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Wolves for Yellowstone: dynamics in time and space

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The reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park is the most celebrated ecological experiment in history. As predicted by population models, the rapid recovery of a wolf population caused both temporal and spatial variability in wolf–ungulate interactions that likewise generated temporal and spatial variation in the expression of trophic cascades. This has amplified spatial variation in vegetation in Yellowstone, particularly with willow (*Salix* spp.) and cottonwood (*Populus* spp.) in riparian areas, with associated changes in food webs. Increasing influences of grizzly bears (*Ursus arctos*), cougars (*Puma concolor*), and bison (*Bison bison*) are making what initially was predominantly an elk–wolf interaction into an increasingly complex system. Outside Yellowstone, however, humans have a dominant influence in western North America that overwhelms trophic cascades resulting in what appear to be bottom-up influences on community structure and function. Complex and unexpected ecosystem responses to wolf recovery in Yellowstone reinforce the value of national parks and other protected areas as ecological baseline reserves.

Key words: bison, *Canis lupus*, *Cervus elaphus*, ecological modeling, elk, hunting, predator–prey dynamics, trophic cascades, wolf, Yellowstone National Park

The reintroduction of gray wolves (*Canis lupus*) into Yellowstone National Park is a well-known ecological experiment, albeit with a lack of replication, randomization, and controls (Kauffman et al. 2013; Ford and Goheen 2015). The trophic cascade that resulted in vegetation being released from herbivory caused by wolf predation on elk (*Cervus elaphus*) is purported to be among the most significant advances in conservation biology of this century (Estes et al. 2011; Ripple and Beschta 2012). I began research on large mammals in the Greater Yellowstone Ecosystem in 1977, thus my involvement in the ecology of the area spans more than 40 years. I will draw from this long-term perspective to reflect on the ecology of wolf recovery in Yellowstone, framed largely on my research and that of my students and colleagues.

BRIEF HISTORY OF WOLVES IN YELLOWSTONE

Although Yellowstone was designated as a national park in 1871, early park management did not provide the protection for wildlife that it does today (Schullery 2003). In fact, the park deliberately eliminated wolves and cougars (*Puma concolor*) by 1926. Within a few years, numbers of elk in Yellowstone had increased substantially, and by the 1930s,

park managers recognized that herbivory was altering vegetation, leading park managers to implement culls to contain the elk population (Houston 1982; Barmore 2003). Public pressure prompted Senator Gale McGee from Wyoming to insist in 1967 that the National Park Service terminate the elk culls. Terminating the elk cull inside the park initiated a period when elk numbers were allowed to reach levels where their abundance would undergo "natural regulation" imposed by the interaction between herbivory and vegetation, i.e., extensive starvation of elk during severe winters (Houston 1982; Merrill and Boyce 1991). Consistent with a review of management of wildlife in national parks (Leopold et al. 1963), the park management committed to restoring wolves to limit elk abundance (Weaver 1978; Despain et al. 1986). Eventually, in 1995, 14 wolves from Alberta were released in Yellowstone, supplemented by another 17 Canadian wolves in 1996 (Smith and Ferguson 2012).

MATERIALS AND METHODS

Modeling wolf recovery.—During the 1980s, the National Park Service began accumulating research and public consultations required to reintroduce wolves. Because of previous research that we had done on population dynamics of elk in

the Greater Yellowstone Ecosystem (Sauer and Boyce 1983; Boyce 1989; Merrill and Boyce 1991), in 1988, John Varley (Director, Yellowstone Center for Resources) persuaded me to develop a model to anticipate probable consequences of wolf recovery to populations of wild ungulates in the park. I proceeded to build a computer simulation model of a predator–prey system focusing primarily on elk–wolf interactions but including alternative prey of bison (*Bison bison*), moose (*Alces alces*), and mule deer (*Odocoileus hemionus*) that were sufficiently abundant to potentially influence wolf recovery. Predation on multiple prey was modeled using a multispecies Holling Type III functional response (Abrams and Allison 1982) to accommodate learning by wolves and density dependence (Maynard Smith 1974).

Parameterization of the elk components of the model relied extensively on data compiled by Houston (1982) for elk populations in the park, and studies of the interaction between wolves and elk in Riding Mountain National Park (Carbyn 1980). Data on predation by wolves on deer (*Odocoileus* spp.) and moose were based on studies in Michigan, Minnesota, Canada, and Alaska (Pimlott 1967; Mech 1970; Garton et al. 1990), whereas the only data for wolf predation on bison were from Wood Buffalo National Park (Carbyn and Trottier 1987). John Varley later asked me to expand my original model focused on the Northern Range (Boyce 1990) to include the Jackson elk herd and the population along the North Fork of the Shoshone River east of the park (Boyce and Gaillard 1992).

Stabilizing features of the model included density dependence for ungulates presumed to be limited by their interaction with vegetation (Houston 1982; Sauer and Boyce 1983; Merrill and Boyce 1991), the logistic functional response affording density-dependent predation at low densities, and density dependence for wolves because of territorial behavior (Cubaynes et al. 2014). In addition, Montana Department of Fish, Wildlife, and Parks had published guidelines for hunter quotas that were density dependent with more licenses being issued when elk numbers on the Northern Range were high (table 2 in Varley and Boyce 2006).

Based on studies of elk ecology on Yellowstone's Northern Range, key to the simulation models was stochastic variation in winter severity (Houston 1982) and summer forage production (Merrill and Boyce 1991). These climate-based perturbations to carrying capacity ensured realistic levels of variation among model predictions; indeed, it was nearly impossible to obtain the same simulation result twice. I programmed a user-friendly interface and we distributed the model on 5 ¼-inch floppy diskettes to high schools, universities, and government agency personnel, encouraging users to explore alternative decisions on how wolf recovery might be managed.

Monitoring dynamics.—For the decade following the reintroduction of wolves, we participated in monitoring elk movements and abundance (Fortin et al. 2005a, 2005b; Mao et al. 2005). Elk were captured in winters of 2000–2002 using netgunning and collared initially with VHF transmitters, and later with GPS telemetry then monitored by Julie Mao (Mao et al. 2005) and Shaney Evans (Evans et al. 2006). Elk on the Northern Range were monitored by the Northern Yellowstone Cooperative Wildlife Working Group in most years using aerial surveys for minimum estimates of abundance not corrected for variation in sightability. Wolves were monitored by park biologists led by Douglas W. Smith following the releases in 1995 and 1996, and beginning in 2004 wolves also were monitored using GPS telemetry.

We used resource selection functions (Mao et al. 2005), step-selection functions (Fortin et al. 2005a), and state-based models (Forester et al. 2007) to document patterns of habitat selection in the context of the distribution of wolves. In addition, we used resource selection functions to study the distribution of sites where wolves killed elk across the Northern Range and performed that analysis each year 1996–2005 to study vulnerability of elk to the spatial distribution of wolves and vegetation (Kauffman et al. 2007). More recently, Kohl et al. (2018) used our telemetry data for elk and data for wolves collected and maintained by park biologists in an analysis of the daily variation in activity by elk and wolves to reveal that they interact in diel patterns of movement and habitat selection.

We revisited the simulation model 10 years after wolf reintroduction in the context of adaptive management (Walters 1986), i.e., to evaluate how well we predicted system dynamics and to adjust the model based on new data (Varley and Boyce 2006).

Vegetation responses.—In the context of trophic cascades, I focus attention on woody plants, in particular aspen (*Populus tremuloides*), willow (*Salix* spp.), and cottonwood (*P. trichocarpa* and *P. angustifolia* and hybrids) that are heavily browsed by both elk and bison.

To study responses of willows to herbivory, 18 stands of willows across Yellowstone's Northern Range were identified, and stems were sampled in 2001. Thin cross-sections of stems were used to measure growth by *Salix boothii* and *S. geyeriana* each year from 1989 to 2001. Variation in growth of willows was modeled relative to browsing, snow depth, elevation, and watershed area, and information-theoretic methods were used to select the best statistical models (Beyer et al. 2007). During the winter of 2003–2004, 7 stands of *S. geyeriana* were monitored 7 times from December through March to document the seasonal pattern of browsing by elk (Varley 2007).

Hydrology is an important factor for riparian vegetation. Marshall et al. (2013) performed 4 replicates of an experimental manipulation of browsing with fenced exclosures and dams to simulate the effect of beavers during 2001–2010. Height and biomass of individually marked willow stems were recorded annually for replicated controls, fenced exclosures, dammed sites, and dammed sites with exclosures. All research was approved by university animal care and conformed to ASM guidelines (Sikes et al. 2011).

RESULTS

Modeling.—The wolf–ungulate model was presented to the United States Congress in support of proposed wolf recovery (Boyce 1990; Boyce and Gaillard 1992). Model predictions

depended on the management alternatives selected by the user, but always resulted in a reduction in the number of elk (Boyce 1995). Yet, density-dependent mechanisms for ungulates and wolves ensured that the model predicted long-term persistence of wolves and all ungulates in the park. Indeed, in over 100,000 iterations of the model, all 4 ungulates and wolves persisted for 100 years (Boyce 1995). Including additional subpopulations in the model also contributed to the stability of the system because fluctuations were not entirely synchronous; therefore, fluctuations in one subpopulation helped to offset those in others (Boyce and Gaillard 1992; Boyce 1995). Consistently, wolf numbers throughout the entire park have been remarkably constant for the past decade at about 100 animals (Fig. 1).

Simulations correctly predicted elk and wolf numbers observed during the first decade after wolf reintroduction (Fig. 2). Early years after wolf reintroduction were dominated by a simple wolf–elk interaction, so the model was most likely to work during the initial period. However, despite these good predictions, we learned that several assumptions and components of the original model (Boyce 1990; Boyce and Gaillard 1992) were incorrect. First, we underestimated the extent to which wolves specialized on elk as prey (White and Garrott 2005), which required revision to the multispecies functional response. Another shortcoming was failure to recognize the strong age selectivity by wolves and hunters (Fig. 3). Hunters preferentially kill bulls but when they kill cow elk they primarily kill prime-age females of high reproductive value (Wright et al. 2006); cows learn to avoid hunters to the extent that individuals older than about 9–10 are essentially "bullet proof" (Thurfjell et al. 2017). In contrast, wolves killed primarily young and old and as a consequence the per capita influence of hunters on elk populations was much greater than for those killed by wolves (Vucetich et al. 2005; Wright et al. 2006). Progressively more elk also began wintering outside the park

on winter ranges secured in part by the Rocky Mountain Elk Foundation, expanding the winter range for elk by about 40% (Taper and Gogan 2002). These deficiencies in the original model structure were accommodated in a revised model that included elk population structure (Varley and Boyce 2006).

Even after making these adjustments, however, during the second decade after wolf reintroduction, the number of elk averaged lower than predicted by the simulation model (MacNulty et al. 2016). I believe that this is because bear (*Ursus arctos* and *U. americanus*) and cougar (*P. concolor*) predation was higher than we had anticipated. In particular, grizzly bears have been shown to be highly effective predators on elk calves (Singer et al. 1997; Barber-Meyer et al. 2008), reducing recruitment by about 7 calves/100 cows (Lukacs et al. 2018). Numbers of bears have not increased appreciably within the park subsequent to wolf reintroduction (Boyce et al. 2001a, 2001b; van Manen et al. 2016), but predation by bears on elk calves has increased (Barber-Meyer et al. 2008; Griffin et al. 2011). Displacement of wolves by bears at kill sites also does not appear to be compensated by increased kill rate by wolves (Tallian et al. 2017). Cougars are highly capable predators on elk and compete with wolves for prey, although they appear to be a subordinate predator (Elbroch et al. 2015).

Another major change in the large mammal community in the past decade has been that the number of bison using the Northern Range has increased to over 4,000 animals, possibly due to reduced competition with elk. Wolves certainly kill bison (Carbyn and Trottier 1987), but bison are more formidable and dangerous prey; thus, when elk are available they are preferred over bison. Consequently, change in the distribution of large herbivores in the park has been one of the most significant responses to wolf predation and this was not anticipated in our predator–prey models.

Monitoring dynamics.—We found that that the interaction between elk and wolves was highly seasonal. During spring
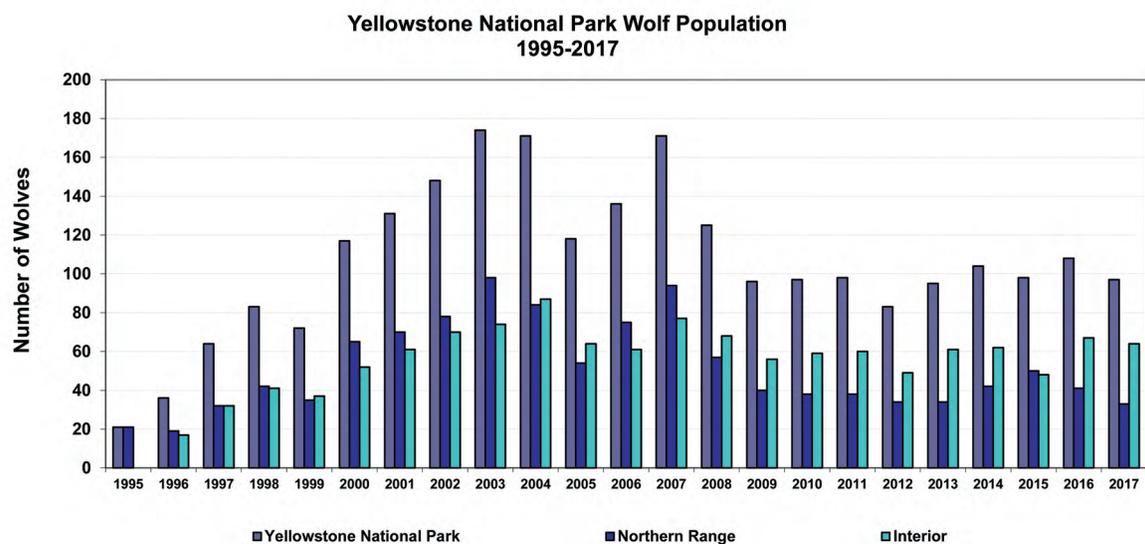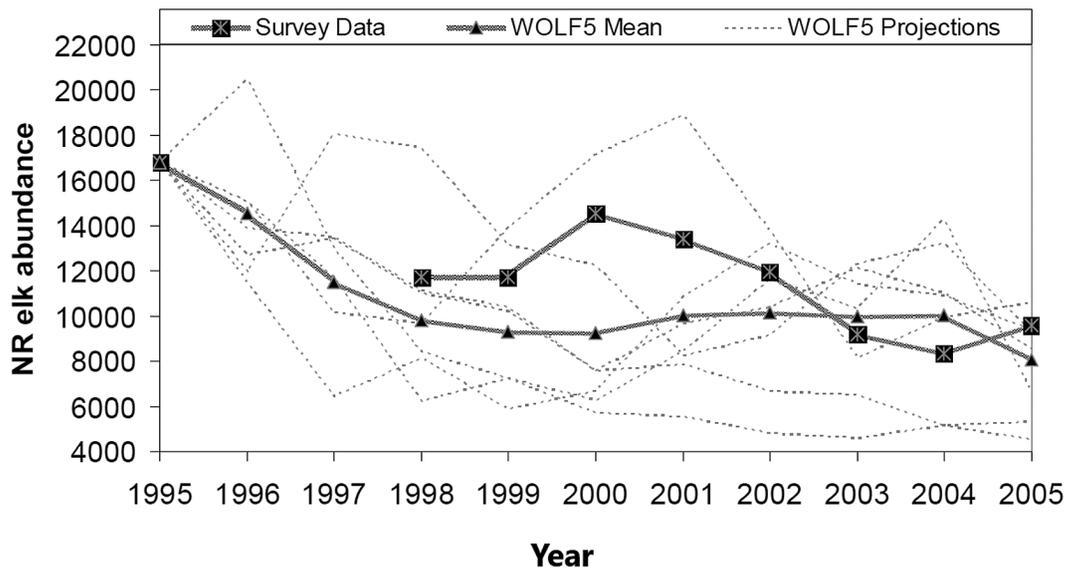

Fig. 1.—Census of wolves (*Canis lupus*) in Yellowstone National Park, 1995–2017, including a breakdown for the Northern Range and the interior portions of the park. Courtesy of Yellowstone National Park.

Fig. 2.—Time series projections from the WOLF5 model (Boyce and Gaillard 1992; Boyce 1995) compared with survey data for the Northern Range elk (*Cervus elaphus*) population, 1995–2004 (from Varley and Boyce 2006).
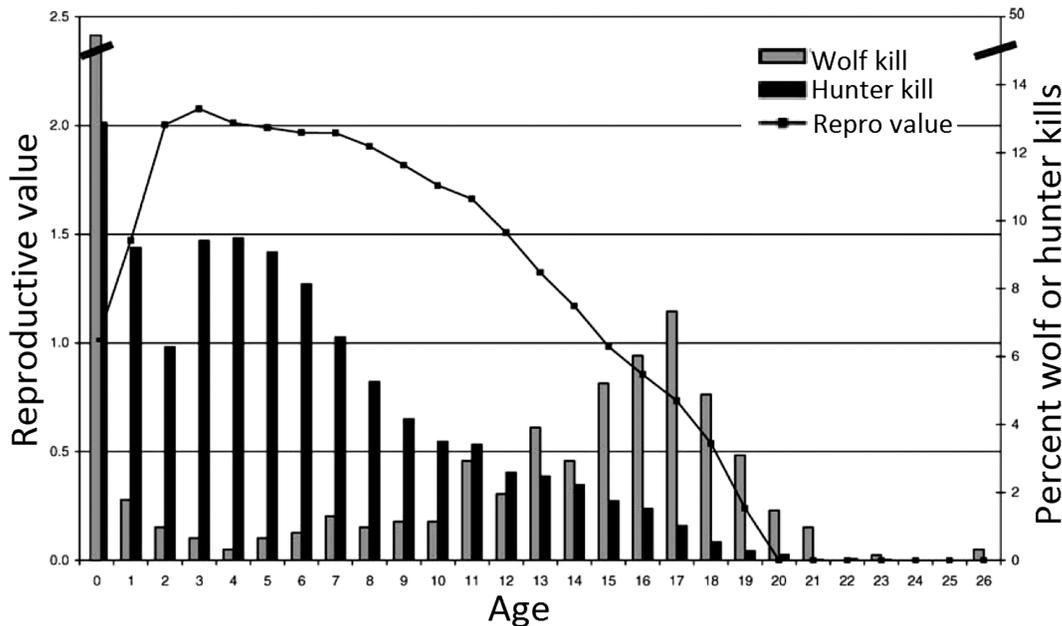
Fig. 3.—Age distributions of female elk (*Cervus elaphus*) killed by hunters versus wolves (*Canis lupus*), 1995–2001. Elk calves killed by wolves is 49% of the total. The line is the reproductive value for females of each age class (adapted from Wright et al. 2006).

and summer, wolf activity was greatest near dens and rendez-vous sites, and resource selection functions for elk showed that they avoided wolves by selecting higher elevations, less-open habitats, more-burned forest, and steeper slopes after wolf rein-troduction. During winter, however, wolves appeared to track the distribution of elk so that elk were unable to select habitats where they might avoid wolves; consequently winter habitat selection by elk did not change much before and after wolf reintroduction (Mao et al. 2005), although in the presence of wolves elk tended to move out of aspen stands toward open grasslands or conifer forests (Fortin et al. 2005a).

Consistent with these elk-based patterns of habitat selection, wolves showed highly seasonal patterns of habitat selection, but

also a substantial year effect, meaning that habitat selection by wolves varied over time (Uboni et al. 2015). Kill sites varied as the wolf population became established and began to saturate the Northern Range. During the first 5 years after wolf reintro-duction, the distribution of elk kills could be attributed in part to the distribution of wolf packs, with remaining variation attrib-utable to landscape and vegetation variables. However, as the Northern Range became saturated with wolf pack territories by year 2000, only landscape and vegetation variables contributed to the distribution of kill sites (Kauffman et al. 2007), again amplifying how the predator–prey system changed over time.

Using our data on elk, Kohl et al. (2018) emphasized that not only was the interaction between wolves and elk highly

seasonal, but it also varied within the day, as had been shown by Forester et al. (2007). Wolf and elk activity are highly crepuscular (Boyce et al. 2010), and the "landscape of fear" is very different during the day and night than during these dawn and dusk activity periods (Kohl et al. 2018). This does not diminish the landscape of fear patterns as reflected by the influence of topography and vegetation on the distribution of wolf kills (Kauffman et al. 2007), but informs a dynamic landscape of fear helping to interpret behavioral observations where elk appeared to ignore wolves during the day.

Vegetation responses.—Foraging by herbivores, especially elk and bison, has substantial consequences to vegetation in Yellowstone National Park (Houston 1982; National Research Council [NRC] 2002; Barmore 2003). Indeed, concern over excessive herbivory precipitated elk culling programs during 1930–1967 and ultimately contributed to wolf reintroduction. Willows, aspen, and cottonwoods were most severely browsed by elk and bison, and reduced browsing resulting from wolf recovery is the expression of a trophic cascade (Ripple and Beschta 2012). Herbaceous grassland plants are important forage for elk and bison as well (Merrill and Boyce 1991; Merrill et al. 1993), but these plants appear to be resilient to grazing (Frank et al. 2016). Yet, grazing amplifies sensitivity of plants to site variation in moisture and nutrients (Frank et al. 2017).

Browsing by elk prior to wolf reintroduction had suppressed growth of willows across Yellowstone's Northern Range (Beyer et al. 2007; Varley 2007). Cross-sectioned willow stem annuli that reflect plant growth for *S. boothii* and *S. geyeriana* show an overall increase in growth at 17 sites across the Northern Range during years following wolf reintroduction, presumably due to reduced browsing by elk (Fig. 4). The best statistical models of willow growth included covariates for elevation, climatic conditions, and the presence of wolves (Beyer et al. 2007). Most important, however, is the enormous variation among sites. This reflects substantial site variation relative to soil type, soil moisture, topography, and vegetation (Tercek et al. 2010). Some sites were released from herbivory, whereas other sites continued to experience substantial herbivory, largely by elk (Varley 2007). Note that these results in Fig. 4 from the analysis by Beyer et al. (2007) are through 2001, before the elk population had begun to decline as a numerical response to wolves, contrary to the interpretation by Creel and Christianson (2009).

Experimental manipulations of the water table and herbivory revealed clear results (Fig. 5). Exclosures to eliminate herbivory enhanced willow growth above that in the control sites, and even stronger response was observed when dams were constructed to simulate beaver dams. The most exaggerated growth by willows was observed at plots behind dams inside exclosures (Marshall et al. 2013).

I visited the Northern Range of Yellowstone in October 2012 at the nadir of elk abundance following wolf reintroduction. Site variation in willow recovery was highly evident. Figure 6 illustrates that willow growth on the Blacktail Plateau is vigorous at a site where willows were suppressed prior to wolf reintroduction. However, south of Mammoth, elk and bison
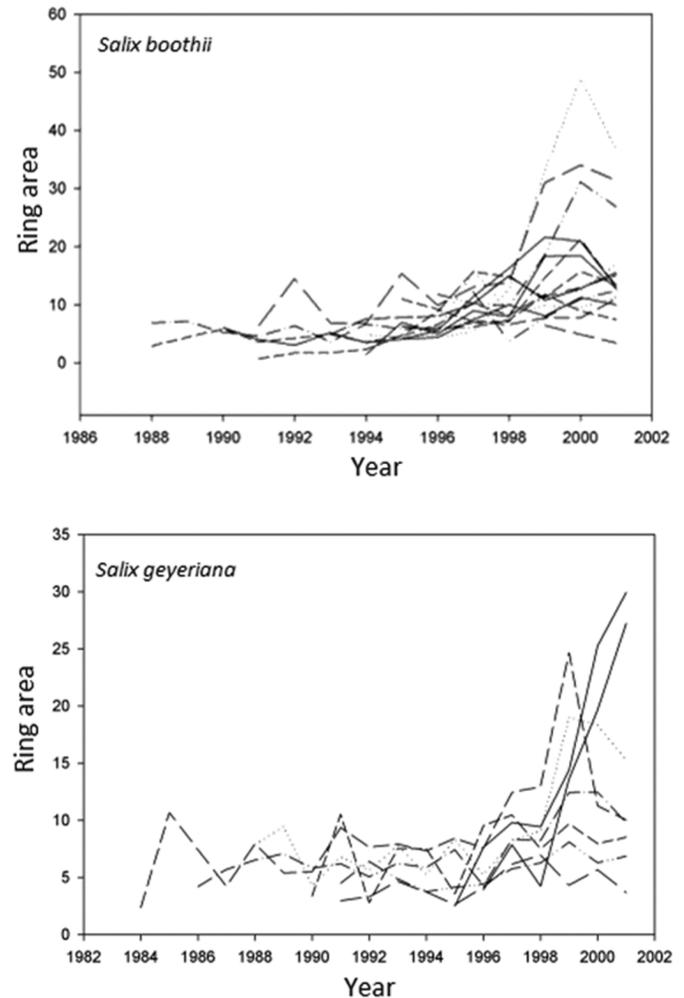
Fig. 4.—Growth by 2 species of willow, *Salix boothii* and *S. geyeriana*, before and after wolf (*Canis lupus*) reintroduction in 1995 measured by dendrochronology (Beyer et al. 2007). Each line is a separate sampling site illustrating substantial variation in the response of willows to wolf recovery. Courtesy of H. Beyer.

continued to suppress willows, revealed by dramatic growth of willows inside an exclosure built in 1958, but no willows persisting outside the exclosure (Fig. 7). I visited this site in 1985 with Don Despain (plant ecologist, Yellowstone Center for Resources), who pointed out that although willow were browsed to the ground every year, the density of stems outside the exclosure was the same as inside. By 2012, however, no willow sprouts could be found outside the exclosure although willows remained robust within the exclosure. Persistent heavy browsing appeared to have killed the plants.

Browsing had largely eliminated cottonwoods from Yellowstone with only a few old trees remaining (NRC 2002; Beschta 2005). However, several flooding events from 1995–2008 resulted in widespread establishment and recruitment of over 1.3 million cottonwoods and an expectation that some of these will survive to form mature stands (Rose and Cooper 2017). Occasional flooding is crucial to the establishment of riparian cottonwoods and release from herbivory is needed for recruitment. Thus, for cottonwoods as well as for willows, we
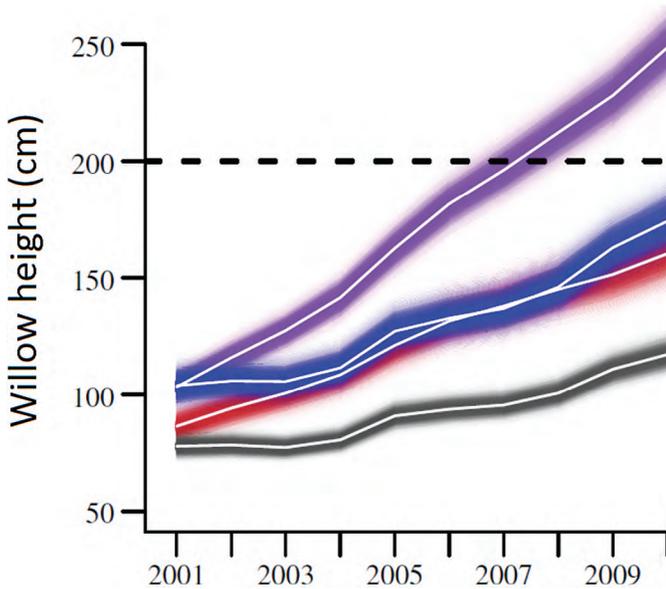
Fig. 5.—Height response of willows (*Salix* spp.) to 4 replicated treatments of herbivory using exclusion fences to eliminate grazing and dams to simulate beaver (*Castor canadensis*) dams. White lines are mean response with shading of 95% prediction intervals for controls in gray, unbrowsed in red, dammed in blue, and both grazing exclosure and dammed in purple. Dashed line at 200 cm is height required to escape herbivory (from Marshall et al. 2013).

Fig. 6.—Willow growth evident in the Blacktail Plateau of Yellowstone National Park, October 2012. A bedded bison (*Bison bison*) is in the middle of the photograph for scale. Photo by M. S. Boyce.

have observed a trophic cascade, albeit associated with flooding conditions required for cottonwood establishment.

Most controversial, however, is the nature of a trophic cascade for aspen. Like cottonwoods, aspen require exceptional conditions to permit recruitment of young trees, especially from seed. Based on sampling of aspen conducted in August and September 1999, Ripple et al. (2001) suggested that due to elk avoiding wolves, aspen might escape herbivory. This could be facilitated by post-fire suckering of aspen (Romme et al. 1995). Aspen were browsed so heavily after the fires of


Fig. 7.—An exclosure 1 km south of Mammoth showing tall willow inside the fenced exclosure, constructed in 1958. I could find no evidence of willow stems outside the exclosure when this photo was taken in October 2012. Photo by M. S. Boyce.

1988, however, that few saplings were able to escape herbivory (Forester et al. 2007; Romme et al. 2011), and high-predation-risk sites were browsed as well (Kauffman et al. 2010).

Consequences of herbivory can be very different among seasons, e.g., elk are typically grazers but browsing is most likely to occur in winter (Fig. 8). Thus, sampling aspen in late summer is not likely to show much site variation in browsing. The ability for a trophic cascade to be expressed also is easily overwhelmed by site and seasonal influences (Marshall et al. 2013). Topography, soils, hydrology, and vegetation all interact to create variation among sites that influences both prey and predator (Bilyeu et al. 2008). Recently, with reduced elk browsing, aspen appear to be recovering in a few stands, especially in eastern portions of the Northern Range (Painter et al. 2015), but not on a broad scale across the Northern Range (Kimble et al. 2011; Kauffman et al. 2013). Again, the outcome is high spatial variability caused by site characteristics and elk herbivory.

DISCUSSION

Several topics regarding wolves in Yellowstone have attracted debate and differences of interpretation, mostly surrounding trophic cascades (Terborgh and Estes 2010). During the first few years after wolf reintroduction, wolves were few and elk still were abundant, leading Beyer et al. (2007) to conclude that behavioral responses released selected willow stands from herbivory. Creel and Christianson (2009) failed to recognize that no decline in elk abundance had occurred during the period studied by Beyer et al. (2007) and incorrectly suggested that the willow response could have been a numerical response. Likewise, during the first 5 years after wolf reintroduction, the distribution of wolf home ranges contributed to the distribution of elk kills on the Northern Range (Kauffman et al. 2007). But after that initial period, the landscape became saturated with wolf home ranges and we found that the
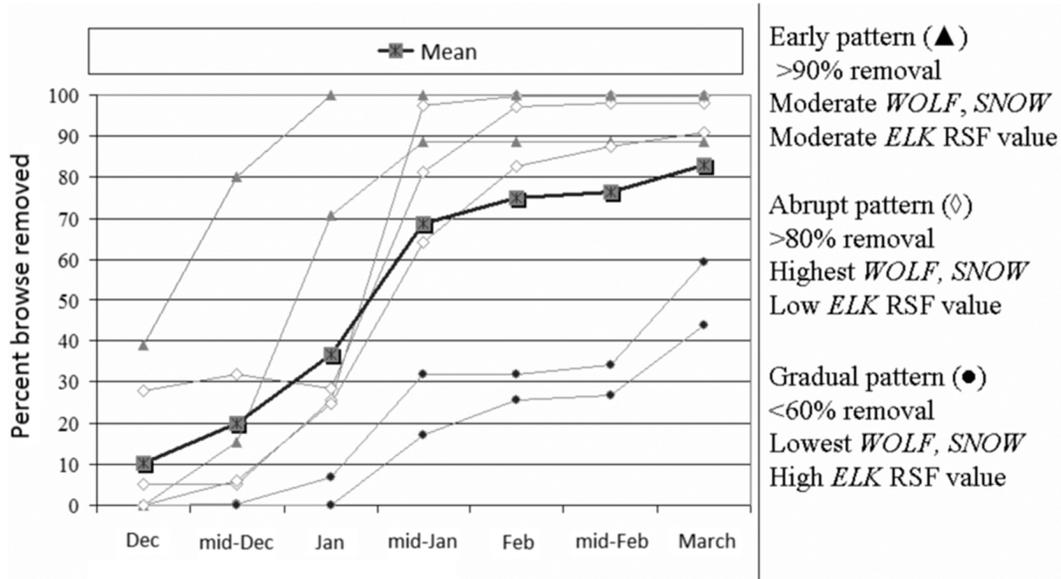
Fig. 8.—Accumulated browsing by elk (*Cervus elaphus*) on willows at 7 stands on the Northern Range, 2003–2004 (from Varley 2007). Patterns of browse removal are indicated by symbols as: early pattern (▲), abrupt pattern (◊), and gradual pattern (●).

distribution of wolf-killed elk was related to topography and vegetation (Kauffman et al. 2007), e.g., elk are easier prey in riparian areas (Bergman et al. 2006). The upshot is that both behavioral and numerical responses have been documented in Yellowstone and these have varied in space and time. I believe that the consensus will be that numerical declines in elk have contributed more to trophic cascades than has behavioral avoidance of wolves, yet behavioral responses clearly exist (Kohl et al. 2018). As vegetation has recovered at some sites, we are now witnessing complex interactions between predation risk and attraction to forage (Gallagher et al. 2017). Clearly, habitat selection by wolves in Yellowstone has varied over time (Kauffman et al. 2007; Uboni et al. 2015; Kohl et al. 2018). Likewise, habitat selection by elk varies seasonally (Mao et al. 2005) and differs among scales (Boyce et al. 2003). Indeed, this heterogeneity in space and time is a hallmark of the expression of a trophic cascade.

My simulation models worked well during the first decade after wolf reintroduction, when the system was dominated by the simple predator–prey interaction between wolves and elk. Density dependence for wolves was debated, and my earlier models were questioned for assuming density dependence in wolves based on their well-known territorial behavior. Yet, this assumption clearly was supported after wolf populations had stabilized and intraspecific interactions were shown to be the most common cause of mortality among wolves (Cubaynes et al. 2014). My assumption of a Type III (logistic) functional response will always be challenging to verify statistically because at low densities we seldom have the sample sizes to show the convex portions of the logistic curve (Marshal and Boutin 1999). The logistic functional response is an important assumption because it contributes to the stability of the system and is highly likely to occur in mammalian carnivores where learning is a mechanism behind the form of the functional response (Maynard Smith 1974; Boyce 2005).

Responses of vegetation to herbivory show remarkable spatial variation. The willow story appears reasonably clear: some drainages began to support good willow growth and populations of willows and songbirds recovered (Beschta and Ripple 2016). However, other sites continue to receive heavy browsing even at reduced elk densities, and might require many decades to recover from 70 years of heavy browsing by elk and loss of beavers (Hobbs and Cooper 2013). Likewise, cottonwoods are recovering not only due to release from elk but largely in response to perturbations created by occasional flooding events (Rose and Cooper 2017); again, this is creating a highly heterogeneous riparian landscape in the park.

The dynamics of aspen and elk continue to perplex us. Beetle (1979) and Gruell (1979) noted that declining aspen could be attributed to heavy browsing by elk as well as an absence of fire. Small fires were ineffective because resprouting aspen attracted heavy herbivory, preventing recovery (Bartos and Mueggler 1979). So, we presumed that what was needed were large fires so that aspen had opportunity to escape elk herbivory. The extensive fires of 1988 gave us the presumed remedy, but elk numbers were so high that aspen could not escape herbivory even though there was extensive resprouting and aspen seed establishment (Romme et al. 2011). Subsequent to wolf recovery, we observed that in the presence of wolves, elk tended to move away from aspen stands toward either open grasslands or coniferous forests (Fortin et al. 2005a). Yet, Kauffman et al. (2010) found that aspen stands were still suffering heavy elk browsing even in high-predation-risk sites. I believe that there are 3 probable explanations: 1) our radiocollars were set to a 5-h fix schedule and with such a long period between fixes, we could not obtain good resolution in a step-selection function (Fortin et al. 2005a); 2) interactions between wolves and elk are highly dynamic in space and time; and 3) we treated all aspen stands as equal in the analysis, whereas in reality there is substantial variation in the perceived threat of wolf approach

among stands because of variation in cover and topography. Nevertheless, Painter et al. (2015) present evidence that some stands of aspen in Yellowstone are now recovering, but there is not convincing evidence that this is driven by a behaviorally mediated response by elk to wolves (Kauffman et al. 2013). Clearly, resolution the dynamics of herbivory and trophic cascades in aspen warrants continuing study.

Although the demonstration that wolves in Yellowstone National Park have shaped a trophic cascade is fascinating ecology, it is not clear that trophic cascades will occur in other areas. We also cannot be confident that these observations have conservation implications for wolf management and ecosystem restoration elsewhere (Estes et al. 2011; Ripple and Beschta 2012; Wolf and Ripple 2018). We need to be cautious about overextending the ecological results from wolf reintroduction in Yellowstone to applications outside parks, where livestock management (Morehouse and Boyce 2011) and hunting have a major influence on ecosystem structure and function (Mech 2012; Muhly et al. 2013).

A principle emerging from wolf recovery in Yellowstone is that trophic cascades have caused increased spatial and temporal heterogeneity. This is evident in the large spatial and temporal variation in growth of willows (Beyer et al. 2007; Varley 2007; Marshall et al. 2013), aspen (Kimble et al. 2011; Brodie et al. 2012; Painter et al. 2015), and cottonwoods (Rose and Cooper 2017). Spatial and temporal variation in predation risk means that the landscape of fear creates an additional source of variation (Abrams 2000). Movement ecology demonstrates how both predators and prey interact in a landscape driven by spatial variation in both energy resources and risk (Fortin et al. 2005a, 2005b; Harvey and Fortin 2013; Gallagher et al. 2017). For example, vegetation resources attract elk to riparian habitats and aspen stands, but these can be risky places because wolves are able to approach and kill prey in these areas (Fortin et al. 2005a; Bergman et al. 2006; Beyer 2006; Ripple and Beschta 2012). In addition, site variation in topography and hydrology create variation in soil moisture that has a large influence on growth of vegetation and thereby the attractiveness of sites to herbivores (Fortin et al. 2005b; Tercek et al. 2010; Brodie et al. 2012; Marshall et al. 2013; Frank et al. 2017; Raynor et al. 2017).

The interplay between predator–prey interactions and spatial heterogeneity includes important connections to scale (Boyce et al. 2003, 2017). Classic studies of predator–prey interactions showed how spatial heterogeneity can stabilize population dynamics and enhance persistence (Huffaker 1958), as we observed when modeling multiple wolf–ungulate populations in the Greater Yellowstone (Boyce and Gaillard 1992). Yet, at finer scales in Yellowstone, we have seen trophic-level interactions amplifying spatial heterogeneity through a trophic cascade. Movement among foraging patches might constitute a "shell game" by bison (Harvey and Fortin 2013) and elk (Boyce et al. 2003; Seidel and Boyce 2016) to avoid wolves, another mechanism amplifying spatial and temporal variation in herbivory. The Huffaker effect applies to wolf–ungulate systems at large scales, where some subpopulations might wink in and out (e.g., Isle Royale and Michipicoten Island in Lake Superior), whereas at finer scales, trophic cascades amplify spatial variation in predation risk and consequent herbivory. Indeed, spatial heterogeneity arising from trophic cascades at small scales could be what stabilizes the system at the larger population scale.

National parks and protected areas serve a crucial function as ecological baseline reserves from which we can evaluate how humans are affecting nature (Sinclair 1983; Boyce 1991, 1992, 1998). The National Park Service has adopted ecological process management, minimizing interference when possible, allowing predation, herbivory, fire, and flooding to shape the ecosystem (White et al. 2013), and this policy allowed wolf recovery with the fascinating dynamics that have emerged. The most immediate threat to this park policy is the increasing bison population that has precipitated political pressure to limit their abundance for fear that heavy grazing and browsing by bison might "damage" vegetation. We do not know how bison will affect Yellowstone, but surely we will learn a great deal more if we allow the bison population to take its course rather than intervening in a fashion that will be arbitrary to the underlying ecological system. Whatever influence we can have as scientists, we must insist that the National Park Service maintain its policy of ecological process management for their Crown Jewel that is Yellowstone National Park.

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