BIOLOGY

A Controversial Equation in Population Ecology

AN equation presented by Nicholson[1] was recently criticized by Andrewartha[2] whose comments were in turn criticized by Varley[3] and Nicholson[4]. So far, the real nature and purport of this equation does not seem to have emerged.

Nicholson[1] leads up to the equation as follows. He defines (p. 29) "the *procurement field* of the species, for the given requisite under the given conditions, as the maximum amount of space an average individual can exhaust of the given requisite in unit time when there are no new accessions of the requisite to the environment". A second characteristic is defined as follows (p. 30) : "For the existence of a species it is clearly necessary that there should be a sufficient quantity of each requisite in the space of the appropriate procurement field to supply at least the minimum needs of an individual. This minimum tolerable quantity is the *maintenance quantum* of the given requisite for the species living under the prevailing conditions. When this quantity is available to an average individual, it is just sufficient to maintain the individuals and permit them to produce sufficient offspring to replace those that die." He then states (p. 31) : "For equilibrium [density] of the animals, an average individual must obtain its maintenance quantum of the governing requisite [food or space] in unit time. This is possible only if the equilibrium density (G_E) of the governing requisite is such that there is one maintenance quantum (q) in the procurement field (i) of an individual. So

$$G_E = q/i.$$

It is necessary for equilibrium of the governing requisite that it should be used at the rate it is generated . . ." All this simply means that if the numbers of an animal are to remain steady then, as a primary condition, the necessary bare sufficiency of the scarcest requisite must be constantly available (cf. the once fashionable 'law of the minimum'). However, elaborating still further (p. 32), Nicholson presents the equation for "the equilibrium density (N_E) of mature animals" as :

$$N_E = (g - lg - wg)/q.$$

This is the controversial equation. According to Nicholson[4], g is "the rate of generation of the governing requisite, l the fraction of this lost to the animals due to other agencies", w "the fraction . . . wasted by the animals which scramble for it" (actually by those individuals which fail to reach maturity—see Nicholson[1]), "and q the amount of the requisite required by an animal for development to maturity". For the sake of clarity, it should be noted that q, as well as g, is a 'rate' ; by definition (see above), q is the amount of requisite needed by the average individual in unit time and g the amount generated in unit time ; and the time taken for the average individual to develop to maturity is the unit of time. It should also be noted carefully that, in the equation, N represents the number of *mature* animals.

For achievement of maturity, N individuals must obviously procure Q ($=Nq$) of requisite in unit time ; that is :

$$N = Q/q$$

if Q is the *effective* level of supply of requisite in unit time. This is simply an equivalence, a formula for rationing which is familiar to farmers. In other words, N is just the *maximum* density possible if the average individual requires q in unit time and Q is made available in unit time. Now it is rational to regard Q as equal to $(g - lg - wg)$ and hence write :

$$N = (g - lg - wg)/q$$

but this does not alter the character of N at all. N remains the maximum possible density as described above. Why does Nicholson append the subscript E to N and call it an "equilibrium" density ? Why is equivalence confused with equilibrium ? Keeping in mind that supply of requisites is a condition of enviroment, the reason is to be found in his theory of natural control of population.

The Nicholson theory[1,5] is that a population must be in a state of equilibrium with its environment and this state is brought about by competition. In the equation the available governing requisite $(g - lg)$ has been reduced to $(g - lg - wg)$ by competition. Hence, according to the theory, the equation represents the "equilibrium density". There are, however, serious flaws in this theory (cf. Milne[6,7]) and one is in the very basis of the primary assumption of equilibrium or balance. Nicholson avers[8] that "the densities of animal populations are known to bear a relation to the environmental conditions to which they are subject, and the existence of this relation shows that populations must be in a state of balance with their environments". But the relation is simply that densities become high in good conditions and low in bad. This relation undoubtedly exists. But the existence of a relation does not show (prove) that it must be one of balance. Relations other than balance can exist. The relation here is essentially one of cause (environmental conditions) and effect (population density). It is true that should population chance to rise sufficiently high, it will itself modify some of the conditions significantly (bringing another condition, intraspecific competition, into play) but the relation remains nevertheless one of cause and effect.

Returning again to the vexed equation : Varley[3] is wrong in holding that w is a function of N ; w is obviously a function of $(N + N')$, where N' is some unknown number of individuals that died at various unknown stages of development short of maturity ; in other words, competition is not functionally involved in the equation. It is therefore not an "equation for intraspecific competition" (see Andrewartha[2]). Nor is it an equation for "equilibrium density" as Nicholson[1,4] claims and Varley[3] accepts. It is merely an equation showing the maximum density possible with an amount of requisite which has been determined by its rate of generation and rate of loss through competition and other agencies. It contributes nothing new to, or useful in, the problem of natural control.

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IT is a fundamental rule of physical equations that the two sides must balance in terms of the dimensions ascribed to the magnitudes that they represent[1]. The same rule should hold when we try to apply physical equations to biological processes.