Physiology & Behavior, Vol. 17, pp. 735–741. Pergamon Press and Brain Research Publ., 1976. Printed in the U.S.A.

Environmental Enrichment and Crowding: Behavioral and Hormonal Effects[1]

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(Received 22 July 1975)

HULL, E. M., C. KASTANIOTIS, G. L'HOMMEDIEU AND J. R. FRANZ. *Environmental enrichment and crowding: behavioral and hormonal effects.* PHYSIOL. BEHAV. 17(5) 735–741, 1976. — Male and female gerbils lived from weaning to adulthood in Enriched Crowded, Plain Crowded, Dense Crowded, or Paired conditions. Daily observations, social interaction tests with one animal from each of the 4 groups, and anatomical measures were made, and levels of cortisol and testosterone were determined by radioimmunoassay. In the social interaction tests Paired gerbils marked and fought the most. Home cage observations estabished that Enriched animals failed to pair bond or establish nests in the small cubicles provided. They also reproduced no more successfully than did other crowded groups, while all crowded groups reproduced less than Paired animals. All groups of crowded animals had lighter testes and adrenal glands than Paired animals, although their cortisol levels were consisderably higher than Paired animals'. This inverse relationship of cortisol and adrenal weight was interpreted as a sign of extreme adrenal activity on the part of crowded animals. Enriched animals had cortisol levels intermediate between those of Paired and of Dense and Plain crowded animals, and their testosterone levels were as high as those of Paired males, indicating some diminution of hormonal effects of crowding. There was, however, little evidence of diminished behavioral and reproductive effects of crowding by environmental enrichment.

Environmental crowding   Hormonal effects   Aggression   Reproduction

IT has been frequently observed that crowding animals leads to decreased reproduction, increased adrenal activity, and behavioral changes, including decreased aggression in social interaction tests and in the home cage if a sufficient period of adjustment is allowed [2, 5, 7, 12, 13, 16, 18, 27]. However, several investigators have reported increased aggressiveness among crowded animals [9, 15, 28], and/or no adrenal hypertrophy [4, 7, 17, 29, 33].

In gerbils we have observed depressed ventral gland marking, aggression, and nonaggressive contacts, as well as diminished reproductive success, resulting from crowding normal animals [17,18]. We have also seen smaller ventral glands (used by gerbils to deposit a sebaceous substance on low-lying objects in the environment) and in some experiments smaller testes and/or enlarged adrenal glands in crowded animals [17,18].

In a previous experiment in this lab [17], one group of crowded gerbils was placed into individual, physically enriched boxes for 2 hr per day for 10 weeks in order to determine whether this intermittent isolation would diminish the physiological and/or behavioral effects of crowding. However, the crowded animals subjected to intermittent isolation became more aggressive both in the home cage and in social interaction tests, and reproduced less than either paired or continuously crowded animals. There was no indication of adrenal hyperactivity, although testes weights were lower in all crowded males. Thus, the enforced periods of isolation did not ameliorate the effects of crowding but rather appeared to exacerbate them.

Most frequently, animals which have been crowded for a relatively long period (at least 2 weeks) exhibit decreased aggressiveness. However, Intermittent Isolation animals in this previous experiment were more aggressive, and this factor may have accounted for their reproduction being poorer than even the Plain-Crowded group. Since isolation is known to increase aggressiveness, and since in the previous experiment much of the aggression was observed immediately after regrouping, the present experiment was designed to provide free access to refuge, rather than enforced isolation. Thus, decreased intensity of social stimulation could be available whenever an animal sought it without the disruptive effects of daily handling, isolation and regrouping. One group of animals lived from weaning to adulthood in a physically enriched environment with access to small tunnels and cubicles leading off from the central area. A second group was housed in a plain square enclosure, with an equal amount of space per animal. A third group lived in a much smaller space. The fourth group lived in male-female pairs, with the same amount of space per animal as the first two groups. Daily observations were made of the animals' behavior in the home cages. At adulthood controlled social interaction tests were made. At the termination of the experiment, animals were sacrificed, organ weights recorded, and blood obtained for radioimmunoassay of cortisol and testosterone levels.

[1]We wish to thank Dr. W. Roy Slaunwhite and Dr. N. Kundu for their help and use of facilities. This work was partially supported by grant No. 1 RO3 MH 25782-01 from NIMH and by Institutional Funds from a Biomedical Support Grant to SUNY/Buffalo.

METHOD

Animals

Sixty-four weanling gerbils (32 male, 32 female) were obtained from Tumblebrook Farms (West Brookfield, Mass.) and individually earmarked. Animals of each sex were randomly assigned to the following four conditions: 16/large enriched cage (Enriched, or E), 16/large plain cage (Plain, or P1), 16/small cage (Dense, or D), or 2/small cage (Paired, or Pr). Food, water, and wooden blocks for gnawing were freely available; paper for shredding was supplied daily. E, Pl, and Pr animals were allowed 64 cm^2 per animal; D animals were allowed 8 cm^2 per animal. All cages were made out of clear Plexiglas. The enriched environment consisted of a large central octagonal space (34 cm/side, 42 cm high), with a small tunnel connecting to a red Plexiglas cubicle emerging from each of the eight sides. Rocks, sticks, a hollow cinderblock, and a food and water dispenser were in the central area. The plain environment was a square (81 × 81 × 42 cm) enclosure with a food and water dispenser in the center. Pr and D animals were housed in standard (10.5 × 40.5 × 16 cm) laboratory cages with overhead food and water dispensers.

Apparatus

Social interaction tests were conducted in a 1 m^2 open field apparatus, painted gray and lined off into 16 squares of equal size. Nine 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 were 48 cm high. A sheet of Plexiglas, with holes into which the pegs fit, covered the floor for easy cleaning. A manual keyboard connected to electromechanical counters was used to record each of the social behaviors.

Procedure

Daily 1 hr observations were made of animals in their home cages. Three observations were made at night. Location and quality of nests, animals most active, instances of aggression, other social interactions, ventral gland marking, and presence of pups were recorded. At 120 days of age social interaction (SI) tests were conducted in the open field apparatus. Each test lasted 10 min., and the number of ventral gland rubs, aggressive encounters, sniff or nonaggressive contacts, and escape attempts initiated by each animal were recorded. Each animal was tested against one other animal of the same sex from each of the 4 environments (4 tests per animal), in counter balanced order.

When behavioral measures were completed, animals were sacrificed by exsanguination under ether anesthesia, and body, ventral gland, adrenal gland, and testes weights were recorded. Blood was collected in heparinized tubes, and plasma levels of cortisol (for all animals) and testosterone (for males) were determined by radioimmunoassay using commercially prepared antibody and standard and tritiated hormones (New England Nuclear). Steroids were extracted from 0.1 ml samples of plasma with methylene chloride. Extraction of relevant steroids was determined to be at least 80% of the total. Blank, zero, standard and sample tubes were run in duplicate. Following an incubation period to allow labeled-unlabeled antigen competition to reach equilibrium, an activiated charcoal suspension was added to appropriate tubes to adsorb unbound antigen. After centrifugation, the supernatant containing the bound antigen was transferred to scintillation vials for counting under conditions optimized for tritium. The percent bound for each sample was used to interpolate the quantity of hormone in nanograms from the standard curve. Calculation of the unknown hormone concentration in $\mu g\%$ was then made, taking into account dilutions, volume extracted, and fractional recovery.

RESULTS

Home Environment Observations

One litter was produced in the E environment; 4, in the Pl; 3, in the D; and 7, in the Pr cages. Parturient females exhibited postpartum estrus, and were frequently chased by numerous males. Although the mothers attempted to retrieve the pups, all 28 offspring in the 3 crowded cages were trampled to death within a few hours. All 37 pups born to the paired animals survived until weaning. In each group some fairly consistent dominance/submissiveness relationships could be discerned, in which a given dominant animal regularly chased and/or attacked one or more other animals. However, a gerbil attacked by one dominant animal was also frequently attacked by others as well. For example, the 4 animals in the Pl condition which were eventually killed were repeatedly attacked by numerous cagemates. In the 3 crowded dages there were somewhat more instances of aggression by females than by males, and most of the aggression by both males and females was directed toward females. Among Pr animals, males and females were equally aggressive, though, of course, same-sex aggression was precluded by the housing conditions. Positive correlations for all animals were found between activity and grooming another animal ($r = .50$, $df = 57$, $p<0.01$). Within-group correlations are given in Table 1. However, correlations between daily observation scores and social interaction scores were near zero.

TABLE 1

WITHIN-GROUP CORRELATIONS AMONG DAILY OBSERVATION MEASURES*

	Activity	Aggression
Aggression	r = 0.6391 for Pl ♂	
	r = 0.9224 for En ♀	
	r = 0.7903 for Pl ♀	
Groom	r = 0.8391 for Pl ♂	r = 0.6691 for Pl ♂
	r = 0.7434 for Pr ♀	r = 0.8054 for Pr ♂
	r = 0.6379 for Pl ♀	r = 0.7666 for Pl ♀
	r = 0.5744 for D ♀	

*For all correlations $df = 8$, $r_{(0.05)} = 0.6319$, $r_{(0.01)} = 0.7646$

In all three crowded conditions, at least half the animals were observed on any occasion to be huddled together. Frequently in the E condition one or two cubicles were literally stuffed with gerbils; the particular cubicles chosen varied from time to time. Also, one or two cubicles were frequently stuffed with wood shavings and shredded paper; the location of these also varied. Neither pair-bonding nor territorial defense was observed. No nests were established in E cubicles, and the one litter produced in this environment was found dead in the central open area. Most animals which were active in the crowded environments on any one day returned periodically to the group huddle. On another day they might not leave the group during the period of observation. Thus, the group huddle seemed to be the focal point from which some animals emerged to be active for a time and to which they returned at the end of that time. There were, however, some animals (2 Pl males, 2 Pl females, and 1 D male) which were more or less permanent outcasts. They were frequently attacked and all 5 were eventually killed (after social interaction tests were completed). They were not replaced. Two Pr females either died or were killed by their cagemates within the first 30 days; the two were replaced by animals of the same age and sex from our colony, and one replacement later produced a litter.

Social Interaction Tests

As can be seen in Table 2, paired males engaged in more ventral marking, $F(3,30) = 5.01$, $p<0.01$, and aggression, $F(3,30) = 4.29$, $p<0.05$, than any other group of males. Paired females also marked more than any other female group, $F(3,30) = 6.65$, $p<0.01$, although their increased aggressiveness did not reach statistical significance. Other groups did not differ significantly according to Newman-Keuls comparisons for either sex. Males marked more frequently than did females ($t = 1.67$, $df = 62$, $p<0.05$). There were no significant main effects in nonaggressive sniffs and contacts. Aggression was correlated with ventral marking ($r = .58$, $df = 57$, $p<0.01$) and with nonaggressive sniffs and contacts ($r = 42$, $df = 57$, $p<0.01$). Housing condition of opponent produced no consistent effect on social interaction scores (Table 3).

Physiological Measures

As can be seen in Table 4, Pr males had the heaviest testes, $F(3,26) = 3.07$, $p<0.05$, while other groups did not differ from each other on Newman-Keuls comparisons. Ventral gland weights of the Pr and Pl groups were higher than those of the other two groups, $F(3,50) = 8.34$, $p<0.01$, and males had heavier ventral glands than did females, $F(1,50) = 138.5$, $p<0.0001$. Males also had heavier adrenal glands than did females, $F(1,52) = 21.75$, $p<0.01$. The Pr group had heaviest adrenals, followed by E, Pl, and D, respectively, $F(3,52) = 4.08$, $p<0.05$, though there was a significant sex × environment interaction with Pr females

TABLE 2

SOCIAL INTERACTION TEST SCORES (MEANS PER INTERACTION FOR EACH GROUP)

	Enriched		Plain		Dense		Paired	
	Mean	S.D.	Mean	S.D	Mean	S.D.	Mean	S.D.
				Males				
Marking	1.31	1.82	0.41	0.68	2.69	4.56	20.13	24.17
Aggression	4.69	5.70	2.31	3.42	1.81	1.64	11.31	9.90
Sniff Contact	57.25	3.70	58.50	7.04	59.72	15.86	70.44	13.90
				Females				
Marking	0.91	1.02	0.25	.08	0.06	0.18	5.97	5.59
Aggression	6.66	5.48	3.66	2.57	5.38	5.12	12.69	14.81
Sniff Contact	70.34	12.07	53.19	8.08	60.16	20.75	63.94	17.61

TABLE 3

WITHIN-GROUP CORRELATIONS AMONG SOCIAL INTERACTION MEASURES

	Sniff & Contact	Marking	Aggression
Marking	r = 0.8226 for Pr ♂ r = 0.8042 for D ♀		
Aggression	r = 0.7807 for D ♂ r = 0.7749 for D ♀ r = 0.6917 for Pr ♀	r = 0.7945 for Pr ♂ r = 0.8098 for D ♀	
Grooming		r = 0.6338 for D ♂	
Escape			r = 0.8498 for En ♂ r = 0.6592 for En ♀

*For all correlations $df = 8$, $r_{(0.05)} = 0.6319$, $r_{(0.01)} = 0.7646$.

TABLE 4

PHYSIOLOGICAL MEASURES

	Enriched		Plain		Dense		Paired	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
				Males				
Body weight (g)	72.62	5.40	68.38	2.01	75.29	10.43	70.38	7.23
Testes (mg)	958.37	83.02	968.75	52.51	944.38	171.35	1095.38	83.93
Ventral gland (mg)	104.75	26.68	120.30	25.24	129.06	63.23	140.84	22.70
Adrenal glands (mg)	31.84	6.13	32.61	3.20	30.84	9.83	31.21	5.50
Relative testes (testes in mg)/(body in g)	13.38	1.41	14.62	1.30	12.75	2.19	15.00	1.31
Relative Adrenal (adrenals in mg)/(body in g)	.438	.118	.477	.054	.410	.085	.443	.083
Relative ventral gland (ventral gland in mg)/(body in g)	1.442	0.352	1.756	0.353	1.67	0.59	2.01	0.343
Cortisol (μg%)	60.52	56.10	88.07	25.91	101.74	24.41	45.14	22.56
Testosterone (μg%)	4.92	5.60	2.23	1.07	3.61	2.40	4.82	4.46
				Females				
Body weight (g)	62.06	5.82	66.21	4.05	61.58	7.35	74.53	7.99
Testes (mg)	—	—	—	—	—	—	—	—
Ventral gland (mg)	25.51	17.82	78.60	28.96	36.29	25.51	66.92	16.77
Adrenal glands (mg)	27.78	5.60	25.88	2.50	21.36	4.80	31.35	2.53
Relative testes wt. (testes in mg)/(body in g)	—	—	—	—	—	—	—	—
Relative adrenal wt. (adrenals in mg)/(body in g)	.447	.096	.390	.050	.347	.090	.421	.037
Relative ventral gland (ventral gland in mg)/(body in g)	.411	.286	1.187	.774	.558	.335	.890	.159
Cortisol (μg%)	39.92	26.82	51.12	30.36	58.24	36.35	24.55	25.56
Testosterone (μg%)	—	—	—	—	—	—	—	—

and Pl males having heaviest adrenals and D animals of both sexes possessing lightest adrenal glands, $F(3,52) = 14.92$, $p<0.01$. As expected, males had heavier body weights than females, $F(1,52) = 9.55$, $p<0.01$, but there were no differences due to environment.

Pr animals had lowest cortisol levels, followed by E, Pl and D in increasing order, $F(3,40) = 5.43$, $p<0.01$. All groups differed significantly from each other according to Newman-Keuls comparisons. Males had higher cortisol levels than did females, $F(1,40) = 12.38$, $p<0.01$. There was considerable variability and no significant differences in testosterone levels. Pr and E groups each had high concentrations of testosterone, while D and Pl males had lower concentrations. Within-group correlations between social interaction behaviors and physiological variables revealed no significant relationship.

DISCUSSION

The E group in this experiment had no better reproductive success than did the Pl and D groups, all crowded groups were much less successful than Pr animals. E animals did not pair-bond, establish cubicle nests, or defend territory. These results were contrary to expectations based on Schwentker's [24] observation that gerbils tend to be monogamous, and Thiessen's [32] report that in a natural setting a pair of gerbils established a territorial claim and drove intruders from their territory. However, Schwentker's observations were made in a breeding colony where adult male-female pairs were housed together for extended periods of time, while Thiessen's paired adult animals were allowed to establish territorial claims before intruders were introduced. In contrast, animals in the present experiment were introduced to their living conditions shortly after weaning and all at the same time. Thus, no animal had prior claim either to a mate or to a particular territory. Most of the crowded animals preferred to huddle to together rather than retreat to cubicles or less crowded corners.

No aggression was observed in home cages until the animals became sexually mature. After that time some animals were frequently engaged in aggressive and nonaggressive contacts with certain other animals. One particular Pl female was observed almost daily to chase and fight with another female, an outcast which was eventually killed. However, in spite of a high home cage aggression score, the attacker was never observed in combat with any other resident during the daily observations, and her social interaction aggression score was low. She was 1 of 2 females which later produced a litter in the Pl environment. Other animals were less restricted in their encounters, but still confined their observed attacks to a small number of residents. Still others were never observed to engage in any aggressive encounters. The lack of correlation between home cage and social interaction aggression is in agreement with several recent papers which have questioned the unitary concept of dominance by pointing out that cross-situational dominant/submissive relationships frequently do not hold [14, 22, 34]. Difference in mean levels of social or environmental stimulation in the 2 situations may have been a factor in this lack of correlation [35] as well as familiarity vs. strangeness of the test conditions and conspecifics encountered.

Although E animals exhibited somewhat more social interaction aggression than other crowded groups, none was killed in the home cage. On the other hand, 4 animals in the Pl condition and 1 in the D condition were killed by cagemates. Thus, the E environment may have offered some protection against injury of its inhabitants.

In this experiment Pr animals possessed the heaviest adrenal glands, yet exhibited the lowest cortisol levels. Furthermore, cortisol levels in the crowded animals were considerably higher than those of paired animals in this experiment as well as those previously reported for gerbils housed singly in standard cages [20,30] or 4/cage [30]. (It should be noted that though Spencer *et al.* [30] report corticosterone levels, rather than cortisol, it is likely that they actually measured cortisol levels, since the extraction method they used did not separate the two. Oliver and Peron [21] report that corticosterone was not detectable in gerbil plasma by their fluorometric technique which employed chromatography to separate the steroids, while cortisol was the major corticoid in peripheral blood.) The present high cortisol levels and low adrenal weights in crowded animals, taken together, would seem to indicate that these animals were approaching the stage described by Selye [26] as adrenal exhaustion. Christian [11] noted a similar decrease in adrenal weight in mice housed 32/cage, though weights increased with greater density from 2 to 16/cage. This was initially explained in terms of deterioration of the social hierarchy in the 32/cage group, but later [12] evidence pointed to adrenal exhaustion in those animals.

It should be noted that cortisol levels of E animals were intermediate between the low values of paired animals and the higher ones of Pl and D animals. This, together with the high testosterone concentrations found in E males as compared to the other crowded groups indicates a diminution of at least the hormonal effects of crowding among the enriched animals. However, except for the lack of deaths in the E condition, there was no evidence for any diminution of behavioral and reproductive effects of crowding.

Testosterone levels in the present experiment are higher than those reported for individually housed rats (0.2 – 1.5 $\mu g\%$, mean = $0.6\mu g\%$) by Bartke *et al.* [3], but within the same range as those reported by the same authors for mice housed 4/cage (0.04 – 4.4 $\mu g\%$, mean = $1.9\mu g\%$). To our knowledge, testosterone levels for gerbils have not been reported.

The finding that all groups of crowded animals exhibited high cortisol levels and low aggression scores would seem to support Brain's [6] and Leshner's [19] proposals that ACTH acts to suppress aggressiveness. However correlation coefficients calculated within groups in the present experiment failed to disclose a consistent significant relationship between cortisol levels (and presumably ACTH) and aggression. Furthermore, Bronson (cited in [8]) reported a failure of either physiological or pharmacological doses of ACTH to alter the frequency of aggression in intact, previously isolated C57 mice, and Sigg [25] found that intact adrenals were not necessary for the induction of aggression by isolation in mice. Indeed, he found heavier adrenal glands in the aggressive isolated animals. Bronson and Desjardins [8] further note that experience in a chronic social situation may serve to increase variability in the adrenal-aggression relationship, and that plasma concentrations of corticosterone may not be significantly different in subordinant and dominant mice allowed to live together for 7 days [10]. Therefore, as noted by Leshner [19], the relationship between pituitary-adrenal hormones and aggression is by no means simple and universal.

Finally, cyproterone acetate (an anti-androgen) administered to male gerbils had no significant effect on their aggressiveness [23], while castration was observed to increase aggressive behavior in gerbils [1]. In the present experiment neither testes weights nor testosterone levels were correlated with aggression scores. Thus the lack of correlation between cortisol, testes weights, or testosterone and aggression scores in the present experiment may reflect a general lack of importance of basal levels of seroid hormones (within the range of physiological concentrations) in the mediation of aggressive behavior in this species. Of course other factors, such as altered neural sensitivity to hormones, may complicate the relationship between hormones and behavior. Nevertheless, it is apparent that in the gerbil at least, there is no simple relationship between basal levels of either cortisol or testosterone and aggressiveness. Furthermore, a recent experiment in our lab (Hull, L'Hommedieu, Kastaniotis, & Franz, in preparation) indicates that even gross manipulations of cortisol and ACTH do not produce significant changes in aggressiveness of either intact or olfactory bulbectomized gerbils. Finally, it should be noted that while four days elapsed between the end of behavioral testing and the beginning of blood collection, blood was obtained at the same time of day for all groups, and this was the same time of day that the behavioral tests had been run.

In summary, environmental enrichment and available refuge did ameliorate the usual hormonal responses to crowding. E animals had intermediate cortisol levels and E males had as high concentrations of testosterone as did Pr males. However, E animals did not pair-bond or establish cubicle nests or territorial claims, and they exhibited no better reproductive success than any other crowded group. Furthermore, all crowded groups had lighter adrenal glands and higher cortisol levels than paired animals; these results may be taken as evidence of approaching adrenal exhaustion. There was no significant correlation between any hormonal index and any behavioral measure. It would appear that there is some factor in the crowded condition which draws gerbils into close groups, depresses their reproductive success, depresses their marking and aggression directed toward a stranger, and which is neither directly related to baseline levels of cortisol or testosterone, nor greatly influenced by type of environmental surroundings.

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