

## Models of ungulate population dynamics

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*Abstract:* A useful theory for analyzing ungulate population dynamics is available in the form of equations based on the work of A. J. Lotka. Because the Leslie matrix model yields identical results and is widely known, it is convenient to label the resulting equations as the "Lotka-Leslie" model. The approach is useful for assessing population trends and attempting to predict the outcomes of various management actions. A broad list of applications to large mammals, and two examples specific to caribou are presented with a simple spreadsheet approach to calculations.

**Keywords:** Modelling, ungulates, Leslie matrix model, Lotka-Leslie model

**Rangifer**, Special Issue No. 7: 24–29

### Introduction

The material presented here was prepared for a workshop session having the theme "Incorporating ecological theory into research design". The major issue in modelling ungulate population dynamics is the lack of suitable field data. We never have enough data and frequently delude ourselves that in any defensible way. This lack of good data leads me to be very pessimistic about many aspects of what seems to pass as ecological theory these days. A few years ago some of these concerns were suggested in a note about testing hypotheses (Eberhardt 1988a).

### The Lotka-Leslie model

There is a body of theory that fits the overall theme of incorporating theory into practice very well indeed, and that has been neglected in practice. This is the theory developed by A. J. Lotka about 80 years ago, which underlies modern studies of demography. Another expression of the same general approach was presented by P. H. Leslie in two papers in the 1940's (Leslie 1946, 1948). Calling the underlying theory the "Lotka-Leslie model" provides a useful reminder of the equivalence of the two approaches.

To justify such a label, one needs to review a little background. Lotka's approach was via continuous mathematics, no doubt inspired by the need to accommodate the human habit of reproducing at any season of the year. His principal result was thus expressed as an integral equation. On the other hand, Leslie used matrix algebra, and thus considered events at discrete points in time, so that the repro-

ductive elements in this model are often described as averages or approximations.

Inasmuch as caribou (and many other wildlife species) give birth only in a short time interval each year, it is possible to avoid many of the complications of the usual demographic analyses. L. C. Cole (1954) developed the necessary equations for such a discrete approach. It turns out the principal equation is the same as that widely used as an approximation to Lotka's equation, which cannot be solved directly in its integral form. Hence, for species like caribou, there is a simple and direct approach in discrete mathematics.

Cole thus provided a very useful formulation and his paper should get more attention in textbooks than usually is the case. Actually, it does get cited quite a bit for another aspect. Probably it is worthwhile to digress here, and mention that issue, in view of the suggestion that we should consider "the demographic parameters that are most influential in terms of caribou numbers". That can be done very simply – adult female survival is the most important such feature. This is readily demonstrated, and there likely are now a dozen papers in the recent literature addressing that point. I have had occasion to stress it in two papers (Eberhardt and Siniff 1977; Eberhardt *et al.* 1982), both of which deal with species (marine mammals and feral horses) having reproductive and survival rates somewhat similar to those of caribou.

Feral horses, however, start giving birth much earlier in life than marine mammals, and thus illustrate

an important secondary feature of population dynamics, i.e., appreciably higher population growth rates are possible when habitat conditions permit first births at age 2 rather than at age 3. Cole was intrigued by this feature and described it for the range of species from bacteria to large mammals. On such a scale, the age of first reproduction does indeed have an impressive effect on population growth rates, and academic types thus often tend to stress that aspect. Hence we need to remember that caribou are not insects, and that much of the population dynamics material found in textbooks is derived from data on insects.

Returning to the main theme here, the Leslie matrix approach starts with a listing (a vector) of the number of individuals in discrete age classes and projects that listing to produce a new such listing one or more units of time in the future, adding in gains from reproduction and losses due to mortality. Recalling that we are dealing with a species that gives birth in a short time period each year, it is most convenient to suppose that the youngest individual in a given population is almost one year of age in the initial listing (age vector). The next observation of the population is made one year later, so that the survivors of the initial population are a year older, and the youngest is again just under one year old. Consequently, the reproductive elements in the matrix which projects the population forward are the product of a birth rate and survival for the first year of life.

In contrast, Lotka's formulation treats the population just *after* births take place, and thus is formulated somewhat differently, leading to a good deal of confusion in the ecological literature. Fortunately, anyone who can make simple calculations with any of the many "spreadsheet" programs now available for personal computers can readily dispose of this confusion by simply calculating the two approaches. However, one further feature of the underlying theory needs to be mentioned first.

This is the "stable age distribution" which is produced if one projects a population having virtually any initial age structure sufficiently far forward in time. The underlying theory shows that not only will the population age structure attain a given form, but that the population will change at a constant rate as that "stable" age structure is attained. Unfortunately, details of the time required to approach the stable state and the nature of that approach depend on the initial age structure and are usually expressed via the calculus of complex domains. Practically speaking, however, one can avoid most of the

se complications by doing some spreadsheet calculations to evaluate the effects of various realistic initial age structures. The theory does, however, give us an equation "characterizing" the Leslie matrix approach (the "characteristic polynomial"), that can be compared with Lotka's equations.

For the present, we need only note that the stable age distribution can easily be computed by a simple equation derived by Lotka. Once this has been done in a spreadsheet, it is then a simple matter to project this age distribution forward in time, using the same reproductive and survival rates as used in Lotka's equations, but proceeding by the rules underlying Leslie's matrix approach. Doing this in a spreadsheet yields exactly the same population growth rate as that predicted by Leslie's matrix approach, providing one retains fractional "animals" in the calculations. Rounding off to the nearest whole individual, as happens in reality, provides a useful reminder not to use many decimal places in expressing a population growth rate.

### Using the Lotka-Leslie model

Thus far, we have considered the elements of a theory of population mathematics established by demographers in some 80 years of research and application. (Books by Keyfitz (1968) and Pollard (1973) describe details, history, and applications to human populations; Eberhardt (1985) described some applications to wildlife populations). Some immediate questions are, "What good is it to wildlife managers?" and "Why isn't it used more in wildlife management?"

I suspect that the answer to the second question lies in part in my initial one-word statement of what matters most, i.e., data. A reasonably short answer can be provided for the first question by considering the kinds of observations collected in wildlife studies and what is done with them. Mostly, one sees a lot of ratios calculated and discussed in general terms and relative to similar ratios from other places and times, such as age ratios, sex ratios, young-adult ratios, and the like. The other common element is some measure of population trend, along with harvest data. If the trend changes somehow, then we try to interpret it in terms of the auxiliary information provided by the various ratios. Too frequently, the results of such interpretations are not very convincing nor very helpful in deciding what to do next.

In my view, the advantage of a theory of population dynamics is that it provides a framework within which the available data can be analyzed and inter-

preted. Whether the analysis is very helpful in management seems to me mostly a matter of the completeness and quality of the information available for a given population. The essential ingredients are survival and reproductive rates, from which one can estimate an expected rate of increase or decrease, subject to the requirement that the stable age distribution holds. In my experience this is not a very important restriction, as can be demonstrated by experimenting with changes in age structure in a spreadsheet model of the kind described previously here. However, this optimistic view does not extend to estimating survival rates from single samples of age structure data. Such estimates are quite sensitive to fluctuations in age structure.

Ideally, one would be able to confirm the findings of an analysis based on censuses or an index of some kind. In practice, it often turns out that some essential rate is not available, such as first-year survival. It is then possible to use the model to estimate the missing item of information.

How can the Lotka-Leslie model be used in real-life management? One obvious way is just as a means to understanding what's going on in a population. Trend data provide a sufficient basis for management only as long as nothing changes, and no change in management action is contemplated. Sex and age ratios usually defy interpretation unless one also has the results of a Lotka-Leslie type of analysis, in

which case the ratios are likely not to be of much interest, anyhow. Table 1 lists some applications of this kind of analysis in practice, but is limited to cases in which I have had some direct experience.

### Some caribou examples

The next question is "how does one obtain the necessary data?" Reproductive rates are not too difficult to obtain. The difficult part, of course, is obtaining survival data. One way is via radiotelemetry, but this approach is very expensive, even for species with a more limited range than caribou. The alternative is to use age structure data. The usual approach is to estimate survival from a single age structure sample. If the population is changing, one has to correct for that fact, using an independent estimate of the rate of change. An example is the data for the George River herd given by Messier *et al.* (1988: Table 5). Their approach involves fitting a smoothed frequency curve, and yields a steadily declining survival rate, which seems somewhat doubtful, on the basis of experience with other large mammals. A problem is that the age frequency curve should decline throughout, but does not in this case. An alternative is to use a subset of age classes in which survival is likely to be nearly constant (say, age 3 to age 12), and the Chapman-Robson "segment" method (Robson and Chapman 1961) to the original data, and correct for changing population size by multi-

Table 1. Some applications of the Lotka-Leslie model.

Species	Application	Reference
Whitetailed deer	Planning and assessing impact of antlerless harvests	Eberhardt (1969)
Feral horses	Assessing population growth rates. Devising management strategies	Eberhardt <i>et al.</i> (1982) On-going
Bowhead whales	Evaluating role of delayed maturity and impact of Eskimo harvests	Breiwick <i>et al.</i> (1984)
Hawaiian monk seals	Searching for causes of persisting low levels after decline	On-going
Fur seals	Appraising population decline and continuing low levels	Eberhardt (1981, 1990)
Grizzly bears	Assessing decline and future prospects (Yellowstone N. Park)	Knight and Eberhardt (1985)
Elk	Evaluating population trends	McCorquodale <i>et al.</i> (1988)
Caribou	Further studies of decline in Nelchina herd	Eberhardt and Pitcher (submitted)
Sea otters	Impact of Exxon Valdez oil spill	On-going
Pacific walrus	Impacts of harvests on population	On-going

plying by  $\lambda$  (cf. Eberhardt 1988b). This gives an unadjusted rate of 0.837 (S.E. = 0.016), which becomes  $0.837(1.11) = 0.929$  on correction. Some allowance for senescence is needed to construct a survivorship curve, and might be obtained by fitting the curves described in Eberhardt (1985).

A second example is available in data presented by Thomas and Barry (1990a). These authors also smoothed age data by fitting a quadratic, using pooled age data from 6 successive years (1981–1986). Trend data were not available, and it was indicated that "a review of the survey data suggests little change has occurred since 1967". It may then be appropriate to pool the age data for the 6 years. This was done by summing the data of Table 3 of Thomas and Barry (1990a) along diagonals, i.e. entries of the same age-class; the data of Table 3 were arranged by cohorts. Using the first 10 age-classes reported and the Chapman-Robson segment method as above, gives  $s = 0.852$  (S.E. = 0.012). An alternative is to calculate survival rates for each year. In this example, the average of the yearly survival rates is virtually that of the pooled data. Because a constant population size is assumed, no correction for population growth is needed (i.e., we assume  $\lambda = 1.0$ ).

Adult survival for the Beverly herd is thus appreciably less than for the George River herd, as might be expected. An immediate question is whether these rates can somehow be checked from the data at hand. Because population trend data were used to correct the apparent survival rates calculated from the age data (explicitly for the George River herd and implicitly for the Beverly herd) it does not, at first glance, seem sensible to use the Lotka-Leslie

model to also calculate a rate of increase. However, it can be argued that such a calculation does provide some evidence as to internal consistency. This is because the age structure depends only on survivorship, and not on reproductive rates. That is, the stable age structure is calculated as (cf. Eberhardt 1985: 998):

$$c_x = B \lambda^{-x} l_x \quad [1]$$

where  $B = 1 / \sum \lambda^{-x} l_x$ . Reproductive rates do, of course, influence population growth, but do so by determining  $\lambda$  from solution of the "Euler equation":

$$1 = \sum_w^a \lambda^{-x} l_x m_x \quad [2]$$

where  $l_x$  = survival to age  $x$ , and  $m_x$  = female births per female of age  $x$ , age of first reproduction is denoted by  $a$ , and  $w$  represents the last age considered.

Calculating  $\lambda$  from the observed survival and reproductive rates thus can provide some evidence of the internal consistency of the data. Rather than attempting to fit a curve to represent senescence, one can use an approximation as suggested by Eberhardt (1985: 1007), but some extra terms are added here to take into account lower reproductive rates in the first few age classes. Messier *et al.* (1988: Table 5) give  $m_x$  values of 0.06 for age 2, 0.35 for age 3 and 0.40 for ages older than 3. If we truncate at age 12 (to compensate for senescence), calculations of  $\lambda$  can be carried out in a spreadsheet model. Messier *et al.* (1988: Table 5) give survival to age 1 as 0.71, and 0.99 for age 1 to age 2. Inasmuch as it appears unlikely that survival in a younger age class would be so much higher than that of adults, the rate calculated above is used here from age 1 onwards, so that  $l_x = 0.5(0.929^{x-1})$ . One can then calculate values of eq. [1] in a spread-

Table 2. Entries for a spreadsheet model for eq. [1], based on data from Thomas and Barry (1990a, 1990b).

Age	$m_x$	$l_x$	$\lambda^{-x} l_x m_x$	$\lambda^{-x} l_x$	$c_x$	$s_x$
0		1		1	0.2242	0.63
1		0.63		0.63038	0.14133	0.8
2	0.06	0.504	0.03028	0.50461	0.11313	0.852
3	0.36	0.42941	0.15487	0.43018	0.09645	0.852
4	0.43	0.36586	0.1577	0.36673	0.08222	0.852
5	0.43	0.31171	0.13444	0.31265	0.0701	0.852
6	0.43	0.26558	0.11461	0.26653	0.05976	0.852
7	0.43	0.22627	0.09771	0.22722	0.05094	0.852
8	0.43	0.19278	0.0833	0.19371	0.04343	0.852
9	0.43	0.16425	0.07101	0.16514	0.03702	0.852
10	0.43	0.13994	0.06054	0.14078	0.03156	0.852
11	0.43	0.11923	0.05161	0.12002	0.02691	0.852
12	0.43	0.10158	0.044	0.10232	0.02294	0

sheet, changing  $\lambda$  until the equation balances. For the George River herd, using the  $l_x$  and  $m_x$  values given above, the result is  $\lambda = 1.096$ , reasonably close to the observed 11% population growth rate.

Thomas and Barry (1990a: Table 2) gave first year survival of 0.50 and second year survival of 0.80. Using these values with the adult survival of 0.852 and the  $m_x$  values of Thomas and Barry (1990b) yields  $\lambda = 0.964$ , appreciably below the value (1.0) needed for a constant population size. Inasmuch as the first and second year survival rates were "developed by assuming 50% survival to 1 year and 20% mortality from age 1 to 2 years". (Thomas and Barry 1990a: 178), it seems reasonable to adjust these rates to see what values are needed to achieve constant population size ( $\lambda = 1.0$ ). Setting  $l_1 = 0.63$  yields the desired result. Entries for a spreadsheet calculation to achieve this result appear in Table 2. The entries in the 4th column ( $\lambda^{-x} l_x m_x$ ) are summed, and  $\lambda$  is varied by trial and error until that sum is virtually unity. The  $c_x$  entries are calculated as in eq. [1], which uses the values in the 5th column of the table ( $\lambda^{-x} l_x$ ). Values of  $s_x$  in the final column are calculated as  $s_x = l_{x+1}/l_x$ , and serve as a check.

## Discussion

I believe that estimates based on a single age structure sample need to be regarded as being useful mainly for exploratory studies. To meet management goals, better estimates should be developed. A prospect that is worth pursuing is to use age structure samples in successive years, weighted by a measure of population trend. One can then estimate survival rates as the ratio of the abundance of an age class in one year to its abundance in a previous year. To minimize chance fluctuations a series of age classes need to be combined. An effort along these lines for fur seals was described in Eberhardt (1990), and a similar attempt for caribou was developed by Eberhardt and Pitcher (submitted).

A final point needs to be considered. The Lotka equations can serve as an analytical device, combining reproductive and survival rates to estimate a rate of increase. These same rates can then be used to project a population forwards in time. However, most practical problems are more complex and need some modifications, and likely a little modelling. One thus uses these tools as a starting place. Perhaps one of the most difficult issues in going further, is "what to do about density dependence?" Often one cannot neglect that issue, but the subject is certainly not well understood as yet. My own inclination at

present is to suppose that density dependence operates initially (and perhaps mainly) on first-year survival, and to represent this by a "generalized logistic" curve, as used, for example, by Breiwick *et al.* (1984). Skogland (1990: Fig. 7) presents data suggesting a decrease in first-year survival with increasing density from which one might approximate the needed curves.

## Acknowledgements

This research was supported in part by the Environmental Research Division of the Office of Health and Environmental Research of the U.S. Department of Energy under contract DE-AC06-76-RLO1830.

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*Printed from manuscript after editorial review.*