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POPULATION DENSITY AND SOCIAL, TERRITORIAL, AND PHYSIOLOGICAL MEASURES IN THE GERBIL (*MERIONES UNGUICULATUS*)[1]

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Gerbils were reared from weaning to adulthood in four same-sex and four mixed-sex density conditions. Ventral gland marking was greatly affected by density and less so by sex in both same-sex and mixed-sex groups. In same-sex but not mixed-sex groups crowding depressed several social interaction measures as well as body, ventral gland, and testis weights. In the mixed-sex groups, paired males and females had heaviest adrenal glands, ventral glands, and marking scores, as well as the highest reproductive rate. Mixed-sex crowding did not depress either social or physiological measures as much as did same-sex crowding. Effects of crowding are discussed in the framework of an information overload concept.

Both isolation and crowding have been cited as stressful conditions in mice and rats. There are contradictory reports, some of which show that isolated animals have heavier adrenal glands compared with grouped animals (Geller, Yuwiler, & Zolman, 1965; Hatch, Wiberg, Balaza, & Grice, 1963; Weltman, Sackler, Sparber, & Opert, 1962), increased activity levels (Bell, Miller, Ordy, & Rolsten, 1971; Bronson, 1963; Essman, 1966; Woods, 1959; Zimbardo & Montgomery, 1957), and/or heightened aggression (Hatch et al., 1963; Kršiak & Janku, 1969; Scott, 1966; Valzelli, 1969). Others find that animals in large groups, as opposed to those in small groups or isolation, have heavier adrenal glands (Brain & Nowell, 1970; Bronson, 1963; Christian, 1955; Rodgers & Thiessen, 1964), increased activity levels (Bronson, 1963; Korn & Moyer, 1968; Myers & Fox, 1963; Stern, Winokur, Eisenstein, Taylor, & Sly, 1960), and/or heightened aggression (Calhoun, 1962; Southwick, 1969). Many of these seeming contradictions are probably based on interstrain and interspecies differences; others on differences between age of onset and duration of the differential housing conditions as well as number of animals in a group. Furthermore, there are discrepancies concerning the effects of grouping vs. isolation on measures of sociability. In some situations, isolated rats seemed less gregarious (Angermeier, 1959; Ashida, 1964), and in others, more so (Casey, 1962; Latané, Cappell, & Joy, 1970; Shelley & Hoyenga, 1966, 1967). In one situation, gregariousness was species dependent, with grouped *Peromyscus* spending more time than isolated *Peromyscus* near a conspecific, and the reverse being true for C57 mice (Bronson, 1963).

Given these discrepancies in effects of grouping animals, the question arises as to the generality, or even the existence, of a "crowding syndrome," in which one or more variables vary systematically with population density. There is some agreement that crowding is stressful but little agreement as to the effects of this stress on the behavior and physiology of the animals. Most of the above experiments have utilized fewer than four dependent variables—many of them, only one or two. Furthermore, most have been done with all-male groups. There is no single study in the literature which has tested a broad range of behavioral and physiological variables using several population densities and both same-sex and mixed-sex groups. The bias toward all-male groups is understandable, since such grouping eliminates the problems of endocrine changes during pregnancy and estrous cycles. However, it is clearly an unnatural sit-

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uation for most animals. Endocrine changes in both males and females have been noted as a result of housing the animals in same-sex, as opposed to mixed-sex, groups. Southwick and Bland (1959) found that males in mixed-sex groups had heavier adrenals than those in all-male groups even though there were no wounds due to fighting in either group. The effect of all-female grouping is even more striking. Whitten (1959) found suspension of estrus for up to 40 days when female mice were housed 30 per cage. Diestrus ended, however, when the animals were placed in individual cages. Whitten (1959) and Lamond (1959) also found that placing a male into the female group or placing one of the grouped females into a separate cage with a male promptly initiated an estrous cycle.

Gerbils were chosen as subjects for these experiments partly because their territorial marking has been extensively studied and is easily observable. Gerbils possess a ventral sebaceous gland which they rub against low objects in their environment. This scent-marking behavior appears to be at least partially a means of making a territorial claim (Thiessen, Lindzey, Blum, & Wallace, 1970). In males, both the size of the ventral gland and the relative frequency of marking behavior have been shown to vary directly with androgen levels (Thiessen, Owen, & Lindzey, 1971). However, there is a base-line gland size and marking frequency displayed by females and castrated males which appears not to be hormone dependent (Thiessen et al., 1971). When a gerbil marks, he glides over an object on the floor, perceptibly lowering his midsection. In contrast, mice and rats apparently mark territory by means of pheromones released with urine or feces, making it difficult for an observer to determine when animals are marking (Gleason & Reynierse, 1969). An additional reason for using gerbils is that they have not been selectively bred for certain traits for many generations, as have most common laboratory animals, and therefore possess a relatively natural repertoire of social behavior. They are active and interesting animals. On the other hand, they are readily available from a reliable supplier, as most wild animals are not, and are the subject of an increasing number of experimental studies.

In the present study, two experiments were performed, one utilizing groups of animals of the same sex and the other utilizing mixed-sex groups. A variety of social, territorial, and exploratory activities and several physiological indices were recorded in an attempt to form a broad picture of the effects of rearing gerbils from weaning to adulthood in several density conditions.

Experiment 1

Method

Subjects

Forty male and 40 female Mongolian gerbils (*Meriones unguiculatus*) obtained at weaning (approximately 30 days) from Tumblebrook Farms, Brant Lake, New York, were used in the experiment. Upon arrival they were randomly divided into the following same-sex groups: 16 isolates, 16 paired animals, 16 animals in two groups of 8 each, and 32 animals in two groups of 16 each. Ten animals died before testing began, apparently due to inadequate shipping procedures. Thus, the following groups were tested: 13 isolates, 16 paired animals, 13 medium-density (8 males, 5 females), and 28 high-density animals (15 males, 13 females).

Experimental Conditions

Each group of 1, 2, 8, or 16 animals was housed in a standard 10-gal. aquarium for 120 days before testing began, at which time all animals were sexually mature. The aquariums housing the isolated animals were painted with flat black paint. The floor was covered with cedar shavings, and paper was available for shredding and nest building. A 2 × 4 in. block of wood was available for gnawing. Food and water were freely available. Overhead fluorescent lights were on from 8 p.m. to 8 a.m. and off the remainder of the day.

Apparatus

The cross maze was constructed of ½-in. plywood, painted gray, with an aluminum floor for easier cleaning. Each of the four arms was 39.5 × 15.8 × 14.5 cm. and had a clear Plexiglas top, hinged so that the animals could be moved into and out of the apparatus. Four chambers, located at the end of each arm, measured 14.0 × 15.8 × 14.5 cm. Each chamber was also painted gray and was separated from the arm by .013-m. wire-mesh screen. One chamber contained a conspecific of the same sex as the experimental animal; another, a white mouse; the third, a small jar of clean sawdust; and the fourth, two shelled walnuts.

TABLE 1

Average Open-Field Marking in 10 Min. for Same-Sex Groups

Group	Marking	
	$\bar{X}$	*SD*
Isolate male	12.6	4.0
Paired male	16.1	10.9
Medium-density male	1.8	1.9
High-density male	1.5	2.0
Isolate female	8.8	10.1
Paired female	6.0	5.4
Medium-density female	2.6	3.1
High-density female	.3	.4

The open-field apparatus was similar to that used by Thiessen, Friend, and Lindzey (1968). It measured 1 sq. m., was painted gray, and was lined off into 16 squares of equal size. Pegs made of clear plastic dowels, 2 cm. high, were inserted into holes at the corners of each square except along the boundary of the field. The sides of the field were 48.0 cm. high and were hinged at the middle to provide access to the animals.

Procedure

All animals were tested first in the cross maze, then all animals were tested individually in the open field, and finally, randomly selected animals from high-density and isolate conditions were paired with another animal in the open field. All testing was done during the dark period of the 24-hr. cycle. The experimental room was dark except for a dim (7.5-w.) bulb placed 2 ft. above the apparatus. The apparatus was cleaned after each trial with a dilute alcohol solution. After all behavioral measures were taken, the animals were sacrificed by means of chloroform inhalation. Age at the time of sacrifice was approximately 180 days. Body weights were measured to the nearest gram; adrenal glands, testes, and ventral glands were weighed to the nearest milligram. The adrenal-gland:body-weight, testes:body-weight, and ventral-gland:body-weight ratios were computed.

TABLE 2

Average Social Interaction in 10 Min. for Same-Sex Groups

Group	Chasing		Sniffing		Marking	
	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*
Isolate male	20.2	5.1	20.0	4.5	18.6	10.0
High-density male	1.4	1.5	12.4	1.6	.8	1.1
Isolate female	8.6	8.1	19.4	4.7	8.8	6.0
High-density female	6.6	5.7	12.0	5.1	.6	.7

Cross maze. Each animal remained in the apparatus for 10 min. divided into five 2-min. intervals. Arm choices and screen contacts were recorded for each interval. A choice was recorded every time an animal entered an arm with all four feet; a contact was recorded every time the animal touched the wire with either face or forepaws, or moved face or forepaws to a new location on the screen.

Open-field activity and marking. Each animal was placed in the open field and observed for 10 min., during which time the number of squares entered with all four feet, the number of ventral-gland rubs on pegs or floor, and the number of boluses defecated were recorded.

Open-field social interaction and marking. Ten same-sex pairs of animals were chosen; one member of each pair was randomly selected from the high-density condition, the other, from the isolate condition. Each pair was allowed to interact in the open field for 10 min. High-density animals were marked on the back of their heads with a red felt-tipped pen; isolate animals were similarly marked with a yellow felt-tipped pen. Each time an animal initiated fighting, chasing, or sniffing of the other animal, rubbed his ventral gland on either a peg or the floor, or defecated, the appropriate score was recorded. If both animals initiated an activity simultaneously, both were credited with the action.

Results

Cross Maze

Analysis of variance computed on total number of choices, percentage of choices for each arm, and on percentage of contacts in each arm revealed no significant main effects for density. However, males chose the arm with the conspecific ($F = 5.77$, $df = 1/62$, $p < .01$) and made more contacts in that arm ($F = 4.15$, $df = 1/62$, $p < .05$) than did females.

Open-Field Activity and Marking

There were no significant differences in number of squares entered during the 10-min. trials. However, marking behavior was greatly affected by density condition ($F = 10.81$, $df = 3/62$, $p < .0001$). Table 1 shows the mean number of times each group marked with their ventral glands. It is clear that the high-density conditions greatly depressed marking behavior. The difference between sexes in marking behavior was not statistically significant. The third measure —number of boluses deposited—showed no significant differences for either density or sex.

TABLE 3

Average Body and Gland Weights for Same-Sex Groups

Group	Body weight (in gm.)		Absolute adrenal weight (in mg.)		Relative adrenal weight (in mg/gm)		Absolute ventral gland weight (in mg.)		Relative ventral gland weight (in mg/gm)		Absolute testis weight (in mg.)		Relative testis weight (in mg/gm)	
	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*
Isolate male	85	8.7	33	5.1	.40	.09	153	30.1	1.8	.4	645	55.8	7.6	.6
Paired male	86	9.1	30	10.0	.35	.10	144	45.5	1.7	.4	596	81.5	6.9	.7
Medium-density male	79	7.1	29	3.4	.36	.04	98	42.5	1.3	.6	522	41.2	6.6	.3
High-density male	76	9.2	34	6.3	.44	.10	62	21.7	.8	.3	475	67.7	6.2	.4
Isolate female	75	9.3	25	7.4	.35	.08	39	13.4	.5	.1				
Paired female	62	14.6	22	7.2	.35	.09	42	15.9	.6	.2				
Medium-density female	65	5.7	24	4.9	.36	.10	38	7.5	.6	.2				
High-density female	57	5.5	20	2.0	.35	.03	40	9.0	.7	.2				

Note. One adrenal gland and one testis per animal were used.

Open-Field Social Interaction and Marking

As shown in Table 2, isolate animals chased ($F = 15.22$, $df = 1/16$, $p < .002$), sniffed ($F = 15.50$, $df = 1/16$, $p < .002$), and marked ($F = 12.12$, $df = 1/16$, $p < .003$) more frequently than did high-density animals. Little fighting was observed, and there was no significant difference in fighting scores or in defecation. Sex differences were not statistically significant on any of these measures.

Physiological Measures

Analysis of variance for body weight indicated significant main effects for both sex ($F = 9.01$, $df = 1/62$, $p < .01$) and density ($F = 3.72$, $df = 3/62$, $p < .05$; see Table 3 for all physiological data). Males weighed more than females, and animals in the low-density conditions weighed more than animals in the high-density conditions. Relative adrenal weights were significantly different when compared according to sex ($F = 6.05$, $df = 1/62$, $p < .05$), with males having heavier adrenal glands than females. There was also a significant Sex × Density interaction ($F = 5.70$, $df = 3/62$, $p < .01$). Female relative adrenal weights were fairly constant over all conditions, while both isolate and high-density males had heavier adrenal glands than the paired and medium-density groups. Analysis of variance performed on relative ventral-gland weights revealed significant differences for both sex ($F = 7.40$, $df = 1/62$, $p < .01$) and density ($F = 3.08$, $df = 3/62$, $p < .05$). Males had heavier ventral glands than females. Whereas density had no effect on females' ventral glands, increasing density led to a progressive decrease in the males' ventral-gland weight, so that glands from males in the highest density condition were almost as small as those of females. Relative testes weights for the males were significantly different when compared by a one-way analysis of variance ($F = 7.67$, $df = 3/34$, $p < .01$).

Experiment 2

Method

Subjects

Forty male and 40 female Mongolian gerbils (*Meriones unguiculatus*), obtained at weaning (approximately 30 days) from Tumblebrook Farms, were used in the experiment. Upon arrival they were randomly divided into the following mixed-sex groups: 16 isolates, 16 paired animals, 16 animals in two groups of 8 each, and 32 animals in two groups of 16 each. Sexes were equally divided in each group. The experimental conditions were the same as in Experiment 1.

Apparatus

The open-field apparatus described above was employed in Experiment 2. Since the cross maze yielded little interesting data in Experiment 1, it was not used in Experiment 2.

Procedure

Open field. All animals were first tested individually in the open field during the dark period of the 24-hr. cycle. The experimental room was dark except for a dim (7.5-w.) bulb placed 2 ft. above the apparatus. Each animal was placed into the open field and observed for 10 min., during which time the number of lines crossed with all four feet, the number of ventral rubs on pegs or floor, and the number of boluses were recorded. The apparatus was cleaned after each trial with a dilute alcohol solution.

Social interaction. Twenty-four male and female representatives were randomly chosen from isolate, paired, and high-density conditions. Each was allowed to interact for 10 min. in the open field with a partner of the same sex but different density level. Thus, four interactions took place between isolate and paired animals, four between isolate and high-density animals, and so on for both males and females. No between-sex encounters were run. Each animal was marked on the back of its head with either a red or a yellow felt-tipped pen. During the test period the animals were identified only by means of these marks, without reference to density condition. Whenever an animal initiated fighting, chasing, or sniffing of the other animal, rubbed his ventral gland on a peg or the floor, or defecated, the appropriate score was recorded. If both animals initiated an activity simultaneously, both were credited with the action. Again the apparatus was cleaned with a dilute alcohol solution after each trial. At the end of the experiment, scores from all animals in each housing condition were added together regardless of the density level of their opponents. In this way, overall fighting, chasing, marking, sniffing, and defecation scores were tabulated for each sex at three density levels.

Physiological measures. After all behavioral tests had been made, the animals were sacrificed by means of chloroform inhalation. Age at the time of sacrifice was approximately 180 days. Body weights were measured to the nearest gram; adrenal glands, testes, and ventral glands, to the nearest milligram. The adrenal-gland:body-weight, testis:body-weight, and ventral-gland:body-weight ratios were computed.

Results

Open Field

There were no significant differences in number of lines crossed during the 10-min. trials. All animals were very active, crossing an average of 300 lines in 10 min. However, marking behavior was greatly affected by density condition ($F = 9.19$, $df = 3/71$, $p < .0001$) and less so by sex ($F = 6.35$, $df = 1/71$, $p < .05$). Table 4 shows that except for the paired males there was a steady decline in marking frequency with increasing density. However, the paired males marked more than twice as much as did isolate males. Medium- and high-density females marked somewhat less than isolate and paired females. There were no differences in defecation frequency on any comparison.

TABLE 4

AVERAGE OPEN-FIELD MARKING IN 10 MIN. FOR MIXED-SEX GROUPS

Group	Marking	
	$\bar{X}$	*SD*
Isolate male	7.3	6.7
Paired male	24.4	19.5
Medium-density male	5.1	8.6
High-density male	1.3	2.8
Isolate female	6.3	6.6
Paired female	7.5	6.2
Medium-density female	1.3	2.0
High-density female	2.2	2.3

Social Interaction

As shown in Table 5, marking was again affected by density condition. High-density males and females showed much lower marking frequencies than isolate and paired animals ($F = 5.15$, $df = 2/42$, $p < .01$). No other social interaction measure showed a significant difference for either sex or density.

Physiological Measures

There were no significant differences in body weight. However, both relative ven-

TABLE 5

AVERAGE SOCIAL INTERACTION MARKING IN 10 MIN. FOR MIXED-SEX GROUPS

Group	Marking	
	$\bar{X}$	*SD*
Isolate male	11	7.3
Paired male	14	16.0
High-density male	1.5	2.7
Isolate female	2.8	3.0
Paired female	13.1	11.8
High-density female	.8	.9

TABLE 6

Average Body and Gland Weights for Mixed-Sex Groups

Group	Body weight (in gm.)		Absolute adrenal weight (in mg.)		Relative adrenal weight (in mg/gm)		Absolute ventral gland weight (in mg/gm)		Relative ventral gland weight (in mg/gm)		Absolute testis weight (in mg.)		Relative testis weight (in mg/gm)	
	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*
Isolate male	75	9.6	23	6.0	.31	.10	101	15.1	1.36	.27	592	29.1	7.88	2.6
Paired male	77	6.4	32	4.0	.41	.08	157	30.3	2.06	.39	590	34.5	7.87	3.4
Medium-density male	77	6.5	25	4.1	.33	.06	106	24.2	1.37	.34	552	49.1	7.35	4.1
High-density male	79	7.4	25	3.8	.32	.07	105	34.7	1.31	.40	528	65.8	6.68	2.7
Isolate female	73	9.3	24	4.7	.33	.05	35	12.4	.46	.11				
Paired female	75	9.1	30	4.5	.40	.07	101	16.5	1.33	.41				
Medium-density female	73	7.5	22	3.8	.30	.05	70	15.0	.96	.26				
High-density female	77	7.3	23	4.1	.30	.08	68	20.4	.87	.31				

Note. One adrenal gland and one testis per animal were used.

tral-gland and adrenal-gland weights were significantly affected by density (ventral glands: $F = 12.52$, $df = 3/71$, $p < .0001$; adrenal glands: $F = 5.48$, $df = 3/71$, $p < .01$; see Table 6). In both cases, paired animals' glands were heavier than those from other density levels. Males' relative ventral-gland weights were significantly greater than those of females ($F = 45.04$, $df = 1/71$, $p < .0001$). There was a slight, nonsignificant decline in relative testis weight with increasing density.

Discussion

The greatest effects of density on both behavioral and physiological measures were seen in animals in Experiment 1. Isolate animals in that experiment produced higher scores in chasing, sniffing, and marking than those from the high-density condition. This is consistent with findings, noted in the introduction, that isolate animals are both more aggressive and more sociable than grouped animals. There were few instances of actual fighting, and, while isolate males initiated the greatest number of fights, the fighting scores were not significantly different among groups. There were some sex differences in chasing, sniffing, and marking; however, the density variable consistently produced the greatest effect. On every measure, the crowded male produced a lower score than the isolate female.

There were no density-related differences in social preference in the cross maze in Experiment 1. Latané et al. (1970) found that their rats showed little social attraction if they could not physically interact with the goal animal. The results of Experiment 1 extend this finding to gerbils as well as rats. Furthermore, two of the most common measures of emotionality (freezing, as determined by activity measures, and defecation) did not discriminate among gerbils reared in different density conditions in Experiment 1.

In Experiment 2, only the marking variable showed density-related differences. Except for the paired animals, there was a steady decrease in marking as population density increased. However, paired males and females in Experiment 2 and males, but not females, in Experiment 1 marked more frequently than even isolated animals. It appears that, for males, some combination of competition and low density in their living cages facilitates the highest levels of marking in the test situation. Thus, isolated animals, lacking competition, do not mark as frequently as paired animals; and high-density animals, having either too little space or too many social interactions in their home cage, hardly mark at all.

Marking by the paired females in Experiment 2, however, requires a different explanation. Marking by females in the same-sex groups in Experiment 1 declined monotonically with increasing density; however, in mixed-sex groups, the paired females marked more frequently than any other females, especially in the social interaction test. At the time of testing, all females in the male–female pairs were pregnant and had a stable, well-formed nest. While some medium- and high-density females were pregnant, there were no nests in their cages. It may be that some aspect of reproduction and/or nesting is responsible for the relatively high levels of marking by paired females.

Physiological measures in Experiment 1 were in general agreement with observations by Brain and Nowell (1970), Bronson (1963), Christian (1955), Christian and Davis (1964), and Rodgers and Thiessen (1964). As expected, body weight declined with increasing density, with males weighing more than females. In the males, both testis weights and ventral-gland weights decreased progressively with increasing density. This is particularly interesting in light of the finding of Thiessen et al. (1968) that the size of the ventral gland is directly related to testosterone levels and that ventral glands of castrated males are approximately the same size as those of females. As seen in Table 3, ventral glands of crowded males in Experiment 1 are not much larger than those of all females. Even in Experiment 2, male–female differences in ventral-gland size decreased with increasing density. However, in Experiment 2 a rather surprising result occurred. Ventral glands of both paired males and females were considerably heavier than those of any other group, and glands of crowded animals were not much smaller than those of isolate animals. Ventral-gland weights for paired females were almost as large as those of isolate and medium- and high-density males. Distribution of open-field marking scores, but not of social interaction marking scores, paralleled the distribution of relative ventral-gland weights.

Adrenal-gland weights of females in Experiment 1 were not altered as a result of density level. However, relative adrenal weights of males showed a J-shaped distribution. If adrenal weights are used as an index of stress (Christian, 1963), it appears that for males in same-sex groups, isolation is more stressful than low and medium levels of density, while high density is most stressful. In Experiment 2, however, both male and female paired animals had heavier adrenal glands than any other group. Christian and Davis (1964) noted that reproductive state is a primary factor in determining adrenal weight in mice and that pregnancy in particular leads to an increase in that weight. While this may account for the females' increase in Experiment 2, it does not directly explain that of their mates. Since both the ventral glands and adrenal glands of paired males—but not their testes—were heavier than those of any other group, it would appear that some social or reproductive factor, rather than testosterone, is responsible for these increases.

We have shown that housing conditions do affect the gerbil's marking—and in some situations, social—behavior and its endocrine and ventral glands. However, we have not found a general crowding syndrome in which several measures consistently increase or decrease monotonically with increasing density. Marking is the one measure which comes closest to an inverse correlation with density in both same-sex and mixed-sex groups. While same-sex groups also showed significant decreases in chasing and sniffing and in body, ventral-gland, and testis weights with increasing density, these decreases were not found in the mixed-sex groups. The opportunity for social and/or reproductive interactions with the opposite sex seems to have offset the effects of density on these measures. Schwentker (1969) reported that gerbils live in herds in their natural environment. Thus, even our crowded conditions may not have been too different from gerbils' normal population density inside their burrows. However, observations of the animals in the high-density groups revealed a number of animals with scarred and bleeding tails and faces. No paired animal had scars or wounds. Furthermore, all of the paired females were pregnant at the time of testing, whereas only 3 of the 16 high-density females were pregnant. One additional high-density female gave birth to a litter before testing had been completed; however, within a day all offspring had been killed. It is clear, then, that high density does have adverse effects on gerbils' reproductive ability as well as on their social and marking behavior.

We would like to emphasize that conclusions drawn from limited laboratory experiments cannot be taken as indicators of a general crowding syndrome. Any results will reflect species differences, gender composition, size of the groups, length of grouping, and ages of the animals as well as the specific variables chosen for testing. However, there is sufficient agreement among reports to infer that relatively severe crowding of any animals depresses one or more aspects of their reproductive ability and usually, though not always, leads to a physiological stress reaction with overproduction of adrenal corticoids. We have added decreased territorial marking to the list of common effects of crowding and have found that in some cases social interactions between strange partners of the same sex are also depressed. Such reactions may be interpreted as an "information overload" situation (Milgram, **1970**), in which a crowded animal fails to seek out new social encounters because it already has had too many social stimuli to process comfortably. The animal may disregard some stimuli, deal cursorily with others, and produce fewer communicative stimuli of its own. Wild animals would normally deal with such a situation by splitting off from the old group and forming a new smaller group in a new territory. This option is not available in the laboratory, so experimental animals simply fail to seek out new interactions and may behave inappropriately in a crowded cage. For example, fighting and trampling on offspring may result from insufficient attention to stimuli which would normally inhibit such behavior. Similarly, isolation is a relatively unnatural situation, and animals isolated early in life may not have learned appropriate methods of communication. They may seek out encounters but not react to them in the normal fashion, often showing greater aggression than normal. Exceptions to general rules do occur, however, and some animals show either less reaction or different kinds of reactions to either crowding or isolation than the average animal. This may be related to relative dominance position or to the social stability of a particular group. However, we still do not understand the specific variables that account for such exceptions.

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