# Population Density and Social Pathology

*When a population of laboratory rats is allowed to increase in a confined space, the rats develop acutely abnormal patterns of behavior that can even lead to the extinction of the population*

by John B. Calhoun

In the celebrated thesis of Thomas Malthus, vice and misery impose the ultimate natural limit on the growth of populations. Students of the subject have given most of their attention to misery, that is, to predation, disease and food supply as forces that operate to adjust the size of a population to its environment. But what of vice? Setting aside the moral burden of this word, what are the effects of the social behavior of a species on population growth—and of population density on social behavior?

Some years ago I attempted to submit this question to experimental inquiry. I confined a population of wild Norway rats in a quarter-acre enclosure. With an abundance of food and places to live and with predation and disease eliminated or minimized, only the animals' behavior with respect to one another remained as a factor that might affect the increase in their number. There could be no escape from the behavioral consequences of rising population density. By the end of 27 months the population had become stabilized at 150 adults. Yet adult mortality was so low that 5,000 adults might have been expected from the observed reproductive rate. The reason this larger population did not materialize was that infant mortality was extremely high. Even with only 150 adults in the enclosure, stress from social interaction led to such disruption of maternal behavior that few young survived.

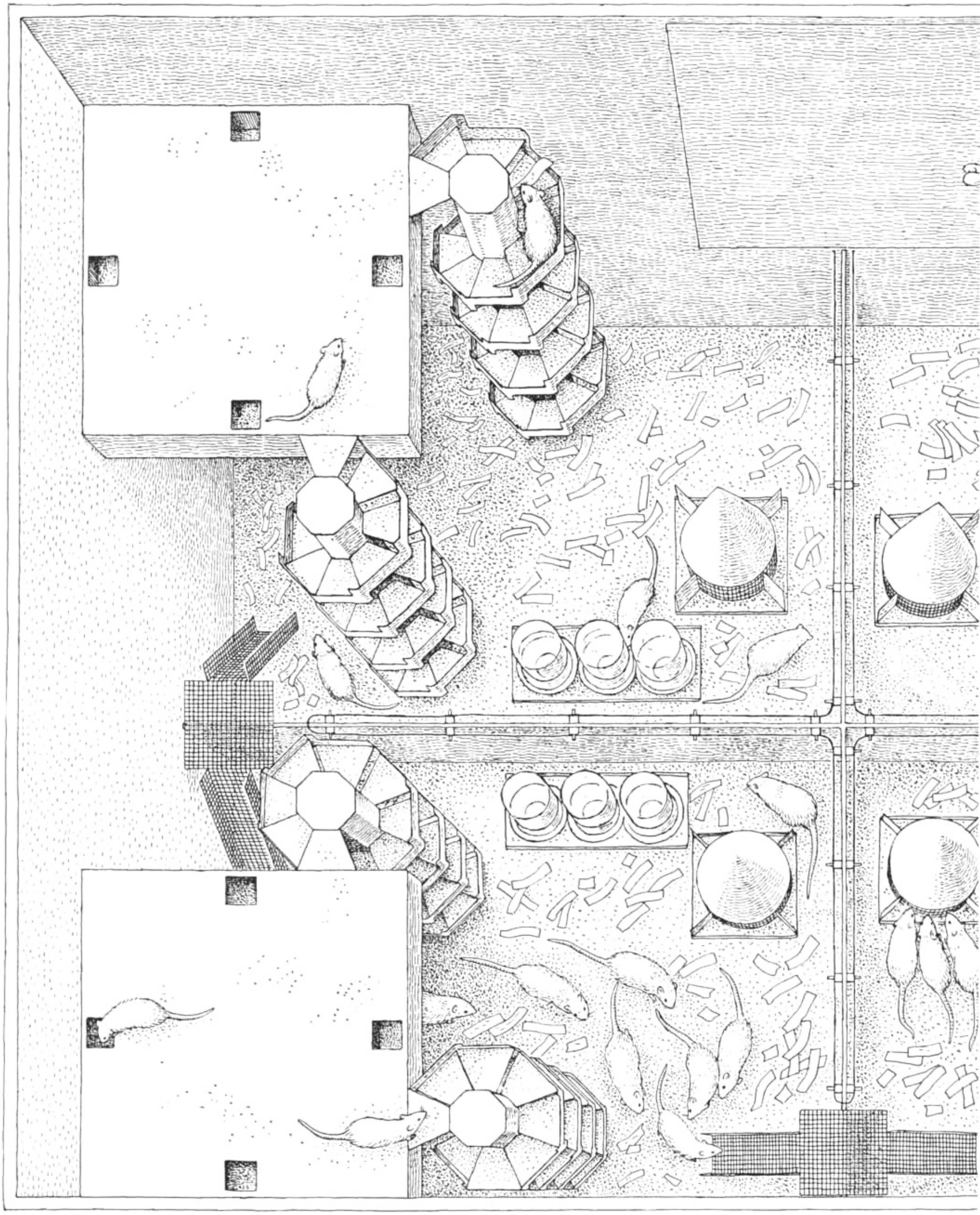
With this background in mind I turned to observation of a domesticated albino strain of the Norway rat under more controlled circumstances indoors. The data for the present discussion come from the histories of six different populations. Each was permitted to increase to approximately twice the number that my experience had indicated could occupy the available space with only moderate stress from social interaction. In each case my associates and I maintained close surveillance of the colonies for 16 months in order to obtain detailed records of the modifications of behavior induced by population density.

The consequences of the behavioral pathology we observed were most apparent among the females. Many were unable to carry pregnancy to full term or to survive delivery of their litters if they did. An even greater number, after successfully giving birth, fell short in their maternal functions. Among the males the behavior disturbances ranged from sexual deviation to cannibalism and from frenetic overactivity to a pathological withdrawal from which individuals would emerge to eat, drink and move about only when other members of the community were asleep. The social organization of the animals showed equal disruption. Each of the experimental populations divided itself into several groups, in each of which the sex ratios were drastically modified. One group might consist of six or seven females and one male, whereas another would have 20 males and only 10 females.

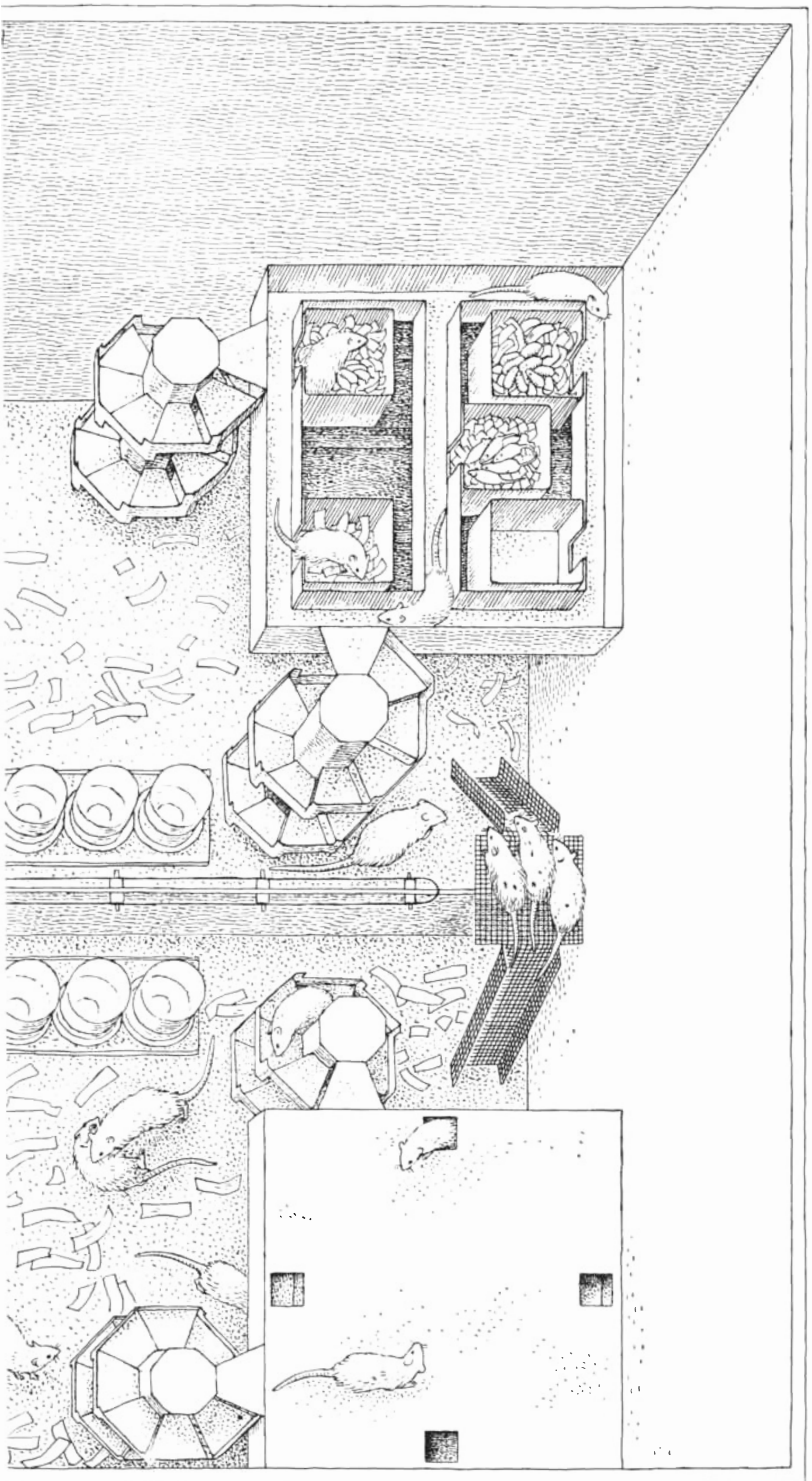
The common source of these disturbances became most dramatically apparent in the populations of our first series of three experiments, in which we observed the development of what we called a behavioral sink. The animals would crowd together in greatest number in one of the four interconnecting pens in which the colony was maintained. As many as 60 of the 80 rats in each experimental population would assemble in one pen during periods of feeding. Individual rats would rarely eat except in the company of other rats. As a result extreme population densities developed in the pen adopted for eating, leaving the others with sparse populations.

Eating and other biological activities were thereby transformed into social activities in which the principal satisfaction was interaction with other rats. In the case of eating, this transformation of behavior did not keep the animals from securing adequate nutrition. But the same pathological "togetherness" tended to disrupt the ordered sequences of activity involved in other vital modes of behavior such as the courting of sex partners, the building of nests and the nursing and care of the young. In the experiments in which the behavioral sink developed, infant mortality ran as high as 96 per cent among the most disoriented groups in the population. Even in the absence of the behavioral sink, in the second series of three experiments, infant mortality reached 80 per cent among the corresponding members of the experimental populations.

The design of the experiments was relatively simple. The three populations of the first series each began with 32 rats; each population of the second series began with 56 rats. In all cases the animals were just past weaning and were evenly divided between males and females. By the 12th month all the populations had multiplied and each comprised 80 adults. Thereafter removal of the infants that survived birth and weaning held the populations steady. Although the destructive effects of population density increased during the course of the experiments, and the mortality rate among the females and among the young was much higher in the 16th month than it was earlier, the number of young that survived to weaning was always large enough to offset the effects of adult mortality and actually to increase the population. The evidence indicates, however, that in time failures of reproductive function would have caused the colonies to die out. At the end of the first series of experiments eight rats—the four healthi-



**EFFECT OF POPULATION DENSITY** on the behavior and social organization of rats was studied by confining groups of 80 animals in a 10-by-14-foot room divided into four pens by an electrified fence. All pens (numbered 1, 2, 3 and 4 clockwise from door) were complete dwelling units. Conical objects are food hoppers; trays with three bottles are drinking troughs. Elevated burrows, reached by winding staircases, each had five nest boxes, seen in pen 1, where top of burrow has been removed. Ramps connected all pens but 1 and 4. Rats therefore tended to concentrate in pens 2 and 3. Development of a "behavioral sink," which further increased population in one pen, is reflected in pen 2, where three rats are eating simultaneously. Rat approaching ramp in pen 3 is an estrous female



**pursued by a pack of males. In pens 2 and 3, where population density was highest, males outnumbered females. In pens 1 and 4 a dominant male was usually able to expel all other males and possess a harem of females. Dominant males are sleeping at the base of the ramps in pens 1 and 4. They wake when other males approach, preventing incursions into their territories. The three rats peering down from a ramp are probers, one of the deviant behavioral types produced by the pressures of a high population density.**

est males and the four healthiest females in each of two populations—were permitted to survive. These animals were six months old at the time, in the prime of life. Yet in spite of the fact that they no longer lived in overpopulated environments, they produced fewer litters in the next six months than would normally have been expected. Nor did any of the offspring that were born survive to maturity.

The males and females that initiated each experiment were placed, in groups of the same size and sex composition, in each of the four pens that partitioned a 10-by-14-foot observation room. The pens were complete dwelling units; each contained a drinking fountain, a food hopper and an elevated artificial burrow, reached by a winding staircase and holding five nest boxes. A window in the ceiling of the room permitted observation, and there was a door in one wall. With space for a colony of 12 adults in each pen—the size of the groups in which rats are normally found—this setup should have been able to support 48 rats comfortably. At the stabilized number of 80, an equal distribution of the animals would have found 20 adult rats in each pen. But the animals did not dispose themselves in this way.

Biasing factors were introduced in the physical design of the environment to encourage differential use of the four pens. The partitions separating the pens were electrified so that the rats could not climb them. Ramps across three of the partitions enabled the animals to get from one pen to another and so traverse the entire room. With no ramps to permit crossing of the fourth partition, however, the pens on each side of it became the end pens of what was topologically a row of four. The rats had to make a complete circuit of the room to go from the pen we designated 1 to the pen designated 4 on the other side of the partition separating the two. This arrangement of ramps immediately skewed the mathematical probabilities in favor of a higher population density in pens 2 and 3 than in pens 1 and 4. Pens 2 and 3 could be reached by two ramps, whereas pens 1 and 4 had only one each.

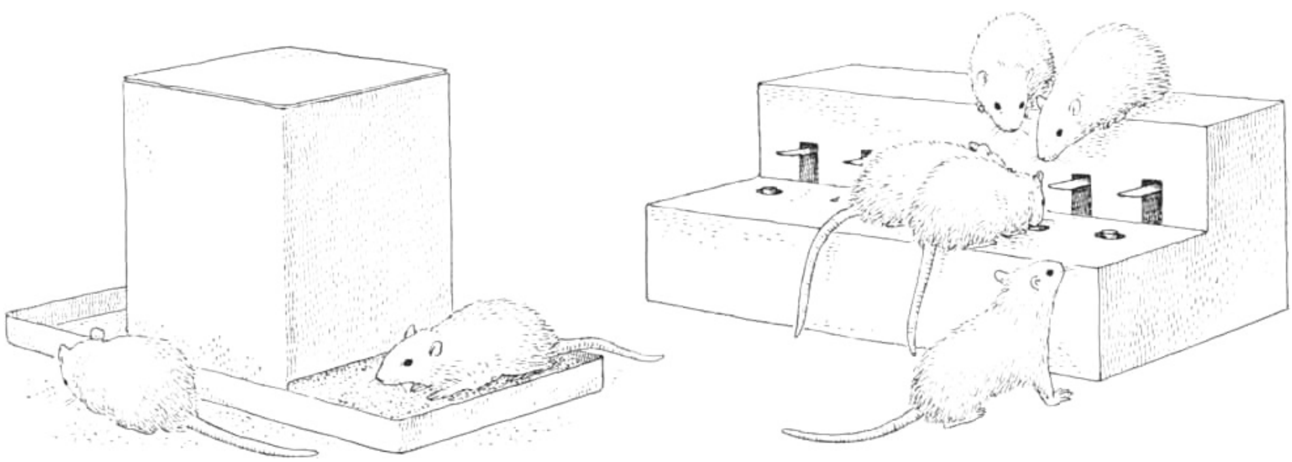
The use of pen 4 was further discouraged by the elevation of its burrow to a height greater than that of the burrow in the other end pen. The two middle pens were similarly distinguished from each other, the burrow in pen 3 being higher than that in pen 2. But here the differential appears to have played a smaller role, although pen 2 was used somewhat more often than pen 3.

With the distribution of the rats

biased by these physical arrangements, the sizes of the groups in each pen could have been expected to range from as few as 13 to as many as 27. With the passage of time, however, changes in behavior tended to skew the distribution of the rats among the pens even more. Of the 100 distinct sleeping groups counted in the 10th to 12th month of each experiment, only 37 fell within the expected size range. In 33 groups there were fewer than 13 rats, and in 30 groups the count exceeded 27. The sex ratio approximated equality only in those groups that fell within the expected size range. In the smaller groups, generally composed of eight adults, there were seldom more than two males. In the larger groups, on the other hand, there were many more males than females. As might be expected, the smaller groups established themselves in the end pens, whereas the larger groups were usually observed to form in the middle pens. The female members of the population distributed themselves about equally in the four pens, but the male population was concentrated almost overwhelmingly in the middle pens.

One major factor in the creation of this state of affairs was the struggle for status that took place among the males. Shortly after male rats reach maturity, at about six months of age, they enter into a round robin of fights that eventually fixes their position in the social hierarchy. In our experiments such fights took place among the males in all the pens, both middle and end. In the end pens, however, it became possible for a single dominant male to take over the area as his territory. During the period when the social hierarchy was being established, the subordinate males in all pens adopted the habit of arising early. This enabled them to eat and drink in peace. Since rats generally eat in the course of their normal wanderings, the subordinate residents of the end pens were likely to feed in one of the middle pens. When, after feeding, they wanted to

**FOOD HOPPER** used in first series of experiments is seen at the left in this drawing. Water tray is at the right. The hopper, covered with wire grating and holding hard pellets of food, made eating a lengthy activity during which one rat was likely to meet another. Thus it fostered the development of a behavioral sink: the animals would eat only in the presence of others, and they preferred one of the four hoppers in the room to all the others. In time 75 per cent of the animals crowded into the pen containing this hopper to eat.



**WATER FOUNTAIN** used in second series of experiments is seen at the right in this drawing. Food hopper is at the left. The fountain was operated by pressing a lever. Thus it made drinking a lengthy activity, associated with the presence of others. But it did not create a behavioral sink. Although the rats would drink only if other animals were present, they engaged in this activity in their home pens immediately after awakening. The fountain therefore acted to produce an even distribution of the population.

return to their original quarters, they would find it very difficult. By this time the most dominant male in the pen would probably have awakened, and he would engage the subordinates in fights as they tried to come down the one ramp to the pen. For a while the subordinate would continue its efforts to return to what had been its home pen, but after a succession of defeats it would become so conditioned that it would not even make the attempt. In essence the dominant male established his territorial dominion and his control over a harem of females not by driving the other males out but by preventing their return.

Once a male had established his dominion over an end pen and the harem it contained, he was usually able to maintain it. Although he slept a good deal of the time, he made his sleeping quarters at the base of the ramp. He was, therefore, on perpetual guard. Awakening as soon as another male appeared at the head of the ramp, he had only to open his eyes for the invader to wheel around and return to the adjoining pen. On the other hand, he would sleep calmly through all the comings and goings of his harem; seemingly he did not even hear their clatterings up and down the wire ramp. His conduct during his waking hours reflected his dominant status. He would move about in a casual and deliberate fashion, occasionally inspecting the burrow and nests of his harem. But he would rarely enter a burrow, as some other males did, merely to ferret out the females.

A territorial male might tolerate other males in his domain provided they respected his status. Such subordinate males inhabited the end pens in several of the experiments. Phlegmatic animals, they spent most of their time hidden in the burrow with the adult females, and their excursions to the floor lasted only as long as it took them to obtain food and water. Although they never attempted to engage in sexual activity with any of the females, they were likely, on those rare occasions when they encountered the dominant male, to make repeated attempts to mount him. Generally the dominant male tolerated these advances.

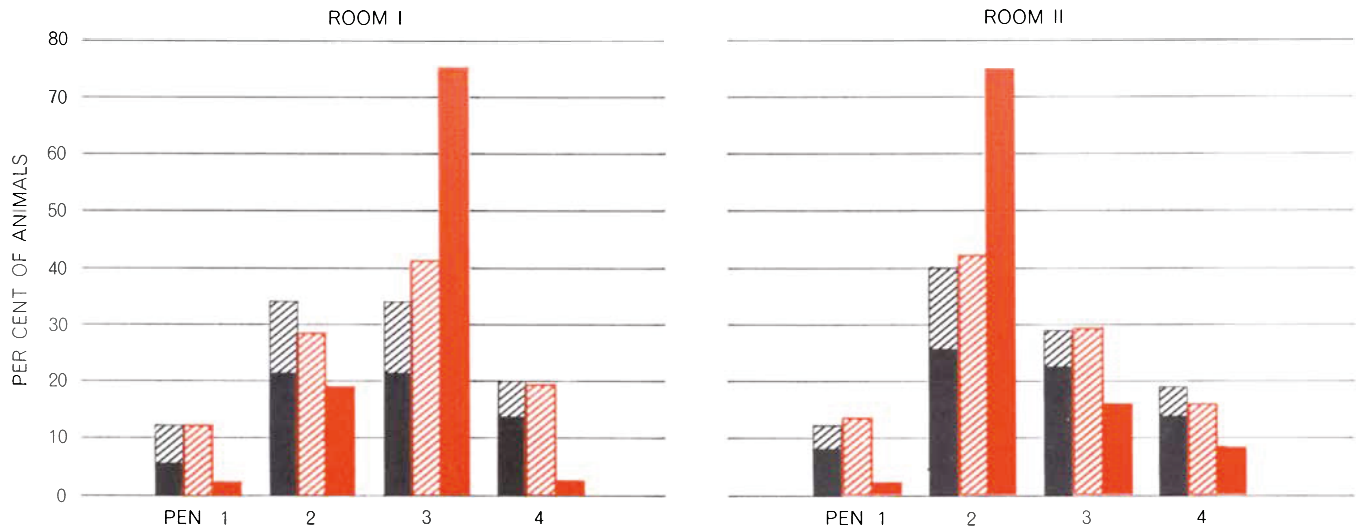
In these end pens, where population density was lowest, the mortality rate among infants and females was also low. Of the various social environments that developed during the course of the experiments, the brood pens, as we called them, appeared to be the only healthy ones, at least in terms of the survival of the group. The harem females generally made good mothers. They nursed their young, built nests for them and protected them from harm. If any situation arose that a mother considered a danger to her pups, she would pick the infants up one at a time and carry them in her mouth to a safer place. Nothing would distract her from this task until the entire litter had been moved. Half the infants born in the brood pens survived.

The pregnancy rates recorded among the females in the middle pens were no lower than those recorded in the end pens. But a smaller percentage of these pregnancies terminated in live births. In the second series of experiments 80 per cent of the infants born in the middle pens died before weaning. In the first series 96 per cent perished before this time. The males in the middle pens were no less affected than the females by the pressures of population density. In both series of experiments the social pathology among the males was high. In the first series, however, it was more aggravated than it was in the second.

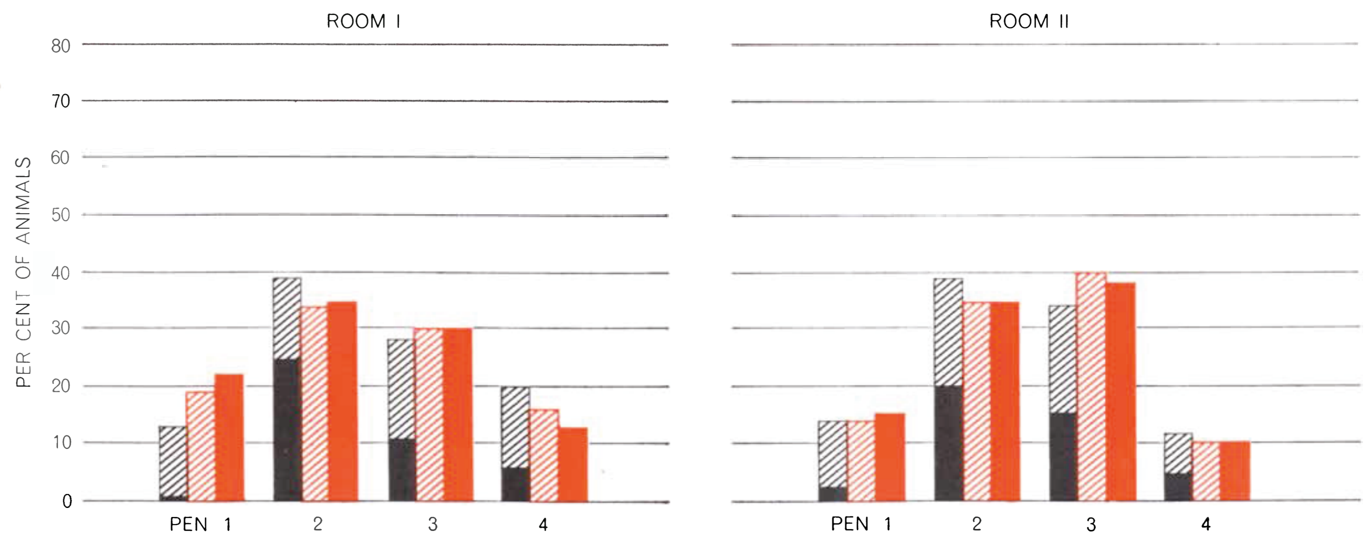
This increase in disturbance among the middle-pen occupants of the first series of experiments was directly related to the development of the phenomenon of the behavioral sink—the outcome of any behavioral process that collects animals together in unusually great numbers. The unhealthy connotations of the term are not accidental: a behavioral sink does act to aggravate all forms of pathology that can be found within a group.

The emergence of a behavioral sink was fostered by the arrangements that were made for feeding the animals. In these experiments the food consisted of small, hard pellets that were kept in a circular hopper formed by wire mesh. In consequence satisfaction of hunger required a continuous effort lasting several minutes. The chances therefore were good that while one rat was eating another would join it at the hopper. As was mentioned earlier, rats usually eat intermittently throughout their waking hours, whenever they are hungry and food is available. Since the arrangement of the ramps drew more rats into the middle pens than into the end ones, it was in

SLEEPING FEMALES
SLEEPING MALES
DRINKING
EATING

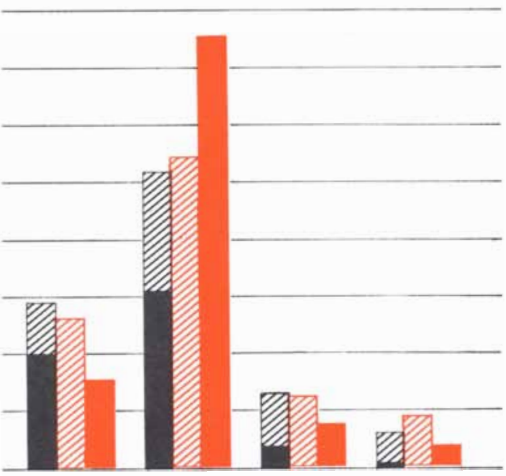



**BEHAVIORAL SINK** developed in the first series of three experiments, drawing half the rats either into pen 2 or pen 3 of each room to drink and sleep, and even more into that pen to eat. Chart describes the situation in the 13th month of the experiment. By then the population distributions were fairly stable and many females in the densely populated pens had died. One male in room

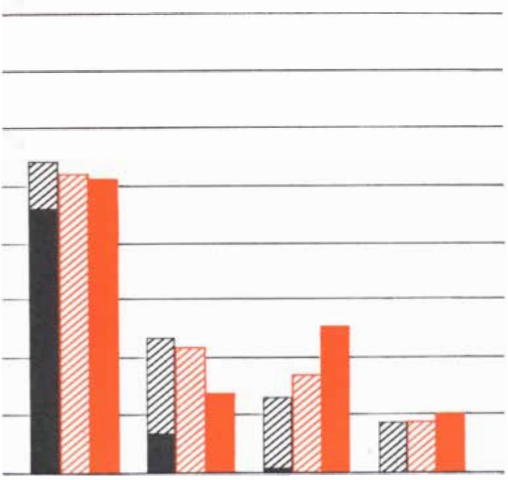



**POPULATION DISTRIBUTIONS** in the second series of three experiments, in which no behavioral sink developed, were more even than they were in the first series, and the death rate among females and infants was lower. Chart shows the situation in the 13th month, when one male had established pens 3 and 4 of room III as his territory, and another was taking over pen 2, thus these pens that individuals were most likely to find other individuals eating. As the population increased, the association of eating with the presence of other animals was further reinforced. Gradually the social aspect of the activity became determinant: the rats would rarely eat except at hoppers already in use by other animals.

At this point the process became a vicious circle. As more and more of the rats tended to collect at the hopper in one of the middle pens, the other hoppers became less desirable as eating places. The rats that were eating at these undesirable locations, finding themselves deserted by their groupmates, would transfer their feeding to the more crowded pen. By the time the three experiments in the first series drew to a close half or more of the populations were sleeping as well as eating in that pen. As a result there was a decided increase in the number of social adjustments each rat had to make every day. Regardless of which pen a rat slept in, it would go to one particular middle pen several times a day to eat. Therefore it was compelled daily to make some sort of adjustment to virtually every other rat in the experimental population.




**III had established pens 3 and 4 as his territory. Subsequently a male in room I took over pen 1, expelling all the other males.**




**forcing most of the males into pen 1. Pen 1 in rooms I and II had also become territories; later pen 4 in room II became a territory.**

No behavioral sinks developed in the second series of experiments, because we offered the rats their diet in a different way. A powdered food was set out in an open hopper. Since it took the animals only a little while to eat, the probability that two animals would be eating simultaneously was considerably reduced. In order to foster the emergence of a behavioral sink I supplied the pens with drinking fountains designed to prolong the drinking activity. The effect of this arrangement was unquestionably to make the animals social drinkers; they used the fountain mainly when other animals lined up at it. But the effect was also to discourage them from wandering and to prevent the development of a behavioral sink. Since rats generally drink immediately on arising, drinking and the social interaction it occasioned tended to keep them in the pens in which they slept. For this reason all social pathology in the second series of experiments, although severe, was less extreme than it was in the first series.

Females that lived in the densely populated middle pens became progressively less adept at building adequate nests and eventually stopped building nests at all. Normally rats of both sexes build nests, but females do so most vigorously around the time of parturition. It is an undertaking that involves repeated periods of sustained activity, searching out appropriate materials (in our experiments strips of paper supplied an abundance), transporting them bit by bit to the nest and there arranging them to form a cuplike depression, frequently sheltered by a hood. In a crowded middle pen, however, the ability of females to persist in this biologically essential activity became markedly impaired. The first sign of disruption was a failure to build the nest to normal specifications. These females simply piled the strips of paper in a heap, sometimes trampling them into a pad that showed little sign of cup formation. Later in the experiment they would bring fewer and fewer strips to the nesting site. In the midst of transporting a bit of material they would drop it to engage in some other activity occasioned by contact and interaction with other individuals met on the way. In the extreme disruption of their behavior during the later months of the population's history they would build no nests at all but would bear their litters on the sawdust in the burrow box.

The middle-pen females similarly lost the ability to transport their litters from one place to another. They would move only part of their litters and would scatter them by depositing the infants in different places or simply dropping them on the floor of the pen. The infants thus abandoned throughout the pen were seldom nursed. They would die where they were dropped and were thereupon generally eaten by the adults.

The social stresses that brought about this disorganization in the behavior of the middle-pen females were imposed with special weight on them when they came into heat. An estrous female would be pursued relentlessly by a pack of males, unable to escape from their soon unwanted attentions. Even when she retired to a burrow, some males would follow her. Among these females there was a correspondingly high rate of mortality from disorders in pregnancy and parturition. Nearly half of the first- and second-generation females that lived in the behavioral-sink situation had died of these causes by the end of the 16th month. Even in the absence of the extreme stresses of the behavioral sink, 25 per cent of the females died. In contrast, only 15 per cent of the adult males in both series of experiments died.

A female that lived in a brood pen was sheltered from these stresses even though during her periods of estrus she would leave her pen to mate with males in the other pens of the room. Once she was satiated, however, she could return to the brood pen. There she was protected from the excessive attention of other males by the territorial male.

For the effect of population density on the males there is no index as explicit and objective as the infant and maternal mortality rates. We have attempted a first approximation of such an index, however, by scoring the behavior of the males on two scales: that of dominance and that of physical activity. The first index proved particularly effective in the early period of the experiments, when the males were approaching adulthood and beginning the fights that eventually fixed their status in the social hierarchy. The more fights a male initiated and the more fights he won, the more likely he was to establish a position of dominance. More than half the animals in each experiment gave up the struggle for status after a while, but among those that persisted a clear-cut hierarchy developed.

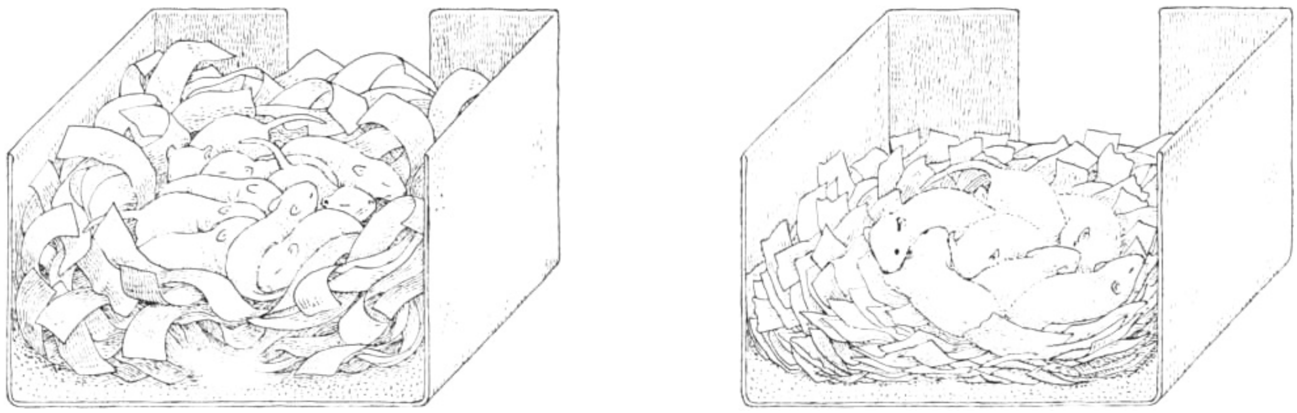
In the crowded middle pens no one individual occupied the top position in this hierarchy permanently. In every group of 12 or more males one was the most aggressive and most often the victor in fights. Nevertheless, this rat was periodically ousted from his position. At regular intervals during the course of their waking hours the top-ranking males engaged in free-for-alls that culminated in the transfer of dominance from one male to another. In between these tumultuous changings of the guard relative calm prevailed.

The aggressive, dominant animals were the most normal males in our populations. They seldom bothered either the females or the juveniles. Yet even they exhibited occasional signs of pathology, going berserk, attacking females, juveniles and the less active males, and showing a particular predilection —which rats do not normally display— for biting other animals on the tail.

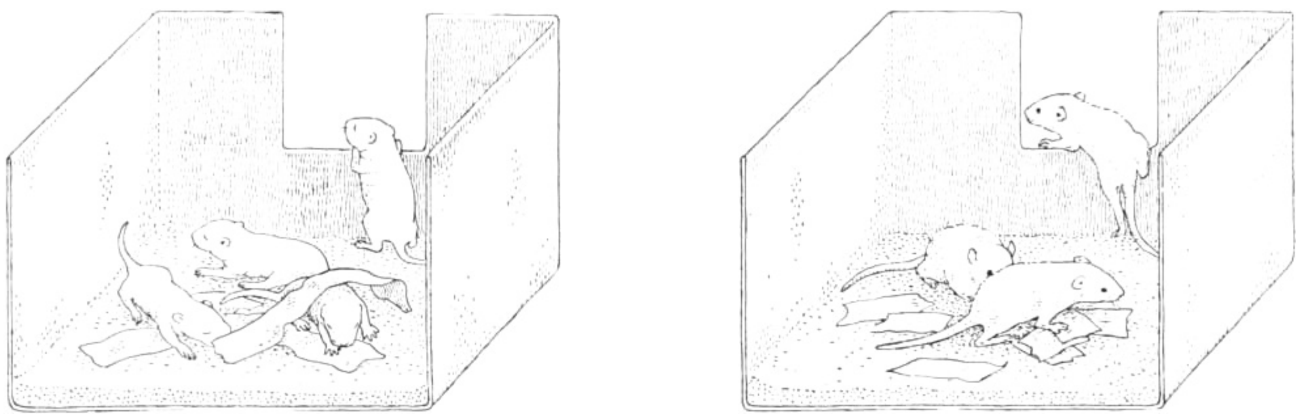
Below the dominant males both on the status scale and in their level of activity were the homosexuals—a group perhaps better described as pansexual. These animals apparently could not discriminate between appropriate and inappropriate sex partners. They made sexual advances to males, juveniles and females that were not in estrus. The males, including the dominants as well as the others of the pansexuals' own group, usually accepted their attentions. The general level of activity of these animals was only moderate. They were frequently attacked by their dominant associates, but they very rarely contended for status.

Two other types of male emerged, both of which had resigned entirely from the struggle for dominance. They were, however, at exactly opposite poles as far as their levels of activity were concerned. The first were completely passive and moved through the community like somnambulists. They ignored all the other rats of both sexes, and all the other rats ignored them. Even when the females were in estrus, these passive animals made no advances to them. And only very rarely did other males attack them or approach them for any kind of play. To the casual observer the passive animals would have appeared to be the healthiest and most attractive members of the community. They were fat and sleek, and their fur showed none of the breaks and bare spots left by the fighting in which males usually engage. But their social disorientation was nearly complete.

Perhaps the strangest of all the types that emerged among the males was the group I have called the probers. These animals, which always lived in the middle pens, took no part at all in the status struggle. Nevertheless, they were the most active of all the males in the experimental populations, and they persisted in their activity in spite of attacks by the dominant animals. In addition to being hyperactive, the probers were both



**NORMAL MATERNAL BEHAVIOR** among rats includes building a fluffy, well-shaped nest for the young. The drawing at the left shows such a nest, holding a recently born litter. The drawing at the right shows this same nest about two weeks later. It has been flattened by the weight of the animals' bodies but it still offers ample protection and warmth, and the remaining pups can still rest comfortably. In these experiments half the offspring of normal mothers survived infancy and were successfully weaned.



**ABNORMAL MATERNAL BEHAVIOR,** shown by females exposed to the pressures of population density, includes failure to build adequate nests. The drawing at the left shows the recently born young of a disturbed female. She started to make a nest but never finished it. The drawing at the right shows her young about two weeks later. One pup has already left and another is leaving. Neither can survive alone. In these experiments the mortality rate among infants of disturbed mothers was as high as 96 per cent.

hypersexual and homosexual, and in time many of them became cannibalistic. They were always on the alert for estrous females. If there were none in their own pens, they would lie in wait for long periods at the tops of the ramps that gave on the brood pens and peer down into them. They always turned and fled as soon as the territorial rat caught sight of them. Even if they did not manage to escape unhurt, they would soon return to their vantage point.

The probers conducted their pursuit of estrous females in an abnormal manner. Mating among rats usually involves a distinct courtship ritual. In the first phase of this ritual the male pursues the female. She thereupon retires for a while into the burrow, and the male lies quietly in wait outside, occasionally poking his head into the burrow for a moment but never entering it. (In the wild forms of the Norway rat this phase usually involves a courtship dance on the mound at the mouth of the burrow.) The female at last emerges from the burrow and accepts the male's advances. Even in the disordered community of the middle pens this pattern was observed by all the males who engaged in normal heterosexual behavior. But the probers would not tolerate even a short period of waiting at the burrows in the pens where accessible females lived. As soon as a female retired to a burrow, a prober would follow her inside. On these expeditions the probers often found dead young lying in the nests; as a result they tended to become cannibalistic in the later months of a population's history.

Although the behavioral sink did not develop in the second series of experiments, the pathology exhibited by the populations in both sets of experiments, and in all pens, was severe. Even in the brood pens females could raise only half their young to weaning. Nor does the difference in infant mortality between the middle pens of the first and second series—96 per cent in the first as opposed to 80 per cent in the second—represent a biologically significant improvement. It is obvious that the behavioral repertory with which the Norway rat has emerged from the trials of evolution and domestication must break down under the social pressures generated by population density. In time, refinement of experimental procedures and of the interpretation of these studies may advance our understanding to the point where they may contribute to the making of value judgments about analogous problems confronting the human species.