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Aggression and Growth in Confined Mouse Populations

Robert Walter Zemore

College of William & Mary - Arts & Sciences

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AGGRESSION AND GROWTH IN CONFINED MOUSE POPULATIONS

A Thesis
Presented to
The Faculty of the Department of Psychology
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

By
Robert W. Zemore
1967
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Arts

Robert W. Jones
Author

Approved, May 1967

Herbert Friedman, Ph.D.
Peter Derks, Ph.D.
Russell Norman, Ph.D.
C. Richard Terman, Ph.D.
Stanley B. Williams, Ph.D.
Chairman, Department of Psychology
I want to express my appreciation to Dr. Herbert Friedman for his encouragement and guidance throughout the investigation. He clarified my thinking upon a number of points and made numerous suggestions as to form and content which greatly improved the manuscript. I am indebted to Dr. C. R. Terman for the information he provided on past research relevant to the present investigation. I am also grateful to Dr. Peter Derks who carefully read and commented upon the manuscript.
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</tbody>
</table>
ABSTRACT

The present study was designed to investigate the relationships between behavior and mechanisms limiting the size of confined populations of mice. The general hypothesis was that aggression, resulting from social instability, may limit a population's growth either directly by interfering with maternal behavior, or indirectly, being mediated by physiological responses to stress. The relationships among social structure, aggression, and mechanisms limiting population growth were studied systematically by varying the ratio of selected and trained aggressive males to selected and trained submissive males in a population and observing the resultant social structure, level of aggression, and growth. After the populations had been assembled for three months the males were sacrificed and inspected for physiological signs of stress.

The main findings of the study were:

1. The level of aggression exhibited by a population was a positive function of the number of selected aggressive males within the population, not the result of social instability.

2. Females in the more aggressive populations took longer to deliver their first litters than the females in the less aggressive populations, lending support to the hypothesis that aggression, mediated by physiological mechanisms, can suppress reproductive activity.

3. Males selected for their aggressiveness weighed more than males selected for their submissiveness. The aggressive males also gained more weight while in the populations than did the submissive males, even though more fighting occurred in the populations housing the aggressive males.

4. The only behavioral mechanism observed to limit population growth directly was cannibalism, which could not be accounted for on the basis of aggression alone.
AGGRESSION AND GROWTH IN CONFINED MOUSE POPULATIONS
INTRODUCTION

Past research on confined populations of small mammals has implicated social behavior as playing an important role in determining natality and mortality, basic components of population growth. However, the mechanisms that relate behavior and population growth remain obscure. The present experiment with confined mouse populations of fixed size and predetermined composition was designed to help define these mediating mechanisms, and to clarify the relationships between behavior and population growth.

Populations of mice confined to a set area with unlimited food and water do not multiply indefinitely. Usually a population reaches asymptote (cessation of growth) far below the numerical level that would exhaust the available space. Wide variations of the number of animals present at asymptote among populations confined under similar physical conditions indicates that the behavioral and physiological mechanisms regulating population growth are not directly related to the numerical level of the population, i.e., growth is not dependent on density per se. Table I lists several typical studies, indicating for each the areas used and the range in size at asymptote of the experimental populations.

Since the several populations of each study were maintained in identical conditions of the physical environment, the variation in final size (Table I) indicates that factors intrinsic to the populations were operating to bring about a cessation of growth without a
TABLE 1*

VARIABILITY OF POPULATION ASYMPTOTE WITHIN EXPERIMENTS

<table>
<thead>
<tr>
<th>Study</th>
<th>Animal</th>
<th>Enclosure Size</th>
<th>Number of Populations</th>
<th>Number of Animals at Asymptote</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown (1953)</td>
<td>Mus musculus</td>
<td>6' x 4'</td>
<td>4</td>
<td>3 - 19</td>
</tr>
<tr>
<td>Christian (1956)</td>
<td>&quot;</td>
<td>29&quot; x 75&quot; x 2 decks</td>
<td>4</td>
<td>21 - 130</td>
</tr>
<tr>
<td>Petrusewicz (1957)</td>
<td>&quot;</td>
<td>80 x 80 x 15 cm.</td>
<td>42</td>
<td>16 - 69</td>
</tr>
<tr>
<td>Southwick (1955a)</td>
<td>&quot;</td>
<td>6' x 25'</td>
<td>6</td>
<td>25 - 130</td>
</tr>
<tr>
<td>Clarke (1955)</td>
<td>Microtus agrestis</td>
<td>67 m²</td>
<td>2</td>
<td>41 - 58</td>
</tr>
<tr>
<td>Louch (1956)</td>
<td>Microtus pennsylvanicus</td>
<td>6' x 25'</td>
<td>3</td>
<td>28 - 67</td>
</tr>
<tr>
<td>Terman (1965)</td>
<td>Peromyscus maniculatus bairdii</td>
<td>20 ft²</td>
<td>8</td>
<td>6 - 47</td>
</tr>
</tbody>
</table>

* This summary of the above studies in table form taken from C.R. Terman (Pers. comm.).
consistent relationship to the number of animals present. Although the dynamics of each population seem to vary with the particular strain employed, the common factor producing the cessation of growth in each of these studies was the lack in production of adult animals, either because of a total absence of reproductive activity, or a failure of offspring to survive through infancy.

Several mechanisms have been proposed to account for this failure to add to the adult population. Christian (1963, 1965), reviewing a number of studies, presents considerable evidence that stress, brought about by social competition, activates the pituitary-adrenal-gonadal system in ways that decrease the natality rate and increase the mortality rate. Support for Christian's concept comes from a number of studies (cf. Christian 1963, 1965), demonstrating that populations approaching asymptote exhibit a progressive inhibition of reproductive activity. Diminished reproductive function in the female was apparent at one or all phases of reproductive activity: inhibition of estrus, reduced numbers of implanted ova, increased intra-uterine mortality, and increased infant mortality due to failure of lactation. Inhibition of male reproductive ability was reflected in the decreasing weights of the testes, seminal vesicles, and preputials.

Although increases in population density usually result in increased adrenocortical function, an important variable determining endocrine response appears to be the increased aggression accompanying population growth (Clarke, 1953; Southwick and Bland, 1959; Bronson and Eleftheriou, 1963). Other factors which have been reported to correlate positively with aggression are aberrant maternal behavior, cannibalism, abandonment of the young, and scattering, trampling, and
crushing of the litters. Although these behavioral variables can effectively limit population growth, they do not appear to be the result of any physiological adaptive mechanism responding to increased stress.

Petrusewicz (1963) suggests that the point at which a population will cease to grow is dependent upon the "ecological structure", based on social hierarchy and fights among males. He emphasizes behavioral mechanisms in population control:

"The simplest is the mechanism that abolishes survival of litters. It is released by noncompetitive fights among males, which become eminently numerous during peaks, i.e., during overcrowding...The increased number of fights among males triggers, as it were, a number of processes; fights between females, lack of care for the young (which are often seen outside the nest), trampling (and crushing) of litters, and frequently general cannibalism." (Petrusewicz, 1963, p. 119).

Southwick (1955a, 1955b) found poor litter survival to be the major controlling mechanism of his confined populations of wild house mice, with litter mortality reaching 100% as aggressive behavior approached one fight per hour per mouse. Louch (1956), working with meadow voles, noted that as asymptote was approached, abandonment and consumption of the young increased as did aggressive behavior. Brown (1953) also noted aberrant maternal behavior in his populations, which he attributed to a breakdown in the female's ability to defend her nest under conditions of increased crowding and unstable social hierarchies.

Brown (1953) and Southwick (1955b) have both pointed out that in an apparently well stabilized hierarchy of mice there is a relatively low level of fighting, but when shifts or disruptions in the social structure occur, as though the maturation of new individuals, an increase in fighting is observed. Aggressive interactions apparently function to determine and maintain a social hierarchy within the popu-
lation (Collias, 1944; Uhrich, 1938). Mice frequently display a "monoarchistic" type of social order in which one dominant male tends to inhibit aggression among all other subordinate males in a group (Scott and Fredericson, 1951). Uhrich (1938) notes that a linear type of social hierarchy, or "pecking order" is also common.

An hypothesis consistent with the above discussion is that aggression, resulting from social instability, may limit population growth either directly, by interfering with maternal behavior, or indirectly, being mediated by the activation of the pituitary-adrenal-gonadal system. There are, however, some observations which do not seem to support this hypothesis. Christian (1956, 1959) and Strecker and Emlen (1953) found no direct relationship between population asymptote and aggressive behavior.

These conflicting observations can be brought into line by postulating that stress is not a function of physical fighting per se, as much as of the perceived threat or danger in the situation (perceived threat being dependent upon past experience with aggressive encounters). Thiessen and Rodgers (1961) review and discuss some of the earlier studies on psychological stress and its relation to social rank, suggesting that social rank is an important factor in determining endocrine response. In a more recent study, Bronson and Eleftheriou (1965) have shown that mice which had previously experienced physical defeat by a fighter showed a much greater adrenal response to the fighter's presence (without direct physical contact) than did mice not having experienced defeat, which suggests that psychological stress may be an important mediator between aggression and physiological mechanisms limiting population growth.
In most fights the mice do not seem to fight over the possession of any object, and Scott and Fredericson (1951) have termed this "non-competitive fighting". The aggressive tendencies of mice may be influenced by genetic makeup (Ginsburg and Allee, 1942; Scott, 1942), hormonal balance (Beeman, 1947), infantile experience (Fredericson, 1951; Kahn, 1954), and learning in later life (Ginsburg and Allee, 1942; Uhrich, 1940). Individual mice may be conditioned to be less aggressive as a result of subjecting them to repeated defeats, or they can be made more aggressive as the result of continued victories over submissive mice. Both types of conditioning affect the ability of a given mouse to secure and maintain high social status (Ginsburg and Allee, 1942; Scott, 1944).

The above analysis leads to the following hypotheses: social structure, aggression, stress, and mechanisms limiting population growth are all dependent upon the relationships formed between dominant and subordinate individuals. These relationships can be studied systematically by varying the ratio of selected and trained aggressive males to selected and trained submissive males in a population, and observing the resultant social structure, level of aggression, and growth.

In order to test these hypotheses, three types of populations were assembled: one in which all the males were selected and trained for aggressiveness, another in which all the males were selected and trained for submissiveness, and another in which there was a single aggressive male with the other males selected and trained for submissiveness. These populations were observed daily for three months. At the end of this period the males were inspected for physiological signs of stress.
METHOD

SUBJECTS

Each population consisted of three male and three female mice, obtained from a colony established in 1964 with 20 pairs of C57BL/6j mice from the Roscoe B. Jackson Memorial Laboratory.

APPARATUS

The mice were raised, isolated, and trained in standard laboratory cages. Cage dimensions were 29 x 19 x 13 cms. The mice were then assembled into population boxes of transparent plastic. Each population box contained approximately 800 cm² of floor space. Food and water were superabundant at all times, with each cage equipped with a water bottle and food basket suspended from the ceiling. Commercial bedding material (Sani-Cel) was placed in all cages. Males were individually marked with a commercial depilatory (Neet). Females were individually ear punched.

PROCEDURE

Group 1. - Twenty-seven male mice were weaned at 21-29 days and isolated in individual cages for four weeks. The purpose of isolating the males during maturation was to prevent the formation of dominant-subordinate relationships that were not under the control of the experimenter. Isolation is also important to training in victory and defeat, as mice more readily fight after a period of isolation from
other mice (Ginsburg and Allee, 1942). Following isolation, selection and training procedures were initiated.

The mice were paired against each other in neutral cages, in a room separate from the one in which they were housed. Aggressiveness was judged by noting which males carried the attack to their opponent, the amount of time elapsed before an attack was initiated and the eventual resolution of the encounter. The more aggressive appearing animals were given additional fighter training. The more submissive males were subjected to a long series of defeats. This additional training in victory and defeat was done simultaneously by placing the more submissive mouse into the more aggressive mouse's home cage.

Selection and training continued for 7 weeks before it was possible to select 9 mice out of the group of 27 who could be counted on to attack as well as defeat most opponents. Also selected were 12 mice judged the most submissive of the 27 original males. With these nine aggressive and twelve submissive males, together with 21 females who had been housed in groups of three since weaning, 7 populations were assembled: two Type A populations consisting of three aggressive males and three females each, two Type S populations consisting of three submissive males and three females each, and three Type DS populations consisting of three females, one aggressive male and two submissive males each.

Group II. - Since Group I had yielded only enough aggressive and submissive animals for 7 populations, another group of 14 males, 39-44 days old, was isolated for 24 days. After isolation, Group II underwent the same selection and training procedures as had been given Group I, with the exception that the members of Group II were matched against
each other in the same room in which they were housed. Only 17 days of selection and training were required with this group to produce four aggressive and five submissive males, enough to assemble three additional populations: A-3, S-3, and DS-4. The females used in these last three populations differed from the females in the first 7 populations in that they had all been mated prior to assembly, and were proven in their fertility and their ability to care for their offspring.

A total of 10 populations were eventually assembled: three Type A populations, three Type S populations, and four Type DS populations. Observations were taken during the first two hours after assembly and were continued each day, one hour a day, for a period of three months. Records were kept on: aggressive activity occurring within the populations as determined by the number of fights and the number of days on which fighting was observed; type of dominance hierarchy formed and each individual's rank within the hierarchy as determined by the results of the aggressive encounters among the males; instability of the social structure as evidenced by the frequency of shifts in social status occurring among the male members of the populations; and natality and mortality rates dependent upon total number of litters born into a population, size of the litters, and number of litters to survive. Litters were recorded as 'surviving' if at least one pup remained alive 10 days after birth. Litters surviving for 10 days were removed from the populations to keep the number of adult mice in each group constant.

Upon termination of the three month period of observation, the spleen, thymus, heart, testes, and preputials of each male in the first 7 populations (Group 1) were removed and weighed.
RESULTS

BODY WEIGHTS OF AGGRESSIVE AND SUBMISSIVE MALES

Table 2 presents the body weights of the selected aggressive and submissive males from Group I. Mean weight on assembly was 25.32 gms for the aggressive males and 23.65 gms for the submissive males ($t = 5.28, p< .01, r_{pb} = .75$). Mean net gain in body weight from assembly to termination of the populations was greater for the selected aggressive males ($\bar{x} = 3.8$ gms) than for the submissive males ($\bar{x} = 1.36$ gms) ($t = 2.45, p< .05, r_{pb} = .45$).

Table 3 compares differences in weight gain according to type of population. Males in the two Type A populations gained the most weight with a mean net gain of 4.0 gms. Males in the two Type S populations actually lost weight, with a mean net gain of -.31 gms. The difference between the Type A and Type S populations is significant ($t = 2.79, p< .05, r_{pb} = .65$).

Body weights of the aggressive and submissive males in Group II (populations A-3, S-3, and DS-4) were given in Table 4. Mean weight on assembly was 21.88 gms for the selected aggressive males, and 20.98 gms for the selected submissive males. Although four of the five submissive males weighed less than the smallest aggressive male, the difference between means was not statistically significant.

Male A-3(1) was found dead 13 days after the population was assembled. His replacement was found dead two days later. The second replacement was not selected for his aggressiveness, so that net body
TABLE 2

BODY WEIGHTS (IN GRAMS) OF THE AGGRESSIVE AND SUBMISSIVE MALES

IN GROUP I ON ASSEMBLY AND TERMINATION OF THE POPULATIONS

Group 1: 101-109 days old on assembly

<table>
<thead>
<tr>
<th>Male</th>
<th>On Assembly</th>
<th>Terminal Weight</th>
<th>Net Gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-1(1)</td>
<td>25.0</td>
<td>29.5</td>
<td>4.5</td>
</tr>
<tr>
<td>A-1(2)</td>
<td>24.2</td>
<td>27.6</td>
<td>3.4</td>
</tr>
<tr>
<td>A-1(3)</td>
<td>24.8</td>
<td>26.0</td>
<td>1.2</td>
</tr>
<tr>
<td>A-2(1)</td>
<td>25.3</td>
<td>30.0</td>
<td>4.7</td>
</tr>
<tr>
<td>A-2(2)</td>
<td>25.5</td>
<td>31.3</td>
<td>6.0</td>
</tr>
<tr>
<td>A-2(3)</td>
<td>25.1</td>
<td>29.3</td>
<td>4.2</td>
</tr>
<tr>
<td>DS-1(1)</td>
<td>26.6</td>
<td>30.1</td>
<td>3.5</td>
</tr>
<tr>
<td>DS-2(1)</td>
<td>26.1</td>
<td>29.7</td>
<td>3.6</td>
</tr>
<tr>
<td>DS-3(1)</td>
<td>25.9</td>
<td>29.0</td>
<td>3.1</td>
</tr>
<tr>
<td>Mean</td>
<td>25.37</td>
<td>29.17</td>
<td>3.80</td>
</tr>
<tr>
<td>S.D.</td>
<td>.55</td>
<td>1.39</td>
<td>1.24</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Male</th>
<th>On Assembly</th>
<th>Terminal Weight</th>
<th>Net Gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>S-1(1)</td>
<td>23.2</td>
<td>26.2</td>
<td>3.0</td>
</tr>
<tr>
<td>S-1(2)</td>
<td>23.7</td>
<td>25.4</td>
<td>1.7</td>
</tr>
<tr>
<td>S-1(3)</td>
<td>23.4</td>
<td>19.6</td>
<td>-3.8</td>
</tr>
<tr>
<td>S-2(1)</td>
<td>25.1</td>
<td>26.0</td>
<td>.9</td>
</tr>
<tr>
<td>S-2(2)</td>
<td>24.1</td>
<td>18.7</td>
<td>-5.4</td>
</tr>
<tr>
<td>S-2(3)</td>
<td>24.1</td>
<td>25.8</td>
<td>1.7</td>
</tr>
<tr>
<td>DS-1(2)</td>
<td>25.4</td>
<td>27.6</td>
<td>2.2</td>
</tr>
<tr>
<td>DS-1(3)</td>
<td>24.5</td>
<td>27.6</td>
<td>3.1</td>
</tr>
<tr>
<td>DS-2(2)</td>
<td>23.2</td>
<td>26.4</td>
<td>4.6</td>
</tr>
<tr>
<td>DS-3(2)</td>
<td>23.2</td>
<td>25.5</td>
<td>4.6</td>
</tr>
<tr>
<td>DS-3(3)</td>
<td>23.4</td>
<td>24.2</td>
<td>.8</td>
</tr>
<tr>
<td>Mean</td>
<td>23.76</td>
<td>25.12</td>
<td>1.36</td>
</tr>
<tr>
<td>S.D.</td>
<td>.78</td>
<td>2.65</td>
<td>2.97</td>
</tr>
</tbody>
</table>

SIGNIFICANCE AND MAGNITUDE OF MEAN WEIGHT DIFFERENCES

BETWEEN AGGRESSIVE AND SUBMISSIVE MALES

<table>
<thead>
<tr>
<th></th>
<th>On Assembly</th>
<th>Terminal Weight</th>
<th>Net Gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>t ratio:</td>
<td>5.28</td>
<td>4.32</td>
<td>2.45</td>
</tr>
<tr>
<td>p value &lt;</td>
<td>.01</td>
<td>.01</td>
<td>.05</td>
</tr>
<tr>
<td>rpb =</td>
<td>.75</td>
<td>.70</td>
<td>.45</td>
</tr>
</tbody>
</table>
### TABLE 3

MEAN AND MEDIAN NET GAIN IN BODY WEIGHT AMONG THE MALES IN EACH OF THE FIRST 7 POPULATIONS

<table>
<thead>
<tr>
<th></th>
<th>Mean Weight on Assembly</th>
<th>Mean Wt. on Termination</th>
<th>Mean Net Gain</th>
<th>Median Net Gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-1</td>
<td>24.67</td>
<td>27.7</td>
<td>3.03</td>
<td>3.4</td>
</tr>
<tr>
<td>A-2</td>
<td>25.23</td>
<td>30.2</td>
<td>4.97</td>
<td>4.7</td>
</tr>
<tr>
<td><strong>Group Mean</strong></td>
<td><strong>24.95</strong></td>
<td><strong>28.95</strong></td>
<td><strong>4.0</strong></td>
<td><strong>4.05</strong></td>
</tr>
<tr>
<td>S-1</td>
<td>23.43</td>
<td>23.73</td>
<td>.3</td>
<td>1.7</td>
</tr>
<tr>
<td>S-2</td>
<td>24.43</td>
<td>23.50</td>
<td>- .93</td>
<td>.9</td>
</tr>
<tr>
<td><strong>Group Mean</strong></td>
<td><strong>23.93</strong></td>
<td><strong>23.62</strong></td>
<td><strong>- .31</strong></td>
<td><strong>1.3</strong></td>
</tr>
<tr>
<td>DS-1</td>
<td>25.5</td>
<td>28.43</td>
<td>2.93</td>
<td>3.1</td>
</tr>
<tr>
<td>DS-2</td>
<td>23.7</td>
<td>28.17</td>
<td>4.47</td>
<td>4.6</td>
</tr>
<tr>
<td>DS-3</td>
<td>24.17</td>
<td>26.23</td>
<td>2.06</td>
<td>2.3</td>
</tr>
<tr>
<td><strong>Group Mean</strong></td>
<td><strong>24.46</strong></td>
<td><strong>27.61</strong></td>
<td><strong>3.15</strong></td>
<td><strong>3.3</strong></td>
</tr>
</tbody>
</table>

SIGNIFICANCE AND MAGNITUDE OF MEAN WEIGHT DIFFERENCES BETWEEN TYPE A AND TYPE S POPULATIONS

\[ \text{t ratio} = 2.79 \]
\[ \text{p value} < 0.05 \]
\[ \text{rpb} = 0.65 \]
TABLE 4

BODY WEIGHTS (IN GRAMS) OF THE AGGRESSIVE AND SUBMISSIVE MALES
IN GROUP II ON ASSEMBLY AND TERMINATION OF THE POPULATIONS

Group II: 83-86 days old on assembly

<table>
<thead>
<tr>
<th>Male</th>
<th>On Assembly</th>
<th>Terminal Weight</th>
<th>Net Gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-3(1)</td>
<td>21.3</td>
<td>*</td>
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<tr>
<td>A-3(2)</td>
<td>21.8</td>
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<td>7.9</td>
</tr>
<tr>
<td>A-3(3)</td>
<td>21.3</td>
<td>27.7</td>
<td>6.4</td>
</tr>
<tr>
<td>DS-4(1)</td>
<td>23.1</td>
<td>26.1</td>
<td>3.0</td>
</tr>
</tbody>
</table>

Aggressive Males

Mean: 21.88  27.83  5.77
S.D.: .58  1.53  2.04

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<thead>
<tr>
<th>Male</th>
<th>On Assembly</th>
<th>Terminal Weight</th>
<th>Net Gain</th>
</tr>
</thead>
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<tr>
<td>S-3(1)</td>
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<td>21.2</td>
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<td>DS-4(3)</td>
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Submissive Males

Mean: 20.98  24.76  3.78
S.D.: 1.39  1.88  2.17

* Male A-3(1) found dead 13 days after the population was assembled.
weight gain for A-3(1) is not given in Table 4. Excluding A-3(1), the mean net gain from assembly to termination of the population for the selected aggressive males was 5.77 gms. Mean net gain for the selected submissive males was 3.78 gms.

AGGRESSION AND SOCIAL INSTABILITY

Table 5 gives the number of fights won, lost, and unresolved for each male in each of the 10 populations. Not shown in Table 5 are the deaths of two males in population A-3 that were attributed to the aggression of male A-3(2).

Table 6 is in part a summary of Table 5, comparing the three types of populations as to total number of fights and number of days on which fighting was observed to occur. The H-values were obtained from the Kruskal-Wallis one-way analysis of variance, testing for differences in aggression between the three types of populations. The population types differed significantly with respect to both the number of fights and the number of fighting days. Type A populations were by far the most aggressive, while Type S populations were the least aggressive.

Social instability, judged either by the percentage of fights lost by the dominant male, percentage of unresolved fights, or frequency of shifts in social status among the male members of the population, showed no relationship to either aggression or type of population.

The amount of fighting observed and the number of selected aggressive males in each population were positively related, with a Spearman rank correlation coefficient of .90 (p < .01).
### TABLE 5

**NUMBER OF FIGHTS WON, LOST, AND UNRESOLVED AMONG MALES IN EACH OF THE 10 POPULATIONS**

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<th>Population A-1</th>
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<th>11-20</th>
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<th>31-40</th>
<th>41-50</th>
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<th>61-70</th>
<th>71-80</th>
<th>81-90</th>
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(cont.)
TABLE 5 (cont.)

NUMBER OF FIGHTS WON, LOST, AND UNRESOLVED AMONG MALES IN EACH OF THE 10 POPULATIONS

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<th>21-30</th>
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Unresolved fights between

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</tbody>
</table>

Total Fights | 10    | 8     | 18    | 9     | 2     | 16    | 10    | 0     | 16    | 9     | 3     | 101   |
TABLE 5 (cont.)

NUMBER OF FIGHTS WON, LOST, AND UNRESOLVED AMONG MALES IN EACH OF THE 10 POPULATIONS

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</table>

Unresolved fights between 1 & 2  13
Unresolved fights between 1 & 3  11
Unresolved fights between 2 & 3  13

Total Fights  53  21  45  19  37  15  50  0  240
TABLE 5 (cont.)

NUMBER OF FIGHTS WON, LOST, AND UNRESOLVED AMONG MALES IN EACH OF THE 10 POPULATIONS

Population S-1

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Unresolved fights
between 1 & 2
1 & 3
2 & 3

0
1
0

Total Fights
0
1
4
0
2
0
0
0
0
0
0
0
7

19
TABLE 5 (cont.)

NUMBER OF FIGHTS WON, LOST, AND UNRESOLVED AMONG MALES IN EACH OF THE 10 POPULATIONS

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TABLE 5 (cont.)

NUMBER OF FIGHTS WON, LOST, AND UNRESOLVED AMONG MALES IN EACH OF THE 10 POPULATIONS

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TABLE 5 (cont.)

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NUMBER OF FIGHTS WON, LOST, AND UNRESOLVED AMONG MALES IN EACH OF THE 10 POPULATIONS

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<td></td>
<td></td>
<td></td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 defeats 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unresolved fights between</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 &amp; 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 &amp; 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 &amp; 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Fights</td>
<td>15</td>
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<td>15</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>42</td>
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</tbody>
</table>
TABLE 5 (cont.)

NUMBER OF FIGHTS WON, LOST, AND UNRESOLVED AMONG MALES IN EACH OF THE 10 POPULATIONS

<table>
<thead>
<tr>
<th>Days:</th>
<th>1</th>
<th>2-5</th>
<th>6-10</th>
<th>11-20</th>
<th>21-30</th>
<th>31-40</th>
<th>41-50</th>
<th>51-60</th>
<th>Total</th>
</tr>
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<tbody>
<tr>
<td>1 defeats 2</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
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<td>3</td>
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<td>1 defeats 3</td>
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<td>0</td>
</tr>
<tr>
<td>2 defeats 1</td>
<td></td>
<td></td>
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<td></td>
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<td>0</td>
</tr>
<tr>
<td>2 defeats 3</td>
<td></td>
<td></td>
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<td></td>
<td>0</td>
</tr>
<tr>
<td>3 defeats 1</td>
<td>2</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>3 defeats 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Unresolved fights</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>between 1 &amp; 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>1 &amp; 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>2 &amp; 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
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<tr>
<td>Total Fights</td>
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<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>12</td>
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</tbody>
</table>

Population DS-4
### TABLE 6

**SUMMARY OF OBSERVED AGGRESSIVE BEHAVIOR FOR EACH OF THE 10 POPULATIONS**

*WITH H-VALUES FROM THE KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE*

<table>
<thead>
<tr>
<th></th>
<th>A-1</th>
<th>A-2</th>
<th>A-3</th>
<th>S-1</th>
<th>S-2</th>
<th>S-3</th>
<th>DS-1</th>
<th>DS-2</th>
<th>DS-3</th>
<th>DS-4</th>
<th>H value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of fights:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>on assembly</td>
<td>20</td>
<td>10</td>
<td>53</td>
<td>0</td>
<td>14</td>
<td>0</td>
<td>9</td>
<td>28</td>
<td>15</td>
<td>5</td>
<td>3.61</td>
</tr>
<tr>
<td>days 2 - 30</td>
<td>87</td>
<td>37</td>
<td>122</td>
<td>7</td>
<td>3</td>
<td>0</td>
<td>12</td>
<td>13</td>
<td>15</td>
<td>7</td>
<td>7.65**</td>
</tr>
<tr>
<td>days 2 - 60</td>
<td>105</td>
<td>63</td>
<td>187</td>
<td>7</td>
<td>3</td>
<td>0</td>
<td>12</td>
<td>14</td>
<td>22</td>
<td>7</td>
<td>7.65**</td>
</tr>
<tr>
<td>days 2 - 90</td>
<td>110</td>
<td>91</td>
<td>-</td>
<td>7</td>
<td>3</td>
<td>-</td>
<td>12</td>
<td>14</td>
<td>27</td>
<td>-</td>
<td>5.36*</td>
</tr>
<tr>
<td>Number of days fighting observed:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>first 30 days</td>
<td>21</td>
<td>14</td>
<td>18</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>7</td>
<td>4</td>
<td>2</td>
<td>2</td>
<td>6.30*</td>
</tr>
<tr>
<td>first 60 days</td>
<td>30</td>
<td>20</td>
<td>27</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>7</td>
<td>5</td>
<td>4</td>
<td>2</td>
<td>7.02**</td>
</tr>
<tr>
<td>total 90 days</td>
<td>32</td>
<td>26</td>
<td>-</td>
<td>3</td>
<td>2</td>
<td>-</td>
<td>7</td>
<td>5</td>
<td>6</td>
<td>-</td>
<td>5.36*</td>
</tr>
</tbody>
</table>

* p<.05  
** p<.01
POPULATION GROWTH

Table 7 summarizes the data on infant natality and mortality over 90 days for each of the 10 populations. Not shown in Table 7 is the death of a pregnant female in population A-2, 37 days after assembly. An autopsy revealed 7 well developed fetuses. Another female was introduced to replace her.

Females in Type A populations took longer to deliver their first litters than the females in Type S and Type DS populations. Table 8 compares the females in each of the 10 populations with respect to the number of days after assembly before each female delivered her first litter. Females from populations S-1 and DS-3 were excluded from the comparison since only two of the three females in each of these populations ever bore litters. Comparing the group mean of Type A populations with the combined group means of Type S and Type DS populations, a significant difference is found ($t = 8.01, p < .001, r pb = .95$).

PHYSIOLOGICAL INDICANTS OF STRESS

Table 9 presents the weights of the spleen, thymus, preputials, testes, and heart for each male in each of the first 7 populations. Table 10 presents the organ weights relative to the initial body weight for each male. Table 11 presents the organ weights relative to the terminal body weight for each male.

The three types of populations differed significantly with respect to relative heart weight (using initial body weight). Type A males had the largest hearts, Type DS males had the smallest hearts (Kruskall-Wallis one-way analysis of variance, $H = 10.22, p < .01$). Relative weights of the spleen, thymus, preputials, and testes showed no
TABLE 7

INFANT NATALITY AND MORTALITY OVER 90 DAYS FOR EACH OF THE 10 POPULATIONS

<table>
<thead>
<tr>
<th></th>
<th>A-1</th>
<th>A-2</th>
<th>A-3</th>
<th>S-1</th>
<th>S-2</th>
<th>S-3</th>
<th>DS-1</th>
<th>DS-2</th>
<th>DS-3</th>
<th>DS-4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of surviving pups:</td>
<td>8</td>
<td>24</td>
<td>44</td>
<td>21</td>
<td>32</td>
<td>0</td>
<td>54</td>
<td>51</td>
<td>46</td>
<td>47</td>
</tr>
<tr>
<td>Number of surviving litters:</td>
<td>1</td>
<td>4</td>
<td>7</td>
<td>4</td>
<td>7</td>
<td>0</td>
<td>7</td>
<td>9</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>Number of litters failing to survive:</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Percent litter mortality:</td>
<td>83%</td>
<td>20%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
</tr>
</tbody>
</table>
TABLE 8

NUMBER OF DAYS AFTER ASSEMBLY BEFORE EACH FEMALE DELIVERED HER FIRST LITTER

<table>
<thead>
<tr>
<th>Female</th>
<th>Female</th>
<th>Female</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>A-1</td>
<td>25</td>
<td>29</td>
<td>65</td>
</tr>
<tr>
<td>A-2</td>
<td>24</td>
<td>37*</td>
<td>50</td>
</tr>
<tr>
<td>A-3</td>
<td>23</td>
<td>32</td>
<td>49</td>
</tr>
<tr>
<td>Group Mean</td>
<td>24.00</td>
<td>32.67</td>
<td>54.67</td>
</tr>
<tr>
<td>S-1</td>
<td>31</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td>S-2</td>
<td>20</td>
<td>25</td>
<td>31</td>
</tr>
<tr>
<td>S-3</td>
<td>21</td>
<td>24</td>
<td>30</td>
</tr>
<tr>
<td>Group Mean</td>
<td>20.50</td>
<td>24.50</td>
<td>30.50</td>
</tr>
<tr>
<td>DS-1</td>
<td>20</td>
<td>23</td>
<td>25</td>
</tr>
<tr>
<td>DS-2</td>
<td>20</td>
<td>24</td>
<td>29</td>
</tr>
<tr>
<td>DS-3</td>
<td>24</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>DS-4</td>
<td>21</td>
<td>23</td>
<td>32</td>
</tr>
<tr>
<td>Group Mean</td>
<td>20.30</td>
<td>23.30</td>
<td>28.67</td>
</tr>
</tbody>
</table>

Type A vs Types DS & S

| t ratio | 5.71 | 3.76 | 4.88 | 8.01 |
| p value | .01  | .01  | .01  | .001 |
| \( \gamma_{pb} \) | .90  | .80  | .85  | .95  |

* Pregnant female found dead 37 days after populations were assembled. Autopsy revealed 7 well developed fetuses.
** Only 2 of the 3 females bore litters during the total 90 days.
TABLE 9

BODY WEIGHT IN GRAMS AND ORGAN WEIGHT IN MILLIGRAMS

FOR EACH OF THE MALES IN THE FIRST 7 POPULATIONS

<table>
<thead>
<tr>
<th>Male</th>
<th>Initial Body Wt.</th>
<th>Terminal Body Wt.</th>
<th>Spleen</th>
<th>Thymus</th>
<th>Heart</th>
<th>Preputials</th>
<th>Testes</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-1(1)*</td>
<td>25.0</td>
<td>29.5</td>
<td>70.3</td>
<td>43.9</td>
<td>171.3</td>
<td>63.93</td>
<td>235.2</td>
</tr>
<tr>
<td>A-1(2)</td>
<td>24.2</td>
<td>27.6</td>
<td>135.5</td>
<td>35.2</td>
<td>147.2</td>
<td>45.97</td>
<td>127.4</td>
</tr>
<tr>
<td>A-1(3)</td>
<td>24.8</td>
<td>26.0</td>
<td>63.5</td>
<td>38.1</td>
<td>156.9</td>
<td>55.96</td>
<td>212.7</td>
</tr>
<tr>
<td>A-2(1)</td>
<td>25.3</td>
<td>30.0</td>
<td>77.1</td>
<td>49.9</td>
<td>152.5</td>
<td>73.90</td>
<td>222.2</td>
</tr>
<tr>
<td>A-2(2)</td>
<td>25.3</td>
<td>31.3</td>
<td>103.1</td>
<td>35.3</td>
<td>171.9</td>
<td>95.68</td>
<td>221.5</td>
</tr>
<tr>
<td>A-2(3)*</td>
<td>25.1</td>
<td>29.3</td>
<td>95.7</td>
<td>41.4</td>
<td>157.8</td>
<td>68.09</td>
<td>235.4</td>
</tr>
<tr>
<td>S-1(1)</td>
<td>23.2</td>
<td>26.2</td>
<td>67.1</td>
<td>35.4</td>
<td>139.9</td>
<td>50.24</td>
<td>90.9</td>
</tr>
<tr>
<td>S-1(2)</td>
<td>23.7</td>
<td>25.4</td>
<td>69.0</td>
<td>46.5</td>
<td>117.4</td>
<td>50.71</td>
<td>202.4</td>
</tr>
<tr>
<td>S-1(3)*</td>
<td>23.4</td>
<td>19.6</td>
<td>107.9</td>
<td>19.5</td>
<td>139.7</td>
<td>46.32</td>
<td>69.7</td>
</tr>
<tr>
<td>S-2(1)</td>
<td>25.1</td>
<td>26.0</td>
<td>59.2</td>
<td>39.7</td>
<td>163.4</td>
<td>47.12</td>
<td>223.6</td>
</tr>
<tr>
<td>S-2(2)*</td>
<td>24.1</td>
<td>18.7</td>
<td>109.6</td>
<td>7.6</td>
<td>151.9</td>
<td>22.80</td>
<td>226.2</td>
</tr>
<tr>
<td>S-2(3)</td>
<td>24.1</td>
<td>25.8</td>
<td>67.7</td>
<td>41.9</td>
<td>120.8</td>
<td>56.30</td>
<td>242.1</td>
</tr>
<tr>
<td>DS-1(1)*</td>
<td>26.6</td>
<td>30.1</td>
<td>94.0</td>
<td>43.3</td>
<td>141.4</td>
<td>52.74</td>
<td>226.1</td>
</tr>
<tr>
<td>DS-1(2)</td>
<td>25.4</td>
<td>27.6</td>
<td>63.7</td>
<td>35.0</td>
<td>113.3</td>
<td>63.04</td>
<td>67.6</td>
</tr>
<tr>
<td>DS-1(3)</td>
<td>24.5</td>
<td>27.6</td>
<td>68.2</td>
<td>42.0</td>
<td>131.9</td>
<td>57.27</td>
<td>252.6</td>
</tr>
<tr>
<td>DS-2(1)*</td>
<td>26.1</td>
<td>29.7</td>
<td>125.9</td>
<td>20.7</td>
<td>149.8</td>
<td>61.22</td>
<td>238.1</td>
</tr>
<tr>
<td>DS-2(2)</td>
<td>23.2</td>
<td>28.4</td>
<td>90.6</td>
<td>31.8</td>
<td>133.1</td>
<td>38.33</td>
<td>78.2</td>
</tr>
<tr>
<td>DS-2(3)</td>
<td>21.8</td>
<td>26.4</td>
<td>85.0</td>
<td>26.2</td>
<td>121.1</td>
<td>50.86</td>
<td>161.4</td>
</tr>
<tr>
<td>DS-3(1)*</td>
<td>25.9</td>
<td>29.0</td>
<td>83.2</td>
<td>39.9</td>
<td>148.2</td>
<td>59.77</td>
<td>251.9</td>
</tr>
<tr>
<td>DS-3(2)</td>
<td>23.2</td>
<td>25.5</td>
<td>54.0</td>
<td>37.3</td>
<td>133.4</td>
<td>80.74</td>
<td>223.5</td>
</tr>
<tr>
<td>DS-3(3)</td>
<td>23.4</td>
<td>24.2</td>
<td>48.2</td>
<td>33.7</td>
<td>123.8</td>
<td>62.51</td>
<td>194.6</td>
</tr>
</tbody>
</table>

* Male winning the greatest percentage of fights in his population.
### TABLE 10

**ORGAN WEIGHTS IN PERCENT INITIAL BODY WEIGHT FOR EACH OF THE MALES IN THE FIRST 7 POPULATIONS**

<table>
<thead>
<tr>
<th>Male</th>
<th>Spleen</th>
<th>Thymus</th>
<th>Testes</th>
<th>Heart</th>
<th>Preputials</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-1(1)*</td>
<td>.281</td>
<td>.176</td>
<td>.940</td>
<td>.685</td>
<td>.256</td>
</tr>
<tr>
<td>A-1(2)</td>
<td>.560</td>
<td>.146</td>
<td>.526</td>
<td>.608</td>
<td>.190</td>
</tr>
<tr>
<td>A-1(3)</td>
<td>.256</td>
<td>.154</td>
<td>.858</td>
<td>.633</td>
<td>.226</td>
</tr>
<tr>
<td>A-2(1)</td>
<td>.305</td>
<td>.197</td>
<td>.878</td>
<td>.603</td>
<td>.292</td>
</tr>
<tr>
<td>A-2(2)</td>
<td>.408</td>
<td>.140</td>
<td>.875</td>
<td>.679</td>
<td>.378</td>
</tr>
<tr>
<td>A-2(3)*</td>
<td>.381</td>
<td>.165</td>
<td>.938</td>
<td>.629</td>
<td>.271</td>
</tr>
<tr>
<td>S-1(1)</td>
<td>.289</td>
<td>.153</td>
<td>.392</td>
<td>.603</td>
<td>.217</td>
</tr>
<tr>
<td>S-1(2)</td>
<td>.291</td>
<td>.196</td>
<td>.854</td>
<td>.495</td>
<td>.214</td>
</tr>
<tr>
<td>S-1(3)*</td>
<td>.461</td>
<td>.083</td>
<td>.298</td>
<td>.597</td>
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<td>.891</td>
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<td>DS-1(3)</td>
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<td>1.031</td>
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<td>.079</td>
<td>.912</td>
<td>.574</td>
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<td>DS-3(1)*</td>
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<td>.154</td>
<td>.973</td>
<td>.572</td>
<td>.231</td>
</tr>
<tr>
<td>DS-3(2)</td>
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<td>.161</td>
<td>.963</td>
<td>.575</td>
<td>.348</td>
</tr>
<tr>
<td>DS-3(3)</td>
<td>.206</td>
<td>.144</td>
<td>.798</td>
<td>.529</td>
<td>.267</td>
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</tbody>
</table>

* Male winning the greatest percentage of fights in his population.
**TABLE II**

**ORGAN WEIGHTS IN PERCENT TERMINAL BODY WEIGHT FOR EACH OF THE MALES IN THE FIRST 7 POPULATIONS**

<table>
<thead>
<tr>
<th>Male</th>
<th>Spleen</th>
<th>Thymus</th>
<th>Testes</th>
<th>Heart</th>
<th>Preputials</th>
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<tr>
<td>A-1(1)*</td>
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<td>.797</td>
<td>.581</td>
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<td>DS-2(2)</td>
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<td>.869</td>
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<td>.199</td>
<td>.139</td>
<td>.804</td>
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</table>

* Male winning the greatest percentage of fights in his population.
relationship to either type of population or social rank. Thymus weight, relative to initial body weight, correlated positively with net body weight gain (Pearson $r = .58$, $p < .05$).
DISCUSSION

SELECTION AND TRAINING

Differences between Group I and Group II in length of time necessary to select and train aggressive and submissive males can be attributed to differences in environmental conditions under which selection and training took place. Members of Group I were paired against each other in a room separate from the one in which they were housed; these two rooms differed with respect to sounds, odors, and light intensity. Members of Group II were matched against each other in the same room in which they were housed. The possibility that unfamiliar stimuli may inhibit aggression has received some support from past research on territoriality and the influence of the home cage on fighting behavior. Uhrich (1938) reported that mice left in their home cage were likely to have more success in fighting than mice who were removed from their home cage. Petrusewicz (1959) reported that mice were more aggressive if left in their home cage or in the presence of their own population than if either were deprived them. Philbrook (1964) found that a period of habituation facilitated fighter training in a strange cage.

BODY WEIGHTS OF AGGRESSIVE AND SUBMISSIVE MALES

Males selected and trained for aggressiveness were found to weigh more on the average than males selected and trained for submissiveness. The aggressive males also tended to gain more weight while in the pop-
ulations than did the submissive males, even though more fighting occurred in the populations housing the aggressive males. Davis and Christian (1957), investigating the relationships between body weight, adrenal weight, and social rank in 18 groups of 6 male mice each, reported that all but the top ranking mouse averaged a weight loss during the 10 day period of grouping. They also reported increased adrenal weights with decreasing social rank, and suggested that low ranking mice are subjected to more physical and psychological stressing stimuli. This suggestion would account for the weight differences between the aggressive and submissive males obtained after the training procedures, which involved subjecting the selected submissive males to a series of defeats by the aggressive males. However, finding that the aggressive males gained more weight in the Type A populations than the submissive males did in the Type S populations suggests that weight loss is not necessarily the consequence of physical stressing stimuli, except in the case where an animal has been severely injured.

If differential weight gain is then the result of psychological stress, this would mean that the males in Type S populations were psychologically more stressed than the males in Type A populations, despite the greater fighting exhibited by the Type A populations. Greater psychological stress among the male members of Type S populations could result from inherent factors which influence both an animal's aggressive behavior and his susceptibility to stressful stimuli, or individuals may tend to be more submissive because they are more susceptible to stressful stimuli. This would suggest that differential stress responses between the dominant and submissive members of a group (cf. Davis and Christian, 1957) are not so much a function of social status
as they are of inherent differences in susceptibility to stress. An alternate explanation to account for these weight differences is that the naturally aggressive males may be predisposed to greater body weights through factors independent of physical and psychological stress.

AGGRESSION AND SOCIAL INSTABILITY

The present study shows that aggression can be varied independently of population size by varying the number of aggressive to submissive males within a population. Populations of Type A, assembled with three selected aggressive males, were more aggressive than populations of Type DS, which were composed of only one selected aggressive male and two submissive males. In turn, Type DS populations were more aggressive than Type S populations, which were assembled with only submissive males.

Perhaps it is misleading to call Type A populations "aggressive populations", since in each of the three Type A populations a single dominant male was involved in 88-96% of the total observed fights, the great majority being initiated by him. This poses an interesting problem. The greater the number of selected aggressive males in these populations, the greater the resultant level of aggression. However, fights are initiated almost exclusively by a single dominant male. In populations DS-1 and DS-3 a similar situation is present, with the selected aggressive male assuming dominance and initiating almost every fight. In spite of the similarities between the dominant males in the three Type A populations and the dominant males in the two DS popula-
tions, a far greater number of fights occur in the three Type A populations.

One possible explanation for this difference in observed number of fights is to attribute greater aggression to greater social instability in the Type A populations. In DS-1 and DS-3 the selected aggressive male assumed exclusive dominance over the selected submissive males within two hours after the populations were assembled. Neither dominant male was ever defeated during the life of the population, and there were only three to five fights involving the dominant male in which the outcome was inconclusive. In Type A populations dominance was not so easily achieved. None of the eventually dominant males were able to assume exclusive dominance until at least the second day after assembly. On the first day of assembly the eventually dominant male in A-1 was beaten twice, and involved in seven inconclusive fights with the other selected aggressive males. In population A-2 the dominant male was beaten once, and involved in five inconclusive fights on the first day. On the first day A-3 was assembled there were 37 inconclusive fights among the three selected aggressive males. The eventually dominant male in population A-3 did not assume dominance until the 6th day after the population was assembled.

An hypothesis that early social instability eventuates in a more aggressive dominant male would account for the differences in aggressiveness between the dominant males in populations DS-1 and DS-3 and the dominant males in Type A populations, but it would not explain the failure of the more unstable DS-2 and DS-4 populations to exhibit a greater number of fights than populations DS-1 and DS-3 (Tables 4 & 5).
Another hypothesis that may account for the greater aggressiveness of the dominant males in Type A populations is that there is simply a greater likelihood of there being an inherently more aggressive male in a population assembled with three selected aggressive males, than in a population assembled with only one selected aggressive male. The third possibility is a combination of the first two hypotheses; social instability leads to greater aggression only if there is an inherently aggressive male in the hierarchy to begin with.

The hypothesis that aggression is dependent upon the number of inherently aggressive males within the population could explain past findings that although aggression tends to increase as population size increases, the effect is not consistent, and may reflect the fact that the greater the number of animals within a population, the greater the probability that it will contain inherently aggressive males.

**POPULATION GROWTH**

The only behavioral mechanism observed to limit population growth directly was cannibalism. This was not related to either the Type of population or the amount of aggression exhibited by a population. Populations A-1 and S-3, one of the most aggressive populations and the least aggressive population, were effectively at asymptote during the first 60 days after assembly, with 100% litter mortality due to cannibalism in both populations. The only litter to survive in A-1 was born 69 days after assembly, two days after the suspected female cannibal was removed from the population and replaced by another female. Male S-3(2) was also observed eating live, new-born pups. However, replacing this cannibal
could not be accomplished without disrupting the social relationships already established among the males in population S-3. The only other population in which a litter failed to survive was population A-2. A litter born 73 days after the population was assembled survived for three days, then vanished without a trace on the fourth day. The destruction of a complete litter in such short time suggests that it was cannibalized.

If cannibalism had occurred only in the more aggressive populations, then the hypotheses of Louch, Petrusewicz, and Brown, would have received some support. Petrusewicz (1963) hypothesized that non-competitive fighting among the males will trigger general cannibalism. Louch (1956) reported a positive relationship between aggression and the consumption of new-born, and Brown (1953) suggests that cannibalism may occur if nest destruction, fights, and physical harassment in general interfere with maternal behavior. However, the fact that cannibalism occurred in population S-3, the least aggressive of the 10 populations, suggests that either there is no relationship between aggression and cannibalism, or that other factors in addition to aggression lead to cannibalism.

To determine if cannibalism would occur in the absence of stimuli intrinsic to the population, the female cannibal was removed from population A-1 while pregnant and placed in isolation. After delivering her litter she promptly cannibalized it. She was kept in isolation another three weeks. A male was then introduced to her cage until she became pregnant, then removed. Seven weeks after having been isolated from population A-1 she delivered her second litter, and again consumed
all the young, leaving little doubt that factors other than social strife are important in eliciting this cannibalism. Possible causes of cannibalism such as protein deficiency, low temperatures, and parasites, do not appear to be relevant factors in the present study. The mice were fed standard lab chow (Purina), temperatures ranged from 70 to 75, and animals from outside the colony were never permitted contact with the populations.

Perhaps the increased incidence of cannibalism that is observed to take place as population size increases reflects the increased likelihood that randomly occurring numbers of individuals with inherent tendencies toward cannibalism will be present.

Another factor which limited growth potential in two of the populations was the presence of nonproductive females. In populations S-1 and DS-3, only two of the three females in each population ever bore litters during the 90 days observations were taken. However, failure to control this aspect of the experiment adequately makes it difficult to interpret these results, or the data on natality and mortality presented in Table 7. The females placed in populations A-1, A-2, S-1, S-2, DS-1, DS-2, DS-3, were untested for their fertility and their ability to care for their litters successfully. Without knowledge of the female's reproductive performance prior to her introduction to a population, an accurate judgement cannot be made as to the effects of the population on her later reproductive performance.

Evidence was found that aggression will suppress reproductive activity at least temporarily. The females in the Type A populations took, on the average, 12 days longer to deliver their first litters
than the females in Type S and DS populations. These temporary effects on mature females may result in more permanent effects on immature females. Terman (1965) working with populations of prairie deermice reports that of the 31 females used to found 8 free growing populations, 38% became pregnant in the populations. In contrast, of the 49 females born into the populations and living a minimum of 90 days only three, or 6.1% produced young. Christian (1965) also presents evidence for the greater selection effects of stress on the young and submissive animals in producing inhibition of maturation, diminished fertility, increased intra-uterine mortality, and developmental abnormalities.

PHYSIOLOGICAL INDICANTS OF STRESS

Failure to obtain any meaningful correlations between the behavioral observations of aggression, social rank, or type of population, and organ weights assumed to reflect physiological responses to stress, suggests that the weights of the spleen, thymus, testes, and preputials are not sensitive and/or reliable measures of differential stress assumed to result from differences in aggression, social rank, or groupings employed in this study. The adrenals of the males in this study were not weighed because too many were crushed or broken during cleaning.

SUMMARY

In summary, the present study has demonstrated that it is possible to examine systematically the relationships between social behavior and mechanisms limiting population growth by assembling populations of pre-determined composition. In contrast to the typical method of observing
free growing populations of mice, the major advantage of the present design is that it allows the experimenter to manipulate such variables as the size of the population, age groupings within the populations, ratio of males to females, ratio of aggressive to submissive animals, and the effects of various kinds of early experiences that may be relevant to population asymptotes.

While it is obvious that the present study did not begin to take advantage of all the potentials inherent in the basic design, nor achieve all its stated goals, there were four results worth mentioning again:

1. Within the ranges investigated by this study, the level of aggression exhibited by a population was a positive function of the number of selected aggressive males within the population, not the result of social instability per se.

2. Females in the aggressive populations took significantly longer to become pregnant than females in the less aggressive populations, which lends support to the concept that aggression, mediated by physiological mechanisms, can suppress reproductive functions.

3. Submissive males grouped together gained less weight than aggressive males grouped together, suggesting inherent individual differences.

4. Cannibalism, in this study, could not be accounted for on the basis of aggression alone.
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Petrusewicz, K. Further investigation of the influence exerted by the presence of their home cages and own populations on the results of fights among male mice. Bulletin de l'Academie Polonaise des Sciences, 1959, 8, 319-322.


VITA

Robert Walter Zemore was born in Flint, Michigan, on April 30, 1938. He graduated from the University of Michigan, Flint College in 1961. From 1965 to 1967 he was a graduate student in the Psychology Department at the College of William and Mary.