# Carrying Capacity: A Primer

The following will seem overly pedantic to most ecologists and wildlife biologists. However, I have heard the term "carrying capacity" and its relative "overgrazing" used carelessly in many public meetings and in high places such as commission meetings and sessions of legislative committees. Consequently, I believe a simple review of the concept is necessary, at least to inform the general public, lest they accept misleading and shallow arguments, often used to propose management for public resources.

I use an old, simple graphic illustration or model of population dynamics. One of its names is the "logistic model". It is not realistic in that it assumes a stable environment, rare at best in the real world. Moreover, the model is focused on a single species population. The complexities of multi-species systems are beyond this discussion. It has been said that, "All models are wrong; but some are useful." This is one of the useful models. Thinking first in simple terms is necessary for dealing with complexities of the real world. Moreover, I am avoiding mathematical rigor in favor of communicating concepts of the model in the most easily understood way.

If we assume a population of animals is newly introduced with a few animals into a limited, stable and suitable environment the growth of the population over time would look like (A).
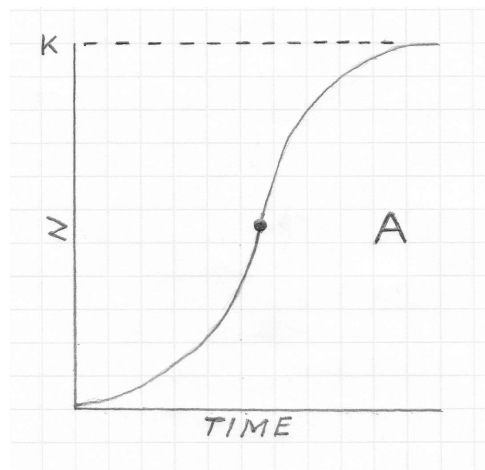
At first the population grows at an accelerating rate (more animals are added each successive year), up to the black dot, which is the inflection point. Beyond the inflection point, the population grows at a decreasing rate (fewer animals are added each successive year). Eventually, the population stabilizes at "K", often termed "ecological carrying capacity". It is important to reiterate that the population grows most rapidly (maximum number of animals added per year) at the inflection point.

In subsequent graphs, I replace T (Time) with N (Number of animals, or population size). Since N increases with T, the replacement is acceptable.

The pattern observed in (A) is due to 3 factors: the number of animals present each year; the mortality rate (%) of those animals; and the reproduction rate (young/female). Mortality and reproduction rates are expected to change as the population grows (B and C).
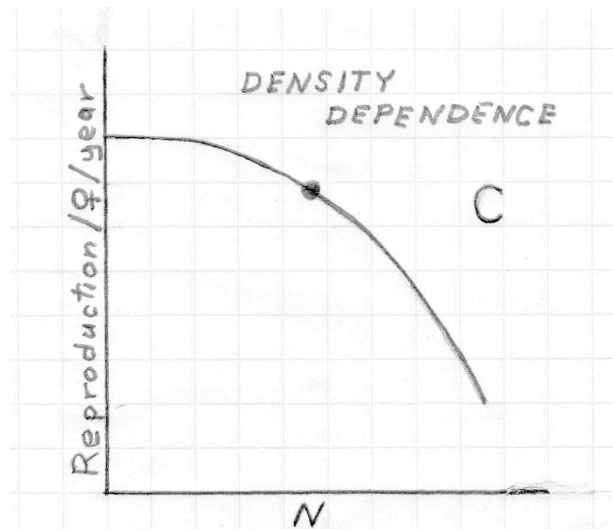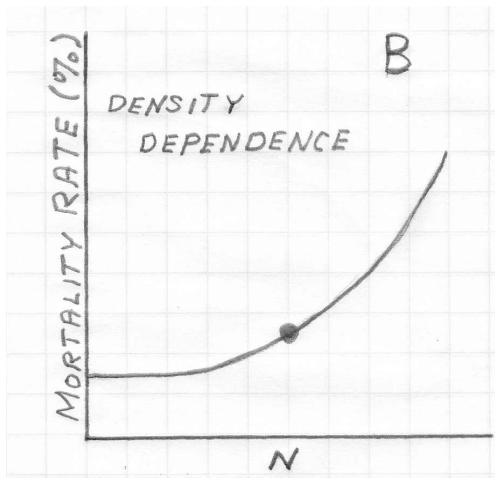

Mortality rates may increase due to increased competition among animals for the limited amounts of habitat resources, often food. However, animals may also compete for water, cover, or security habitat. Thus, as the population grows, an increasing proportion of the population is living with less and/or lower quality resources. In addition, the increasing population may transmit diseases more easily and may become more attractive to predators seeking lower quality animals in less secure habitats. In the real world, the mechanisms of increased mortality vary greatly, but the trend is an increasing rate of mortality with increasing population size. We might call this pattern "N-dependent" mortality for this model. Most biologists use the term "density-dependent" where "density" is the number of animals per unit of habitat (such as deer/square mile). Note in (B) that, at the inflection point (black dot), the mortality rate is not minimal. More animals die each year compared to the mortality rate at a lower population size.

In contrast, reproduction rates decline with increasing population size (C), for some of the same reasons that mortality rates increase. In the model, as the population grows, rates of mortality and reproduction change until they become equal and the population stabilizes with births = deaths, as in (A) at ecological carrying capacity. Note again that, at the inflection point, the reproduction rate per female is not maximum. In early population growth, the decline in reproduction rate is overcompensated by the increasing number of female animals and population growth continues to accelerate up to the inflection point.

An important derivative of (A) describes the annual production of the population. While rates of mortality and reproduction change as in (B) and (C), the number of animals added to the population annually is illustrated in (D). Production is greatest at the inflection point, the steepest part of the population growth curve in (A). Note that maximum production occurs, not with maximum population size, but at some intermediate population size. Maximum annual production is, of course, a paramount consideration in the livestock industry.

TOTAL ANNUAL PRODUCTION OF YOUNG

D
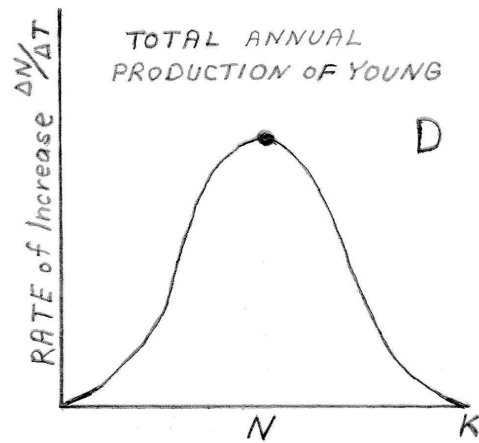
As has already been alluded, the condition of animals declines with increasing population size (E). Animal condition may be evaluated in terms of individual growth rates, ultimate body sizes, or body-size ratios such as the girth/length ratio, or weight/height ratio. The frequency of trophy-sized animals may be another measure of population/animal condition. We should also expect there are declines in less measurable characteristics such as disease-resistance, agility, and alertness. Again, the maximum abundance of the highest-quality animals occurs with a population size below the inflection point.

E

F
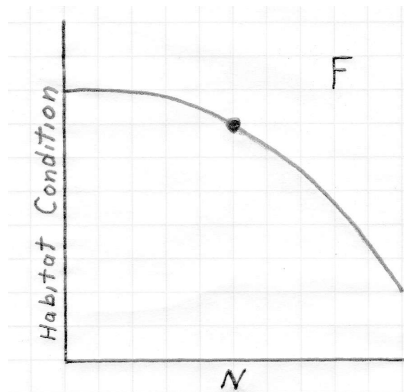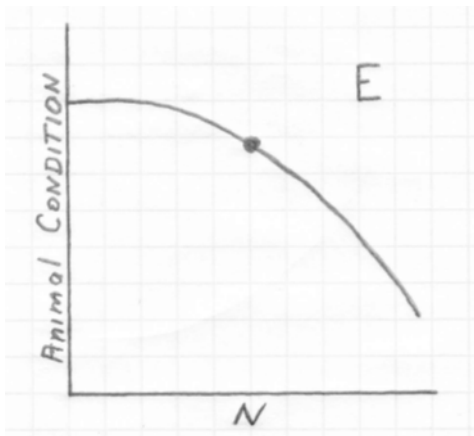
Lastly and importantly, a larger population will have impacts upon its environment, especially upon food resources such as forage. The relationship (F) is most often applied to forage conditions for a population of large herbivores. It is assumed that the best forage conditions occur when the population using the forage is small. With a small population, animals may choose only the best parts of the abundant best plant species to provide for nutrition. But, as the herbivore population grows and consumes more forage, the most favored plant species usually decline and are replaced by less favored and less nutritional plants. With an even larger herbivore population, the vegetation may consist mostly of plant species avoided by the animals, and bare spots may increase amongst the vegetation.

Since most livestock are large herbivores, this concept is much embraced in livestock management. Cattlemen often classify plant species as "increasers", "decreasers" and "invaders". Decreasers are initially abundant, but decrease with increased grazing impact. Increasers are initially less common and increase with grazing up to intermediate levels of

grazing. Invaders are absent with little or no grazing, but invade and increase with more grazing. Generally, decreasers are considered the best forage; increasers are less valuable; and invaders are poor or non-forage. The ratios of decreasers, increasers, invaders, and bare ground may be used as indices to the condition of the foraging habitat as indicated in (F). (However, the concept is a generalization, as some increasers are valuable, even preferred, forages for some herbivore species.) Note, even when the concept is limited to forage conditions for large herbivores, the very best forage conditions occur with numbers of animals below the inflection point.

The concept in Fig. (F) is somewhat overused in wildlife management. First, even for wild herbivores, forage may not be the most important population-limiting factor. For such populations of wildlife, habitat condition must be measured with some habitat characteristic other than forage. Second, the pattern in (F) does not apply to many species of small herbivores. The best forage conditions for pronghorn often occur with rather high levels of ungulate grazing, including pronghorn grazing. Thus, what is good habitat (forage) condition for bison or for domestic cows, is not the best for pronghorn, not for jackrabbits, nor for many other wildlife species adapted to live in heavily grazed environments.

So what do all these relationships tell us about carrying capacity or about "overgrazing"? Carrying capacity is the ability of the habitat to "carry" (support) animals on a sustained basis. If we accept or desire nature's regulation of the quality of the animals (E), the productivity of the population (D), and resulting habitat conditions (F), carrying capacity is "ecological carrying capacity" (A). (At ecological carrying capacity, wildness and the preponderance of natural selection acting upon the population are maximized – a topic I have addressed elsewhere.) But, often, we have other intentions for the qualities of populations and habitats. The profession of wildlife management was born on the assumption that we would control a population size at some point along the continuum in (A). Of course, selecting a desired population size is concurrently selecting, intentional or not, for positions along the continua in (B), (C), (D), (E) and (F).

Likewise, "overgrazing" is a level of foraging that is excessive for achieving, on a sustained basis, some desired condition for the foraging habitat, or for all the related parameters in (A) – (E).

The point is that "carrying capacity" and "overgrazing" are meaningless terms until one has specified a goal for the management program. Moreover, opportunities to simultaneously maximize achieving more than one goal are rare. (Factors affecting such goals must be 100% correlated.)

In most livestock management, the goal is a maximum, sustained production of harvestable animals. Thus, a rancher's "carrying capacity" is found at the inflection point illustrated in (A) – (F), with primary emphasis on (D). Above the inflection point, impacts on forage resources ultimately reduce the population's production of animals. Below the inflection point, ranchers may see a "waste" of good forage. The inflection point is often termed "economic carrying capacity".

Too often, "carrying capacity" and "overgrazing" are invoked in public meetings on wildlife issues with an implication that sustained annual production of animals is the only appropriate

management goal. (Sometimes I think there is an overbearing attitude that "All the world should look like a ranch.", and be managed accordingly. The goal of harvesting animals is particularly inappropriate for our National Parks.) While many game populations are managed with a goal of maximizing sustained harvestable surpluses, there are other appropriate goals for managing some wildlife. In any management program, the <u>primary</u> goal may relate to some habitat condition, to some quality of the animals, or to some other affected public or private resource or desire. Thus, the primary goal may relate to any one of (A) – (E), with consequent effects from all the other parts of the model.

Populations may be managed above the inflection point for purposes of maintaining wildness with the benefits of natural selection, to provide animals for predators and scavengers that may be rare species, to foster impacts on forage resources that will benefit other herbivore species, or to enhance recreational or esthetic benefits for people.

Populations may be managed below the inflection point to limit negative impacts, perhaps on rare plants; to limit competition with domestic livestock; or for purposes of human health or safety.

In discussing wildlife management goals, it is important that wildlife managers and the public recognize all the model components (A) – (E). Selecting a parameter from one graph automatically selects parameters from all the others. For example, the Interagency Bison Management Program for Yellowstone National Park currently has a goal of having 3000-3500 animals for compromise purposes of maintaining but limiting the number of animals annually visiting Montana. It is seldom recognized that 3000-3500 bison likely is near the inflection point, maximizing the number of animals that must be removed annually in a controversial harvest and through expensive capture-and-slaughter operations.

In conclusion, hearing the terms "carrying capacity" and "overgrazing" should send up red flags in the audience and foster often-needed deeper thinking. – Jim Bailey, 2016