Volterra's Principle*

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September 19, 2006

The Australian cottony cushion scale insect, a citrus pest, was introduced to the United States in 1868. Much later, DDT was used in an attempt to eradicate this pest, yet seemingly paradoxically the scale population *increased*. In fact, the pest was already partially controlled by a predator - the ladybird - and the indiscriminate use of the pesticide had removed this natural check on scale numbers in accordance with *Volterra's principle*:

> *An intervention in a prey-predator system that removes prey and predators in proportion to their population increases prey populations.*

Which, considering the scale insects as prey, the ladybirds as predator and DDT as the intervention, explains the observed increase in scale population.

As phrased, the principle illustrates how increased intervention favours prey levels; thus reduced intervention favours predators. This was the result Volterra, a post-first world war Italian mathematician, had been attempting to explain: during the war, the proportion of predatory fish caught in the Adriatic sea had increased, due to a decline in fishing (the intervention).

Volterra's principle is fairly simple to capture mathematically, modelling the interaction within a prey-predator system by what have become known as Lotka-Volterra equations. Letting U be the number of prey and V the number of predators, we can formulate the conservation equations in words as follows:

$$\text{Rate of growth of } U = \begin{array}{c}\text{rate of growth in}\\ \text{absence of predation}\end{array} - \begin{array}{c}\text{rate of loss due}\\ \text{to predation}\end{array} - \begin{array}{c}\text{rate of loss}\\ \text{due to fishing}\end{array}$$

$$\text{Rate of growth of } V = \begin{array}{c}\text{rate of growth due}\\ \text{to predation}\end{array} - \begin{array}{c}\text{rate of loss in}\\ \text{absence of predation}\end{array} - \begin{array}{c}\text{rate of loss}\\ \text{due to fishing}\end{array}$$

*First appeared on Everything2, at *http://www.everything2.com/index.pl?node_id=1834554*

Which gives rise to equations of the form

$$\frac{dU}{dt} = \alpha U - \gamma UV - pEU$$

$$\frac{dV}{dt} = e\gamma UV - \beta V - qEV$$

Where α, β, γ, e are positive constants: α denoting the growth rate of the prey population; $-\beta$ the growth rate of the predators (negative, indicating decline without prey- this model assumes an exponential decay); γ the decline in prey due to predation (with a linear relation between the quantity of prey and the level of predation); e the increase in predators due to successful predation. Further, E indicates the amount of effort invested in fishing, with p and q being positive quantities indicating the 'catchability' of each type of fish; again the catch is asssumed to increase linearly with effort.

We thus have a two variable system of differential equations. The equations describe how the variables change with time; we describe a constant state as a steady state. Thus, to be a steady state, the pair of population values (U, V) must be unchanging- that is, each of dU/dt and dV/dt, their rates of change, must be zero:

$$\frac{dU}{dt} = \alpha U - \gamma UV - pEU = 0$$

$$\frac{dV}{dt} = e\gamma UV - \beta V - qEV = 0$$

Or, factorising, a population pair (U^*, V^*) will be a steady state if

$$U^*(\alpha - \gamma V^* - pE) = 0$$

$$V^*(e - \beta - qE) = 0$$

A trivial steady state is thus given by $(0, 0)$- obviously if there are no fish of either type, then this will continue to be the case. Seeking a non-trivial case, we can safely assume that prey levels are non-zero, and thus from the first of the above two equations we conclude $(\alpha - \gamma V^* - pE) = 0$. Rearrangement gives

$$V^* = \frac{\alpha - pE}{\gamma}$$

which by the second equation leads us to a value of

$$U^* = \frac{\beta + qE}{e\gamma}$$

By inspection, therefore, evaluating these expressions for greater values of E gives greater values of U^* and lesser values of V^*- it also emerges that the model is only biologically realistic if $E < \alpha/\beta$ else it predicts negative predator levels!

Moreover, we may compute the ratio of prey to predators caught at steady state:

$$R = \frac{pEU^*}{qEV^*} = \frac{p(\beta + qE)\gamma}{e(\alpha - pE)}$$

Which, giving rise to Volterra's principle, is an increasing function of E.

Limitations

The above analysis describes the effect of varying the level of intervention in a system at steady state- and thus implicity assumes that such a steady state has been reached. However, it is entirely possible for dynamical systems such as those governed by Lotka-Volterra equations to have a steady state which is not asymptotically stable- that is, the population values are free to oscillate close to the steady state rather than inevitably settling down. However, all is not lost should these oscillations turn out to be periodic- repeating in a predictable way over time. Then, further analysis confirms that Volterra's principle holds for the mean population values, i.e., by averaging to take account of the fluctuations. Is the assumption of periodic oscillation itself reasonable? Often it holds in the lab, but rarely in the field- although data for the interaction of hare/lynx populations provide a real-world example of such behaviour, along with the examples already discussed.