Chapter 3: Population Processes

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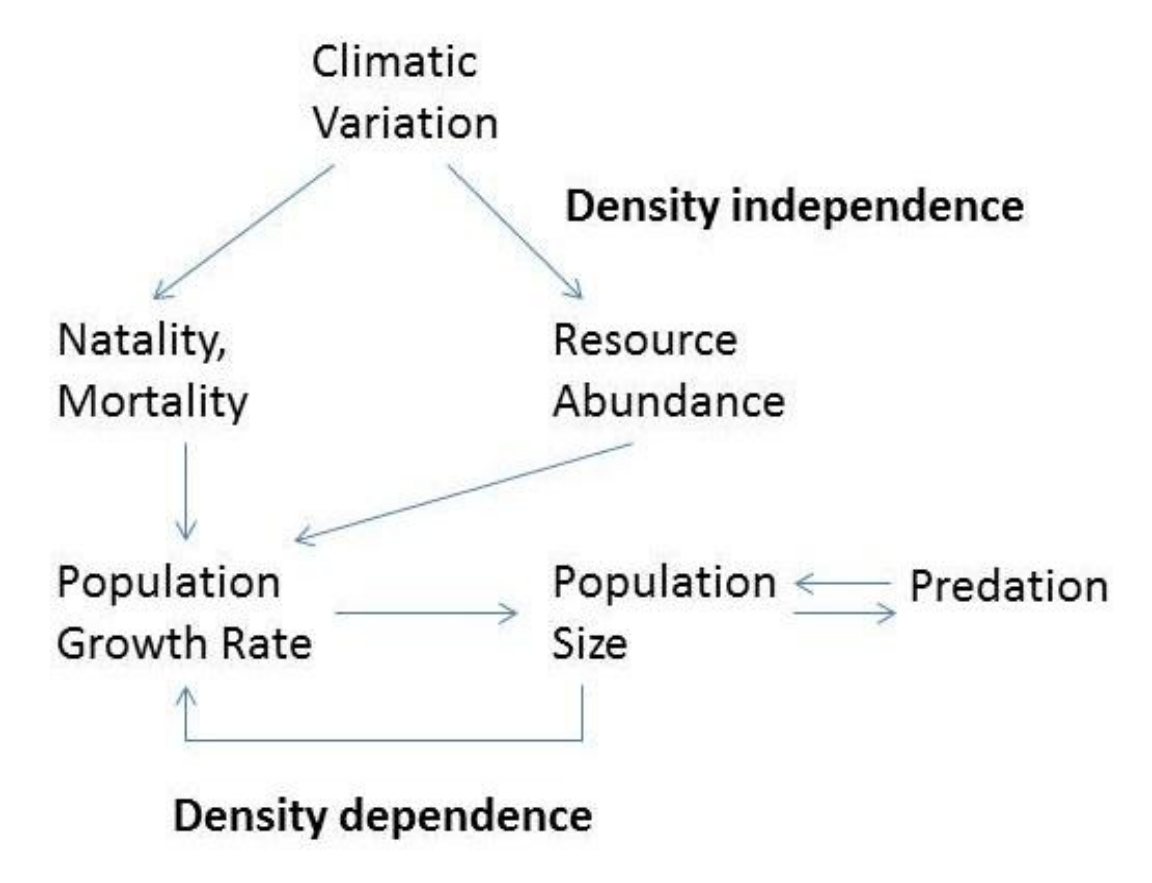
Questions for Committee

- Would free-ranging horse and burro populations self-limit if they were not controlled? If so, what indicators (such as rangeland condition, animal condition, and health) would be present at the point of self-limitation?
- Is there compensatory reproduction as a result of population size control. Compensatory reproduction is defined as an increase in reproduction as a direct or indirect consequence of management reductions

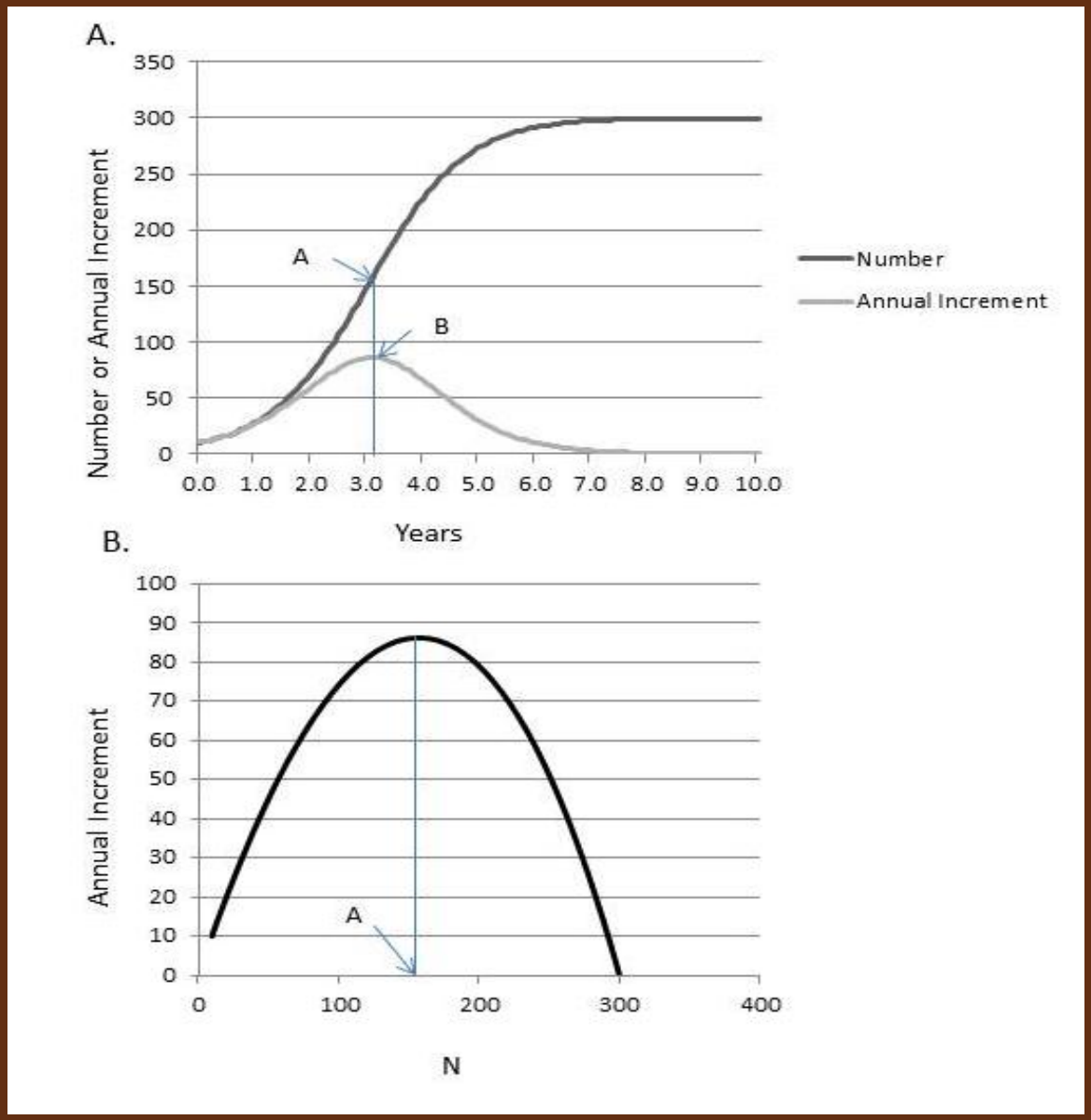
Self-limitation

- For self-limitation to occur, it is necessary for population processes to respond to population density. That is, population processes—such as population growth rates, age-specific survival rates, natality, and age of bearing first offspring - must be density-dependent.

Population processes involved in population regulation, including density dependent and independent controls.



Logistic population growth



Carrying Capacity – Different Concepts

- Food-limited or ecological carrying capacity - when a population comes into quasi-equilibrium with food supply and/or predators
- Appropriate Management Level (AML) – stocking rate set to preserve a thriving ecological balance
- Economic carrying capacity - the stocking rate that maximizes animal or vegetation productivity

Evidence for Density Dependence

- Numerous reviews and meta-analyses have shown that density dependence is common in large herbivore populations (Fowler, 1987; Sinclair, 1989; Gaillard et al., 2000).
- It is manifested through reductions in pregnancy, fecundity, twinning rate, number of offspring per female, percentage of females lactating, and young-to-female ratios and increase in age of first reproduction.

Nutritional and Physiological Mechanisms

- The mechanisms through which food limitation affects population vital rates are most likely: effects of poor nutrition, energy balance, and body condition on reproductive processes and survival rates (e.g. Gaidet and Gaillard, 2008).
- Poor nutritional status may also impair animal feeding and predator avoidance and increase susceptibility to adverse weather.
- Climatic conditions and spatial accessibility determine the availability of forage for herbivores.

Behavioral Mechanisms

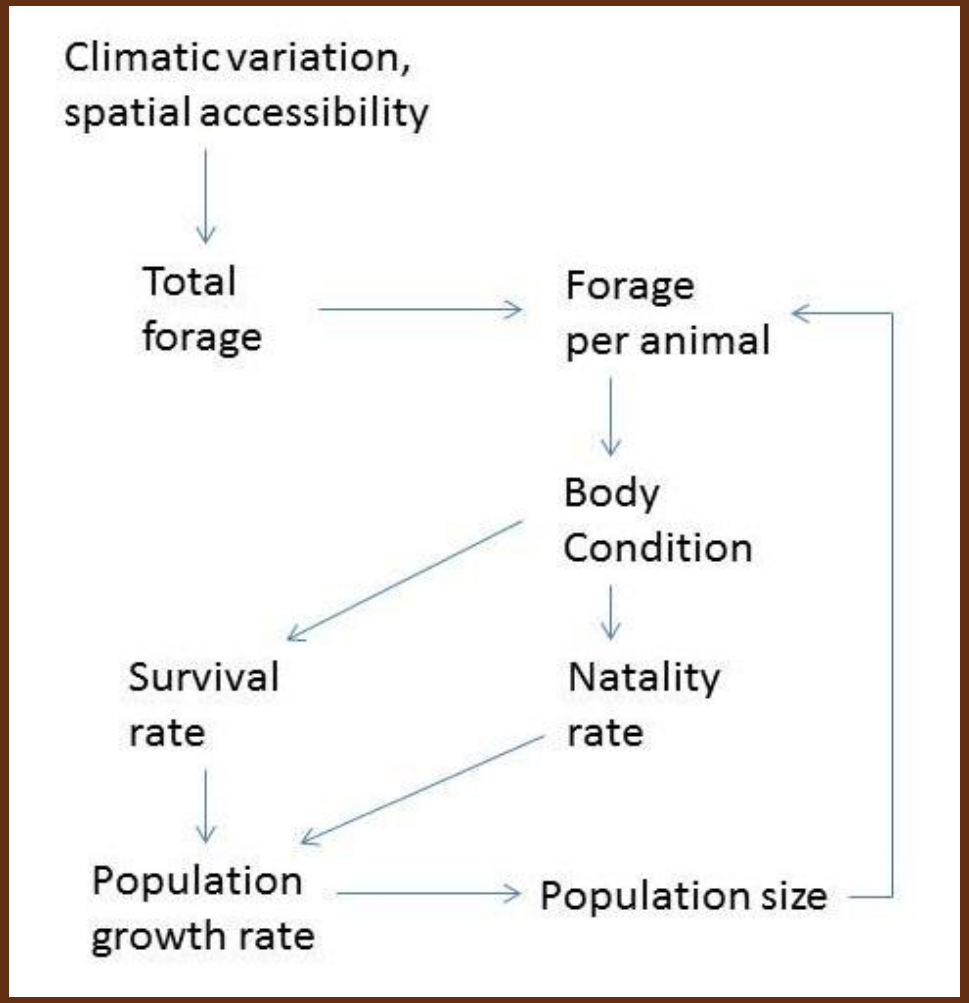
- Two fundamental mechanisms of behavior-mediated density dependence:
  - increased dispersal at high densities - dispersal sinks, migration, density becoming proportional to forage distribution
  - changes in social interactions that affect reproduction – e.g. more rapid turnover in the tenure of harem males or increased competition among females that leads to female movements among groups

Including Density Dependence in Models

- Argentina wild horses - fit a simple logistic equation with a best-fit intrinsic rate of increase and carrying capacity (Scorolli and Lopez Cazorla, 2010).
- Kenya zebra - density dependence in the form of a ratio of rainfall (as a surrogate of food availability) to density (Georgiades et al. 2003).
- Ecosystem/population modeling - the energy balance of the herbivore population is simulated as an outcome of forage intake and energy expenditure. The energy balance determines storage (fat) reserves, a measure of body condition. Condition, in turn, affects survival and fecundity (Coughenour et al).

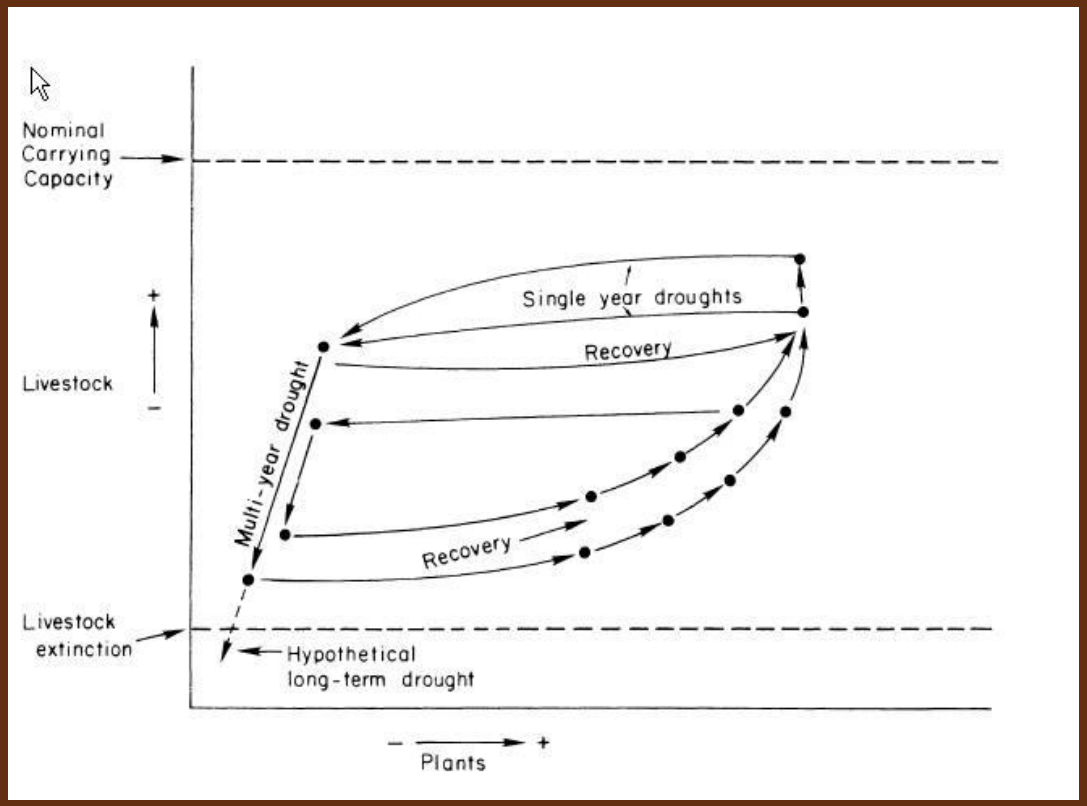
Density Independent Controls

- Variable precipitation and winter weather conditions affect population growth independent of density.
  - Precipitation affects forage production, and snow can affect availabilty.
  - Periodic large mortality events in severe winters have been well documented in horse populations.
- Note how it can be represented in models.


Climatic variation,
spatial accessibility
Total
forage
Forage
per animal
Body
Condition
Survival
rate
Natality
rate
Population
growth rate
Population size

Density Independent Controls

- In climatically variable environments herbivore populations should not be expected to reach a steady state in which population density is in stable equilibrium with forage production.



A herbivore population in an environment subject to periodic droughts is periodically reduced to a low level independently of density. The population then recovers slowly until the next drought causes another reduction. As a result, the population is kept below food-limited carrying capacity.(Ellis and Swift 1988).

Predation

- Zebras and other ungulates were not limited by food in Namibia but most likely by predation or disease (Gasaway 1996).
- Predation was suspected of being a major population control in a collection of ungulate populations in Kruger National Park (Owen-Smith et al 2005).
- Grange et al. (2004),found evidence that rates of predation on zebras in the Serengeti were high and hypothesized that predation potentially holds the population in a “predator pit.”

Wolf Predation

- In southern Europe, equids constituted 6.2
- percent of wolf diets (range, 0-24 percent) (Meriggi and Lovari, 1996).
- In northwestern Spain, a population of free-ranging ponies is heavily preyed upon by wolves (Lagos and Barcena, 2012).
- Wolves in a multi-prey system have been reported to prey on feral horses in Alberta, Canada. Webb (2009).

Mountain Lion Predation

- Mountain lion predation on free-ranging equids in North America is, with few exceptions, considered uncommon.
- An exception is the free-ranging horse population on the central California-Nevada border (Turner et al. (1992). Mountain lions were responsible for the deaths of 45 percent of the foals that were born. (Turner and Morrison 2001).
- Horses were documented to have been consumed as prey by collared mountain lions in eight mountain ranges throughout the study area in western Nevada (Andreasen – U. of Nevada, in progress)

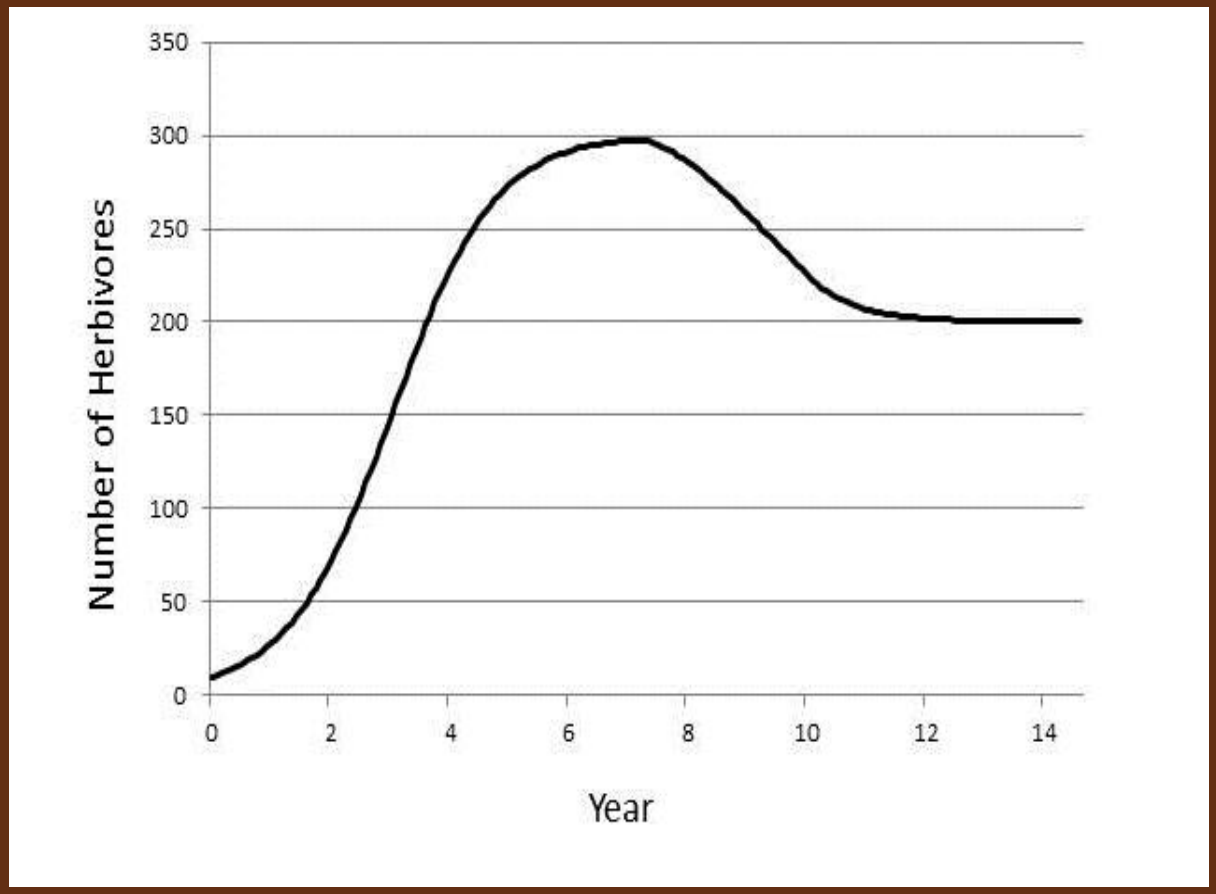
Mountain Lion Predation

- The potential for mountain lions to affect the sizes of populations of free-ranging horses in North America is limited by the fact that most HMAs are in areas that have few mountain lions.
- Mountain lions are ambush predators and require habitats that provide opportunities for stalking or finding prey without being seen.
- Among free-ranging horse populations, foals are the usual prey. Population size is not affected as much by foal survival as it is by adult survival.

Consequences and Indicators at Self-Limitation

- Riney (1964) and Caughley (1970, 1976) proposed that, on introduction of a large herbivore into an ecosystem not previously occupied, there would be an initial irruption of the population that would lead to a decline in vegetation conditions, which would in turn lead to a decline in the herbivore population and allow partial vegetation recovery.
- The resulting plant-herbivore system may be less productive, have less standing herbaceous biomass, and have a different plant species composition, but it may nevertheless be functional and sustainable.

Herbivores and vegetation coming into equilibrium (Riney 1964, Caughley 1970, 1976)



Consequences and Indicators at Self-Limitation

- Large herbivores have numerous effects on their environments that result from grazing, browsing, trampling, and behavioral and competitive interactions with other species. (Just what they do)
- If resulting feedbacks to equid population growth are ineffective or if they have been disrupted by human activities, rangeland ecosystems can be pushed across thresholds into degraded states (Chapter 7).

Consequences and Indicators at Self-Limitation

- Grazing pressures can be expected to be spatially heterogeneous. Some areas will be heavily, perhaps “excessively,” grazed while other areas are little used (even in “natural” ecosystems).
- Horses will have poorer body condition on average. As a result, mortality will be greater, particularly in times of food shortage resulting from drought or severe winter weather.

Difficulty of Generalizing About the Role of Food Limitation in Nature

- Indeed, many large-herbivore populations are regulated through food limitation as a natural process.
- Predation is a factor in some large-herbivore populations and some equid populations.
- However, in North America predators are absent or present at low densities.
- The degree of “naturalness” is also affected by other human activities (e.g. land use).

Case Studies

- Central Australia (Berman 1991)
  - 206,000 animals. Numbers increased then decreased in response to dry conditions, suggesting food limitation. High densities associated with degradation, but difficult to definitively prove how much was due to horses.

Case Studies

- Argentina (Scorolli and Lopezx Casorla 2010)
  - increased according to a logistic curve and was beginning to show signs of density dependence,
  - hypothesized that fecundity was reduced at higher densities because of reduced pregnancy in mares that had low body condition
  - reduced plant cover, reduced plant diversity and species evenness and altered the composition of communities, declines in wildlife

Case Studies

- Shackleford Banks (Rubenstein 1981)
  - horse population was clearly food limited
  - removal of competing domestic stock resulted in increased horse body condition and numbers, then numbers declined again
  - behavioral responses included decreased harem stability
  - decreased plant cover, increased bird diversity, decreased fish diversity

Case Studies

- Oostvardersplasen (ICMO 2006 , ICMO2 2010)
  - unmanaged horse population grew to food limited carrying capacity
  - periodic large winter die-offs
  - dying, starving animals are culled on ethical grounds
  - average body condition has declined
  - grazing produces short vegetation, prevents woody regeneration, increased plant diversity at small scales but not at a large scale

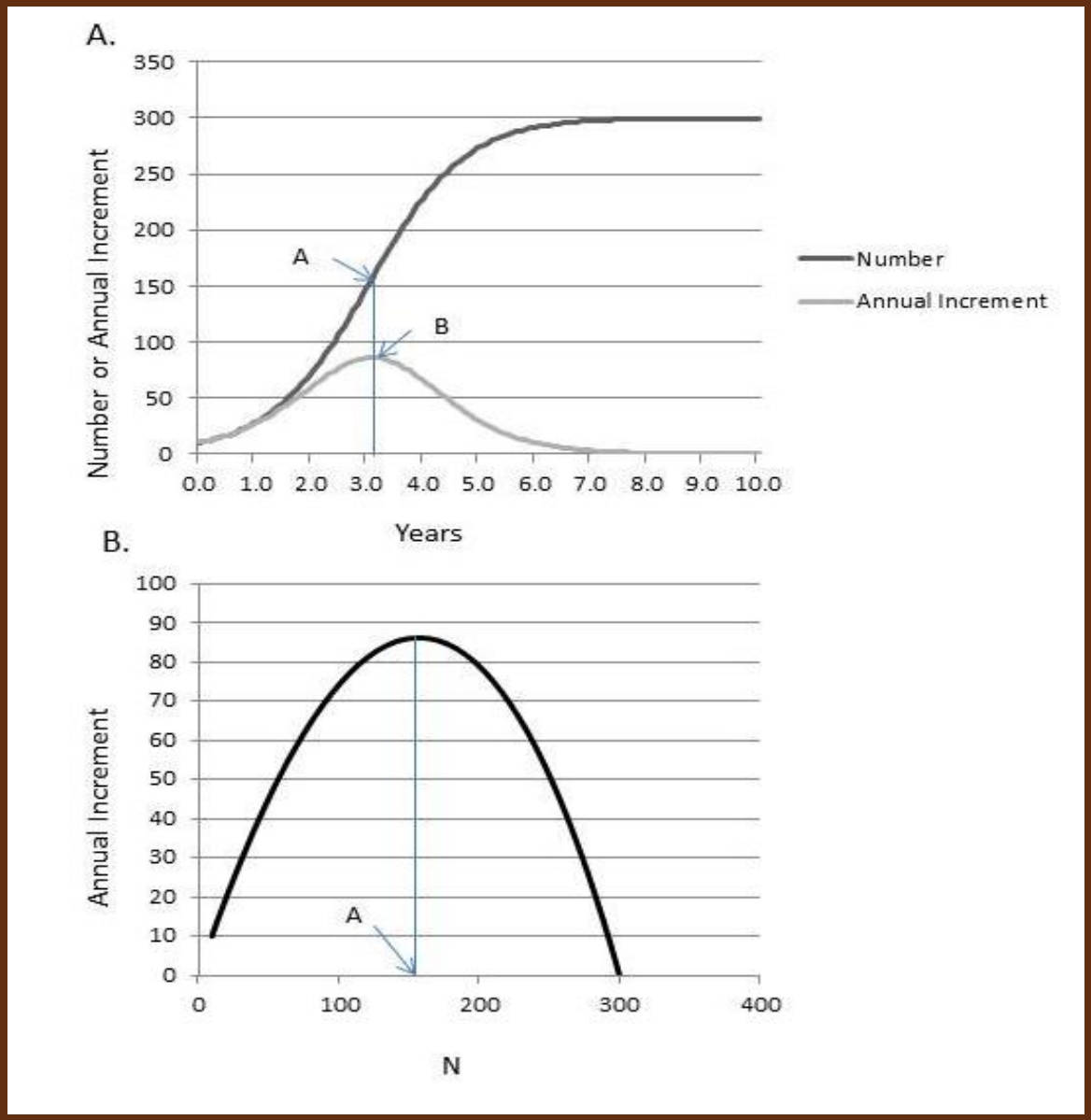
Case Studies

- Pryor Mountains
  - Horses present at least since 1901, possibly the 1700's, first roundup in 1971
  - For last half century, range conditions have been assessed as poor to fair.
  - Despite reductions since 1971, range condition is still considered to be unhealthy.
  - An ecosystem-population modeling exercise (Coughenour 1999) predicted outcomes at food-limited carrying capacity, and represented the underlying processes involved in density dependence, including food limitation, reduced body condition, and resulting reduced vital rates.

Management Implications of Compensatory Growth

- Horse and burro populations are seldom limited by density because they are kept below food-limited carrying capacity.
- Removals are likely to keep the population at a size that maximizes population growth rate, which in turn maximizes the number of animals that must be removed and processed through holding facilities (compensatory reproduction).
- HOWEVER, removals to even lower levels WILL reduce the number of animals removed.

Logistic population growth



Management Implications – Compensatory Growth at Chicoteague vs. Assateague

- Higher foaling rates were observed in the population managed with foal removals
- Although hypothesized to be due to cessation of lactational anestrus, there was no direct evidence of that.
- It is possible that pregnancy and foaling rates are reduced in lactating mares because of the lower body condition that results from the energetic demands of lactation.
- Not relevant to BLM herds as they are not managed through foal removals

Does PZP Cause Compensatory Population Growth?

- Effects of PZP on population growth, longevity, and body condition were studied over a 10-year period on Assateague Island (Turner and Kirkpatrick, 2002).
- Body condition of untreated mares, or of treated mares in which the treatment has lost effectiveness, could have increased because of reduced competition for forage. In treated mares, contraception reduces the energetic costs of reproduction, and this also results in increased body condition and longer lifespan.
- Might be termed compensatory population growth; however, it is unlikely that the degree of compensation would be sufficient to overcome the degree to which contraception reduces reproduction and population growth.

The End