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Carrying Capacity

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Carrying capacity is typically defined as the maximum population size that can be supported indefinitely by a given environment. The simplicity of this definition belies the complexity of the concept and its application. There are at least four closely related but nonetheless different uses of the term in basic ecology, and at least half a dozen additional definitions in applied ecology.

Basic Ecology

Carrying capacity is most often presented in ecology textbooks as the constant K in the logistic population growth equation, derived and named by Pierre Verhulst in 1838, and rediscovered and published independently by Raymond Pearl and Lowell Reed in 1920:

$$N_t = \frac{K}{1 + \mathrm{e}^{a-rt}} \quad \text{(integral form)}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(\frac{K-N}{K}\right) \quad \text{(differential form)}$$

where N is the population size or density, r is the intrinsic rate of natural increase (i.e., the maximum per capita growth rate in the absence of competition), t is time, and a is a constant of integration defining the position of the curve relative to the origin. The expression in brackets in the differential form is the density-dependent unused growth potential, which approaches 1 at low values of N, where logistic growth approaches exponential growth, and equals 0 when $N = K$, where population growth ceases. That is, the unused growth potential lowers the effective value of r (i.e., the per capita birth rate minus the per capita death rate) until the per capita growth rate equals zero (i.e., births = deaths) at K. The result is a sigmoid population growth curve (Figure 1). Despite its use in ecological models, including basic fisheries and wildlife yield models, the logistic equation is highly

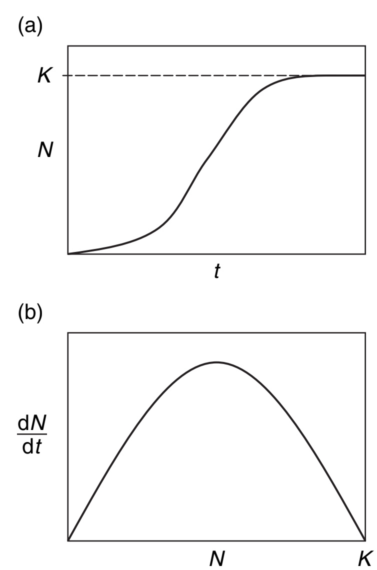

Figure 1 The definition of carrying capacity most frequently used in basic ecology textbooks. (a) Logistic population growth model, showing how population size (N) eventually levels off at a fixed carrying capacity (K) through time (t). (b) Logistic population growth rate ($\mathrm{d}N/\mathrm{d}t$) as a function of population size. Note that the growth rate peaks at $0.5K$ and equals zero at K.

simplistic and much more of heuristic than practical value; very few populations undergo logistic growth. Nonetheless, ecological models often include K to impose an upper limit on the size of hypothetical populations, thereby enhancing mathematical stability.

Of historical interest is that neither Verhulst nor Pearl and Reed used 'carrying capacity' to describe what they called the maximum population, upper limit, or asymptote of the logistic curve. In reality, the term 'carrying capacity' first appeared in range management literature of the late 1890s, quite independent of the development of theoretical ecology (see below). Carrying capacity was not explicitly associated with K of the logistic model until Eugene Odum published his classic textbook *Fundamentals of Ecology* in 1953.

The second use in basic ecology is broader than the logistic model and simply defines carrying capacity as the equilibrial population size or density where the birth rate equals the death rate due to directly density-dependent processes.

The third and even more general definition is that of a long-term average population size that is stable through time. In this case, the birth and death rates are not always equal, and there may be both immigration and emigration (unlike the logistic equation), yet despite population fluctuations, the long-term population trajectory through time has a slope of zero.

The fourth use is to define carrying capacity in terms of Justus Liebig's 1855 law of the minimum that population size is constrained by whatever resource is in the shortest supply. This concept is particularly difficult to apply to natural populations due to its simplifying assumptions of independent limiting factors and population size being directly proportional to whatever factor is most limiting. Moreover, unlike the other three definitions, the law of the minimum does not necessarily imply population regulation.

Note that none of these definitions from basic ecology explicitly acknowledges the fact that the population size of any species is affected by interactions with other species, including predators, parasites, diseases, competitors, mutualists, etc. Given that the biotic environment afforded by all other species in the ecosystem typically varies, as does the abiotic environment, the notion of carrying capacity as a fixed population size or density is highly unrealistic. Additionally, these definitions of carrying capacity ignore evolutionary change in species that may also affect population size within any particular environment.

Applied Ecology

The term carrying capacity may have first appeared in an 1898 publication by H. L. Bentley of the United States Department of Agriculture, with an original focus on maximizing production of domestic cattle on rangelands of the US southwest. The first use in wildlife management was apparently associated with classic studies of deer populations on the Kaibab Plateau in northern Arizona in the 1920s. The concept was popularized in wildlife ecology by Aldo Leopold and Paul Errington in the 1930s.

There have been four typical uses of carrying capacity in applied ecology, illustrated in Figure 2: (1) the maximal steady-state number or biomass of animals an area can support in the absence of exploitation (the original use of carrying capacity, K); (2) the maximal sustainable yield (MSY) of biomass of animals an area can produce for exploitation, which equals $0.5K$ in the simplest form of the logistic model; (3) the maximal sustainable economic yield (MEY) of animals an area can produce for exploitation, which equals the maximum difference between yield value and cost of exploitation; and (4) the open-access equilibrium (OAE), where the value of the yield equals the cost of exploitation, which is the upper economic limit of exploitation in the absence of economic subsidies and restrictive management regulations. Note that open access, typical of historical marine fisheries, often leads to severe overexploitation because the population is reduced to sizes far below the other types of carrying capacity. Indeed, even the application of maximum sustainable yield in single-species fisheries management has proven elusive and often disastrous, as evidenced by the poor state of most marine fishery stocks so managed.

Two additional uses of carrying capacity in applied ecology focus on optimal stocking of rangeland with cattle,

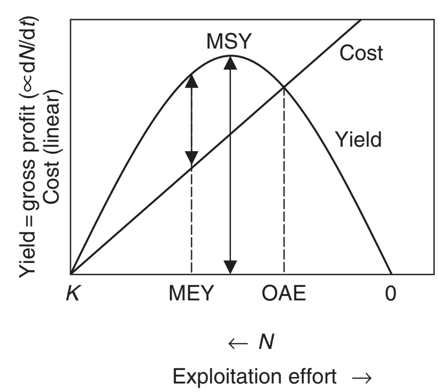

Figure 2 Four definitions of carrying capacity used in applied ecology. Yield (or so-called surplus production, which directly translates to gross profit and which varies directly with the growth rate of the exploited population) initially increases and eventually decreases as exploitation effort increases, whereas the cost of exploitation presumably increases linearly with effort. The conventional carrying capacity (K) occurs in the absence of exploitation (i.e., zero effort). MSY occurs where total yield peaks (i.e., $0.5K$ in the logistic model). MEY occurs where net profit (i.e., gross profit minus cost) is maximal (i.e., where the slopes of the cost and yield curves are identical). The OAE occurs where gross profit equals cost. Typically, as illustrated, $K > \mathrm{MEY} > \mathrm{MSY} > \mathrm{OAE}$.

sheep, etc. The Society for Range Management defines the term as the maximum stocking rate possible which is consistent with maintaining or improving vegetation or related resources. A more general definition is the optimum stocking level to achieve specific objectives given specified management options. These practical definitions implicitly acknowledge that carrying capacity is not a constant, but rather is affected by a variety of environmental factors.

The elusive applied goal has been to determine number of animal-unit-days per unit area that produces a desired objective. A typical simplistic formulation follows:

$$A = (B \times C)/D$$

where A is the number of animal-unit-days an area can support ($(\# \times d)$ per square kilometer), B is biomass of food in the area ($\mathrm{kg\,km^{-2}}$), C is the metabolizable energy of that food ($\mathrm{J\,kg^{-1}}$), and D is the metabolizable food energy required per animal unit per day ($\mathrm{J}/(\# \times d)$). Obviously, such formulas ignore the reality of environmental variation, species interactions, etc.

A classic field study of wildlife carrying capacity was published by David Klein in 1968. In 1944, some two dozen reindeer were released on St. Matthew Island in the Bering Sea, where previously there had been none. Lichens were plentiful and the population increased at an average rate of 32% per year for the next 19 years, reaching a peak of about 6000 in 1963. During the severe winter of 1963–64, nearly all the animals died, leaving a wretched herd of 41 females and 1 male, all probably sterile. It was not so much the inclement weather that devastated the herd as it was a deficiency in food resources caused by overgrazing. After careful study, Klein concluded that 5 reindeer per square kilometer would have been the carrying capacity of an unspoiled St. Matthew Island. An animal census taken in 1957 gave 4 animals per square kilometer. A further 32% increase during the ensuing year brought the population to 5.3 per square kilometer, in excess of the predicted carrying capacity and a prelude to the eventual population crash.

Conclusions

Overall, the many and varied definitions of carrying capacity, typically stated in rather vague and ambiguous terms, render the concept to be most useful in theoretical ecology. Efforts to parametrize and measure carrying capacity in the field have proven problematic, such that the practical utility of the concept is questionable. This dilemma is especially true when considering the worldwide carrying capacity of humans, which seems better approached by the concept of ecological footprint. Nonetheless, the carrying capacity concept is clearly of heuristic value given the fundamental truth that no population can grow without limit, and especially given the fact that many human societies have behaved as if no limits exist.

See also: Abundance; Biomass; Death; Ecological Footprint; Evolutionary Ecology: Overview; Fecundity; Fisheries Management; Fishery Models; Grazing Models; Grazing; Growth Constraints: Michaelis–Menten Equation and Liebig's Law; Growth Models; Human Population Growth; Limits to Growth; Maximum Sustainable Yield; Mortality; Prey–Predator Models; Stability; k-Dominance Curves; r-Strategist/K-Strategists.

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