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THE INTERRELATIONS OF SOME APPROACHES TO THE CONCEPT OF DENSITY DEPENDENCE IN ANIMAL POPULATIONS

H. KLOMP

*Department of Zoology, Agricultural University,
Wageningen, The Netherlands*

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During the last fifteen years the process of density dependent operation in animal populations has repeatedly been the subject of theoretical considerations. These considerations have been helpful in clarifying density regulation, and in providing a clue to the analysis of density dependence in empirical population data.

Though the starting points of some of these considerations appear to be different, they have a common background and are closely interrelated. This aspect in particular will be discussed in this paper. In addition the limitations of their application to natural conditions will be considered.

The relation between density and the net rate of reproduction.

HALDANE (1953) has discussed the movements of animal numbers in non-overlapping populations, such as those of annual insects, if the net rate of reproduction (R = the quotient of densities of the same stage in successive generations) is density dependent with various degrees of sensitivity. He expressed density as a multiple or fraction (a) of the equilibrium density (p), being ap , and he formulated R as a function of a . If $R = 1/\sqrt{a} = a^{-1/2}$, it follows that the population will return asymptotically to equilibrium after each deviation. If for instance the population were $4p$, it would fall to $4p \cdot R = 4p \cdot 4^{-1/2} = 2p$ in the next generation, and then to $2p \cdot 2^{-1/2} = 1.4p$, etc. (see fig. 1A).

HALDANE further considered two cases of increasing sensitivity of density dependence by putting $R = a^{-1}$, and $R = a^{-3}$. In this paper a sequence of increasing sensitivity of density dependence is studied, R being successively $a^{-1/2}$, $a^{-2/2}$, $a^{-3/2}$, $a^{-4/2}$ and $a^{-5/2}$. The population movements resulting from

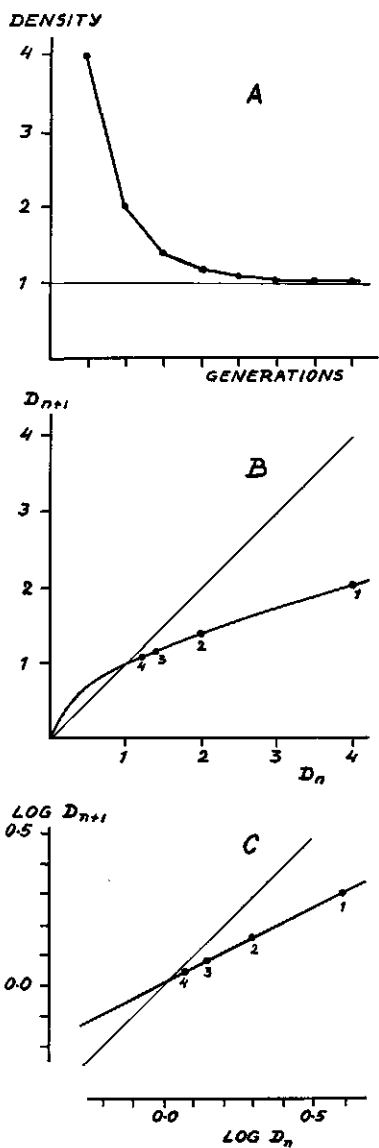
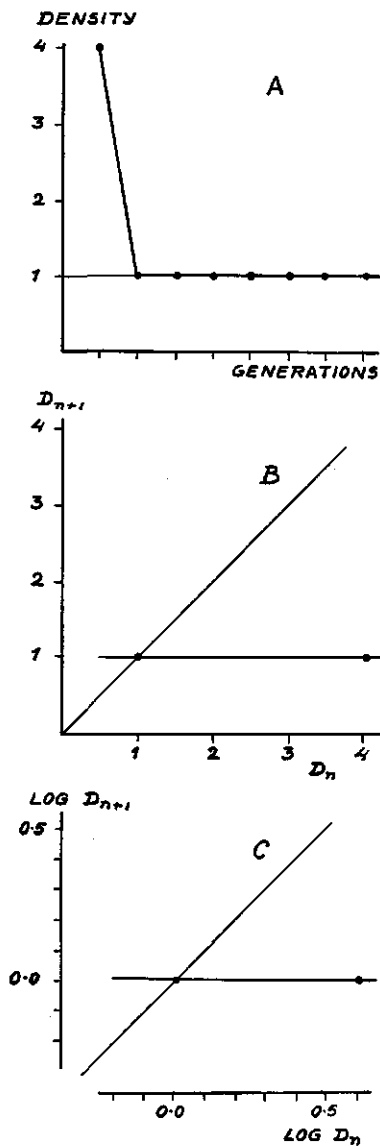


FIG. 2. Graphs showing the density dependent relations in a population where $R = a^{-2/2}$. See the text for further explanation.

FIG. 1. Graphs showing the density dependent relations in a population where $R = a^{-1/2}$. The numerals near the curves refer to generations. See the text for further explanation.



these relationships are given in the figures 1A, 2A, 3A, 4A, and 5A. We have further simplified the formulations by reducing all cases with different equilibrium densities to the same standard by putting $p = 1$. This facilitates the comparison of the various methods as will become evident later in the paper.

The formulation employed in fig. 2A gives the most stable population. Any deviation of equilibrium is immediately restored.

In fig. 3A it is shown that a somewhat more sensitive reaction leads to a small overshooting of equilibrium, resulting in oscillations with decreasing amplitude. A still greater sensitivity results in oscillations with constant, or even with increasing amplitudes, as shown in fig. 4A and 5A. It will be shown later (p. 7) that HALDANE's formulations of the more sensitive cases of density dependency have some implications, particularly away from the equilibrium position, which make them inapplicable to natural conditions.

The relation between the densities of successive generations; the reproduction curve.

RICKER (1954) has studied various degrees of density dependence by using graphs, called reproduction curves, in which density in any one generation is plotted over density in the preceding generation. The principle of this method is explained in fig. 6. Let us assume that the relation between the successive densities is given by the reproduction curve l . It will then be evident that at a low density (q) the population density increases to q' in the next generation, and at a high density (r) the population decreases to r' . Where l crosses the 45-degrees line the population is at equilibrium (p). Consequently, a density dependence as established by this curve necessarily leads to an asymptotical approach of density to equilibrium once the equilibrium state is disturbed, like in the first formulation of Haldane.

We will now study the reproduction curves corresponding with the various formulations of density dependence according to Haldane's method. They can easily be derived as follows.

(1) $R = a^{-1/2}$, $D_{n+1} = D_n \cdot R_n = a_n \cdot p \cdot a_n^{-1/2} = a_n^{1/2} \cdot p$, where D_n and D_{n+1} are densities of the same stage in successive generations. In the standard formulation referred to above p equals unity, and consequently $D_n = a_n \cdot p = a_n$, from which follows $D_{n+1} = D_n^{1/2}$. Hence the reproduction curve is part of a parabola (fig. 1B).

(2) $R = a^{-2/2}$, $D_{n+1} = a_n \cdot a_n^{-2/2} = 1$. This implies that the reproduction curve is a straight line parallel to the abscissa (fig. 2B).

(3) $R = a^{-3/2}$, $D_{n+1} = a_n \cdot a_n^{-3/2} = a_n^{-1/2} = D_n^{-1/2}$, and consequently the reproduction curve approaches a hyperbola (fig. 3B).

(4) $R = a^{-4/2}$, $D_{n+1} = a_n \cdot a_n^{-4/2} = a_n^{-2/2} = D_n^{-2/2}$, which shows the reproduction curve to be a hyperbola, symmetrical with regard to the 45-degrees line (fig. 4B).

(5) $R = a^{-5/2}$, $D_{n+1} = a_n \cdot a_n^{-5/2} = a_n^{-3/2} = D_n^{-3/2}$, which makes the reproduction curve again to be approximately a hyperbola (fig. 5B).

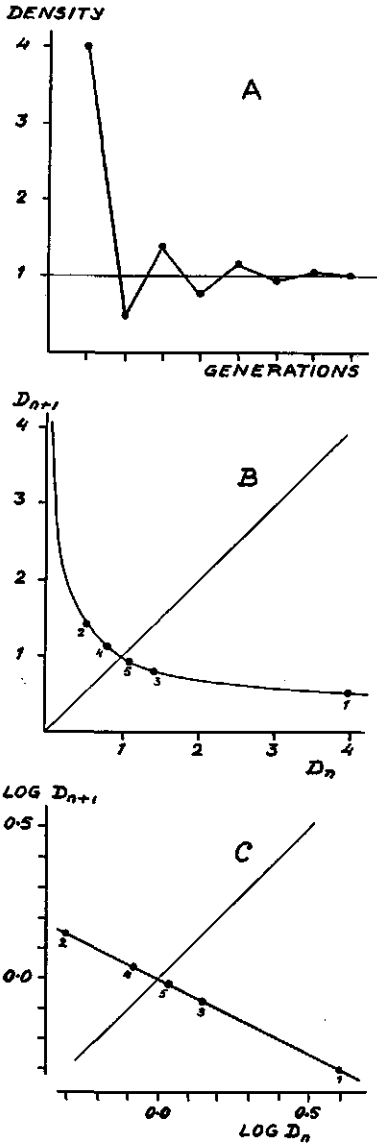
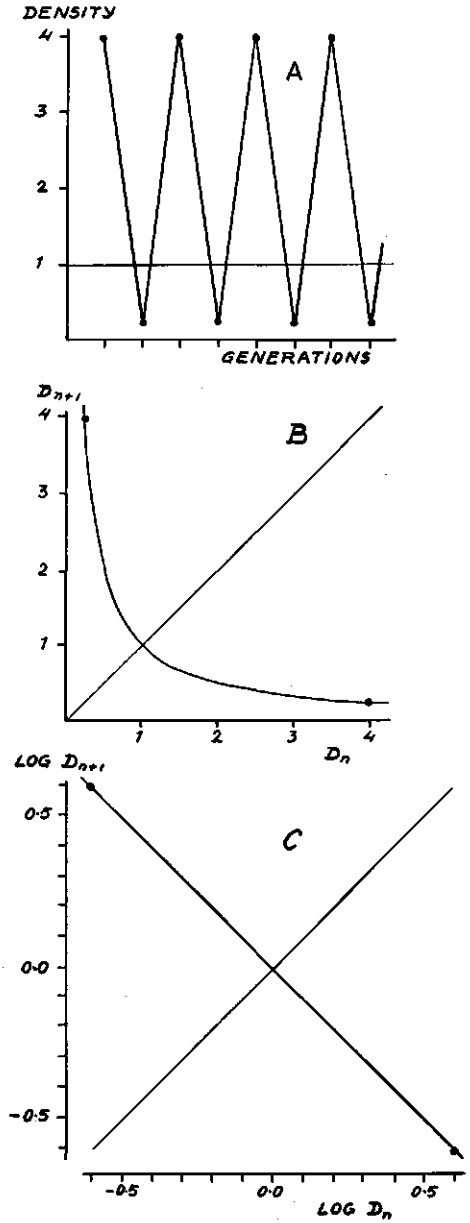


FIG. 4. Graphs showing the density dependent relations in a population where $R = a^{-4/2}$. See the text for further explanation.

FIG. 3. Graphs showing the density dependent relations in a population where $R = a^{-3/2}$. The numerals near the curves refer to generations. See the text for further explanation.



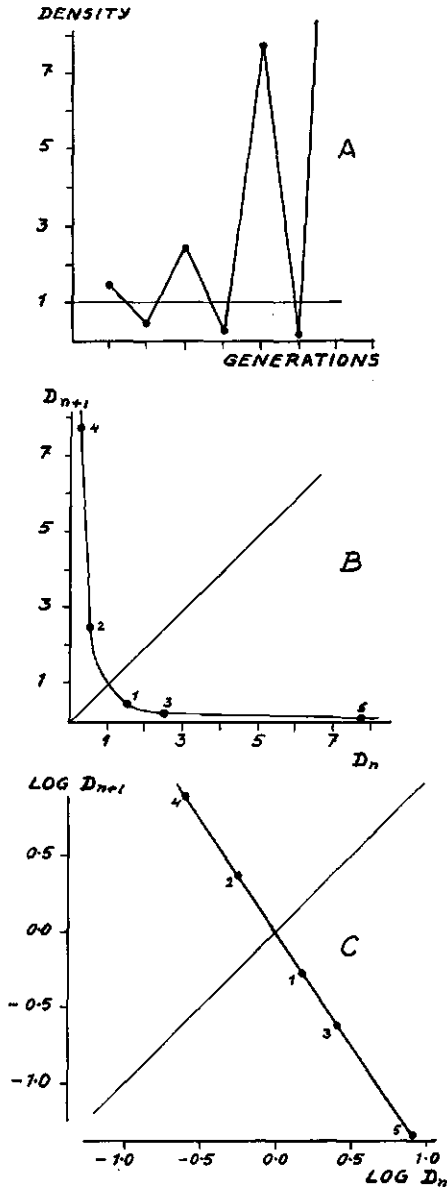


FIG. 5. Graphs showing the density dependent relations in a population where $R = a^{-5/2}$. The numerals near the curves refer to generations. See the text for further explanation.

RICKER (l.c.) has presented a series of curves, which were not mathematically formulated, but principally describe the same density dependent relationships. At one point, however, they deviate essentially: RICKER's curves all pass through the origin. Those derived here do not – except curve 1B – as readily follows from their respective algebraic formulations. This point of major deviation is restricted to the lower density range. This implies that the density dependence expressed by RICKER's curves, at least in the more sensitive cases, cannot be under the same simple formulation at all densities. It will be shown that this assumption is correct.

The index R is composed of two factors, namely the numbers added to the population by natality (v), and the fraction surviving (s). Starting from HALDANE's first formulation we have

$$R = v \cdot s = a^{-1/2},$$

from which follows

$$s = v^{-1} \cdot a^{-1/2},$$

where a is density.

If we assume v to be density independent, then for different values of v curves can be drawn showing how s changes with decreasing values of the density (fig. 7). When $v = 10$ the fraction surviving is unity, and hence maximal, when the density (called critical density further in this paper) is 0.01 times equilibrium density (log density = -2). At still lower densities, e.g. log $a = -2.3$, R can never

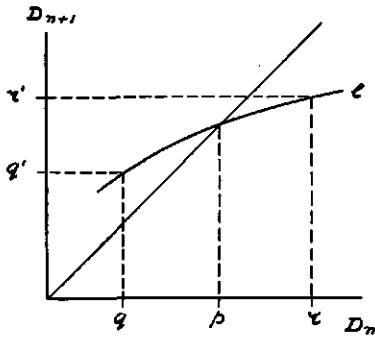


FIG. 6. The reproduction curve of a population with an asymptotical approach to equilibrium after disturbance of the latter. D_n and D_{n+1} are densities in the generations n and $n+1$. See the text.

reach the value necessary to fulfil the requirements of the formulation, according to which R should be $a^{-1/2} = 0.005^{-1/2} = 14.2$. The value which R can reach maximally is $v \cdot s = 10.1 = 10$.

For values of v greater than 10 the critical densities are lower (fig. 7).

Should v be density dependent so that it increases with decreasing density, then this would bring down the critical level.

As far as reproduction curves are concerned these facts have definite implications. They involve a geometric increase of density up to the critical level (for instance with the net rate of reproduction $R = 10$, when $v = 10$ and $s = 1$), giving a straight line through the origin as first part of the reproduction curve. At densities higher than the critical level the curve can follow the course dictated by the density dependent relationships involved. With respect to the curve 1B this means a small correction only; the others are more drastically affected,

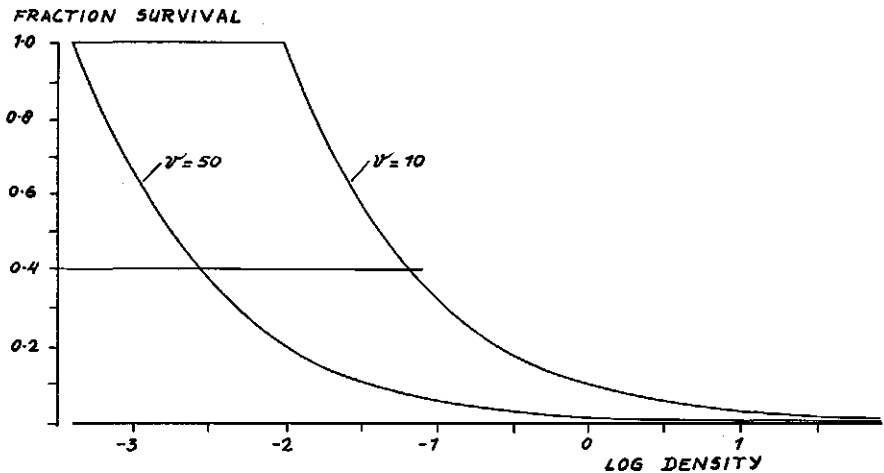


FIG. 7. Graphs showing the fraction survival in an animal population for two different values of the rate of natality (v), and a density dependent net rate of reproduction (R) according to the formulation $R = a^{-1/2}$, where a is density. See the text.

and in the sequence 2B to 5B over increasing density ranges as a result of higher critical density levels (see fig. 8).

In connection with natural populations there is one question which needs further consideration. In the above calculations of the critical densities it was assumed, that at decreasing density the fraction surviving could increase up to unity. This implies that all the mortality should be density dependent, which seems to be a very unrealistic assumption. Let us quite arbitrarily assume that there is a sixty percent mortality on the average at all densities, then in general s cannot reach values higher than 0.4, which gives a further rise of the critical levels in all cases (fig. 7 and 8). This rise may well bring the critical density within the range of normal fluctuations of populations. Thus in univoltine insects for instance, to which the above considerations apply (see p. 1), numbers often

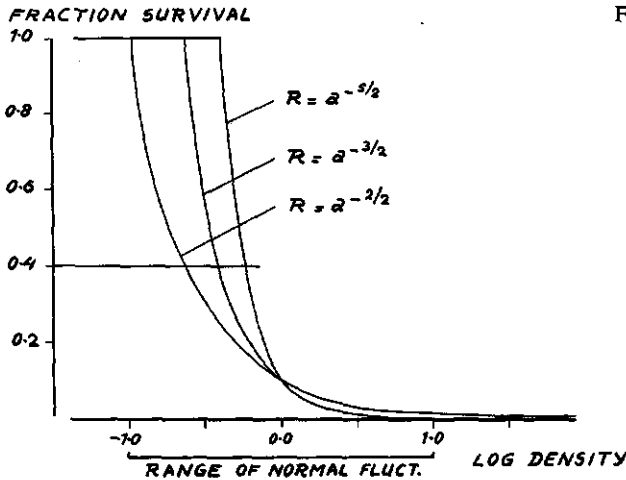


FIG. 8. Graphs showing the fraction survival in an animal population with a density independent rate of natality ($v = 10$), for three different density dependent formulations of the net rate of reproduction (R). a is density. See the text.

fluctuate within a range of one tenth and ten times the equilibrium value, and as shown in fig. 8 for relatively low values of v , the critical density is well within this range in the more sensitive density dependent cases. This implies that HALDANE's formulations of the more sensitive cases of density dependence have no practical significance, and that reproduction curves as given in the figures 2B - 5B are unlikely to be found for natural population data of such insects. The curves of RICKER, which pass through the origin in all cases appear to be more in accordance with the facts. The density dependence expressed by these curves results in a more gradual return to the higher densities than indicated in the figures 3A to 5A, after a crash due to a very sensitive density dependent reaction to high population numbers.

The precise course of the curves in the low range depends on the density relationships at these levels. The first part of the curve is linear when the net rate of reproduction is density independent, as is assumed above; it is convex when there is still a weak density dependent factor in operation, as is expressed

in RICKER's curves (see also fig. 1B); it is concave when the relationship is inversely density dependent.

The relation between the densities of successive generations; the study of density dependence by regression analysis.

MORRIS (1959, 1963) has studied density dependence in natural populations by way of regression analysis. He plotted, just as RICKER did, the density in any one generation of an insect over the density of the preceding generation. However, unlike RICKER, he plotted the logarithms of density. Moreover, MORRIS used actual field data in which variable factors come into play, with the result that the points plotted do not arrange on a single line, but are scattered around it. The course of this line can be estimated by regression analysis. It was for this reason that MORRIS plotted logarithms, for in doing so he provided linearity for the data of the insect species studied, and in addition, the variance of the density measurements was stabilized, which is a condition for a correct use of the regression analysis.

That the plotting of logarithms provides linearity in all cases of density dependency formulated according to HALDANE's method can easily be demonstrated. This immediately follows by taking the logarithms of the functions given in the foregoing section.

$$\log D_{n+1} = \log D_n^{1/2} = 1/2 \log D_n \quad (\text{fig. 1C})$$

$$\log D_{n+1} = \log 1 = 0 \quad (\text{fig. 2C})$$

$$\log D_{n+1} = \log D_n^{-1/2} = -1/2 \log D_n \quad (\text{fig. 3C})$$

$$\log D_{n+1} = \log D_n^{-2/2} = -2/2 \log D_n \quad (\text{fig. 4C})$$

$$\log D_{n+1} = \log D_n^{-3/2} = -3/2 \log D_n \quad (\text{fig. 5C})$$

Comparing the graphs A and C in each of the figures 1 to 5 shows that the regression coefficient is an index for the sensitivity of the density dependent mechanism in operation. If the coefficient is unity (for field data: does not deviate significantly from unity) then there are no density dependent factors in action. The points in MORRIS' graphs will be scattered around the 45-degree line. If the coefficient is between unity and zero, then the net rate of reproduction is weakly density dependent, and the population tends to approach the equilibrium position asymptotically. The points will then, for instance, be scattered around the line shown in fig. 1C, and so forth.

In the foregoing paragraphs it was inferred that in the very sensitive cases of density dependence the reproduction curves of natural populations will deviate essentially from those portrayed in the figures 3B to 5B at the lower levels of density (p. 7). It will be evident that in these cases the conversion to logarithms can not lead to linearity over the whole density range. If the field data of such a case is plotted in a diagram according to MORRIS' method, then the points will be scattered around a regression line with a coefficient smaller than zero for densities higher than the critical one. The position of the points at levels lower than the critical one is depending on the kind of the density relationships which come then into action (see p. 7). That MORRIS did not meet complications in

this respect shows that the insects studied all fluctuated at levels higher than the critical density, a supposition supported by two facts. First, the regression coefficients found were never smaller than zero, and secondly, the insects studied all had a relatively high rate of natality. As discussed above both these facts induce a low critical density. However, in other cases – more sensitive density dependencies and (or) lower reproductive rates – a curvi-linear rather than a linear approach deserves recommendation. For instance, where population numbers are reduced to a low level in one generation by competition for food, followed by a gradual return to the high density. The study of density dependence by regression analysis has some more statistical complications, but these will not be discussed in the present context.

From these considerations the interrelations of the various working methods published earlier in literature may be evident. The concept of density dependence has long been a source of controversy among ecologists. We will not enter into the causes of these differences of opinion, but only express our hope that a better understanding of the rather complicated principles of the concept will not only contribute to the growth of a more uniform view on density regulation, but also to a more successful analysis of density dependence in field data. It is for those reasons that we emphasized the common background of the various ways of considering of the concept we have met with in the literature.

SUMMARY

Some of the more pertinent considerations from the literature on density dependent operation and analysis in animal populations are discussed against their common backgrounds. It is shown that the principles of HALDANE's algebraic formulations agree with RICKER's graphical representation of various degrees of density dependence. Further it is demonstrated that both the mathematical and graphical expressions are helpful in the understanding of some of the basic aspects of MORRIS' method of analysis of density dependence by means of regression calculus. The limitations of the application of the models and methods to natural conditions are discussed.

SAMENVATTING

Gedurende de laatste 15 jaren zijn er enkele beschouwingen over de werking en de analyse van dichtheidsafhankelijke processen in de bevolkingsdynamiek van dieren verschenen. Hoewel de uitgangspunten van deze beschouwingen verschillend zijn, blijken zij op vele punten in elkaar te grijpen en een gemeenschappelijke achtergrond te bezitten. Zo stemmen de principes van HALDANE's algebraïsche formuleringen overeen met het leidende thema uit de grafieken van RICKER. Voorts zijn de principes van beide methoden van betekenis voor een goed begrip van de methode van MORRIS voor analyse van de dichtheids-afhan-

kelijkheid door regressieberekening. De formuleringen van HALDANE zijn op enkele punten in strijd met de regulatie-processen, zoals die in veldpopulaties werkzaam zijn. De consequenties van deze discrepancies voor de methode van MORRIS worden besproken.

REFERENCES

- HALDANE, J. B. S. , 1953, Animal populations and their regulation. *New Biology* **15**, 9-24.
MORRIS, R. F., 1959, Single factor analysis in population dynamics. *Ecology* **40**, 580-588.
MORRIS, R. F., 1963, Predictive population equations based on key factors. *Mem. Ent. Soc. Can.* **32**, 16-21.
RICKER, W. E., 1954, Effects of compensatory mortality upon population abundance. *J. Wildlife Manag.* **18**, 45-51.