HOW TO MODEL MOOSE POPULATION ECOLOGY?

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ABSTRACT: Modeling population dynamics of a species like moose, living under intense selection due to heavy exploitation, must consider both short term and long term dynamical processes. Population dynamics are constrained by the distribution of the environment, effecting both short and long term dynamics, and the genetic distribution, mainly effecting long term dynamics. Both, the short and long term dynamical processes are determined by the individuals' survival probability and rate of reproduction. This observation is fundamental. If field studies effectively are to enhance our ability to predict moose population dynamics, various factors supposed to effect the moose ecology must be evaluated in terms of survival and reproduction. These general problems are briefly discussed. To highlight these problems a simple example is given that considers variation in population growth rate when reproduction is determined by both environmental as well as genetical factors.

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There are several reasons why moose population dynamics need to be modeled carefully. In Sweden about 150 000 moose are killed each year (Anon. 1980-1989) making moose the single most important hunted species and, consequently, an intensely exploited species. Important modeling issues are the avoidance of over-exploitation or that of receiving maximum yield of e.g. meat production. Moose also browse on economically important trees, particularly on the pine (e.g. Lavsund 1987). Consequently there are demands that the population should be kept at some economically defendable level. This adds further restrictions to be consider in a population dynamic model and again we have to face an increased risk of over killing.

In the proceeding section I discuss the main components of a successful population model, measured by the ability to predict the future population size and composition. Finally I consider an example of how the population growth rate might vary when both the genetic and the environmental state of a population are considered.

THE SHORT AND LONG TERM POPULATION DYNAMICS

Alike many other species, the moose is characterized by long and short term variation in population size (e.g. Bishop and Rausch 1974, Danilov 1987 and Haagenrud *et al.* 1987). Consequently, we must consider processes that systematically change populations over long time periods and processes that vary the populations "unsystematically" around the long term, systematical change.

Studies on population dynamics should not to be restricted to changes in *number* of moose. It should also concern the shift in the distribution of individuals within a population of a constant size, changes in age structure, sex-ratio, mass distribution, number of individuals using a particular food source etc.. For instance, when predicting the future meat yield from a moose population, the dynamics of mass distribution within the population, might be as important to consider as the total number of individuals.

A population's dynamics is determined by the pattern of survival and reproduction. This is always the case when concerning changes in population size (of course emigration and immigration will effect population dynamics, but only when population studies are geographically restricted). But, there are situations when the dynamic of survival and reproduction does not apply. For instance, the habit of stripping bark on coniferous trees, observed in the Swedish moose, could be spread in the population by learning (e.g. Edwards 1976). Consequently, if this would be true, a change in distribution of individuals using this behaviuor is not determined by nighter survival nor reproduction.

Presently three main processes are responsible for changes in populations: 1) Dynamics of the surrounding environment such as climate and food availability. 2) Natural selection resulting in Darwinian evolution of characters such as sexual dimorphism and age specific reproduction. 3) Cultural evolution of certain behaviours, such as food choice and migratory behaviours. The last two processes are very much alike and might not always be separable. The most important difference between cultural and Darwinian processes, is that the first occurs between generations as well as within generations, while the second only occurs between generations. Also, cultural evolution is probably constrained to behavioural characters primarily. Thus, the cultural process is not necessary tightened to reproduction and/or survival as is the Darwinian process.

All three processes can give rise to long term changes in a population. Short term variation of populations is only known to have environmental origin. But in the case of the cultural process, our knowledge is very limited. The three processes will of course also influence each other causing an inter-process dynamic.

To make useful models, we must identify the processes that cause long term trends and those that cause short term fluctuations. For instance, in the Swedish moose long term changes in the population might be caused by natural selection, as there is an intensive, systematical, national-wide exploitation of the population. An example of an existent selection is that cows lacking calves have a much larger probability of being killed than cows with calves, since the shooting is firstly directed towards the calves. Consequently, at each hunting occasions, cows with twin-calves have the highest probability to survive. Thus, the hunting strategy in Sweden results in a strong selection on the reproductive rate, which might favour an increased reproductive effort in terms of a larger twining rate as well as a decreased age of first reproduction. This scenario is just one among several possible selective consequences expected from intense exploitation. Hence, an important issue for modeling is to predict consequences of different hunting strategies.

Even though natural selection could cause long term changes in the population, so could also environmental alterations. For instance, large scale clearcutting and plantations, have greatly increased the availability of moose food. The proximate variation in population size between years is most likely caused by pure environmental impact on the time-specific survival and reproduction. Such environmental factors might for instance be variation in winter climate and shoot production of important food trees.

GENES, ENVIRONMENT AND POPULATION GROWTH RATE

The purpose of this model is to show what effects genetic and environmental variation can have on population dynamics. My main suggestion is that we must start considering the kind of problems described in the model. I also have to point out that this model does not try to mimic the true situation in the moose. But still, the moose most likely have genetic variation in reproduction as well as some responce in reproduction due to environmental variation. These are the main effect of the variables in the model.

The model is an example of how gene action and environmental variation can effect variation in population growth rate. I consider a situation where calf production is both genetically, which is the case in many animals (e.g. Falconer 1981) and environmentally determined (e.g. Franzmann and Schwartz

1985). The analysis is simplified by assuming the model moose as haploid. I further assume that only two moose genotypes, A and B, exist. The A-genotype can only produce one calf while the B-genotype can produce two calves. A and B occur with the frequencies '$1-q$' and q respectively. The expression of the calf-number-gene is affected by the environment and the gene can only set the upper limit of calf production. If a cow has insufficient resources for reproduction, fewer calves are produced. This is important, as it specifies how genes and the environment give rise to the phenotypic expression.

The home rang quality of a cow is classified into: poor, intermediate and good home-ranges. This classification depends on the available food resource, r, in the cow's home-range. The frequency of home-ranges with a given resource is $f(r)$. An example of a frequency distribution of home range quality is shown in Fig. 1. In poor home-ranges, the resource level is less or equal to level p, $r \leq p$, and does not admit any calf production, regardless of the cows' genotype. The frequency of such home-ranges is $f(r \leq p)$. Cows inhabiting good home-ranges, above or equal to resource level g, $r \geq g$, will produce one or two calves depending on genotype. The frequency of good home-ranges is $f(r \geq g)$. The remaining home-ranges are of intermediate resource levels, $p<r<g$. In these all cows produce one calf, independent of genotype with a frequency of $1-[f(r \leq p)+f(r \geq g)]$ (Fig. 1). Below I will use the notation $f(p)$ and $f(g)$ instead of $f(r \leq p)$ and $f(r \geq g)$, respectively. The frequencies of home-ranges of different resource levels might differ between years and/or areas as illustrated by the two distributions in Fig. 1.

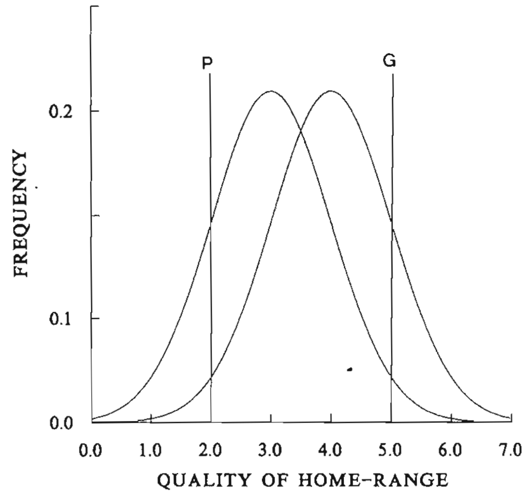

Fig. 1. Two frequency distributions of cows inhabiting home-ranges of different resource quality. The two distributions could represent different years and/or areas. The vertical line, P is the limit above which a cow can reproduce and G above which B-genotype cows are able to produce twins (more details are found in the text).

The frames of the model has now been described and we are ready to analyse the system. For simplicity, I will only concider the exponential growth phase of the population. That is $N_t = \partial^t N_0$, were ∂ is the time-specific growth rate of the population and N_t is population size at time t.

The time-specific growth rate could be determined from the Lotka-Euler equation (e.g. Charlesworth 1980), which gives a very simple expression if we assume a constant calf survival, s_c, a constant adult yearly survival, s_a, and age-independent calf production, m (e.g. Schaffer 1974). In this situation, $\partial = ms_c + s_a$. Inserted into the exponential population model we get, $N_t = (ms_c/2 + s_a)^t N_0$, assuming a sex-ratio of 1/2.

We are now in the position to introduce the effects of genetic and environmental variation on reproduction and to study the effect on the population dynamics. First, we estimate the average reproductive rate of the population, that is

$$
\begin{aligned}
E[m] &= 0\{qf(p)+(1-q)f(p)\} + 1\{q(1-(f(p)\\
&\quad +f(g))+(1-q)(1-f(p))\} + 2qf(g)\\
&= qf(g) + 1-f(p).
\end{aligned}
$$

Inserted into the population growth model we get the following expression

$$
\begin{aligned}
N_t &= [E[m]s_c/2 + s_a]^t N_0\\
&= [\{qf(g) + 1-f(p)\}s_c/2 + s_a]^t N_0.
\end{aligned}
$$

To keep the population from declining $[qf(g) + 1-f(p))s_c/2 + s_a] \geq 1$, or

$$[1 + qf(g)-f(p)] = E[m] \geq 2(1-s_a)/s_c \qquad (1).$$

This inequality demonstrates the genetic composition and environmental requirements for the population to persist in the long term.

Consider a hypothetical population example: The yearly calf survival, s_c=0.40 and yearly adult survival s_a=0.70, the proportion of cows living on poor home-ranges, $f(p)$=0.1. Substituting these figures in eq. 1, we get $1 + qf(g) - 0.1 \geq 1.5$ or $f(g) \geq 0.6/q$ (Fig. 2). Thus, even if all individuals in the population carry genes to give birth to twins, that is when q=1, the population can only persist if the proportion of good habitats, $f(g)$, is larger or equal to 0.60 (Fig. 2). This provides an insight why and how populations are geographically restricted and varies in density from one area to another (e.g. Pease *et al.* 1989). In some areas the distribution of good home- ranges may not be sufficient to support the moose population requirements (e.g. Lande 1987).

Finally, consider the variation in population growth rate as it might be important due to its effects on the probability of population extinction. The larger the variation, the greater the risk of extinction. The growth rate variation is defined as, $V[\partial] = Var[E[m]s_c/2 + s_a] = s_c^2 Var[E[m]]/4$. From general statistical theory the variation in the expected value equals the variation in the studied variable divided by sample size, which in our situation is $V[m]/t$. Thus, to determine $Var[\partial]$ we must first determine $V[m]$, which is

$$\begin{aligned} \mathrm{V[m]} &= \{\mathrm{qf(p)+(1-q)f(p)}\{0-\mathrm{E[m]}\}^2 + \{\mathrm{q(1-(f(p)+f(g))+(1-q)(1-f(p))}\}\{1-\mathrm{E[m]}\}^2 \\ &\quad + \mathrm{qf(g)}\{2-\mathrm{E[m]}\}^2 \\ &= qf(g)(1+2f(p)-qf(g)) + f(p)(1-f(p)). \end{aligned}$$

Consequently, the variation in population growth rate is

$$V[\partial] = s_c^2\{qf(g)(1+2f(p)-qf(g)) + f(p)(1-f(p))\}/4t.$$

This expression indicates under what environmental and genetic state we should expect the largest variation in growth rate. The size of growth rate variation is particularly important in the perspective of population extinction probability. This probability is proportional to the growth rate variation and, consequently, the risk of extinction is largest when the variation is at some maximum. The maximum is found by deriving $V[\partial]$ and solving the equations $V'[\partial]=0$. The Fig. 3. depict how the variation is effected by the gene and good home-range frequency at a

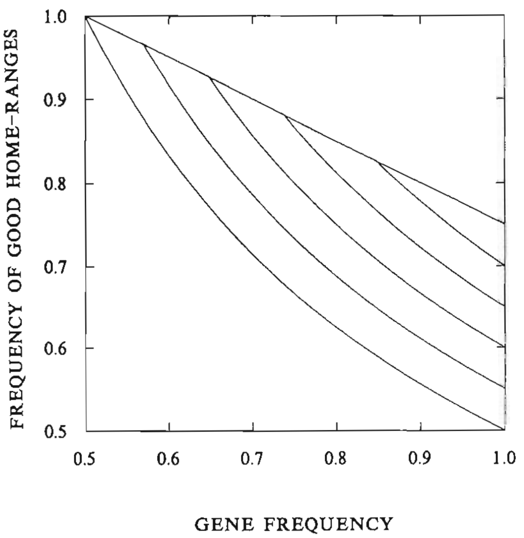

Fig. 2. There are environmental and genetical states where populations can not persist. This figure depicts when the model population increases, decreases and are stable. The isoclines represents the state where the population is stable for different frequencies of poor home-ranges, from 0 (lowest isocline) to 0.20 (uppermost isocline). Above an isocline the population will increase, below it decreases. Above the straight line diagonal there are no possible combinations of home ranges of different quality.

given frequency of poor home-ranges. The Fig. 3 also gives a restricted picture of how the maximum variance can shift due to the genetical and environmental state of the population. The solutions where $V[\partial]$ is at a maximum for the frequences f(p),f(g) and q are rather cumbersome (see Appendix).

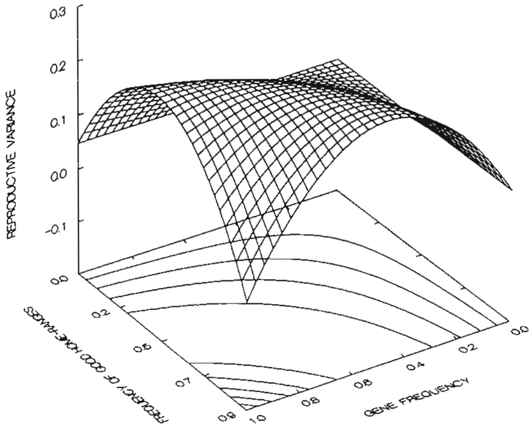

Fig. 3. Reproductive variance as a function of frequency of cows inhabiting good home-ranges and twin-calf allele frequency among the cows (at a given frequency of poor home-ranges, *f(p)*=0.1). The variance maximum shifts as the frequency of good home-ranges and allele frequency alters.

ACKNOWLEDGEMENT

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APPENDIX

The solutions of $V'[\partial]=0$ gives the maximum variance for unique combinations of gene frequency, frequency of poor and good home ranges, which are as follows

$$q = -\{[4f(g)^4-8f(g)^3-8f(g)H^2f(p)+4f(g)(2f(p)-3)+4f(p)H^2+4f(p)+1]^{1/2}-2(f(g)H^2-f(g)+f(p)+^{1/2})\} / 4f(g)$$

$$f(p) = [2qf(g)^2-2f(g)(q^2+q+)+q-1] / [2(f(g)-(1+q))]$$

$$f(g) = -\{8[f(p)^2-f(p)(2q^2+2q-1)+q^4+2q^3+3q+]^{1/2}-(f(p)+q^2+q+1/2)\} / 2q$$

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