

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

ROBERT L. BESCHTA<sup>1,2</sup> AND WILLIAM J. RIPPLE<sup>1</sup>

By the early 1900s, Euro-Americans had extirpated gray wolves (*Canis lupus*) from most of the contiguous United States. Yellowstone National Park was not immune to wolf persecution and by the mid-1920s they were gone. After seven decades of absence in the park, gray wolves were reintroduced in 1995–1996, again completing the large predator guild (Smith et al. 2003). Yellowstone's "experiment in time" thus provides a rare opportunity for studying potential cascading effects associated with the extirpation and subsequent reintroduction of an apex predator. Wolves represent a particularly important predator of large mammalian prey in northern hemisphere ecosystems by virtue of their group hunting and year-round activity (Peterson et al. 2003) and can have broad top-down effects on the structure and functioning of these systems (Miller et al. 2001, Soulé et al. 2003, Ray et al. 2005).

If a tri-trophic cascade involving wolves–elk (*Cervus elaphus*)–plants is again underway in northern Yellowstone, theory would suggest two primary mechanisms: (1) density mediation through prey mortality and (2) trait mediation involving changes in prey vigilance, habitat use, and other behaviors (Brown et al. 1999, Berger 2010). Both predator-caused reductions in prey numbers and fear responses they elicit in prey can lead to cascading trophic-level effects across a wide range of biomes (Beschta and Ripple 2009, Laundré et al. 2010, Terborgh and Estes 2010). Thus, the occurrence of a trophic cascade could have important implications not only to the future structure and functioning of northern Yellowstone's ecosystems but also for other portions of the western United States where wolves have been reintroduced, are expanding their range, or remain absent. However, attempting to identify the occurrence of a trophic cascade in systems with large mammalian

predators, as well as the relative importance of density and behavioral mediation, represents a continuing scientific challenge.

In Yellowstone today, there is an ongoing effort by various researchers to evaluate ecosystem processes in the park's two northern ungulate winter ranges: (1) the "Northern Range" along the northern edge of the park (NRC 2002, Barmore 2003) and (2) the "Upper Gallatin Winter Range" along the northwestern corner of the park (Ripple and Beschta 2004b). Previous studies in northern Yellowstone have generally found that elk, in the absence of wolves, caused a decrease in aspen (*Populus tremuloides*) recruitment (i.e., the growth of seedlings or root sprouts above the browse level of elk). Within this context, Kauffman et al. (2010) initiated a study to provide additional understanding of factors such as elk density, elk behavior, and climate upon historical and contemporary patterns of aspen recruitment in the park's Northern Range. Like previous studies, Kauffman et al. (2010) concluded that, irrespective of historical climatic conditions, elk have had a major impact on long-term aspen communities after the extirpation of wolves. But, unlike other studies that have seen improvement in the growth or recruitment of young aspen and other browse species in recent years, Kauffman et al. (2010) concluded in their Abstract: "... 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."

In the interest of clarifying the potential role of wolves on woody plant community dynamics in Yellowstone's northern winter ranges, we offer several counterpoints to the conclusions of Kauffman et al. (2010). We do so by readdressing several tasks identified in their *Introduction* (p. 2744): (1) the history of aspen recruitment failure, (2) contemporary aspen recruitment, and (3) aspen recruitment and predation risk. Task 1 covers the period when wolves were absent from Yellowstone and tasks 2 and 3 focus on the period when wolves were again present. We also include some closing comments regarding trophic cascades and ecosystem recovery.

1. *History of aspen recruitment failure.*—Although records of wolf and elk populations in northern Yellowstone are fragmentary for the early 1900s, the Northern Range elk population averaged ~10 900 animals (7.3 elk/km<sup>2</sup>; Fig. 1A) as the last wolves were being removed in the mid 1920s. Soon thereafter increased browsing by elk of aspen and other woody species was noted in northern Yellowstone's winter ranges (e.g., Rush 1932, Lovaas 1970). In an attempt to reduce the effects this large herbivore was having on vegetation, soils, and wildlife habitat in the Northern

Manuscript received 13 January 2011; revised 10 June 2011; accepted 20 June 2011. Corresponding Editor: C. C. Wilmsers.

<sup>1</sup> Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331 USA.

<sup>2</sup> E-mail: Robert.Beschta@oregonstate.edu

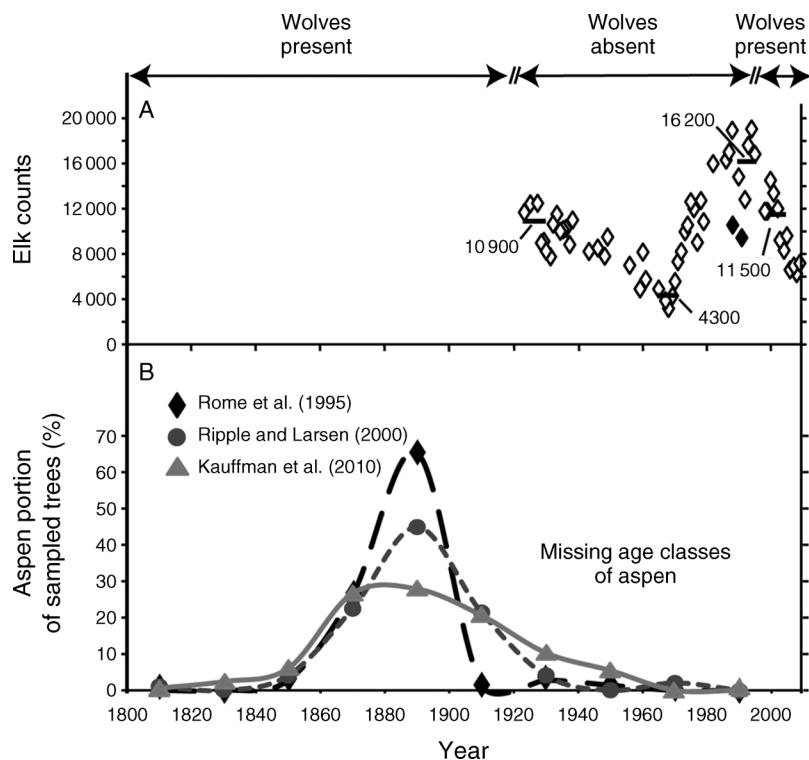


FIG. 1. (A) Status of gray wolves (absent/present) and annual elk census data from years 1923–2009 for the Northern Range of Yellowstone National Park, USA. From 1920 to 1968, elk were culled from the Northern Range herd by the park service while some that left the park were hunted, resulting in declining numbers over time; park service culling ceased in 1968. Average number of elk for 1923–1929, 1965–1970, 1990–1995, and 2003–2007, based on five years of count data, are identified by horizontal lines and numbers. Elk counts did not occur every year; a substantial underestimate due to poor survey conditions (solid diamonds) occurred in 1989 and 1991 (adapted from NRC [2002]; White and Garrott 2005). (B) Aspen age structure expressed as the percentage of sampled trees by date of establishment from studies in northern Yellowstone (adapted from Romme et al. [1995], Ripple and Larsen [2000], and Kauffman et al. [2010]). “Missing age classes of aspen” denotes a period of severely reduced aspen recruitment that has occurred since the early 1900s.

Range (Yellowstone National Park 1961), the park service undertook a program of culling elk. Culling continued over a period of four decades and was the primary cause of declining Northern Range elk numbers (NRC 2002). By the late 1960s to early 1970s, the elk population had been reduced to  $\sim 4300$  animals ( $2.9$  elk/km<sup>2</sup>; Fig. 1A).

The historical age structure (number of trees by date of establishment) for aspen in the Northern Range had previously been reported by Romme et al. (1995) and Ripple and Larsen (2000). Nevertheless, Kauffman et al. (2010) also determined the age structure of Northern Range aspen. While there are some differences in study outcomes based on the selection of trees for age determination, number of trees sampled, or location of study sites, resultant age structures are convergent in that they demonstrate a pronounced decline in aspen recruitment since the early 1900s (i.e., missing age classes in Fig. 1B). The huge downturn in aspen recruitment not only has major implications for the potential sustain-

ability of this species in northern Yellowstone, but is indicative of pronounced changes to other plant communities and ecosystem processes (Ripple and Beschta 2004a). Cottonwood (*Populus* spp.) recruitment in the Northern Range similarly declined (Beschta 2005) following the extirpation of wolves. Thus, we agree with Kauffman et al. (2010) when they conclude for the period without wolves, as have previous studies, “that elk are indeed responsible for aspen decline on the Northern Range of Yellowstone.”

With regard to any association between historical trends of aspen recruitment decline and elk populations, Kauffman et al. (2010) indicate in their *Abstract*: “This pattern of recruitment failure appears more consistent with a gradual *increase in elk numbers* [emphasis added] rather than a rapid behavioral shift in elk foraging following wolf extirpation.” Their conclusion as to causation is in error since the major decline in aspen recruitment occurred concurrently with *decreasing* elk numbers in Yellowstone’s Northern Range (Fig. 1A). By

the late 1960s to early 1970s, when elk numbers on the Northern Range were at their recorded low, elk browsing had essentially terminated the recruitment of aspen (Fig. 1B). A similar situation occurred in the Gallatin Winter Range where elk numbers declined following the extirpation of wolves (Peek et al. 1967), yet recruitment of aspen (Halofsky and Ripple 2008) and willow (Ripple and Beschta 2004b) severely declined. The fact that aspen recruitment declined concurrently with declining elk numbers in both winter ranges indicates that these large herbivores, even at reduced densities, were capable of causing browsing-suppressed plant communities in the absence of wolves.

2. *Contemporary aspen recruitment.*—In the summer of 2004, Kauffman et al. (2010) sampled aspen suckers (root sprouts) in 16 Northern Range aspen stands, four stands from each of four geographic strata. Their results indicated that aspen suckers, nearly a decade after wolf reintroduction, were “not surviving to the juvenile (or unbrowsable) stage” of 200 cm, a height that approximates the upper browse level of elk. Furthermore, average sucker heights for plants from 5 to 18 years of age were generally unable to exceed 80 cm, indicating heavy browsing suppression by ungulates.

We understand that sucker measurements by Kauffman et al. (2010) indicate aspen recruitment was not occurring as of 2004 in the 16 stands they sampled. However, the conclusion in their *Abstract* that “aspen are not currently recovering in Yellowstone” is factually incorrect since previously published research has demonstrated that young aspen, as well as cottonwoods and willows (*Salix* spp.), have been experiencing reduced herbivory and growing taller in various northern Yellowstone locations, in some cases plant heights are exceeding the browse level of elk. For example, in 2006 we sampled 98 Northern Range aspen stands (44 riparian stands and 54 upland stands [Ripple and Beschta 2007]) within the Lamar River catchment where Kauffman et al. (2010) had sampled 8 of their 16 stands. Within each stand, we measured the five tallest suckers using a plant architecture methodology (Keigley and Frisina 1998) that allowed us to analyze for trends in browsing and sucker height over time. If the return of wolves had initiated a trophic cascade, assessing herbivory and growth patterns of the five tallest suckers within various aspen stands could potentially provide an “early view” of that cascade.

Although wolves had been reintroduced in 1995–1996, results from our 98 aspen stands indicated average annual rates of aspen sucker browsing remained high and heights were less than 100 cm from 1998 through 2003 (Ripple and Beschta 2007); these results are consistent with the 2004 results of Kauffman et al. (2010). However, our measurements also indicated a trend of decreased browsing and increased sucker heights, predominantly in riparian stands, beginning in

about 2004 and continuing to 2006 (our last year of measurement). By 2006, browsing levels for the five tallest aspen suckers had dropped to an average of 25% for riparian stands while remaining at 74% for upland stands. Heights of the five tallest suckers averaged 214 cm in riparian stands indicating recruitment was occurring in some of these stands. In contrast, sucker heights in upland stands averaged only 105 cm indicating continued suppression by browsing (Ripple and Beschta 2007). Site productivity, as indexed by current annual growth, was not significantly different between riparian and upland stands. In 2010, we revisited the 98 aspen stands and found that aspen recruitment has continued to occur in many of these stands (photographs *available online*).<sup>3</sup> Improved recruitment of young riparian aspen is consistent with other studies that have documented increased growth or recruitment of riparian cottonwoods and willows following wolf reintroduction in portions of Yellowstone’s northern winter ranges (Ripple and Beschta 2004b, 2006, Beschta and Ripple 2007a, 2010, Beyer et al. 2007, Baril et al. 2009). Similarly, aspen recruitment was found to recover after wolves recolonized Jasper National Park in the mid-1900s (Beschta and Ripple 2007b).

As to why Kauffman et al. (2010) did not observe recruitment on their sites, we suggest such results may have occurred for several reasons: (1) they utilized average sucker heights in their study whereas we (Ripple and Beschta 2007) selected for the tallest suckers to assess any potential “leading edge” changes in browsing patterns and height growth following wolf reintroduction and/or (2) most of their aspen stands may have been in non-riparian settings, thus increases in sucker heights had not yet begun to occur. With regard to site locations, Kauffman et al. (2010) did not specify the proportion of their stands in riparian or upland settings. With regard to the location of their 16 sampled aspen stands, it is unclear how these stands were selected “within 3 km of a random location.” Additional information on these issues would help readers understand their methods and basic findings.

3. *Aspen recruitment and predation risk.*—One goal of Kauffman et al. (2010:2744) was to analyze for the occurrence of a behaviorally mediated trophic cascade (BMTC). To test “whether differences in current levels of aspen recruitment observed across the landscape are related to spatial variation in the risk of wolf predation on elk” they selected nine aspen stands spanning a range of variation in predation risk and measured annual survival and growth of aspen suckers from 2004 to 2007. Kauffman et al. (2010) did not find increased sucker heights or recruitment occurring in their landscape

<sup>3</sup> <http://ir.library.oregonstate.edu/xmlui/handle/1957/25603>

assessment of 16 aspen stands or within the nine stands they monitored.

To 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 (e.g., decreased herbivory, increased sucker heights, increased recruitment). Because Kauffman et al. (2010) did not find these herbivory/plant responses in any of their aspen stands (i.e., no evidence of a trophic cascade), it is puzzling that they undertook an analysis of “sucker survivorship” to assess the strength of a BMTC. Without confirmation of a trophic cascade on their sites, attempting to assess a behaviorally mediated trophic cascade can provide no insight regarding changes in aspen recruitment in response to predation risk, their stated concern.

We propose for future studies of woody browse species in northern Yellowstone that increased height growth of young plants, along with measurements of browsing levels, are the appropriate variables for assessing the occurrence of a trophic cascade, as well as for discerning the potential importance of density or behavioral mediation. Species such as aspen, cottonwoods, and tall willows need to grow above the browse level of elk so that they can provide ecosystem functions associated with mature plants (e.g., microclimate mediation, nesting and roosting sites, extensive root networks for stream bank stability, sources of downed wood, sexual reproduction). Recruitment of woody stems is a particularly important criterion. It should also be noted that browsing from an increased bison (*Bison bison*) population in the Northern Range during recent years may be additionally affecting the capability of browse species to establish and grow along valley bottoms and uplands (Ripple et al. 2010). Discerning the relative effects of elk and bison herbivory on young woody plants represents an important research need in the Northern Range.

In regard to predation risk, we have concerns whether an analysis of kill sites fully represents “the landscape of fear,” as Kauffman et al. (2010) indicate. Even if such an assessment accurately characterizes the statistical likelihood of predation across a landscape, there are strong reasons to doubt that kill-site locations are necessarily related to the predation risk that foraging elk perceive. For example, the spatial distribution of kill-site density results from a complex interaction of factors including the joint probability that prey will encounter predators, predators will attack prey given an encounter, and that prey will be caught and killed from a given attack (Lima and Dill 1990, Hebblewhite et al. 2005). Additionally, encounter sites and kill sites in Yellowstone occur, on average, nearly one kilometer apart (Kauffman et al. 2007).

Regardless of kill-site locations and predator-prey dynamics, it is ungulate herbivory and plant heights

across northern range sites that ultimately provide information capable of discerning spatial and temporal patterns of perceived predation risk as well as conformation, or not, of a trophic cascade. Because browse plants are present year-round, they represent an important herbivory “sensor” that can be effectively used to assess a prey species perception of predation risk across landscapes with varying terrestrial, biotic, and cultural conditions (Laundré et al. 2010) and over time (e.g., Ripple and Beschta 2006, 2007). The amount of plant material “removed vs. left behind” by herbivores under the risk of predation is similar to the experimental approach of “giving up densities,” a highly favored method of determining perceived predation risk with depletable food patches and for analyzing tradeoffs between food and safety. Measurement of risk “from a feeding animal often provides a more accurate behavioural indicator of predation risk than direct observations of predator-inflicted mortality” (Brown and Kotler 2004). Cresswell (2008) similarly suggests that prey may respond more to perceived predation risk based on local conditions than to actual per capita mortality rates.

#### *Trophic cascades and ecosystem recovery*

At the end of their paper, Kauffman et al. (2010) indicate that “If the Northern Range elk population does not decline to levels considerably lower than current numbers, many of Yellowstone’s aspen stands will likely continue to decline in the coming decades.” Such an “experiment” of fewer elk numbers in the absence of wolves had been previously tested, from the 1920s until 1968, and it failed. Even though elk numbers were drastically reduced during that four-decade period, intense elk browsing in the absence of wolves continued to cause a decline in the recruitment of aspen, cottonwoods, and willows to the point of nearly total failure. With the return of wolves and a Northern Range elk population in 2003–2007 that averaged  $\sim 11\,500$  animals ( $7.7$  elk/km<sup>2</sup>), or nearly three times greater than that of the late 1960s to early 1970s, a spatially patchy recruitment of riparian aspen, cottonwoods, and willows has been documented, although most upland aspen stands continued to be suppressed from high levels of herbivory. In other words, during the historically low elk densities of the 1960s when wolves were absent, no significant improvement in Northern Range vegetation occurred, whereas at the relatively higher elk densities and presence of wolves in recent years, some recovery is underway.

Since changes in elk densities over time have not satisfactorily explained historical or contemporary patterns in the recruitment of aspen, cottonwood, and willow recruitment in northern Yellowstone, and climate has not been found to be a major factor in these patterns, this would seemingly indicate behavior medi-

ation may be having a significant role. Such a hypothesis is supported by research documenting that elk, under the risk of predation by wolves, alter their vigilance, foraging patterns, movements, group size, habitat use, and other traits (Wolff and Van Horn 2003, Ripple and Beschta 2004a, Creel et al. 2005, Fortin et al. 2005, Hernández and Laundré 2005, Beyer 2006, Halofsky and Ripple 2008, Laundré et al. 2010). Overall, there seems to be little doubt that elk behavior in northern Yellowstone today with wolves is quite different than what it was without wolves. Even so, we would consider it imprudent of ecologists and others to expect wolves to entirely “fix” Yellowstone’s aspen recruitment problem, as well as that of other browse species, within the first decade or two of being reintroduced.

Overall, we are concerned that Kauffman et al. (2010) provide little recognition of the potential for behavior mediation in the presence of wolves for having a role at either site-specific or landscape scales. In addition, they downplay the accumulating evidence that some recruitment of multiple woody species, including aspen, is again occurring since wolves have returned. If the reintroduction of wolves had not occurred, there is nothing to indicate from a large number of studies that intensive herbivory by elk, the primary factor affecting the collapse and impairment of northern winter range ecosystems, would have abated (e.g., Chadde and Kay 1996, Ripple and Beschta 2004a, b, Beschta 2005, Wolf et al. 2007, Kauffman et al. 2010).

The fact that at least some riparian plant communities are beginning to recover represents a fundamental shift from the multiple decades of browsing-caused suppression that had occurred throughout Yellowstone’s northern winter ranges when wolves were absent. Even so, any recovery processes currently underway will need to continue if a broader range of ecosystem services are to accrue, such as improved habitat and food-web support for terrestrial and aquatic wildlife (e.g., Smith and Tyers 2008, Baril et al. 2009). The need for continued ecological recovery and increased resiliency of these critical ecosystems in northern Yellowstone is perhaps even more urgent given the ongoing and impending changes in region’s climate.

Finally, the potential recovery pathways for Yellowstone’s ongoing experiment in passive restoration via tri-trophic cascades will require continual and creative evaluation by the scientific community of all three trophic levels, as well as their interactions, since we may get to do so only once. Improved understanding of ecosystem structure and functioning associated with the reintroduction of a formerly extirpated apex predator could also help inform predator management policies on vast areas of public land in the western United States that lie outside of Yellowstone National Park, where wolves could someday return or have already done so.

#### *Acknowledgments*

We are greatly appreciative of review comments from C. Eisenberg, J. Estes, D. Fortin, N. Johnson, L. Painter, O. Schmitz, M. Soulé, and three journal reviewers.

#### *Literature cited*

- Baril, L. M., A. J. Hansen, R. Renkin, and R. Lawrence. 2009. Willow–bird relationships on Yellowstone’s northern range. *Yellowstone Science* 17:19–26.
- Barmore, W. J. 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park; Research and Synthesis 1962–1970. Yellowstone Center for Resources, Yellowstone National Park, Mammoth, Wyoming, USA.
- Berger, J. 2010. Fear mediated food webs. Pages 241–253 in J. Terborgh and J. A. Estes, editors. 2010. *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington, D.C., USA.
- Beschta, R. L. 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone’s northern range. *Ecology* 86:391–403.
- Beschta, R. L., and W. J. Ripple. 2007a. Increased willow heights along northern Yellowstone’s Blacktail Deer Creek following wolf reintroduction. *Western North American Naturalist* 67:613–617.
- Beschta, R. L., and W. J. Ripple. 2007b. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Canadian Journal of Forest Research* 37:1–13.
- Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142:2401–2414.
- Beschta, R. L., and W. J. Ripple. 2010. Recovering riparian plant communities with wolves in Northern Yellowstone, USA. *Restoration Ecology* 18:380–389.
- Beyer, H. L. 2006. Wolves, elk and willow on Yellowstone’s National Park’s northern range. Thesis. University of Alberta, Edmonton, Alberta, Canada.
- 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.
- Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.
- Brown, J. S., J. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385–399.
- Chadde, S., and C. E. Kay. 1996. Tall-willow communities on Yellowstone’s northern range: a test of the “natural regulation” paradigm. Pages 165–184 in F. J. Singer, editor. *Effects of grazing by wild ungulates in Yellowstone National Park*. Technical Report NPS/NRYELL/NRTR/96-01. National Park Service, Denver, Colorado, USA.
- Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397.
- Cresswell, W. 2008. Nonlethal effects of predation in birds. *Ibis* 150:3–17.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Halofsky, J., and W. Ripple. 2008. Linkages between wolf presence and aspen recruitment in the Gallatin elk winter range of southwestern Montana, USA. *Forestry* 81:195–207.
- Hebblewhite, M., E. Merrill, and T. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos* 111:101–111.
- Hernández, L., and J. W. Laundré. 2005. Foraging in the landscape of fear and its implications for habitat use and diet

- 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.
-