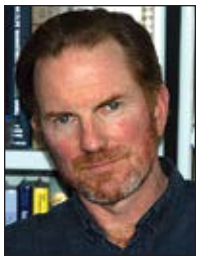
THE HARVESTABLE SURPLUS CONCEPT REVISITED



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Nearly 100 years ago Aldo Leopold, the father of game management, coined the term "harvestable surplus." The intended meaning of the term is that some wildlife species and populations may produce more young in a given year than can survive to the following year. Those individuals doomed to die over the winter, for example, represent the "surplus" in the population. Leopold observed that those surplus animals could be killed by hunters during the fall, instead of succumbing to winter mortality, and there would be little impact on the population. So, in theory, hunting would be sustainable because the population would not change.

My overly-simplistic explanation of this concept is, for better or worse, dogma in many hunting circles. I'm sure most readers are quite familiar with the concept. The problem is that this concept applies only to certain kinds of species under certain circumstances. Leopold based his concept largely (but not solely) on observations of ruffed grouse and bobwhite quail—species that are relatively short-lived, reach breeding age relatively young, and produce large broods.

Under the concept of a harvestable surplus, hunting mortality compensates for "natural" mortality. Compensatory mortality has been the objective of many hunting programs intended to sustain harvests year-in and year-out. It has often been associated with ungulate hunting, but as professional members Dr. Terry Bowyer and Dr. Vernon Bleich and colleagues have documented in a recent paper in the journal *Alces*, basing ungulate hunting management on the premise that animals harvested are surplus is a flawed approach.

Most ungulates, particularly members of the deer family, tend to be large-bodied, longer-lived, produce relatively few offspring, and have relatively higher survival than game birds. The assumptions inherent in the harvestable surplus concept do not bear out with ungulates, for the most part. Determining whether a moose harvest was, is, or would be compensatory to natural mortality, versus additive (adding to what would have been the natural mortality in lieu of hunting) requires data that are difficult and costly to obtain, if not near impossible. What Bowyer and Bleich, et al., maintain is an entirely different concept that is more appropriate.

The million dollar question that wildlife biologists hate to be asked: "How many [deer, elk, moose, pronghorn] are there in our state?" This is an impossible question to answer with any precision; providing estimates with narrow confidence intervals requires lots of data and work—and the number is not static. Fortunately, in managing ungulates, it is not necessary to know this (although biologists would love to know). What is more important, and this is the gist of Bowyer and Bleich's paper, is estimating where the population is relative to carrying capacity (typically defined as the number of animals that a particular environment can support at an equilibrium).

Carrying capacity, or *K*, itself is difficult to estimate for a number of reasons, including the fact that it varies over time and space. However, there are metrics that when estimated, can help in determining where a population is in reference to carrying capacity.

First, there are two terms that are key to this and are foundational to Bowyer and Bleich's analyses.

Density dependent: This describes species that exhibit changes in demographics and population dynamics based on the density of the population. Ungulate and other large mammal populations exhibit density dependent responses.

Density independent: These are factors that affect a population regardless of its density, such as catastrophic weather events. Some game bird species may be more vulnerable than ungulates to density-independent effects, such as severe spring rains that can cause losses of entire broods.

What drives ungulate populations is the availability and quality of food resources. At low densities, food is more available per capita than at high densities. Lower density ungulate populations are expected to be in better physical condition, produce more offspring, and have higher survival than high density populations in the same environment. As the density of a population increases, it closes in on, or maybe exceeds *K*, resulting in poorer physical condition and body size, lowered reproduction, older age

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structure, and increased mortality. Theoretically, harvest of ungulates at high population densities reduces the density, and more food per capita becomes available, resulting in increased reproduction and fitness of the population. This is the essence of why harvest of ungulate populations is sustainable.

Getting back to the concept of harvestable surplus, Bowyer, Bleich, and colleagues make a powerful point: The surplus determines the harvest for density-independent species, while the harvest determines the surplus for density-dependent species. What this means is that for a species like ruffed grouse that is more vulnerable to density-independent effects, good weather and abundant forage can result in high survival of offspring leading to a higher harvest (surplus) the following fall, whereas a high harvest of a deer population near *K* that reduces density and increases reproduction will result in a future "surplus."

I've only touched the tip of the iceberg of what Bowyer and Bleich have covered in their excellent paper. A critical facet that relates to managing ungulate harvest that they emphasize is the relationship of recruitment number (number of young recruited into the population) to population size relative to *K*. Graphically, this represents a parabola, or upside-down U with the legs stretched out. The highest part of the parabola representing highest recruitment should be when the population is at 60 percent of *K*. When an ungulate population is less than that, harvest should be conservative, as it could become additive to natural mortality and not result in a surplus. When the population is at 60 percent or higher, harvests can be more liberal, and productivity is more likely to increase, resulting in a surplus.

Bowyer, Bleich, and their colleagues provide guidance on what metrics will best enable wildlife managers to assess where ungulate populations are relative to *K*, so that ideally, harvests will provide a surplus and those surpluses can continue to be harvested. Thanks to Drs. Bowyer, Bleich, and their colleagues for their continued efforts to enhance ungulate management! ■