Crowding and Animal Behavior

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In our increasing concern with the environment, symbolized by the widespread response to the first "Earth Day" of April 22, 1970, and emphasized by the proliferation of media output on "ecology" and "overpopulation," we are in danger of becoming too narrowly focused. What is the environment? We often fail to consider the total environment or more than one or two levels of coping with environmental problems. We frequently leave man as an evolving cultural species out of our thinking. We consider him only as a victim or as a despoiler of the physical environment. But man is of the environment, and the understanding of his social environment, including his interrelationships with the physical environment, will enable the growing concern to evolve toward a true environmental awareness.

The solution to our environmental crisis encompasses more than repairing our polluted waters and fouled air. It does and must include the promotion of man and his quality of life. Hopefully, this volume, largely representing the views of psychologists, will be a step in the direction of putting man back into the environment and of putting *mental* back into environ*mental.* But the present chapter is about behavior and crowding and animals. What insights can we gain from studies of crowded animal populations relevant to the corresponding problems of man?

There is a hierarchy of levels of organization in biological systems from the molecular, through the cellular, tissue, and organ levels, to the individual, his social groups, and the entire population of the species and the surrounding community complex. There is little question of the utility of animal studies at the lower organizational levels. Results are often directly applicable to man. Physiological processes are frequently identical at the biochemical level in mouse or man. An insulin molecule and its potential action are not species-specific, fortunately for millions of diabetics. When we reach the individual

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and go beyond to the realm of social behavior or the dynamics of populations, there is an abrupt shift in attitude toward nonacceptance of animal studies as being relevant to man, even on the part of a great many highly qualified professional scientists. But the author believes there can be a true intellectual interface between studying the social dynamics of animals and those of man. This interface is possibly most fruitful in generating ideas and insights during the process of the study itself, not always at the study's termination when all results are in and are fixed, definitive, and final for the animal species in question. Hopefully, the reader will judge and ponder as some of the ongoing animal studies in the laboratory of John B. Calhoun of the National Institute of Mental Health are described.[1] The studies are not final, nor are the traditional scientific results completely tabulated, but the idea-generating interface has been almost continuously productive.

ONGOING ANIMAL STUDIES

In designing the animal studies, we consider the relationship between the social and physical environments throughout. The animal's habitat becomes an integral part of the living whole. We deal with crowding in freely growing mouse populations; thus, we are concerned with density (number of animals per unit area), but density related to the richness of the physical environment and its structure as it affects the availability of resources. We also relate density to the individual animal and his role or status in the social structure of the crowded environment.

The BALB/c is a highly inbred albino strain of laboratory mouse. The genetic template of an individual BALB/c is nearly identical to any other with the obvious exception that there are two sexes. Thus, within each sex there is no diversity of potential for expressing those behaviors that are characteristic of the strain and the species. There is homogeneity, not heterogeneity; equality, not inequality. Indeed, within a true biological definition, all inbred mice are created equal.

Let us take a sweeping overview of the history of a population of such mice that has evolved within a structured physical environment. This environment was designed by man for mouse but encompasses an abundance of resources: food, water, and varied living space. A traditional failure in similar animal population studies has been in the design of the physical environment. The environment must be structured to make sense in terms of the ecological

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[1] This chapter hopefully represents a constructive distilling and synthesis of ideas and viewpoints gained from a year's association with John B. Calhoun and the staff of the Unit for Research on Behavioral Systems. Much of the material was gleaned from personal discussions or unpublished unit documents generated during the course of the mouse population studies. The author is indebted to John Calhoun for increasing his personal awareness of the environment, but success or failure of the present synthesis is the author's own responsibility.

requirements of the species, and the elements of the environment must be such that they can be identified (coded), controlled, and related directly to the behavior of the animals. The physical environment designed for this study, with its virtually unlimited availability of food and water, provides a potential utopia, or paradise, for mice. A measure of richness has been provided in terms of what and how opportunities are given to the individual, group, or population to realize and express the genetic potential of the species. A brief description of this physical environment is now required. The designed habitat is called an experimental mouse universe. It is bounded physical space. Thus, one possible divergence from utopia is that there can be no escape if things go awry. It is tempting to point out that the concept of "Spaceship Earth" fits a similar definition. With the absence of predation or major population-wide disease, the mouse universe of this study provides a model closer to the human situation than can be derived from animals living in natural field habitats.

A mouse universe consists of one or more identical cells. The population under consideration evolved in a 16-cell universe, each cell consisting of the following elements (see Figure 1):

1. There are 640 square inches of triangular floor space covered with finely ground corncobs to a depth of 3 inches and bounded by low, wooden partitions.

2. An elevated metal ring stand holding a small cup is located in the center of the cell with nesting materials at the base (paper strips).

3. On the wall in each cell are four vertical wire screen tunnels that lead to a complex of 16 nesting compartments, a food hopper accessible from all surfaces, and two waterspigots above the hoppers.

4. The surface area in the wall complex is approximately equal to that of the floor space. Wire mesh is used throughout the structured portion of the environment so that the mice can readily climb to all locations except the boundary walls. The overall spatial arrangement permits more than 250 mice to live in each cell before physical space per se is exhausted, access to food and water resources becomes limited, and a density of "standing room only" is reached. In this 16-cell universe, standing room only thus becomes greater than 16×250, or more than 4,000 mice.

Eight mice were introduced into this potential utopia. These were the original colonizers, four males and four females. The BALB/c is an excellent reproductive performer. A female, when sexually mature at 3 months, can become pregnant and bear a litter of four to eight pups once a month. The reproductive potential for quickly reaching standing room only is in the genetic template. Converting from mouse to man time, 6 mouse months equal 25 man years; 150 years of reproductive history are compressed into 3. The eight mice had the capacity to double their population size every 60 days. They could fill the universe in less than 3 years.

The genetic potential for exploiting this mouse paradise was qualitatively and quantitatively present in equal proportion in each of the original eight colonizers and would remain essentially unchanged even to the *n*th generation.

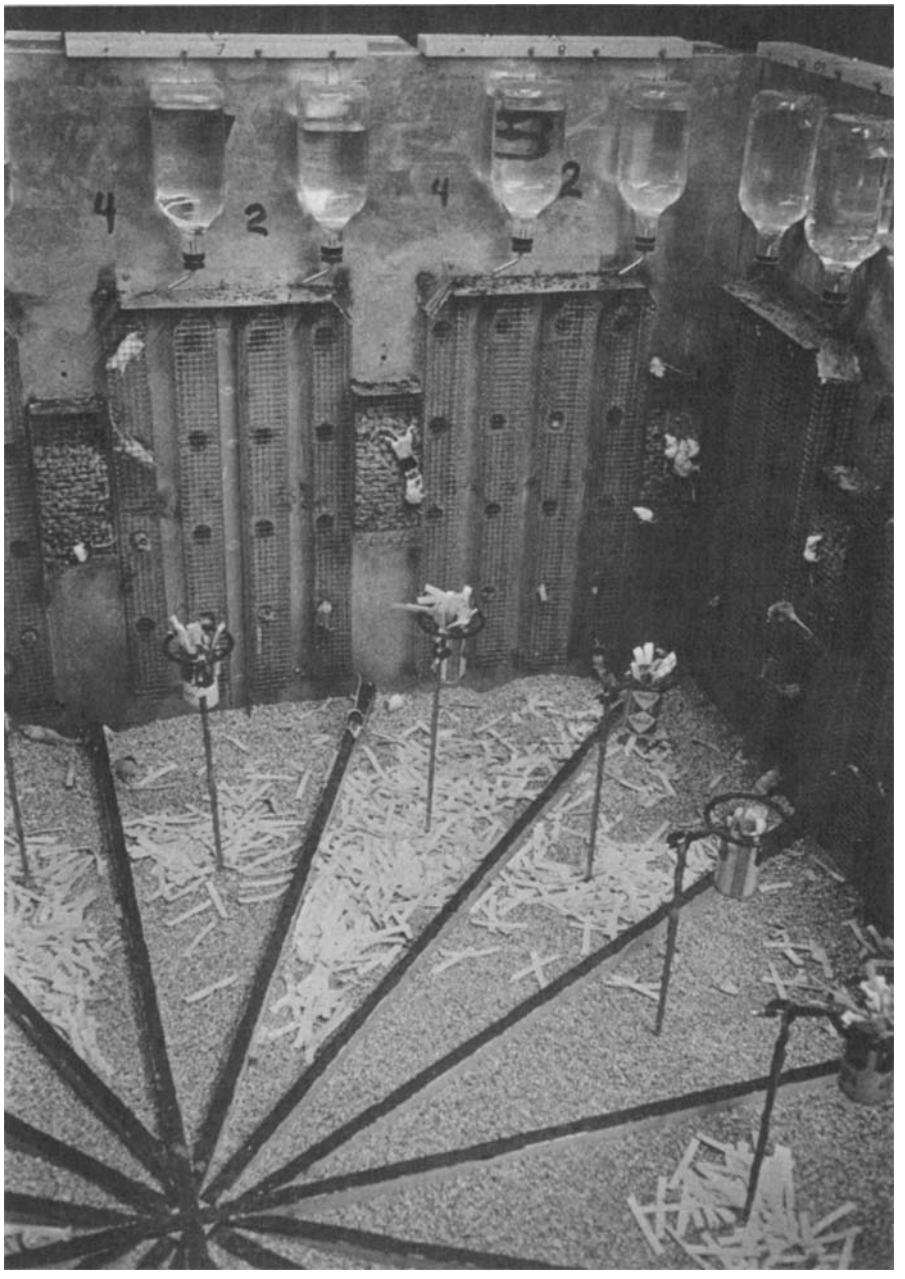

Fig. 1. Picture of the experimental mouse universe showing 4 of the 16 cells making up the living space for the mouse colony. (Photograph by Calvin Nophlin, National Institute of Mental Health.)

For a male BALB/c, realization of the coded genetic instructions of the species means to become dominant over his fellow males, to establish a territory, and to mate with females. Territory is defined as that portion of the physical environment that the male identifies as part of himself and that he is capable of aggressively defending against other males who might intrude upon his extended personal space. For a female, full expression and attainment of genetic potential are found in mating, constructing an appropriate nest in a favorable site, bearing young, and successfully rearing them to weaning. Thus, the definition of the realization of potential is put in terms of what is fulfilling for the individual, and all that is expected of a mouse is total involvement in perpetuation of the species. The most complex kind of social behavior in mice is that which culminates in successful reproduction. This is normalcy.

Like men, mice have no preawareness of what the optimum population size of their universe should be. Even in optimum-sized groups or populations not all mice attain full potential, full gratification. Some are frustrated in fulfilling their role. There is always a mixture of frustration with gratification. In the universe of this study, optimum size is probably less than 150 adults forming 14 social groups. Each group contains a dominant or territorial male, associated subordinate males, reproducing females, and young. With the young, the upper optimum is about 1,000 individuals filling all of what we can identify as social space. This is the density at which role-fulfilling potential is attained by the greatest number of adult mice. The ultimate limit of the numerical occupation of the universe is standing room only. Yet, in this study, although the theoretical optimum was grossly exceeded, standing room only was never reached. The population in the 16-cell universe reached a maximum of 2,200, about half the theoretical maximum and about 15 times the optimum number of adults.

As the population exceeded the optimum and proceeded toward the maximum, processes evolved that resulted in the emergence of proportionally more and more divergent types of animals, animals deviating strongly from the ideal of how a normal mouse should behave, that is, a male being occupier and defender of his personal space and procreator of his species and a female being bearer and rearer of healthy young. In the population as a whole, successful reproduction slowed down and finally ceased. The era of exploitation of genetic potential was over. The population stagnated and began to die. At this writing, there were 1,800 physically adult mice and no young. Utopia had become hell. The growth and decline of the population is shown in Figure 2.[2]

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[2]Since the writing of this chapter, an additional census of the population has been taken, at 960 days after colonization. At that time, there remained about 1,650 animals in the colony, thus confirming the steady decline of the population which was projected for it, though as yet the rate of decline has not accelerated as much as Figure 2 would suggest.

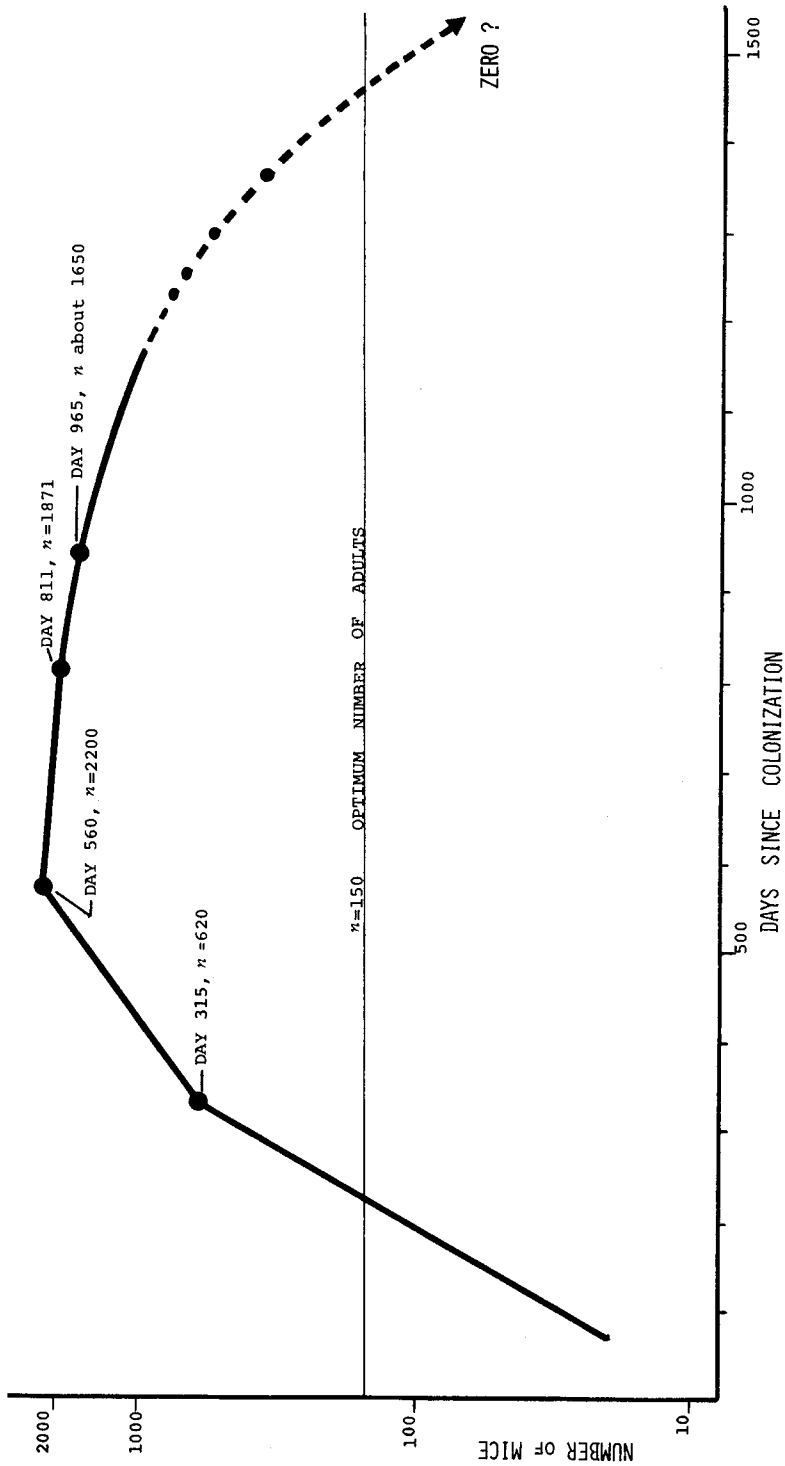

Fig. 2. Growth and decline of the mouse population. (Portion of curve beyond 870 days represents a projection beyond the last recorded value as of the writing of this chapter, cf. Footnote 2.)

The emerging abnormal behavioral types were recognized, first, as being males and, second, as having been ejected from the usual living quarters of the apartment sites. They now lived in the open, on the floor, in large pools of similar individuals. These mice were now spending their lives in public space, moving to food and water, but then returning to the masses on the floor. What characterizes the males living in aggregates on the floor is an almost total withdrawal from normal social interaction. They do not mate with females; their personal space as an extension of self is reduced to the point where no territory is recognized or defended. Aggression remains, but it is characterized by sporadic, undirected outbursts of violence ending in wounding and serving no adaptive purpose. Following such outbreaks of violence, the participants quickly merge again into the closely packed pools. These males had ceased to be normal mice in that they no longer contributed to the perpetuation of the species.

Accompanying the emergence of the deviant types was the disappearance of animals exhibiting the normal kinds of mouse behaviors (dominant, territorial males and successful mothers). When the population reached 2,200, territorial males were no longer present, and all effectively reproducing females were gone. Sexual mounting between the sexes was still seen, but it was abnormally prolonged and often disoriented. Some females did become pregnant, but failed either to bring embryos to term or to raise pups to weaning. Normals had been replaced by abnormals. Although the pooled withdrawn male mice on the floor were the first deviants to emerge and be readily recognized, other types of individuals soon began to appear. There were solitary withdrawn males living singly at the base or at the top of the food hoppers, or on the platforms beneath the water bottles. These mice constitute a second rejected group. Perhaps both groups contain mice that at one point in their history attempted to compete with the remaining dominant males, to try and express their emerging awareness of the genetic command to get involved, that is, to defend territory and to mate. Unable to find any unoccupied social space that they might successfully compete for and exploit as extended personal space, they withdrew singly or in pools.

Withdrawal has taken another form, another route among a third contingent of deviant males. These mice never attempted to become involved. They are called the "Beautiful Ones," for their coats are sleek and well groomed and their wounds few or absent.

They live together in the apartment units; they do not participate in sex or compete for territory. Historically, they have been even less involved than the pooled or solitary withdrawns, not experiencing defeat but never approaching their potential as members of society. They can be looked on as arrested juveniles, physically adult but neurologically immature, never exercising their genetic capacities. If mice could make rational decisions, theirs was, "Don't go out, don't get involved, you can't win. Stay where you are, stay out of it." It is possible that a peculiar type of maternal neglect or behavior produced these Beautiful Ones.

The Beautiful Ones are unstressed. Julius Axelrod, of the National Institute of Mental Health, ran adrenal enzyme assays in his laboratory on animals selected from the crowded universe. The Beautiful Ones, in contrast to the pooled withdrawn mice, showed low assays of the enzyme that converts noradrenalin to adrenalin, a good indicator of an unstressed individual. But unstressed or not, the Beautiful Ones remain outside of society. The pooled withdrawns resulted from too many frustrating interactions in the high-density situation. The Beautiful Ones seldom interacted, achieving neither gratification nor frustration.

Except for the fact that they do not reproduce (and inadequate male performance plays a definite role here), less is known about the emerging female deviants. However, female aggressors—females that apparently have taken on the male role of attacking within physically extended personal space —have been identified. This behavior is not normal for the female.

Thus, all mice were equal at the onset of conception, but, despite an unvarying physical environment providing adequate surface space and physiologically substantive resources, the population increased to a density that prevented normal mice from developing. This density resulted in a pathologically high frequency of nonadaptive social interaction and fostered the creation of a multiplicity of deviant types incapable of becoming involved in meaningful social relations. In mouse ecological terms, this was disastrous.

One possible end to the story is that the population, having entered a period of slow decline, will finally die, ending with a single mouse. With 2,200 mice in a 16-cell universe, there were no longer any mice, that is, none capable of behaving as normals and producing a new generation. All 2,200 had "overlived." Certain experiments now in progress tend to support this prediction. We removed all but 24 animals, 16 females and 8 males, from a population of 300 mice in the slow-decline phase of population history in a 2-cell universe. For two months after this dramatic reduction in density, zero reproduction continued; no sex, no pregnancies, no pups. Then, even after removing these male and female groups from their universe and putting them in new ones with young, vigorous, normal mice of the opposite sex, reproductive performance remained extremely poor. All stages of the reproductive cycle were affected: sexual relations, carrying the embryos to term, and caring for the young. Among females, spontaneous abortion, resorption of embryos, cannibalism, inability to find and utilize appropriate nesting sites, and poor nest construction were some of the components in this reproductive failure. A particularly dramatic example of the retention of the behavioral anomalies in a new, uncrowded universe was given by the 16 females. With 32 individual nest sites now available, they chose to remain in only one. With their new, normal male partners, only half became pregnant; of those litters brought to term and delivered, all were dropped in the same nest site on a flattened, almost nonexistent nest soaked with urine and packed with the adult females. Only 5 pups, of a normal potential of about 100, survived to 14 days of age. This is a manifestation of the "behavioral sink" phenomenon

as described by Calhoun (1962a, 1962b) for rats; in this case, a reproductive behavioral sink.

At some point in the history of this mouse population, there was a maximum diversity of types—a balance between the normal, traditional animals and the emerging deviants. In the slow decline or die phase of the population's history, there appears to be a turning once again toward sameness, equality, and uniformity. But the type of mouse that will probably survive is similar to a Beautiful One and possibly one not capable of becoming involved again. It remains to be seen whether a few of the remaining arrested juveniles can break through and achieve a rebirth of population growth as the population continues to decline in number.

CONCLUSION

In his recent and provocative book, *Future Shock,* Toffler (1970) challenges the thesis that our human population (society and culture) is moving toward an imposed standardization, stasis, and rigid conformity—the "fear of bureaucracy" projected into the social nightmare depicted by many authors in recent history. Orwell's *1984* and Huxley's *Brave New World* are two striking examples. Toffler's position is that we are becoming more and more diverse. His evidence for the acceleration of change and the proliferation of diversity in all things (roles, people, groups, organizations, material things) is impressive. But Toffler admits that he is really dealing with the present. Despite the title of his book, he is not projecting beyond an expectation of more of the same kind of increase in diversity. Diversity can be creative. If interaction between diverse types of individuals can achieve a balance between what is gratifying and what is frustrating and if the overall interaction rate does not rise too high, then creativity can arise from those individuals at the interface between the normal, traditional forms of behavior and the inevitable withdrawn or nonadaptive forms—individuals not traditional and not withdrawn, but probing for new insights and ideas. Toffler states convincingly that new behavioral types are emerging in our society with terrifying speed. He also states that as new types emerge, the old drop out. He does not state with clarity which changes are adaptive and which are nonadaptive, only that traditions are repeatedly being shattered.

The social dynamics that Toffler describes parallel the mouse model at many points: the acceleration of change, the increasing diversity, and the sudden emergence and dropping out of behaviors. This change and increase in diversity could be productive of a new creative phase in man's history; or if carried too far, too fast, it could result in mass "future shock" and the setting in of a preponderance of social withdrawal and noncreative pathological deviants (Esser, 1971). The course could eventually lead to the rigid conformity that Toffler does not see coming but that the mice are attaining. Unlike the mice, however, we are theoretically and hopefully capable of

choosing and designing a different course for our future social evolution (Wigotsky, 1970).

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