Relationships between groundwater use, water table, and recovery of willow on Yellowstone's northern range. *Ecosphere* 2:art20.
- Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742–2755.
- Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters* 10:690–700.
- Kimble, D. S., D. B. Tyers, J. Robison-Cox, and B. F. Sowell. 2011. Aspen recovery since wolf reintroduction on the northern Yellowstone winter range. *Rangeland Ecology and Management* 64:119–130.
- Liley, S., and S. Creel. 2008. What best explains vigilance in elk: characteristics of prey, predators, or the environment? *Behavioral Ecology* 19:245–254.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decision making under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction into Yellowstone National Park. *Journal of Wildlife Management* 69:1691–1707.
- Morell, V. 2007. Aspens return to Yellowstone, with help from some wolves. *Science* 317:438–439.
- Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23:57–69.
- Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184:299–313.
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* 54:755–766.
- Ripple, W. J., and R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* 230:96–106.
- Ripple, W. J., and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138:514–519.
- Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* 95:361–370.
- Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102:227–234.
- Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk and fire on the northern range of Yellowstone National Park. *Ecology* 76:2097–2106.
- Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952–954.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163.
- Schullery, P. 2004. Searching for Yellowstone: ecology and wonder in the last wilderness. Montana Historical Society Press, Helena, Montana, USA.
- Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161:1–68.
- Skinner, M. P. 1925. Migration routes of elk in Yellowstone National Park. *Journal of Mammalogy* 6:184–192.

- Skinner, M. P. 1928. The elk situation. *Journal of Mammalogy* 9:309–317.
- Tercek, M. T., R. Stottlemeyer, and R. Renkin. 2010. Bottom-up factors influencing riparian willow recovery in Yellowstone National Park. *Western North American Naturalist* 70:387–399.
- Tyers, D. B. 2006. Moose population history on the northern Yellowstone winter range. *Alces* 42:133–149.
- Winnie, J., and S. Creel. 2007. Sex-specific behavioral responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behavior* 73:215–225.
- Wolf, E. C., D. J. Cooper, and N. T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications* 17:1572–1587.
-