

## Issues of Elk Productivity for Research and Management

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### Introduction

Elk (*Cervus elaphus*) populations in western North America have been intensively managed for the past century. The species' popular appeal as an animal for hunting and viewing, and its potential to damage agricultural crops and compete with livestock make it a species that is closely scrutinized by managers and many public interests. Today, elk continue to have significant ecological, cultural, and economic values. For example, the species provides substantial revenue for rural communities from hunting and viewing (Bolon 1994). Since the 1960s, elk in some areas of the western United States caused economic damage to farming and ranching operations. Elk managers spent considerable effort to maintain populations at levels compatible with these private land uses, while also striving to provide sufficient hunter opportunities on public lands to meet recreational demands.

More recently, concern about elk has changed from how to manage increasing populations to that of population maintenance. Elk recruitment, defined here as number of calves per 100 females that survive to one year of age, has declined in many areas of the western United States. Elk recruitment gradually declined since the 1960s in areas of northeast Oregon (Oregon Department of Fish and Wildlife 2003) from more than 50 calves per 100 females to fewer than 20 calves per 100 females in some areas during the 1990s, resulting in lower elk populations and fewer hunting tags issued. In Wallowa County of northeast Oregon, the number of antlered elk tags was reduced from 7,030 in 1995 to 4,620 in 2000 and from 4,140 to 350 for hunting antlerless elk (Oregon Department of Fish and Wildlife 2001). Elk populations declined 25 percent in the Clearwater Basin in Idaho, 50-70 percent in the North Rainier, 30-50 percent in the South Rainier, and 30 percent in the Blue Mountains elk herds in Washington during the late 20<sup>th</sup> century, and most of these declines were concurrent with low recruitment (Cook et al. 1999).

The focus of our paper is to describe biological factors that affect elk population dynamics and focus on some potential causes of recent declines in elk recruitment. We identify interacting factors that may explain recent declines in elk recruitment, and describe the most likely hypothesis as a combination of several factors. We provide this discussion as context for the many subsequent papers that focus on elk productivity or related issues as part of research conducted by the Starkey Project and its partners.

### Factors Affecting Elk Recruitment and Populations

The question of what regulates elk productivity is of practical interest because effective management depends on understanding how the multitude of factors may limit or interact to affect populations. Questions have centered on whether factors that most affect ungulate productivity are density dependent or density independent and if predation can limit elk populations. Following Skogland (1991), we define regulation as any positive density-dependent (effects increase as density increases) process that tends to stabilize population numbers over time. Any process that causes changes in population size is termed limitation. Limitation processes normally operate independently of density and thus do not stabilize populations. Both regulatory and limitation factors have been proposed to explain the long-term decline in elk recruitment. Factors that are usually listed as regulating include food, disease, and perhaps other key habitat resources that may be in short supply as populations increase. Changes in elk population characteristics such as reproduction and survival have been correlated with changes in population size (or density) (Houston 1982). Factors that are often listed as limiting ungulate populations include human

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harvest, stochastic events (usually weather related), and predation. Predation effects can be density dependent, density independent, or inversely density dependent (Messier and Crête 1985, Skogland 1991, Messier 1994). Because territoriality of predators will restrict their density at some point, there should be a point at which predation should no longer be positively density dependent as prey populations increase (Skogland 1991). Messier (1994) identified three scenarios where predation can have varying effects on ungulate populations. Predation can be (1) density dependent at low prey densities when predation rates increase as prey density increases, (2) density independent when predation rates remain constant, and (3) inversely density dependent when predation rates decrease as populations increase often at higher prey densities (Messier and Crête 1985).

Density independent and density dependent factors affect population parameters (e. g., rates of birth, growth, fertility, mortality), and the statistics that quantify these parameters are vital rates (Caswell 2001). Temporal variation in vital rates have a major effect on population growth ( $\lambda$ ) of elk. Eberhardt et al. (1996) estimated a maximum rate of increase ( $\lambda$ ) of 1.33, or about 27 percent per year. Survival of adult female elk is the most important vital rate for long-term stability of populations (Nelson and Peek 1982, Wisdom and Cook 2000, Garrott et al. 2003) followed by fecundity of prime-aged adults, fecundity of primiparous females, and finally juvenile survival (Gaillard et al. 2000). In practice, however, survival of juveniles is an important component of ungulate population dynamics even though this vital rate has disproportionately less effect on population growth than other vital rates (Gaillard et al. 1998, 2000; Eberhardt 2002).

How might density independent and density dependent factors act separately or interactively to control vital rates and growth of ungulate populations? The literature contains theoretical and empirical works that address ungulate productivity and are often contradictory when read in the absence of a broad examination of the issue. For example, within the Serengeti, smaller ungulate species were controlled by predation, and available resources controlled larger species (Sinclair et al. 2003). Moreover, density dependent and density independent factors may act simultaneously, such that effects of density independent factors (drought or severe winter) increase with higher population density (Gaillard et al. 2000).

A related concept to density dependence is that of compensatory versus additive sources of mortality. Compensatory sources of mortality are those that have little influence on population growth, because other factors interact or negate their effect (e.g., Bartmann et al. 1992). By contrast, additive sources of mortality are direct, minimally influenced by other factors, and cause a predictable increase in mortality and reduction in population growth. Predation can be an additive source of mortality when density dependent effects are minimal but compensatory at high population densities if food is limiting (Messier 1994). Hunting also can have an additive effect in heavily exploited populations (Dusek et al 1992).

### **Density Dependent Effects**

Effects of density dependence on population growth are well-documented in theoretical and experimental work (Holling 1959; Fowler 1981, 1987). Density dependence in ungulates has been most evident in isolated populations, often on islands, and in predator-free or nearly predator-free environments (Grubb 1974, McCullough 1979, Coulson et al. 1997, Gaillard et al. 2000, Garrott et al. 2003, but see Houston 1982, Lubow et al. 2002, Taper and Gogan 2002 for exceptions with elk). Density dependent regulation evidently was caused by intraspecific competition for food that decreased reproductive performance, increased juvenile mortality rates, and in some cases increased adult mortality rates. Density dependent changes in vital rates were most obvious in ungulates when populations are close to carrying capacity (Fowler 1981). Eberhardt (2002) summarized how density dependent regulation of ungulates manifests itself via four sequential steps as populations approach carrying capacity: (1) juvenile mortality increases, (2) age at first reproduction increases, (3) reproductive rate of adult females decreases, and (4) mortality of adults increases.

Nutrition fundamentally controls reproduction in ungulates, with effects that can carry over from one season or year to the next. Inadequate nutrition of cow elk in winter and spring reduced calf weight and survival at birth (Thorne et al. 1976). Reduced spring ambient temperature also reduced calf birth weight (Smith and Anderson 1996). Poor condition of moose (*Alces alces*) cows resulted in low birth mass of their calves (Keech et al. 2000). Nutrition in summer has marked effects on growth and development of deer fawns (Holter and Hayes 1977, Verme and Ozoga 1980) and elk calves (Cook et al. 1996, 2004). Steinheim et al. (2002) found that lifetime reproductive performance of free-ranging domestic sheep (*Ovis aries*) was related to body mass at birth: ewes with an initial low body mass produced fewer offspring at first and second parturition. Summer nutrition influenced black-tailed deer (*Odocoileus hemionus*) body fat and weight dynamics (Parker et al. 1999) and probability of survival in winter (Mautz 1978, Parker et al. 1999, Cook et al. 2004). This effect might be most pronounced in ecosystems occasionally or frequently experiencing relatively harsh winters.

Nutritional demands of lactation during late spring through early autumn can affect pregnancy rates in autumn because nutritional condition (e.g., body fat) of cow elk is the prime determinant of successful breeding (Trainer 1971, Kohlmann 1999, Cook et al. 2001c, Cook et al. 2004). The energetic demands of lactation are high, and if the digestible energy in summer forage is low or marginal relative to requirement, cow elk may not rebuild sufficient body reserves by autumn to enter estrous. However, Cook et al. (2004) found that if the cow loses its calf early after parturition she can accumulate sufficient fat reserves to successfully breed in autumn even when forage quality in summer is markedly inadequate for lactating cows. Trainer (1971) suggested that at a kidney to fat ratio (KFI) < 60 [9 percent body fat (Cook et al. 2001a)], probability of pregnancy was reduced. Cook et al. (2004) also found that female elk in poor condition would not conceive and suggested that 8-9 percent body fat was a threshold for cow elk in autumn, below which pregnancy rates decline.

It is not clear about the degree to which density-dependent nutritional effects in winter versus those in summer most influence populations. Density dependent mortality has been well-established in Yellowstone as a function of elk density on winter range (Houston 1982, Taper and Gogan 2002). Lubow et al. (2002) also concluded that density dependence on winter range regulated the elk herd in Rocky Mountain National Park. Beuchner and Swanson (1955) suspected density dependent influences on primiparity of young cow elk in southeast Washington. Merrill and Boyce (1991) reported significant correlations between elk calf survival and abundance of green phytomass during summer in Yellowstone. Crête and Huot (1993) reported marked effects of nutrition during summer on reproductive processes in caribou at relatively high herd density.

Whatever the case may be regarding seasonal influences, it follows that as elk populations approach carrying capacity, recruitment should decrease because increased intraspecific competition for high quality forage lowers nutrition. Moreover, selective grazing at high herbivore density may effectively erode the nutritional value of plant communities available to herbivores, enhancing the food-based density effect over time (Irwin et al. 1994, Riggs et al. 2000). Forest succession patterns also may exacerbate density dependent effects despite little or no change in animal numbers, because amount of forage may decline markedly from early-successional stages to advanced stages in forest ecosystems (Hett et al. 1978, Peek et al. 2001). Such influences might be pronounced where wildfire and logging have been reduced and precipitation is adequate to support high rates of forest succession. These effects may require many years to develop and thus may be hard to document with typical short-term studies (but see Peek et al. 2002). Finally, nutrition may be inadequate at low animal densities, simply because available forage, no matter how abundant, may not adequately satisfy requirements. This density independent aspect of nutritional influences is rarely recognized, but may be important in some ecosystems (Cook et al. 2004).

### **Density Independent Effects**

Climate is typically identified as having a density independent effect on ungulates (Gaillard et al. 2000) that can limit populations. Effects of climate, however, can be more severe when populations are

close to carrying capacity (Garrott et al. 2003). Variation in climate caused juvenile survival to vary widely even though adult survival was high (Gaillard et al. 1998). Sæther (1997) argued that climate is the most important density independent variable in the absence of predation. In temperate and montane habitats, climate is characterized by distinct warm and cold seasons, with corresponding variation in forage quality and quantity. During late spring and early summer, forage typically is abundant and high in quality, but in winter quality is low and abundance may be low.

Among seasons, temperature and precipitation may be highly variable, resulting in summer drought or severe winter conditions. Summer drought can decrease forage quantity and quality (Vavra and Phillips 1980), thus reducing fat accumulations in yearling and lactating cow elk that can delay or cancel estrus (Cook et al. 2004). The result can be lower pregnancy rates of yearling cow elk (Bruce Johnson, unpublished data, 2003) and prime-aged elk, and increased susceptibility to harsh winter conditions. Variation in winter severity can cause wide variation in survival of elk calves but have little affect on survival of prime-aged females (Garrott et al. 2003). Severe winter climate followed by cold, wet springs that delayed green up of vegetation lowered survival of neonate caribou (Rangifer tarandus) (Adams et al. 1995) and caused higher predation on neonates in semi-domestic reindeer (Tveraa et al. 2003).

Diseases and parasites can infect elk (Thorne et al. 2002); however, most of the common livestock diseases do not affect elk recruitment. The one exception is brucellosis that can reduce pregnancy rates up to 12.5 percent annually (Thorne et al. 2002). Elk populations in Oregon have been monitored for brucellosis and the disease has not been detected in any sample. In general, elk populations are little affected by parasites, and problems are often restricted to local situations (Thorne et al. 2002).

## **Predation**

Predation can have highly variable effects on ungulate population growth, and in many areas of western United States, predator populations are increasing (Mech et al. 2001, Keister and Van Dyke 2002). Predator to prey ratios are not sufficient to describe the effects of predation on ungulate populations because the functional response of predation may vary with prey density (Messier 1994). Manipulative experiments with ungulates and predators can be difficult to accomplish because of the long time periods required. Several manipulative or correlative studies, however, have been conducted. Sinclair et al. (2003) described a 40-year experiment in Africa where small to medium sized ungulate populations increased when predators were poached or poisoned in the Serengeti from 1980-1987. When predator populations were allowed to return to previous levels, the ungulate populations returned to their former levels. Jedrzejewski et al. (2002) found that wolf (Canis lupis) predation had an inverse density dependent effect, in that predation limited red deer (C. e. elaphus) numbers but did not regulate the population; by eliminating a large portion of the juvenile age class, wolves dampened the rate of deer population growth. Jedrzejewski et al. (2002) also summarized the effects of wolf predation on red deer in temperate forests of Poland from 1850 to the present. Wolves were extirpated twice. During both periods of wolf extirpation, populations of red deer increased dramatically to the point where density dependent effects were obvious. When wolf populations were reestablished, deer populations decreased in proportion to the increase in wolf populations.

Hayes et al. (2003) manipulated wolf densities across 10 sites in Canada to evaluate the population responses of woodland caribou (R. t. caribou), moose, and Dall sheep (Ovis dalli) and found that predation lowered caribou and moose recruitment and adult moose survival. Populations of Dall sheep, however, did not respond to changes in wolf density. Kunkel and Pletscher (1999) found that when wolves colonized a study area in northern Montana, survival of white-tailed deer (Odocoileus virginianus) and elk decreased and concluded that wolf predation was an additive mortality.

Predation does not necessarily affect sympatric prey species in the same manner (Hayes et al. 2003). Robinson et al. (2002) compared recruitment parameters and cause-specific mortality factors for sympatric white-tailed deer and mule deer (Odocoileus hemionus). While there were no differences in fetuses per female or fawn survival between the species, survival of adult white-tailed deer was higher.

Predation by cougar (*Puma concolor*) was the major source of adult mortality for each species but predation rates on adult mule deer were two times higher than on white-tailed deer. As a result, the mule deer population was about 30 percent lower than that of white-tailed deer.

Further complications with interpreting effects of predation on ungulates involve sources of alternative prey and multiple predators on one prey species. Messier and Crête (1985) and Messier (1994) suggested that wolf predation of moose was less pronounced when multiple species of prey were present. If a second predator was present, however, effects of predation may increase. By contrast, Wakkinen and Johnson (2001) suggested that woodland caribou numbers were declining in the Selkirk ecosystem because of predation by cougar. They hypothesized that the dependable, alternate prey source provided by the expanding white-tailed deer population allowed the cougar population to remain high, which in turn, resulted in increased predation on caribou. Kunkel and Pletscher (1999) found that the survival of moose increased when white-tailed deer and elk were present when cougars, grizzly bears (*Ursus arctos*), wolves, and black bears (*Ursus americanus*) were sympatric with the three prey species. Finally the degree of seasonal migration may affect the extent to which predation acts on prey populations (Crête and Huot 1993).

The composite picture from these studies suggests that effects of predation can operate in multiple ways, depending on the suite of prey species present and the number and abundance of predator species. Prey population responses to predation can vary, and few, if any conclusions can be drawn without site-specific information on the predator and prey species that occur. Skogland (1991) stressed that although predators may limit prey populations, there is little evidence that predators regulate prey populations. Territoriality of predators may place upper limits on predator densities, potentially precluding predation as a regulating factor (Skogland 1991).

### **Hunting**

Hunting can have an important influence on ungulate populations, diminishing the evidence of density dependence by reducing density below carrying capacity. For example, Swihart et al. (1998) evaluated the nutritional condition and pregnancy rates of white-tailed deer from areas with and without hunting. In areas without hunting, pregnancy rates, body size, and body fat were lower than in areas where hunting controlled deer numbers. In addition, Swihart et al. (1998) found that pregnancy rates varied inversely with density among the five sites evaluated. Messier and Crête (1985) warned that ungulate populations appearing to be healthy (high recruitment) may change if human exploitation increases in the presence of predator populations. If predator to prey ratios change, predation can shift from inverse density dependence to density dependence, resulting in a further decrease in ungulate density and resulting in predation being sufficient to keep ungulate populations suppressed (Messier and Crête 1985). In recognition of such effects, Hayes et al. (2003) suggested hunter harvest of moose and caribou populations be set at low levels (2-5 percent) in areas where wolf and bear populations were high.

### **Pervasive Human Disturbances**

Recreational activities on public lands are increasing as human populations increase, and may decrease animal fitness or expose animals to higher rates of mortality (Knight and Gutzwiller 1995). Since the 1950s, road construction on public lands of the western United States has provided access, resulting in increased use of areas that were previously undisturbed (Trombulak and Frissell 2000). Examples of increased recreational activities include mushroom and berry picking, fire wood gathering, mountain biking, all terrain vehicle use, cross country skiing, back packing, camping, and snowmobiling. Elk have responded by moving away from roads open to the public (Rowland et al. 2000, 2004), especially roads with higher rates of traffic (Wisdom 1998). Elk have also moved away from off-road recreation activities, especially ATV and mountain bike riding (Wisdom et al. 2004). Conner et al. (2001), Vieira et al. (2003), and Wertz et al. (2004) found that displaced animals moved to areas where disturbance was minimal.

During hunting seasons, energetic consequences of the increased disturbance include increased energetic costs associated with movements (Johnson et al. 2004) and perhaps shifts to habitats where foraging conditions are diminished (J. G. Cook, unpublished data, 2003). Disturbance during parturition and calf rearing resulted in higher calf mortality (Phillips and Alldredge 2000) or decreased reproductive performance of mule deer in the following year (Yarmoloy et al. 1988). These added energy costs could lead to higher winter mortality rates as animals deplete stored fat reserves to avoid human activities.

### **Competing Hypotheses to Explain Declines in Elk Productivity**

Several factors or hypotheses may explain long-term decline in elk recruitment across large areas of the northwestern United States. Each factor is plausible but not likely to operate independently of other factors. Exact mechanisms causing declines likely vary from location to location depending on habitat, climate, and predator populations. We hypothesize that recent declines in elk productivity are a result of a combination of factors that interact in both density dependent and independent ways. Our hypothesis is built on the following assumptions:

1. Intraspecific competition for forage.--Elk populations have gradually increased concomitant with reductions in forage biomass and quality over the last six decades in much of western United States. In turn, this may have increased intraspecific competition for nutritious forage, resulting in lower pregnancy rates and higher mortality rates of elk. Effective fire suppression on forestlands over the last 60 years has had a substantially greater, negative effect on forage production than the counteracting, positive benefits of wildfire, timber harvest, and insect-caused mortality of trees that has occurred in the last two decades. The effect in total may be a slow erosion of carrying capacity on many elk ranges. For example, the elk populations increased dramatically in the 1980s and subsequently declined in the late 1990s following the volcanic irruption at Mount St. Helens in Washington.
2. Decrease in highly palatable forage.--Elk may exert strong and highly selective grazing pressure on the forage species that are relatively palatable and available, especially if animals are displaced because of human activities. Coupled with increasing density, nutritional limitation occurs, reducing population parameters.
3. Increase in predator populations.--Cougar, black bear, and wolf populations have increased substantially during the past four decades, resulting in lower recruitment of elk.
4. Summer drought and winter severity.--Abiotic factors of summer drought and winter severity may not be operating in the traditional, density independent manner. Instead, these factors may increase the vulnerability of elk to predation or increase winter mortality due to nutritional constraints.
5. Legal and illegal hunting.--In situations where recruitment is lowered due to predation, cow elk hunting has an additive and substantial effect on growth rate of elk populations.
6. Human activities.--Human disturbance activities have increased across all elk ranges, and may be exerting a negative effect on elk populations not observed in the past. The energetic costs of elk avoiding pervasive human disturbances can be substantial, and have been overlooked as affecting elk nutritional condition.

Considering the above assumptions together, we hypothesize that the underlying basis for elk productivity is nutrition and that predation, hunting, weather variation, and human disturbance factors currently are additive in their effects on the decline in productivity, and that the relative effects of each may vary among herds. Where limiting factors are prevalent, density dependent effects may not be apparent. Ratios of predators to prey are critical in understanding how the several factors outlined above result in increasing or decreasing rates of population growth. At high levels of nutrition and appropriate (but unknown) predator to prey ratios, we hypothesize that effects of predation, human disturbance, and hunting would reduce but not limit population growth. That is, elk recruitment would respond positively

even with these sources of mortality under high levels of nutrition, thus providing an inherent resilience to population change. If, however, predator to prey ratios were shifted dramatically due to reduction of elk populations due to hunting, severe winter mortality of elk, or increases in predator populations, then predation could keep elk at a lower equilibrium such that elk populations and recruitment remain low. The point at which mortality factors tip the balance between growth and decline of the prey population should vary along a gradient of nutritional adequacy.

### **Challenges to Research and Management**

We believe our hypothesis deserves careful examination within a research framework. Obviously, no single factor can explain either the variability or the long-term decline in elk recruitment across the northwestern United States. Several factors are interacting, in different ways in different areas, making it difficult to impose any one management strategy that can ensure recovery of elk populations.

One of the principal goals of the Starkey Project was to examine management activities that affected elk productivity. The original studies of the Starkey Project were directed at understanding how single factors affected elk fitness, distribution, or reproduction (e.g., Cook et al. 1998, Rowland et al. 2000, Noyes et al. 2002). Subsequent research at Starkey and associated study sites was then expanded to examine how two or more factors might interact to affect elk reproduction, survival and recruitment (e.g. Cook et al. 1999, 2004; Johnson and Jackson 2001). The next step is to further expand research to address the full complexity of factors and their interactive effects on elk productivity and population growth.

We suggest three complementary approaches to gain better knowledge about elk productivity: (1) adaptive management, (2) retrospective and meta analysis, and (3) simulation modeling. Under adaptive management, research would be designed and tested as manipulative experiments in real-world conditions (Walters 1986). Researchers and managers would jointly develop hypotheses for testing and implementing treatments, and work together to measure and interpret the results. For example, a set of watersheds could be selected for intensive habitat improvements and subsequent reduction in human disturbances, and another set of similar watersheds used as controls. Researchers could measure and compare a variety of population responses of elk to the habitat improvements and reduction in human disturbances. On the other hand, predator populations could be reduced, and responses of prey populations monitored, probably providing a more rapid assessment that would not require waiting on habitat changes.

Retrospective and meta analysis provide alternative analyses of potential value. Meta analysis could be used to analyze the multitude of studies that have evaluated the effects of nutrition, predation, and weather on population dynamics of ungulates as case studies (e.g., Messier 1994, Linnell et al 1995, Sæther 1997, Unsworth et al. 1999, Gaillard et al. 2000, Hayes 2002). The synthesis of many studies of elk recruitment (Schlegel 1976, 1983; Smith and Anderson 1996; Singer et al. 1997; Myers et al. 1998; Gratson and Zager 2000; Jedrzejewski et al. 2002; Zager and White 2003 and unpublished results from the region) could yield general, predictive patterns about the interactive effects of various factors on ungulate productivity and population dynamics. However, most of these studies had no measure of nutritional condition of the prey populations or imprecise estimated of predator populations, making analysis and interpretation more difficult.

Simulation modeling also can provide insights about the potential interactions of factors that affect elk productivity and growth rates of populations. For example, a series of models could be constructed under different competing hypotheses, and each model run under a set of standard simulations to gain a more formal understanding of potential effects. Model parameters could reflect empirical data, but also hypothesized data, to further understand the range of potential effects, and to identify the most plausible effects and outcomes. The challenge will be to link habitat conditions, prey populations, and predator populations, an undertaking that has rarely been attempted. Hobbs (1989) and Weisberg et al. (2002) provided examples of models that link weather and habitat conditions with animal population characteristics, but neither incorporated predation effects. Typical predatory-prey models (Skogland 1991) rarely explicitly addressed contributions of habitat and nutrition. Further, if simulation models are

to consider habitat/nutritional conditions on summer ranges in forest ecosystems, then plant succession patterns following disturbance and the interaction of herbivore numbers and plant succession patterns will be key elements of models.

Without these types of new research, managers face the difficult challenge of dealing with the high uncertainty about the proximate and ultimate causes of declines in elk recruitment. Even then, long-term monitoring of elk recruitment, survival, and nutritional condition are critical to understanding when predation, weather variation, and hunting may be limiting and nutrition is regulating. Nutritional condition of elk populations can be measured inexpensively by using cow elk hunters to collect reproductive tracts, suitable indices of condition, and mammary tissue for animals harvested in autumn (Kohlmann 1999; Cook et al. 2001a, b). In situations where hunter collections are inadequate to satisfy research/monitoring objectives, nutritional condition of live elk can be assessed reliably (Cook et al. 2001a, b).

When elk recruitment is low or declining, managers will need to gain insights about how density dependent factors, long-term vegetative successional trends, variation in summer precipitation and winter severity, hunting, and predation may be interacting. If nutritional characteristics and climatic variability are implicated, then management alternatives to address habitat conditions; where hunting or predation appear to be limiting recruitment, then alternative actions may be required to increase recruitment. Public acceptance of predator management evidently is waning, creating challenges for managers to meet the social and economic needs of the various public groups interested in wildlife. Consequently, a strong partnership between managers and researchers, with the use of modeling and adaptive management approaches, appears to be the most suitable strategy increasing understanding and for effectively dealing with emerging challenges of declining elk productivity.

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