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THE UNITY OF ANIMAL POPULATIONS

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For many years now there have been appearing in the biological literature references to the actions of groups of organisms reminiscent of the actions of individual animals. A basic philosophy running through these discourses is the subordination of the individual of a species and the consideration of it only as it contributes to the existence of the species.

The subordination of the individual to the group, the contribution in a specialized way of the individual to the group, has given rise to the concept of the supra-organism. This concept analogizes population activities with those of an individual organism. Depending on the field of interest of the investigator, or his bias in thought, the definition of the supra-organism varies and becomes inclusive or restrictive. To some ecologists it is the ecological community. Therefore it consists of many species living together under broad restrictions. To some entomologists it is limited to insects which display a social structure. Emerson (1952), while not defining the supra-organism, defines the organism and thus gives us a base for analogy with attributes of groups of individuals. According to Emerson an organism possesses, among others, the following characteristics:

(1) It is an open system importing and exporting component materials and energy, and exhibiting orientation in space.

(2) It maintains a relatively steady state as a unit system. There is a tendency toward dynamic equilibrium, balance, periodicity, and self-regulation.

(3) It performs specific synthesis of its substance and repeats or duplicates its pattern.

(4) It exhibits division of labor in its parts, and integration of the whole.

(5) It has a temporal ontogeny and a temporal phylogeny.

Activities of nonsocial animals have not generally been considered as analogizing with the activities of an organism, but it appears that such analogies do exist.

If one attempts to find evidence of supra-organismic activity among nonsocial organisms, one must broaden his concept of division of labor or discard it. One must also question highly developed social or ecological integration as a criterion. Supra-organism analogies are most easily discovered among the higher social forms, but do they exist among lower social orders? One cannot eliminate division of labor completely from any bisexual species for bisexuality in itself is a division of labor. Nor can one divorce it from species which care for their young. Adults perform the functions of protection and provide for nutrition of the young. This is especially apparent in altricial forms.

If we take Emerson's definition of a multicellular organism as a starting point, we may look for analogies with lower social units or even non-social species.

1. *An organism is an open system importing and exporting component materials and energy, and exhibiting orientation in space.*—I do not at this time analogize activities of diffuse populations with the nutritional activities of an organism. However, in exhibiting orientation in space we find parallels which may be of value. Migratory animals have a high degree of orientation. As surely as an individual may orient itself in relation to external stimuli, a flock of yellow warblers or golden plover orient themselves. With individuals this orientation expresses itself in various, often obvious, tropisms. The causes bringing about the orientation effects in diffuse populations are not so well understood.

The more highly migratory species often follow certain temperature movements but studies such as those of Rowan (1925) and others have cast doubt on temperature as a motivating factor. Day length has a profound effect on the physiology of migratory birds, and this effect may initiate migratory orientation. But this orientation is probably the result of a chain of factors, and we are far from unraveling the causes and their interrelationships at this time. Unidirectional, nonreturning migrations may have still other initiating causes. Why does the thistle butterfly indulge in these movements? Why will bands of mormon crickets or beet webworms move in one direction, often without dissipating food supplies through which they pass? Why are there mass movements of tree squirrels? Of lemmings? Complete utilization of a food supply or some essential part of a food supply might initiate movement, but there is evidence in muskrats that a high population is a restless one. Perhaps in some forms there is a minimum spatial limitation which, when reached, sets up psychic disturbances which in turn release a unidirectional movement.

2. *An organism maintains a relatively steady state as a unit system. There is a tendency toward dynamic equilibrium, balance, periodicity, and self regulation.*—Perhaps the most important attribute of nonsocial populations is their tendency, which almost amounts to an obsession, to be regulated in size. Much of this regulation is self-induced by the population. Cannibalism in closed cultures of *Tribolium* is a self-regulating mechanism. Intraspecific intolerance among muskrats or upland game birds is self-regulatory. Dissipation of a food supply is self-regulatory. Territoriality and consequent spacing is self-regulatory. That populations of nonsocial animals are held stable is one of the most consistent phenomena in nature. A population may in successive generations have a potential of increasing from 2 to 200 to 20,000 to 2,000,000. Instead it progresses from generation to generation possibly as 2 to 1.9 to 2.2 to 2.1 to 1.8 to 2.0. This stabilization in size is parallel to the stabilization, the "steady state as a unit system," of an organism. And much of this steadiness is directly or indirectly self-induced.

The phenomenon of inverse ratios is a conspicuous example of self-regulation. By inverse ratios we mean that as the breeding population increases there is an inversity in the success of the breeding. Several dramatic examples can be given. Errington (1942) has described one as follows:

> On roughly one-half of the marsh, losses (to muskrats) from causes other than intraspecific strife were not great but breeding stopped by midsummer. . . . On the other half, losses through disease and predation predominated, . . . and nearly all of the late summer litters —usually the third and fourth of the season for individual females—were born on sections of the marsh where known early-summer mortality of the young had been highest.

Allen (1943) has shown that, after a population of squirrels with a known breeding pattern had suffered decimation through loss of food supply, a higher percentage of females became pregnant and young squirrels started breeding three months before their normal time. The New York grouse study (Bump, et al, 1947) reports that where low densities of ruffed grouse occurred young were produced in greater numbers.

Periodicity in nonsocial populations has long been the subject of surmise and study. Much time could be spent discussing the ups and downs of populations which seem to recur at rather regular intervals. There is the so-called ten-year game cycle. Ruffed grouse seem to fluctuate at about ten-year intervals, the varying hare from 8-11, etc. Siivonen (1948) has recently postulated a cycle of about 3⅓ years for several animals, each third peak being larger and representing the 10-year period. Hamilton (1937) has seen a cycle in meadow mice of approximately 4 years. There is much contradicting as well as corroborating evidence concerning this cycle; Cole (1951), however, believes that a series of random numbers will show fluctuations of about the same amplitude as those seen in nature.

Contradictory data are to be expected, for much of our information on cycles is based on gross numbers, which may be quite misleading. There are two sets of factors which will produce variations in numbers. One set consists of external factors which will affect populations after birth or hatching. The other set affects populations by varying the numbers which are produced for the first set to work on. Gross numbers are the results of the combined actions of both sets and are therefore polyvalent. True cyclic behavior may be masked in part or in the whole by this nonsegregation of causations. Storms, disease, and the like are illustrations of the first set, and differences in ovulation or in susceptibility to disease are examples of the second. Until we are able to differentiate between these internal and external factors, between the true and pseudo cycle, there will be contradictory data. In spite of this there does appear to be some sort of population periodicity analogous to physiological periodicity in the individual.

3. *An organism performs specific syntheses of its substances and repeats or duplicates its patterns.*—As far as my thinking has gone, it appears that a specific synthesis of materials is not paralleled in nonsocial populations. However, such populations duplicate their pattern from year to year and from area to area. Population expressions such as host predilection or migratory pattern are carried over from one gener-

ation to another. The English sparrow has the same habits, the same loquacity, the same nests, in America and in Europe. A small colony which I observed at Camaguay, Cuba, was still unmistakably sparrow-like in its habits. Norway rats are Norway rats all over the world, whether in Illinois or on an isolated Pacific island. The pattern is duplicated.

4. *An organism exhibits division of labor in its parts and integration of the whole.*—We have already noted that bisexuality, which is universal in the higher vertebrates, can be construed as an expression of division of labor in a primitive sense. In some species this goes beyond the division of the sexual responsibilities. The hornbill female lays its eggs in a hollow trunk and incubates them. The male plasters the opening shut with mud, leaving a small aperture through which it feeds the female. At hatching time the closure is removed.

There are interesting variations from the normal pattern. The case of the phalaropes is classical: the usual plumage pattern is reversed, the male being the modestly clothed sex and the female relieving herself of household duties after oviposition, which duties devolve on the male. This is true to a lesser extent among other shore birds. Certain birds are communistic—the smooth billed ani, for example—in that the females lay eggs in a communal nest.

What may not quite be a division of labor but an assumption of responsibility by the parents on a temporary basis is often seen. The feeding and protection of altricial young, and the protection of precocial young are examples. The alleged "watchman function" of certain individuals in flocking birds or herding mammals would be a primitive division of labor. And in colonial hydroids, which are certainly not social in the accepted sense, there is a continuity of nutrition but a strong division of labor among different organisms in the same colony.

Demands of a rather constant nature on a population may be met by some individuals in the population, thus satisfying the levy and protecting the remaining population. Compensatory loss may express this phenomenon. Where a carrying capacity is evident in an environment, a population may be pinched down in one or several of many ways. Disease, predation, emigration with consequent increased hazard, climatic extremes—all may play a part in wiping out a surplus. Even within one loss-producing mechanism this compensation may be seen. When one predator does not assess the usual tax, possibly through reduction in numbers of the predator or a new protective device on the part of the prey, other species not commonly considered as predatory on the host take over the function. In New York the destruction of the common predators attacking ruffed grouse brought on attacks by pine squirrels (Bump, et al, 1947). In Illinois we have noted that protection of wood ducks from raccoons, snakes, and squirrels was accompanied by nest destruction by woodpeckers.

5. *An organism has a temporal ontogeny and a temporal phylogeny.*—All populations, whether they be social or nonsocial, go through waxing and waning periods. They have

a development and a senescence. Bodenheimer (1937) has said that the growth of colonies of social insects may be divided into three periods: (1) the initial period of colony foundation, (2) the period of expansion and vigor, and (3) the period of senescence and death. "The growth of these colonies resembles that of organisms." In looking for analogies with diffuse, nonsocial populations we must extend time greatly over that which concerns us in the colony cycle. In organisms introduced into new areas it is easy to see the growth of populations and the invasion of ecologically acceptable habitats. The origin of new populations at the species level (or above) is characterized by expenditure of time in units which extend beyond the time which has yet been expended in scientific endeavor. However, methods in nature have been postulated and there are reasonably creditable theories.

It is much easier to note senescence and decay during our period of scientific thought and observation. Many species have disappeared, some of them without the direct intervention of man insofar as we know. The Labrador duck disappeared before gunning for waterfowl was a factor, and it was not esteemed as food. The large coastal mink of the north Atlantic possibly suffered a somewhat similar fate. Ground sloths and the native elephants disappeared before recorded history but after the appearance of man in North America. That the California condor may be on its way to oblivion is indicated by the records of an earlier wide distribution. It would appear, then, that there is a process analogous to the ontogeny of the individual at work among species.

Reversing the usual procedure of defining terms in advance, we can now define the supra-organism, in the sense used above, as follows:

> A supra-organism is a population of organisms of the same species which as a unit carries out some functions analogous to those of an individual.

The concept of the supra-organism is in its infancy. It has, possibly, caught up with its food supply and must wait for continued growth until it can be nourished by future discoveries to be made in the population dynamics of a wide variety of animals. It may have considerable value in the future in elucidating and allowing prediction of activities of populations, in predicting what certain variations of population treatment will do. It may, for example, be a philosophical tool of high importance in economic entomology or in fish and game management.

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