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A NOTE ON THE STABLE POINT OF POPULATIONS SHOWING BOTH INTRASPECIFIC COOPERATION AND DISOPERATION[1]

A humpback curve frequently results when some representative measure of the well-being of a population is graphed as a function of population density (Allee 1940, 1951: 31, Allee *et al.*, 1949: 396). Such curves make use of many types of measures of the condition of the population for a great variety of organisms. It can be said, therefore, that the humpback curve is sufficiently frequent to be a generalization.

In the present discussion, the specific survival rate, which is the specific birth rate minus the specific death rate, is used as the measure of the immediate condition of the population. Ludwig and Boost (1939) plotted this population parameter as a function of density; they used data from several authors and thus demonstrated such humpback curves as are shown in Figure 1. This constitutes confirmation of the generalization in terms of survival rates and a demonstration that the simple logistic equation does not apply in these cases. A logistic has a slanting straight line in this plot. The humpback curve indicates that the distribution of beneficial and detrimental density dependent factors affecting the excess of births over deaths generally produces a maximum survival tendency at a moderate population density. Those populations that lack the humpback and left slope of the curve (Figure 3A) can be considered to be special cases of the general curve which have the optimal survival tendency at the lowest possible density.

Customarily, the left portion of the curve is referred to as a zone of cooperation. Until the density is above the optimum, there is an increase in survival tendency as the density increases. The right side of the curve to the right of the hump is referred to as the zone of disoperation, since the survival tendency decreases as the density increases.

A hump-shaped curve like the one in Figure 2 can be

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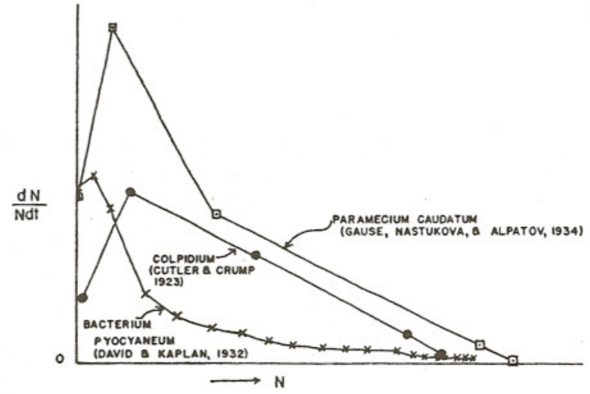

FIG. 1. Specific rate of population change as a function of density (modified from Ludwig and Boost 1939). Coordinates are adjusted to permit comparison of curves.

expressed in the form of an equation for clarity as is shown below. This expression avoids the difficulty of introducing a fictitious biotic potential or requiring determination of the intrinsic rate of natural increase which is determined with difficulty. Instead b represents any operationally determined growth rate.

This discussion strictly applies where there is only one specific growth rate for each density. If the organism changes its basic nature, or if the environment is not kept constant, the curve will change. Therefore, the density growth-rate curve should be used for comparisons in open steady state systems. Some of the curves from Ludwig and Boost (1939, Fig. 16) do not properly meet this requirement in the higher density range where waste product accumulation causes change in the growth rate even at identical population densities.

$$\frac{dN}{N\,dt} = b + f_1(N) - f_2(N)$$

N Is the population density

t Is the time

$\frac{dN}{N\,dt}$ Is the specific survival rate (specific growth rate)

b for operational simplicity, is the specific growth rate of some small population under favorable and reproducible environmental conditions. (The assumption of an intrinsic rate of natural increase with a stable age distribution does not seem necessary to the study of the density-dependent factors.)

$f_1(N)$ is some positive function of N representing intraspecific cooperation effects. This term contributes component curve B in Figure 3.

$f_2(N)$ is some negative function of N representing disoperative effects.

When the cooperative term is zero, the remainder of the equation contributes component curve A in Figure 3. The basic biotic potential term b, the cooperative term, and the intraspecific disoperative term together produce the humpback curve that relates the specific survival rate to the population density. Note how the overall curve becomes concave on its right leg as a result of cooperation as suggested by Ludwig and Boost (1939).

The stability principle discussed by Holmes 1948 suggests that systems trend toward a stationary steady state by the natural selective elimination of all states that are not stable. A stable state is here defined as one with a self-regulating mechanism so that if the system is displaced from its stable state it will return like a cork bobbing on water. Biological natural selection has been considered a special case of the stability principle (Holmes 1948), and applications have been suggested for geochemical systems (Odum 1951).

The stability principle suggests that regardless of its initial state, a population of organisms will either increase or decrease until a population density is reached that is characterized by a self-regulating mechanism. A point on a graph with a self-regulating mechanism can be referred to as a stable point as has already been described in inter-specific competition systems by Gause (1935). As indicated in Figure 2, there is only one stable point for a population that possesses a survival-density curve of the types in Figure 2 or Figure 3A. The stable point is the intersection of the curve with the zero line of equal births and deaths on the right side of the hump. Here, stability results from a self-regulating mechanism. Should the population increase, deaths would begin to exceed births and the population would decrease to the stable point again. Should the population decrease past the stable point, births would exceed deaths and again the population would return to the stable point. A population whose density is in the zone of disoperation will move to the stable point.

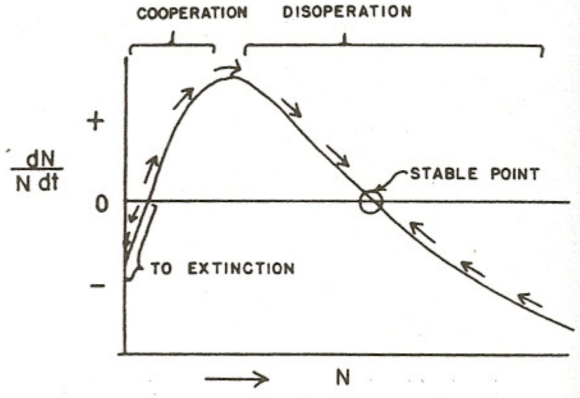

FIG. 2. Generalized survival-density curve characteristic of populations which have a negative survival rate at low densities.

On the left side of the hump, the population behaves in a different manner. Should the population possess a density in the cooperative range above the line of equal births and deaths, the population will move to the right and eventually end up at the stable point on the right side of the hump. Should the population possess a density below the birth-death balance line on the left, unless conditions change it would move to extinction. Thus, no population can remain at a density in the cooperative zone for there is no stable point there. Isolated populations cannot, therefore, conceivably survive without some form of disoperative intraspecific competition in operation. They will either become extinct or increase until a disoperative intraspecific competition does begin to operate. Applying this conclusion to human populations, one might state that non-competitive utopias are unstable and impossible unless, of course, some new kind of self-regulating mechanism can be introduced to permit a stable point on the left side of the hump.

The absence of a stable point on the left side of the curve helps to explain why cooperation among organisms is often overlooked. The important question arises: why is cooperation so widely distributed in the living kingdoms even though populations are rarely found in the density range corresponding to predominantly cooperative interaction? It is suggested that the presence of cooperation in a species has the function of raising the density of the stable point thus giving a species an edge in competition with other species. In terms of the equation above, the cooperative term illustrated in Figure 3B when added to the remainder of the equation in Figure 3A produces a curve in Figure 2 whose stable point is shifted to the right. Thus, other things being equal, cooperative animals have higher densities in their stable population levels than non-cooperative animals. But in all cases, the stable point is characterized by an excess of disoperative competition over cooperation. The intraspecific cooperative effect above may be either linear or a more complex function such as the second power term suggested by Hutchinson (1947) for social animals.

In man's evolution, we have apparently had continual shifting of the stable point to the right as man's cooperation increased. The great question before us all is not how to increase cooperation or how to avoid the inevitable disoperation but what form of disoperation will ultimately determine our stable point and at what density will this take place.

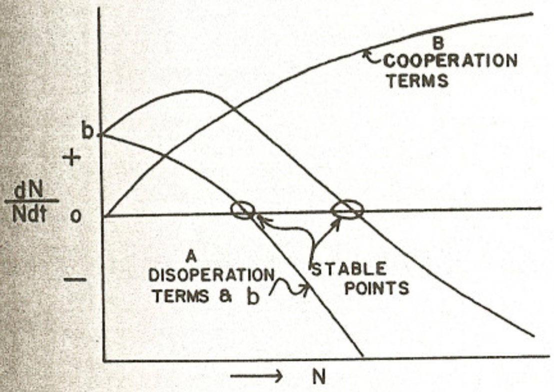

Fig. 3. Survival curve and components for a species with a survival rate that is positive at minimum densities.

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