

## ISSUE 18:

Both commenters and peer reviewers presented comments surrounding our discussion and analysis of the carrying capacity for grizzly bears in the GYE. Both commenters and peer reviewers raised concerns that Figure 1 of the proposed rule is an oversimplification of a population at carrying capacity. They proposed including an explanation of the variables, in addition to those presented in Figure 1, that influence carrying capacity (e.g. food availability and emigration in search of food, mates, or territory). One commenter noted that a graph illustrating how the Chao2 estimate of the GYE grizzly bear population is leveling off might provide a clearer demonstration of carrying capacity. Additionally, commenters doubted our conclusion that the GYE population is approaching carrying capacity; one commenter noted that grizzly bears only occupy 25% of the GYE (i.e. carrying capacity has not been met), and that we acknowledge the inherent difficulty in calculating carrying capacity.

Commenters and peer reviewers suggested alternative hypotheses to our claim that GYE population is approaching carrying capacity. Commenters suggested that a decrease in food availability may be the driver behind a slowing growth rate in the GYE grizzly bear population. Another commenter noted that carrying capacity itself may have declined as a result of decreasing food availability (specifically of the four major grizzly bear food sources). One peer reviewer concurred with this suggestion, noting that the stabilizing trend for grizzly bears in the GYE could be a result of a shrinking biological carrying capacity. This peer reviewer cited [Van Manen et al. \(2016, page 309\)](#), who noted that a decrease in carrying capacity was a possible alternative explanation for the demographic changes apparent in the GYE population; this peer reviewer suggested that we should note this possible explanation in the rule. Another peer reviewer proposed that grizzly bears in the GYE may have reached a *social* carrying capacity, not a biological one.

### Current language from the Conservation Strategy

[Harris et al. \(2006\)](#) [Schwartz et al. \(2006, entire\)](#) analyzed estimated survivorship of cubs-of-the-year, yearlings, and independent bears as well as reproductive performance to estimate population growth. They examined geographic patterns of population growth based on whether bears they lived inside Yellowstone National Park, outside the Park but inside the [Recovery Zone](#) or Primary Conservation Area (PCA), or outside the PCA entirely. The PCA boundaries (containing 23,853 sq km (9,210 sq mi) correspond to those of the Yellowstone Recovery Zone (U.S. Fish and Wildlife Service 1993) and will replace the Recovery Zone boundary (Figure 1). They concluded that grizzly bears were approaching carrying capacity inside Yellowstone National Park. Consistent with this [conclusion interpretation](#), the IGBST (2012) documented lower cub and yearling survival than in the previous time period. Importantly, annual survival of independent females (the most influential age-sex cohort on population trend) remained the same while independent male survival increased (IGBST 2012). Collectively, these two studies indicate that the growth rate of the grizzly bear population inside the DMA had slowed as bear densities may bear nearing carrying capacity in portions of the GYE, particularly in the core area of occupied range. Recent work by van Manen et al. (2016) confirms provided further that the population is showing evidence of density-dependent population regulation in portions of the DMA where bear densities are high.

### Current language from the Proposed Rule

#### Population Ecology—Background

**Comment [FTvM1]:** This is indeed a simplification but that is necessary to explain the general principles behind the concept of K. The text addresses the complexity of this concept.

**Comment [FTvM2]:** These are addressed in the narrative of the carrying capacity concept, such as: "Population stability (i.e., fluctuation around carrying capacity or a long-term equilibrium) is often influenced by a combination of density-dependent and density-independent effects."

**Comment [FTvM3]:** Interesting idea but using actual data would not be conducive to conveying the concept of K.

**Comment [FTvM4]:** It is unclear where this estimate comes from. If we use the DMA as a reasonable boundary to delineate "suitable habitat" and social acceptance, very few areas of the DMA remain unoccupied.

**Comment [FTvM5]:** The paragraph discussing the general concept of K clearly states that K is difficult to estimate.

**Comment [FTvM6]:** These are addressed in the summary of the Food Synthesis analyses.

**Comment [FTvM7]:** This is indeed recognized as an alternative explanation in van Manen et al. (2016, p. 309). However, in that same paragraph, the authors provide evidence that the scientific evidence for this is not strong: "If bears were responding to a decline in carrying capacity, however, we would have expected home-range size and movements to have increased (McLoughlin et al. 2000), bears to have relied on lower energy food resources (McLellan 2011), and body condition to have declined as a consequence (Rode et al. 2001, Robbins et al. 2004, Zedrosser et al. 2006). To date, there is little support for these conditions in the Yellowstone Ecosystem: female home ranges have decreased in size and are less variable in areas with greater bear densities (Bjornlie et al. 2014b), daily movement rates and daily activity radii have not changed for either sex during fall (Costello et al. 2014), bears continue to use high-quality foods (Fortin et al. 2013), and body mass has not declined (Schwartz et al. 2014). As we discussed previously, ...

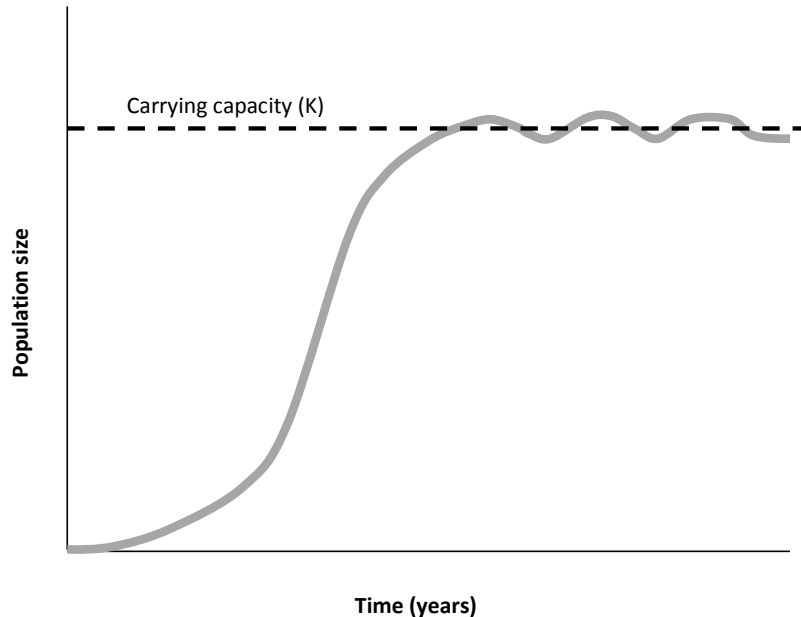
**Comment [HMA8]:** I would add that our studies point to a density-dependent effect for leveling off of the population. Male survival has undoubtedly increased, more males in the population compete for mating opportunities may be a possible cause. ...

**Comment [FTvM9]:** We assume this refers to human social carrying capacity (social tolerance). This is certainly a consideration but IGBST data do not support the interpretation that this is contributing to the slowing of population growth. ...

**Comment [HMA10]:** I agree with Frank, no evidence that social carrying capacity or human tolerance for grizzly bears has been reached.

**Comment [FTvM11]:** I think it may be best to cite the entire Wildl. Monograph here, as all chapters contributed to the population projections.

No population can grow forever because the resources it requires are finite. This understanding led ecologists to develop the concept of carrying capacity (expressed as the symbol “K”). This is the maximum number of individuals a particular environment can support over the long term without resulting in population declines caused by resource depletion (Vandermeer and Goldberg 2003, p. 261; Krebs 2009, p. 148). Classical studies of population growth occurred under controlled laboratory conditions where populations of a single organism, often an insect species or single-celled organism, were allowed to grow in a confined space with a constant supply of food (Vandermeer and Goldberg 2003, pp. 14–17). Under these conditions, K is a constant value that is approached in a predictable way ~~that and~~ can be described by a mathematical equation. However, few studies of wild populations have demonstrated the stability and constant population size suggested by this equation. Instead, many factors affect carrying capacity of animal populations in the wild, and carrying capacity itself typically varies over time. ~~and p~~Populations usually fluctuate above and below carrying capacity, resulting in relative population stability over time (i.e., lambda value of approximately 1.0 over the long term) (Colinvaux 1986, pp. 138–139, 142; Krebs 2009, p. 148). For populations at or near carrying capacity, population size may fluctuate ~~s just above and below carrying capacity~~ around a long-term mean, sometimes resulting in annual estimates of lambda showing a declining population (figure 2). However, to obtain a biologically meaningful estimate of average annual population growth rate for a long-lived species like the grizzly bear that reproduces only once every 3 years and does not start reproducing until at least 4 years old, we must examine lambda over a longer period of time to see what the average trend is over that specified time. ~~This is not an easy task; f~~or grizzly bears, it takes at least 6 years of monitoring as many as 30 females with radio-collars to accurately estimate average annual population growth (Harris *et al.* 2011, p. 29).



**Figure 2.—Typical Population Trend with Respect to Carrying Capacity (K). When the population is low, growth rate is rapid. When the population is at or near K, growth rates decelerate and may temporarily decrease as population size fluctuates around K.**

**Comment [FTvM12]:** The “swings” above and below carrying capacity should be quite a bit greater than what the figure suggests.

When a population is at or near carrying capacity, mechanisms that regulate or control population size fall into two broad categories: density-dependent effects and density-independent effects. Generally, factors that limit population growth more strongly as population size increases are density-dependent effects, or intrinsic factors, usually expressed through individual behaviors, physiology, or genetic potential (McLellan 1994, p. 15). Extrinsic factors, such as drought or fire that kill individuals regardless of how many individuals are in a population, are considered density-independent effects (Colinvaux 1986, p. 172). These extrinsic factors may include changes in resources, predators, or human impacts and may cause carrying capacity to vary over time. Population stability (i.e., fluctuation around carrying capacity or a long-term equilibrium) is often influenced by a combination of density-dependent and density-independent effects. Among grizzly bears, indicators of density-dependent population regulation can include: (1) decreased yearling and cub survival due to increases in intraspecific killing (i.e., bears killing other bears), (2) decreases in home-range size, (3) increases in generation time, (4) increases in age of first reproduction, and (5) decreased reproduction (McLellan 1994, entire; Eberhardt 2002, pp. 2851–2852; Kamath *et al.* 2015, p. 10; van Manen *et al.* [2015](#)[2016](#), pp. [8307–3089](#)). Indicators that density-independent effects are influencing population growth can include: (1) larger home-range sizes (because bears are roaming more widely in search of foods) (McLoughlin *et al.* 2000, pp. 49–51), (2) decreased cub and yearling survival due to starvation, (3) increases in age of first reproduction due to limited food resources, and (4) decreased reproduction due to limited food resources. As a result of these sometimes similar indicators, determining whether a population is affected more strongly by density-dependent or density-independent effects can be a complex undertaking. For long-lived mammals such as grizzly bears, extensive data collected over

decades are needed to understand if and how these factors are operating in a population. We have these data for the GYE grizzly bear population, and the IGBST has ~~been able to examine~~ tease apart some of these confounding ~~effects~~ factors. The slowing of population growth since the early 2000s was primarily a function of lower survival of dependent young and moderate reproductive suppression (IGBST 2012). Survival of cubs-of-the-year and reproduction were lower in areas with higher grizzly bear ~~to find densities but showed no association with estimates of decline in whitebark pine decline~~ tree cover, suggesting that density-dependent factors contributed to the change in population growth (van Manen *et al.* 2016) ~~that density-dependent effects are the likely cause of the recent slow in population growth~~ (see *Changes in Food Resources* under Factor E, below, for more detailed information).

#### *Population and Demographic Recovery Criteria*

Schwartz *et al.* (2006, entire) estimated survivorship of cubs-of-the-year, yearlings, and independent bears as well as reproductive performance to estimate population growth. They examined geographic patterns of population growth based on whether bears ~~Harris *et al.* (2006, p. 29) analyzed survivorship of cubs-of-the-year, yearlings, and independent bears based on whether they~~ lived inside Yellowstone National Park, outside the Park but inside the Recovery Zone or PCA, or outside the PCA entirely. The PCA boundaries (containing 23,853 sq km (9,210 sq mi) correspond to those of the Yellowstone Recovery Zone (U.S. Fish and Wildlife Service 1993, p. 41) and will replace the Recovery Zone boundary (see figure 1, above). They concluded that grizzly bears were approaching carrying capacity inside Yellowstone National Park. The IGBST (2012, p. 33) documented lower cub and yearling survival than in the previous time period, results consistent with the conclusion by Schwartz *et al.* (2006b). Importantly, annual survival of independent females (the most influential age-sex cohort on population trend) remained the same while independent male survival increased (IGBST 2012, p. 33). Collectively, these ~~two~~ studies indicate that the growth rate of the GYE grizzly bear DMA population has slowed as bear densities have approached carrying capacity, particularly in the core area of occupied range.

Comment [FTvM13]: Just made it consistent with the suggested language for CS

#### *Changes in Food Resources*

Key findings of the Synthesis Report are summarized below. To address the first question about how diverse ~~diets of GYE grizzly bears~~ diets in the GYE are, Gunther *et al.* (2014, entire) conducted an extensive literature review and documented over 260 species of foods consumed by grizzly bears in the GYE, representing four of the five kingdoms of life ~~(for more information, please see Nutritional Ecology, above). If whitebark pine seeds are highly selected over other fall foods. Regarding the second research question, if whitebark pine was a preferred food or if individual grizzly bears were dependent on this food source, we would expect movement rates and grizzly bear selection of whitebark pine to increase as its availability decreased and bears had to search further and longer to find this food source. grizzly bears would continue to seek this food even as availability declined. However, However, Costello *et al.* (2014, p. 2013) found that grizzly bear selection of whitebark pine habitat and duration of use had actually decreased between 2000 and 2011. Additionally, They also found that movement rates had not changed over the study period, further supporting the notion that grizzly bears were simply finding alternative foods within their home ranges as whitebark pine seeds became less available over the past decade (Costello *et al.* 2014, p. 2013). Regarding the third research question, if grizzly bears were dependent on whitebark pine to meet their nutritional requirements, we would expect body condition would be expected to have decreased since 2002. Instead, Schwartz *et al.* (2013, p. 75) and the IGBST (2013, p. 18) found body mass and percent body fat in the fall had not changed significantly from 2000 to 2010. When they examined~~

Comment [FTvM14]: I tried to edit this as a narrative to avoid having to list the 8 research questions.....

trends in females only, the data ~~seemed to show~~ed a ~~slightly moderate~~ decline ~~ing trend~~ in female body fat during the fall, starting around 2006 (Schwartz *et al.* 2014, p. 72). However, they suggested it could be the result of ~~very~~ small sample sizes ( $n = 2.6$  bears/year) and noted the data for 2011 (not included in their published paper) showed an increase in fall body fat for females, ultimately cautioning that more data were needed before it could be determined if there was truly a trend (Schwartz *et al.* 2014, p. 76). In the Food Synthesis Report, the IGBST revisited the previous analysis with ~~information data collected~~ since 2010, and ~~found~~ ~~concluded that~~ "body condition ~~was~~ not different between poor and good years of whitebark pine production" (IGBST 2013, p. 18). In years with poor whitebark pine seed production, and that grizzly bears shifted their diets and used consumed more meat in years with poor whitebark pine seed production (Schwartz *et al.* 2013, p. 68). ~~In response to the fourth research question, the IGBST found that ungulate carcass use had increased since 2002, and that bears used more meat in years with poor whitebark pine seed production (Schwartz *et al.* 2013, p. 68).~~ These results were ~~expected and are~~ consistent with previous findings (Mattson 1997, p. 169). Given these observations of diet shifts, Ebinger *et al.* (2016, p. 705) examined whether grizzly bear use of ungulate carcasses in fall had increased during the period of whitebark pine decline. This was indeed the case, supporting the interpretation that responses to changing food resources were primarily behavioral. If overall food resources were declining, ~~Because we one would expect daily movements, and fall movements, and home range sizes to increase if food resources were declining and bears were roaming more widely in search of foods.~~ However, ~~To answer the fifth and sixth research questions identified in the previous paragraph, the IGBST examined movement rates and home range sizes. They found movement rates did not change during 2000–2011, suggesting that grizzly bears were finding alternate foods within their home ranges as whitebark pine seeds became less available over the past decade (Costello *et al.* 2014, p. 2013). daily and fall bear movements had not increased from 2000 to 2011 (Costello *et al.* 2014, pp. 2011, 2013).~~ For females, Additionally, they documented that home ranges actually decreased significantly for females in size from the period before (1989–1999) and after (2007–2012) whitebark pine decline, whereas male home ranges did not change in size. ~~and that~~ This decrease was greater in areas with higher grizzly bear densities ~~but showed no relationship with amount of live whitebark pine in the home range (Bjornlie *et al.* 2014b, p. 4–6).~~ Male home ranges did not change in size (Bjornlie *et al.* 2014b, p. 4–6). Finally, at the population level, bear density, but not whitebark pine decline, was associated with lower cub survival and reproductive suppression, factors contributing to the slowing of population growth since the early 2000s. The IGBST compared pre (1989–1999) and post whitebark pine impact (2007–2012) periods and did not find a relationship between home range size and amount of live whitebark pine in the home range (Bjornlie *et al.* 2014b, p. 4–6). ~~Because we would expect daily and fall movements and home range size to increase if food resources were declining and bears were roaming more widely in search of foods.~~ Combined, these findings ~~offer strong suggest support~~ that changes in population vital rates since the early 2000s are more indicative of the population approaching carrying capacity than a shortage of resources (van Manen *et al.* 2016, p. 24310).

Formatted: Font: Italic