UTILITY OF MULTIPLE EQUILIBRIUM CONCEPTS

APPLIED TO POPULATION DYNAMICS OF MOOSE

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Abstract: Despite the occurrence of several long term studies, including the celebrated Isle Royale case history, little progress has been made in developing a general theory of natural regulation of moose numbers and much controversy still surrounds the roles of food supply and predation as they relate to moose population dynamics. Recent attempts to formulate such a theory for moose and other northern ungulates include efforts to employ models originally developed by insect and fisheries ecologists. These models include concepts of multiple equilibria in which predation has an increasingly greater impact on recruitment at lower prey densities, thus producing sinuous stock-recruitment curves with stable upper and lower equilibria. When moose numbers are reduced to low levels by hunting or other outside disturbances, the system collapses to very low densities and moose numbers stay in the vicinity of a lower equilibrium unless predators are reduced. These arguments have been used to explain recent moose population declines in Alaska and to suggest remedial management actions. This paper reviews these ideas and concludes that the multiple equilibrium models generated to date may be inappropriate models for moose population dynamics. This results from their failure to capture several important qualitative and quantitative features of moose-predator systems and from the basic inability of stock-recruitment curves to produce realistic moose recruitment functions. Validation of these models has not been possible because existing field data are inadequate.

The behavior of moose *(Alces alces)* populations subject to predation by naturally regulated predators has long attracted the attention of population ecologists. This interest was stimulated largely as a result of the well publicized Isle Royale studies that, since 1959, have amassed

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an impressive array of long term data. References to Isle Royale regularly appear in theoretical discussions of predation and ecosystem stability (May 1973, Botkin and Sobel 1975, Caughley 1977); indeed Murdoch and Oaten (1975) identified the moose-wolf *(Canis lupus)* interaction on Isle Royale as the main worked-out example of a predator stabilizing its prey in a natural environment. Keith (1974) reviewed the history of Isle Royale moose and concluded that a stationary wolf population had stabilized the moose herd at a density below the carrying capacity dictated by available browse. Caughley (1977) reached the same conclusion.

A second factor which, along with predation, has often been identified as a determinant of moose density is food. Its role in the irruptive behavior of ungulate populations has been championed by Caughley (1970, 1976) who stated (Caughley 1976:198): "The eruption is the typical pattern of ungulate growth. It occurs in the presence of predators and in the absence of predators... . Whenever an ungulate population is faced with a standing crop of vegetation in excess of that needed for maintenance and replacement of the animals an eruption and crash is the inevitable consequence." Geist (1971) offered a similar theory for moose and recent interpretations of the Isle Royale data collected during the early 1970's stress the importance of plant succession and judge its long-term role in determining moose numbers as more important than predation (Peterson 1977, Allen 1979). These views suggest that in boreal forest environments moose exist at low densities until fires create a superabundance of forage. Moose then irrupt despite the presence of predators and decline rapidly when plant succession reduces the supply of browse. Predation's role in this cycle is mainly to act in an inverse density dependent fashion during the decline thus driving moose numbers lower than they would go in the absence of predators.

Recent moose population declines in Alaska have reportedly followed this
pattern (Bishop and Rausch 1974, Gasaway et al. 1977).

Despite these speculations it is important to note that little
progress has been made in developing a general theory of natural regulation
of moose numbers and much controversy still surrounds the relative roles
of food supply and predation as regulators of moose density. Keith
(1974) listed four examples where moose irrupted when wolves were either
rare or absent and listed three different lines of evidence suggesting
that North American ungulates were limited by predation, rather than
food, in presettlement times. Pimlott (1967) presented similar arguments.
A.T. Bergerud in a series of papers (Bergerud 1971, 1974, 1978a, 1978b)
has argued that predation on boreal forest caribou *(Rangifer tarandus)*,
in many cases augmented by hunting, has caused high caribou populations
to decline and has prevented low caribou populations from recovering
throughout North America. Bergerud (1978a) has discussed the role of
moose as alternate prey for wolves and has identified possible consequences
of such predation for caribou.

During the past decade when this controversy was debated in the
literature moose populations in several areas of North America declined
and simulation modelling emerged as a powerful tool for a new generation
of systems ecologists. Several recent papers have modelled moose-
predator relationships using the functional components approach of
Holling (1959) and data from field studies in Mount McKinley National
Park (Haber et al. 1976, Haber 1977, Walters et al. in press). This
approach employs concepts of stability and resilience of ecosystems
wherein prey populations tend to exist at equilibrium and remain there
unless perturbed severely by natural catastrophies or man-caused events
(Holling 1973). If the perterbation is hard enough, the population

rapidly moves to a much different density where it remains at equilibrium despite the removal of the original disturbance. Thus, prey populations in natural environments are seen as capable of occupying two or more equilibria separated by a zone of instability that, once crossed, results in drastically different system behavior. This approach has also been used to model caribou-wolf interactions (Haber 1977, Haber and Walters in press).

ORIGIN OF THE THEORY AND ITS APPLICATION TO MOOSE

Ricker (1954) pioneered the use of reproduction curves in the fisheries literature as an attempt to correlate the density of spawning adult fish with the recruits they produced. This technique was widely used by fisheries biologists during their early attempts at population modelling and several variants of it have been applied to insect populations (Morris 1963, Hassell 1976). According to one school of thought reproduction curves are normally dome shaped in the absence of predation (Fig. 1a) but when efficient predators acting in an inverse density dependent manner suppress recruitment at low prey densities a sinous reproduction curve results (Fig. 1b). The range of densities where the reproduction curve dips below the replacement line (Fig. 1b) represents a "predator pit" from which the population must escape in order to increase from low densities. Because net increments are negative in the predator pit, a population that declines into this range of densities will rapidly decline farther until predators either decline or switch to other prey.

When the reproduction curve crosses the replacement line with a negative slope (Fig. 1b) a potential equilibrium density exists toward which the population tends to return if displaced. This results from the nature of the net increments above and below these equilibrium
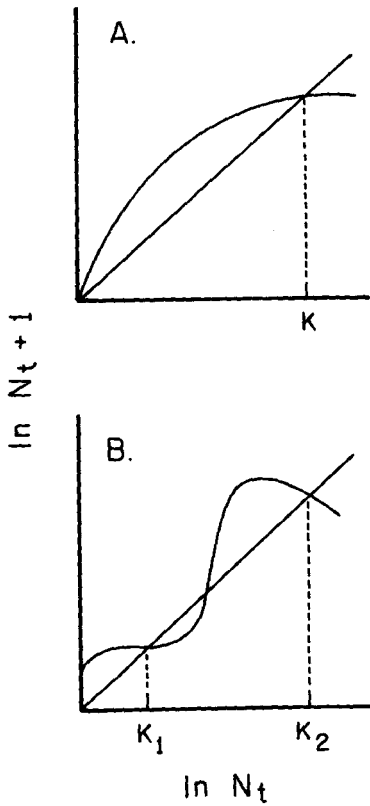
Figure 1. A. Reproduction curve in absence of predators.
Numbers are compared in successive years and increments are
positive until equilibrium density denoted by K is reached.

B. Reproduction curve in the presence of predators. Predators
act to produce negative increments over a certain range of prey
densities. Once prey exceed this range they "escape" predation
and move to an upper equilibrium (K_2) where intraspecific
competition regulates the population.

points; positive net increments increase the population while negative increments produce declines. Two such stable equilibria are portrayed in Figure 1b, a lower point where predation prevents population increase and an upper point where intraspecific competition limits population growth. Because the predators are limited by satiation and limited potential for growth of their own populations, predation alone cannot regulate at the upper equilibrium. When the reproduction curve crosses the replacement line with a positive slope (at some point between the two stable equilibria) the population moves away from this density because increments are negative below and positive above. These simplified processes are the basis of the multiple equilibrium model that has been used by Haber (1977) to simulate the population dynamics of moose and caribou.

Haber (1977) plotted recruitment as a function of herd density for 9 North American caribou herds and concluded that net annual increments tended to be negative at densities lower than 0.4 caribou per square kilometer when wolves were present at "normal" densities. Net increments declined when caribou exceeded 1.2 per km^2; the presence of two or more equilibria was suggested by a recruitment curve fit to these data. Because similar data were not available for moose, Haber simulated a recruitment curve for them based on available information and assumptions. Several of the most important assumptions include:

> 1. Moose deaths from nonwolf causes were assumed to be density independent, i.e. a constant fraction of the population died as density increased. In the absence of data on such mortality, it was assumed to range from 5-10 percent of the total population per year of average snowfall. Baseline mortality rates were assumed to

generate a pool of carrion that was treated as a separate type of prey for wolves. At high prey populations this pool absorbed a large share of the predation impact that was normally directed toward living individuals.

2. A linear density dependent effect on moose birth rates was assumed such that birth rates fell to zero for cows 4 years and older when population density rose to about 0.7 moose per km^2. At densities of 0.4 moose per km^2, birth rate was estimated at about 100 calves per 100 cows. These birth rates were further adjusted for the impact of snow during the winter of pregnancy so that birth rates were approximately halved after a severe winter.

3. Moose mortality caused by wolves was calculated with a multispecies disc equation (Charnov 1973) that requires knowledge of time spent by a wolf pack searching for prey, time spent at kills, the proportion of prey encounters that result in kills, and rates of encounter with prey over a broad range of prey densities. Of these, the last two were the most difficult to estimate. These data must exist for all prey types (sheep *(Ovis dalli)* and moose) and age classes.

The resulting model predicted stable moose numbers at a density of about 0.5 per km^2 in the absence of wolves. With wolves present moose remained near an upper equilibrium density of about 0.4 per km^2, very close to the density observed by Haber (1977) during field studies. If, with average sheep numbers, the moose population was driven down by an outside disturbance to a density below 0.2 per km^2 it would collapse to

a lower equilibrium of about 0.02 per km^2. Sheep numbers would also

decline and recovery of sheep and moose would not occur until all wolves

starved. Population collapses did not occur in the absence of outside

perterbations such as hunting even when winters were severe. These

predictions were dependent on several other parameters including adjustments

in wolf pack territory size.

EVALUATION OF THE MODEL

The perfect ecological model contains realistic biological details,

is precise, and has general application to a variety of natural phenomena.

Haber's (1977) model employs the functional components approach to

predation, a method much praised by insect ecologists and fisheries

biologists struggling with similar problems (Larkin 1979). At first

glance the multiple equilibrium model accurately portrays many qualitative

aspects of moose-predator interactions. Over a certain range of high

densities the model predicts stability of moose populations that coexist

with naturally regulated predators. It also provides for sharp declines

accelerated by predation similar to those that have recently been described

in Alaska (Bishop and Rausch 1974). But the model also has some serious

qualitative flaws. Grizzly bear *(Ursus arctos)* predation is not considered

despite the fact that bears are common in the park and are known to kill

moose. Forage dynamics are not considered. Loss of predators or prey

switching are considered necessary and sufficient conditions for moose

population increases from low densities. Wolf pack size is assumed to

be naturally regulated and not influenced by man. Moose cannot exist

with wolves if sheep are absent, or can exist only at high density. The

impact of predation on caribou numbers is ignored and a fixed number of

caribou is available to wolves during bimonthly periods from January

through August; this number exceeds the number of moose present during
May and June when loss of calf moose to predators should peak.

These qualitative deficiences rob the model of realism but what is
their effect on the quantitative predictions that result? The model
relies heavily on density dependent reductions in birth rate to produce
a stable upper equilibrium. Major birth rate reductions occur rapidly
over a density range of 0.4 - 0.7 moose per km^2. An assumed birth rate
of zero for adult cows at 0.7 moose per km^2 seems clearly inappropriate
and is contrary to field data presented by Haber (1977). The effect
of this assumption is to markedly underestimate the effect of predation
at high moose densities and to predict the presence of an upper equilibrium
at a density much lower than its actual occurrence in nature.

The field data from McKinley Park strongly suggest that the moose
population there is not presently subject to poor recruitment as a
result of a low birth rate. Twinning frequencies are high (W. Troyer,
personal communication) but recruitment is low probably as a result of
combined predation on neonates by wolves and grizzly bears. If this
moose herd is currently at equilibrium it must be a low equilibrium
where predation, not competition for forage, it dominant. If that is
the case, one would expect a dramatic increase in calf survival and
population growth in the absence of predators, perhaps resulting in a 3
to 4-fold increase in moose numbers before an inevitable crash. This
has been the scenario for other moose herds in Alaska, including those
adjacent to McKinley Park, and seems to have occurred generally throughout
North America. The limited potential of the climax plant communities in
McKinley Park to support high moose densities would perhaps make this
irruption less spectacular than others, but the pattern of moose population
growth and its causes would be identical to the irruptions that followed
predator reductions elsewhere in Alaska.

An additional quantitative deficiency in the model stems from its failure to predict realistic moose population densities signalling the start of population declines and accelerating predation. Such declines have begun throughout Alaska at densities well above the predicted upper equilibrium of 0.4 moose per km^2 (Bishop and Rausch 1974). This lends additional support to the idea that an upper equilibrium, if one exists, is considerably higher than that predicted by Haber's model and suggests that the "predator pit" extends over a much wider range of densities.

Although the model predicts a lower equilibrium density for moose at about 52 square kilometers per animal, this equilibrium was not stable during long simulations (C. Walters, personal communication). The model actually provides no means for moose populations to increase if they decline below densities of about 0.2 per km^2 as alternate prey also collapse. Haber and Walters (in press) suggested several mechanisms that would allow caribou populations at low density to escape predation, most notably massive immigration from adjacent herds. Similar mechanisms were not proposed for moose and one is left with the impression that moose simply cannot recover from low densities unless the resident wolves disappear or expand their territories greatly. These predictions also run counter to empirical observations.

I believe these deficiencies in the model are symptomatic of deeper problems. When recruitment is expressed as a function of density, all other factors are assumed to be constants in time. Recruitment depends only on the density of the population. This approach is valid only when density effects act without lags; when delayed density dependent mortality acts there are two values of recruitment at each density (Morris 1959). When species like moose exhaust their food supply or decline rapidly from other causes, they may return to a low density by a much different

route from that by which they increased. Also, for longlived animals the effects of skewed age distributions on total adult mortality rate can be so severe that net increments can be negative at any density. In addition, the well known link between nutrition and fecundity of ungulates suggests that net reproduction is tied more closely to relative food supply than to density per se. In light of these problems it seems legitimate to question the application of reproduction curves and the models they generate to ungulate population dynamics.

Krebs (1972) reviewed the use of stock-recruitment models in fisheries management and concluded that in no case of a major fishery was there any detectable relationship between density and recruitment. Holling (1973) recognized that reproduction curves are imprecise, that data to produce them are seldom complete over a wide range of densities, and variability is high. Larkin (1978:64) concluded: "Because of environmental vicissitudes, there is a wide gap between the theory of stock and recruitment and what seems to happen naturally. Whenever there are data sufficient to test theory, actuality departs significantly from the deterministic expectation. It is the common gossip that if you didn't have the certain knowledge that zero adults produce zero offspring, you could fit a Ricker model, or a Beverton-Holt model, or a straight line, or a circle, with equal satisfaction."

McCullough (1979) documented a parabolic relationship between number of recruits and population size for white-tailed deer *(Odocoileus virginianus)* in Michigan. He found the right hand segment of the curve to be "a morass of unpredictability" (McCullough 1979: 101) with extremely wide confidence limits. Meaningful predictions based on the curves generated by McCullough's data could only be made below densities about half that of carrying capacity because most of the response at higher

densities depended on survivorship of young, not reproduction. Environmental factors produced extreme variations in survivorship and far outweighed the effects of density. Similar relationships can safely be postulated for moose.

Finally, a serious quantitative deficiency in the model is its failure to accurately predict the proportion of the moose population killed by wolves as a function of moose density, i.e. determine the shape of the wolves' functional response curve. The field data gathered by Haber were simply inadequate to simulate these relationships but were used in lieu of stronger data from McKinley Park or elsewhere. In subarctic ecosystems where wolf territories are large and prey are migratory good data on the parameters necessary to accurately construct these curves are exceedingly difficult to collect. But functional response curves are critical components of the models discussed here. If they are lacking in quality, or the problems with them resemble those surrounding the use of reproduction curves, the model's ability to predict is severely compromised.

MOOSE, EQUILIBRIA, AND ECOLOGICAL THEORY

Several concepts surround the idea of equilibrium and many different definitions have been applied to it. Often, stability and equilibrium are used interchangeably. But a population may be stationary in numbers while not at equilibrium in the sense that a stable equilibrium state is one to which the population tends to return if displaced. Carrying capacity may also be confused with equilibrium by the underlying assumption that food is the only factor capable of regulating population density. Equilibrium concepts include the notion that instantaneous rate of increase of the population is zero. For long-lived animals like moose

with age distributions that are seldom stable, achieving a zero rate of increase often sets the stage for population change solely as a result of a skewed age distribution. The ecological literature is full of terms such as contancy, persistence, inertia, elasticity, cyclical stability, etc. (Orians 1975) coined by people trying to force ecological events into the conceptual framework of classical physics and systems theory. Basic differences between these areas of science may impede progress in our understanding of population dynamics and predator-prey relationships (Botkin and Sobel 1975).

During the past decade ecological literature on predator-prey relationships has mushroomed. Many of the papers stress stability and employ models. Collection of field data for many species including moose has lagged far behind and it appears that the process of inferring theory from empirical observations has been reversed. One first constructs a model and then casts about for field data to confirm the model's predictions. The emphasis is on what can happen in nature rather than what does happen. For managers whose emphasis must be on real events this approach is frustrating at best and may prove dangerous. An unfortunate result is that modelling loses its credibility with those who need it most and all theoretical arguments become suspect.

Currently, our understanding of moose population dynamics and moose-predator relationships is still in its infancy. Because moose have high individual biomass and long generation time, actual population biomass turnover is slow; there are inherent components of stability in the life cycle of moose. Long-term field studies of naturally regulated predators interacting with moose have not yet revealed whether or not moose populations experience the kind of stability associated with equilibria. Until they do, my view is that models based on multiple

equilibrium concepts are best used for generating hypotheses or for
pontifications after the event, rather than for predicting what will
happen before the event or for managing moose populations.

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