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Density dependence in mule deer: a review of evidence

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Wildlife managers often need tangible evidence of density dependence in populations to support decision making. Field experimentation to identify density dependent effects is often cost and time prohibitive. Thus, assimilation of existing knowledge into a balance of probabilities can serve as a surrogate for experimental research. A case study of such a process is found in the mule deer *Odocoileus hemionus* herds of Colorado. Wildlife managers and hunters expressed concern over a recent decline in western Colorado mule deer herds, yet the underlying cause of this decline is yet to be determined. In response to this management concern, we conducted a review of scientific evidence on Colorado's mule deer population dynamics. This review was done in the context of a conceptual model that portrays population growth as a function of population size, per capita growth rate and population carrying capacity. Similar declines that occurred during the 1960s and early 1990s resulted in similar reviews that identified research and management topics that would benefit mule deer. These topics included: harvest, predation, intraspecific competition, disease, interspecific competition, and habitat loss and degradation. Between the late 1990s and present time, many of these topics were addressed by research. The conventional working hypothesis in Colorado is that mule deer herds are limited by winter range habitat. We identify new gaps in knowledge and suggest potential, future research topics, as well as potential management strategies. We suggest a focus on integrated studies of multiple herbivores with density reduction experiments to address intra- and inter- specific competition. In addition, we suggest focused experiments that address the roles of mountain lion predation, black bear predation, and disease in mule deer population dynamics.

Density dependence in populations can be summarized as a series of biological feedback mechanisms that lead to high population growth rates when density is low and low population growth rates when density is high. The scientific literature is replete with explanations of how density dependence can be manifest in populations (Tanner 1966, Sinclair 1989, Hixon et al. 2002). Examples of density dependence in free-ranging herbivore populations also exist (Sæther 1997, Gaillard et al. 1998, Brown 2011). However, wildlife managers often need direct, tangible evidence to support decision making at local scales. Yet experimental inquiry of density dependence is typically cost and time prohibitive. Thus, scientific reviews that generate a preponderance of evidence provide an important alternative to direct inquiry. These reviews serve a role in decision making processes, but also for identifying gaps in knowledge. As a case study, we consider the population dynamics of mule deer in Colorado.

Colorado's mule deer population has demonstrated several dramatic shifts in abundance during the past six to seven decades. Typically these fluctuations have mirrored regional mule deer population dynamics (Workman and Low 1976, Gill 2001). However, biologists, managers, and hunters have expressed concern over a recent decline in some western Colorado mule deer herds (Fig. 1). Preliminary evidence suggests that this recent decline in Colorado is again part of a broad, regional pattern (Walker 2011). Within Colorado, this recent decline has primarily been observed in the herds that are located in the western most third of the state (Fig. 2). However, these areas have also historically comprised the most abundant herds and this trend has thus driven broad perceptions about all of Colorado's mule deer herds. Despite this pattern, model based abundance estimates for the smaller herds located in the higher central mountains have appeared to increase during the last decade (Fig. 2).

Historical declines in mule deer populations have resulted in similar reviews (Workman and Low 1976, Gill 2001). In particular, a decline in mule deer populations during the late 1960s and early 1970s resulted in a regional symposium that was focused specifically on identifying potential causes of that decline (Workman and Low 1976). After a period of population increase during the late 1970s and 1980s, mule deer populations declined again during the early and middle portions of the 1990s. While this second decline was also observed at the regional scale, it was the impetus for a Colorado-centric symposium in 1999, resulting in a report to Colorado's legislature that called for a renewed focus on mule deer research and increased population monitoring activities (Gill 2001). A product of both symposia was the

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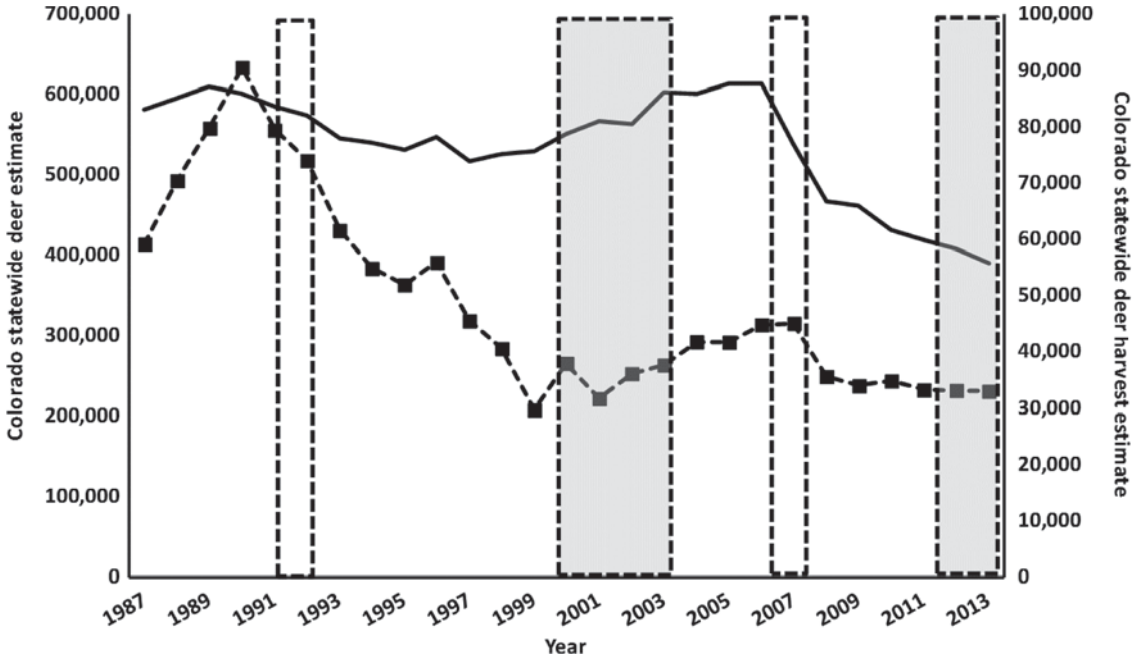


Figure 1. Historical statewide estimates of modeled total deer abundance (solid black line) and statewide deer harvest (dashed line) from Colorado. Harsh winter events during 1992 and 2007 are denoted by white boxes with dashed perimeters. Drought conditions from 2000–2003 and 2012–2013 are represented by gray boxes with dashed perimeters. The perceived population decline beginning in 2007 and driven by several large mule deer herds in the western third of Colorado served as the impetus for this review.

identification of several recurring potential causes for mule deer population decline: habitat loss, habitat degradation, predation, disease, interspecific competition (i.e. with elk *Cervus elaphus* and livestock) and intraspecific competition (i.e. increased density or overabundance of mule deer relative to available habitat). For these causes, the definition of habitat was primarily concentrated on browse availability and browse condition, and to a lesser extent escape and thermal cover provided by vegetation. In particular to Colorado, the review by Gill (2001) identified shortcomings in the

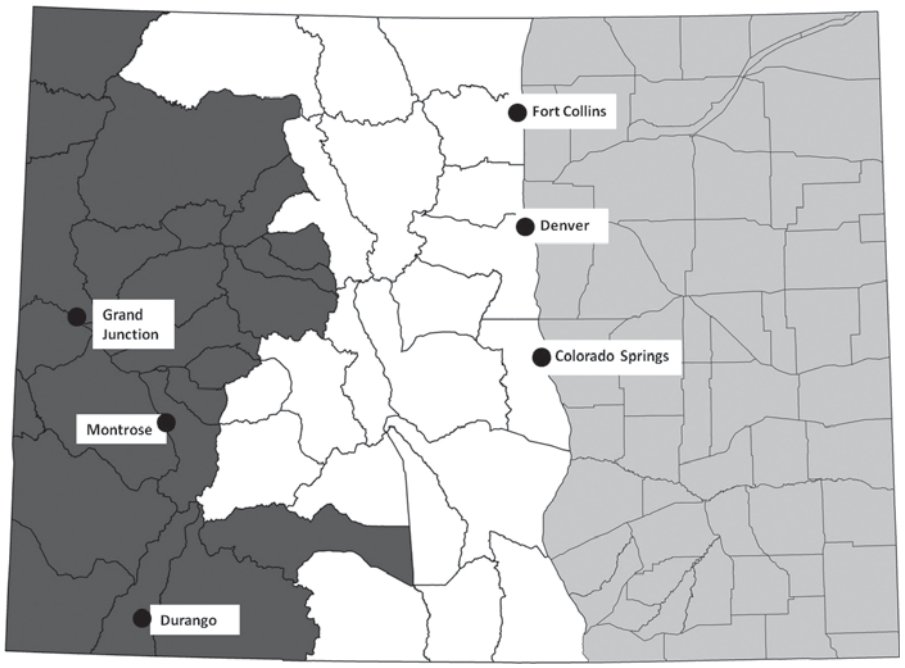


Figure 2. Map of Colorado reflecting mule deer herd management unit boundaries. Herd units that are shaded dark gray in the western third of the state reflect mule deer herds that have historically represented the largest herds, but also herds that have experienced perceived declines since 2007. White herd units in the central third of the state primarily occupy the higher, central mountains, and have been perceived as stable during the same time period. Herd units that are shaded light gray in the eastern third of the state are comprised of grassland and prairie ecosystems with extensive private land agriculture. These herds have been perceived as stable during the period of interest.

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collective knowledge base, and thereby indirectly provided a recipe for research, management experiments, and population monitoring that would benefit deer management. Many of these studies have been completed, yet a collective review of research results has not occurred.

Terminology and assumptions

In order to provide a review of scientific evidence and to assess key characteristics of a population, terminology must be clearly defined. A key component of many vertebrate population models is that populations are limited (i.e. unlimited population growth is not feasible). Under this constraint, the number of deaths eventually equals the number of births, resulting in no population growth. While the factors setting this upper limit to populations are debated and commonly researched, the notion that an upper limit exists (i.e. carrying capacity – *K*) is fundamental to other population attributes. For example, the terms 'regulation' and 'limitation' can easily be confused. For the purposes of this paper, and following the distinctions drawn by Messier (1991) and Boutin (1992), we define a regulating factor as any factor that has the ability to bring a population back into equilibrium after perturbation. The strength of a regulating factor is dependent on overall deer density and population size relative to *K*. Stronger regulating effects occur at higher deer densities when populations are near *K*. Regulatory effects are weaker when populations and deer densities are lower. Alternatively, a limiting factor is defined as the single factor that prevents populations from increasing beyond a threshold. Removal or adjustment of the limiting factor would result in a population that is capable of reaching a new, presumably higher, threshold. The rate at which a population achieves this new threshold is dictated by regulating factors.

Population regulation and population limitation can also be expressed as part of theoretical population growth models. In a generic form, population growth can be written as

$$\frac{dN}{dt} = f(N,r,K)$$

in which the change in population size (dN) occurs during a discrete time interval (dt). This rate of population growth is a function (f) of the current population size (N), the intrinsic rate of increase (r), and carrying capacity for the population (K). The value dN/dt is a population's growth rate. The function relating population size, population growth rate and carrying capacity can take many forms (e.g. logistic growth, theta-logistic growth) and can be expanded to include harvest (Williams et al. 2001). Such derivations have been extensively explored (Ricker 1954, Hassell 1975, Hassell et al. 1976, Williams et al. 2001, Gotelli 2008). While the major differences between different theoretical population growth models are often manifest when populations are below carrying capacity, with each model having a different set of ecological circumstances under which it is most useful, any single mathematical function is of nominal consequence to this review.

Expanding our theoretical model to accommodate the per capita rate of change (R)

$$R = \frac{\left(\frac{dN}{dt}\right)}{N}$$

reveals a value that can be easily confused with the intrinsic rate of increase (r). As noted above, whereas r is a constant value, R changes depending on population size (N). In keeping with the definitions of population regulation and population limitation, the strength of regulating factors manifested in R are dependent on current population size (N). Limiting factors are those that influence carrying capacity for the population (K).

Regardless of how population models are conceptualized, several noteworthy assumptions and simplifications are commonly made. First, the perspective that populations have a single limiting factor is a common oversimplification. This simplification facilitates both communication and study design. In reality, populations may be limited by an interaction of factors, such as habitat condition and weather severity: interactions that are partially driven by random processes that complicate scientific and management endeavors. Another common oversimplification for many conceptual models is that K is assumed to be known and fixed. In applied settings, neither of these assumptions is valid. A simple demonstration of how K can change over short time intervals can be found by considering the influence of weather on browse availability. During harsh winters during which the snowpack greatly exceeds normal depths and temperatures are lower than those traditionally experienced, winter browse for deer can be buried under thickly crusted snow layers, rendering it unavailable for immediate use. Under these extreme conditions, the quantity of available food is reduced. If deer are food limited on the winter range that is experiencing these conditions, K is reduced. Alternatively, during mild winters in which snow depths are below average and temperatures are higher than traditionally expected, access to plant resources on winter range is unrestricted and K is increased. Similarly, extended periods of drought or abundant moisture can change the long term trajectory of available browse, and subsequently K. Due to the dynamic nature of browse availability, managers rarely know how many deer can be supported by current conditions. A similar assumption that is commonly made for simplification purposes is that all mule deer browse is of equal quality. As demonstrated by Hobbs and Swift (1985), forage quality is often inversely related to forage quantity. Thus, traditional range food supply/animal food requirements models require a simplification that fails to accommodate the interaction between K and the nutritional status of animals. One final oversimplification that is commonly made when considering K is that all animals have an equal competitive advantage, a similar nutritional response, and an equal likelihood of facing mortality when K is reached. However, an extensive body of literature has demonstrated that adult mule deer are more robust in terms of survival than fawns (Unsworth et al. 1999, Lukacs et al. 2009, Bishop et al. 2009). In particular, studies that have assimilated mule deer survival data over broad spatial and temporal scales have demonstrated that the variation in fawn survival exceeds that of adult survival (Unsworth et al. 1999, Lukacs et al. 2009). Similarly, other studies have provided evidence that adults have a competitive advantage over fawns

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(Garrott and White 1982, Bishop et al. 2005, Bergman et al. 2011). Ultimately, this can be viewed as evidence that *K* is different for adults and fawns.

Much of the research on mule deer population dynamics has also investigated the principals of additive and compensatory mortality (Bartmann et al. 1992, Bishop et al. 2009). Compensatory mortality is a phenomenon that is dependent on a population being above *K*, implying that by the end of an annual cycle the number of individuals exceeding that threshold will have necessarily died. The portion of the population that will have necessarily died has been referred to as the 'doomed surplus' (Errington 1934, Kokko and Lindström 1998, Boyce et al. 1999). For simplicity in communication, all of the doomed individuals will die from causes related to the limiting factors for the population. However, this scenario is not necessarily the case and is unlikely. A hypothetical example can be found in a nondescript deer population that is limited by winter habitat, but is also exposed to hunter harvest. In this example, the available habitat is capable of supporting no more than 500 individuals during the winter months and annual hunter harvest is 25 individuals. During some years far more than 500 animals arrive on winter range, such as 600, but harvest may remain static at 25 individuals. Under this scenario, 100 individuals are expected to die, presumably of malnutrition (i.e. the doomed surplus is 100 individuals). If 25 individuals die due to hunter harvest and 75 still die of malnutrition, harvest-caused mortality is completely compensatory with malnourishment-caused mortality. During years in which fewer than 500 animals arrive on winter range, yet 25 animals are harvested, those 25 deaths can be considered completely additive as resources were available to support those animals had they not been harvested. These two scenarios represent opposite ends of a mortality spectrum, thereby also creating a false dichotomy in the illusion that mortality is either always additive or always compensatory. A final derivation of this example can be found during years in which slightly more than the carrying capacity of deer arrive on winter range, such as 510, with harvest remaining static at 25 deer. During these years, partially additive mortality is expected as the loss of 10 deer can be considered compensation between harvest and starvation, yet the loss of 15 extra deer is additive. While these scenarios are for a hypothetical example, they reflect the driving principals of harvest management programs in which harvest objectives are based on the desire for hunter harvest to be compensatory, and to accommodate the relationships between density dependence, mortality and timing of harvest (Kokko and Lindström 1998, Boyce et al. 1999).

The biological feedback mechanisms experienced by populations as they reach *K* have been a topic of interest to ecologists and managers for several decades (Eberhardt 1977). In particular, among many taxa, predictions of the sequence and role of density-dependent feedback mechanisms are surprisingly consistent – density-dependent effects are predicted to impact populations sequentially in the order of reduced juvenile survival, increased age of first reproduction, declines in the reproductive rates of adult females, and reduced survival of the adult age class (Eberhardt 1977, Gaillard et al. 1998, 2000). The perspective that populations demonstrate shifts in life history characteristics as overall abundance nears carrying capacity is a logical extension of the objectives of Hobbs and Swift (1985). Hobbs and Swift (1985) demonstrated that when the interaction of forage quality and forage quantity was considered in carrying capacity models, they could predict the maximum number of animals that could maintain a diet of a specified quality, or they could predict the maximum quality of diet for a specified number of animals. However, despite the foundational premise of density dependence and the repetition of predictions, the effect of density on the dynamics of free-ranging ungulate populations is difficult to demonstrate.

A review of evidence – potential limiting factors

Due to the uncertainty surrounding the geographic extent of this most recent decline, but also to the certainty that it has occurred in Colorado, we focused this review on research and analyses that are particular to mule deer herds in Colorado. However, research and collaboration among Colorado and other western states is common, and we expanded this review to include pertinent literature from outside Colorado, and from other North American ungulates, to gain insight on ecological processes that have not been the focus of research in Colorado. In particular, this review is focused on harvest, predation, intraspecific competition, disease, interspecific competition, and habitat loss and degradation.

Harvest

Many harvest management systems are based on the premise that a doomed surplus, or harvestable surplus, of animals exist in populations. As described above, this surplus occurs when populations are at or near *K*. The most publicized of these systems pertains to harvest of waterfowl in North America (Burnham and Anderson 1984, Nichols et al. 1995, 2007). However, similar examples can found in the ungulate literature (Wallmo 1981, Swenson 1985). Alternative harvest management strategies also exist. A well-known example of one of these alternatives, which was embraced by marine fishery managers during the 1950s, is based on the desired outcome of maximizing a sustained yield (Hilborn et al. 1995). The principal of maximum sustained yield is that populations can be held below *K* in order to maximize production and recruitment of new individuals into the population (Williams et al. 2001). From a numerical perspective, the same number of individuals recruited into the population can be harvested with no change in overall abundance (Williams et al. 2001). These two harvest management philosophies represent opposite ends of a continuum – the harvestable surplus strategy assumes harvest is completely compensatory while the maximum sustained yield strategy assumes harvest is completely additive – yet both philosophies are based on the premise of density dependence. The fundamental difference between the two strategies is that they exploit different aspects of *R*, a population's per capita rate of change. These two strategies also create a false dichotomy as managers rarely know how many animals are in a population, what *K* is for a system, or if *K* is changing. This is particularly evident for mule deer when considering that harvest recommendations are set and harvest occurs prior to winter. Winter is commonly the period in which *K* can be stochastically suppressed by deep snow depths and

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low temperatures. In the face of this uncertainty, the potential for harvest to drift between being completely additive, partially additive and completely compensatory is high. The most complete documentation of this harvest management dilemma for large ungulate systems stems from moose *Alces alces* management in Alaska, where multiple harvest objectives were placed on a system that was subjected to periodic and harsh environmental fluctuations, as well as a rich predator assemblage (Gasaway et al. 1983, 1992, Boertje et al. 2009, Young and Boertje 2011).

This diversity in harvest management strategies can also be found in Colorado's deer herd management plans (Colorado Parks and Wildlife unpubl.). For example, some of Colorado's deer herds are managed such that *N* (abundance) is maximized. While the total number of animals that can be supported in these herds remains unknown, this approach to herd management reflects the principals of a doomed surplus – herd abundance is maximized after each winter and is thus capped by winter habitat (*K*). Specifically, summer and fall abundance of these herds are believed to exceed winter range *K*. Thus, harvest is intended to capture this doomed surplus, making it a compensatory source of mortality. Alternatively, other herds that experience harsh winter events at more frequent intervals are managed such that *N* is preferentially kept at *K* set by those extreme winter conditions and thus below *K* that is set by mild winter conditions. During mild winters when range capacity is less restricted, this approach to herd management reflects sustained yield principles. The last example stemming from Colorado's deer herd management pertains to an entirely separate objective that is geared towards providing individual hunters with a high quality hunting experience. High quality hunting experiences are typified by: 1) herds that have high adult male:adult female ratios, 2) opportunities for hunters to encounter male deer that have reached older age classes and thus have more developed antler structure, and 3) lower encounter rates between hunters.

Two evaluations of Colorado's harvest management decisions have occurred (Bishop et al. 2005, Bergman et al. 2011). Each of these was an evaluation of restrictions to deer hunting, and primarily within this, restrictions on the hunting of adult male deer. In each case, as harvest was restricted, an increase in adult male:adult female ratios was observed. In particular, ratios increased by as many as 4.52 adult males per 100 adult females in one study (Bishop et al. 2005) and by as many as 21.86 adult males per 100 adult females in the other study (Bergman et al. 2011). However, simultaneous declines in fawn:adult female ratios were observed as part of each study. Declines were as high as 6.96 fawns per 100 adult females (Bergman et al. 2011) and 7.51 fawns per 100 adult females (Bishop et al. 2005). While neither study was a direct experimental evaluation of intraspecific competition or density dependence, both studies provide circumstantial evidence that increasing the proportion of adult male deer in the population came at the expense of population productivity. Interaction between the male, female, and young components of populations, similar to that presented by Bishop et al. (2005) and Bergman et al. (2011), can result in second order feedback effects that are non-trivial (Mysterud et al. 2002). If lowered fawn:adult female ratios can be interpreted as an indicator of suppressed population growth, the studies of Bishop et al. (2005) and Bergman et al. (2011) may provide evidence that harvest decisions that change the sex and age structure of deer herds to favor mature animals may have a regulating effect – thereby slowing the rate of population growth (dN/dt) by reducing the per capita rate of change (R) in our conceptual model. Moreover, at a given population size (N), a herd with a higher proportion of males has a lower reproductive potential because it has a lower proportion of females. In the event of stochastic reductions in K due to harsh winters, die-offs in herds with a higher proportion of males may experience delayed rebounding (i.e. sex ratio may have a regulating effect on population growth). Colorado's current statewide ratio of total males to adult females, when weighted by herd size, is 33.4 adult males per 100 adult females (Colorado Parks and Wildlife unpubl.). However, it is unknown if sex ratios at this level have a regulating effect.

The effect of hunting on wildlife species extends beyond population management. In particular, the indirect effect of hunters on ungulates, specifically movement patterns and animal behavior, has received recent attention (Conner et al. 2001, Vieira et al. 2003, Ciuti et al. 2012). Similarly, the effect of trophy-focused hunting pressure on large ungulates, and the subsequent effect on trends in antler size, has also been the focus of recent research (Allendorf and Hard 2009, Monteith et al. 2013).

Predation

The role of predation in shaping ungulate population dynamics is a common research topic with many different conclusions being possible, depending on individual circumstances. In the Rocky Mountain West, the motivation to study coyote *Canis latrans* predation on mule deer is several-fold. First, encounter rates between coyotes and hunters (i.e. observation of coyotes and coyote tracks, hearing coyote howls, and finding coyote kill sites) are likely higher than those for any other predator of deer. Stemming from this, an intuitive reaction by hunters is often that coyote predation has a stronger effect on deer population dynamics than other sources of predation. Thus, pressure from the public for a more complete understanding of the impact of coyote predation on deer populations has frequently been articulated (Willoughby 2012). Secondly, investigations into the causes of mortality of mule deer have consistently identified coyote predation as a common source of mortality (Bartmann et al. 1992, Whittaker and Lindzey 1999, Pojar and Bowden 2004, Bishop et al. 2009). Stemming from this demand and from these patterns, the effect of coyote predation on mule deer has been more thoroughly investigated than other sources of predation. Experimental manipulation of coyote density as a treatment effect on deer population dynamics has occurred as part of two studies. Research conducted by Bartmann et al. (1992) in northwest Colorado evaluated the effectiveness of coyote control as a management strategy to increase productivity within a deer herd. While the annual removal of 47–93 coyotes from the 140 km^2 winter range study area reduced coyote predation, a simultaneous increase in malnourishment deaths occurred and no overall increase in survival rates was detected. This switch between mortality causes, with no increase in survival, was viewed as strong evidence that coyote predation was compensatory

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with starvation. Specifically, if this were a top–down system in which coyotes were limiting (i.e. predation determined *K*), removal of coyotes should have increased *K*, translating to an increase in *R* as the deer population responded. No change in *R* was observed.

More recently, research conducted by Hurley et al. (2011) in southeast Idaho also tested the effectiveness of coyote removal from mule deer winter range as a management strategy to improve mule deer population performance. Hurley et al. (2011) removed an average of 53.3 coyotes/1000 km^2 per year during a six-year period. Coyote removal did result in increased neonate survival during years in which lagomorph populations were low; however, the increase in survival was temporary. Subsequent December fawn:adult female ratios showed no population level increase stemming from coyote control efforts. No effect of coyote removal was observed during years of normal lagomorph abundance. As was the case with Bartmann et al. (1992), no change in *R* was observed.

In addition to these large scale predator manipulation studies, several other studies have quantified coyote predation on mule deer in Colorado. In particular, work by Bishop et al. (2009) reported coyote-caused mortality rates for two groups and age classes of deer. In the first group, comprised of animals that had received a nutrition enhancement, fawns had a coyote-caused overwinter mortality rate of 0.04 (SE = 0.01) and adults had an annual coyote-caused mortality rate of 0.01 (SE = 0.01). Alternatively, fawns that had not received the nutrition enhancement experienced an overwinter coyote-caused mortality rate of 0.12 (SE = 0.03) and adults experienced an annual coyote-caused mortality rate of 0.02 (SE = 0.01).

Other, non-experimental, research has also been conducted in Colorado. Work conducted by Whittaker and Lindzey (1999) assessed the frequency of coyote predation on mule deer neonates ($\leq$ 30 days old) on Colorado's Front Range. Whittaker and Lindzey (1999) reported a 30-day survival rate of 0.66 for mule deer neonates during a two-year study, with coyotes accounting for 79% of the mortality. When compared to other neonatal survival data during the first 30 days of life (Pojar and Bowden 2004), the survival rates reported by Whittaker and Lindzey (1999) appeared to be slightly lower, with coyotes accounting for a higher proportion of the mortality. In each study, coyote predation diminished after the first 30 days of life, highlighting the role of prey vulnerability in the predation process. While this example links vulnerability to age and immaturity, vulnerability can also be associated with malnourishment (Bartmann et al. 1992) or landscape features (Bergman et al. 2006). Because neither the study conducted by Whittaker and Lindzey (1999), nor the study conducted by Pojar and Bowden (2004) measured survival to the stage of recruitment into the adult age class, determining if the predation they documented was additive or compensatory is not possible. However, if the deer herds studied by Whittaker and Lindzey (1999) and Pojar and Bowden (2004) were above *K*, predator caused neonate mortality during the first one to three months of life would be compensatory with winter fawn mortality that would be linked to malnutrition.

Other research in Colorado assessed the secondary impact of coyote removal, for livestock protection purposes, on mule deer (Harrington and Conover 2007). Based on sex ratio data, Harrington and Conover (2007) found that coyote control efforts had no effect on deer herd productivity. An extensive literature review conducted by Ballard et al. (2001) resulted in several general conclusions about predation. First, as noted by studies from Colorado, coyote predation can be a significant mortality factor for mule deer. However, Ballard et al. (2001) also noted that discerning the role of coyote predation on deer population dynamics was often confounded by other factors such as weather and habitat condition. This confounding between mortality factors highlights the necessity of discerning between proximate and ultimate mortality causes.

While the role of coyote predation has been the focus of deliberate research, in Colorado there have been no studies that have directly assessed the effect of increased mountain lion *Puma concolor* harvest, or mountain lion removal, on mule deer population dynamics. However, the research conducted by Hurley et al. (2011) in Idaho provides experimental evidence on this topic. Hurley et al. (2011) found that overwinter mortality of adult mule deer decreased and fawn:adult female ratios increased in areas of intense mountain lion removal, indicating that mountain lion predation was partially additive. Despite these patterns, no significant change in population trend was documented. This result was partially attributed to the conclusion that winter severity was the most significant factor limiting mule deer population growth (Hurley et al. 2011). Thus, the process variation in *K* stemming from weather had a stronger influence on deer population dynamics than predation. In Colorado, Pojar and Bowden (2004) reported a 3.2% mountain lion caused mortality rate for mule deer $\leq$ 6 months old. Also in Colorado, Bishop et al. (2009) reported a mountain lion caused mortality rate of 0.5% for adult female deer that had received a nutrition enhancement and 3.2% for adult females that had not received the enhancement. While Bishop et al. (2009) found that felid predation comprised nearly 15% of all mortality for deer $\geq$ 6 months old, predation on deer that had received a nutrition enhancement was greatly reduced. This was interpreted as evidence that mountain lions selected for animals in poorer condition, which can also be interpreted as that mountain lion predation was at least partially compensatory with starvation.

The role of black bear *Ursus americanus* predation on mule deer population dynamics has not received focused attention in Colorado or elsewhere in the Rocky Mountain West. While bear predation on neonates has been reported in numerous studies (Pojar and Bowden 2004, Bishop et al. 2009), this predation appears to be highly synchronous with birth pulses. Specifically, predation by bears peaks shortly after the peak in parturition before quickly waning during the subsequent three to five week period. This pattern has largely lent itself to the perspective that bear predation is not likely a limiting factor in mule deer population dynamics. Literature reviews conducted by Ballard (1992) and Zager and Beecham (2006) identified conditions under which the pulse in bear predation following parturition was most likely additive. In particular, bear predation appeared to be additive when bear densities, particularly black bear densities, were high and ungulate densities were low. However, this evidence was largely specific to brown bear *Ursus arctos*

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and black bear predation on moose in Alaska and Canada (Stewart et al. 1985). More recent evidence provided by Barber-Meyer et al. (2008) has extended this perspective to elk populations as well. Pojar and Bowden (2004) reported a bear-caused mortality rate of 4.0% for mule deer fawns ≤ 6 months old, although the bulk of this mortality occurred between early June and the middle of August. Bishop et al. (2009) reported low bear-caused mortality rates for adult female deer (0.0%–0.8%), with bear predation probabilities that quickly decayed from a maximum of 0.20 during the first 100 days of life for newborn fawns. Thus, while black bear predation likely does not affect *K*, it could affect *R*. However, if herds are winter habitat limited, black bear predation during this period would be compensatory with overwinter malnutrition related deaths.

Intraspecific competition

The research projects that have addressed intraspecific competition on mule deer in Colorado can be broken into three broad categories: stocking experiments, density reduction experiments, and habitat manipulation studies. Of note, with the exception of general management studies, all of these research projects were focused on winter range. Bartmann et al. (1992) used deer-proof fenced pastures, stocked with different densities of deer, to test the effect of intraspecific competition on overwinter fawn survival. Three pastures, ranging from 0.66–1.69 km^2 were stocked with mule deer during three separate winters. Deer densities in the pastures were 44, 89 and 133 deer km^{-2}. Bartmann et al. (1992) found that overwinter survival of fawns was inversely related to density during all years of the study, although malnourishment was the primary cause of mortality in all three pastures. The fact that malnourishment related mortality occurred in even the lowest density pasture was considered to be evidence that food limitation was occurring on this winter range. No coyote predation was reported.

The effect of deer density and intraspecific competition was tested under free-ranging conditions as part of two different studies. Each of these studies relied on a reduction in deer density as a treatment effect. The first of these utilized deer removal from a non-fenced, winter range study area in order to conduct the previously described stocking experiment (Bartmann et al. 1992). During a two-year study period, overwinter mule deer density on a treatment study unit was reduced by 22% and 16%, whereas density was left unaltered on control units. Despite these reductions in density, no difference in overwinter survival of fawns was observed between the treatment and control study units. Bartmann et al. (1992) concluded that density reductions were not high enough to induce a treatment effect on overwinter survival of fawns. No differences in mortality causes were observed between treatment and control study units, although as winter severity increased, the percent of fawns that died due to malnourishment increased. Following this initial project, a second density reduction experiment was conducted in which hunter harvest was increased in a treatment study unit, whereas no increased harvest occurred in a control study unit (White and Bartmann 1998). Building on the results of Bartmann et al. (1992) in which reductions in density of 22% and 16% resulted in no detectable treatment effect, desired reduction in density for this second study was > 50% (White and Bartmann 1998). Conducted over a four-year period, the increased harvest resulted in a 76% reduction in density. The reduction in density resulted in increased fawn survival from 0.31 to 0.77 during the treatment period, an increase of 0.46, whereas an increase of 0.29 was observed in the control unit. Despite the fact that an increase in survival occurred in both the treatment and control study units, the higher survival that occurred in the treatment area – the area with lower deer density – was evidence that population regulating effects were occurring.

As an alternative to reducing the density of deer, recent research has focused on habitat alteration as a mechanism to increase the finite supply of food. The first of these studies was an experimental manipulation of winter resource availability delivered via pelleted food (Bishop et al. 2009). Using a cross-over study design, Bishop et al. (2009) delivered ad libitum food to mule deer on two winter range experimental study units. Average overwinter survival of fawns on the treatment study unit was 0.905, whereas it was 0.684 on control units. Bishop et al. (2009) found that nutritional enhancement did not affect pregnancy or fetal rates, but enhancements did increase neonatal survival in treated animals. Ultimately, this nutritional enhancement led to a projected population rate of change of 1.17 on treatment study units, versus 1.03 on control study units. The increases in survival rates and productivity were viewed as evidence that *K* for mule deer was set by nutritional limitation. Bergman (2013) extended the results of Bishop et al. (2009) by replacing pelleted food with mechanical habitat treatments on mule deer winter range. While the treatment effect on the overwinter survival of fawns was smaller, Bergman (2013) documented a 1.15 times magnitude increase in survival in study units that had received mechanical disturbance treatments, reseeding, and chemical control of weeds over study units that hadn't received any treatments. Changes to vital rates impacting long-term population performance (i.e. pregnancy rates, twinning rates, neonatal survival, and adult body mass) were not documented. However, the increase in fawn survival translated to an increase in the projected finite population growth rate from 1.10 in untreated study units to 1.15 in treated study units (E. Bergman, Colorado Parks and Wildlife, unpubl.). As part of concurrent research, Bergman (2013) failed to conclusively demonstrate an effect when determining if habitat treatments extended to overall abundance. This lack of effect, in regards to abundance, was attributed to insensitivity of the abundance estimation procedures, annual variation in weather patterns that periodically forced additional animals on to study units, and to a lag effect between increased survival of fawns and an attending increase in abundance.

Disease

Research on disease within Colorado's mule deer population, especially during the past 15 years, has primarily focused on Chronic wasting disease (CWD). However, the focus of much of this research has been on the spatial ecology of the disease (Conner and Miller 2004, Farnsworth et al. 2006) and mechanisms for reducing the prevalence of the disease in deer herds (Wolfe et al. 2004, Conner et al. 2007).

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Extension of CWD research to deer population dynamics has largely been based on simulation. Results from these simulation efforts have been variable, although Gross and Miller (2001) demonstrated that population growth and productivity could be strongly influenced by low infection rates, implying a potentially regulating influence. Extension of simulation results to field assessment demonstrated weaker effects. In particular, Dulberger et al. (2010) concluded that while effects were present, the influence of CWD on recruitment was weak and could be ignored when considering the effects of the disease on population growth rates. Part of the difficulty in making conclusions about the population level impact of CWD on mule deer is imbedded in the evidence that infected deer are more vulnerable to predation (Miller et al. 2008, Krumm et al. 2009). Mountain lions have demonstrated the ability to select for CWD positive deer, demonstrating that compensation between predation and disease-related mortality occurs.

Other diseases, particularly bluetongue and Epizootic hemorrhagic disease (EHD), also occur in Colorado, but outbreaks of these diseases tend to be spatially localized and unpredictable. Thus, the frequency and magnitude of outbreaks has remained undocumented. However, Thorne et al. (1988) estimated that 1000 mule deer died during a bluetongue outbreak in Wyoming, providing evidence that disease impacts may not be trivial. In such cases, disease outbreaks would likely impact N, but not K or R.

Interspecific competition

Competition between mule deer and other species has received attention since the 1950s (McKean and Bartmann 1971). The majority of competition research, when focused on other wild ungulates, has focused on elk (Beck and Peek 2005, Torstenson et al. 2006). In consideration of domestic livestock, the majority of research has focused on competition between mule deer and cattle (Beck and Peek 2005, Torstenson et al. 2006). A common trend among all of these research projects has been the quantification of dietary and spatial overlap between different species. Studies have consistently concluded that in regards to dietary overlap between mule deer, elk, and cattle, mule deer demonstrate a high degree of diet partitioning as compared to the other two species (Beck and Peek 2005, Torstenson et al. 2006). Although not in Colorado, Beck and Peek (2005) found evidence of moderate (45%–59%) diet overlap between mule deer and elk during summer months. Torstenson et al. (2006) reported similar overlap (45%) between these two species during spring, although mule deer showed preference for forbs and shrubs, whereas elk showed preference for graminoids. In Colorado, research focused on range response to different stocking rates of mule deer, sheep, and cattle was conducted during the 1950s and 1960s (McKean and Bartmann 1971). This research demonstrated variable preference for different species of plants by all three species. However, McKean and Bartmann (1971) concluded that only under higher density stocking rates of multiple species did deterioration of range conditions occur. Unfortunately, research focused on competition between mule deer and other species has not been extended to population-level effects. Specifically, a robust estimation of how many mule deer may be replaced by other species in locations of range overlap has not occurred. While the need for such research has been identified (Lindzey et al. 1997), the financial and logistic constraints to accomplish such work are high. While the research results noted above demonstrate that the direct effects of competition between mule deer and other species are likely low, the indirect effects such as displacement of deer from optimal foraging locations or periods, and the subsequent cascade effect on body condition and productivity can only be speculated.

Habitat loss and degradation

Loss of habitat for wildlife species is incremental, with likely effects eventually stemming from the accumulation of those incremental losses. Thus, unlike many other factors that have a negative impact on mule deer, the impact of habitat loss is subtle and effects may only be realized after many years of compounding. Evaluation of the impacts of habitat loss on wildlife populations thus becomes a long process in which repeated quantification of both impacts and populations is necessary. For example, Nellemann et al. (2003) studied the impacts of hydroelectric reservoir infrastructure development on reindeer *Rangifer tarandus* during a 10-year period. This effort required monthly surveys of reindeer, but subsequently documented an overall reduction to 8% of pre-development densities in areas within 4 km of developed sites. Similar results for mule deer facing habitat loss due to energy development in Wyoming were reported by Sawyer and Nielson (2011). In the case of Sawyer and Nielson (2011), a 43% decline in mule deer abundance was observed in herds facing energy extraction and development, whereas a congruent decline of 23% was observed in nearby control areas. In each of these cases, habitat loss was slow (i.e. spread out over multiple years), but quick enough to be documented during a 10-year period. Habitat loss or habitat deterioration due to other causes, such as exurban and rural residential development, or vegetative succession to less desirable species, may occur over a time period spanning multiple decades. Documenting effects over such long time periods is increasingly difficult. Extension of historical trends into forecasts or predictions of future conditions is subsequently a difficult challenge to overcome. For example, Schwartz et al. (2012) linked projections of road density models with brown bear demographic criteria to estimate the loss of source habitat through 2020, and thus predicted that future exurban development would result in conversion of suitable habitat into sink habitat for brown bears. Similar efforts were made for mule deer in Oregon, although predictions about future habitat conditions were not extended to mule deer abundance (Kline et al. 2010). While recognized as a management dilemma in Colorado, no assessment of mule deer habitat loss or habitat conversion has occurred. Modeling efforts initiated by Johnson et al. (2012) will be the first effort to quantify this habitat conversion by land type as well as by landowner (e.g. private lands, state owned lands and federally owned lands). Thus, while the effects of habitat and nutritional limitation on deer herd productivity are well documented, the effects of habitat loss and conversion on population size have not been quantified. However, the modeling work by Johnson et al. (2012) may ultimately provide a data-based link between dN/dt and reductions in K.

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In addition to direct habitat loss, vegetational conversion within mule deer habitat to new, less desirable or less palatable species can also occur. While not quantified, a subtle example of such a conversion that has likely impacted mule deer in Colorado has been the conversion of mixed agricultural fields that included a higher non-native alfalfa *Medicago sativa* component to predominantly grass fields. More widely identified problems that result in lower quality and less palatable species include drought, expansion of exotic species such as cheatgrass *Bromus tectorum*, and overgrazing (Watkins et al. 2007).

Discussion

Based on published evidence from Colorado and elsewhere, the working hypothesis continues to be that many of Colorado's mule deer herds are limited by habitat, and more specifically, quality of winter range habitat. Refining this hypothesis leads to the conclusion that herds are limited by overwinter fawn survival, which in turn is a function of *K* for that winter. The preponderance of evidence, particularly the evaluations of winter nutrition and habitat management, but also evidence of compensation between predation and starvation support this position. Under the habitat limitation assumption, which assumes that a population is at or above *K*, the cause of mortality for deer is largely irrelevant as it pertains to the doomed surplus in a population; removal of one source of mortality would result in an increase in other mortality causes. Due to the partial dependence of *K* on weather and other stochastic events, even populations that are thought to be slightly below *K* may be subject to a doomed surplus if harsh or extreme conditions occur. Several of the key mule deer research projects discussed in this review demonstrate the phenomena of additive and compensatory mortality. This was particularly evident when coyotes were removed as part of the work conducted by Bartmann et al. (1992). A clear exception to this generalization, but an exception that provides support for the working hypothesis, is the lack of compensation that occurred when Bishop et al. (2009) reduced the opportunity for malnutrition by providing pelleted food. In this case, survival rates increased. Bishop et al. (2009) also demonstrated a consistent pattern of higher predation occurring, in the absence of enhanced nutrition, regardless of treatment location. In the case of harvest management studies (Bishop et al. 2005 and Bergman et al. 2011), reductions in fawn:adult female ratios were observed following increases in the male component of different herds. While not direct evidence of a cause-and-effect relationship, these results were potentially indicative that resource limitation was occurring and competitive interactions between different sexes and age classes of deer resulted in shifts in population ratios. A review by Mysterud et al. (2002) also emphasizes the asymmetric and non-trivial effects that males can inject into population dynamics.

In line with the hypothesis that mule deer are limited by winter range habitat, the role of coyote predation on mule deer does not appear to be limiting. The experimental evaluation of coyote removal on deer population dynamics has been robust. However, whether the effects of mountain lion predation on adult female deer in Colorado are additive or compensatory remains unclear. It is likely the impact of this predation is variable, depending on other environmental factors such as deer density, alternate prey species, winter severity, or disease incidence. Based on the abundance of mountain lion habitat in Colorado, as well as conservative mountain lion harvest management strategies, assuming that mountain lion predation on Colorado's mule deer is weakly additive may be reasonable. The population-level effect of bear predation on mule deer neonates ($\leq$ 2 months old) also remains unclear. Evidence from other predator–prey systems that are comprised of a more complex predator assemblage (e.g. brown bears, black bears, wolves *Canis lupus* and mountain lions) indicates that bear predation during this period is additive. In the absence of robust experimentation on the roles of mountain lion and bear predation, their impact on mule deer population dynamics will remain elusive.

Despite the existing research and knowledge, other key factors that may influence Colorado's mule deer population dynamics remain untested. For example, despite a large increase in Colorado's elk population between the 1960s and present time, interspecific competition between mule deer and elk has not been evaluated. An additional factor that limits the inference of this review is the fact that the research pertaining to density-dependence and winter range limitation on Colorado's mule deer herds has occurred at small spatial scales. To extend the existing body of knowledge to field management levels, we recommend a large scale integrative study that would address interactions between multiple predator and prey species, and multiple sources of mortality. In particular, experimental manipulations of the density of multiple herbivores at the herd level would allow investigation of interspecific competition, while also providing further insights into intraspecific competition. When put in the context of harvest management and herd management plans, managers and biologists would benefit from a quantitative assessment of deer and elk population interactions. A specific example might include the experimental reduction in herd size of one species, with the desired outcome being a positive response in population parameters (e.g. young:adult ratios, or survival rates) for both species, or an increase in overall abundance for the other species. Such an integrated study would also allow for an evaluation of the interactive effects of multiple mortality sources on populations. While winter browse availability and quality appears to set the upper limit for deer herds in Colorado (i.e. habitat is population limiting), a suite of other factors may regulate how quickly a deer herd reaches that limit. A hypothetical example can be constructed for Colorado's Front Range where CWD prevalence is high. Krumm et al. (2009) and Miller et al. (2008) found that mountain lions are capable of selecting for CWD infected deer. However, mountain lion diets are diverse and also included non-infected deer. Similarly, due to private land ownership and limited hunter access, hunter harvest of mountain lions is typically low in this region, potentially leading to high densities of mountain lions. The interaction of disease and predation, coupled with high predator/prey ratios could conceivably have a strong regulatory effect on deer population growth.

An integrated density experiment could also evalauate the regulating effects of coyote predation on deer. Evidence from a white-tailed deer *Odocoileus virginianus* and coyote

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predator–prey system demonstrated that coyote predation may have greater impact on deer populations, and thereby become additive in nature, when deer populations are at lower densities, although this result was confounded by the fact that predation rates on deer were also linked to densities of alternative prey, snowshoe hares *Lepus americanus* (Patterson and Messier 2000). To date, there are insufficient data to make similar conclusions about the impacts of coyotes on low density mule deer herds in Colorado. Specifically, if coyote predation becomes additive at low deer densities, determining the density at which that switch begins to occur is currently impossible. An ideal study would assess the inflection points at which the effects of predation switch from being additive – likely at low prey densities – to compensatory – likely at high prey densities.

Finally, research focused on the roles of weather, climate and summer range has not been conducted. A growing body of evidence has shown that plant phenology during spring, summer, and fall plays an important role on large ungulate demography. In particular, the role of forage abundance and quality outside of winter months has been shown to drive body mass for several North American ungulates (Cook et al. 2004, Giroux et al. 2014, Hurley et al. 2014). Declining body condition and body mass of adult females can impact age of first reproduction, neonatal rates, and also annual pregnancy rates, all of which are components of lagged density dependence. However, mule deer research in Colorado has been narrowly focused on winter habitat. Similarly, the relationship between climate phenomena and Colorado's mule deer population performance remains unexplored. While addressed more frequently for European and arctic ungulates, and North Atlantic weather patterns (Post and Forchhammer 2002, Stien et al. 2012), the relationship between weather, climate and mule deer remains largely uninvestigated (but see Marshal and Bleich 2011). Particularly as they relate to shifts in abundance in Colorado, linking the contribution of El Niño and La Niña weather events to large declines in mule deer may prove to temper concerns over herd health.

In conclusion, understanding of mule deer population ecology and management remain constrained by several gaps in knowledge. While research can be expected to continue, other useful sources of data can be exploited in the interim. For example, age, mass and reproductive data from hunter harvested deer are not currently collected. If these data can be collected in an unbiased manner, they will lend insight to important population attributes such as population age structure, cohort effects, and overall productivity. Likewise, in the absence of further information, herd management strategies can be re-evaluated. Based on the premise that K is variable, and largely dependent on stochastic weather patterns, setting abundance (N) objectives to align with K during extreme conditions may be prudent. By maintaining N at or below the perceived K for harsh winters, the per capita rate of change (R) will increase, thus minimizing the negative impacts of stochastic weather events, and also allowing quick population growth if forage quality or quantity improve.

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