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CRITIQUE OF CARRYING CAPACITY CONCEPTS CONCERNING DALL SHEEP

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Abstract: The classic concept of nutritional carrying capacity tends to complicate management of Dall sheep (*Ovis dalli dalli*) populations because they often exist at relatively constant population sizes over extended periods. The fundamental axiom taught in the wildlife management curriculum is that population growth will follow the logistic curve until it reaches or exceeds carrying capacity where further growth is limited by nutritional constraints. A common extension of this is concept is that any numerically static population has reached nutritional carrying capacity. Obviously, Dall sheep populations grew to present-day levels by overcoming environmental resistance until the equilibrium we typically observe in continental climates was established. Hence, managers reason that lowering population density will result in compensatory increases in productivity, recruitment, and individual growth as the population tries to reach carrying capacity again. However, in northern ecosystems with abundant predators, environmental resistance resulting from non-nutritional causes is highly dynamic, and probably more influential than density-dependent nutritional constraints in limiting population growth. This calls the fundamental axiom and its commonly assumed postulate into question. It is important for managers to recognize this confusion because managed cropping mortality of a population limited by density-dependent nutritional constraints may result in compensatory increases in productivity or growth as the axiom predicts. However, managed cropping mortality in a population limited by non-nutritional environmental resistance will be additive. The former cropping scheme will not lower population size or productivity; the later will.

When articulating the working hypothesis of Dall sheep management (Heimer 1988), I stated that Dall sheep should not be expected to show explosive population growth, and that we should anticipate relative stability in population size over time. This hypothesis was based on the conclusion that Dall sheep are adapted to continuous use of climax vegetative systems. Adaptation to a stable food source (in contrast to the cyclically transient forage bonanzas which occur in successional habitats) should confer no selective advantage for nutrition-mediated increases in reproduction such as the multiple births or accelerated sexual development seen in seral-adapted species such as moose (*Alces alces*) and deer (*Odocoileus* spp.) under ideal conditions.

Dall sheep populations which exhibit relatively consistent sizes, particularly where sheep densities are high, have often been assumed to be at nutritional carrying capacity. This conclusion has typically resulted from the assumptions which underlie the carrying capacity theory. Population reduction, the classic management action suggested by this conclusion, is risky. If the assumptions and conclusions are correct, managers succeed; if not, they fail. Hence, understanding our general thinking and its relevance to specific situations has significant management implications.

Review of Dall sheep adaptations to their environment, as well as awareness of their specific ecological relationships, will show that assuming populations of Dall sheep are at carrying capacity because they exist at relatively static population sizes is not dependable. The purposes of this paper are to identify general adaptations of Dall sheep, to discuss specific biological findings about Dall sheep, and to highlight the likelihood of incorrect reliance on classic population "symptoms" to diagnose nutritional limitation. Clearly, management actions are recommended as results of diagnosis by managers. Hence, incorrect diagnosis may lead to inappropriate management actions. An alternate approach to management will be offered.

METHODS

The common, operational understanding of carrying capacity theory and its underlying assumptions were assessed by interviewing wildlife managers and hunters over the last 15 years. Literature relevant to Dall sheep population adaptations as well as their autecological relationships to classically defined symptoms of nutritional carrying capacity constraint were also reviewed. Findings were related to the prevailing interpretations of the carrying capacity model as assessed by the interviews.

RESULTS

The Carrying Capacity Model

About 15 years ago, I began to question the relevance of carrying capacity theory to management of Dall sheep in intact ecosystems (ecosystems where natural predators still exist). At that time, I began to raise the question with working wildlife managers and hunters. I interviewed managers because most approach management from this perspective. I interviewed hunters because they are commonly taught to use carrying capacity in their justifications for hunting. Whatever the original and true intent of the carrying capacity model may have been, the common understanding among those I interviewed was as follows.

The carrying capacity model is commonly expressed as a plot of population size over time (Fig. 1). It is based on several assumptions. These include:

1. Range resources are fixed and finite while ungulate populations are dynamic and capable of outgrowing their food supply.

2. When ungulate populations reach a certain size or density, access to nutritional resources becomes an inverse function of the number of animals present in the population, i.e. the higher the number of animals, the lower the per capita food.

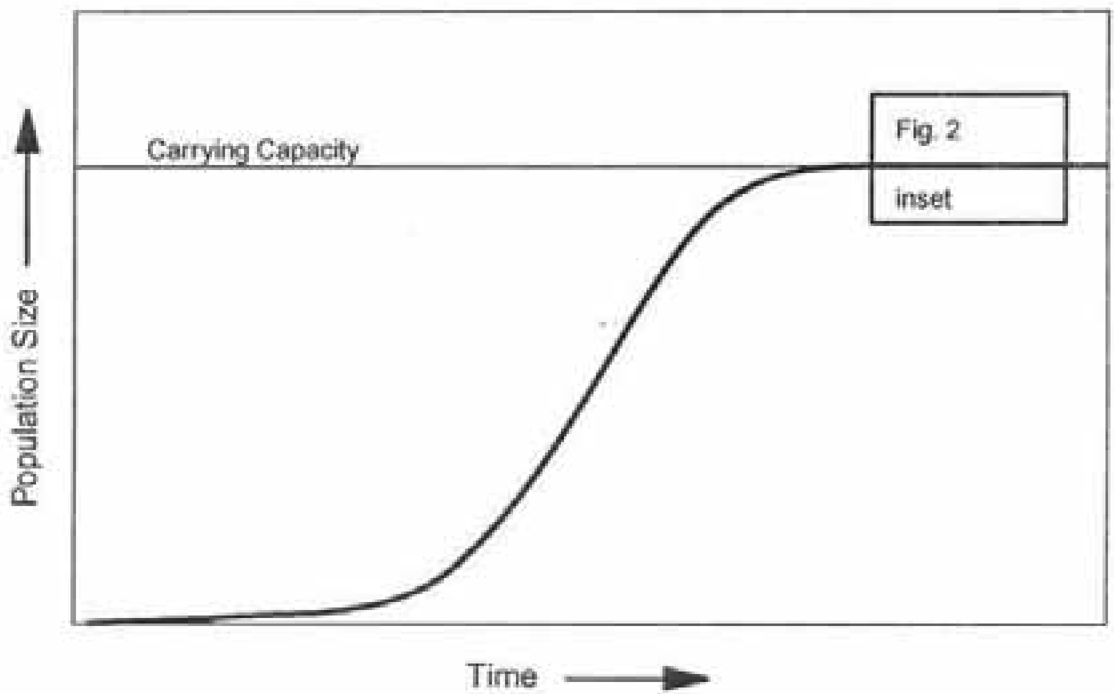

Fig. 1. Classic logistic growth curve.

3. A result of this inverse function is a symmetrical second degree polynomial we call the logistic growth curve. It predicts that population size in a "new" population will increase geometrically until food becomes limiting. Then the rate of increase will slow, initially to linearity, and eventually approach a "zero growth" asymptote when food resources can no longer support higher population numbers.

4. The asymptotic population size defines nutritional carrying capacity.

5. Populations always strive to reach carrying capacity.

Alternately, in temperate or sub-tropical climates where predators are absent, environmental resistance may be so low that introduced populations reach a level greatly above carrying capacity. This over-population may then result in a nutrition-mediated population crash. As a result of overgrazing which occurred when the population was above carrying capacity, habitat is presumably damaged; and the post-crash population size is projected to stabilize at a lower nutritional carrying capacity (Caughley 1970).

Dall Sheep Adaptations and Autecology

Dall sheep exhibit relatively slow population increases compared with seral-adapted ungulate species. In spite of observations of aloe-mothering (Hoefs 1978), multiple births are unknown in Dall sheep.

With respect to their relatively small body size, onset of reproductive activity among Dall ewes is typically delayed--to 3 or 4 years of age. However, this delay is not a result of delayed ovulation resulting from poor nutrition but of delayed breeding (Heimer and Watson 1986a,b).. Available data show Dall ewes uniformly ovulate at 18 months in the wild (Heimer and Watson 1986a, b, Nichols 1972) and in captivity (R. Bullerman, Milwaukee County Zoo, P. Smith, Denver's Zoo pers commun.). In captivity ewes typically breed at 18 months and have their first lamb at 24 months of age (Heimer and Watson 1986a). However, in the wild Dall ewes normally don't deliver their first lambs until age 3 or 4 years (Bunnell and Olsen 1981, Heimer and Watson 1986a). In unusual circumstances associated with a scarcity of mature rams (which is frequently the case in zoos), a significant percentage of ewes breed at 18 months and have their first lamb in the wild at 2 years of age (Heimer and Watson 1986a).

In addition, mortality during the first year is typically high for Dall lambs, averaging about 40% in measured herds, (Murie 1944, Deevey 1947, Heimer and Watson 1986a). Dall sheep live in hazardous ecosystems where unfavorable weather, snowslides, falling rocks, and falling sheep combine with full compliments of predators to produce formidable environmental resistance to population growth. This environmental resistance is variable, but when coupled with comparatively low, climax-adapted fecundity it appears to have resulted in populations which tend toward slow growth or maintenance.

I previously suggested (Heimer 1988) nutritional limitations are more probably produced by a "bottleneck" in winter food quality than by chronically insufficient forage quantity or compromised food quality resulting from overgrazed ranges. Summer food quality and abundance are very high (Whitten 1975, Winters 1980). Conversely, winter food is of such uniformly poor quality (Heimer 1983) that slow passage rates through the digestive tract probably limit the ability of Dall sheep to gather energy. Hence, Dall sheep lose weight during winter (Heimer 1983). I think it follows that these circumstances result in a relative abundance of low quality food being available under normal winter foraging conditions. If so, the number of individuals on winter range is not critical as long as there is enough low quality food to keep each rumen filled and functioning.

Still, sheep show greater mortality during (Watson and Heimer 1984), and lower productivity after (Heimer and Watson 1986b) winters with deep snow accumulation than they do when winters are less severe. This is probably because lighter snow interferes less with access to the higher quality food plants which occur on the lower fringes of their ranges (Heimer 1983). Severe winters preclude access to these more nutritious plants by confining sheep to windblown ridges throughout winter and delaying their access to high quality forage at lower elevations during late winter and early spring. Hence, at observed population levels, winter severity should be expected to influence population productivity and survival more than does sheep density. Even crowded populations (where the quantity of forage is most likely to be limiting) produce spectacularly high lamb:ewe ratios when environmental conditions are favorable (Heimer and Watson 1986b, F. Mauer, USFWS, pers. commun.). That is, when environmental resistance is transiently lowered, populations which otherwise appear to be at carrying capacity produce lambs at the rate of 70 to 85:100 ewes instead of their usual 30-40.

Further confounding the definition of carrying capacity for Dall sheep is the demonstration that several classic indicators of nutritional insufficiency in other species are mimicked by unusually low ram abundance and the accompanying distortions of ram age and social structures (Heimer and Watson 1986a). These symptoms appear in populations where ram age structure is radically skewed toward young rams. In 1980, I raised the question of whether population quality (Geist 1971), then considered a function of food quality, was a result of nutrition or other factors (Heimer 1980). Subsequently, Sarah Watson and I (Heimer and Watson 1986a,b) demonstrated that several classic indicators of nutritional carrying capacity were more rationally attributable to behavioral than nutritional factors. These indicators included low lamb production (Heimer and Watson 1986b), low ovulation rates (Heimer and Watson 1986a), and low ram survival (Heimer et al. 1984). We now have data that suggest even ram horn growth may be compromised by these conditions (Heimer unpubl. data).

DISCUSSION

Reviewing the suite of evolutionary adaptations and the specific autecology of Dall sheep reveals an almost bewildering array of circumstances which may conspire to produce relatively unchanging population sizes. Still, high Dall sheep densities, and relatively static population sizes, have led many managers to suppose Dall sheep populations typically exist at or above nutritional carrying capacity. Extending the density-dependent assumptions of nutritional limitation, which derive from the carrying capacity model, typically leads managers to 1 of 2 conclusions.

The first is that sheep populations are "too high" for their food resource, and that any decrease in population performance is an indicator of insufficient nutrition. Based on these assumptions, managers frequently suggest reducing the number of sheep will increase the amount of food available to each remaining sheep. Hence, as a result of increased food availability, each survivor will eat better. The cumulative result of better per capita nutrition will be a collective increase in population productivity and growth.

The second conclusion is that because Dall sheep populations are at or above carrying capacity, and because the carrying capacity model stipulates populations will always grow until constrained by density-dependent nutrition, any reduction (below carrying capacity) will result in sustainable production of a harvestable surplus as the population tries to return to carrying capacity. It is assumed that this surplus will be produced annually, and that the population will be stabilized below carrying capacity by annual removal of this surplus. In this scenario, it is assumed that reducing the population to generate the surplus and then removing it annually will become stable and manageable, limiting components of environmental resistance.

However, if Dall sheep populations, or populations of other ungulates, are already being held below carrying capacity by cumulative environmental resistance, density dependent nutrition should not be a factor. When this is so, managers should not expect downward adjustment of population size by managed cropping to produce the theoretically expected increases in productivity and growth. Instead, cropping should be expected to lower population size because the increased mortality (which would be expected to stimulate productivity in a population limited by density dependent factors) will be additive, not compensatory. Continued cropping will, in all likelihood, result in continued population declines.

Kuck (1980) reported carefully managed cropping of female mountain goats (Oreamnos americanus) in Idaho produced this exact result. This experience, and the arguments presented here suggest managers should critically evaluate their assumptions with awareness of adaptations common to K-selected species before applying carrying capacity theory to climax-adapted species. Similarly, managers should be careful when assigning causes to changes in population performance and status.

Even climax-adapted species selected for population stability or maintainence, like Dall sheep, exhibit population fluctuations about the stable level or "asymptote" (Figs. 1 and 2). Consequently, it may be productive for Dall sheep managers, or managers of other ungulates which do not exhibit radical, density-dependent "boom and bust," cycles, to

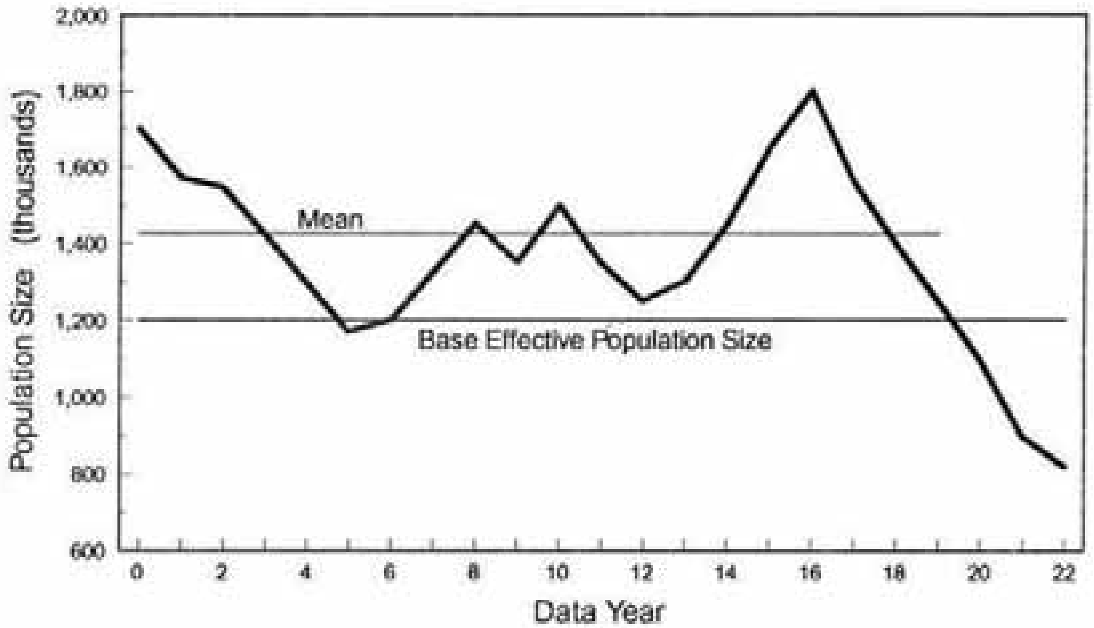

Fig. 2. Stylized population size modeled from Dry Creek, Alaska Range. (Greatly magnified from Fig. 1.)

reconsider the causes and biological significance of population size fluctuations. I suggest that we consider the notion of "base effective population size" as the relevant population statistic rather than mean population size (Fig. 2).

Variations in environmental resistance produce the observed variations in population size through a variety of mechanisms. Given a data set with fluctuations over time, our natural inclination is to draw a line through the middle with positive and negative fluctuations about the mean (Fig. 2). However, if we consider the typical lower level reached by population size fluctuations as the base effective population, and any fluctuations above this line as results of transient decreases in environmental resistance, management is simplified.

Setting population objectives at the base effective population offers practical advantages not available when the mean population size is used to define the population size objective. If a manager selects the mean, the population objective will not be met about half of the time. That is, the population objective will not be obtained whenever population size is below the mean. Hence, the manager will face uncertainty about whether corrective management actions are appropriate. This will not be a problem if the population objective is set at base effective size.

When populations are above base effective population size, managers must monitor; but need not take corrective action for every observed downward fluctuation. Only those dips which fall below the population size objective, which was set at base effective population size (Fig. 2), will require corrective management actions. The appropriate management responses in these cases are actions to reduce environmental resistance. Further lowering of population density in hopes of increasing _per capita_ nutritional benefits to survivors is unlikely to succeed in increasing production or survival.

For example, Dall sheep populations in Interior Alaska experienced population declines which approached 25% during winter 1981-82 (Watson and Heimer 1984). These changes were results of variations in cohort size precipitated by changes in environmental resistance (Watson and Heimer 1984). The declines were alarming, but actually of little management import because mild weather (transient, low environmental resistance) had produced transiently high population sizes by allowing several strong cohorts of sheep (which were earlier results of transient decreases in environmental resistance) to survive longer than normal. Hence, these decreases from "high" populations did not require corrective management actions. I do not recommend ignoring longer-term downward population trends, particularly if their cause and nature are not understood.

Here it should be emphasized, that base effective population need not represent the lowest level reached by naturally regulated, unmanaged populations. Base effective population size should be set by the manager to produce a level of human benefits sustainable by practical management actions. For example, in the Eastern Alaska Range 25 years of experience have shown that satisfactory ram harvests by humans are associated with a trend-indicator population size of 1,200 sheep in the Dry Creek study area (Heimer and Watson 1986a, b, 1990). Recorded high population sizes in this trend-indicating population have approached 1,800 sheep, and the Eastern Alaska Range has yielded increased ram harvests resulting from periods with higher population levels. Unregulated lows have not been observed because past management practices, including predator reduction programs (Heimer and Stephenson 1982), have maintained population size in the indicator area above 1,170 sheep. Experience suggests the base effective population required to produce acceptable ram harvests from the Eastern Alaska Range is indicated by a minimum population of about 1,200 sheep in the Dry Creek study area.

Obviously, determining the base effective population size requires a fairly long-term data base including population size, the magnitudes of documented fluctuations, and the level of human benefits desired. However, we should remember management has always, and will always, require application of specific information about the managed population.

As a manager, I think this approach has merit because I consider carrying capacity theory secondary to specific observation. That is, as a sheep manager, I am willing to rely more on the specific autecology of Dall sheep than on the synecology of ungulates in general. While reliance on the observed specifics of Dall sheep biology has produced management benefits (Heimer and Watson 1990), my past failure to directly address the carrying capacity question, which is fundamental to the thinking of most traditionally trained wildlifers, has interfered with their ability to consider and understand my arguments. I hope this discussion results in creative interchange among biologists regarding components of environmental resistance in addition to density-dependent nutrition. I also hope it results in greater direct application of what we know specifically instead of what we postulate in general.

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