

## **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**

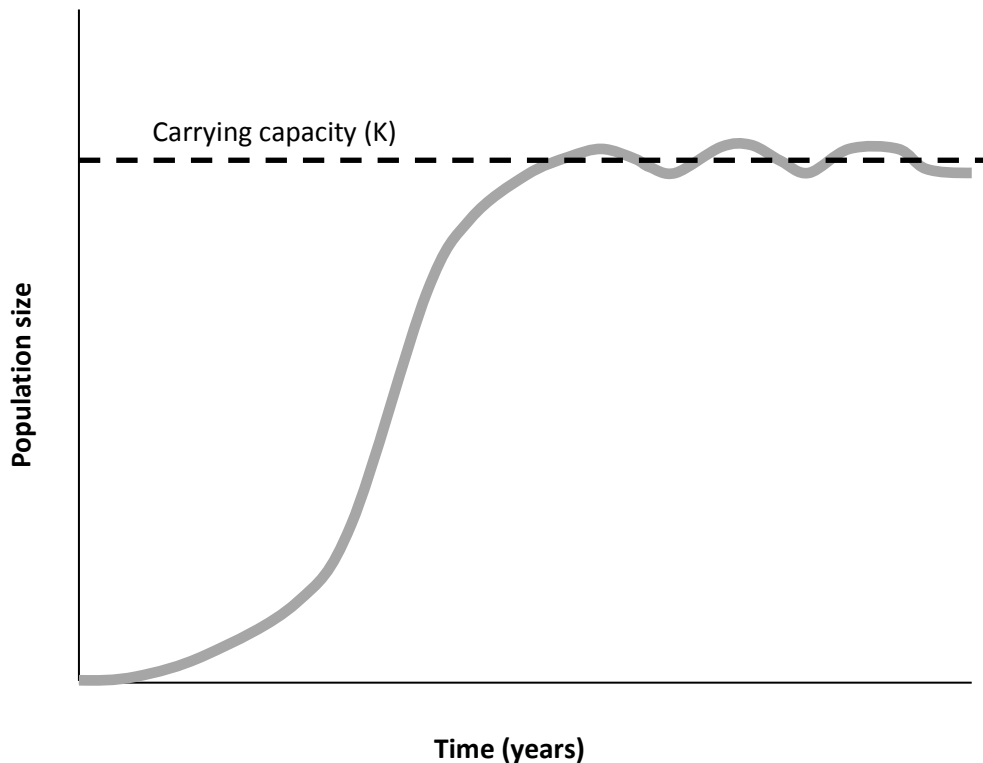
Harris *et al.* (2006) analyzed survivorship of cubs-of-the-year, yearlings, and independent bears based on whether they lived inside Yellowstone National Park, outside the Park but inside the Recovery Zone or Primary Conservation Area (PCA), or outside the PCA entirely. The PCA boundaries (containing 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, 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, particularly in the core area of occupied range. Recent work by van Manen *et al.* (2016) confirms 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**

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 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 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 fluctuates just above and below carrying capacity, 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; for 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.**

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. 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, pp.8–9). 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 tease apart some of these confounding effects to find 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*

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.

#### *Changes in Food Resources*

Key findings of the Synthesis Report are summarized below. To address the first question about how diverse GYE grizzly bear diets 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). 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. However, Costello *et al.* (2014, p. 2013) found that grizzly bear selection of whitebark pine habitat had actually decreased between 2000 and 2011. 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 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 trends in females only, the data seemed to show a slightly declining 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 since 2010, and found “body condition is not different between poor and good years of whitebark pine production” (IGBST 2013, p. 18). 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). To answer the fifth and sixth research questions identified in the previous paragraph, the IGBST examined movement rates and home range sizes. They found daily and fall bear movements had not increased from 2000 to 2011 (Costello *et al.* 2014, pp. 2011, 2013). Additionally, they documented that home ranges actually decreased significantly for females and that this decrease was greater in areas with higher grizzly bear densities (Bjornlie *et al.* 2014b, p. 4–6). 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, these findings offer strong 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.* 2015, p. 21).