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Kenneth E. F. Watt
University of California, Davis

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Kenneth E. F. Watt Department of
Zoology, University of California, Davis

Expensive, extensive and apparently lethal control measures have been applied against many species of pest vertebrates and invertebrates for decades. In spite of this, few pests have been annihilated, and in many cases the stated goals have become progressively more modest, so that now we speak of saving foliage or a crop, rather than extermination. It is of interest to examine the reasons why animals are so difficult to exterminate, because this matter, of course, has implications for the type of control policy we pursue in the future. Also, it has implications for the problem of evaluating comparatively various resource management strategies.

There are many biological mechanisms which could, in principle, enhance the performance of an animal population after control measures have been applied against it. These are of four main types: genetic, physiological, populational, and environmental.

We are all familiar with the fact that in applying a control measure, we are, from the pest's point of view, applying intense selection pressure in favor of those individuals that may be preadapted to withstand the type of control being used. The well-known book by Brown (1958) documents, for invertebrates, a tremendous number of such cases. Presumably, vertebrates can show the same responses.

Not quite so familiar is the evidence that sub-lethal doses of a lethal chemical may have a physiologically stimulating effect on population performance of the few individuals that happen to survive (Kuenen, 1958). With further research, we may find that this phenomenon occurs throughout the animal kingdom.

Still less widely recognized is the fact that pest control elicits a populational homeostatic mechanism, as well as genetic and physiological homeostatic mechanisms. Many ecologists, such as Odum and Allee (1950, Slobodkin (1955), Klomp (1962) and the present author (1961, 1963) have pointed out that the curve for generation survival, or the curve for trend index as a function of last generations density is of great importance in population dynamics.

Suppose we measure the density of populations every generation at the same stage in the life of the animals. The density estimate at any time can be designated as N_t, and the corresponding estimate at the same place in the previous generation can be called N_{t-1}. It is obvious, a priori, and it is also demonstrable for any natural population, that these two densities bear a relationship to each other which can be described by the following curve.

$$\frac{N_t}{N_{t-1}}$$

C

A

B

1.0

D

0

log N_{t-1}
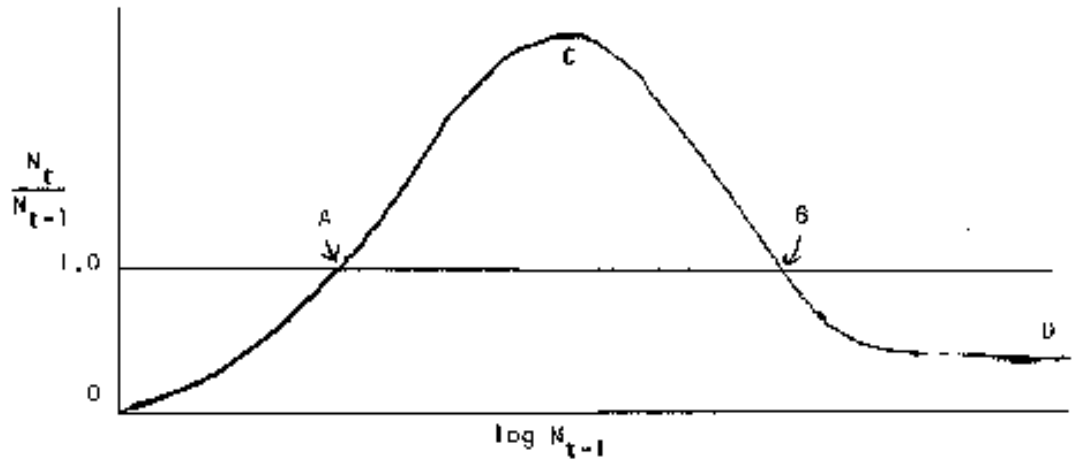
This curve merely states the obvious fact that when any animal population becomes very rare, the probability of prospective mates finding each other sinks very low, and if the density sinks low enough, the population will become extinct. On the other hand, while rising densities enhance population growth prospects up to the point C, increasing density beyond this point increases intra-population competition for resources (food, breeding sites, etc.) and the ratio N_t /N_{t-1} drops.

This is, of course, an oversimplified theoretical picture, which is complicated in practice by the fact that great scatter about the line can be produced by the operation of extrinsic factors, such as weather. Indeed, further research is probably going to prove that the difference between pest species and non-pest species (which represent a much larger group) is that the former are more weakly density-dependent than the latter. However, even so, it must be true, a priori, and careful population work has proved, that by averaging enough data, even weakly density-dependent animals are described by the curve I have presented.

Hence, it is of great interest to examine the implications of this curve. Note that if we draw a line parallel to the X-axis at N_t /N_{t-1}. = 1.0, this line crosses the curve at two points, A and B. If a population is slightly more dense than at A, it will tend to increase, but. if slightly less dense than at A, it will tend to decrease. Therefore, A is an instable equilibrium point. B, however, is a stable equilibrium point, because if a population is at pest densities (e.g. D), it will tend to get smaller (approach B), and if it is at below-equilibrium density (e.g. C), it will tend to get bigger (approach B).

Suppose an animal is a pest. By definition, its density is at D, and using some types of control at least, we merely drive the population to C, which forces it back up to D. Hence the population is constantly rocking about B, and this is why pest populations are not annihilated by decades of intensive control, of traditional types. What is needed is some selfaccelerating method of control that forces populations down to A by eroding their homeostatic capability. The new genetic and biological control techniques are like this.

The fourth, or environmental type of homeostatic mechanism will occur where control produces some change in the environment that enhances population success for the survivors of control. For example, if trace elements of a lethal chemical become incorporated into plant tissue, and produce a physiologically stimulating effect on animals that eat the plants, population performance could improve.

Considerations such as the foregoing, combined with the spectacular success of the Florida screw-worm eradication program using radiation-sterilized males, has produced a revolution in pest control thinking in recent years. First, there has been a great deal of thought about techniques for exploiting Achilles heels in the biological mechanisms of pest populations, and second, a large array of new types of control have become available. Also, the sophistication of research on traditional control procedures is in-creasing.

Two examples will illustrate the types of new thinking about exotic methods of control.

Most animals, vertebrate and invertebrate, have difficulties with various types of parasites. One might ask, "Why don't they have more difficulty?" The effectiveness of parasites will be limited by various environmental factors, such as the abundance of the right type of food at critical stages in the life cycle of the parasite. Some research organizations are exploring the possibility of increasing the effectiveness of parasites by increasing the availability of such foods in the environment.

A second "exotic" possibility is to change the shape of the curve I drew. If we were to introduce into a pest population, at a time of low population densities, a gene for high reproductive success at low densities, but low success at high densities, this would swamp a low-density population. Thus, we would have changed the population curve from A to B, below.
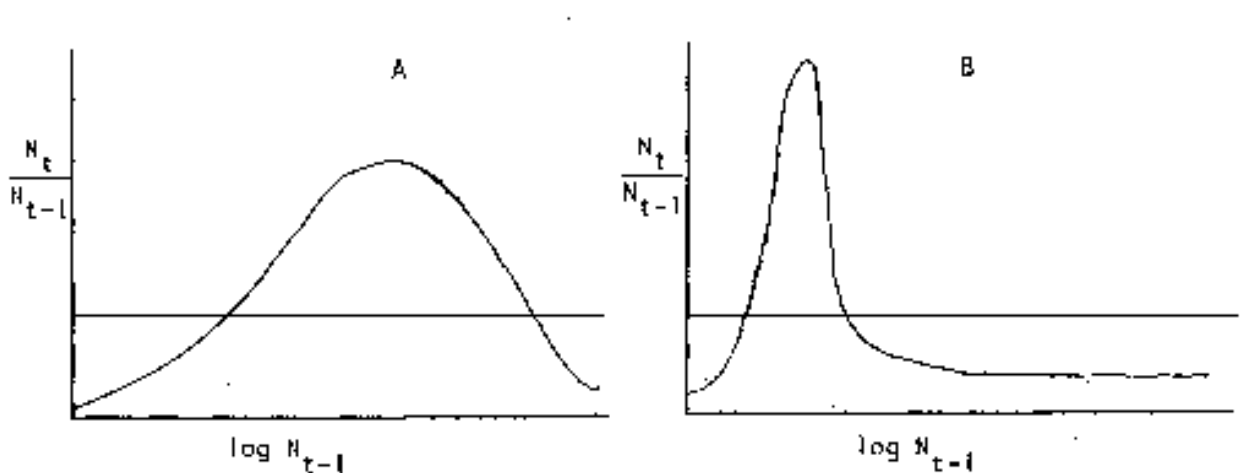
This is not so unreasonable as it seems, because both these types have been discovered in animal populations. A is known as the "Allee type" curve, and B is known as the "Drosophila type". To effect this change, considerable insight into the genetics, behavior and physiology of mating and reproduction is required (Watt, 1960).

A principal implication of the plethora of new control strategies becoming available is that it is increasingly difficult to decide what strategy of control is best. This is particularly true where various combinations of control techniques are considered, because the number of possible combinations can be very large.

Therefore, research on the evaluation of pest control strategies using simulation studies on computers can be expected to gradually assume the importance of analogous work in business, engineering, water resources planning, and salmon gear limitation studies.

Simulation has become enormously popular in many fields, because time and money are typically in too short supply for it to be possible to test in real experiments all possible courses of action. Therefore, we do enough experiments to get the data required to build a mathematical model of the phenomenon, then this model is programmed for computer analysis. The computer then performs a large number of experiments to test the consequences of various control measures, very rapidly.

Because of the great arithmetic speed (500,000 additions a second), input-output speeds (75,000 characters on magnetic tape a second), and vast memories of the new computers (32,000 10-digit units of information can be stored for access in 2 microseconds each), enormous masses of detail, and hence great realism can be built into the computer.

Hence, the following features of vertebrate pest, control strategy evaluation studies can be handled on large magnetic tape machines.

1) Spread of pests outward from a focal point, in addition to changes in population density at any given point can be simulated, and maps of population distribution can be printed at great speed.

2) The effects of weather over a sequence of 20-100 years can be simulated by means of tables of historical weather data stored in the memory of the machine.

3) The very different type of action that different types of control have in space and through time can be simulated, and objective economic comparisons can be made. The computer does this by simulating the consequences of pursuing a specific strategy over, say, 35 years. Each year the computer evaluates losses from damage, and costs of control, and adds these to the cumulative total for all years. The object of the computer research is to find the type of strategy, and the specific materials and operational procedures that minimize the cumulative sum of costs and losses over a long period of time. Thus, cheap control measures which are applied once, have a small initial effect, but grow in importance from year to year, and expensive control measures which have dramatic effect but which have to be used repeatedly can be compared on an objective and equal basis.

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