The subject of population dynamics is more commonly treated from the demographic point of view. This view stresses the fact that a population grows, remains stable, or declines, dependent upon the interrelationships of natality, mortality, and migration. Interactions of these phenomena determine density; that is, the number of organisms inhabiting a given space. Customarily, the results of such demographic studies are graphed as growth curves which pictorially show the change in density through time, or they are given as life tables from which such factors as life expectancy or age structure of the population may be derived.

In the analysis of those factors which alter the pattern of changes in density, consideration is normally given to the relative abundance of food or other prerequisites of life, to the incidence of disease and similar factors as they affect the general health of the population, and to the occurrence of favorable or unfavorable climatic conditions. Such factors are viewed as they depress or accelerate the growth and expansion of a population (Allee, et al., 1949; Cole, 1948; Park, 1946). Scant attention is paid to the role of the individual or to the internal phenomena of those sub-groups of the population to which every individual of most species is normally a member, such as the family or other reproductive aggregates, feeding aggregations, harborage aggregations, and finally regional aggregations. This latter consists of individuals or groups which occasionally come in contact with each other without normally participating in the attaining of common goals. If social behavior really does alter the character of population dynamics, it is just such an understanding of the role of the individual and his group which we must seek. We might have rephrased our problem as "Does population dynamics alter the character of social behavior?"

Both aspects will be examined here.

In the following discussion there is no attempt to review the literature. Rather, we shall hazard to discuss a wide variety of phenomena that are involved in a full appreciation of the interrelationship between sociality and population dynamics. Through such a "stock-taking" of relevant data from diverse fields of research, we shall endeavor to demonstrate the need for multi-discipline approaches to these complex problems. The writer, as an ecologist, no doubt expresses bias in his treatment of this discussion.

We might first wonder if sociality really does have any influence at all on population dynamics. Perhaps it will be best for me to describe briefly a situation with which I have had intimate experience. This concerns the role of social
behavior in limiting numbers among wild Norway rats. (This study of the Norway rat is still largely unpublished. It was a phase of the research program of the Rodent Ecology Project of the Johns Hopkins University School of Hygiene and Public Health, which was sponsored through a grant from the International Health Division of the Rockefeller Foundation.) (Calhoun, 1949a, 1949b.) For 28 months I observed a colony of rats (Rattus norvegicus) near Towson, Maryland, as it grew from a few individuals to the point of saturation in numbers. This colony was maintained in a 10,000-square-foot pen where there was a super-abundance of food at all times, and where harborage space was never completely utilized by the rats. At the time the colony was killed off there were considerably less than 200 adult rats, and all the evidence pointed to the fact that the adult population would never have exceeded 200 individuals. The number is particularly instructive when we compare it with the number of rats that might have been raised in the available space had each individual been isolated as a juvenile into two square feet of cage space, as is customarily done in the laboratory. Under such laboratory conditions 5,000 healthy rats might have been reared in 10,000 square feet of space instead of the 200 which utilized such space under free ranging conditions. This figure of 5,000 rats is actually a conservative one in regard to representing the biotic potential expected from this free-ranging colony. The studies of Emlen and Davis (1948) and Davis (1949) supplemented by my own observations indicate the following conditions for determining the potential reproduction were other limiting factors not in operation: (1) 8 per weaned litter with equal sex ratio; (2) first litter by 5 months of age; (3) one litter every two months; (4) no breeding during the four mid-winter months; (5) all rats born the first breeding season should be dead by the end of the third; (6) it is within the potential life span of a rat for all others to have been alive at the end of the experiment; (7) the study lasted from March 1947 to June 1949. With these conditions as a basis for judgment, 50,000 rats might have been alive in June 1949 as descendants from the original five females. Nevertheless, in the comparison above, it is believed that the figure 5,000 is a more realistic one in indicating the potential density of 10,000 square feet, although it is conceivable that 50,000 healthy rats could be maintained in a similar space by confining each to a cage somewhat less than eight inches on a side. What, then, was the cause of this 25-fold decrease in utilization of space under naturalistic conditions? The obvious explanation is that under free ranging conditions the rats expressed genetically determined and culturally modified behavioristic potentialities, which were impossible under caged conditions. This explanation has philosophically broad implications. Whenever the density of a population becomes increased beyond that level to which the heredity-to-environment relationship provides optimum adjustment, then the individual and the group must forfeit some of their potentials of behavior if all members are to maintain an adequate state of health.

There are three basic ways in which the social behavior of this colony of rats altered the population growth. They are as follows:
1. Development of local groups which maintain their integrity restricts the utilization of space.—Local colonies or aggregates were formed primarily on the basis of continued association in the locality of birth. There was sufficient conflict existing between these local colonies that there developed intermediate buffer zones in which burrows were never constructed and across which there was a reduced incidence of locomotion. The development of these social buffer zones seems essential to the maintenance of group integrity and it is a major factor in reducing the number of animals which utilize a given amount of space.

2. Social stability favors successful reproduction.—A stable group is one in which there is a well-developed dominance hierarchy, is one where there are well-established relationships between all the members of the group, and is one in which the individual members have experienced few behavioral disturbances and have exhibited favorable patterns of growth. Among such stable groups the frequency of conception is high, and most of the young born are successfully raised.

On the contrary, among socially unstable groups the frequency of conception is reduced and very few of the young born survive to weaning, and if they do the chances of their, in turn, leaving any progeny are very slim indeed. Socially unstable groups are those consisting of members who have had few associations in common, and/or who have experienced many behavioral disturbances and have exhibited retarded rates of growth. Among such stable groups the frequency of conception is high, and most of the young born are successfully raised.

3. Social stability favors decreased mortality.—Predation from flies was the chief direct cause of death. During the immediate post-weaning period, when the young rats are making their adjustments to colony life, flies frequently lay eggs in the fur of the young. The young most likely to succumb are those which have received excessive punitive action from their associates or who, for various reasons, have no permanent home. Flies also kill adults by laying eggs in open wounds, even fresh wounds. Rats low in the social order receive more wounds and are thus more subject to being consumed “alive” by maggots.

As the population increased in numbers there was an increase in the frequency, intensity, and complexity of behavioral adjustments necessitated among and between groups of rats. This forced more and more rats to be characterized by social instability with the accompanying result of lowering the biotic potential to the point where there was a balance between natality and mortality—all this in the continued presence of a superabundance of food and unused space available for harborage.

This influence of social behavior upon population growth in the Norway rat is exhibited in various degrees among other animals. However, in the time and space available here, no attempt will be made to present a critical review of the field. Rather, we shall examine the phenomena of social behavior and the condition of sociality as they relate to the broad problem of growth exhibited both on the individual and on the population level. Through this discussion we
shall place sociality in perspective to other biological phenomena and suggest avenues for further research.

Various concepts of levels or types of sociality exist. According to Allee (1940) these are: 1. "Sociality includes all integrations of two or more organisms into a supra-individualistic unity on which natural selection can act;" 2. Sociality is coextensive "with the existence of an innate pattern of a certain specialized appetite" whose satisfaction demands that animals live together and engage in common activities; 3. "True sociality occurs only in the presence of abstract values of which members of the group are more or less conscious." Thus, sociality ranges from unconscious automatic co-operation (Allee, 1945) to conscious cooperation in which the members react to socially conditioned symbols (Northrop, 1948). A bridging of this range of social characteristics is begun as soon as the association between a social behavior and its consequences is modified by the learning process. For example, when a mouse who has repeatedly lost in combat makes the adjustment of running away upon sight of his opponent, values are affecting social behavior. Approaching the opponent will result in pain, while avoidance prevents pain. Not only does such a behavior illustrate the realization of values, but also that such values may be generalized. A case (Allee, 1942) in point is that of an albino mouse, who submits to other albino mice on first encounter, after having previously been conditioned from repeated defeats by the more aggressive C57 black mice. To such a mouse any other mouse, and not just the one by which it had been beaten, serves as a symbol of the dire consequences which will result, if he fails to submit or run away. Such generalizations from prior experience form the major basis for the origin of abstract values.

For our consideration of the interrelationship of sociality to growth phenomena, the most important considerations cover those conditions permitting a population to develop and express those characteristics of sociality which are possible within the limitations imposed by the genetic potentialities of the species in question.

Wherever animals live they are constantly altering the environment about them. This occurs through such diverse phenomena as release of excreta, alteration of surrounding temperature and humidity, construction of trails and burrows, and the development of habits, all of which may alter the behavior of members of their own or later generations. These phenomena are spoken of as biological conditioning of the environment. Such activity has repeatedly been shown to alter the welfare of existing members of a population as well as the density exhibited by later generations (Allee, 1942, 1945; Allee, et al., 1949). Under essentially random dispersal of individuals through the environment, any effect of biological conditioning upon the welfare of the members of a population may be assumed to be dissociated from social phenomena. However, when such effects are associated with animals which live in aggregates (as opposed to different effects occurring when the same kind of animals live dispersed) we may, with assurance, infer that sociality is a factor in affecting the welfare of the group. There is a tendency among many animals toward group activity, the result of which ameliorates the environment so that their physiology is more efficient or that survival rate is increased. Such biologically conditioning phe-
nomena are the result of co-operative activity. Beyond a certain point the same activity may become deleterious as the participating group increases in numbers, to the point that the formerly beneficial activity lowers survival rate or physiological efficiency. The merits of any social behavior are thus relative to the condition and history of the group within which they occur. For example, copulation among mammals is a desirable and necessary social behavior if the species is to survive. Yet, among certain socially disturbed groups of my Towson colony of rats, which lacked a well-integrated dominance-hierarchy, copulation rarely led to conception despite, or perhaps because of, its high frequency.

As soon as animals begin to condition their environment through the elaboration of relatively permanent artifacts such as trails, nests, burrows, and the like, biological conditioning assumes a more definite cultural aspect. To be sure, such artifacts satisfy primary organic requirements; dens are a place of retreat from enemies or inclement weather; nests are places where the young are safe; trails lead to food or harborage, and food caches serve to make food more accessible. However, beyond such primary functions, dens, nests, trails and the like further serve as a physical mold in which the social matrix takes its form.

It is with reference to the construction and utilization of these animal-made structures that many patterns of behavioral relationships become established. Where more than one animal uses one of these biological artifacts either conflict, tolerance, or the acceptance of rank-oriented priority develops (Collias, 1944). When two rats, who are familiar with each other, meet along a trail, each usually steps slightly aside and passage occurs with no sign of conflict, even where difference in rank occurs. Furthermore, young animals who develop within an artifact-conditioned environment find life much easier than did the original colonizers. They not only find previously established places of retreat and established pathways of movement between harborages, sources of food and the like, but they also encounter an artifact-oriented stabilized social structure within which their own integration during maturation is facilitated.

This alteration of the habits and social behavior of one generation by the activities of generations which precede it represents a cultural process, when culture is considered from a broad biological viewpoint. The term culture will here be used in this limited sense, without attempting to discuss the further elaborations which are expressed among human societies. If this restriction is placed upon the concept of culture, there exists the possibility of treating it comparatively in experiments with infra-human organisms. By so doing we may hope to arrive at generalizations which are useful on the human level. For such comparative purposes we can deal with effects and modifications produced by inherent behavior as well as those which are further structured through the process of learning.

There are striking similarities between the culture of man and that of some of the other vertebrates. Artifacts are constructed, learned patterns of social behavior are developed, and both are passed on to influence the life of later generations. Chance behavior or superstition may affect the pattern of learned social behavior (Skinner, 1948), and the character of vocalization may be handed down through cultural inheritance. Regarding the cultural modification of vocali-
zation, Altmann (1950) has recently described an interesting situation among elk. In herds whose social structure has been upset by hunting, very little vocalization occurs. However, in a herd which lived far back in the Teton Mountains, where they had escaped being hunted, there was a continual calling back and forth between members of the herd.

Much in common exists between the patterns of culture among different species of vertebrates. Culture, particularly when continuity through many generations is insured, provides a stabilizing influence on the activities of the members of a population and permits them to make more effective use of their environment. Although there is as yet no experimental data to verify this postulate, it is quite likely that the genetic inheritance of many species is such that optimum adjustment by the individual or the group is made only under those conditions favoring the existence of a stabilized culture with its accompanying biologically produced artifacts. However, we must realize that cultural stability also restricts the potentialities of behavior, since other patterns of culture are automatically excluded.

It is through the alteration of the complexity and stability of culture that sociality exerts a controlling influence upon population dynamics. One of the inherent aspects of this concept concerns the relative continuity through space and time of both the population and the physical and social alterations which have been produced by the population. Discontinuities impose conditions of cultural instability as well as inhibit the maintenance of developing complexities of social organization. As mentioned previously, for the Norway rat such social control of population dynamics operates by influencing reproductive capacity, growth rate, mortality rate, incidence of disease, and behavioral adjustment. Our problem, then, resolves itself into a consideration of factors which may influence the complexity or stability of the culture of a population.

Analysis of operant factors must take into consideration the perception of the environment by the individual. The manner in which animals perceive their environment is socially important because it largely determines the rate and manner in which animals contact each other, and the manner in which they utilize the space about them. We often overlook the fact that the same physical environment, such as a mat of grass, may be differently perceived or is differently reacted to by different organisms (Schneirla 1949). Similarly, the same environment may have different meaning to two different individuals of the same species, due to differences in heredity or experience. In this discussion we shall treat the responses (or lack of responses) of animals as resulting from their perception of the environment. However, we must realize that the physiological state of the individual may alter the response regardless of how the environment is perceived (Fuller, 1950).

There are two phenomena relative to perception of the environment which must be kept in mind upon interpreting observations. First, an animal may react to an environmental situation as if it were complete, whereas portions of it are actually missing. Second, an animal may fail to perceive or react to portions of its environment which are actually present, and which it is capable of
perceiving and reacting to. In either case, unfavorable usage of the environment, with resultant density effects, may occur.

The first phenomenon of reacting to an incomplete environmental situation is a derivative of the "releaser" concept developed by Lorenz and by Tinbergen (1948). A releaser is a structure of the environment or a behavior of one animal, which elicits a sequence of behavior by another animal. It is characteristic that the releaser is only a segment of the complete goal-object or goal-situation to which the reacting animal responds. Under usual conditions the behavior of the reacting animal proves satisfactory, since the complete goal-object or goal-situation is actually present. Tinbergen showed that the red belly of male stickleback fish during the breeding season served as a releaser, which elicited the female to follow the male to the spawning ground. Females will follow objects with ventral red areas which only remotely resemble fish in appearance. Under such conditions the behavior of the female can have no effective solution. Admittedly, much research needs to be done in the field of elicitation of behavior of social implication by releasers, but the releaser concept, nevertheless, provides a useful theoretical framework for orienting research.

Harris (1950) has made some interesting studies of spatial orientation in the deermouse, Peromyscus, which bears on the problem of the role of "releaser phenomena" on population dynamics. Peromyscus maniculatus bairdi inhabits grassland, whereas Peromyscus maniculatus gracilis inhabits woodlands. These two closely related subspecies may live in adjoining habitats and yet never interbreed, although they do so freely in the laboratory. Adjoining rooms with an inter-connecting passage were arranged to simulate the natural habitats. "Grassland" was made of bunches of thin strips of heavy paper, while "forests" were simply sections of small trees standing on end. When given a free choice of movement between these two rooms each of these subspecies of mice spent a significantly greater amount of time in the habitat simulating their natural one. Such orientation was just as efficient by mice born and raised in small laboratory cages as it was by mice trapped in the wild. It showed that these mice possess an innate capacity for tropistic behavior for which only a small segment of the environment is required as a releaser. This type of behavior is one of the keys as to why animals make differential usage of the available environment—space in particular being considered. Although extrapolating from experimental situations sometimes leads to false conclusions, one would strongly suspect that both the spacing and form of vegetation are important factors in both the occurrence of a deermouse in a habitat and the size of its home range, perhaps irrespective of the supply of food and harborage. Certainly, these ideas present a provocative subject for both observational and experimental studies. In fact, one is led to wonder how the behavior of animals is altered when they find themselves confined, as on islands, to habitats from which they cannot escape and to which their heredity does not permit their proper adjustment. Such an area of investigation might be designated as "comparative esthetics." Its ultimate analysis presumably would concern the manner in which the art forms of the material world about him affect man's behavior and peace of mind. Further theoretical
aspects of releaser phenomena to social behavior have been pointed out by Ginsburg (1949). He says: "What interests me here is that a phylogeny of such releasers amounts to a phylogeny of symbolic behavior and indicates an innate capacity to derive meaning from abstract symbols. It is true that we do not know what this meaning is on an ideational level; nevertheless, it has its counterpart in human behavior if we accept the findings of orthodox Freudians."

The second phenomenon of failure to react to those existing portions of the environment, which potentially should contribute to the well-being of the organism, is one with reverberations in the dynamics of populations. The point involved here is that conditions arise which preclude the organism making the optimum use of available resources, whether they be physical, biological or social. In the field of psychology a large portion of the research in learning theory and abnormal behavior is actually involved with this problem. Likewise, it is the crux of the endeavors of psychoanalysis to reveal the origins of such situations. Field workers in ecology frequently observe animals whose reactions are out of harmony with their environment, and it is one of the aims of wildlife management to prevent their origin. In the experimental field we find such attempts to designate the problem, as in Tolman's (1949) concept of "perceptual blindness," or we find the conditions exemplified in such artificial situations as Liddell's (1942) work in producing "abnormal behavior" in his investigation of conditioned reflexes.

I would like to cite an observation of my own from my free-ranging colony of Norway rats. It exemplifies the complexities which may arise in an open society. Most rats, particularly those which have received mild degrees of punitive action from their associates, stored food in their burrows. The food might or might not be eaten immediately upon taking it to the burrow. Transportation of food in itself might satisfy a drive; however, it is to be noted that these rats deposited the transported food in locations where they themselves would have a good chance of securing it later. On the other hand, the storing behavior of rats who have experienced excessive punitive action from their associates is quite different. Repeated trips would be made from the food hopper depositing food at scattered points nearby, usually not more than 15 feet away, whereas the burrows were all further away. Once this food was left the rats which had done the transporting paid no further attention to it. Whatever the mechanism of development of this behavior may be, it is readily evident that the rats exhibiting it are no longer making a favorable use of this aspect of their environment.

An interesting aspect of this behavior, which is certainly abnormal from the individual's viewpoint, is beneficial with reference to the entire colony. (This type of behavior occurred in less than five percent of over 200 rats observed. Associated characteristics in such rats formed a syndrome which included (1) accentuated pre-weaning competition with older sibs, (2) inhibited growth during entire life span, (3) "freezing" when cornered in a trap or harborage, (4) lack of successful reproduction.) This scattering of the food made it more available and thus reduced competition at the main source of food. This observation
raises the question, "how abnormal is abnormal behavior?" Though an individual rat may have its behavior so disturbed that its own effective reproduction is prevented and its own proper usage of food inhibited, it may, nevertheless, make a significant contribution to the welfare of its society through making the environment more favorable for its associates. For proper evaluation the range of variation in individual behavior needs to be viewed both as it affects the individual and the group.

Perception of spatial relationships and the manner in which animals utilize the space available to them have important social implications and exert a controlling influence on density. Territoriality, the active defense of a given tract, and home range, the occupancy of a preferred area, function as active or passive means of maintaining dispersion of individuals or groups (Allee, et al., 1949, page 412; Burt, 1943; Nice, 1941). Although we lack sufficient knowledge to state exactly why an animal occupies a territory or home range of a given size, one rather general characteristic is that more food exists in the occupied area than is utilized.

This restriction of the privilege of occupying space irrespective of food imposes limitations to population growth not realized by the earlier students of this subject (Davis, 1950). Social hierarchies provide an elaboration to the complexity of territory or home range. The development of rank-order systems permits the organization of group integrity and stability which in turn leads to in-group and out-group status. Attraction between members of a group and antagonism between members of different groups produce local concentrations with intervening buffer zones which are little used by the members of adjacent groups (Keith, 1949; Scott, 1943; and author’s observations on rats).

Perception of spatial relationships may have repercussions directly or indirectly on both social behavior and population dynamics, because patterns of locomotion through an environment alter the rate of contact between associates, as well as their orientation to the physical structures of the habitat.

At the Jackson Laboratory litters of dogs are raised in 20 x 70-foot pens. Snow trails reveal the manner in which the dogs utilize their confined area. Wirehaired Fox Terriers beat a single path about the periphery; Cocker Spaniels also beat a path about the periphery of the pen, but they also beat a few trails diagonally across the pen; Beagles and Basenjis form trails as do Cocker Spaniels, but in addition there are occasional to frequent wanderings away from the paths through the otherwise unbroken snow; and finally, the opposite extreme from the Wirehaired Fox Terriers is exhibited by Shetland Sheep Dogs—their tracks appear to be distributed completely at random over the pen with very little indication of a peripheral trail adjacent to the fence. Of course, we do not know what sort of natural population these breeds are capable of developing, but the snow-trail patterns exhibited indicate that these breeds would markedly differ in their utilization of their home range.

Another factor which has direct implications for population dynamics, particularly among social species, is that of preadaptation (Allee, et al., 1949, page 642). Although natural selection may have been operating on a species with
the result that this species exhibits the ability to make an optimum adjustment to some particular environment, the species may, nevertheless, make a very excellent adjustment to some new environment with which it has had no prior association. In fact, some animals prosper in the new situation, as indicated by expansion of the population into new areas or by increases in density. Such adaptation is particularly prominent among such birds as robins, chimney swifts, bluebirds, wrens, and kingbirds (Kennedy, 1915), which have utilized many man-made structures to increase their available nesting or feeding niches. This same utilization of environments, highly altered by man, is especially exhibited by such forms as the house mouse and the Norway rat. Preadaptation phenomena include the ability to engage in complex behaviors in entirely new situations. Under the artificial environment of the laboratory myriads of experiments with the derived strains of the Norway rat have amply demonstrated this ability. Under completely free-ranging conditions ground squirrels will engage and solve many intricate problems presented to them in their normal environment (Gordon, 1943).

The phenomenon of preadaptation becomes of particular importance when the opportunity for it to be exhibited occurs in a population characterized by cultural continuity. Although the original manner of exploitation of a new environmental situation may be by chance, by learning, or by reasoning, its
continued contribution to the welfare of the population is greatly enhanced by the new patterns of behavior being passed on to later generations through cultural processes. In time, the behavior may be further elaborated, so as to further the biological conditioning of the environment and also to modify the cultural pattern. In the long run, what preadapted and culturally modified behavior does is to permit the population to make more effective use of available energy. A striking example of this is reflected in the population growth (Fig. 2) of Germany (Dewey and Daikin, 1947). One cycle of growth during an agricultural economy had just about terminated at the beginning of the industrial revolution. At that time there arose a new growth curve which has only recently approached completion. Thus, the carrying capacity of an environment must also be considered from the ability and opportunity of its inhabitants to exploit the available energy. Each new type of exploitation gives rise to a heightened level of population density. (Many similar examples could be cited utilizing infra-human animals. An outstanding one is that of the chimney-swift. Prior to the arrival of white man in North America it nested in hollow trees, and during the migration seasons they aggregated in fairly large flocks which spent the night together. With the replacement of hollow trees by myriads of chimneys as a nesting

![Population growth in Germany](after Dewey and Daikin). This figure typifies the influence upon the resultant population growth of the ability of an organism to utilize the available energy. Such changes in ability may arise through either genetic or cultural changes within the species.
niche, the abundance of this species has greatly increased. In addition to the increase in social contacts imposed by the proximity of chimneys, much larger aggregates—at times reaching many thousands—are formed in chimneys of large buildings during migration. Similar phenomena are characteristically observed in the changes of population densities during the succession of plant and animal communities (Allee, et al., 1949). Animals or plants characteristic of a later stage of succession are commonly found as scarce invaders of an earlier stage. As the community structure changes and as conditions become more favorable for the invader its numbers increase. An important aspect of this situation is that the organism participates in the production of an environment more favorable to itself. From a research viewpoint the investigation of this phenomenon resolves itself into two aspects: (1) In what ways do organisms alter their environment to make them more favorable? (2) How can animals be induced to make more rapid and more efficient alterations and yet maintain their cultural stability?) The repetition of this process requires continued increase in complexity of the social organization. And as has been previously remarked, after a time there are continued restrictions to the development and expression of behavioral potentialities—a process, which we may anticipate, will terminate with the individual being only a hollow shell of his potential self. Opportunity for free expression of hereditary potentials of behavior and the drive toward increased utilization of available energy by the group are in part complimentary and in part conflicting tendencies.

Natural selection toward the survival of organizations of life which make more effective use of available energy is exhibited in the succession of plant and animal communities (Allee, et al., 1949). The final stages are characterized by an increased rate of energy intake from the sun (by plants), by an increased rate of release of free energy (particularly by animals), by greater complexity of organization, and usually by a greater weight of living matter per area. In our search for guide posts for human civilization we would do well to examine closely the dynamics of community succession whose terminal stage is self perpetuating as long as drastic changes in climate do not occur.

Nor can we consider the utilization of available energy without taking into account the growth of a population (that is, its density) with reference to the growth of the individual members of the population. Fishery research has shown that in a given body of water a relatively large number of stunted fish or a much fewer number of large fish may live. Density cannot be considered irrespective of the welfare of the individual. If the rat is at all typical, mammals behave much as do fish. In my Towson colony of Norway rats, as the population increased, more and more individuals were physically stunted despite having plenty of food available. Such stunted rats seemed healthy, as judged by the occurrence of fat—they simply failed to grow very large and attained their mature weight very slowly. These stunted rats were characterized by behavioral disturbances imposed by the increasing complexity of the social structure. Dwarfism or abnormal growth in man may also be associated with behavioral disturbances arising from unstable social environments (Binning, 1948; Fried and Mayer, 1948; Talbot, et al., 1947).
Thus, we see that several growth processes are closely interrelated: (1) the rate of physical growth and skeletal maturation in the individual, (2) the level of mature growth of the individual, (3) the level of sexual and behavioral maturity in the individual, (4) the degree to which an individual or group is enabled to express genetic potentialities, (5) the growth rate of a population and its density at maturity, and (6) the social integration of a population—all these are inter-dependent variables whose expression is in turn influenced by the structure of the environment and the degree of cultural continuity possible.

The extent to which one of these growth phenomena may be enhanced through the partial suppression of the others raises the problem of value systems. Population density may be intensified at the expense of reduction in individual growth, and an increase in social tension. Maximum individual growth may be assured, through isolation with the resultant induced social sterility, irrespective of population density. A realization of the interdependence of these growth phenomena provides the viewpoint for the establishment of a truly comparative science of sociobiology.

As our human society becomes more highly technical, there arises the tendency to accentuate one of these growth phenomena without any consideration as to its effect on other aspects of life. This is particularly so as regards increasing population density, which in many quarters is accepted as a desirable objective. Bateson (1912) long ago realized the fallacy of this concept when he said: "It is not the maximum number but the optimum number, having regard to the means of distribution, that it should be the endeavor of social organization to secure. To spread a layer of human protoplasm of the greatest possible thickness over the earth—the implied ambition of many publicists—in the light of natural knowledge is seen to be reckless folly."

Yet such accentuation of a single aspect of the value systems relating to growth phenomena continue. E. G. Rochow (1949) predicts that it will be possible to feed a population of one billion persons (this is over five times the upper level indicated by the present trend) living within the boundaries of the United States. In a letter to me, Dr. Rochow made this further elaboration: "The chief difficulty arises, of course, in feeding so large a population, particularly if it is to spread over and inhabit a large part of the present farm lands. This is the part of the problem that becomes a challenge to chemists" and "I should also like to point out that the high population density in large cities is in part alleviated by purposeful isolation of many of the inhabitants." The choice before us is to develop a society whose numbers are limited, but whose members live a full life, or, as Rochow believes, to develop a society of maximum numbers whose members have had a restricted experience accompanied by an inhibition of many potentialities of expression. Maximum production of protoplasm is a valid concept and objective in the field of animal husbandry, but it is of doubtful value when applied to human society or even to game management. Current discussions of increasing agricultural production are also frequently so worded as to imply that what is possible is desirable—with little critical thought as to the consequences on the human population.

In this whole problem of the social aspects of population dynamics an im-
portant consideration is the individual's learning the nature of his physical and social environment. Although some behavior does not reach full development until an animal is quite mature, such as copulation and defense of territory, nevertheless, most contacts that an animal has with his environment begin very early in life. In fact, even where the complete behavior pattern or the full experience only occurs during adult life, the experiences of infancy and the juvenile period markedly alter later life (Hymovitch, 1949). The learning process among immature animals is qualitatively different; where the young are prevented from perceiving the environment, they, as adults, do not profit as well from similar experiences. Experiences during early life have a profound effect upon adult behavior and health. These conclusions apply to both physical and social aspects of the environment. Among dogs the latter part of the nursing period and the period just following weaning form a brief but critical one for the development of social adjustments (Scott and Marston, 1950). My own observations on wild rats were not such as to result in any clear-cut conclusions regarding the role of pre-weaning experience, but they amply demonstrated that the immediate post weaning and preadolescent periods were critical for future development. Among these rats social status, rate of growth, adult size, and stability of behavior were in large part determined during this juvenile period. In our observations of animals under natural conditions, in experimental studies of population ecology, and in laboratory studies of isolated animals or small groups, we need to give increasing attention to the manner in which the environment and experience of juvenile animals affect their behavior as adults.

In all species, regardless of their degree of sociality, natural selection operates on all levels of organic complexity from the individual to the population (Allee, 1945). By a population we mean: any contiguously distributed grouping of a single species which is characterized by both genetic and cultural continuity through several generations. Therefore, if we are to make real progress in understanding the inter-relationships of sociality and population dynamics, our observations need to be focused upon the population as the major unit in which the lives of individuals find reality. Particular stress needs to be laid upon those factors which alter the maturation of the individual on the one hand, and, on the other, to the variations in the structure of the environment, which mold the fate of both individuals and populations. From an experimental standpoint this means that we must use populations as our experimental units; these to be followed from their inception with a few members to the maturity and possible senescence of the population, and to be studied in environments where many of the physical factors of the environment are controlled and organized into meaningful patterns. Fuller (1950), in his Situational Analysis, has provided a framework for the experimental manipulation of the field parameters of behavior (incentive, barriers, and complexity) into meaningful patterns. This framework coupled with Calhoun's (1950) approach to the experimental manipulation of population as the unit of investigation presents the necessary background for objective investigation of the social aspects of population dynamics. Many helpful suggestions for plan-
ning experimental studies of sociality are included in the "Minutes of the Conference on Genetics and Social Behavior" (Scott, 1946).

In the planning of such experiments we may rely on the great wealth of ecological field observations and the equally great wealth of laboratory studies of the psychology and physiology of individuals and small groups. At best, experimental studies into population dynamics, even with those vertebrates characterized by high reproductive potentials, take several years for completion. They require substantial sums of money and should be pursued simultaneously by investigators trained in several diverse disciplines. To be sure, this is a large order, but small in comparison to the likely contributions to the welfare of man and the world about him. Any interpretation of results pertaining to the interrelationship between sociality and population dynamics involves judgment values. This is as it should be. However, such judgment values can only gain reliability when viewed against a background of experimentation, which enables manipulation of the variables, as well as repetition of experiments with the view of determining the variability of the end results of social equilibrium, when the accompanying static aspects of the environment (and heredity) are maintained constant.

Initial studies under controlled conditions of the interrelationship between sociality and population dynamics are likely to be most fruitful if we utilize some of the common experimental mammals and their wild counterparts. Of these the most useful will be: (1) the mouse, Mus musculus; (2) the rat, Rattus norvegicus; (3) the rabbit, Oryctolagus cuniculus, (4) the dog-wolf complex, Canis lupus; and (5) the rhesus monkey, Macaca mulatta. This arises from the fact that there is a great backlog of biological information concerning them, and that scientists in several biological disciplines are accustomed to working with these forms. Four of these forms (mouse, rat, rabbit, and dog-wolf) are particularly suitable, since for them there is available a large number of highly inbred strains or genetically divergent breeds. This variability may be used to exploit the heredity parameter of the organism-environment complex. Scott (1949) has discussed in detail the value of inbred strains for experimental work relative to behavior, and Heston (1949) has similarly treated the usage of inbred strains in physiological studies. Inbred strains or breeds exhibit accentuation or inhibition of behavior characteristic of the wild form. It is this type of variability from the wild type which makes the use of such genetic derivatives useful. On the primate level we should have available breeds or inbred strains of a species suitable for use in the laboratory and in the field situation required by experimental population ecology. The rhesus monkey (Carpenter, 1942) is probably most suitable for such genetic work leading to further behavior studies. Although I have mainly stressed environmental influences in the present discussion, we must bear in mind that an analysis of the social aspects of population dynamics must be based upon a consideration of both heredity and environment. Sumner (1922) long ago ably pointed out that, insofar as the existence of life was concerned, neither heredity nor environment had reality in the absence of the other.
It so happens that all five of the species are characterized by rather complex social structure in comparison with many other representatives of their orders. To produce the fullest understanding of sociality and population dynamics some of those species with less complex social structure should also be thoroughly investigated.

Although present knowledge, derived from ecological studies of animals living in their native habitat, and from psychological studies of animals in the semi-isolated unsocial conditions of the laboratory, gives us a firm foothold for planning controlled studies of population ecology, much additional basic information is desirable. We particularly need many more detailed life-history studies of animals in their native habitats. These will be most effective when parallel life histories are made comparing related species known to differ in social structure. In practically all orders and many smaller taxonomic categories of mammals, there exists a wide range in the degree of sociality between different species. Table 1 presents examples of the wide range of sociality existing between related genera. In each instance the degree of sociality is judged on the basis of the size and permanence of groups, as well as the complexity of interrelationships between individuals and groups.

The existence of wide ranges of sociality among many groups of mammals, even including the primitive marsupials, makes it highly likely that determination of social structure is in large part independent of the degree of evolution of the cerebrum.

Investigation of the following topics by those making life history studies will be most helpful in bringing about a better understanding of the relationship between sociality and population dynamics.

1. What are the goal-objects toward or between which animals orient?
2. How are these goal-objects distributed through space and time, particularly as they relate to the energy expenditure of the organism in re-encountering a goal-object?

<table>
<thead>
<tr>
<th>COMMON NAME</th>
<th>ORDER</th>
<th>SLIGHTLY SOCIAL</th>
<th>MORE HIGHLY SOCIAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deer</td>
<td>Artiodactyla</td>
<td>Moose (Alces)</td>
<td>Elk (Cervus)</td>
</tr>
<tr>
<td>Rabbits</td>
<td>Lagomorpha</td>
<td>Cottontails (Sylvilagus)</td>
<td>European rabbit (Oryctolagus)</td>
</tr>
<tr>
<td>Rodents</td>
<td>Rodentia</td>
<td>Deermouse (Peromyscus)</td>
<td>Norway rat (Rattus)</td>
</tr>
<tr>
<td>Opossums</td>
<td>Marsupialia</td>
<td>American opossum (Didelphis)</td>
<td>Australian opossum (Trichosurus)</td>
</tr>
</tbody>
</table>

1 Literature references: Moose (Denniston, 1949); elk (Altmann, 1950); cottontails (Trippensee, 1934); European rabbit (Southern, 1940, 1947); deermouse (Howard, 1949; Nicholson, 1941); Norway rat (Calhoun, 1949a, 1949b); American opossum (Lay, 1942); Australian opossum (Pracy and Kean, 1949).
3. What are the physical barriers of the environment and the complexity of their arrangement, which modify the likelihood of an animal perceiving or reaching a goal-object or of contacting other individuals?
4. What are the pain-producing barriers (both physical and social) which may occur between an animal and its goal-object?
5. How are the physical barriers or the pain-producing barriers distributed through space and time?
6. Describe each observed type of behavior in terms of:
   A. Composition of group involved (sex, age, relationship, etc.—see especially Carpenter, 1942).
   B. Type of behavior as regards its origin and function (see Scott, 1946, p. 23).
   C. Innate drives whose satisfaction depends upon the occurrence and distribution of goal-objects and barriers.
7. What are the conditions of juvenile life as related to:
   A. Relative maturity at birth.
   B. Length and pattern of dependency of young upon their mother or other associates, including frequency and kind of contact.
   C. Manner in which the young are integrated into the social structure.
   D. The maturation of each goal-object oriented behavior.
8. In what ways do the animals biologically condition their environment, and how does such conditioning influence the expression of either innate or learned behavior?
9. What is the social structure of groups in terms of rank-order relationships or other inter-individual adjustments?
10. What is the pattern of relationships between different groups?
11. How is the growth of the individual, its reproductive success, and likelihood of survival associated with the above types of data?

Whereas, other types (refer to the outlines appearing from time to time in Ecology, whose publication is sponsored through the Committee for Life History Studies) of observations are useful in preparing life history studies, the systematic accumulation of data of the above type will be of great usefulness in the next step of analysis—the planning and execution of controlled experimental studies into population ecology. Such data will facilitate a systematic arrangement of environmental components. In the native habitats of most animals goal-objects, barriers, and other physical structures are so irregularly arranged as to enable us to arrive at only vague approximations of their influence. From these life history-derived approximations we may logically plan the arrangement of goal-objects, barriers, and the like so that we may derive general principles as to their influence on population dynamics, social structures, and evolution of culture.

Concepts and techniques developed in the science of psychology will also be of great usefulness in planning and conducting experiments in population ecology. In its development, psychology has relied mainly on clinical studies of man and of experimental studies of various laboratory animals, the latter under
essentially unsocial conditions. Both of these approaches are atomistic in the sense that they must perforce view the individual, whose past history and environment is little known, or which is living essentially out of context with its natural physical and social environment. Nevertheless, these two psychological approaches have given us great insight into the manner in which the individual perceives, learns, and adjusts, and to a more limited extent it has shown how individuals react to and with others of their kind in rather simple stereotyped environments. The time is now ripe to utilize this great host of information in planning experiments and analyzing results in which the unit of investigation is the population.

The potential contribution of psychology to the investigation of the behavioral aspects of population dynamics may not be realized by current trends in psychological research. Psychology has stressed the development of concepts at the expense of the descriptive aspects of behavior. Such comparative psychological endeavors can provide a cataloging of the range of behavior exhibited by a species and of the range of conditions which elicit such behaviors. Such data needs to be available both for the wild-type representative of each species and also for genetically similar isolated groups of the species, such as subspecies, inbred strains, or breeds. Such descriptive studies will form the building blocks of behavior with which we can proceed with greater assurance in planning experimental studies into group dynamics and population ecology.

With each new increase in complexity of life new properties arise, and the phenomena exhibited by the less complex forms of life take on new meaning. Thus, our knowledge of the behavior of individuals and small groups will assume richer connotations and reveal new concepts when applied to the social population level of organic organization. In turn, it is inevitable that investigation at this level of organization will produce new topics for investigation under strictly laboratory conditions.

Concepts of the social aspects of population dynamics are of potential value to three spheres of human activity. They contribute to man's management of himself through the development of a "preventive medicine" of mental hygiene, through its contribution to psychiatry by providing a better appreciation of the relationship of the total individual to his total environment (Cameron, 1948); through the provision of principles of community planning; and through the assessment of desirable population densities. They contribute, in the sphere of animal husbandry, to man's management of domestic animals, so that they will most economically provide him with sustenance. They contribute to the essential problem of man's management of the world about him in the broad fields of conservation and wildlife management; for man lives not alone, but in context with the "balance of nature," which he disrupts at his own peril. Admittedly, the concepts of the social aspect of population dynamics are as yet in an embryonic state. Their development to the point where we may safely and surely apply such knowledge presents a challenge to research. To meet this challenge we must plan long-term observational studies of the social ecology of man and other animals under their normal conditions of existence; we must plan long-term ex-
perimental studies of population ecology where conditions of the physical environment, which mold social structure, are systematically controlled, and where the history of the population is followed through the years from infancy to maturity; we must have the courage and foresight to depart from the laboratory in its customarily accepted sense, and take with us into the broader laboratory of field situations our extensive knowledge derived from analytical studies of the individual and small groups. Such procedures will lend greater insight into the dynamics of group behavior as well as provide new problems to carry back with us into the laboratory for other analytical treatment.

LITERATURE CITED


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[This article is based upon a paper delivered June 27, 1950 at the annual meeting of the American Society of Mammalogists as a part of the Symposium on Dynamics of Mammalian Populations.]

Division of Behavior Studies, Hamilton Station, Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine. Received June 18, 1951.