EVALUATION OF THE STATE AND PRODUCTIVITY OF MOOSE POPULATIONS USING LESLIE MATRIX ANALYSES

V. N. Lopatin and S. V. Rosolovsky

Institute of Evolutionary Animal Morphology and Ecology, Russian Academy of Science, 117071, Moscow, Russia

ABSTRACT: We examined the use of a Leslie Matrix analysis for estimating moose (*Alces alces*) population parameters and allowable harvests from a moose population near Leningrad, Russia, during 1959–1975. Leslie Matrix analysis indicated that moose fecundity and mortality exhibited cyclic fluctuations.

ALCES SUPPLEMENT 2: 77-80 (2002)

Keywords: Alces, fecundity, harvests, Leningrad, Leslie Matrix, mortality, populations, productivity

Evaluation of population status is a traditional problem of modern ecology. Closely associated with it are the practical problems of determining management strategy. Many population models have been used to mimic populations, but the question remains if these models are representative of nature. Many quantitative methods have been used, but solution of many mathematical and ecological problems necessitates expansion of the traditional methods of examining ecological problems (Watt 1971, Jeffers 1981).

One method of expressing population dynamics is through the use of a Leslie Matrix model (Leslie 1945), which considers age-specific birth and survival rates. Rusakov (1979) used a Leslie Matrix model to examine a moose population in northwestern Russia. Also, Peterson (1977) used a Leslie Matrix model to examine moose populations on Isle Royale, Michigan, USA. Based on these and similar analyses (Aivazyan 1968, Pesaran and Slater 1984), we refined these methods for this study as provided by Lopatin and Rosolovsky (1988). These modifications result in rates of fecundity and mortality of individuals dependent on changes in density. For example, knowing the fecundity and death rate, one can determine the relative change in numbers over time and can estimate death rate. The purpose of this paper is to examine the dynamics of a moose population near Leningrad, Russia for the period 1959 - 1975.

METHODS

We used a Leslie Matrix analysis to examine moose population fluctuations within the Leningrad Region, Russia, during 1959 - 1975 (Rusakov 1979). Under natural conditions, fecundity rate is often difficult to obtain under field conditions. Often, field managers use the average number of calves per cow as an estimate of fecundity rate. These ratios can be represented as number of calves per female (X axis) and death rate (Fig. 1). This indicates that population numbers are more sensitive to changes in death rate than fecundity. If the numbers of calves per female and total number in the moose population are determined accurately, equations derived from Fig. 1 can be helpful in managing the moose population.





Fig. 1. Changes in moose population numbers in relation to fecundity and mortality rates.

RESULTS AND DISCUSSION

The moose population increased during 1959 - 1963. The average finite rate of increase was 1.165. To maintain this rate of increase, total mortality should have been about 14.2% of the autumn population. A harvest rate of 3.6% would have increased the total mortality rate to 17.8%. During the period of population reduction (1964-1966), the average rate of change was 0.895. At a fecundity rate of 0.45 calves per female, the death rate reached greater values and was estimated at 33%. Mean harvest over that period was 9.3%, and natural death rate was estimated at 23.7%. The calculated rate of increase for that death rate was 0.945, a decline in the population. Thus, even a complete cessation of harvest would not have prevented reduction of the moose population. The moose population was declining naturally, and additional human harvests would have accelerated the decline.

During 1967 - 1970, average change in the population was about 1%. Thus, another 1% of the population could have been removed without reducing total numbers. By adding an additional 8.0% harvest, a total mortality of 9.0% could have stabilized moose population numbers. During 1971 – 1975 the mean value of change was about 2%, which allowed a harvest of about 2% of the population. By adding this value to the mean size of harvest (8.6%), one obtains the admissible harvest, which is now equal to 10.6%.

Initial harvests were too small to halt population growth. Thus, in managing the initial population, harvests were too conservative. Conversely, when the population was declining, harvests were too large which increased the rate of population decline. The two harvest strategies during periods of population increase and population decline, in theory, should have stabilized the population. Subsequently, harvest can provide a balance in fecundity and mortality, if all factors are equal. However, determination of optimum population size is difficult to determine, much less manage.

We suggest that the fluctuations observed during this study resemble longterm cyclic fluctuations. According to the theory of dynamic systems, the limit cycle is a stationary trajectory of the real system, which is in the oscillatory regime (Smith 1975, Andronov et al. 1981, Butenin et al. 1987). Rusakov (1979) has provided the equations describing the cyclic nature of moose populations as depicted in Fig. 2.



Fig. 2. Moose population trajectory as a result of cyclic changes in fecundity and mortality (A = maximal productivity, B = maximal numbers, C = minimal productivity, and D = minimal numbers).



We suggest cyclic changes in fecundity and mortality explain moose population dynamics. The stationary trajectory of this process is presented in a 3-dimensional diagram as illustrated in Fig. 3. Increases in the D-A-B range result in increased fecundity. However, death rates change differently. During the first stage of the rise in numbers (D-A), death rate declines, which results in an increase in moose population size. During the A – B phase, rate of increase increases, and despite high fecundity, the population rate of growth declines and results in a stable population (B).

The phase of population decline (B–C– D) is accompanied by a decrease in fecundity. During the period B – C, death rates increase, and despite high fecundity, leads to a rapid population decline. During the second period of the population decline phase (C–D), death rate reaches a maximum (C), and declines, which leads, despite the lowering of fecundity, to stabilization of the population size at a minimal level (D).

Productivity also cycles at different phases of population dynamics (Fig. 4). For example, maximum productivity, similar to a logistic model, is attained during the increase phase at numbers roughly equal to the mean between maximal and minimal (A). At the same time, minimal productivity is attained during the decline phase, when



Fig. 3. Moose population numbers as a function of cyclic changes in fecundity and mortality (A–D as in Fig. 2).



Fig. 4. Changes in moose productivity as a function of cyclic changes in birth and death rates (A–D as in Fig. 2).

numbers are roughly mean between the maximal and the minimal (C).

We suggest, that based upon the above examples, the demography of moose populations can be expressed by simple graphs resulting from a Leslie Matrix analysis. These models allow evaluation of status, simple population dynamics, and productivity of individual moose populations which could be useful for determining harvest strategies.

REFERENCES

- AIVAZYAN, S. A. 1968. Statistical investigation of dependencies. Metallurgy, Moscow, Russia. (In Russian).
- ANDRONOV, A. A., A. A. VITT, and S. E. KHAIKIN. 1981. Oscillation theory. Nauka, Moscow, Russia. (In Russian).
- BUTENIN, N. V., Y. I. NEIMARK, and N. A. FUFAEV. 1987. Introduction to the theory of nonlinear oscillations. Nauka, Moscow, Russia. (In Russian).
- JEFFERS, D. 1981. Introductions to systems analysis: application in ecology. Mir, Moscow, Russia. (In Russian).
- LESLIE, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.
- LOPATIN, V. N., and S. V. ROSOLOVSKY. 1988. Demographic analysis and its use



for evaluation of the state of populations. Pages 24–39 *in* Population studies of animals in reserves. Nauka, Moscow, Russia. (In Russian).

- PESARAN, M., and L. SLATER. 1984. Dynamic regressions: theory and algorithms. Finances and statistics. Moscow, Russia. (In Russian).
- PETERSON, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Park Service Science Monograph 11:1–200.
- RUSAKOV, O. S. 1979. Moose. Pages 174–271 *in* Ungulates in northwestern USSR. Nauka, Leningrad, Russia. (In Russian).
- SMITH, D. M. 1975. Models in Ecology. Mir, Moscow, Russia. (In Russian).
- WATT, C. W. 1971. Ecology and management of resources. Mir, Moscow, Russia. (In Russian).

