California Fish and Game 100(3):550-572; 2014

Density dependence in ungulates: a review of causes, and concepts with some clarifications

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Understanding population dynamics of ungulates is not conceptually simple, in part, because there are many counterintuitive processes. We attempt to disentangle important concepts, including density dependence, density independence, limitation, regulation, compensatory and additive mortality, and top-down versus bottom-up forcing by examining how those ideas are related to the carrying capacity (*K*) of the environment. We contend that the *K*-selected, life-history characteristics of ungulates account for major components of their population dynamics. Those density-dependent attributes of ungulates require different management strategies than for species with attributes that are influenced primarily by density-independent processes. We offer a conceptual framework to help explain how density-dependent processes can be confused with those that are density-independent. We also discuss why regulation is the correct term for describing demographics of ungulates when limiting factors have density-dependent feedbacks. We emphasize that density *per se* is not valuable for understanding density dependence—rather, the population size relative to *K* is the critical factor. Comparisons among populations or within a population through time based on density alone are flawed, because *K* is not necessarily constant and can result in misleading results and conclusions. Whether mortality is compensatory or additive is a function of where the population is in relation to *K*, which is critically important when determining if and when predator control is biologically justified. We provide a model based on life-history characteristics to help parameterize where the population is in relation to *K*, and discuss a new nutritional model (nutritional carry capacity; NCC) for determining the relative degree of compensatory or additive mortality and the proximity of a population to its food supply.

Key words: additive mortality, compensatory mortality, demographics, density dependence, density independence, forcing, life-history characteristics, limitation, predation, regulation, ungulates

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Density dependence is an essential component for understanding the population ecology of large mammals—as well as a thoroughly established principle (Caughley 1977; McCullough 1979, 1999; Fowler 1981; Kie and White 1985; Skogland 1985; Clutton-Brock et al. 1987; Boyce 1989, and many others). Nevertheless, debate and confusion continue over exactly what density dependence entails and how it operates, or fails to do so, in populations of large mammals (Fowler 1981, McCullough 1979, Mackie et al. 1990). Misunderstandings abound and stem, in part, from failing to recognize that density dependence is both a life-history characteristic of a species (Stearns 1977), and a measureable parameter of populations (Caughley 1977). Our purpose is to clarify many of the misconceptions concerning the role of density dependence in ungulate population dynamics, relying heavily on our previous experiences and publications.

Ungulates (hooved mammals) exhibit a complex, yet predictable, suite of life-history characteristics. Although variation exists among species (Feldhamer et al. 2007), especially within pigs (Suidae) and peccaries (Tayasuidae), many of those large mammals display an array of traits that result in them being categorized as *K*-selected (i.e., density dependent and slow paced in their life histories) (Williams 1966; McCullough 1979, 1999). Compared with many small mammals, which often are termed *r*-selected (i.e., density independent and fast paced in their life histories), large mammals—in addition to large body size—are characterized by long lives, low adult mortality, delayed reproduction, small litter size, high maternal investment in young, iteroparity (multiple reproductive efforts over a life time), and high, but variable, survival rates of young. Individuals of species that exhibit strong density dependence also may trade reproduction to enhance adult survival (Martin et al. 2010, Monteith et al. 2014), or tradeoff current against future reproduction (Morano et al. 2013). Those life-history traits lead to low intrinsic rates of increase (*r*) for populations compared with their smaller-bodied counterparts (Stubbs 1977, Pianka 1983). As a result of those life-history characteristics, ungulates exhibit striking competitive abilities, and their population dynamics can be affected strongly by intraspecific competition, which changes in relation to the ecological carrying capacity (*K*) of the environment—a topic we will return to later. A characteristic growth curve of numbers over time for these large mammals in a constant environment would be S-shaped, reaching an asymptote at *K*.

Small animals are more likely to be affected by density-independent factors, with populations only occasionally reaching *K* except in unusual environmental situations or under controlled conditions in an experimental setting. Mammals with strong density-independent characteristics tend to be small, have short life-spans, high reproductive rates, and may reproduce but a single time (semelparity; Pianka 1983). Those organisms usually are not limited by intraspecific competition, or the resources available in the environment—for these species *K* is seldom attained because their populations are reduced (and may crash) because of density-independent factors, such as severe weather. Species with strong density independent characteristics are more likely to sacrifice survival for reproduction, because short lifespans generally preclude tradeoffs between current and future reproduction (Ghalambor and Martin 2001). Accordingly, density-independent organisms tend to exhibit a series of J-shaped growth curves over time, with populations that seldom, if ever, approach *K*. The irruptive phase of those J-shaped curves results from high population productivity and is associated with a high *r*. Of course, this stark dichotomy does not hold for all organisms. A continuum of species, with their accompanying life-history characteristics occurs from species exhibiting strong density dependence to those displaying clear density independence (McCullough 1979). Even among ungulate species and the landscapes they occupy, the strength of influence of density dependence and the ability to detect it is not ubiquitous (McCullough 1999, DeYoung 2011).

Disentangling effects of density-dependent and density-independent factors on ungulate populations is not straightforward. Density-independent effects can be masked in populations of most ungulates at low density, because females are in good nutritional condition (Pierce et al. 2012). Hence, variance in most measures of productivity would be low because individuals are well-buffered against climatic extremes, with correlations between weather and productivity of the population most apt to be weak (Milner et al. 1999, Kie et al. 2003). Conversely, populations at high density and near *K* would have a large proportion of animals in poor nutritional condition, and those individuals would be poorly cushioned against effects of severe winter weather or drought (Monteith et al. 2014). Populations at high density in relation to *K* also may be physiologically compromised, and therefore more susceptible to diseases (Sams et al. 1996). Variance in measures of population performance in such populations would be high, as would correlations between weather and productivity of the population. This outcome occurs because those animals in poor condition would be more likely to be helped or hindered by a variable climate than would individuals in good condition (Kie et al. 2003), or because a pulse of high-quality food associated with optimal weather conditions in arid climates promotes productivity (Shea et al. 1992, DeYoung 2011). At sufficiently high density in relation to *K*, however, density dependence may override even beneficial density-independent events (Stewart et al. 2005). Likewise, low population density relative to *K* may mitigate detrimental effects of climate, including drought (McCullough 2001). One circumstance in which the expected relationship between low density with respect to *K* and high productivity of ungulates may not occur is where disease has lowered the nutritional condition of individuals. Even low-density populations of bighorn sheep (*Ovis canadensis*) may exhibit poor nutritional condition after being infected with bacteria causing respiratory disease from contact with domestic sheep (Shannon et al. 2014). Our point, however, is that correlations may not always reflect cause and effect, and strong relationships between the productivity of ungulate populations and weather-related variables can be driven largely by density-dependent feedbacks, via changes in available resources and amount of intraspecific competition for those resources (Stewart et al. 2005, Monteith et al. 2014).

Consider a population that is at low density relative to *K*, and in which forage availability is high and intraspecific competition is low. Individuals would attain a high nutritional plane with resultant excellent nutritional condition, including high fat reserves that, in turn, would promote a high reproductive rate and survivorship. Winters of mild to moderate severity would have little influence on the overwinter survival of those animals, because they are well-buffered against those climatic events by extensive body reserves (Bowyer et al. 2000). An extremely severe winter, however, could still cause high rates of mortality, even among animals in good nutritional condition (Figure 1a).

Now consider a population near or at *K*. Intraspecific competition would be intense, per capita forage availability low, and nutritional condition poor. Under such circumstances, even a winter of moderate severity would be capable of causing high overwinter mortality (Figure 1b). Although mortality caused by winter severity is commonly interpreted as a density-independent factor (Severinghaus 1947, Verme 1968, Bartmann and Bowden 1984), those situations seldom are entirely density independent, because individuals can be buffered against such weather anomalies depending upon the level of density dependence experienced (Figure 1c). In this example, density-dependent processes produce a near-linear relationship between mortality and winter severity, which might be misinterpreted as a strong density-independent effect.

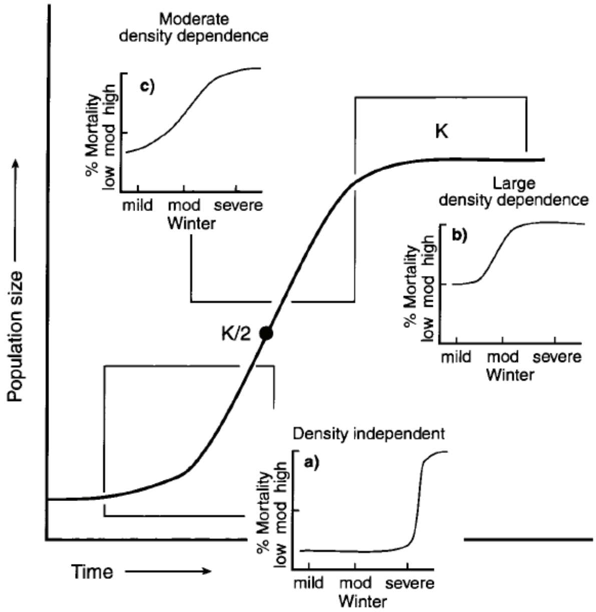

Figure 1.—A conceptual model illustrating relationships among ungulate population density, winter severity, and rate of overwinter mortality. Representative curves are provided for (a) density independent, (b) large density dependence, and (c) moderate density-dependent effects interacting with winter weather. The lines around the inset graphs indicate the area of the growth curve (population size over time) to which each inset corresponds. The shape of the population-growth curve need not be symmetrical for the postulated relationship to hold (from Bowyer et al. 2000).

Winter conditions may interact with density-dependent processes, sometimes with unanticipated outcomes. Mitchell et al. (2015) sampled density of Dall's sheep (*Ovis dalli*) before and during gray wolf (*Canis lupus*) and coyote (*C. latrans*) harvests for 3 years on adjacent treatment (predator harvest) and reference (no predator harvest) areas. Density of sheep on the reference area was similar over 3 years, while density of sheep where canids were harvested increased markedly. A winter of above-normal snowfall combined with crusted snow occurred during the final year of the study. Sheep on the reference area (where predators were not harvested) did not experience a change in density, whereas the population of sheep on the treatment area crashed precipitously. Sheep on the treatment area initially benefited from the harvest of predators, but their population crashed, ostensibly the result of a combination of increased population density brought about by removal of predators, and a subsequent severe winter (Mitchell et al. 2015).

Winter has long been a focus for management and research on ungulate populations, especially in temperate and arctic environments (Mautz 1978, Bergman et al. 2015); however, mounting evidence indicates that nutritional quality of summer range also plays a critically important role in their population dynamics (Cook et al. 2004, Stewart et al. 2005, Couturier et al. 2009, Monteith et al. 2013, Shallow et al. 2015, among others). In separate manipulative experiments, while holding effects of winter constant, Stewart et al. (2005) documented effects of summer nutrition on pregnancy rates and nutritional condition of North American elk (*Cervus elpahus*) by manipulating population density, and Tollefson et al. (2010, 2011) demonstrated effects of summer nutrition on reproduction of adult mule deer (*Odocoileus hemionus*) and growth and survival of young mule deer by manipulating summer diets. Nevertheless, nutritional contributions from seasonal ranges are not independent because carryover effects, including provisioning of young, influence the nutritional state of an individual entering the next season (Bardsen and Tveraa 2012; Monteith et al. 2013, 2014). Consequently, the question of which seasonal range is more important is probably moot, because strength in one may help compensate for the weaknesses in another—thus, they are both important (Kie et al. 2003, Monteith et al. 2013).

The preceding generalizations and examples concerning the life-history strategies and population dynamics of ungulates are at the center of misunderstandings concerning the demographics, conservation, and management of large mammals. Variable environments will seldom have the capacity to support the same number of animals on an annual basis, thereby confounding interpretations and resultant management alternatives (Mackie et al. 1990, DeYoung 2011, Pierce et al. 2012, Monteith et al. 2014). Consequently, the number of animals in relation to *K* determines the potential productivity of the population; identical densities of large herbivores inhabiting a variable environment can exhibit either similar or differing measures of productivity depending upon environmental conditions (Monteith et al. 2014). As a result, density of animals *per se* cannot be used to compare the dynamics of different populations directly. Rather, the relative amount of food on a per capita basis effects nutritional condition of individuals. Thus, the number of animals in relation to *K* determines the potential productivity of a population (Caughley and Gunn 1993, Bishop et al. 2009, Pierce et al. 2012, Monteith et al. 2014). Indeed, searching for direct relationships among metrics of productivity with density can yield spurious results in variable environments, even when strong density-dependent processes are at play (Pierce et al. 2012; Starns et al. 2014, 2015). Unless environmental conditions remain constant, which they rarely do, studies seeking to compare productivity of ungulate populations based on density alone are logically flawed, and likely provide misleading or unreliable results. Density, likewise, can be a misleading indicator of habitat quality (Van Horne 1983).

Density dependence in ungulates manifests itself in changes in vital rates, which is a function of where the population is with respect to *K*. Indeed, such changes in vital rates in relation to *K* often occur in a predictable pattern with increasing population size as a consequence of a conservative life-history strategy: decreased survival of young; increased age at first reproduction; reduced fetal rate; reduced pregnancy rate; and reduced survival of adults (Gaillard et al. 2000, Eberhardt 2002, Bonenfant et al. 2009, Monteith et al. 2014), all of which can affect *r*. In particular, recruitment rate (the number of young recruited per adult) changes as an inverse linear, or relatively linear, function of population size (McCullough 1979, 1999), with recruitment rate being highest at low population size relative to *K*, and lowest at high population size relative to *K* (Figure 2). Moreover, recruitment rate varies with changes to *K* within a population, such that modifications to improve habitat will have a pronounced effect near *K*, but substantially less influence for populations at low density relative to *K*, where predation or other factors may occur and, consequently, competition for forage is low and nutritional condition is high (Figure 2). Thus, inferring that density dependence is not operating at low density relative to *K* simply because that variable is difficult to detect is inappropriate, because there may be other reasons that density-dependent responses are not readily evident. For instance, observations might have been made over too short a period to identify a trend in reproductive rates (McCullough 1990), time lags associated with recovery of resources or intergenerational effects may have delayed a density-dependent response (Fryxell et al. 1992, Monteith et al. 2009), or density may not have changed sufficiently to note differences in that variable over time, especially given the difficulties in reliably measuring that variable (McCullough 1990).

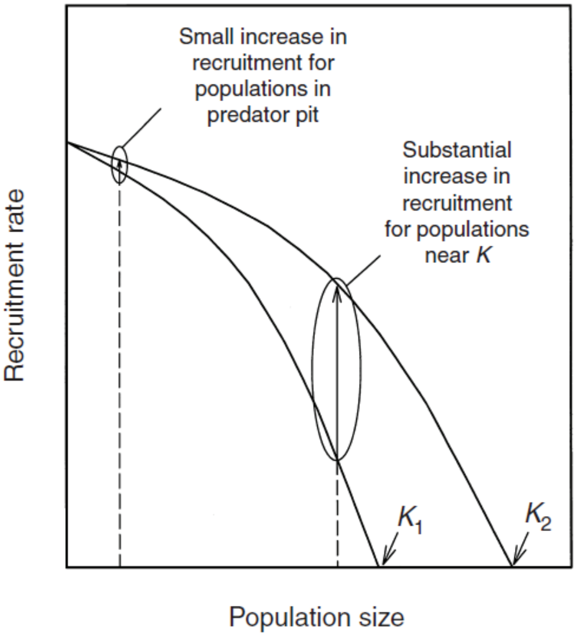

FIGURE 2.—Variation in recruitment rate (young/adult) with increasing population size relative to *K*. Note that for small population size (such as when ungulate populations are held at low density by predation) there is little increase in recruitment rate from improving *K* (i.e., moving from K_1 to K_2). There is a sizeable increase in recruitment rate, however, for populations initially near K_1 (from Kie et al. 2003).

Life-history characteristics related to density dependence among ungulate populations result in a continuum of reproductive rates that change with population size relative to *K*. Detecting density-dependent changes in demographic parameters for a particular population, however, may be difficult at low density, where productivity is high. In such situations, those demographic changes are less variable across changing densities. Demographic adjustments, however, are relatively easy to detect at high densities relative to *K*, when productivity is low and changes markedly with density (Figure 3). We suggest that most ungulates will exhibit a density-dependent response because of their unique life-history characteristics, but acknowledge, that under particular conditions this outcome may be difficult to detect.

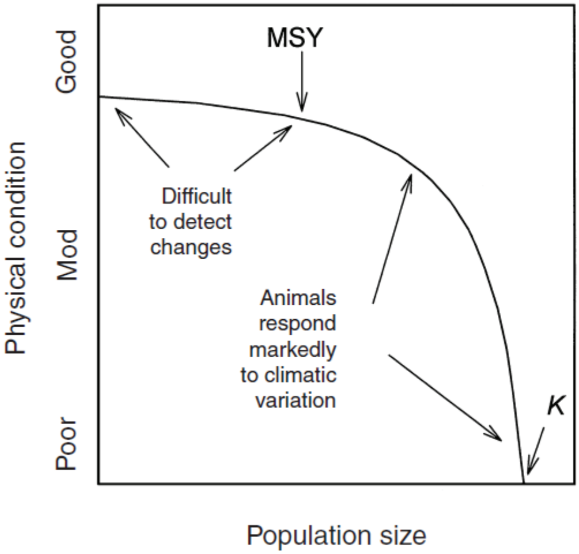

FIGURE 3.—Relationship between physical condition of ungulates and changing population size. Changes in condition and subsequent effects of reproduction and survival may be difficult to detect below maximum sustained yield (MSY), but changes in condition between MSY and carrying capacity (*K*) can be marked (from Kie et al. 2003).

In arid environments characterized by low productivity, but with abundant low-quality forage that meets requirements of maintenance, populations may respond negligibly to changes in density. Large amounts of maintenance forage sustain adults in poor nutritional condition and potentially across a wide range of densities, but yields insufficient resources to enhance recruitment of young (Shea et al. 1992, Owen-Smith 2002, DeYoung 2011). Nonetheless, density-dependent effects can occur at very low density relative to *K* when small amounts of high-quality food are available seasonally, or when density increases following multiple years of optimal forage production (McCullough 1999, DeYoung 2011). In normal years of typically unproductive forage production, populations may fluctuate up and down with no apparent signs of density dependence because of the large forage base that supports maintenance, but not reproduction (DeYoung 2011).

In contrast with the near-linear change in recruitment rate with increasing density, the total number of young recruited has a parabolic relationship with population size for ungulates, which results from the product of population size and recruitment rate at various sizes of the population (Figure 2, Figure 4). Very high and very low recruitment rates (Figure 2) result in a low number of recruits, but intermediate levels of recruitment rate and population size yield the greatest number (Figure 4). The point at the apex of the parabola is termed Maximum Sustained Yield (MSY), and is the maximum annual harvest that a particular population can withstand without moving the population toward extirpation (McCullough 1979; Figure 4).

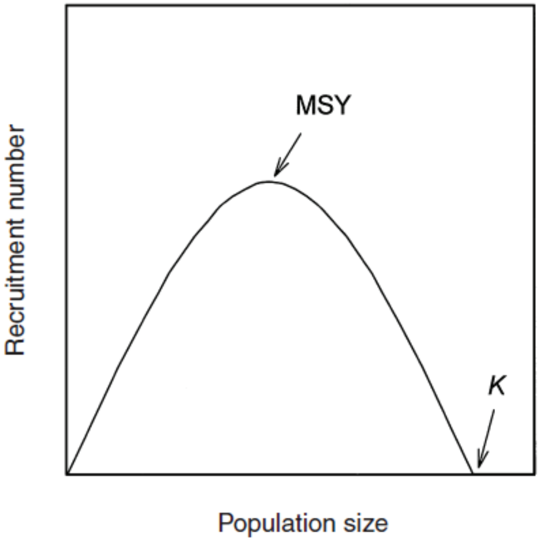

FIGURE 4.—The parabolic relationship between recruitment number (i.e., the number of young successfully added to the population) and size for an ungulate population. MSY is maximum sustained yield, which is the maximum harvest (or other mortality) that can be sustained by the population. The relationship need not be symmetrical to infer density dependence (from Kie et al. 2003).

Several critical points emerge from these simple theoretical models. First, species with strong density-independent and density-dependent characteristics require different management strategies (McCullough 2001). The J-shaped curves of abundance indicative of density independence denote that there is a surplus of animals that will perish even in the absence of a harvest; moreover, the population rebounds each year following a crash. Those animals that will perish, then, become the "harvestable surplus" described by Leopold (1933) that has been used to set hunting regulations (i.e., the surplus determines the harvest). We caution, however, that the concept of a harvestable surplus has been criticized by McCullough 1979) and Connelly et al. (2012). For density-dependent species, the harvest determines the surplus (McCullough 2001). For example, if the population depicted in Figure 4 is near *K*, and is moved toward MSY by harvesting animals, the surplus initially increases until MSY is achieved, but declines thereafter. As a result, large ungulates in particular cannot be managed effectively by trying to set harvests according to observed surpluses—at best this management results in a very conservative harvest. If the population was near *K* and exhibited low recruitment (Figure 4), then setting a low harvest would result in poor recruitment again the following year (all else being equal), and harvest would remain well below what the population is capable of sustaining over time (McCullough 2001). If a population is already at or near MSY, however, a danger exists in assuming that increased recruitment will result from an increased harvest (Figure 4)—such management may result in declining recruitment numbers, which is the general pattern for an overharvest. This situation does not mean that density-dependent processes were not operating; rather, density-dependent response in recruitment simply was not sufficient to compensate for a sustained overharvest. Furthermore, in the aforementioned example depicting an arid environment with abundant, poor-quality food for maintenance, increasing harvest in a similar fashion would not increase productivity if the density reduction does not concomitantly reduce competition for forage and, thus, yield increased production (DeYoung 2011). This outcome, of course, will vary with the types of habitats and ungulate species involved; the wide distribution and diverse environments inhabited by white-tailed deer (*Odocoileus virginianus*) offer a good example of this variability (McCullough et al. 1999, DeYoung 2011). Such complexity enforces the notion of having a firm understanding of population dynamics to aid in implementing harvest strategies.

Another mechanism that has the ability to reduce the *K* of a habitat for a particular species is interspecific competition. Life-history characteristics of ungulates should make them among the most competitive of all organisms (Stewart et al. 2002). Most studies of ungulates, however, infer competition from the amount of resource partitioning (Putnam 1996). Manipulative experiments are necessary to unequivocally demonstrate competition, yet those are exceptionally difficult to conduct on large, vagile, animals in a natural setting (Stewart et al. 2002, 2011a). Competition may be exploitive, when one competitor uses resources, thereby making them unavailable to another competitor, or involve interference competition wherein a competitor is prevented from using a resource even if it is not reduced in abundance by the competing species—both mechanisms likely operate in ungulates, and could lower *K* for one or both competitors (Stewart et al. 2002, 2011a). Apparent competition also may occur where 2 ungulates share a common predator. If one ungulate is abundant and the other rare, the greater number of predators supported by the more common species can adversely influence the population of the rarer ungulate where their distributions overlap (Johnson et al. 2013). The mechanisms underpinning the population dynamics of competing species of ungulates, however, remain the same. The relationship of population size to *K* helps determine the dynamics of both populations.

Density-dependent species also can exhibit irruptive growth, such as when a population at low density rebounds rapidly towards *K* (Leopold 1943, Klein 1968, Forsyth and Caley 2006, Ricca et al. 2014). This phenomenon occurs when a population has been held well below MSY (e.g., by harvesting animals), which allows for food resources to accumulate (McCullough 1979). In the absence of harvest or a marked reduction in harvest, populations will respond with rapid growth toward and a potential overshoot of *K*. In such an example, the magnitude of the overshoot of *K* will be related to the magnitude of the accumulation of resources; and, the degree of depletion of resources and subsequent population crash will exceed the magnitude of the overshoot of *K* (McCullough 1979, Person et al. 2001).

Irruptive growth in ungulate populations also can occur following newly abundant resources resulting from the creation of large areas of new habitat (McCullough 1979), introduction of ungulates to new areas, or release onto islands without predators (Klein 1968, Ricca et al. 2014). Under the previously listed examples, an overshoot of *K* can cause a concomitant decrease in *K* from overgrazing and resultant loss in habitat quality, thereafter leading to reductions in productivity (McCullough 1979; Starns et al. 2014, 2015). Ungulates possess the capability to have either detrimental or beneficial effects on the ecosystems that they inhabit, which largely are related to their population density relative to *K* (Hobbs 1996; Cote et al. 2004; Stewart et al. 2006, 2009; Speed et al. 2010).

Another term that is sometimes misused is anti-density dependence (also called inverse density dependence). This term has been applied correctly to carnivores preying on declining ungulate populations (Boutin 1992). For ungulate populations themselves, however, this process is thought to occur when the growth of a population is facilitated by increasing population density. For a population increasing from low density toward MSY (Figure 4), the population indeed will grow larger with increasing density. This is a normal part of the density-dependent process; there is nothing "anti" about it. The population would need to increase from the point of MSY toward *K* (Figure 4) as density increased for this to be anti-density dependent (a situation that at best is uncommon among ungulates). The Allee Effect (Allee 1938), wherein a population at a sufficiently low density facilitates a decline in growth rate (perhaps because of a lack of social facilitation necessary for mating or other causes—Berec et al. 2007, McLellan et al. 2010), is an example for which the term may be appropriate. Hoffmann et al. (2010) noted that some evidence for an Allee Effect existed for pronghorn (*Antilocapra americana*), and was thought to be produced by variation in rangeland condition over time. Such changes in condition of rangelands, however, also would likely involve changes in *K*, and hence density dependence. We contend the concept of anti-density dependence often is misused primarily because of the failure to conceptualize the parabolic nature of the curve for recruitment number (Figure 4), and its relationship to the more linear curve for recruitment rate (Figure 2)—nothing represented by those curves can be construed as anti-density dependent. Stephens and Southerland (1999) review circumstances where inverse density dependence is thought to occur without invoking rates of predation.

An additional misunderstanding regarding population dynamics relates to a life-history characteristic of ungulates (Bleich et al. 1997, Barboza and Bowyer 2000, 2001; Bowyer 2004; Stewart et al. 2011b, 2015)—sexual segregation. The sexes of dimorphic ungulates spatially separate from one another for much of the year, but aggregate for mating. This means that females, rather than males, compete most intensively for resources with other females and young for much of the year, thereby affecting nutritional condition of females. Accordingly, the female component is most closely related to the overall dynamics of a population (McCullough 1979). Among polygynous species exhibiting sexual segregation, harvesting males will do little to move a population away from *K* and, consequently, reductions in harvest of males will do little to bolster population growth (Freeman et al. 2014) because abundance of males has little effect on recruitment of young (McCullough 1979, 2001). Nonetheless, males may influence the dynamics of ungulate populations under some circumstances (Mysterud 2002), but those effects are not autonomous from density-dependent processes and sometimes may be overridden by them. Differences in space use, habitat selection, and diets between the sexes have led investigators to suggest that the sexes should be managed as if they were different species (Kie and Bowyer 1999, Stewart et al. 2003, Schroeder et al. 2010, Whiting et al. 2010), and have important implications for conservation (Bleich et al. 1997, Rubin and Bleich 2005). Indeed, examples exist wherein a management action undertaken to benefit the species differentially helps one sex to the detriment of the other (Bowyer et al. 2001, Stewart et al. 2003).

An additional problematic area in the understanding of ungulate population dynamics is the difference between compensatory and additive mortality (McCullough 1979, Bartmann et al. 1992). The concept of compensatory mortality was introduced by Errington (1934), Errington and Hammerstrom (1935) and Errington (1946) based on situations in which prey populations were observed losing what was termed a surplus of animals each year. Under compensatory mortality, one source of mortality compensates for another; with additive mortality, the effects of the sources of mortality are summed. Female ungulates generally attempt to produce more offspring than the habitat can support: attempted recruits exceed actual recruits (McCullough 1979; Figure 5). The difference between the number of attempted recruits and actual recruits that the habitat can support is the component of mortality that is compensatory (Monteith et al. 2014). That is, regardless of the proximate cause of mortality (e.g., predation, malnutrition), resources were insufficient to support those animals that did not survive (Figure 5). Therefore, the consequences of mortality and the degree to which mortality is compensatory or additive result from density dependence and resource limitation, whereby an increase in per capita resources reduces natural mortality rates and enhances potential for survival and reproduction (Boyce et al. 1999).

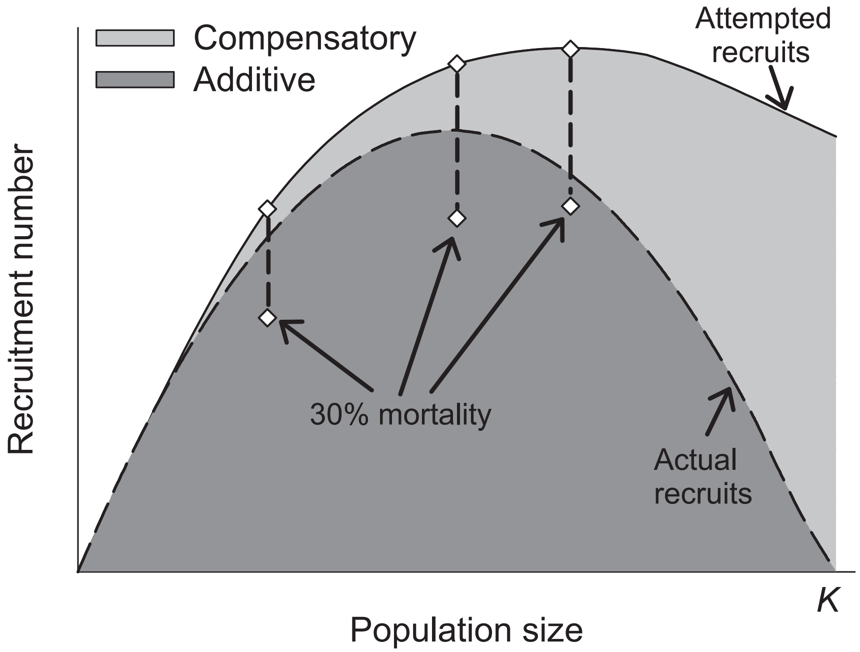

Figure 5.—Changes in recruitment number and attempts to recruit with increasing population size of adult female ungulates. Females attempt to add more young to the population than can be sustained by the environment at densities ranging from maximum sustained yield (MSY) to *K* where mortality becomes increasingly more compensatory (one source of mortality substitutes for another). Attempts to recruit young below MSY, however, are more successful because females are in excellent nutritional condition. Consequently, mortality is additive (one source of mortality is added to another) (from Kie et al. 2003, Monteith et al. 2014).

In populations at low density relative to *K*, females are in an enhanced state of nutritional condition, and the resources exist to support most of the attempted recruits (in the absence of predation or other sources of mortality), compared with populations near *K* when females are in poor nutritional condition and most attempted recruits will be lost because resources do not exist to support them. Between those two endpoints is a gradient of an increasing proportion of mortality that is compensatory as resource limitation increases concomitant with rising density relative to *K* (Figure 5). Consequently, unless a population exists at one of those two endpoints, conclusions that all mortality was either compensatory or additive are suspect. Depending upon proximity to *K*, mortality up to a certain point is compensatory, with higher levels of mortality becoming increasingly additive (Monteith et al. 2014). Indeed, compensatory and additive mortality both can operate, to varying degrees, in the same population (Pierce et al. 2012, Monteith et al. 2014).

Another topic of concern is the application of the terms compensatory and additive to characterize contributions of mortality among different predators preying on the same ungulate population. For instance, attempting to differentiate if mortality caused by particular predators was compensatory or additive is meaningless to the dynamics of ungulate prey; only the relationship of population size to *K* and, hence, level of resource limitation affects the degree to which mortality is additive or compensatory (Figure 5). Although a specific predator may have greater potential to have an additive effect than other predators—for example bears killing young within a few days of birth when those neonates are most vulnerable (Bowyer et al. 1998, Zager and Beecham 2006, Monteith et al. 2014)—it is the nutritional potential of the prey population to recruit young, and not the predators, that determines the consequences of mortality (Bartmann et al. 1992, Tveraa et al. 2003, Monteith et al. 2014).

Outcomes from compensatory versus additive mortality, indeed, have huge implications for interpreting effects of predation on ungulate populations (Ballard et al. 2001). For example, if a sample of radio-marked ungulates for a population experiencing strong resource regulation near *K* indicates that mortality of young was largely a result of predation, the need for predator control to benefit the ungulate population would be nil—most young would not have been recruited into the population and removing predators would have little effect on the ungulate population (i.e., most of the mortality was compensatory; Figure 5). Conversely, an identical mortality rate attributed to predation for an ungulate population at low density (or size) in relation to *K*, would lead to a far different conclusion—such mortality would be largely additive because the resources existed to support most of the young lost to predation. Consequently, predator control could be biologically justified (i.e., at least some mortality was additive), if the management objective was to increase the population of ungulates.

The terms "limitation" and "regulation" have engendered considerable debate (Van Ballenberghe and Ballard 1994, Berryman 2004, White 2007). For regulation to occur, there must be a density-dependent feedback (in prey for instance, as a result of predation, or changes in population size as an outcome from harvest) (Holling 1959). Limitation simply requires the death of individuals. Therefore, when limiting factors operate in a density-dependent manner they are, thus, regulating and have the potential to maintain populations at densities lower than what their habitat would allow. Therein, regulation can imply some level of equilibrium (between predator and prey, or harvest and populations size)—albeit uncommon and difficult to attain—among some populations of ungulates (McCullough 1999). For example, a predator pit can result in a prey population maintained at low density by density-dependent predation (Gasaway et al. 1992, Person et al. 2001, Bowyer et al. 2005, Wittmer et al. 2005). The pervasive influence of density-dependent limitation of resources on ungulate populations assures that resource limitation is a regulating factor.

As our previous discussion demonstrates, determining where an ungulate population is in relation to *K* is critically important for understanding its dynamics, and may affect decisions concerning conservation and management. Regression (McCullough 1979) and forage-based models (Hobbs and Swift 1985), as well several other methods (such as time series; Boyce 1989, Beck et al. 2006, Forsyth and Caley 2006) exist to parameterize *K*, but those approaches are data hungry and often cost prohibitive; many years may be needed to parameterize the necessary information (Bowyer et al. 2005, 2013; Monteith et al. 2014). Issues related to the conservation and management of ungulates likely would have been resolved for either good or ill long before many of the aforementioned models could be adequately parameterized (Bowyer et al. 2013). Meanwhile, habitat or environmental changes may well have occurred, potentially nullifying conclusions from the models.

Instead, we recommend using a model based on life-history characteristics of ungulates to determine the relative position of a population in relation to *K* (Table 1). Variation in those population characteristics, with regard to whether the population is near or backed away from *K*, results from changes in nutritional condition of females as a function of resource availability relative to density (Stewart et al. 2005). That suite of variables (Table 1), when considered as a whole, can provide valuable information on where the population is in relation to *K*. Likewise, this same approach can be used to evaluate whether population regulation or limitation is top-down (i.e., from predation) or bottom-up (i.e., via resource availability) (Pierce et al. 2012). Indeed, we contend that this approach is more meaningful and less difficult than collecting data on predator-prey ratios or kill rates, both of which can be misleading (Bowyer et al. 2013).

Table 1.—Life-history characteristics of ungulates that reflect the relative differences in a population regulated by top-down versus bottom-up processes (from Bowyer et al. 2005, 2013).

Life-history characteristic	Top-down regulated	Bottom-up regulated
Physical condition of adult females	Better	Poorer
Pregnancy rate of adult females	Higher	Lower
Pause in annual reproduction by adult females	Less likely	More likely
Yearlings pregnant[a]	Usually	Seldom
Corpora lutea counts of adult females[a]	Higher	Lower
Litter size[a]	Higher	Lower
Age at first reproduction for females	Younger	Older
Weight of neonates	Heavier	Lighter
Mortality of young	Additive	Compensatory
Age at extensive tooth wear	Older	Younger
Diet quality	Higher	Lower

[a] Some species of ungulates may show limited variability in particular characteristics.

Whether regulation is top down or bottom up ultimately can dictate important management decisions. We prefer the term "forcing" rather than regulation, because it allows for either top-down or bottom-up effects to change in a particular direction with population size, but without requiring equilibrium—use of the term forcing also avoids the regulation-limitation debate. Making judgments about top-down or bottom-up forcing, however, cannot be based solely on population trajectories. Information on the life-history characteristics of the ungulate population (Table 1) is required to identify such differences (Pierce et al. 2012). Moreover, both top-down and bottom-up forcing can operate in the same population and change in magnitude over time (Pierce et al. 2012, Monteith et al. 2014). This approach for assessing life-history traits also can be used to infer the degree to which predators are regulating prey (Bowyer et al. 2013). In some systems, predators may hold prey at low density in a predator pit in which reduced intraspecific competition results in good nutritional condition of prey with concomitant changes in life-history characteristics (Gasaway et al. 1992, Person et al. 2001, Bowyer et al. 2005). In other ecosystems, however, predators may be less successful in suppressing prey populations (Hurley et al. 2011). Consequently, the relationships presented in Table 1 may offer an alternative to other measures of predation in assessing whether regulation of ungulates is either top down or bottom up (Pierce et al 2012, Bowyer 2013).

The concept of carrying capacity (*K*) is at the heart of most models we have discussed. Contrary to some opinions, we do not find *K* to be a slippery notion (Macnab 1985) but, rather, to be one that is essential for understanding population dynamics of ungulates. We do, nevertheless, recognize that *K* can be easily misconstrued, especially in variable environments, and estimating *K* can be difficult (Monteith et al. 2014). Ecological carrying capacity (i.e., *K*) traditionally has been defined by the number of animals that a particular area can support at equilibrium (Caughley 1979, McCullough 1979). Directional changes (increases or decreases) in *K* can be brought about by perturbations of habitats (Holl and Bleich 2010, Holl et al. 2012), such as intentional manipulation, fire, drought, overgrazing, or overshoots of *K*. Results of such alterations to habitat can include differing equilibria between ungulates and the areas they occupy, which might be accompanied by fluctuations, or time lags of ungulate numbers and in density-dependent influences (McCullough 1999, Monteith et al. 2009, Pierce et al. 2012). Where directional changes in *K* do not occur over time, however, fluctuations in populations could still ensue. Such an outcome results from weather influencing the food supply (or in the instance of deep snow, also the energy budget) for these large herbivores. Managing ungulate populations based only on those fluctuations will, however, result in a very conservative harvest (McCullough 2001).

Productivity may vary from year-to-year depending on patterns of weather; thus, the net number of animals that available habitat can support fluctuates on an annual basis. Nevertheless, those short-term changes in productivity of habitat, and consequently the degree of density dependence each year, create difficulties in understanding the relative role of habitat and number of animals that can be sustained over the long term. To overcome difficulties of parameterizing *K* in a variable environment, Monteith et al. (2014) proposed the use of a new model termed "animal-indicated nutritional carrying capacity" (NCC). NCC is parameterized based on the nutritional condition of a population when $r = 0$ (i.e., no population change), because nutritional condition of a population signifies the position of a population relative to its current food supply (Monteith et al. 2014). Poor nutritional condition of animals relative to that threshold implies a population near or above NCC, and for which the resources for sustained growth of the population are not available, compared with a population in comparatively good nutritional condition, which is typical of a population below NCC and for which resources exist to support population growth. Indeed, the nutritional status of a population at a particular point in time integrates nutritional history relative to forage quality and abundance as a function of density and potential nutritional carryover to the following season (Monteith et al. 2013). Not only does this approach provide a tractable tool for assessing NCC, it also yields the mechanism for examining the consequences of mortality on population dynamics (Figure 6) that is essential for managing populations of ungulates. This innovative approach allows for more comprehensive management of ungulates, because density-dependent processes and potential fluctuations in food supply are inherently integrated in the nutritional status of the population of interest. We note, however, that the conservation and management of ungulates may require more than just an improved understanding of their population dynamics (Krausman and Bleich 2013).

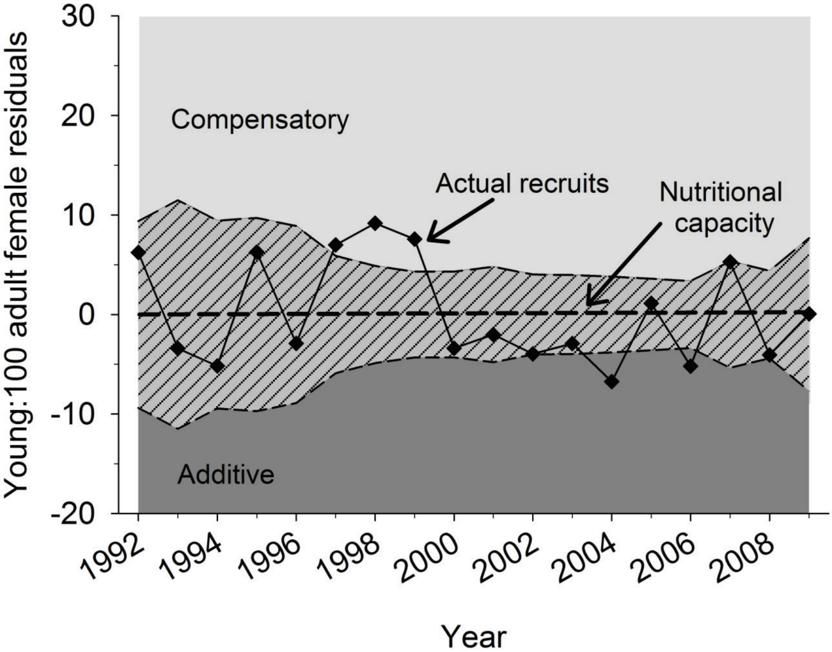

Figure 6. —Residuals from a mixed-effects model used to predict the nutritional capacity of female mule deer (*Odocoileus hemionus*) to recruit young relative to attempted recruits (based on fetal rates) and observed recruits (based on the ratio of young to adult females) over time. Residuals in ratios of young to adult female above those predicted (dashed line) indicate mortality was compensatory (light gray); ratios below that expected indicate the amount of mortality that was additive (dark gray). The model included the variables mean March ingesta-free body fat (IFBFat) of the current year, mean March IFBFat of the previous year, mean March body mass, mean litter size, per capita snowpack, summer precipitation, and summer temperature. The hashed areas around the predicted line represent 95% confidence intervals (from Monteith et al. 2014).

MANAGEMENT IMPLICATIONS

We highlight the importance of determining where an ungulate population is in relation to carrying capacity (*K*) to understand the dynamics and, thereby, the management and conservation of that population. Density-dependent processes underpin the nutritional condition and life-history characteristics of ungulates. We offer a method that incorporates such information to parameterize where a population is relative to *K* (Table 1). This cost-effective approach also can be used to help establish and adjust harvest goals in an adaptive manner, and determine whether the population might be regulated by predation. We caution that what appears to be density-independent regulation of a population also may have a strong density-dependent component, especially when there are correlations between population productivity and weather variables (Figure 1). Comparisons among populations based only on density can be misleading, because *K* may vary among populations independent of their density. Winter range has long been thought to be the primary factor influencing productivity of ungulate populations in temperate and arctic regions. Nonetheless, the importance of summer range recently has been documented—both seasonal ranges may be critical in determining the productivity of populations, and carryover effects in nutritional condition may occur across seasons.

Different management strategies are required for species displaying density-independent compared with density-dependent components to their life-history characteristics. Harvesting just the surplus of populations that are strongly density-dependent when near *K* (which will be low) results in low recruitment in the following year (Figure 4), and very conservative management, if the goal is to increase harvest. For density-dependent ungulates, the harvest determines the surplus, and increasing harvest until MSY is reached will continuously increase recruitment; harvesting beyond MSY, however, can move the population toward extirpation (Figure 4). Harvesting only males will do little to affect the dynamics of ungulate populations. When released from harvest or introduced into new environments, ungulate populations may irrupt, with an overshoot of *K* resulting in disproportional damage to habitat relative to the size of the overshoot—a circumstance that should be avoided if possible. Creating new habitat when the population is at low density will do little to promote increased reproduction, yet can be a successful strategy when the population is near *K* (Figure 2). The sexes of ungulates typically spatially separate outside the mating season. Males and females select habitats differently, and effective management may require treating the sexes as if they were separate species—examples exist where habitat manipulations benefited one sex to the detriment of the other.

Understanding differences between compensatory mortality (one source of mortality compensates for another) and additive mortality (one source of mortality is added to another) and how this changes with increasing population size in relation to *K* is critical for the sound management of ungulate populations (Figure 5). Mortality near *K* is mostly compensatory, and reducing harvest or predation will have little influence on changing the size of the ungulate population. Conversely, if a population is at low density in relation to *K* (and, hence, most mortality is additive), the same harvest or losses to the population from predators could have dire consequences by further reducing population size. Under such circumstances predator control may be biologically justified. The relationship of the ungulate population to *K* is the critical element in determining whether mortality will be additive or compensatory—that one predator causes more additive mortality than another is meaningless to the dynamics of ungulate populations—the number of ungulates killed and the relationship of the population to *K* is what is critical. Finally, we offer a new method for understanding year-to-year variation in the nutritional carrying capacity (NCC) of an area, and a technique to determine whether mortality is additive or compensatory (Figure 6). This method should be useful in the long-term management of ungulate populations, especially in variable environments.

Acknowledgments

We thank numerous colleagues and students for many productive discussions that occurred over an extended period of time, dating back to 1988. The results of those discussions and their suggestions were refined over the years, resulting in this contribution. We also thank H. Wittmer, F. Weckerly, and an anonymous reviewer for providing stimulating comments that resulted in an improved manuscript. We thank J. W. Connelly for his editorial expertise. This is Professional Paper 108 from the Eastern Sierra Center for Applied Population Ecology.

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Guest Editor was J. Connelly
Received 24 November 2014
Accepted 20 January 2015