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The Effect of Population Density on the Development of an Androgenmediated Marking Response of Meriones Unguiculatus

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THE EFFECT OF POPULATION DENSITY ON THE DEVELOPMENT
OF AN ANDROGEN-MEDIATED MARKING RESPONSE OF
MERIONES UNGUICULATUS

John Patrick Bell

A Thesis Submitted to the Faculty of the Graduate School
of Loyola University in Partial Fulfillment of
the Requirements for the Degree of
Master of Arts

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1973
ACKNOWLEDGEMENT

The author wishes to express his appreciation and gratitude to Dr. Richard A. Maier and Dr. Homer H. Johnson who served on his thesis committee. Special thanks go to Charlene T. Bell for providing technical assistance during the research and for typing the several drafts of the manuscript. A debt of gratitude is expressed to Dr. Eugene Zechmeister, Mr. Ronald Szoc, and Mr. Greg Ozog for their assistance with data analysis.
VITA

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He is a member of the American Association for the Advancement of Science, Animal Behavior Society, and the Midwestern Psychological Association.
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ABSTRACT

The hypothesis that population density suppresses the secretion of gonadotropic hormones in developing Mongolian gerbils was investigated using gland pad parameters and the marking frequency as dependent variables. There were obvious differences in the marking frequencies of isolated and grouped gerbils, but these differences were not reflected in between group comparisons of gland pad parameters. A third group of animals, which were first grouped and then isolated, showed a significant increase in marking frequency and in gland pad width, but not gland pad length. Since both variables are known to be androgen-mediated, it is suggested that the repeated measures design is more sensitive to changes because of the reduction of within-subject error variance compared to the randomized groups design.
Introduction

Observers of rodent behavior have noted that population density can exert an inhibiting effect upon reproduction and development (Parkes and Bruce, 1961). It has been suggested that the retardation of development was caused by a failure of the animal's system to secrete the necessary amounts of hormones (Christian, Lloyd, and Davis, 1965). Although behavioral evidence of reproductive retardation has been suggested by many studies of rodents (Archer, 1970), physiological data directly supporting this hypothesis have been difficult to obtain because of the small amounts of hormones that must be assayed. The low androgen titer is generally inferred from the presence of high ACTH titer and increased adrenal size, since testosterone is antagonistic to these parameters. The androgen-mediated marking response of the Mongolian gerbil provides us with a convenient physiological and behavioral measure of hormonal level for investigating the Christian, Lloyd, and Davis hypothesis.

Thiessen (1968) suggested that territorial marking, aggression, and mating behavior in the male Mongolian gerbil formed a sex-specific behavioral complex which was possibly modulated by the androgen titer of the animal. Evidence supporting this
statement has accumulated since that time. Lindzey, Thiessen, and Tucker (1968) found that the marking behavior develops rapidly with the onset of puberty, and that this marking behavior as well as the gland pad integrity was found to be androgen dependent in the male (Thiessen, Friend, and Lindzey, 1968); the marking level of castrates fell off until it matched the levels of females (Thiessen and Lindzey, 1970). This observation supports Komisaruk's (1970) suggestion that the same circuits serve the behavior in both sexes, but the appearance of high androgen titers at puberty begin to increase the functionality of those neural circuits responsible for sex-specific behaviors.

Thiessen and Yahr (1970) found that the marking behavior could be elicited by chemical implantation of the testosterone propionate into the preoptic area of the gerbil, while Baran and Glickman (1970) found that olfactory ablation virtually eliminated the marking behavior in males. Murphy and his colleagues have found that olfactory ablations eliminate both mating (Murphy and Schneider, 1970) and territorial defense (Murphy, 1970) in the golden hamster, while Singer (1968) found that the medial preoptic area is necessary for mating behavior in the male rat. Bunnel, Sodetz, and Shalloway, (1970)
found that the amygdala is necessary for aggressive behavior in the hamster, but there has been no comparable work done on the gerbil at this time. The interesting thing about these studies is that Stumpf (1970 a and b) has presented evidence that these various regions mediating sex, aggression, and marking behavior are joined together into circuits which are highly responsive to estrogen and testosterone. Thus, there seems to be a neural-hormonal circuitry in the brain of rodents for the organization of these three types of behavior which can be modulated by the type of hormone which is present.

Several authors (Baran & Glickman, 1970; Blum, 1970; Thiessen & Yahr, 1970) have found evidence that the primary target tissue of the androgen is in the central nervous system. Baran and Glickman found that animals with gland pad excisions did continue to mark. In a recent paper, Blum and Thiessen (1970) reported upon a detailed study of the gland in marking behavior, and concluded that the "marking behavior is not regulated by some aspect of the gland". Thiessen and Yahr (1970) reported that hypothalamic implantations and intraventricular injections of testosterone propionate caused a marked increase in the frequency of marking. Blum (1970) found that marking frequency varied as a function of the androgen titer of the
animal. This evidence suggests that the androgen acts on the central nervous target tissue and in doing so controls the frequency of marking. Hence, we would expect that the animal with a higher androgen titer would mark more often, defend his territory more often, and mate more often, than an animal with a lower androgen titer. Blum's data further reveals that androgens modulate marking in a continuous rather than an all-or-none fashion and suggests the possibility that a dominance hierarchy could be organized along this physiological measure.

Thiessen (1968; Thiessen and Lindzey, 1970) has provided evidence that the effect of testosterone also included a significant increase in the gland secretion. Arluk (1970) performed a series of bioassays on the gland pad and found that testosterone was most effective in stimulating it. Next most effective were the female hormones estrogen and diethylstilbestrol. The sebum composition of glands stimulated by both testosterone and estrogen was identical suggesting that the role of these hormones is to trigger the stimulation of lipogenesis in the sebaceous cells of the ventral gland. Hence, testosterone is capable of acting both as a frequency and an amplitude modulator which interacts to increase the redundancy of the territorial claims and thus maintains stability within
populations of Mongolian gerbils. In this respect, Blum (1970) reported a low correlation between gland area and marking frequency, and his data suggested a logarithmic relationship between the gland pad and androgen titer.

If the ventral gland and marking behavior actually serve a territorial function, it would be expected that the presence of the sebum would inhibit other gerbils' entry into the territory. Thiessen, Blum, and Lindzey, (1970) found that male scores (marking, sniffing, urination, defecation, and activity) "tended to be lower on a previously contaminated field", but could not demonstrate clear cut differences. Nyby, Thiessen, and Wallace (1970) found that animals which had been exposed to defeat at the hands of the residents decreased their marking to about 25% of control males while in the resident's territory. These authors conclude that gerbils defend their territorial claims primarily by "olfactory intimidation". Hence, a defeated animal discontinues territorial behavior in the presence of olfactory cues from all animals that are associated with his past defeat. Unfortunately, these authors do not elaborate further on the nature of these olfactory cues.

In an earlier study (Bell and Maier, 1972), it was found that crowding of immature gerbils suppressed marking behavior
after maturity but that the marking behavior appeared with subsequent isolation of the animals. The present study was designed to retest the earlier hypothesis and to investigate the possibility that gland pad size would show correlated changes with marking behavior.

**Method**

**Subjects.** The subjects were twenty-eight male Mongolian gerbils obtained from Tumblebrook Farms at one month of age. The animals were divided into four groups upon their arrival at the laboratory and maintained as described below with only minimal handling until testing began at one hundred and fifty days of age. The members of group IC (N=7) were assigned to individual polypropylene cages (14" x 9", or 19" x 6") with metal grid covers. Group GC (N=8) were housed in a 3' x 3' stainless steel pen. During the first half of the experiment, group GI (N=13) was housed in a 2' x 3' wood and glass pen; during the second half of the experiment, they were individually housed in polypropylene cages as described for the isolated condition (see above). Fresh bedding was placed in all living conditions at the beginning of each block of trials, so that fresh bedding changes in the two control groups corresponded to housing changes in the grouped-isolated condition. All
Figure 1. a, top view of the Blum testing apparatus showing marking pegs larger than scale. b, front panel of testing apparatus showing location of plexiglass window.
animals were maintained in the same room in which testing took place, and all animals had ad libitum water and guinea pig chow. The animals were maintained on a 13L:11D reversed photoperiod with a temperature range of 68° - 72° Fahrenheit.

**Apparatus.** Testing for marking scores was done using a modified version of Blum’s testing apparatus (Blum, 1970; Blum and Thiessen, 1970). The basic testing apparatus was 2' x 2' black wooden box with 1' walls and covered by a stainless steel grid. The floor and the walls (to a height of 4") were covered by black ContactR paper to facilitate cleaning. A small clear plexiglass window, measuring 6" x 3" was set in the center of the front wall of the apparatus (see Figure 1a) for purposes of observation. On the floor of the apparatus were six white plexiglass pegs measuring 1" x 0.5" x 0.25". The surface of the pegs had been roughened in order to increase tactile stimulation (see Figure 1b). A single white 15-watt lightbulb was affixed two feet above the surface of the apparatus.

**Gland Pad Measurements.** Measurements were made on two gland pad parameters, length and width, three times during the course of the experiment. The first measurement was taken on the evening prior to the first block of trials; a second measurement was taken on the evening of the final trial of the second
block of trials.

Prior to taking the first measurement, the ventral gland area of the animals was shaved with surgical clippers, and this procedure was repeated as needed on the other occasions. The animals were also shaved in spots as part of the recognition system. During the actual measurement, the experimenter held the animal in a supine position while the assistant measured the length and width of the gland pad with a transparent millimeter ruler.

**Testing Procedure.** Trials for marking frequency were given every other day, and administered in two blocks of six trials. The first block corresponded to the grouped-isolated condition. All animals were tested individually in the Blum apparatus and testing took place during the middle of the dark period (i.e., late afternoon). Testing sessions were conducted in the same room in which all animals were housed.

Animals in the isolated control condition were brought to the testing apparatus in their individual cages, while animals in the grouped control condition were placed together in a single 14" x 9" polypropylene cage and brought to the testing apparatus as a group. The transportation of the grouped-isolated condition animals corresponded to the related control
group.

On any given trial, the experimenter placed the animal in the center of the testing apparatus and simultaneously started a stopwatch. The animal was observed for a five-minute period and the frequency of marking recorded. A score was recorded each time that an animal rubbed its abdomen against a plexiglass peg. Marking behavior directed to the floor or the walls was ignored. At the conclusion of a trial, the animal was removed from the testing apparatus and replaced in its home cage. Prior to the first trial of each day, and after each trial, the testing box surface and plexiglass pegs were cleaned with a 15% solution of Pinesol® in water. The apparatus was dried before the next trial.

**Design.** A multiple time series design (Campbell & Stanley, 1966) composed of a treatment group and two control groups was used:

<table>
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<tr>
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<th>M₁</th>
<th>M₂</th>
<th>M₃</th>
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<tr>
<td>IC</td>
<td>0₁ 0₂ 0₃ 0₄ 0₅ 0₆</td>
<td>0₇ 0₈ 0₉ 0₁₀ 0₁₁ 0₁₂</td>
<td></td>
</tr>
<tr>
<td>GI</td>
<td>0₁ 0₂ 0₃ 0₄ 0₅ 0₆</td>
<td>X 0₇ 0₈ 0₉ 0₁₀ 0₁₁ 0₁₂</td>
<td></td>
</tr>
<tr>
<td>GC</td>
<td>0₁ 0₂ 0₃ 0₄ 0₅ 0₆</td>
<td>0₇ 0₈ 0₉ 0₁₀ 0₁₁ 0₁₂</td>
<td></td>
</tr>
</tbody>
</table>

where the left-hand column corresponds to the conditions;
Figure 2. The mean marking scores of the three groups over both blocks of trials.
$M_1, M_2, \text{ and } M_3$ correspond to the time at which gland pad measurements occurred; $O_1 - O_6$ and $O_7 - O_{12}$ correspond to the two blocks of marking trials and $X$ corresponds to the isolation of the previously grouped animals in the grouped-isolated condition.

Results

Figure 2 describes the mean marking scores of the three groups over both blocks of trials. It is apparent from visual inspection of the data that a large difference exists between the grouped and isolated control conditions. No statistical analysis was made since the means of the grouped control were due to the activity of only two animals. The mean marking scores on the post-isolation trials of the "grouped-isolated" condition were analyzed by a subjects X trials analysis of variance and found to be significant ($F=10.39$, df=5 and 60, $p<.005$). Trend analysis indicated both significant linear ($F=39.97$, df=1 and 60, $p<.005$) and quadratic ($F=8.21$, df=1 and 60, $p<.025$) trends in the data.

t-tests were used to analyze the data for possible differences in gland pad width ($t=1.91$, df=13, $p<.05$) and length ($t<1$, df=13, p=NS) but only an initial difference in width was significant with a 1-tailed test. Subjects X trials analysis of variance failed to reveal any within group differences over
Figure 3. Changes in mean gland pad length of the three groups during the study.
Figure 4. Changes in mean gland pad width of the three groups during the study.
time for the group GC's length (F=1.00, df=2 and 12, NS) and width (F=1.50, df=2 and 12, NS). The same type of analysis failed to detect significant differences in width (F=1.15, df=2 and 12, NS) and in length (F=3.74, df=2 and 12, NS) for Group IC (Figure 3).

Figure 4 indicates that the widths for the two groups had converged by the second measurement and were identical on the third measurement. A subject X trials analysis of variance on gland pad parameters demonstrated a significant increase in width (F=12.36, df=2 and 24, p < .001) but not in length (F=12.36, df=2 and 24, NS) for the grouped-isolated condition. Orthogonal analysis of the width data indicated that the significant increase occurred following the isolated block of trials (F=22.07, df=1 and 24, p < .001). A comparison of the grouped-isolated condition with the grouped-control using a t-test demonstrated a significant difference in gland width on the third measurement (t=5.33, df=18, p < .001).

The binomial test was applied in determining the probability associated with the number of animals marking in the grouped condition. In determining this probability, the number of marking animals in the grouped control and the number of animals marking in the grouped phase of the grouped-isolated
conditions were combined to give an N=2l. The number of animals marking on one or more trials was six, and had an associated p=.039; the number of animals marking on two or more trials was four and had an associated p=.004.

A series of correlation coefficients were computed for the isolated condition pad parameters and marking score on the trial most closely related to the measurement. The values for the three successive correlation coefficients are shown in Table 1. Table 2 presents correlation coefficients between gland pad width and length for all groups at all three measurement points.

Discussion

The present study was undertaken in order to test two hypotheses related to the effect of population density on the frequency of ventral marking behavior. The data clearly supported the hypothesis that density or crowding resulted in a suppression of marking. The difference between groups IC and GC on marking were obvious (Figure 1), although statistical significance could not be tested. Likewise, a significant increase in marking behavior followed the isolation of the animals in group GI. Finally, an analysis of the number of animals marking under crowded conditions revealed significant suppression of marking using the binomial test of probability.
Table 1

PEARSON PRODUCT-MOMENT CORRELATIONS BETWEEN MARKING FREQUENCY AND GLAND PAD PARAMETERS FOR ISOLATED CONTROL GROUP

<table>
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<tr>
<td>$r_{m \cdot l}$</td>
<td>-0.19</td>
<td>0.06</td>
<td>0.19</td>
</tr>
<tr>
<td>$r_{m \cdot w}$</td>
<td>-0.26</td>
<td>-0.27</td>
<td>-0.21</td>
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Table 2

PEARSON PRODUCT-MOMENT CORRELATIONS BETWEEN GLAND PAD LENGTH AND WIDTH FOR ALL GROUPS

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<th>M2</th>
<th>M3</th>
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<tbody>
<tr>
<td>Isolated Control</td>
<td>0.52</td>
<td>0.76</td>
<td>0.38</td>
</tr>
<tr>
<td>Grouped-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isolated</td>
<td>-0.42</td>
<td>0.06</td>
<td>-0.14</td>
</tr>
<tr>
<td>Grouped</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.41</td>
<td>-0.37</td>
<td>0.17</td>
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The second hypothesis stated that the difference in marking scores should be accompanied by a related change in ventral gland pad parameters. An analysis of the differences between groups IC and GC on gland width data revealed a significant difference on the initial measurement, but not on the two other measurements. Within-subject analysis of the gland pad width data of group GI indicated a significant (p<.001) increase following isolation of the animals. No significant differences were found for any of the comparisons using length data.

While the within-subject analysis of group GI supports the predicted change in gland pad parameters concurrent with an increase in frequency of ventral marking, the between-groups comparison of IC and GC fails to do so. The initial difference on the gland width data was significant at p<.05 if the one-tailed probability distribution was used, but failed to reach significance if a two-tailed probability distribution was used. No further significant differences were found for the width data, and no significant differences were found in the analysis of the length data. Considering the objections that have been raised against testing with one-tailed probability distributions (Eysenck, 1960), it would seem that a conservative interpretation of no significance between groups on any gland pad param-
eters would be advised. This interpretation would have the added advantage of being in agreement with the results reported by Thiessen, Lindsey, Blum, and Wallace (1971). The fact that highly significant within-subject differences were found for group GI may indicate that the random error reduction that occurs by using this type of analysis makes it more sensitive to changes.

Several criticisms are applicable to the use of the ventral gland as a measure of androgen levels involved in marking behavior. First, the amount of androgen necessary to maintain behaviors in rodents is less than the amount necessary to maintain peripheral organs and glands and anti-androgen drugs tend to exert their effect on peripheral organs and glands rather than behavior (Davidson and Levine, 1972). Thiessen (1968) and Blum (1970) both reported low correlations between gland pad area and marking frequency, and suggested that this low correlation was due to the fact that both variables were correlated with a third variable, androgen. Our data (Table 1) on marking and gland pad parameters in group IC are in agreement with their results. Thiessen and Yahr (1970) were able to stimulate marking behavior with testosterone implants in the preoptic region of the brain, although the hormone levels were too low to affect
the involuted gland. While this supports the criticism, it must be kept in mind that there is no reason to assume that the plasma concentration of testosterone reflected the brain concentration of testosterone, a relation that would be expected to hold under normal conditions. Finally, treatment with an anti-androgen drug reduced gland pad and other hormonally dependent structures but did not affect aggressive behavior (Sayler, 1970).

Secondly, as indicated in our study, animals may have the same size gland pads and yet show obvious differences in marking behavior frequencies, suggesting that some factor other than androgens may be operating here. Results from other studies indicate that olfaction (Baran and Glickman, 1970; Thiessen et al., 1970) and olfactory cues (Nyby et al., 1970; Thiessen and Dawber, 1972) play a significant role in the regulation of marking behavior. Olfactory bulbectomy results in a sharp and immediate decline in marking behavior, with no noticeable change in androgen levels; therapy with androgens can result in some recovery of marking behavior, although the level is not that expected on the basis of dose-marking relationships found in other studies. However, olfactory ablation has been shown to decrease levels of brain neurotransmitters in areas of the brain involved in the cyclic release of testosterone (Pohorecky et al.,
1969), so that factors other than the loss of sensory information may be involved here. If a gerbil intrudes into the territory of a colony and is attacked, it will later avoid entering areas permeated with colony scent even if the residents are not present. Furthermore, it will avoid areas marked by other intruder gerbils, and its marking frequency will be significantly reduced.

Thirdly, it is possible that mere size of the ventral gland pad is not a sensitive enough measure of small increases in androgen levels that significantly affect brain function. There is evidence that the rate of change of hormone concentrations and neurotransmitter concentrations provide more information to the brain than do the actual levels of concentrations. Perhaps marking behavior is preceded by some type of luteinizing hormone surge such as accompanies ovulation in the female. It is doubtful that this would be necessarily reflected in an increase in gland pad size. Arluk (1968) has demonstrated that the effect of testosterone on the gerbil gland is to increase lipogenesis. It is possible that a measure of this parameter may be more sensitive to changes in circulating testosterone levels.

Three studies performed by Thiessen's group at the University of Texas are closely related to the present report.
Thiessen, Owen, and Lindzey (1971) reported that social competition resulted in the reduction in marking frequency of the defeated animal, and that there was a tendency for initially high markers to become dominant in a competitive situation. No physiological data were reported in this study, but an earlier study by Nyby, Thiessen, and Wallace (1970) reported essentially the same behavioral findings along with a lack of evidence for androgen inhibition or stress effects in the defeated animals. In both of these experiments, the intruder animals were present for relatively short period of time, as compared with the chronic four-month housing arrangements in the present study. Thus, the physiological results of Nyby et al. (1970) are probably not the same as those which would be expected in the long-term present study. This conclusion is supported by the study of Thiessen, Lindzey, Blum, and Wallace (1971) which demonstrated significant differences in seminal vesicle weight between grouped and isolated animals. It is interesting that despite the between group differences in seminal vesicle weights, no differences were found for gland pad areas. In view of these results, the suggested use of within-subject analysis may be more sensitive to androgen-related changes in gland pad size, and may explain why we found significant differences in gland pad size with this
type of analysis.

Finally, a distinction made by Stokols (1972) between density and crowding may be applicable here. Density can be defined in terms of the number of animals within a particular set of spatial parameters, while crowding is due to an interaction of spatial parameters, social factors, and personal factors. We have found in the present study, and in an earlier one (Bell and Maier, 1972), that under grouped conditions there is always a relatively high marking animal whose presence seems to inhibit marking behavior in the other animals. While it is not known what the density of Mongolian gerbils is in their natural environment, nor at what density androgen-mediated behaviors would be affected, our results would seem to indicate that the presence of a high frequency marker may be more important than the actual number of animals involved.
References


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The thesis submitted by John Bell has been read and approved by members of the Department of Psychology.

The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Arts.

May 8, 1973

DATE

Richard A. Mayer
ADVISOR'S SIGNATURE