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Presidential Address—Kansas Academy of Science, Seventy-third Annual Meeting

CROWDING AND ITS EFFECT ON ORGANISMS

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We are gathered here today, a group of men and women, activated by some internal drive which has directed our endeavors toward a common cause—the seeking of truth through the method of science. We are scientists, not because of some distinctive anatomical, physiological, or psychological constitution, but because of training, method of procedure, and objective that have become a part and parcel of our very being.

A true scientist is not a cold-hearted, fact finding, materialistic being as is often pictured by many among the laity. On the contrary he is sensitive, responsive to harmony and beauty, and highly endowed with the sense of value for truth and balance in his researches into nature and her secrets. He knows that every result has a cause; every action has a reaction; and that truth is often more strange than fiction.

It is the function of the scientist to investigate, weigh, measure, compare, and classify the truths nature has in store, and share freely of his findings. The poet may sing, the artist may paint, and the dictator may abuse and censor, the industrialist may appropriate the fruits of scientific achievements for material progress and profit, but the scientist is ever seeking the truth which when discovered is given to humanity without stint or favor. The entire universe is his sphere of action, and all humanity is made the beneficiary of the fruits of his labor.

"Be fruitful and multiply, and replenish the earth, and subdue it." (Gen. 1:28).

Philosophers, scientists and thinkers since time immemorial have been impressed by the essential and fudamental resemblances that exist among all organisms. Because of this fundamental oneness of all life there has arisen an ever greater human interest in all living things.

A fundamental property of all living matter is irritability. By virtue of this property, living matter not only responds to stimuli, but reacts through conduction so that the cell, or a group of cells, respond as a coordinated unit, making possible those structural and functional adaptations necessary for existence. This property also serves as a criterion for distinguishing between living and non-living, between the organic and the inorganic.

Our basic study of the biological nature of man has been through the lower organisms in which the life processes are reduced to their simplest terms; and this has supplied us with material which could be subjected to rigid experiments. Upon these fundamental likenesses between the life processes of man and those of the lower animals are based much of our knowledge of physiology, genetics, and experimental medicine, a knowledge which ranks among the highest achievements of science. This fundamental likeness between man and the lower animals has also enabled us to arrive at a number of conclusions regarding the effect of environment upon the internal and external adaptations of organisms, both as isolated individuals and members of the social structure.

In the discussion that follows the writer aims to present some fundamental reactions exhibited by a number of organisms in relation to their environment; and since man has much in common with the other organisms an attempt will be made to indicate that in the main, he also is subject to the same laws and processes that call forth reactions and species of behavior.

On the other hand, since man has been endowed with a massive brain capable of the superior functions of intelligence and reason, he alone can perceive himself objectively and profit from experience; he alone can control his environment through an intelligent application of the laws of nature. In addition we must not lose sight of those higher attributes with which man is endowed, such as honor, sympathy, morality, and sentiment; his appreciation of higher values and beauty; his religious nature; and his ability to form an intelligent philosophy of life—attributes which have placed him upon a pedestal far above the beasts of the field.

The urge or internal drive towards reproduction of its kind is present in all living things. Protoplasm, whether it be organized as a simple cell, a spermatozoan, an ovum, a protozoan, or as a complex organism like a mammal, obeys the dictum: "Be fruitful and fill the earth."

In its attempt to comply with this dictum, nature appears to be very wasteful. Millions upon millions of potential organisms in the form of spores, sperms, ova, pollen grains or ovules must of necessity fail to materialize. Even after fertilization, there are myriads of embryonic forms which fail to germinate, hatch, or attain individual existence. Even among those which do begin life as young independent organisms, only a small number survive in the struggle for existence, to the stage which makes it possible for them to become potential reproducers of their kind. Yet life persists, and, while nature is lavish with the individual organisms, she preserves them in numbers sufficient for the survival of the species which she guards with the greatest of jealousy.

In the constant struggle for survival and dominion each species attempts to reproduce its kind literally in numbers sufficient to cover the surface of the earth. However, during this struggle the organisms are engaged in ceaseless competition in their search for food, for space, a mate, and a suitable breeding habitat. They must also seek escape from their enemies, overcome barriers and find a habitable environment. As a result, there arises a constant need for adjustment and readjustment until an approximate balance is reached. At some point a decided over-crowding occurs, while at another the population is reduced to a point which endangers extinction. Each of these conditions has its defects, while observations and experiments have shown that in a large number of instances there is an optimum population density for best species survival. Of necessity, this optimum in numbers varies among the several species and within any one species as well, due to the diversity of and the variability in the environment. Hence, in this discussion general principles will be dealt with only. In support of these principles we shall refer to specific examples met with in the writer's work as well as that gleaned from other workers in the field of biology.

Until a few years ago, it was generally believed by all investigators on animal, plant, and human population density that crowding was uniformly harmful. Exceptions were made only in case of hibernation and at breeding time. More recently, however, there has been accumulated evidence by some ecologists, students of general physiology, psychology and sociology indicating that within certain limits crowding and aggregation do have definite beneficial effects in a number of ways, especially in regard to survival value and longevity. In support of this problem it is not proposed to defend the thesis that all crowding has merits. Quite to the contrary we find that excessive crowding is in general uniformly harmful except where this condition promotes migration, which in turn will serve as a factor in the distribution of the species over a wider area and thus have a survival value.

In a large number of cases investigated there seems to obtain a quite definite so-called optimum condition of crowding or aggregation. (5), (11), (17), (22), (30), (51), (54), (56). Since single individuals, the smaller groups and very large groups do not reproduce nor survive as well as do groups of intermediate sizes, it is concluded that there may be found an optimum size or group number for most organisms. This optimum is not necessarily constant or static for the conditions of environment, both physical and biological, must be taken into account. Yet for each set of conditions there seems to be an optimum under which the survival value and group activities are most beneficial.

The problem of aggregations and crowding has been extensively worked out by Dr. Allee of Chicago and his students, and among these the writer had the good fortune of being one of the workers. Although the observations and experiments have yielded a variety of results, many of them negative, yet the general trend has shown that there is an optimum in numbers of crowding governing the well being of most organisms.

Many animals like mosquitoes and midges among insects (46) (50), and amphibia (12) (27), snakes (34), birds (2a) (64), and bats (69a) (38) (44) among vertebrates, form active aggregations under certain conditions. Nereis limbata (47), (23a) for instance, swarm and assemble most frequently at full moon, and least at the third quarter phase. Again, the activity is at its maximum the hour following twilight. Land isopods (3) tend to aggregate in bunches when the environment is unfavorable as for example when too dry, and to scatter when moisture is supplied. Likewise they assemble when exposed to noxious gases, and again scatter when normal air is supplied. Wheeler (70) (71) reports that similar results have been obtained with certain ants. Fruit flies (Drosophila) exposed to excessive moisture aggregate at a location higher up where it is less moist, but under optimum conditions they stay farther apart or form small groups only.

Among poultry (56) it has been found that rate and quantity of egg production is affected by crowding. Even where the floor space per hen is constant, a group of 50 hens yield superior results to groups of 100 or 150. Chapman (22) in his experiments with the confused flour beetle (Tribolium confusum) showed that there was an optimum initial number (four) for most rapid production. He found that this mean number of individuals per gram of flour after equilibrium had been established was 43.9. However, the time required before this equilibrium was reached differed with the initial seeding per gram of flour. Land isopods show decided advantage when bunched over that of isolated individuals (51). While this may be due to conservation of moisture, heat and rate of metabolism, yet there is quite definite optimum size to the groups (3). Aquatic animals from paramecium to gold fish, survive longer in moderate sized groups than do those isolated or in smaller groups (45a) (8). This is especially true when colloidal silver or other poisons are added to the water. The group in this case probably produces a protective substance which aids in warding off the initial shock. Also grouped animals may, in some cases, resist high temperature better than do the isolated individuals. The boxelder bug (Leptocoris trivittatus) was found by the writer (31) to aggregate in regions of higher temperature in a vessel having a graduation from 10° C to 70° C, when introduced in considerable numbers. The larger numbers came to rest in regions of higher temperature than did the isolated individuals or smaller groups.

The effect of violet rays (43) (5) has been tested with a number of animals including sperms and protozoa. In the case of planaria (10) it has been shown that the groups of 60 resisted better than groups of 15 and these again survived better than isolated individuals or in groups of two. Wild Drosophila (54) (55) has been found to survive longer under a variety of conditions when grouped in numbers ranging from 35 to 55 than in smaller or larger groups. Those reared in groups of 35 and later placed in groups of 200 lived longer than those originally reared in groups of 200. This survival factor proved true even when the two kinds were mixed in the 200 groups. Those originally reared in the 35 groups survived longer under these conditions also.

Resistance to adverse conditions have been demonstrated in the case of many bacteria. B. Coli inoculated in agar plates containing gentian violet failed to grow when the initial number was small. However, when the plates were inoculated with larger numbers they grew successfully (20) (25) (26). When single bacteria were introduced in agar plates, there was no growth, but in numbers of 30 they grew very well, probably due to a so-called "communal activity"[1]. Similar results have been obtained in exposure to sunlight. Burnet (20) (20a) reported that when one part of a plate was seeded with a group of 30 and another part seeded with single bacteria the latter would grow if seeded to within a range of one centimeter of the group. Here it appears that some diffusion product may have been developed and served as a promoter. Spermatozoa in large masses have greater fertilizing power and are longer lived than single sperms or smaller groups. (37) (39) (49). This may be interpreted to be due to the difference in the rate of metabolism (47). Single spermatozoa or smaller masses, exhibit greater activity than do the larger masses. Hence products of metabolism such as (CO_2) and the expenditure of energy may be responsible for the reduced survival and lowered efficiency of the single or small groups of sperms. Similar results have been obtained in the cases where larger masses of sperms from Ar-

1. Churchman and Kahn concluded that 30 bacterial cells are able to accomplish more than 30 times as much as a single cell, and this discrepancy between the work actually accomplished by 30 individuals and that which they might be expected to accomplish on a quantitative basis is what is meant by the expression "Communal activity of bacteria."

bacia were diluted with sea water (47) (49) (43). The increase in volume of the fluid and the range of activity thus afforded reduced the longevity and penetration efficiency of the spermatozoa. (32) (37) (39).

The problem of sex and sex ratio has interested all peoples since time immemorial. It has been found that in the case of many kinds of nematode infection of grasshoppers, there always resulted males when the egg infestation was small (5 or less). (23). Again many workers have found that in the case of several species of Cladocera and other small crustaceans, sex was largely determined by crowding (13) (65). Normally reproduction was carried on by parthenogenetic females, but when these were crowded, the young were predominantly males (7) (14). These males would in turn fertilize the eggs of the next generation (6) (16). Since fertilized eggs can resist dessication and other adverse conditions we have here a survival value of the species. Again, where crowding is moderate the young produced consist of both males and females and it thus appears that there exists an optimum in numbers or crowding among these animals (11). When the number of individuals (e.g. Cladocera) become too great in a given area, the offspring is chiefly or entirely males, and since these have no issue there will be a reduction until an optimum is again attained (66) (67). This optimum will favor production of both sexes, and eggs produced at this time are capable of withstanding adverse conditions which will also serve as a factor in the distribution of the species over a wider area. This response to a variety of physical and biological environmental conditions seems to indicate that the organisms develop an adjustment which has definite value for the survival of the species.

Morphological changes occur in many organisms due to crowding. Barnacles, snails, planaria and a large number of insects and crustaceans among animals as well as trees and other plants in the vegetable kingdom when crowded differ greatly in form from those living farther apart. Reinhard (1927) states that aphids have a larger per cent of winged forms when crowded but apterous forms predominate when given more space. (63). Experiments indicate that in general scarcity of food, unfavorable temperature etc. do not produce more winged forms but crowding does, even though the insects are wingless under normal conditions (63). It therefore appears from these results that since crowding results in a larger percentage of winged forms these may fly away and locate new, less crowded habitats which aids in the survival and promotes the distribution of the species.

Uvarov (68) (69), Plotnikov (57) (58) (59), Buxton (21), and others have studied dimorphism and "phases" in certain grasshoppers (locusts). Buxton (21) states that the dark forms of the nymphs were found to have a temperature of 4 to 5 degrees higher than those of the same species having a lighter color. That would be an advantage during the seasonal and daily periods of lowered temperature. The darkers forms were more active and hence a physiological factor was involved. Faure (35) also has stated that larger swarms of adult locusts fly faster and farther than do the smaller aggregations. This activity would tend to scatter them more widely and hence they may reach the needed food more quickly. Need for food, however, is not the dominant factor for they migrate even though food is plentiful. Some deeper seated cause is to be sought (35).

Extensive studies have been made of the morphology, habits, "phases" and of environmental influences upon the closely related forms, Locusta migratoria, and L. danica (35) (58) (68) (69). Johnson (45) has in a similar way made a study of Schistocerca gregaria and S. flaviventris. In addition others have studied African and American locusts with results that corroborate the general principles of crowding (28) (29) (35) (42) (46). Although the migratory and the solitary forms differ quite distinctly in color, habits, and certain morphological features, there are also found intermediate forms. The outstanding differences between the migratory phase and the solitary phase is the darker color of the former. In addition there are distinctive morphological differences between the two in the pronotum and the wing (59) (59). Faure (35) reported that when the eggs were deposited in large and crowded masses by aggregations of females the resulting nymphs developed all the features of the migratory locusts. On the other hand when the depostition of the eggs is made under less crowded conditions the nymphs are said to take on all the features of the solitary locusts; the resulting adults retained in each case the habits expected from the nymphal stage. No doubt a combination of factors enter in but among these that of crowding seems to be the chief contributing factor.

Bridges, Eigenbrodt, Plunket, Harnly, and others have found that morphological features are definitely affected by crowding in Drosophila (18) (33) (40) (60). Reduction in size and suppression of normal morphological features obtained under these conditions. When 20 to 25 larvae developed in 8-drachm bottles the adults were normal. Under most favorable conditions a maximum of 40 may be raised in an 8-drachm bottle but when this number was exceeded the flies were decidedly affected. Here again when taking into consideration the factors of food, temperature, and ventilation, crowding was the determining factor.

In the foregoing discussion there has been presented a number of examples from nature and from the laboratory which should throw some light on the effect of crowding or the relation of numbers to the well-being of animals. Might the results of these studies throw some light upon the problem of human social organization? Under stress, panics, starvation, suppression and the like members of the human species come together in crowds, may even form mobs, but disperse when conditions are again favorable. The colonists, early settlers and immigrants sought out the company of their respective nationals or were kept together by other social, psychological or economic or political interests which they had in common. Even in the present day, foreigners tend to seggregate and form local groups, especially in the larger cities. They are more comfortable there in each other's company for various mutual relations and for protection when subjected to a new environment or when surrounded by unusual conditions.

It has been set forth that overcrowding among humans may be harmful. That children raised in the crowded slums are smaller on the whole than those raised under less crowded and more favorable conditions (17) (34a). Overpopulated countries like India may have a dominance of frail people, both men and women. Men weighing scarcely 100 pounds are quite common. Their life span is also short and their usefulness to the community is next to nil. On the other hand, there appears to be some evidence indicating that people raised in sparsely settled regions are also less favored. Their average size is smaller than that of those living in more populated regions. Statistics gathered from tombstones (40a) and other records in sparsely settled regions indicate that the life span here also is relatively shorter. It seems, then, that even among humans there might be found an optimum as to numbers present in a given area. Standards of living are largely dependent upon optimum crowding among people. Too few people results in less social intercourse and inferior educational facilities, longer distance of travel, greater monotony, inferior artisans and professional men, and inadequate facilities for law enforcement. Too crowded means interference, undue competition, unfavorable conditions of employment, lack of wholesome and stimulating recreation and the development of an artificial mode of living from lack of closer contact with nature. The present suburban movement is an example of the desire to relieve the congested and crowded conditions of the large city. The unfavorable conditions in the metropolis are thus relieved by this type of dispersal and serves to bring about a more favorable and balanced community life.

The majority of our great leaders in all useful walks of life have been born and raised in the country, the village or the smaller and less crowded community. Great discoveries and inventions have been made in the small laboratory and the modestly equipped shop. The small to medium sized college has contributed a larger per cent of leadership than has the great university when considered in terms of total attendance. The same condition prevails in the family of states and nations from ancient times to the present day. However, we must not overlook the fact that much of the detailed, well planned research work that requires special technique and expensive and refined instruments and material can be carried out only in a large institution or by a large company. Yet, this is not a case of crowding, for here the work is performed under favorable or optimum conditions by a few gifted and scientifically trained persons. On the other hand we may refer to the ill effects of crowding that obtain in the mechanized, industrial plant or shop where mass production is effected under over-crowding that militates against the well-being of the group and the individual worker alike.

It seems, therefore, that the constant yearning in men for more territory, larger populations, imperialism, subjugation of smaller nations, and the unlimited increase in the size of population is tantamount to the initiation of disorder. A scientific study of man as a rational being should lead us to strive for moderation rather than excess. In the light of the history of mankind, and from evidences gleaned from the study of other organisms we must conclude that there is an optimum to be attained in the matter of numbers, crowding and size in the unit of aggregation. None of these factors are stereotyped or static, for the various environmental conditions, both natural and man made, must be taken into account. Nevertheless, it would be an act of madness to interpret the dictum "Be fruitful and multiply and fill the earth, and subdue it," to mean that any one people or few peoples shall usurp this prerogative. Neither does it mean that quantity and size have no limits. By far greater importance must be placed upon optimum conditions for the attainment of the highest possible quality in all endeavors. This is the spirit of the scientific attitude and the methods of science. As long as our Academy will champion this cause it must of necessity continue its present high standards of achievement and become an ever greater factor for good in our local and national life.

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