MANAGING MOOSE WITH THE KNOWLEDGE OF POPULATION DYNAMICS THEORY

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Abstract: Moose managers have historically operated under the implicit assumptions that either hunting was compensatory or the population was very stable and could absorb the impacts of hunting without change. The experience of declines of moose populations throughout North America has proven both assumptions false. Many theoretical forms of population response to harvesting are possible, from no change to catastrophic declines. Different management strategies are required for different expected scenarios . The presence of predators is particularly critical in determining the range of system behaviours that could be expected. A more scientifically precise method of reaching management decisions that incorporated hypothesis testing would lead to quicker gain of knowledge. An active adaptive approach to moose management is recommended to reduce the risks and costs of failure.

Ecological theory seems to have outstripped wildlife management in recent years. That is not necessarily bad because management requires innovative ideas to handle increasingly complex tasks and decisions. The difficulty arises because many of the most advanced and powerful ideas are commonly couched in mathematical terms and formulations that are obscure to biologists. There has been relativley little attempt by biological mathematicians to reach field level biologists. Journals such as Mathematical Biology are full of valuable ideas that cannot be read by the biologists that presumably stimulated the work in the first place.

The second problem arises because of the status of many of the moose populations in North America. Severe declines in population or harvest have occurred in Alaska, British Columbia and Ontario (Gasaway et al. 1983, Macgregor and Child 1981, Bergerud 1981). None of the declines were planned or anticipated by management agencies. If management agencies have any single common function, it is likely to maintain harvest levels. The conclusion that must be drawn then, since that objective has not been met, is that historical management strategies have been tested and found lacking.

The question to be addressed is "How can the ideas being developed in theoretical population dynamics and other fields be applied to the next generation of moose management?"

MODELLING AS A SOLUTION

The answer lies in modelling. After all, "modelling is just figuring out the implications of a set of assumptions" (Stephens and Charnov 1982), and these assumptions are the foundations of hypotheses. Developing hypotheses about the way the world operates is critical to science.

Models often reach their final formulation in a computer program, but by no means are all models computer models. In fact, whether we acknowledge it or not, we use models in our work and daily lives. The Copernican model of the earth's movements around the sun helps us to predict the seasons and the rising of the sun. That model ,too, was formulated and tested in mathematical terms.

The modelling exercise merely brings the subconscious ideas gained through observation, experience and training into the conscious realm for logical examination and scrutiny. Any hypothesis contains an associated set of assumptions that act in a method defined by the hypothesis to produce a result. Simple correlation of results without the causal explanation (ie. the hypothesis) is insufficient (Salmon 1978). The hypothesis is predictive in the sense that every time the assumptions are met the result must occur. If the predicted result does not occur, the hypothesis in that form is falsified. It is this method of hypothesis testing and falsification that seems most productive for scientific advancement (Popper 1959, Lakatos 1965).

Results that agree with the hypothesis increase our faith in the validity of the hypothesis but provide little new information or learning. False results, though, are highly informative. They may lead to rejection of the hypothesis in favour of an alternative, or modification of either the assumptions or hypothesis for further testing (Fig. 1). This exploratory approach to learning is fundamental to the technique known as adaptive management.

ADAPTIVE MANAGEMENT

It may initially sound ludicrous, but wildlife management decisions should also be made to risk failure. Failure is guaranteed given the uncertainties of the biological world, but unanticipated failure leads to catastrophe and excessive cost. Anticipated failures probe the unknowns of a system, stimulate change and generate knowledge (Yorque 1976).

Planning for uncertainty and failure has been formalized in the process known as adaptive management. Adaptive management seeks to balance the future returns of a constant policy against the experience and knowledge gained by exploratory policies, while maintaining flexibility toward the unexpected (Holling 1978). It is the shortest route toward optimal policies and the reduction of future uncertainty. Active adaptive management differs from passive adaptive management in that information is actively sought about unknown situations by experimental perturbations of the system. Passive management merely observes and uses available knowledge.

BEHAVIOURS OF A MOOSE SYSTEM

To understand the applications of these management approaches, we will investigate the assumptions of some common management schemes. A convenient illustration of the effects of hypotheses can be demonstrated graphically with the use of recruitment curves.

Many ungulates, including moose, have been shown to exhibit density dependent reproduction that results in dome-shaped curves of population change on population density (Fowler *et al.* 1980, McCullough 1979, Van Ballenberghe 1983). Recruitment data from Isle Royale in the 1960's, when the population was increasing, were well fit by a Ricker curve with a=0.7 and b=0.0009 (Fig. 2). Calf recruitment was adjusted upward for known loss to wolves. The

predicted carrying capacity for 12% non-wolf mortality was 2150 moose or 3.99 moose/km^2 (Page and Peterson in prep). The maximum growth rate (r_m) of this population was 0.368 or 36.8%.

This form of the density dependent relationship is the simplest possible, yet can still lead to extreme population fluctuations and instability (May and Oster 1976). The long life span of moose leads to further potential instability due to age structure effects (Goodyear and Levin 1980). Overshoot of the forage-based carrying capacity occurred for moose invading Isle Royale, but the relatively low rate of increase of moose suggests that a stable equilibrium with food should have been attained (Peterson and Page 1982, McCullough 1979, Caughley 1976).

An initial assumption of management programmes was that hunting was totally compensatory, or that any animals removed by harvest would be replaced by increased survival or reproduction of those remaining (Errington 1954, Eastman and Hatter 1983). It was hypothesized that wildlife populations could absorb the impact of hunting and return to previous levels. This was an appealing concept because little or no management intervention would be required after harvest to ensure continued maintenance of that harvest level. Total compensation implies no change in the recruitment curve between a hunted and an unhunted population (Fig. 3a). This idea was falsified when populations were found to decline under heavy harvest. Hunting as a compensatory mortality factor was modified to partial compensation. Partial compensation would lower the curve but reduction in the population level would be less than the harvest (Fig. 3b). No compensation (or additivity) implies that reduction in population is equal to the harvest (Fig. 3c). Another assumption included in these graphical formulations is that any effect would be density independent. In fact, compensation, if it occurred, would most likely be found at high population densities when competition between individuals was greatest. At low densities, any compensatory effect due to the lessening of competition with the removal of harvested animals would be insignificant.

More problematic is the effect of harvest on the form of population dynamics and the behaviours to be expected from the system. Clark (1976) has undertaken extensive analysis of the potential effects of harvest on the behaviour of animal populations. Harvest levels are rarely just a percentage of the population as in Fig. 3 but can take many different non-linear forms. Many of his analyses are dependent on investment in equipment and economic return from harvest for their characteristic behaviours. While relevant to fisheries and whaling, they have comparitively little relevance to sport moose hunting. Some cases are informative though, particularly the effects of depensation. Depensation occurs when harvest is proportionately heavier at low population densities than at high levels.

Let's suppose that a harvest of 11% has been tried on Isle Royale (without wolves) and found sustainable (Fig 4a). On that basis, a quota of 114 is set for the population at carrying capacity and the population declines close to the maximum sustained yield (Fig 4b). The behaviour of a system under an 11% harvest is quite different from that of a system under a quota of 114, though for years of harvest both populations would seem the same. The difference would occur if the population was unexpectedly or unknowingly decreased below the level of positive recruitment in Fig. 4b. The population in Fig. 4a would recover to its previous level, while the other would be hunted to extinction. In reality, most managers would be aware of the disaster in the population and reduce the harvest but perhaps not until a very significant decline. Quota systems cannot be considered a safe strategy on the basis of previous success.

AGE AND SEX SELECTIVE HARVESTING

Another management scheme is age selective harvesting. The problem that has led to the initiation of these new schemes is low moose densities, with a significant portion of the blame due to overharvest, and frequently confounded by predation. The solution being promoted is to shift the harvest to calves. This argument assumes compensation in calf survival, but compensation is only able to occur at high densities where competition for resources is strong. What is frequently overlooked is that all subsequent age classes are dependent on the initial cohort. Age class 2 is limited by the number of moose in Age class 1. In other words, the number of moose in Age class N+1 is primarily determined by the number of moose in Age class N (Fig. 5). Compensation assumes the converse, that Age class N+1 also has a very great effect on Age class N. The impact of one animal in Age class N on Age class N+1 will be much, much greater than the impact in the reverse direction. The sacrifice of calves will not be compensated for as much as future populations will be limited, especially at low densities. Shifting harvest to calves would then be expected to cause a decline in future populations and harvest levels.

The other reason for age selective harvesting strategies was to help correct baldly skewed sex ratios due to disproportionate male harvest (Macgregor and Child 1981). Sex selective harvesting has also been instituted. Again there is an interaction with density that should be acknowledged. Moose bulls are physiologically capable of breeding at least 7 females (Bubenik pers. comm.), but breeding in later estrous periods has been found in populations that have many fewer than 7 females per bull. I suspect the males are incapable of finding the females in these low density populations. I also hypothesize that the relationship between the maximum allowable sex ratio and density is different for taiga and woodland moose (Fig. 6). Females in the taiga aggregate around males before the onset of estrous insuring impregnation at the earliest estrus even if males are rare. Sex ratios of 5 cows per bull cannot be said to be a problem of too few males, but primarily are due to too low a density. The problem will not likely be corrected by harvesting of females, but only by reduction of the harvest of males and a subsequent reduction of total harvest.

The work of Tony Bubenik has primarily stimulated the interest in age and sex specific harvesting, but his recommendations have been misinterpreted in these harvest strategies. Tony recommends a balanced age and sex structure in the population to reduce social strife and produce healthy moose with better trophy antler growth. These results were produced in an experimental manipulation of chamois, but total population and the resultant harvest declined (Stringham and Bubenik 1974). Age and sex specific harvesting strategies as presently formulated in North America appear likely to cause declines in populations rather than increases as intended, unless total harvest levels also decline.

CONCLUSION

A rigorous scientific approach to moose management decisions acknowledging the tentative nature of our knowledge is recommended. Explicit delineation of the assumptions of our hypotheses and models and the incorporation of the results into an active adaptive management scheme will increase the success of future management efforts. Advanced techniques of linear and dynamic programming and optimal control theory can be incorporated to produce models that can rank economic return of harvest strategies and incorporate diverse effects such as predator control (Walters et al. 1979). These complex models can be very useful if coupled will understanding of the assumptions and shortcomings of the model. In fisheries, they have produced notable successes, such as the tuna fishery . Perhaps in moose management our knowledge is sufficient only for simple models, but the need for useful models is great.

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Figure Legends

Figure 1. Learning through model testing.

Figure 2. Recruitment curve for moose on Isle Royale. Data has been corrected for known wolf mortality and assumes 12% non-wolf mortality. Maximum rate of increase is 36.8%.

Figure 3. Effects of different hypotheses of compensatory mortality on recruitment.
  a. Effect on recruitment curve of total compensation under a harvest equal to 20% of the natural mortality
  b. Effect of partial compensation.
  c. Effect of no compensation (additivity).

Figure 4. Depensatory effect of a quota harvest compared to a proportional harvest.

Figure 5. Assumptions of age selective harvesting.

Figure 6. Proposed relation between density and allowable sex ratio skewness.

MODEL TESTING

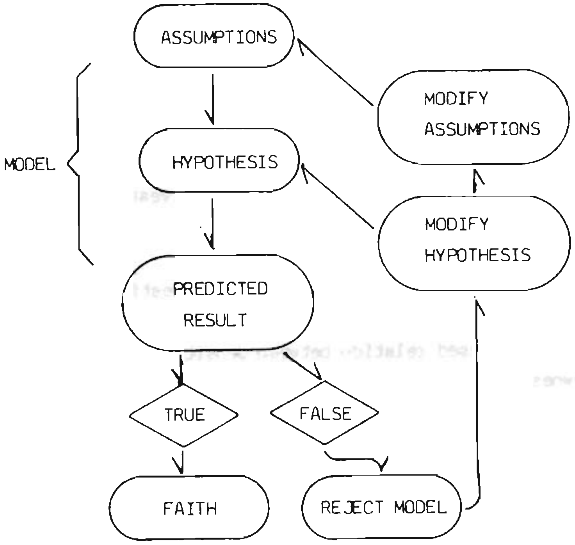
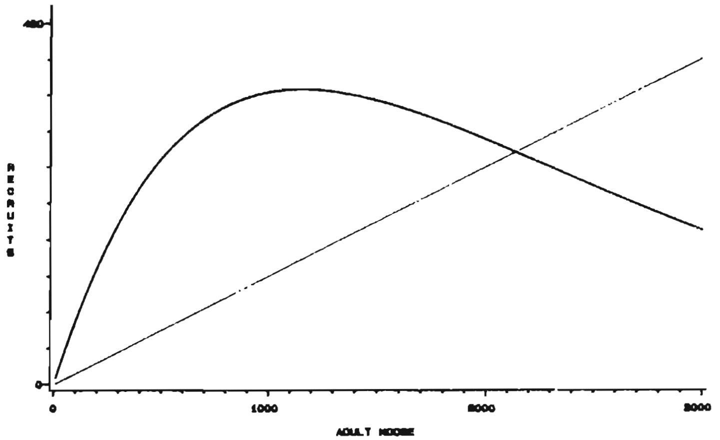
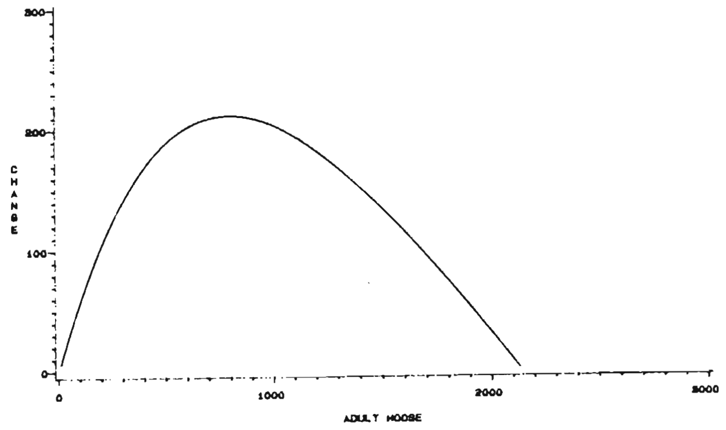


FIG. 1



RECRUITMENT CURVE FOR ISRO MOOSE
ADULT MORTALITY OF 12% ASSUMED



RECRUITMENT CURVE FOR ISRO MOOSE

FIG. 2

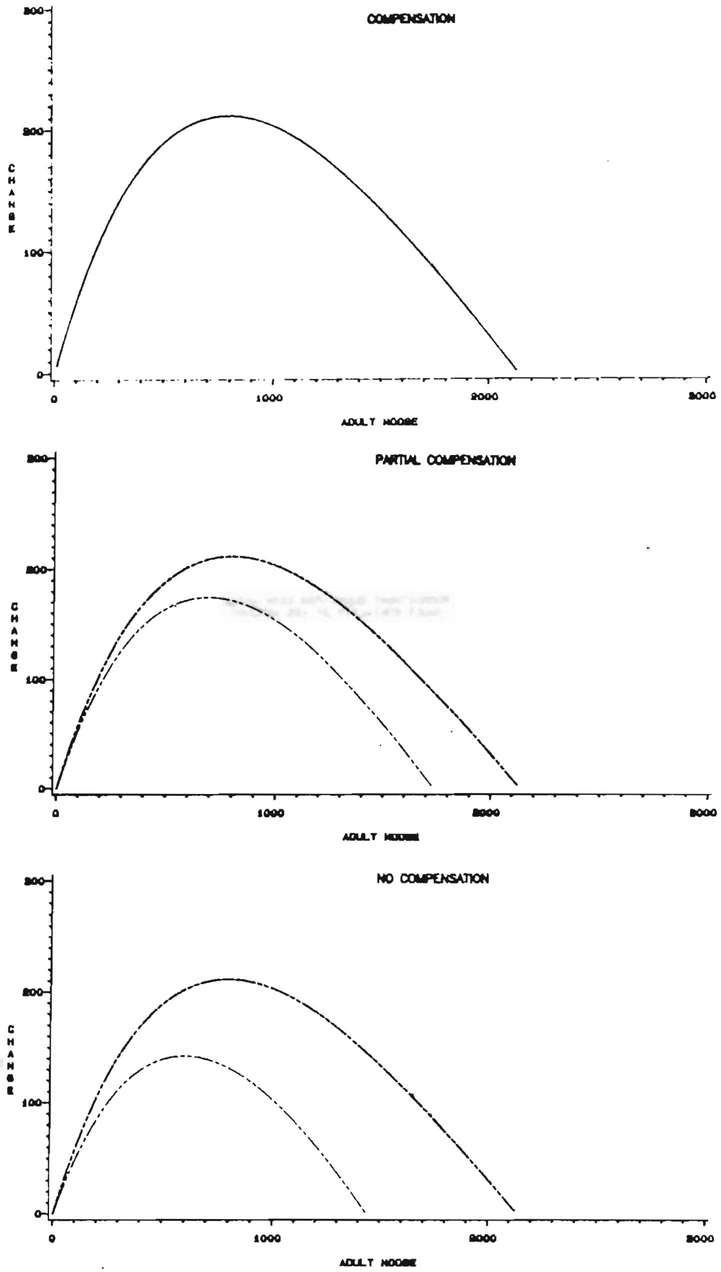
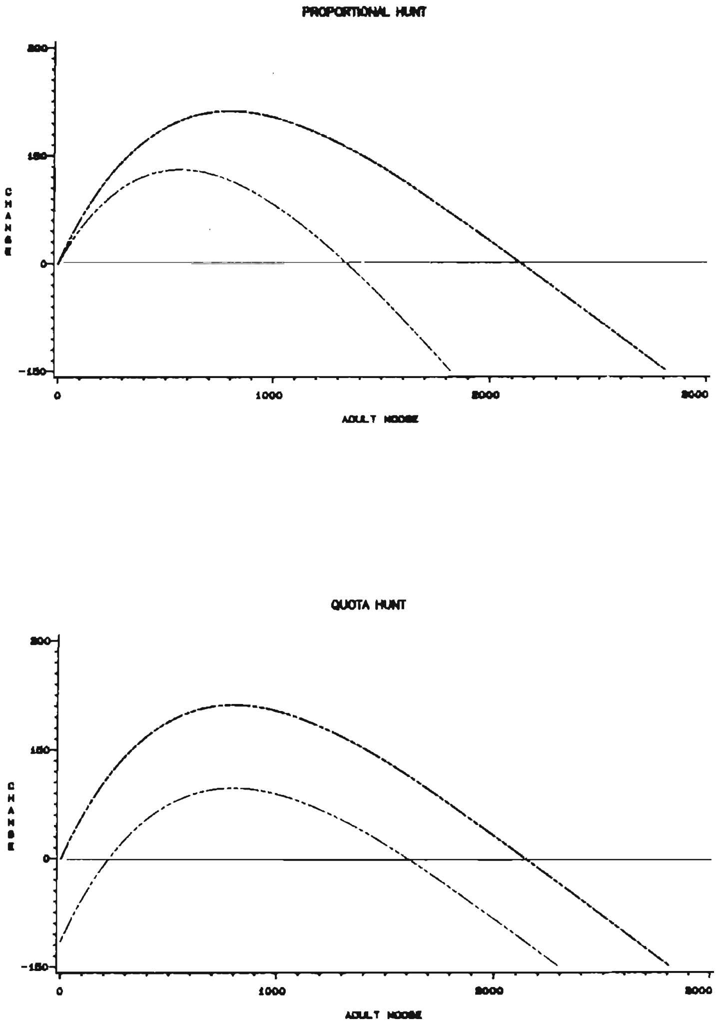


FIG. 3



RECRUITMENT CURVE AFTER HUNTING

FIG. 4

$\text{Age 1} \xrightarrow{\text{determines}} \text{Age 2} \xrightarrow{\text{determines}} \text{Age 3} \ldots$

but Compensation (Social Stress) also implies :

$\text{Age 1} \xleftarrow{\text{determined by}} \text{Age 2}$

$\longleftarrow\!\!\longleftarrow \text{Age 3}$

$\longleftarrow\!\!\longleftarrow \cdot$

$\cdot$

$\cdot$

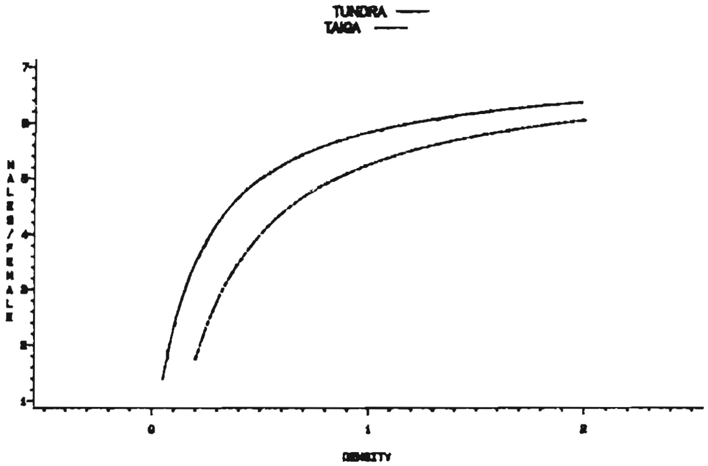
But

$\text{Age 1} \rightleftarrows \text{Age 2}$

$\therefore$ sacrificing Age 1 will not likely be compensated for as much as future populations will be limited, especially if populations are not already close to carrying capacity.

Shifting harvest to calves without reduction in total harvest, in a population in decline, will cause further decline in future populations and harvest levels.

FIG. 5



SEX RATIO AT WHICH ALL FEMALES ARE BRED

FIG. 6