



METRICS OF HARVEST FOR UNGULATE POPULATIONS: MISCONCEPTIONS, LURKING VARIABLES, AND PRUDENT MANAGEMENT

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ABSTRACT: Biologists often must use incomplete information to make recommendations concerning harvest of large mammals. Consequently, those recommendations must draw on a firm understanding of the ecology of the species in question, along with selection of the most applicable population characteristics on which to base harvest—both essential components for prudent management. Density-dependent processes, which are ubiquitous among populations of large mammals, may be counterintuitive because of unexpected patterns in recruitment coincident with changes in population size. Misconceptions concerning population dynamics of ungulates also can occur when demographics are based solely on correlations with environmental factors. Further, the concept of a harvestable surplus can be misleading for managing ungulate populations, because of the parabolic relationship between population size and number of recruits—harvest determines the surplus rather than *vice versa*. Understanding consequences of mortality, especially relative components of compensatory or additive mortality, also is necessary. Knowledge of the proximity of an ungulate population to ecological carrying capacity (K) is required to fully assess whether most mortality is compensatory or additive. We describe selected life-history traits and population characteristics of ungulates useful in parametrizing where populations are in relation to K , thereby allowing for a reasonable harvest despite some uncertainty in population size. We advocate an adaptive-management approach while monitoring those life-history traits to evaluate the suitability of a particular harvest strategy.

ALCES VOL. 56: 15–38 (2020)

Key Words: adaptive management, additive mortality, compensatory mortality, density dependence, harvest metrics, harvestable surplus, harvesting females, life-history characteristics, modeling, prudent management

Humans have engaged in organized hunting for millennia (Hull 1964). In the past 2 centuries, considerable effort has been focused on restoring and conserving populations of wildlife in North America (Leopold 1933, Allen 1954, Trefethen 1975, Bowyer et al. 2019), and conducting research to understand effects of harvest on those populations (McCullough 1979, 2001, Connelly et al.

2012, Monteith et al. 2013). Herein, we define harvest to be the legal and regulated killing of game species by licensed (i.e., authorized) hunters, as typically practiced throughout most of North America, Europe, and parts of Africa. Hunting also incorporates ethical considerations such as “Fair Chase,” whereby hunters must not take an unfair advantage over animals they pursue (Posewitz

1994). Culling—another term for hunting that may not meet those preceding criteria—typically occurs when removals are designed to reduce population size to diminish conflicts with agriculture or to regulate predators (Quirós-Fernández et al. 2017), to combat the spread of diseases (Myserud et al. 2019), or for the removal of individuals with undesirable phenotypic traits (Torres-Porras et al. 2007); these are not subjects of this essay.

Regulation of hunting effort, means of take, seasons, and harvest quotas reflect a biological and ethical approach to harvest management that has been aspired to since Leopold (1933). Indeed, a sound and scientifically based harvest is the benchmark that exemplifies prudent management of wildlife, and is one of seven pillars of the North American Model of Wildlife Conservation (Organ et al. 2010, Mahoney and Geist 2019). Biologists, however, frequently must make harvest recommendations with a limited understanding of population characteristics, often because fiscal constraints hinder intensive monitoring or surveys (Dinsmore and Johnson 2012). In such instances, management decisions must rely firmly on an understanding of the ecology of any species, in addition to data available for a particular area. Managing harvest based on imperfect information might be necessary, but selecting the correct population characteristics on which to base prudent management is essential. Our purpose is to examine populations metrics for large mammals in general, and ungulates in particular, within the context of density-dependent processes. In addition, we clarify how such measurements relate to the reliable and prudent management of ungulate populations.

LIFE-HISTORY CHARACTERISTICS OF LARGE MAMMAL POPULATIONS

Many demographic characteristics exist with which to assess populations of large mammals (Caughley 1977, Williams et al.

2001, Skalski et al. 2005 for reviews). Population dynamics of those species have been widely studied (Schmidt and Gilbert 1978, McCullough 1979, Sauer and Boyce 1983, Skogland 1985, Boyce 1989, 2018, Grøtan et al. 2009, and others). Moreover, life-history traits of large mammals differ markedly from those of small mammals (Caughley and Krebs 1983), and those differences help form the basis for understanding and assessing the population dynamics of large mammals (McCullough 1979, Bowyer et al. 2014).

Large mammals possess numerous attributes consistent with a slow-paced life history. These species exhibit a Type I Survivorship Curve, wherein survival of young initially declines, sometimes markedly (Gaillard et al. 1998), but then quickly approaches an asymptote with survivorship remaining high throughout mid-life, followed by high mortality late in life that is reflected in a precipitous decay of the curve (Deevey 1947). Concomitantly, large mammals exhibit slow development, a delay in age at first reproduction, are iteroparous, possess small litters with large-bodied progeny, are long-lived, provide high maternal investment in young, and exhibit a low intrinsic rate of increase (r) (Stubbs 1977, Gaillard et al. 2000). This suite of characteristics leads to strong density dependence among large mammals not only in their demographics, but also in their population dynamics (Bowyer et al. 2014). Large body size buffers them against environmental extremes, and the slow life-history characteristics result in strong competitive abilities of ungulates compared with small mammals. Further, individuals of species exhibiting density dependence and having long lives may forgo or restrict allocation to reproduction to increase probability of their survival (Monteith et al. 2014a), or tradeoff current against future reproduction (Morano

et al. 2013). These traits should not be considered a dichotomy (i.e., large vs. small mammals); rather, they should be viewed as a continuum across the range of life histories. Moreover, not every large mammal will subscribe perfectly to these life-history traits (Stearns 1977, Kleiman 1981, McCullough 1999). Nonetheless, density dependence resulting from these attributes is the critical factor in understanding and managing populations of large mammals (McCullough 1979, Fowler 1981, Bowyer et al. 2014).

DENSITY DEPENDENCE AND POPULATION CHARACTERISTICS

Unimpeded population growth of density-dependent species typically follows an S-shaped (or logistic) curve of number of individuals over time (Verhulst 1838). This curve, which often is depicted as symmetrical, shows exponential growth up to an inflection point, and then moves toward an asymptote at ecological carrying capacity, K (McCullough 1979). The curve need not be perfectly symmetrical and can include an overshoot of or oscillations around K (McCullough 1999). Nonetheless, this growth curve provides a heuristic framework for understanding the population dynamics of large mammals, so long as it is recognized that some departures from this basic pattern can occur (Fowler 1981, McCullough 1999).

The principal reason the curve of population size over time is S shaped in ungulates relates primarily to nutrition (Fowler 1981, Fowler and Smith 1981). As the population increases, *per capita* availability of food declines, eventually causing negative effects on reproduction and survival; those effects become especially prominent once abundance surpasses the inflection point of the curve (McCullough 1979, 1999, Monteith et al. 2014a). Indeed, several of those traits that characterize large mammals as having a

slow-paced life history change with the size of the population relative to K , including survival of young, age at first reproduction, litter size, and weight of neonates (Albon et al. 1983, Gaillard et al. 2000, Eberhardt 2002, Bowyer et al. 2014). This relationship between population size and K , rather than density *per se*, has critically important implications for population dynamics, because K differs among environments and can change over time. Hence, dynamics of populations at differing densities is dependent on their relation to K (Kie et al. 2003). The ultimate cause of population regulation—food—can vary in complex ways and interact with other factors, such as weather (Mitchell et al. 2015), human disturbance (Lendrum et al. 2012), disease (Eve and Kellogg 1977, Sams et al. 1996), or immune function (Downs et al. 2015). Therefore, care must be taken when interpreting factors other than density dependence to avoid errors in managing populations of ungulates. There is a risk of making such errors by accepting the fit of observations to an explanation as evidence for the correctness of that premise. The danger lies in that those observations may be consistent with other hypotheses; correlation may not reflect causation (McCullough 1979). With respect to ungulates, such correlations may be spurious, because nutritional condition may result in other factors being correlated with but not the actual cause of the observed population dynamics.

Convincing empirical and experimental evidence has documented the widespread occurrence of strong density dependence among ungulates (McCullough 1979, 2001, Sauer and Boyce 1983, Kie and White 1985, Fowler 1987, Boyce 1989, Stewart et al. 2005, Bonenfant et al. 2009, Monteith et al. 2014a), especially for sexually dimorphic artiodactyls. A useful approach for understanding how density dependence underpins population dynamics of ungulates involves

plotting the number of recruits (the number of animals successfully added to the population in a reproductive effort) as a function of population size (McCullough 1979, Fowler 1981; Fig. 1). This parabolic curve illustrates that number of young added to the population is low at extremely low numbers because few adults exist to produce young, and low at high numbers (near K) because few young survive—most young are successfully added to the population at intermediate numbers, a point termed maximum sustained yield (MSY). MSY is the product of population size and recruitment rate, and lies at the peak of the parabola, which also indicates the maximum annual harvest that a population can sustain under a given set of ecological conditions without causing a decline in

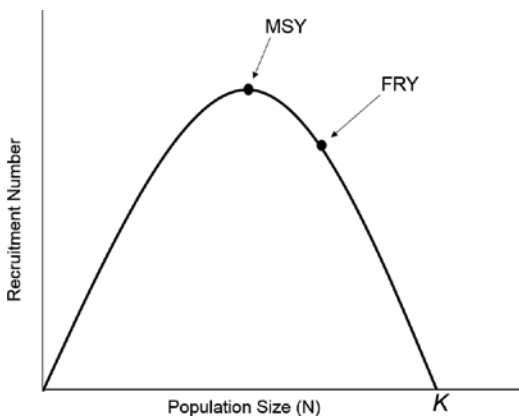


Fig. 1. The parabolic relationship between recruitment number (i.e., the number of young successfully added to the population) and population size for an ungulate population. MSY is maximum sustained yield, which is the maximum harvest (or other mortality) that can be sustained by the population, FRY is a fixed removal yield, and K is the number of individuals that the environment can support under equilibrium conditions (adapted from Bowyer et al. 2014). The yield curve is derived from the near-linear inverse relationship between recruitment rate (young/adult) and population size (McCullough 1979:88, 93; Boyce 1989:84).

numbers (Fig. 1). This model is not fully age structured and considers only adults and young. The assumption is that recruited young compensate for adults removed in the harvest. Consequently, the age structure of the population becomes younger with an increasing harvest that reduces population size relative to K (Bowyer et al. 1999).

The concept of ecological carrying capacity (K) is central to understanding density dependence (McCullough 1979). Traditionally, K has been defined by the number of animals that a particular environment can support at equilibrium (Caughley 1977, McCullough 1979), a concept that is reflected in the conceptual models we present. Long-term changes in K (either increases or decreases) can be brought about by perturbations to habitats, including via mechanical manipulation, fire, climate change, grazing, or population overshoots of K (Klein 1968, Bleich and Hall 1982, Kie et al. 2003, Holl and Bleich 2010, Holl et al. 2012, Berger et al. 2018). Short-term changes in K also occur. For example, temporary variation in productivity or winter severity can alter the extent of density-dependent processes in any particular year (Loison and Langvatn 1998, Bowyer et al. 2014, Monteith et al. 2014a). Although average population size may decrease with a fluctuating K (Boyce and Daley 1980), the effect of those interannual shifts in K is comparatively modest relative to those brought about by large perturbations to the environment.

Harvest of ungulates is sustainable, in part, because of their density-dependent attributes (Kokko 2001, Bowyer et al. 2014, 2019). Harvest reduces population size, resulting in increased availability of food on a *per capita* basis. In situations when populations become increasingly food limited as they exceed MSY and approach K , heightened nutrition that follows reductions in population size can increase survival,

fecundity, or both, and thereby compensate for animals harvested (Owen-Smith 2006). Density-dependent responses to reduced population size include increased survival of young (Eberhardt 2002, Bonenfant et al. 2009, Monteith et al. 2014a), large body mass of neonates (Keech et al. 2000), and enhanced rates of growth (McCullough 1979, Schmidt et al. 2007, Monteith et al. 2018). In addition, large litter sizes (Keech et al. 2000, Hanson et al. 2009), rapid growth to large body size (Monteith et al. 2009), high pregnancy rates (Stewart et al. 2005), and early age at first reproduction (Monteith et al. 2014a, Jensen et al. 2018) are associated with a high nutritional plane typical of a population well below K , whether from harvest or other causes (Gasaway et al. 1992, Hayes et al. 2003). Those density-dependent responses facilitate resilience to harvest and promote persistence of hunted populations of ungulates (Bowyer et al. 2019).

THE HARVESTABLE SURPLUS AND DENSITY DEPENDENCE

Leopold (1933) proposed the concept of the harvestable surplus—populations of most animals produce more young than are necessary to ensure persistence. Accordingly, that excess could be harvested without adversely affecting the population. This idea may be particularly relevant for species with comparatively fast-paced life histories. Those species exhibit J-shaped growth curves, are especially sensitive to annual variation in weather, and exhibit no evident relationship between population density and mortality. Hence, for those density-independent species, the number of surplus animals in a particular year determines the harvest (Leopold 1933, Errington 1945). Those animals constitute Leopold's "doomed surplus"—death might occur from a variety of causes, including harvest, but remaining animals allow the population to rebound the

following year with few adverse effects from harvesting the surplus individuals (Leopold 1933). Populations of many upland game birds are limited by primarily by weather (Perkins et al. 1997, Flanders-Wanner et al. 2004, Terhune et al. 2019), and management often follows this harvest paradigm. Many organisms can have density-dependent components to their life histories (Sibly et al. 2005), even for species with fast-paced characteristics. The essential question is whether population density or weather-related events primarily regulate their populations.

McCullough (1979) contended that the concept of a harvestable surplus was of limited value in understanding the harvest of highly density-dependent species, which includes most ungulates. The principal conceptual difference between harvest paradigms is that for density-independent species the surplus determines the harvest, whereas for density-dependent species the harvest determines the surplus. For animals exhibiting a strong influence of density dependence (i.e., characterized by marked changes in vital rates under changing densities relative to K), the harvest, through its effects on abundance, becomes a determinant of the surplus in subsequent years (Fig. 1). Progressively increasing the harvest (thereby reducing the population) along the x-axis of population size from K toward MSY in Figure 1, theoretically results in an increase in the number of young recruited into the population until population size falls below MSY—harvest is regulating the surplus. Convincing empirical data support this premise (McCullough 1979).

Leopold's (1933) concept of a harvestable surplus is inadequate for managing density-dependent species, because recruitment of young when the population is near K would be low, and there would be little surplus (Fig. 1). Decreasing harvest to account for that poor recruitment ultimately would

be counter-productive, with the result that the population remains near K and again exhibits poor recruitment the following year, even though harvest might have been reduced with the expectation that it would compensate for poor recruitment. The best outcome from such management is a loss of hunting opportunity; the worst is a population in poor physical condition, with small-bodied individuals that are more likely to succumb to adverse weather or other maladies such as predation or disease (Bowyer et al. 2014). Harvests that reduce the population well below MSY also will diminish recruitment (Fig. 1). Managing populations below MSY is unlikely to be sustainable. Unless the intent is a large reduction in population size, such management can be risky because of the vagaries of dealing with small populations (Lande and Barrowclough 1987). Judging where the population is with respect to K will be addressed later.

COMPENSATORY VERSUS ADDITIVE MORTALITY

Another attribute of populations of large mammals that can muddle interpretation of data needed for prudent management is the shifting pattern of compensatory and additive mortality (Errington 1946). Compensatory mortality occurs when one source of mortality compensates for another (e.g., animals killed during hunting season would have died anyway from harsh winter conditions or predation—Bartmann et al. 1992, Boyce et al. 1999). With additive mortality, sources of death are summed (e.g., animals killed by hunters would be added to those dying from other causes, but in the absence of harvest would not have otherwise died). Additive mortality varies with the dynamics of ungulate populations and the proximity of those populations to K (McCullough 1979, Bowyer et al. 2014, Monteith et al. 2014a).

Females that exist in populations at low to moderate numbers with respect to K tend to be in excellent nutritional condition (McCullough 1979, Monteith et al. 2014a); attempts to recruit young into the population often are successful, because they have the necessary resources to complete gestation and provision young—food is not limiting (McCullough 1979; Fig. 2). As the population increases toward K , however, intraspecific competition intensifies and *per capita* availability of food diminishes. With increased competition and fewer resources, nutritional condition of females declines, resulting in lower recruitment of young into the breeding population (McCullough 1979, Bishop et al. 2009, Bowyer et al. 2014; Fig. 2). At those higher numbers, females attempt to rear more offspring than the environment can support; these are young that might perish from a variety of sources, but irrespective of the cause of mortality, they are destined to die—mortality is compensatory (Fig. 2). In some situations, compensatory mortality also can occur as a result of seasonally determined processes of density dependence (Boyce et al. 1999). Harvest may not influence spring breeding or pre-harvest numbers of animals. With “seasonality,” density dependence following harvest can increase seasonal abundance or annual survival, resulting in compensatory mortality. This outcome occurs via the interaction between reduction in size and the density-dependent response of the population (Boyce et al. 1999).

A critically important consideration is that ungulate populations undergoing additive effects of mortality tend to be those at low density with respect to K , with mortality becoming increasingly compensatory as population size and, thus, nutritional limitation increases (Monteith et al. 2014a). For populations near K , predators killing young is less of a concern, and there is no need to reduce the

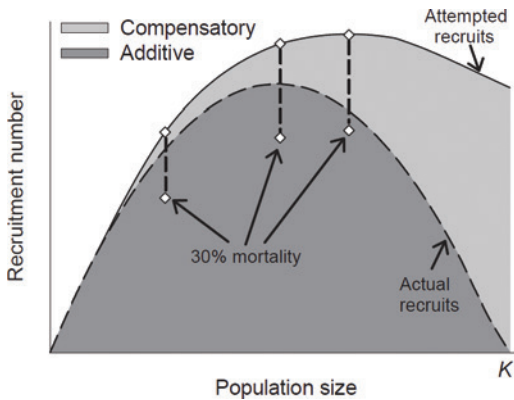


Fig. 2. Changes in number of successful recruits, as well as unsuccessful attempts to recruit, in relation to increasing size of an ungulate population. Females attempt to add more young to the population than can be sustained by the environment as a function of its carrying capacity (K). Note that mortality becomes increasingly more compensatory (one source of mortality substitutes for another) as the population approaches K . In contrast, a similar level of mortality becomes increasingly additive (one source of mortality is added to another) as populations size backs further away from K , because the number of young that females attempt to recruit approaches the number they can recruit given improvements in nutrition (adapted from Monteith et al. 2014a). Prescribing a 30% harvest, for example, results in mortality that varies in its distribution between successful and attempted recruits as the population changes in size.

size of the planned harvest to compensate for other sources of mortality (Fig. 2). Additive and compensatory mortality, however, do not represent a discrete dichotomy. Notice how prescribing a 30% harvest, for example, induces mortality that varies in its distribution between successful and attempted recruits as the population changes in size (Fig. 2). These differing patterns of mortality also mean that predator control near K is unlikely to enhance survival of young, whereas such control may be justified at lower population sizes where mortality is additive (Bowyer et al. 2013, 2014).

DENSITY DEPENDENCE, WEATHER, AND POPULATION MODELING

Populations of wildlife have been modeled using a variety of approaches (Lack 1954, Starfield and Bleloch 1986, Royama 1992, Caswell 2001, MacKenzie et al. 2006, and others). Kokko (2007) recommended the inclusion of density dependence in population models; failing to do so results in a less-general model, which reduces the usefulness of that approach, especially for large mammals. Indeed, a sustainable harvest is not possible without incorporating the concept of density dependence (Mendelsohn 1976). Numerous reasons exist why density-dependence can be difficult to measure (McCullough 1990, Bowyer et al. 2014), and outcomes from density-dependent processes may be counter-intuitive (e.g., harvest potentially increasing the number of recruits; Fig. 1). Nonetheless, incorporating density dependence is essential to building harvest models, no matter how tempting it might be to construct simpler models based on variables that are easier to measure.

In highly stochastic environments, food resources available during any particular year may vary widely (Mackie et al. 1990, Marshal et al. 2005, Heffelfinger et al. 2017). Hence, capacity of the habitat to support large herbivores can vary annually, creating what could appear to be an absence of density dependence when density itself displays no obvious relationship with nutritional or demographic variables (McCullough 1999). Density dependence, however, remains firmly in operation because resources available *per capita* are a function of both population abundance (i.e., density) and the availability of food within a particular year (McCullough 1990, Monteith et al. 2014a). Consequently, a seemingly absent short-term relationship with density does not necessarily imply an absence of density dependence (McCullough 1990, Kie et al. 2003).

One shortcoming of basing models for ungulates solely on density-independent variables, such as rain, snowfall or temperature, is that those variables can interact with population density of animals in relation to K (Monteith et al. 2014a). Ungulate populations close to K will be in poor nutritional condition, and weather is likely to help or hinder those individuals disproportionately compared with animals existing at lower numbers where their physical condition is good (Bowyer et al. 2014 for review). At sufficiently high numbers relative to K , density dependence may outweigh even density-independent events that might be beneficial (Stewart et al. 2005). Conversely, severe weather, such as extreme drought, may be overridden by effects of increased nutrition related to reduced population numbers (Thalmann et al. 2015). Furthermore, body mass of reindeer (*Rangifer tarandus*) was more important than spring phenology in determining production of young in a severe arctic environment, largely because of carry-over effects from reserves accumulated in previous seasons (Veiberg et al. 2016).

Spurious correlations between weather and fitness components such as pregnancy, young recruited, and survival can exist for density-dependent species and may lead erroneously to the conclusion that weather, rather than population size, is regulating a population, especially for populations near K . Incorporating density-independent variables for ungulates based on such misconceptions can result in models that will not cope with variation in population size relative to K . In this example, weather metrics, including winter severity, are lurking variables (i.e., those that are correlated with the variable of interest but are not its primary cause), and their misinterpretation can lead to the mismanagement of populations. As in our previous example, reducing harvest because of a perceived effect of weather—such as

from high snowfall or severe drought for a population near K —would result in the loss of potential hunting opportunity, and poor recruitment again the following year because the population remained near K . We concede that there are rare weather events that kill animals without regard to their physical condition (Bleich and Pierce 2001, O’Gara 2004, Bleich 2018), but such events cannot be common or few animals would persist in those environments.

We argue that the starting point for models and tests of hypotheses concerning the population dynamics of ungulates should begin with the key assumption of density dependence. We further propose that results from correlational studies implicating weather as a cause of changes in demographic traits be viewed with care and skepticism, in the absence of ascertaining the position of the population in relation to K . This is a critical point in selecting which metrics to use in evaluating effects of harvest.

ROLE OF THE SEXES AND HARVEST OF FEMALES

Sexual segregation—the differential use of space, forage, or habitat by the sexes outside the mating season—occurs widely among polygynous ungulates (Bowyer 2004). Ungulates exhibit primarily polygynous mating systems, wherein relatively few large males are necessary to inseminate females within a population (Darwin 1872, Geist 1974). Increased polygyny intensifies male-male competition for mates, which in turn has led to the evolution of increased sexual dimorphism in body size and weapons (Geist 1966, Weckerly 1998, Loison et al. 1999, Emlen 2015). Avian models, which ascribe sexual dimorphism to intersexual competition, do not suffice for mammals (Ralls 1977).

Spatial segregation of the sexes tends to be most pronounced near and following parturition, when provisioning of young is

critically important, and neonates are most vulnerable to predation (Bowyer 2004). Indeed, differences in body size between sexes of ungulates foster intersexual disparities in susceptibility to predators, with females and young being more vulnerable than adult males (Berger 1991, Bleich et al. 1997, Bowyer et al. 2001). Avoidance of predators by females and neonates can result in marked differences in behavior (Bleich 1999) and their resultant use of space compared with males and nonparturient females (Barten et al. 2001).

In addition, sexual dissimilarities in digestive morphology and function occur, and also can explain sexual segregation in ruminants based on the allometry of metabolic requirements, minimal food quality, and retention of digesta (Barboza and Bowyer 2000, 2001). Adult males eat abundant forages high in fiber, because ruminal capacity prolongs retention, and consequently allows greater use of fiber for energy than in females (Fig. 3). Females, which typically are smaller-bodied than males, are better in postruminal digestion of forage, especially when energy and protein requirements needed for reproduction increase (Monteith et al. 2014b). Lactating females also increase rumen size, as well as the length and width of rumen papillae beyond that of nonreproductive females (Zimmerman et al. 2006). Increased nutrient requirements of pregnant females, including the costs of remodeling their digestive tracts to facilitate lactation, underlie differential use of habitats and forages and can lead to sexual segregation (Barboza and Bowyer 2000, 2001). Although a number of hypotheses have been forwarded to explain sexual segregation, predation (Bleich et al. 1997) and the gastrocentric model (Barboza and Bowyer 2000, 2001) are the prevailing views concerning how this phenomenon relates to the spatial ecology of ungulates (Stewart et al. 2011 for review).

Males and females may partition space at fine scales in species such as white-tailed deer (*Odocoileus virginianus*), or large scales as in moose (*Alces alces*) (McCullough 1979, Stewart et al. 2003, Oehlers et al. 2011). Increasing population density (i.e., the number of individuals relative to K) results in greater overlap in the distribution of the sexes and a reduction in degree of sexual segregation (Stewart et al. 2015), but with that overlap comes a divergence in diets of males and females (Kie and Bowyer 1999, Schroeder et al. 2010). The upshot is that males and females avoid competing for resources, and arguably should be managed as if they were separate species (Bowyer 2004), including developing separate management plans for the sexes. Consequently, the harvest of males does little to promote population productivity when compared with the harvest of females (McCullough 1979). For sexually dimorphic ungulates, harvesting males to such low numbers that females might not be fertilized occurs infrequently (Schwartz et al. 1992, Laurian et al. 2001). A particularly heavy harvest of males will reduce their age structure, and thereby reduce the size of males and their horn-like structures (Jenks et al. 2002, Monteith et al. 2013).

Throughout most of North America, harvest of female ungulates is either rare or limited but varies by species and area (Monteith et al. 2013, 2018). Management paradigms typically have focused on the harvest of males, ostensibly because of the low-risk and conservative approach that male harvest offers for maintaining population size. Mysterud et al. (2002) provides insights into how the harvest of males might affect population dynamics. Nonetheless, a male-biased harvest is expected to have a negligible influence on population dynamics (Freeman et al. 2014), because abundance of males has little effect on nutrition of females, and thereby recruitment of young (McCullough

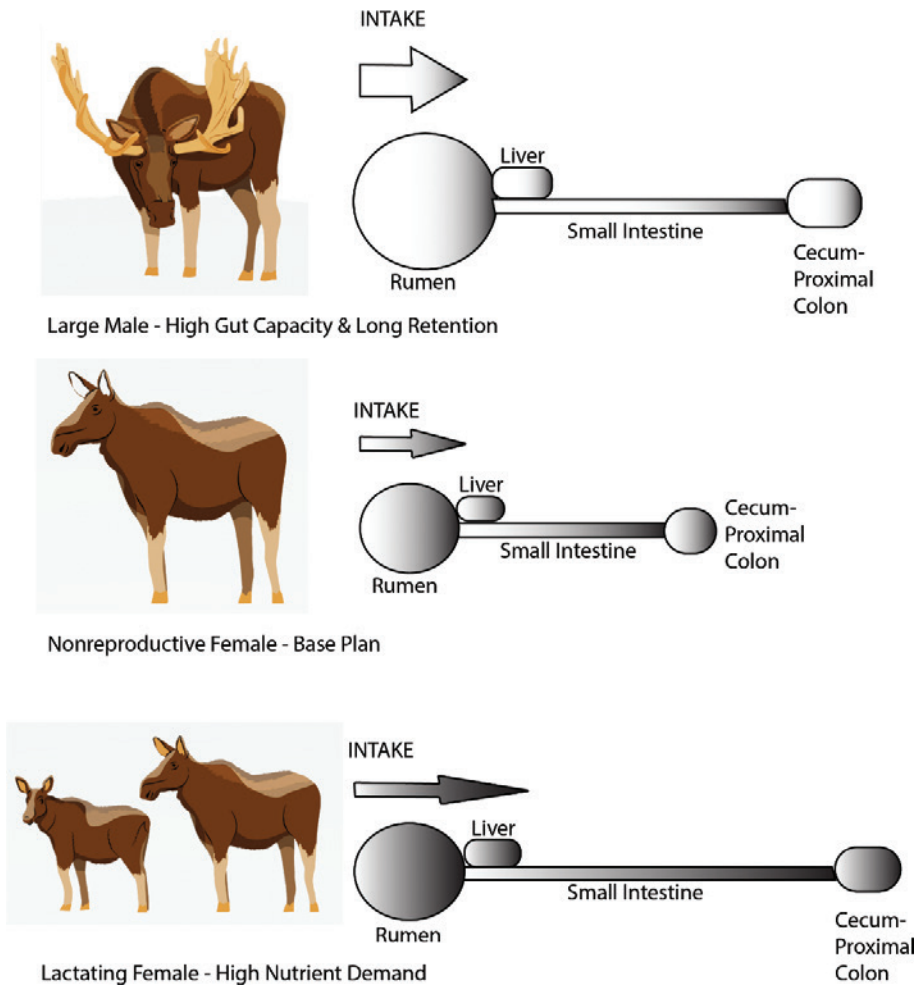


Fig. 3. Model of intake and digestive function in nonreproductive females (middle) compared with large males (above) and lactating females (below). Width of arrows reflects amount of food intake, length of arrows indicates rate of digesta passage, and shading indicates density of nutrients in food. Diagrams of the digestive tract are stippled to reflect potential changes in fibrosity of food for males and increases in post-ruminal size and function of lactating females (modified from Barboza and Bowyer 2000, Zimmerman et al. 2006).

1979, 2001, Monteith et al. 2018). Indeed, harvest that only targets males can have little controlling influence on population sizes except under exceptionally high rates (McCullough 1979, Milner-Gulland et al. 2003), and primarily only influences the age structure of males in the population.

Harvest of females may provide an important, yet undervalued and underused, management tool for regulating density-dependent

processes for many ungulate populations by holding population numbers below K (Monteith et al. 2018). Females play the predominant role in the dynamics of most ungulate populations. Consequently, harvest of adult females can allow managers to manipulate population sizes to decrease nutritional limitations and competition for resources (McCullough 1979, 2001, Solberg et al. 2002, Doak et al. 2016).

Further, when maintaining or increasing size of secondary sexual characteristics (i.e., horns, antlers, or pronghorns) in males is a management objective, harvest of females may be an effective management option (Monteith et al. 2018). As *per capita* resources decline with rises in population size, females are limited in the resources they can allocate to offspring (Festa-Bianchet and Jorgenson 1998, Monteith et al. 2009), and females that are in poor condition will produce sons that have smaller bodies and smaller horn-like structures that can persist into adulthood (Festa-Bianchet et al. 2004, Solberg et al. 2004, Monteith et al. 2009, 2013, 2018). Another strategy for increasing the size of horn-like organs is allowing males to reach the age of asymptotic body growth prior to harvest (Stewart et al. 2000, Jenks et al. 2002, Monteith et al. 2009).

Although maintaining populations at or near K may be viewed as an ideal management outcome when considering only animal abundance, if management goals are aligned with increased nutritional condition or large horn-like structures, maintaining populations at a moderate population size via female harvest can result in a productive and more stable population with a greater yield of large males (McCullough 1978, Monteith et al. 2018). Predation also has the potential to hold ungulate populations at densities well below K (Gasaway et al. 1992, Hayes et al. 2003). The role of K in understanding predator-prey dynamics and its relevance to management has been discussed elsewhere (Person et al. 2001, Bowyer et al. 2005).

METRICS FOR HARVEST

Many methods exist to estimate abundance and trends of animal populations (Krebs 1998, Maier et al. 2005, Ryan 2011, Pierce et al. 2012a for reviews), most of

which entail considerable expense, time, and sometimes risk (Boyce 2012). Our approach has been constrained chiefly to understanding harvest metrics; thus, we will focus on harvest-based characteristics that provide information concerning populations.

Among methods for estimating population size from harvest are population reconstructions (i.e., cohort analysis) (McCullough 1979, Bowyer et al. 1999, Ueno et al. 2009), and catch-per-unit-effort (CPUE), which in addition to other shortcomings, requires the size of a population to be reduced sufficiently to observe changes over time (Bishir and Lancia 1996, Bowyer et al. 1999, Schmidt et al. 2005). Those methods, however, may require several years to parametrize equations necessary to estimate population size. We contend that specific attention to understanding the position of population abundance in relation to K offers another potential and more immediate approach for managing populations of ungulates.

Sophisticated metrics, such as a reliable estimate of population size, may not be necessary for management purposes, although most managers would welcome such detailed information. We maintain that prudent management of ungulate populations relies on one critical point—knowing where the population is in relation to K . The importance of that knowledge is illustrated by considering a harvest strategy termed the fixed removal yield (FRY) by McCullough (1979), which results in a population being on the right-hand “hump” of the recruitment parabola (Fig. 1). A harvest at this level is the near-maximum harvest that a population can sustain without causing a decline in numbers, but is less than the maximum harvest (MSY) to avoid an inadvertent overkill. Moreover, such a harvest would be buffered by compensatory mortality (Fig. 2). An identical amount of sustained harvest applied to

a population on the left-hand side of the parabola would drive a population toward extirpation (Fig. 1). If the objective is a high yield, managing for FRY is prudent. Nevertheless, without some benchmark to identify K , applying such a harvest strategy can be precarious.

Estimating K can be a daunting proposition. Regression methods of plotting recruitment rate over population size can be used to estimate K , but that technique tends to overestimate K , and may entail many years of data collection (McCullough 1979, Bowyer et al. 1999). Forage-based models (Hobbs and Swift 1985, Beck et al. 2006) for estimating K have been developed but are labor intensive; forage measurements also may lag declines of large herbivores. Other methods (Boyce 1989, Forsyth and Caley 2006) exist to determine K , but those approaches require large data sets and can be costly; again, years may be needed to obtain the information necessary to parameterize those models (Bowyer et al. 2005, 2013, Monteith et al. 2014a). Issues related to the conservation and management of ungulates likely would have been decided before many of the aforementioned models could be developed (Bowyer et al. 2013). In addition, habitat or environmental changes might have occurred, potentially invalidating conclusions from the resulting models.

Monteith et al. (2014a) proposed the use of “animal-indicated nutritional carrying capacity” (NCC), and identified methods necessary to parametrize that metric. NCC is based on the nutritional condition of individuals comprising a population when $r = 0$ (i.e., no population change). Animals in poor nutritional condition infer a population near or above NCC—where resources sufficient to sustain good body condition are not available. A population consisting of individuals in relatively good nutritional condition typifies a population below NCC, where

resources exist to support population growth (Monteith et al. 2014a). This approach offers a workable means for assessing NCC and tracking the status of populations over time. Although, this approach was developed for mule deer (*O. hemionus*), NCC should be a concept useful for managing numerous species of ungulates, in part, because it allows for interannual variation in K .

The life-history characteristics and population parameters in Table 1 provide a conceptual framework with which to assess the nutritional status of ungulate populations and calibrate their relationship to MSY and K . These variables change with the size of a population relative to MSY and K , and can be used to help assess effects of harvest. Knowing the size of a population may not be essential for management purposes—what is needed is an understanding of where the population is in relation to K . Moreover, ungulate populations exhibit a sequence of changes in life-history traits that tend to be modified as the population approaches K . The most sensitive of those characteristics is declining recruitment of young, followed by increasing age at first reproduction, declining litter size, lower rates of pregnancy, and finally diminishing adult survival (Gaillard et al. 2000, Eberhardt 2002).

Care should be taken to collect appropriate data concerning multiple metrics to ensure a reliable assessment of the status of a population. For example, young to adult ratios commonly are used to index population productivity. Interpretation of such ratios are inherently chancy, however, because of their double-variable nature (Caughley 1974, Theberge 1990, Person et al. 2001, Bowyer et al. 2013). Nevertheless, ratios are tempting to use because they are readily obtainable (Bowyer et al. 2013), and because mortality in adult females should be relatively constant given the Type I Survivorship Curve of ungulates (Deevey 1947). Nonetheless,

sufficiently strong density-dependent mechanisms can adversely affect adult survival (Pierce et al. 2012b). A situation in which both adult females and young were decreasing would result in a ratio indicative of a population that was unchanged, when the population was in decline. If survival of adult females were known, however, the ratio could be interpreted (Monteith et al. 2014a), but those data would require additional monitoring of survival of adult females instead of merely sampling ratios. Caughley (1974) warned that the use of such ratios could be problematic without some indication of population size and trajectory, and if r were known, the ratio would be superfluous; others have echoed similar concerns for ratio data (Theberge 1990, Person et al. 2001, Bowyer et al. 2013). We contend that measures of animal condition and related metrics (Table 1) offer a stronger basis for prudent management so long as several variables (Table 1) are considered in concert. We make no specific recommendations on which metrics in Table 1 to employ to accomplish that goal—those would be a function of the species under consideration and which variables might be collected most effectively and economically. Likewise, we make no recommendations as to where to manage an ungulate population in relation to K . Such management decisions are both socioeconomic and biological in nature, and likely vary with the objectives or responsibilities of the management agency. We do, however, provide the background to interpret the likely biological outcomes from such management decisions.

ADAPTIVE MANAGEMENT

Several studies of density dependence in ungulates have been based on experimental manipulations of density over large areas with free-ranging animals (McCullough 1979, 2001, Stewart et al. 2005); such

research allows for much stronger inference concerning cause and effect than from observational or correlative studies. Moreover, the use of a hypothetico-deductive approach provides a rigorous framework for testing predictions, including those concerning density dependence, because that approach allows for falsification (Popper 1959). Illogic ensuing from observational or correlative studies that rely solely on inductive reasoning can fall victim to Popper's white-swan fallacy—no number of sightings of white swans can verify the hypothesis that all swans are white, because the observation of a single black swan falsifies that premise (Popper 1959).

When more in-depth research is possible, critical tests of properly framed hypotheses will answer questions about *why* particular phenomena occur, and hold the potential to be generalizable, thereby yielding an overall understanding and greater certainty in processes underpinning population regulation. Less-general tests, focused on questions about *what* happened, inevitably will be narrow in nature and scope, and necessarily will require repeated testing to judge the importance of a phenomenon. These patterns are particularly germane to understanding population dynamics of ungulates. Hypotheses that consider harvest within the broad framework of density-dependent processes are likely to provide a sound understanding of population dynamics and yield prudent management. Studies that assess only a few environmental factors related to productivity are too restrictive and too narrow to provide a reliable understanding of population dynamics, and offer, at best, a chancy tactic for management. Yet, hypothetico-deductive tests stemming from in-depth research are not always possible.

Adaptive management has been advocated as a method for dealing with the presence of uncertainty in biological systems

(Walters and Hilborn 1978, Westgate et al. 2013). The harvesting of ungulate populations clearly holds a degree of ambiguity given that biologists often must set management objectives with limited information concerning the status of populations (Dinsmore and Johnson 2012). Where more structured and reliable data related to population dynamics are unavailable because of time or expense, we suggest that varying the harvest of females and monitoring selected life-history characteristics and related metrics (Table 1) can resolve the status of a population relative to whether the harvest is sustainable, and thereby result in prudent management decisions. Also, the sequence in which those life-history traits are observed can provide insights into where the population is relative to K . A similar approach has been used for adaptive management of stock-recruitment curves for fisheries (Smith and Walters 1981).

There are several caveats to this approach. Not all density-dependent variables increase linearly with population size,

including population growth and recruitment of young into the population. Further, the parabolic relationship between recruitment number and population size may not be symmetrical (McCullough 1999, Sibly et al. 2005). Nonlinearities can confound interpretation needed for adaptive management particularly when linear responses were expected. For instance, a harvest of females that initially resulted in increased recruitment of young, might eventually cause a decline in recruitment if that harvest exceeded MSY (Fig. 1).

Maternal effects are widespread in cervids (Freeman et al. 2013) and might further confuse interpretations from employing an adaptive-management approach. Body size and antlers of young white-tailed deer took several generations to respond to enhanced nutritional condition of their small mothers (Monteith et al. 2009). Moose that were born small relative to larger offspring failed to compensate in size over time (Keech et al. 1999), whereas young caribou (*R. tarandus*) did compensate (Dale et al. 2008).

Table 1. Variation in life-history and population characteristics of ungulates in relation to the proximity of the population to MSY (maximum sustained yield) and K (ecological carrying capacity) (modified from Bowyer et al. 2014).

| Life-history and populations characteristics | \leq MSY | Near K |
|--|-------------|--------------|
| 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 ^b | Additive | Compensatory |
| Diet quality | Higher | Lower |
| Population age structure | Younger | Older |
| Age at extensive tooth wear | Older | Younger |

^aSome species of ungulates may exhibit limited variability in particular characteristics.

^bAdditive and compensatory mortality would be inferred from other variables in this table.

Further uncertainty in interpreting population dynamics may be caused by delayed density dependence, wherein recruitment is lagged further than expected following harvest (Fryxell et al. 1991, Lande et al. 2006). Deteriorated rangelands may take time to recover from overgrazing or other perturbations (Heady 1975), and ungulate populations inhabiting such ranges may not respond immediately to harvest in the expected manner. In addition, interspecific competition holds potential to lower K for sympatric ungulates (Stewart et al. 2002), and some large carnivores can regulate ungulate populations at densities below K (Gasaway et al. 1992, Tatman et al. 2018). Diseases and parasites likewise can affect populations of large mammals (Cassirer and Sinclair 2007, Jones et al. 2017). Provided that managers are mindful of these caveats, the variables in Table 1 offer a useful method for judging where the population is with respect to K , and thereby determining harvests without requiring estimates of population size. Clearly, an adaptive management approach offers many strengths for prudently managing ungulate populations, but being knowledgeable, observant, and patient is necessary.

CONTEXT AND CONCLUSIONS

The conservation of mammals worldwide is a pressing concern (Ceballos and Ehrlich 2002). Unregulated or illegal hunting continues to be a threat to the conservation of some mammals, especially in underdeveloped countries (Van Vliet et al. 2015). Terrestrial families within the *Certartiodactyla* (i.e., the even-toed ungulates) are especially vulnerable to threats to their existence (Bowyer et al. 2019). Ungulates possess life-history traits that make them more susceptible than other mammals to extinction, including large body size and slow-paced life histories (Cardillo et al. 2005). Based on the IUCN Red List, threats to mammals from

hunting still exist (Bowyer et al. 2019). Many of those threats, however, concerned the historical depletion of a species, or illegal killing; nowhere is legal and regulated recreational hunting of mammals recognized as a threat (Bowyer et al. 2019).

In North America, Europe, and parts of Africa, hunting has been the foundation for successful programs to ensure conservation of critically important habitats or to restore wild populations (Geist 1995, Organ et al. 2010, Krausman and Bleich 2013). Selecting the best metrics for managing the harvest of ungulates is a refinement of existing management practices and a critically important step in their scientific stewardship, but this procedure needs to be viewed in the proper context. Today, in North America and Europe, populations of wild mammals are thriving, and legal hunting remains not only a cornerstone to financial return in support of their persistence, but also a useful tool to regulate their abundance at either ecologically or socially acceptable levels (Organ et al. 2010).

ACKNOWLEDGEMENTS

We thank J. A. Jenks, C. D. Mitchell, and M. S. Boyce for their helpful and insightful comments on our manuscript. This is Professional Paper 129 from the Eastern Sierra Center for Applied Population Ecology.

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