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Behavioral changes due to overpopulation in mice

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AN ABSTRACT OF THE THESIS OF James Robert Hammock for the Master of

Science in Psychology presented July 26, 1971.

Title: Behavioral Changes Due to Overpopulation in Mice.

APPROVED BY MEMBERS OF THE THESIS COMMITTEE:

Ronald E. Smith, Chairman

Robert Powloski

Roger Jennings

Previous research has found that if a population were allowed
to exceed a comfortable density level, then many catastrophic events
occurred such as increased mortality among the young, cannibalism,
homosexuality, and lack of maternal functions. The most influential
researcher in this area is Calhoun (1962), after whose experimental
design a pilot study was fashioned to replicate his results. The
results of this pilot study inspired a more detailed research project
of which this thesis is an account.

Forty-eight albino mice of the Swiss Webster strain were divided
into three groups of sixteen each. Each group consisted of ten fe-
males and six males chosen randomly; two groups were to serve as ex-
perimental groups and the other group as the control. The experi-
mental groups were placed into apparatus 15 5/8" x 20 1/2" x 8" and

the control group in an apparatus 47 7/8" x 61 1/2" x 8". The three

groups were allowed to multiply freely with nesting material, food

and water provided proportionately as their numbers grew. The ex-

perimental groups were allowed to overpopulate while the control

group was not.

There were six behavior variables noted as the experiment pro-

ceeded: (1) grooming, (2) homosexuality, (3) nest building, (4)

retrieving of young, (5) fighting, and (6) mortality of the young.

It was predicted that grooming, nest building, and retrieving of the

young would decrease in frequency as the population increased, while

fighting, homosexuality and mortality of the young would increase

with the rising population density. The experiment was conducted

for six months and fourteen days.

The result of this experiment was a total lack of overpopulation.

The two experimental groups never weaned any pups though they produced

many, and the control group grew to the comfortable limits of its

apparatus and then ceased weaning any further pups. In an effort to

ascertain the reasons for these results, one of the experimental

groups was artificially reduced in number; whereupon it promptly

weaned forty-one percent of its first litter, thirty percent of its

second, and none of its third. At the time of its first weaning, this

group was technically overpopulated.

In conclusion an hypothesis is proposed to explain the results.

It is felt that each population has an innate knowledge of its comfort-

able limits with regard to density and will maintain this crucial den-

sity level if necessary. The group's ability to control its popula-

tion is directly related to a time factor in that if a population

were allowed to approach its crucial density level gradually it would

not exceed it; however if there were little or no approach time,

then this level would be exceeded.

BEHAVIORAL CHANGES DUE TO OVERPOPULATION IN MICE

by

JAMES ROBERT HAMMOCK

A thesis submitted in partial fulfillment of the
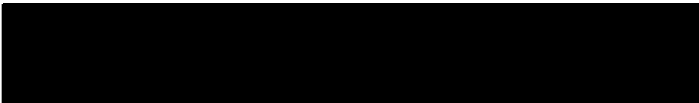requirements for the degree of

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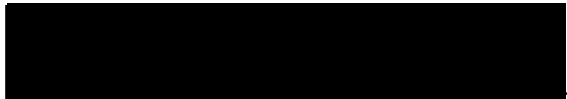TO THE OFFICE OF GRADUATE STUDIES:

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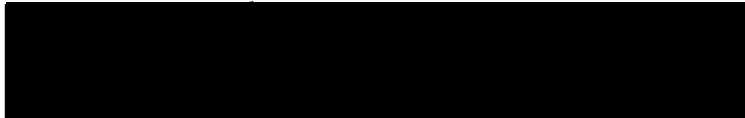James Robert Hammock presented July 26, 1971.

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REVIEW OF THE LITERATURE

The concern with populations-- their growth, demise, movements, and effects upon the behavior of the individual-- has been the topic of much speculation and little scientific research. The term population has been defined as any contiguously distributed grouping of a single species which is characterized by both genetic and cultural continuity through several generations (Calhoun, 1952). This population at a given time is the result of the interaction of three general forces: (1) reproduction which increases the population, (2) mortality which decreases the population, and (3) movement which either increases or decreases the population depending upon the net result of immigration or emigration (Davis, 1953). The primary concern of most population research has been the growth of populations by either reproduction or immigration. Pearl (1927) suggested that population growth followed a "logistic curve". This curve was explained by Strecker (1955): the population tends to multiply according to a growth curve which rises slowly at first and then picks up momentum until it shoots upward almost vertically. Pearl felt that as the population grew, as represented by the logistic curve, it would begin to stabilize at some asymptotic level that could be determined mathematically. Using his mathematical formulation, Pearl (1930) determined the asymptotic population level for the United States was 197.27 million. He felt this number would never or should never be reached although it would be close by the year 2100. If there has

been a serious or cataclysmic alteration of the conditions under
which the earlier growth of the population took place then a popula·
tion will not follow this logistic curve (Pearl & Reed, 1930). Pearl
(1930) defined these conditions as climatic, geological, biological,
economic, and social. It is interesting that he does not include
ecology as one of his conditions; however with his list of conditions,
he can explain any deviation in the population growth. For example,
the national depression of the 1930's would have an effect on the
population growth. Unfortunately he does not specifically state the
effects of these conditions on a population's growth pattern. Pearl
(1927) determined that the rate of population growth included the
following: (1) a population grows according to the same mathematical
laws that individuals follow in the growth of their bodies, (2) a
human population grows according to the same laws as does an experi-
mental population of lower animals, and (3) the rate of fertility of
a population is negatively correlated with the density of this popula-
tion. Woolston (1929) argued against these assumptions and the logis-
tic curve. He stated that all populations do not either increase or
remain stationary; nor when they do grow, do they always follow the
logistic curve. Woolston would seem to be justified in his criticism
of Pearl's (1927, 1930) logistic curve theory for the population of
the United States, as of 1970, is approaching 210 million. However,
the assumption that a human population grows according to the same
laws as does an experimental population of lower animals has inspired
many experimenters to use lower animal populations to study the
effects of overpopulation.

The effects of overpopulation on behavior have been dramatic. Pearl (1932) studied the effects of overpopulation on egg production in <u>Drosophila</u> <u>Melanogaster</u> (fruit fly). He found that as the density of population within a limited, closed universe (a bottle) increased, the rate of egg production per female decreased. This decrease was considered an indication of a change in physiological equilibrium resulting in part from collisions. The effects of increased population also showed itself in an alteration in food intake and energy out-put in muscular work. If the flies were switched from a high density group to a low density group, the rate of egg production was higher in the low group and lower in the high group. This study supports the third assumption of growth rate, that the rate of fertility is negatively correlated with population density. Pearl's (1932) study was later supported by Maclagan and Dunn (1934).

The most comprehensive work on animal overpopulation and resultant behavioral changes was done by Calhoun (1962). In his study, Calhoun used Norway rats of the albino strain and divided them into six different populations. Each population was allowed to increase to approximately "twice the number that could occupy the available space". He determined this number based on his own past experience with rat populations. The experiment was conducted in two series; in the first series thirty-two rats were used and in the second series, fifty-six. The number was divided equally between males and females. The apparatus used was ten feet by fourteen feet. Calhoun observed each population carefully for sixteen months. The pathology of overpopulation was most apparent in the females. They were unable to

carry their litters to full term or survive delivery of their litters, if they did give birth. Christian (1956) found there was a thirty-one percent decline in the number of normal embryos per mature female in his experimental population, when all experimental mice were considered as one group and all controls as another. In a later study, Christian and Lemunyan (1958) found that the number of young per litter was significantly less in the crowded females. They concluded that crowding resulted in intra-uterine mortality and probably in diminished fertility, explaining why none of the mice in their seven populations ever appeared pregnant during crowding and why almost half never bore litters, even after segregation.

Calhoun (1962) found most of the females, if they gave birth, neglected their maternal functions, which resulted in their litters dying. The females were less adept at nest building and eventually quit building nests at all. Brown (1953) states that the survival of the litters is a direct result of the type of nest building activity occurring prior to birth. As his population increased, the females could not or would not, build and defend adequate nests. The decrease in nest building was sixty-eight percent. Those with inadequate nests did not have a successful litter while those with adequate nests did. He concluded that the isolation of the female and her nest from the activities of other mice is important in the successful weaning of the litters born. The partial or complete breakdown of nest defense appears one of the key factors in the destruction of subsequent litters and hence population control. This inability in nest construction and defense was also noted by Strecker (1955).

Southwick (1955) explained another variable in his discussion of nest destruction and the females' inability to construct nests. He found that the intermingling of sexes at the nest site apparently influences litter survival. The presence of one or more adult males in a nest box had a detrimental effect on survival of the pups. In an experimental group of 107 litters, survival with one or more adult males attending was between nineteen and thirty-one percent, whereas survival of 129 litters, attended by females alone or in groups, averaged fifty-nine percent. The number of adult males in attendance with a litter made little difference to its survival; the presence of one male was as harmful as the presence of several. Southwick also found that the type of nest constructed, if there was one, played a role in the survival rate of the litters. If there were no nests constructed, there were no survivors. A bowl shape nest resulted in a sixty to ninety percent survival rate. A platform nest resulted in a fifty-nine percent survival rate and a platform nest with two or more adults resulted in an eighteen percent survival rate. The females in Calhoun's study (1962) discontinued transporting their pups from one place to another. The young were left or dropped and not retrieved which in turn resulted in their deaths. Southwick also found desertion of the young a major contributor in population control.

Is the death rate of adults more prevalent in an overpopulated environment? When examined experimentally, this question has produced mixed results. Calhoun (1962) found the females died readily from disorders in pregnancy and parturition; however, this condition has not been found universally in studies of overpopulation. Southwick found

that the mortality rates of weaned sub-adults increased significantly after the population had reached its peak, while the mortality rates of adults was largely unaffected.

The inability of females to nourish their young has also been cited as a contributor to population control. This upsetting of maternal physiology was noted by Christian and Lemunyan (1958). They reported that suppressed growth of progeny nurtured by mothers crowded for at least two generations was due to quantitative and/or qualitative deficient lactation. This effect of overpopulation may explain the long continued decline in natural populations following peak levels and a sharp decrease in total numbers. In conclusion, Calhoun (1949) noted that the upsetting of maternal physiology might be one of the limiting factors in population growth.

Calhoun (1962) found the males to be hypersexual, sexually deviant and hyperactive in an overpopulated environment. The sexual deviancy exhibited itself in the form of homosexuality. Homosexuality is not uncommon in normal animal populations; however, Calhoun found this behavior in excess of what he had expected. Most of the homosexuals seemed unable to distinguish a sex object and would attack males, females, and juveniles. The males also exhibited a frenetic over-activity level. This high activity level due to overpopulation was also noted by Southwick (1955). A review of the literature suggests that in any overpopulated environment there is an increase in activity and a decrease in fear generally. These conditions depend on the number of individuals present. Davitz and Mason (1955) found that the presence of one rat tended to reduce the strength of a fear re-

sponse exhibited by another rat. This reduction of fear response has also been reported by Masserman (1943) and Liddell (1950).

In an attempt to explain this heightened activity level as found by Calhoun (1962), Morrison and Thatcher (1969) compared the body weight and adrenal weight in albino rats in different size groups. The group sizes were one, four, sixteen, and thirty-two rats. Only minimal differences were obtained between subjects housed one and four per cage. The major effect of the density variable was seen between these two conditions on the subjects housed sixteen and thirty-two per cage. Group differences in corrected adrenal weights, as measured by analysis of variance across the four population groups, indicated that adrenal weight increases with increased population density. An earlier study by Bronson and Eleftheriou (1963) also found an increase in adrenal weight as population density increased.

Calhoun (1962) found some males displayed a pathological withdrawal syndrome, in which they would eat and drink only when others of the community were asleep. Some became passive to the point of being somnambulistic. Even females in estrus were not approached by these males. A good portion of the males went berserk, attacking females, juveniles and less active males, and even biting others on the tail. This tail-biting is very abnormal behavior for a rodent (Calhoun, 1962).

When the population became large, Calhoun (1962) found that the males began to struggle for status. This struggle manifested itself in a great deal of fighting. Brown (1953) found a definite social hierarchy among house mice caged together. This hierarchy was deter-

mined and maintained to a considerable degree of fighting. In all cages observed, there appeared to be a social hierarchy set up in which one male was dominant over all other males. Not only males but also females seem to form a hierarchical status. Christian (1961) who found that reproduction by female mice declines with increased population size, also found that the dominant females in a group do most of the reproducing. In an earlier study, Scott and Fredericson (1951) found that overpopulation tended to increase the probability of fighting; however, overpopulation did allow for better escape by defeated mice. These results had been observed by Calhoun .(1949) and Strecker (1955). When the dominant male had been determined, he immediately established a territorial dominance and claimed many females in his harem. The dominant males would often submit to homosexual advances of subordinate males. Fighting among the subordinate males was common (Calhoun, 1949, 1962). Archer (1970) found that the occurrence of aggressive behavior was correlated with a higher adrenocortical function in overpopulated groups than in isolates.

When is a mouse or rat actually fighting and not engaged in a similarly appearing activity? Investigation, grooming, and sexual behavior are three forms of behavior often confused with fighting. Scott and Fredericson (1951), realizing the difficulty, studied fighting behavior in rats and mice and devised a system for determining fighting behavior. They divided fighting into four stages: (1) preliminary behavior, (2) attacking behavior, (3) defensive and escape behavior, and (4) noncompetitive fighting. The preliminary behavior consists of hair-fluffing, tail-rattling, and mincing. In hair-

fluffing, the hair literally stands on end over most of the body, with no emphasis on particular regions as with the cat and dog. One problem is that a poorly groomed animal may give somewhat the same appearance. This becomes a problem in overpopulated environments because the animals in this culture tend not to groom themselves. In tail-rattling, the mouse rapidly twitches its tail from side to side so that it takes on a wavy appearance. Mincing occurs when mice are fighting in round-robin fashion. Beeman and Alee (1945) define round-robin fighting as each mouse meeting every other mouse. Before attacking, the mouse circles around or near the opponent with his body humped up and takes short, rapid steps. In the attacking stage, the behavior takes on two forms; either two mice attack each other or one mouse attacks while the other runs away. When the mice attack, they will bite, scratch, and wrestle. The third stage, defense and escape behavior, begins at the end of the attack stage. When a mouse is beaten, it squeaks when attacked, and if the space allows, will run away. If no escape is possible, the mouse will rear up on its hind feet, holding out the front paws toward the aggressor and remain motionless until attacked, when it may squeak and jump. The above behavior is known as "submissive reaction". The final stage, noncompetitive fighting, seems to serve no particular purpose. Calhoun (1950) suggests that this form of fighting is for undisturbed possession of living space. Noncompetitive fighting should become frequent as the population density increases and the available living space decreases.

The final consideration in Calhoun's study (1962) was the change in the area of social behavior with the population as a whole. As the

population grew, it divided itself into several groups, in each of
which the sex-ratios were drastically modified. One group consisted
of six or seven females and one male, while another group might con-
sist of twenty males and ten females. The subjects would congregate
in one area to eat rather than eat alone. Eating and other biologi-
cal activities were transformed into social events in which the prin-
cipal satisfaction was interaction with other rats. Because of the
communal activities such as eating and drinking, the animals tended to
live in this same general area even with space available elsewhere.
Calhoun called this a "behavioral sink". It was hypothesized this
togetherness caused a rise in the mortality rate of the young because
of neglect. The young that died were usually eaten by the adults.
Brown (1953) states that in overpopulated groups partial or complete
destruction of the litters occurred after parturition. This was
caused either by killing or abandoning them. Southwick (1955) found
the major mechanism of population limitation was excessive litter mor-
tality due to cannibalism and desertion. Calhoun (1962) observed that
the estrous females found themselves pursued by packs of males violat-
ing all rules of the ritual mating behavior of their species. He hypo-
thesized that, in time, failures of reproduction combined with mortal-
ity of the young would cause the colonies to die out completely. To
test this hypothesis, Calhoun removed eight healthy rats (four of each
sex) from his experiment. The rats were six months old. These rats
produced fewer litters in the next six months than expected and none
of their offspring survived to reach maturity.

Calhoun (1962) never suggests any reasons for his colonies'

extinction. At this point one might speculate as to some possible causes for this extinction phenomenon. As stated earlier, migration is a key factor in population growth; and in Calhoun's experiment this was not allowed. Crowcroft and Rowe (1958) found that reproduction recovered after it had been inhibited completely, when migration was permitted. They concluded that such densities, and therefore total inhibition of reproduction, would not occur in natural populations. Christian (1961) states that if migration is permitted from a population when it reaches levels which would completely suppress reproduction, then reproduction continues rather than being totally inhibited. D'Aulaire and D'Aulaire (1970) found that lemming populations recovered from overpopulation when mass migration occurred. These experiments limit the significance of Calhoun's results if one wishes to generalize to human populations; however, not all findings agree with the findings of Crowsroft and Rowe, Christian, and D'Aulaire and D'Aulaire. Kalela (1957) and Evans (1949) cite examples of extreme densities obtained by house mice in the wild; these populations exhibited suppression of reproduction. They also found the possibilities for emigration became restricted. One might assume from these studies that if migration was curtailed in the wild, as it was in Calhoun's study, extinction of the population could occur.

Another possible cause for the extinction of Calhoun's populations was a lack of gonadotropic activity. Deevey (1960) found that overpopulation disturbed the entire pituitary-adrenal system and diverted or suppressed the hormones governing sexuality and parental care. Thiessen (1964) found that gonadotropic activity was antagonized

and reproductive capacities failed when a population becomes over-
populated. He also found that in super-saturated populations, as was
Calhoun's, the intensity of these effects was maximized-- social con-
flict was widespread, hormonal aberration greatest and mortality ex-
tensive. This lack of reproduction by females has also been found by
Retzlaff (1938), Brown (1953), and Christian (1961). The combination
of this lack of reproduction and a high mortality rate of young could
very well lead to extinction.

In a recent study, Gandelman (1971) found that removal of the
olfactory bulbs eliminated maternal behavior in lactating and virgin
mice and in most instances initiated cannibalism. He felt that ol-
factory cues emitted by the young stimulate the area of the lateral
hypothalamus involved in the expression of maternal behavior. He con-
cluded that without such stimulation, maternal behavior might not be
elicited. This study predicted that destruction of the lateral hypo-
thalamus could cause a cessation of maternal behavior. One might
assume that in super-saturated environments like Calhoun's (1962) the
lateral hypothalamus would be affected resulting in a lack of maternal
instincts and if this affect were permanent it would explain the ex-
tinction of Calhoun's population.

In a pilot study (1969), this author followed Calhoun's (1962)
study design to determine if his findings could be replicated. Six-
teen adult albino mice (eight males and eight females) of the Swiss
Webster strain were placed in a confined enclosure and allowed to
reproduce freely. The subjects were provided food and water propor-
tionately as their numbers grew. Strecker and Emlen (1953) found

when food shortage was tested in reference to population growth, the
discontinuance of population growth was due to a cessation of repro-
duction and did not involve any increase in mortality rate of adults
or of young born before the food crisis. The behavioral changes of
both individuals and the group were of primary importance and each was
observed twice daily as the population grew. The population was per-
mitted to increase to approximately four times the number that could
occupy the available space comfortably.

The results of this pilot study were similar to those found by
Calhoun (1962). The lack of maternal care combined with inefficient
nest construction and poor defense resulted in a high mortality rate
among the second litter (71%), while the mortality rate for the first
litter was only two percent. The young that died were eaten by the
adults. Nest building by the females was abandoned entirely with the
second litter. Retrieving and transporting of the young by the females
also ceased by the second litter. Homosexuality increased greatly
among the males after the second litter, while normal sexual behavior
decreased; the males would attack juveniles as well as other adults.
As the population grew, an increase in fighting among the males was
noted. The fighting seemed more vicious and each fight lasted for a
longer period of time. As the population grew, a frenetic overactiv-
ity level was noted among all subjects. This frenetic behavior ceased
only when the subjects slept. The individuals within the group would
endeavor to isolate themselves from the others. In trying to isolate
themselves, the subjects would spend a great deal of time chewing at
the wire covering of the apparatus. Some spent as long as thirty

minutes continuously engaged in this single activity. Any estrous females were pursued by a pack, consisting of three to five males all trying to mount simultaneously. The total number of births per female decreased as the population grew. For example, the first litter consisted of sixty-three while the second litter was only thirty-five, although there were more productive females. The subjects would lie in any available space, with their eyes open, completely ignoring all others even though they were walked and defecated upon. Finally, it was noted that complete grooming all but ended. The subjects would clean their faces but not the rest of their bodies. This resulted in a matted unkempt appearance for the total population.

Some of Calhoun's findings were not observed in the pilot study. He found that many females did not survive delivery of their litters. While one female in the pilot study did die shortly after giving birth, her death alone was not significant. This finding agrees with South-wick (1955).

Males alone displayed a pathological withdrawal syndrome in Calhoun's study while the entire population of this pilot study demonstrated this behavior. One possible cause for this difference might be in the total size of the two populations. Calhoun's populations were allowed to expand to only twice the number for the available space, while this author's population was four times larger than the space available. The pilot study population was more super-saturated than was Calhoun's. Being a more super-saturated population, any behavior change might be manifested by all the inhabitants, not merely a few.

Calhoun found tail biting occurred as his populations grew, while

this mannerism was not found in the pilot study. This could have
been caused by Calhoun's use of rats while this pilot study employed
mice, although according to him the choice of rodent should not matter
when considering this behavior. In the pilot study, there was no
struggle for status among males nor any establishment of territorial
dominance, harems, or a "behavioral sink". Calhoun found that as the
population grew it divided itself into several groups in which the sex
ratios were drastically modified. This did not occur in the pilot
study; again the species difference in subjects used could account for
these discrepencies. While the population of the pilot study did not
die out as Calhoun hypothesized, there was a drastic decrease in the
number of young from the first litter (N=63) to the second (N=35),
and it might be assumed that given a longer period of time, this popu-
lation might also have become extinct.

CHAPTER II

PROCEDURE

METHODS--PART I

Of the many possible behavior variables that can be affected by
overpopulation, six were chosen to be examined by this experimenter.
This choice was based on past research of overpopulation and on ear-
lier pilot study. The six behavioral changes examined were: (1)
grooming, (2) homosexuality, (3) nest building, (4) retrieving of
young, (5) fighting, and (6) mortality of the young. For each of
these variables, the experimental groups were compared with the
control group and with each other for any change due to overpopulation.

Grooming

Grooming was defined as the cleaning and caring of the entire
body by the subject. It was assumed that as the population within the
experimental groups increased beyond the crucial density level, the
ratio of unkempt mice would exceed the ratio found within the control
group. The ratio was defined as the number of unkempt mice observed
once a week divided by the total number in the population for that
week.

Homosexuality

Homosexuality was defined as any attempted mounting, mounting,
or intromission by like sexes; a frequency count of the number of such
occurrences per group compared with the total number within that group
was made. It was predicted that as the population density increased

homosexual activity in the experimental groups would be greater than in the control group.

Nest building

Nest building included construction and defense of a nest. The observations were made on a "yes-no" basis for each litter, either the females built nests or they did not. The hypothesis was that as the population density increased within the experimental groups, nest building and defense would decrease until eventually no nests would be constructed. It was hypothesized that there should be no change in nest building or defense within the control group.

Retrieving of young

Any pup that was moved from one position to another was considered retrieved. By broadly defining this variable, any personal attention received by a pup could be recorded; therefore besides measuring just the return of a dropped pup, it also measured personal attention given the pups by the adults. As the population would exceed asymptote, there should be proportionately fewer retrievals in the experimental groups than in the control group. The ratio was determined by dividing the number of retrievals observed by the total number of pups at the time of observation (number of retrievals/number of pups).

Fighting

Fighting was distinguished from similar appearing behavior by using the Scott and Fredericson system (1951). The proportion of fights observed within the experimental groups was predicted to exceed those in the control group as the population density increased. Here

the ratio was the total number of fights per week, based upon a pre-
determined schedule of observations, divided by the total population
for that observed period (number of fights per week/total population).

Mortality of the young

The mortality of the young was defined as the death of any pup
for any reason before it was weaned. The normal weaning period for a
mouse is twenty-one days (Gandelman, 1971). The survival rate of pups
was expected to decrease rapidly once the experimental populations
exceeded their asymptotic level, while no significant decrease in the
survival rate was anticipated in the control group. The survival rate
was calculated as the number of pups alive divided by the number of
pups born (number of live pups/number of births).

Observation schedule

The observation schedule for each of the six behavioral changes
was as follows: grooming was observed weekly, the frequency of homo-
sexual activity and the number of fights was recorded for one-quarter
hour three times per week for each group, nest building was recorded
daily by observing the total number of nests per group, retrieving was
observed for one-quarter hour four times per week for each group as
pups were available, and mortality of the young was recorded daily
when pups were available. All observations were made at random times
during the week to avoid any possible effects of a fixed schedule. Be-
fore each observation period, there was a fifteen minute delay from the
time the observer entered the room until he began recording. This
allowed the subjects time to become accustomed to the presence of the

experimenter.

To aid in the insurance of as little experimenter bias as possible, a trained observer was employed at five different points throughout the experiment to make independent observations with the primary experimenter; and an interrater reliability coefficient was calculated. Each variable was tested except for mortality of the young which was obvious and needed no reliability check. For each variable tested, the resulting Pearson $r = 1.00$.

METHODS--PART II

The subjects were adult albino mice of the Swiss Webster strain. A total of forty-eight mice were used, eighteen males and thirty females. The purpose of having more females than males was to increase the population more rapidly than would occur with an even number of subjects. Mice were chosen primarily because of their small size and the limited amount of laboratory space available. To insure the fastest population growth, the Swiss Webster strain was chosen because of its breeding capability.

There were a total of three apparatus used varying primarily in their dimensions. Two of the apparatus measured 15 5/8" x 20 1/2" x 8" and one apparatus measured 47 7/8" x 61 1/2" x 8". Because of the sanitation problem, each small apparatus was equipped with a wire screen floor having a removable tray just beneath it. In the case of the large apparatus instead of a tray, paper was used to accumulate the waste. The wire mesh floors were constructed of 1/4" hardware cloth, which was sufficiently small to prevent the pups from falling

through while large enough for defecated material to pass onto the
paper below. The two smaller apparatuses were each equipped with a
food bin made of 1/2" hardware cloth and two water bottles, while the
large apparatus had a similar food bin but three water bottles. The
layout of the living area for each apparatus was essentially identical.
Along the walls of the rectangular structure there were small cubicles
or "apartments". The cubicles allowed the animals a place in which to
build their nests, raise their young, or find solitude. The central
portion of the apparatus was open-- much like a courtyard-- with food
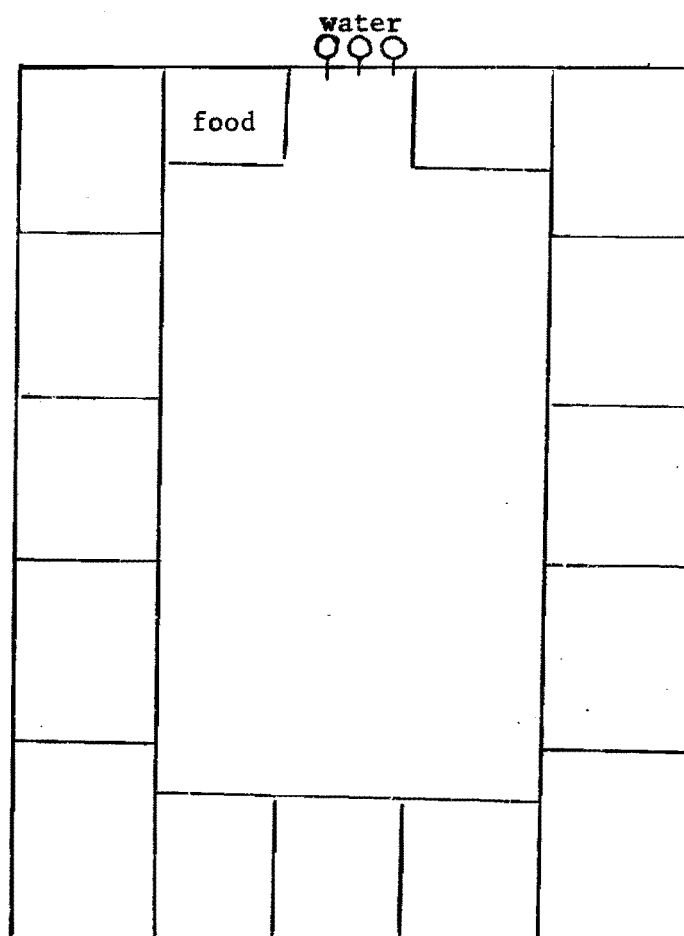

Figure 1. Apparatus for control group

and water supplied at one end. Figure 1 illustrates the larger apparatus. To insure adequate nesting material, strips of paper were provided as needed and removed when soiled. The top of each apparatus was covered in 1/2" hardware cloth which allowed the removal of soiled paper and dead pups. This removal was accomplished with the use of a "grab all" tool which was inserted through the top, and pulled back without the need of removing the attached top each time. Any adult animals that died were removed by detaching one corner of the wire top and pulling the animal out with the "grab all" tool.

From the previous pilot study, it was found that the asymptotic level for the population was approximately fifteen square inches per mouse. This figure was used in establishing each experimental group in this study. Upon arrival, the mice were separated into three groups; each group consisted of six males and ten females. No attempt was made to mark each mouse separately upon his arrival, because of the eventual number of mice anticipated and the impossibility of marking each one. The ability to distinguish males from females was easily accomplished because the genital region on the males was quite visible. One group was placed in each of the two small apparatus to serve as an experimental group. The density level in each of these groups was approximately eighteen square inches per mouse which approximated asymptotic level. By placing of these groups so near asymptotic level, an overpopulated condition would result with the weaning of the first litter. The remaining group was placed in the large apparatus to serve as the control group. Each group was allowed to reproduce freely and each was provided food and water proportionately as their

numbers increased. Once placed in the apparatus with the top secured, the subjects were not disturbed except to remove any dead and to count any pups. The counting of pups was crucial to the success of this experiment and was accomplished by pushing any adults in the nest out of the cubicle and barring the door with heavy wire inserted through the ceiling and floor. Once the pups were counted the wire was removed. The control group would not be allowed to multiply beyond the comfortable limits of their apparatus which was estimated to accommodate 197 mice. Should this figure have been exceeded, the extra subjects would have been removed. The experiment was terminated after six months and fourteen days.

CHAPTER III

RESULTS

The results were not as anticipated-- there was no overpopula-
tion in either experimental group, nor did the control group reach its
earlier calculated asymptotic level. Each group controlled its popu-
lation growth with respect to the density of its environment. Each ex-
perimental group began with active sexual behavior and within a month
after arrival both groups began delivery of their first litters. With-
in no more than three days after delivery, each pup was subsequently
killed and cannibalized by the adults. The methods by which the pups
were exterminated varied with no one method paramount. Some were
killed in the retrieval process. For a short period of time after the
birth of each batch of pups, the females engaged in "baby swapping".
Each female would endeavor to accumulate as many pups as possible into
her nest. This activity could become quite frenetic and in the ex-
citement the females often killed the pup they were trying to retrieve.
Some pups were literally pulled apart by the females trying to retrieve
it. Other pups died as a result of cannibalism. The cannibalism was
performed by the entire population and not exclusively the female.
Many pups were removed from the nest by members of the general popula-
tion and eaten. Others were eaten in the nest area by either the fe-
male or some intruder. Finally, some pups died as a result of mater-
nal neglect.

Figure 2 illustrates the survival rate for each group in the ex-
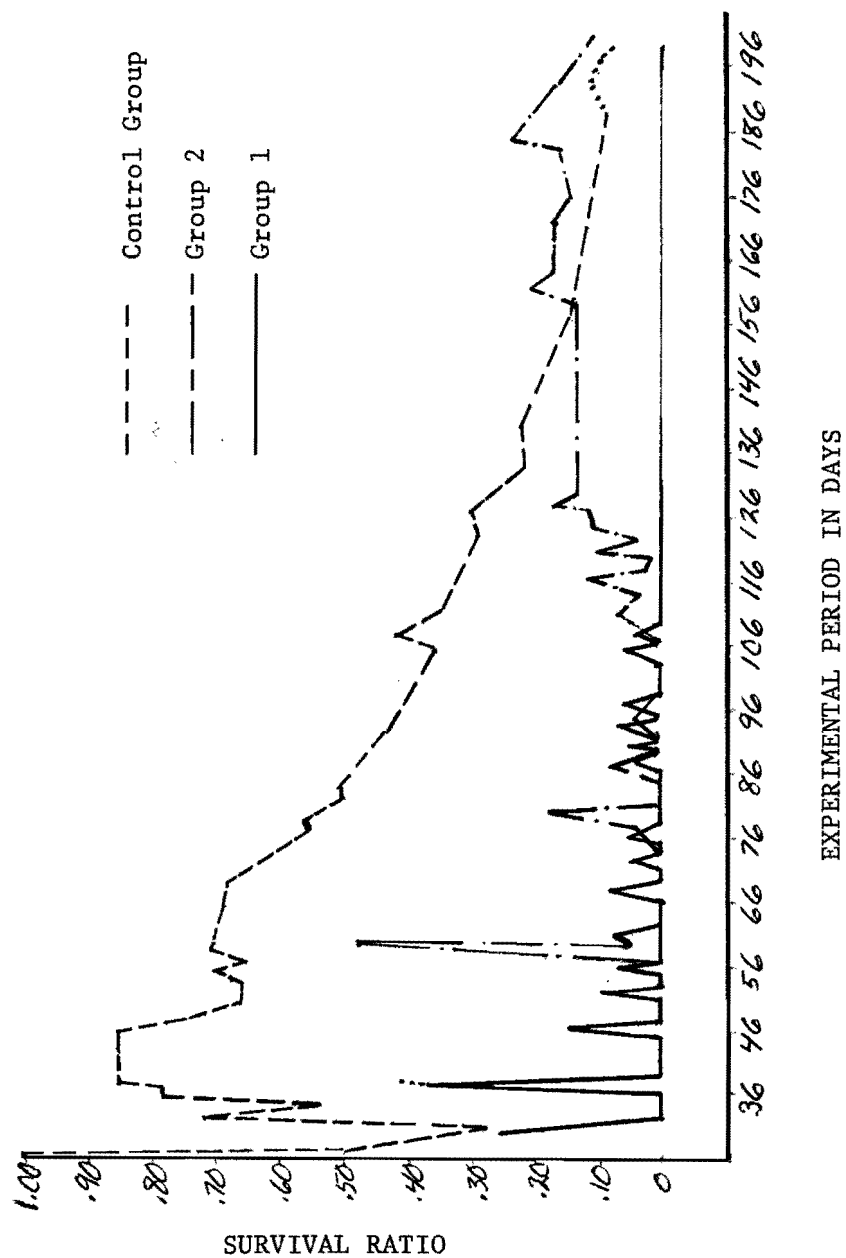periment. This rate is illustrated on a daily basis. The zero survi-

Figure 2. Mortality rate for the three population groups.

val rate continued in experimental group one for seventy-seven days and a total of 130 pups, whereupon delivery ended for the remainder of the experiment (ninety-one days without a birth). Sexual activity within this group did not seem to diminish perceptively and there appeared to be pregnant females during the entire ninety-one day period. Since the gestation period for mice was only nineteen days (Gandelman, 1971), at least four more litters should have been born. It would appear that intrauterine mortality existed during this final ninety-one day period. This differs from Christian and Lemunyan (1958) for this effect did not appear in their groups until after overpopulation had occurred. By the ninety-fourth day of the experiment, twelve days before the final pup was born, the total population had reduced itself to twelve adults; eight females and four males remained. After this date, there were no more births or deaths among the adults.

Experimental group two followed much the same pattern as did experimental group one. For seventy-three days after its first births, this group delivered and exterminated 113 pups (see figure 2); and by the seventy-second day, it had reduced its total population to fourteen; ten females and four males. On the 108th day of the experiment, three months prior to the experiment's termination, experimental group two was artificially reduced in population to eight, seven females and one male, to see if this trend of a zero survival rate would change and at what density level this change might occur. The results of this artificial population reduction were dramatic. In the next litter after reduction, twenty-three pups were weaned out of a total of fifty-six births (forty-one percent survival). The total popula-

tion of adults was now thirty-one. In the second litter after popula-
tion reduction, twelve pups were weaned out of a total of forty births
(thirty-percent survival). The total population was now forty-three.
In the third and final litter, there were no survivors out of eighty-
four births. Figure 3 illustrates the survival rate of experimental
group two after its population was artificially reduced.

After an initial fluctuation period, the survival rate of the
control group stabilized at eighty-four percent and began to drop
immediately until it reached ten percent at its lowest point, nine
days prior to the termination of the experiment. On the 136th day,
the control group reached its maximum density level of 116 adults;
and from that point until the termination of the experiment, some
fifty-one days later, there were no pups weaned. During that time
period there were some 479 pups born. At the time the experiment was
terminated, there was a total of thirty-five pups alive and it cannot
be said with absolute certainty that all of these pups would have died;
however on the 188th day, the number of young was zero and in the
following nine days some ninety pups were born of which these thirty-
five remained. The overall survival rate for the control group on the
188th day reached its lowest point of 10.66 percent. These final nine
days are represented in Figure 2 by a broken line. At the time of
termination, there was a total of 112 adults and there had been a
total of 1056 births within this population. An interesting point
emerges from a comparison of the density level of experimental group
one and the control group at its highest adult population level of 116.
The livable area in cubic inches for group one was 2237.50 and for the
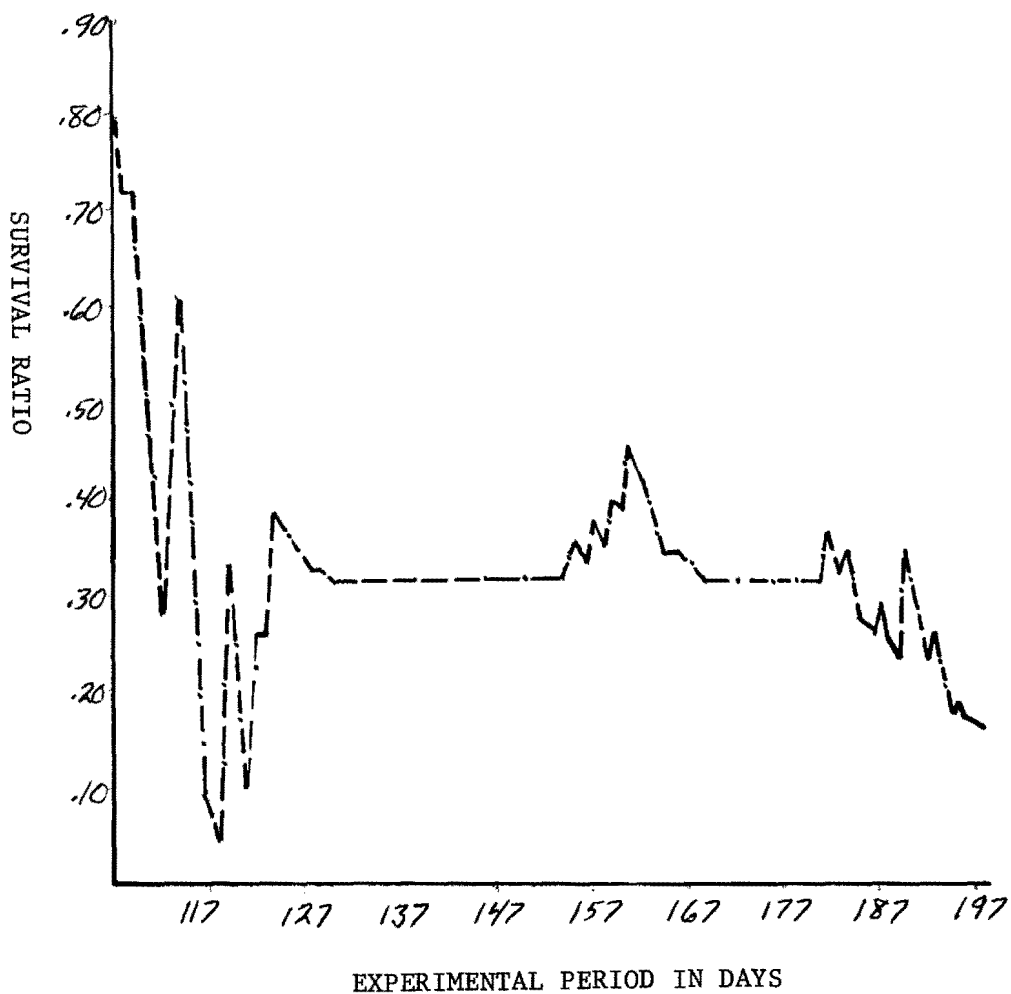control group was 22,443.375. When calculated for each mouse the

Figure 3. Survival rate for experimental group two after artificial population reduction.

results are 186.46 cubic inches/mouse for group one and 193.48 cubic

inches/mouse for the control group. At its widest range there was

only a 13.92 cubic inch/mouse difference between group one and the con-

trol group. It would appear from these results that the two popula-

tions both stabilized at nearly the same density level; one by reduc-

ing its adult population and exterminating its young; the other by

controlling the survival rate of its young.

The other five variables were analyzed even though overpopula-

tion did not occur. With the lack of overpopulation there was no ob-

served decrease in grooming activity for any of the three groups. At

no time during the experiment were any unkempt mice seen. There was

no increase in homosexual behavior in any group. In fact, only upon

one occasion was a homosexual act observed and it occurred in the

control group.

Nest building for individual females could not be determined as

earlier proposed. Females did not construct separate nests, instead

they combined their efforts and built communal nests, usually shared

by two or three females in the experimental groups and from two to

eight females in the control group. It was also noted that non-preg-

nant females and even males constructed nests, and at times pregnant

females would comandeer these already constructed nests. For

the entire experiment there was a mean of 3.4, 2.3, and 5.3 nests for

the control group, group one, and group two respectively. The only

noticeable change in this variable occurred in the control group: at

first only bowl type nests were observed, but as the survival rate be-

gan to decline more and more platform nests were constructed until at

a twenty-nine percent survival level no more bowl type nests were ob-
served. Southwick (1955) noted a sharp decline in survival when the
type of nest construction changed. There was no change in nest type
observed in the experimental groups. Both constructed only bowl type
nests.

The results for the retrieval of the young are illustrated in
Figure 4. For each group there were periods of time in which no pups
existed; rather than represent this time period in Figure 4 the graph
for each group was collapsed, and each illustration is for the time
period in which there were pups for possible retrieval. The abscissa
represents the total number of days there were pups in each group and
the ordinate is the ratio of retrievals per group. For each experi-
mental group the highest number of retrievals came at or near the time
of birth and then began to drop off immediately until, at the time of
weaning, the pups were too large to retrieve and the ratio fell to
zero. In Figure 4 the births and weaning periods are noted for each
experimental group. This same phenomenon does not seem to hold for
the control group: there seems to be no relationship between the time
of birth and the increase in retrieving. In comparing the two experi-
mental groups with the control group, it was noted that at the time of
the births the interactions between adults and pups as measured by the
retrieval ratio was considerably higher for the experimental groups
than for the control group. The frequency of interaction (retrieval)
began to increase in the control group as the population neared its
crucial density level.

The results of the fighting variable are illustrated in Figure
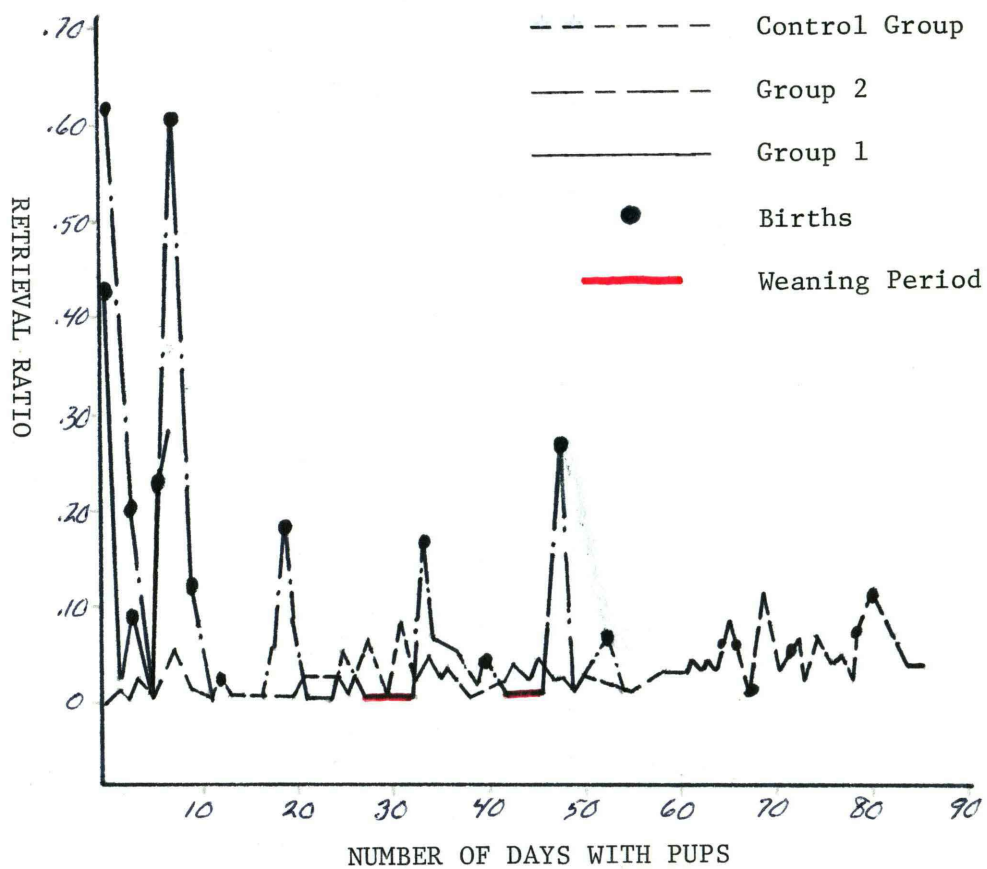
Figure 4. Frequency in retrieval of the young for all three groups.

5. For the first fifteen weeks there appears to be no particular trends being established. Each group begins with an initial low period soon followed by a rapid increase in fighting. From this point (about the sixth week), the groups begin to vary in their fighting behavior with no particular predictable pattern. From the fifteenth week until the termination of the experiment, group one and the control group continue the same fighting behavior that they had established in the first fifteen weeks; however, group two changed. At the fifteenth week experimental group two's population was artificially reduced and within a week the frequency of fighting had been reduced by more than one-half. By the second week after reduction, fighting had stopped and was nonexistent for four weeks. When the first pups were weaned during the twenty-first week, fighting promptly rose and at the second weaning during the twenty-fifth week fighting reached its highest point for the entire experiment. All notable points are illustrated in Figure 5. In the control group an interesting aside was noted: when the fighting began to increase many males would escape by hanging from the wire screen top of the apparatus. As the population began to grow and the hiding places became more limited, this peculiar behavior increased. Many animals would sleep while hanging in this position. There were occasions when as many as twenty males would be seen hanging from the top. In the entire experiment no female was ever observed engaged in this behavior nor was this behavior ever evidenced in either experimental group.

Another variable which was not tested but was noted because of curiosity and the fact that Calhoun (1962) found it to be important
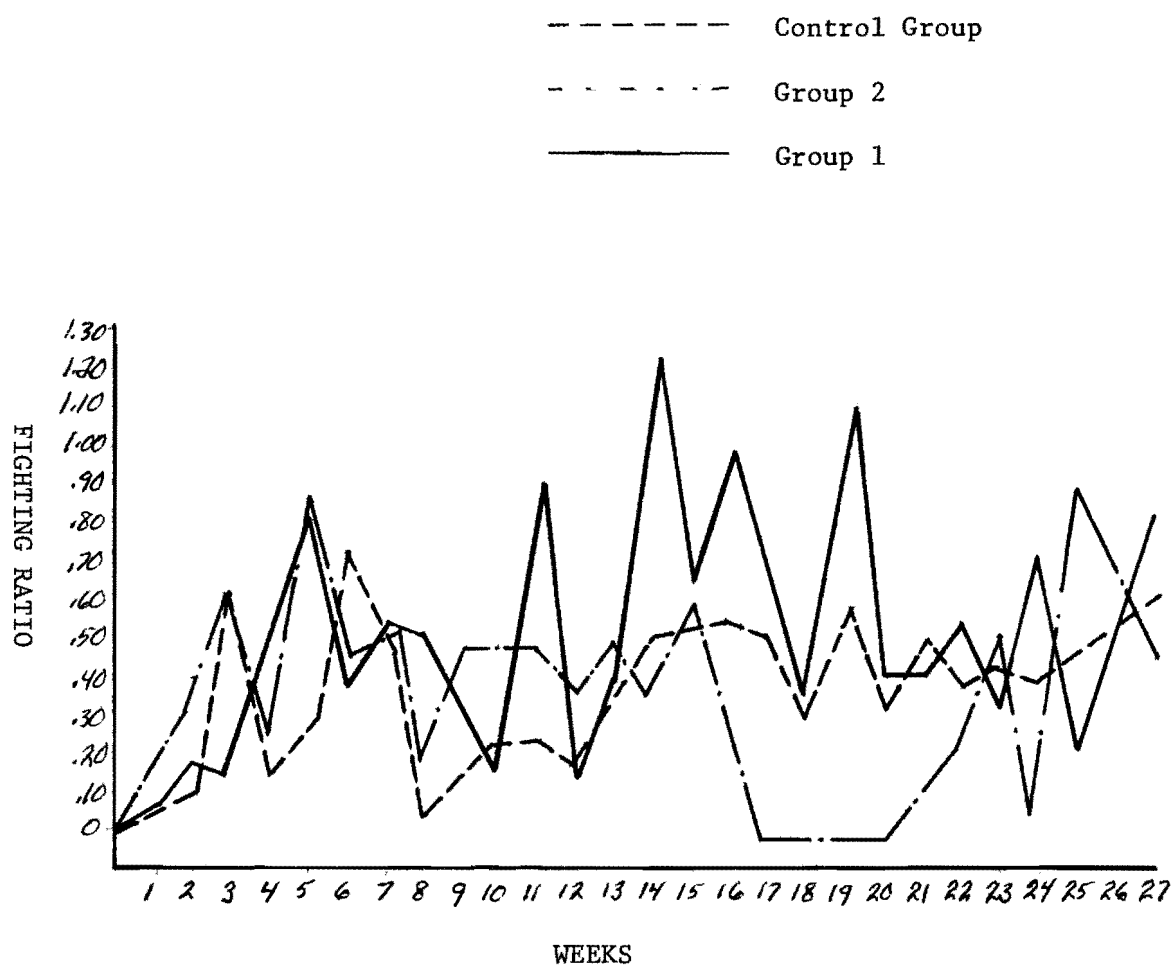
Figure 5. Fighting behavior for all groups.

was the defining of territories and collecting of harems. Neither of
these characteristic behaviors were observed in either experimental
group; however early in its population growth, the control group set
up territories. There seemed to be no apparent harems just terri-
tories. After an initial adaptive period most of the mice in the con-
trol group settled down in the cubicles nearest the food and water.
In appearance it was much like Calhoun's "behavioral sink". At this
time there was one group of males who were driven out of this living
area and foeced to live at the far end of the apparatus. This group
varied in size from two to eight males. Each time one of these ani-
mals left his cubicle to acquire food or water he was promptly attack-
ed and driven back to his cubicle. The attacks came from both males
and females and, at a later time, even juveniles. There never appear-
ed to be any females in this group, however females would enter the
cubicle to engage in mating activities. As the density level began to
increase within this group, the territorialism began to break down as
did the "behavioral sink". Finally there were no more territories,
nor was there a "behavioral sink" as described by Calhoun (1962).

Another curious behavior manifested itself in all three groups
shortly after the birth of the first litter. For some reason the popu-
lation would periodically move the entire nest, paper and pups, to a
new cubicle. For example, in one three week period the control group
moved their nest forty-three times. Often there was more than one
nest constructed; therefore the movement figure includes any building
of a new nest and movement of pups from an already constructed nest to
it and movement of the entire nest. This behavior tapered off and

soon ended as the population grew in the control group. This behavior

occurred sporadically in experimental group two and terminated on the

108th day in group one. Other than the behaviors described, no other

variables were observed or recorded.

CHAPTER IV

DISCUSSION

The most important single factor in this experiment was the fact

that experimental group one and the control group never overpopulated,

and that experimental group two never weaned a pup until artificially

reduced in number. No other experiment reviewed had this phenomenon

occur. In all other research, the populations first overpopulated

then reduced their numbers. This experiment suggests an inborn popu-

lation control mechanism based upon the density available per mouse;

and as this crucial density level is approached, the population will

stop its own growth. The term crucial is here defined as that partic-

ular point or range which, if exceeded, results in overpopulation.

This crucial density level is variable and determined by each popula-

tion independently. From the initial reaction of groups one and two,

both reduced their adult population, it would appear that a population

can also reduce its adult members to this "inborn" density level. The

crucial density level which was determined by noting the control group

at its highest adult level (N=116) and experimental group one (N=12),

at its constant level after initial population reduction, was calcu-

lated as 189.97 ± 3.51 cubic inches/mouse. If the calculation were

made using the control group at its lowest adult level (N=112), the

resultant crucial density level is 193.42 ± 6.96 cubic inches/mouse.

There is only a ± 3.45 cubic inch difference per mouse between these

two crucial density levels depending upon how they are calculated.

From the examination of these results, one could hypothesize that when

a given population of mice neared this calculated crucial density

range (189.97 $\pm$ 3.51 in^3 to 193.42 $\pm$ 6.96 in^3) it would begin to con-

trol its growth to stay within this range, and that any population

placed in an environment with a higher crucial density range would re-

duce itself to meet this level. The results of this experiment sub-

stantiate such a hypothesis.

Experimental group two, after artificial population reduction,

exceeded this crucial density level; however this increase can be

accounted for under the innate population control hypothesized earlier.

When the experiment began, group two followed the same trend as did

group one in that it quickly reduced its adult population from sixteen

to fourteen and did not allow any pups to survive. On the 108th day,

this group was artificially reduced to eight. At the time of reduc-

tion its density level was 159.82 cubic inches/mouse; therefore we

cannot state with any accuracy that this group would have reduced it-

self any further. However one cannot say that it would not have con-

tinued as did group one, eventually reaching the calculated crucial

density level. At group two's reduced level of eight, the density

level per mouse was 279.69 cubic inches. After reduction this group

weaned twenty-three mice in their first litter, twelve mice in their

second litter, and non in their final litter (note Figure 3). The

high survival rate for its first litter, forty-one percent, can be

accounted for: until the pups are weaned and start interacting with

the general population, they do not significantly affect the density

level for the group. When these twenty-three pups were weaned, the

population density was reduced to 72.18 cubic inches/mouse. From the

earlier hypothesis one would assume that the survival rate for the second litter would be zero, however the survival rate was thirty percent. The density level after the second litter was 59.03 cubic inches/mouse.

What seems to have occurred is a time lag between the number of births and the effects of those births on the population controls; the population was soon affected as demonstrated by the zero survival rate for the third litter. This group did terminate its survival rate and, although it is only conjecture, it is possible that given more time experimental group two would have continued a zero survival rate and reduced its adult population to the crucial density level. This group would not have exceeded the crucial density level if it had gradually approached it. The evidence for this statement is based upon the population growth of the control group. This group never exceeded the crucial density level because it had time to alter its growth before reaching this limit. Group two was below the crucial level before weaning the pups and upon weaning exceeded this level. Before the effects of the higher population density could be a factor, group two had produced its second litter. It was evident the effects of a high density level had begun to make its presence known because the survival rate for this second litter was only thirty percent. The full effect was felt by the third litter for none of the pups survived. It would appear that the effects of population growth on the inborn population control factor are directly tied to time. If the population has the time to approach the crucial density level gradually, it will not overpopulate; if, however, the crucial density level is met

with little or no approach time, it will be exceeded and the population will be overpopulated. If overpopulation should occur, the group will then begin to return to its inborn crucial density level by reducing the adult population and reducing their survival of new born pups to zero.

The results of this experiment have not been found in any other study on overpopulation. What is it about these groups which makes them uniquely different from all other populations studied? At this point the question seems to defy answer. Populations, both experimental and natural, seem to control their growth; however the variables that affect this control do not begin until after overpopulation has occurred (Calhoun, 1962; D'Aulaire and D'Aulaire, 1970). Possibly the difference in results is due to a procedural difference between this experiment and all others reviewed. Some experimenters like Calhoun (1949, 1962) and Morrison and Thatcher (1969) have used rats in their studies on overpopulation, and their findings might differ from this experiment's due to a species difference. Since one cannot generalize from the results of animal studies to a prediction of human behavior, one might also assume that he cannot generalize from the results of studies using rats to those using mice. Also any studies such as Pearl's (1932) which used a different animal (fruit flies) cannot be compared to mice for the same reason. Another group that can be eliminated in this quest for universality are those experimenters who artificially overpopulated their groups and did not allow natural overpopulation (Christian & Lemunyan, 1958; Thiessen, 1964). One cannot assume that the behavioral changes that result from arti-

ficial overpopulation would be the same as those for natural over-
population. Even those experimenters who used mice and allowed natu-
ral overpopulation might argue that these results are not equivalent
because we used a different strain of mice (Brown, 1953; Southwick,
1955). The one study which cannot be eliminated for any of these
reasons is the pilot study conducted prior to this experiment. In
that study the same strain of mice were used and the procedures for
conducting the experiment were identical. However the result was
overpopulation. Essentially the only difference between the pilot
study and this experiment was the flooring in the pilot study appara-
tus. The flooring in the pilot study apparatus was solid wood co-
vered with litter material, while the apparatuses of this experiment
were florred with quarter inch hardware cloth. What effect this dif-
ference in apparatus might have cannot be determined without further
research. It would seem that none of these differences can adequately
explain why no overpopulation occurred in this experiment but did in
all others. All other experiments-- regardless of species of animal
used, apparatus, or general procedure-- got overpopulated.

Without further research it would seem highly presumptuous to
postulate a cause for the paradoxical situation thus described; how-
ever if one is allowed to speculate, a plausible solution is possible.
Assume that a population is more than just a collection of individuals.
A population has inherent characteristics of its own with its own per-
sonality and idiosyncrasies. If a population could be considered a
single entity with one personality, the same psychological tenets
could apply to that population as to the individual. The concept of

individual difference, applied to the population would become this: because one population overpopulates does not mean that all populations will overpopulate.

Because of the results of overpopulation studies like Calhoun's (1962), many contemporary writers have generalized from these results to the possible outcome of human population growth. Based upon these studies, Ardrey (1970) has postulated that much, if not all, of our violence in the world is directly attributable to overcrowding which is a byproduct of overpopulation. He feels the overcrowded society may be headed for chaos or dictatorship. Ehrlich (1968) has hypothesized the annihilation of the human race if it does not stop its rapid population growth. Morris (1967) concluded from the results of other studies that a "catastrophic upheaval" must result from overpopulation but that if some "controlled anti-reproductive device" could be introduced at the first signs of overpopulation, chaos could be averted. From the results of this experiment it would appear that this is exactly what occurred, each group employed anti-reproductive devices and avoided inevitable overpopulation and chaos. All of these authors have risked an obvious violation, that of generalizing from the behavior of non-human species to humans; this generalization cannot be made with any degree of certainty.

Besides the growth of the population, the density level also affected other variables tested. Without overpopulation, grooming and heterosexual behavior were unaffected and this was as one might expect. Nest building was not directly affected by density, and as earlier noted the females combined efforts and constructed communal

nests. Indirectly the physical size and shape of the apparatus did seem to affect nest building and to a certain degree the retrieval of the young. The cubicles in the experimental groups were smaller than those in the control group which allowed fewer females to inhabit them. No more than two pregnant females were ever observed to occupy a single nest in the experimental groups, whereas up to eight pregnant females were observed occupying a single nest in the control group. Because of this inequality in nest dispersal, there was less opportunity or need for retrieval of the young in the control group. With nearly all the mothers and their pups confined to one nest, there was less need to move the pups; and little or no "baby swapping" occurred. The greater number of nests in the experimental groups allowed more "baby swapping" to occur where the pups were available. This availability is reflected in the greater retrieval ratio exhibited by both experimental groups (see Figure 4).

Another interesting phenomenon occurred with the retrieval variable. In each experimental group the retrieval process increased rapidly with each birth and then dropped off equally as fast. This pattern of retrieval did not occur in the control group; in this group there was little correlation between the retrieval frequency and time of birth. The central factor determining the cause of this difference in behavior seemed to be the age of the young. The pups did not survive long enough in the experimental groups for the adults to accustom themselves to their presence; whereas in the control group there were always pups alive so the birth of new pups did not cause frenetic "baby swapping" as it did in the experimental groups.

The final variable directly influenced by the density level was fighting. Until the fifteenth week there was no way of determing if the density level was having any effect on the fighting behavior of the groups. No group had established any pattern in its fighting behavior. At the fifteenth week experimental group two was artificially reduced in number and its fighting behavior almost immediately dropped to zero and remained there until the first population addition some six weeks later. From this result it would appear that aggression in the form of fighting is directly tied to the density level. This would seem to support Ardrey's (1970) conclusions with regard to aggression and overcrowding. The interesting point noted with this variable is that fighting is directly correlated with population density at all levels of population growth. Overpopulation does not have to occur for there to be a substantial increase in fighting frequency. Ardrey may be correct when he attributes aggression to overcrowding and not directly to overpopulation as does Calhoun (1962). At this point a distinction should be made between overcrowding and overpopulation for they are not synonymous terms. Overcrowding is the substantial increase in the density within a section of a particular environment, while the entire environment is not particularly affected. For example, Australia is not considered a high density environment while Sidney is a highly dense area within that environment. Overpopulation occurs where the entire environment is densely populated. These two terms are often used interchangeably when, it is felt, there is a distinct difference between them.

Future research

It has been demonstrated in this experiment that not all populations need overpopulate. Unfortunately because no other experimenter has had similar results, more research is needed to substantiate these findings. First, another experiment should be done in an effort to replicate the findings of this experiment. If these results are replicated, one should then begin to compare these findings to those of other researchers like Calhoun (1962) in an effort to find that variable or variables which might be involved in producing the differing results. One would need to test the differences of species, apparatus, and procedures to evaluate what affect each had on population growth. If the results are not replicated, the effort must be focused on why they were not and on the variables that might be involved. No variable regardless of seeming insignificance should escape testing. Such variables as the lighting schedule, heat, ventilation, nesting material, apparatus design, and frequency of personal encounter might all play a significant role in the growth of a population. Incorporated into any future research on population growth must be the physiological affects of density. Gandelman (1971) may have given an important clue with his implication that the lateral hypothalamus may be directly involved in maternal care. If this area of the brain is affected by fighting, this could be the determining factor in the differing population growths observed. This experiment implies that, to date, not all the influences upon population growth are known nor can it be assumed that a population if allowed to grow will overpopulate.

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