GERBILS FOSTERED TO RAT MOTHERS:

EFFECTS ON ADULT BEHAVIOR

by

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ABSTRACT

At 72 hrs after birth gerbil litters were divided and half the pups fostered to lactating mother rats whose own pups were removed. Remaining pups were returned to their natural mothers. Rat-reared gerbils had a higher mortality rate than control gerbils but weighed more at weaning. At 60 days control gerbils weighed more and at 100 days there was no difference in weight. When tested in the open-field from Day 128 to Day 135, rat-reared gerbils were found to locomote and rear less than control subjects. There was no difference in defecation or in the tendency to enter the central squares as a result of fostering. The paper shredding and territorial marking activity of the subjects were also measured but no clear cut effects of fostering emerged on these tests. The results were discussed in relation to those obtained with rat-reared mice and it was suggested that species differences in maternal behavior, especially handling and retrieving of pups, may be the crucial factor responsible for fostering effects.

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A number of treatments, when imposed on infant rodents during the preweaning period of development have been found to modify certain behavioral and physiological characteristics of the adult organism. Such treatments include handling, shock, and hypothermia. There is some controversy, however, as to the manner in which these variables exert their effect. Recent evidence suggests that their effects are extremely complex and may be mediated by altering the mother's behavior towards her offspring as well as through direct action on the offspring themselves (Hudgens, Chilgren, and Palardy, 1972). Early experience studies are now beginning to concentrate on the mother and her interactions with the young as important variables mediating the handling phenomenon and similar effects.

One approach to studying the maternal influence on later behavior is the method of cross-fostering, i.e., fostering one species or strain to another. By this procedure, one can begin to separate the genetic-prenatal contributions to behavioral variance from the postnatal maternal factors. In the normal development of the young animal these factors are usually confounded. If animals which are cross-fostered exhibit behaviors which differ significantly from those of control animals, we can conclude that such behaviors are affected by the nature of the postparturient environment (Denenberg, 1970). By directly manipulating the mother-infant relationship and analyzing the maternal behavior patterns which affect the offspring's performance, we may soon be in a position to isolate the critical aspects of motherhood.

The majority of cross-fostering studies have involved the mouse, Mus musculus, as the fostered species and the rat, Rattus norvegicus as the foster mother species. For the purposes of the present paper,

the term "fostering treatment" will refer exclusively to fostering to a rat mother, and following Denenberg (1970), the term "fostering effect" will refer to the rather consistent pattern of results obtained from C57BL/10J mice fostered to rat mothers.

Denenberg, Hudgens, and Zarrow (1964) first reported that mouse pups which had been fostered to a lactating mother rat displayed behavioral characteristics in adulthood which differed markedly from those of mice reared by their natural mothers. Rat-reared mice were found to be less active in an open-field, to prefer a rat to a mouse on a two choice social test, and to show a lower incidence of fighting compared to mouse-reared controls.

In subsequent studies, Denenberg and his co-workers have attempted to narrow down the range of possible variables that could be responsible for the fostering effect as well as extending the number of dependent measures employed. Apparently fostering per se is not important since in studies where this variable has been controlled, i.e., where mouse pups are fostered to a mouse mother, it was found to be without effect (Hudgens, Denenberg, and Zarrow, 1967).

In order to eliminate the possibility that observed differences between rat-reared and mouse-reared mice are due to biochemical differences between rat and mouse milk, Denenberg, Rosenberg, Paschke, and Zarrow (1969) developed a rat "aunt" preparation. This was a nonpregnant, nonlactating female that had first been primed by exposure to a rat mother and her pups for six days. It was then placed in a cage with a mouse mother and her pups. As expected such aunts behaved maternally towards the mouse offspring, nest-building, retrieving, and hovering above them. It was found that mice tended by rat aunts had a significantly lower corticosterone response

to novel stimulation, thereby confirming an earlier result but with the milk factor controlled. Although these mice were also less active in the open-field than control mice, this difference was not significant. It therefore appears that the rat aunt preparation has a similar, although somewhat less potent effect to the true foster rat mother.

Since the milk factor did not appear to be the primary variable responsible for the fostering effect, Denenberg, Paschke, Zarrow, and Rosenberg (1969) investigated the possibility that the effect was mediated by noncontact stimulation including vision, olfaction, and audition. The only dependent measure taken in this study was the plasma corticosterone response to a novel stimulus since previous studies had shown this measure to be most sensitive to the fostering treatment. Experimental mice were placed with their own mothers in a cage separated from an adult female nonlactating rat by a double mesh partition, so presumably they could see, hear, and smell the rat, but no physical contact was possible. Control mice were reared similarly in the presence of an adult nonlactating female mouse. At the time of weaning the plasma corticosterone response was found to be identical, thus indirectly supporting the hypothesis that actual physical contact between the rat mother and the mouse pups is necessary to mediate the observed physiological changes in the mouse.

The role of physical contact was observed somewhat more directly by Rosenberg, Denenberg, and Zarrow (1970). They used two types of rat aunt preparation that differed in the amount of maternal behavior they exhibited. One was similar to the type described previously with the addition that their nipples were thalectomized. The second type were adult female thalectomized rats who had just given birth to their own

young. Thus neither type could give milk. The rat aunts were placed with mouse mothers and their litters and their maternal behavior was rated twice daily on a seven-point scale from Day 5 through Day 20. The post partum rat aunt preparation was found to result in a greater degree of maternal interaction with pups compared to control aunts. In addition, the open-field activity and plasma corticosterone response of the pups reared by these two types of aunts were compared with each other and with a group of pups raised by mouse mothers.

The open-field activity of the post partum aunt group was found to be greatly reduced compared to the two control groups. The adrenal response to novelty was also found to differ among the three groups. The control group gave the greatest response, the control aunt group gave a lesser response, and the post partum aunt group gave the lowest response but the only significant difference was between the two extreme groups. In addition to the between-group comparisons, within-group correlations were calculated. A significant negative relationship was obtained between maternal ratings and corticosterone level after exposure to a novel stimulus although correlations between maternal ratings and activity scores were small and nonsignificant.

In view of these findings, it is interesting to note that physical contact between the mother and pups has also been implicated as an important mediator of the handling phenomen. Bell, Nitschke, Gorry, and Zachman (1971) found that when neonatal pups of the species, Peromyscus maniculatus bairdi were handled for 3 minutes, they differed from nonhandled pups in the average number of ultrasonic vocalizations emitted. In another study using rat pups, Bell, Nitschke, Bell, and Zachman (in press) correlated ultrasonic vocalization produced by cold exposure with increased maternal retrieving

and grooming. These data strongly suggest that handling pups results in modified maternal behavior which may be responsible for later changes in offspring behavior. An analysis of infant vocalization and maternal behavior associated with cross-fostering has not been carried out but the latter studies suggest the possibility of similar mechanisms operating in both cases.

All studies of rat-reared mice conducted in Denenberg's laboratory used the C57BL/10J strain with the exception of one by Paschke, Denenberg, and Zarrow (1971) which compared the effects of the fostering treatment on Swiss albino and C57BL/10J mice. They found that the effect of the treatment was similar on some measures but differed on others as a function of strain. The treatment by strain interaction was most pronounced on the fighting measure. A reduced incidence of fighting in C57BL/10J mice reared by rats is one of the most consistent findings obtained in these fostering studies yet fostering Swiss albino mice to rat mothers has no detectable effect on their aggressive behavior.

Southwick (1968) employed a reciprocal cross-fostering procedure with two inbred strains of mice that differed in their level of aggression. He found that fostering males of the passive strain (A/J) to mothers of the aggressive strain (CFW) significantly increased their aggression over that of controls whereas fostering to A/J mothers did not reduce the aggression of CFW males.

Southwick's study demonstrates maternal influence on the development of aggression in A/J mice but the kinds of conclusions one can draw from his study (or any study involving a reciprocal cross) are not the same as one can draw from situations where the strain of the mother is constant and the strain or species of fostered offspring is varied, e.g., Paschke,

Denenberg, and Zarrow (1971). However, because pups of different strains may differ in certain stimulus characteristics, the foster mother might respond differently to pups of one strain than she would to pups of another. Ressler (1962) has presented evidence that the strain of pups does, in fact, influence maternal behavior. He found that BALB/C pups received more handling from both BALB/C mothers and C57BL/10 mothers than did C57BL/10 pups.

Hudgens, Denenberg, and Zarrow (1967) studied the open-field activity of rat mothers as a function of species reared. For mothers which had reared rat pups, activity decreased over the first four days following weaning, while the activity of mothers rearing mouse pups increased over the same period. Thus, not only is the mother an important variable in determining the behavior of the pups, but the pups influence the behavior of the mother as well. When attempting to interpret the results of cross-fostering, it therefore seems necessary to consider the dynamic nature of the mother-infant relationship.

In the present study gerbil pups were fostered to rat mothers and the effects of the treatment on the gerbils' adult behavior were measured. There were reasons for choosing the gerbil other than simply to extend the generality of the fostering effect to a different species.

Firstly, the mouse and the gerbil are known to differ physiologically in a number of ways, most notably in regard to adrenocortical function. The Mongolian gerbil is a desert animal and can manufacture all its water requirements from its solid food diet and concentrate its urine to a marked degree (Cortez and Peron, 1963). Furthermore, biochemical analysis of the steroids found in adrenal venous blood of gerbils shows that 19-hydroxydeoxycorticosterone constitutes one of the major adrenocortical

secretions whereas corticosterone is found in barely detectable amounts (Oliver and Peron, 1964). In the mouse adrenocortical reactivity to a novel situation, as measured by plasma corticosterone level, has been found to be sensitive to the fostering treatment, rat-reared mice exhibiting a reduced response compared to controls (Denenberg, Rosenberg, Paschke, and Zarrow, 1969). It is possible that this alteration in adrenocortical reactivity may underlie certain behavioral alterations produced by fostering. Therefore the effect of fostering gerbils to rats would be of interest.

Secondly, gerbils exhibit a variety of behaviors which might prove sensitive to the fostering treatment but, because of their species-specificity, have not been possible to investigate in mice. These include shredding of paper and territorial marking.

The function of paper shredding is unknown. It may have some function in nest-building but gerbils in the laboratory will shred paper in excess of that required to construct a nest. They also engage in most vigorous paper-shredding when seemingly excited or disturbed. In support of this casual observation is the finding that gerbils paper-shred immediately after mild foot-shock (Dunham, 1971). Although paper-shredding is a poorly understood behavior, it may be related to other forms of activity such as locomotion and may therefore be sensitive to the fostering treatment.

Territorial marking, on the other hand, has been thoroughly investigated and its basis is fairly well understood. Both males and females rub a ventral sebaceous gland over low lying objects, males marking approximately twice as frequently as females. This difference corresponds roughly to the sex difference in gland size (Thiessen, 1968). A variety of evidence suggests that marking is androgen dependent and that marking frequency as

well as gland size reflects the titre of androgen. Castration in males almost eliminates marking; the gland undergoes a parallel reduction in size (Thiessen, Friend, and Lindzey, 1968). However, the marking response is restored by testosterone propionate and the extent of response recovery is directly proportional to the amount of hormone administered. In gonadally intact males marking frequency correlates positively with both gland size, ($r=.22$), (Thiessen, 1968) and seminal vesicle weight, ($r=.54$), Blum and Thiessen, 1971).

Although marking appears to be androgen dependent, it is clear that marking will not occur unless evoked by the appropriate environmental stimuli. Baran and Glickman (1970) showed that olfactory bulb removal completely eliminates marking and testing animals in the dark significantly reduces it. Thus, olfactory, visual, and probably tactual cues play a role in eliciting and maintaining ventral marking.

A variety of indirect evidence suggests that the function of ventral marking is, in fact, territorial. Thiessen, Owen, and Lindzey (1971) found that males with the highest marking frequencies usually emerge as dominant individuals in paired fighting encounters. However, prior knowledge of marking scores is not a perfect predictor of success in competition, ($r=.44$, $p>.01$), since marking frequency is modified by social stimuli. When two males are introduced both initially mark at a high frequency but once dominance of one male has been established, the defeated male will cease to mark while the dominant male will continue to do so at a high frequency, actually showing a preference for his opponent's territory. A defeated male will even show an avoidance of his opponent's odor in a Y-tube preference test (Nyby, Thiessen, and Wallace, 1970). These authors also found that repression of marking in subordinates was not necessarily

related to decreases in adrogen titre. Thiessen, Owen, and Lindzey (1971) offer the interpretation that given optimal surroundings and no social competition hormonal influences predominate but that there is neural control over marking irrespective of hormone levels.

Because such measures as frequency of territorial marking, gland size, and defecation have been shown to differ for male and female gerbils (Thiessen, Blum, and Lindzey, 1969), it is important to study the effects of the fostering treatment on both sexes. Early experience investigators have typically included only male subjects in their experiments, thereby ignoring any possible interactions the treatment may have with the sex variable.

To summarize, the major purposes of the present study were to assess the effects of the fostering treatment on a variety of adult behaviors of the Mongolian gerbil, to compare the obtained results with the results of previous studies using mice, for those measures in common, and to study any differential effects of the fostering treatment on males and females.

METHOD

Subjects. The subjects were Mongolian gerbils born and raised in the Department of Psychology's animal colony at the University of British Columbia. The parents were obtained from Tumblebrook Farm, Brant Lake, New York and bred at approximately 100 days. The rat mothers were derived from the Long-Evans strain and had been born and raised in the animal colony. At weaning there were 30 rat-reared (RR) pups and 31 control (C) pups. When behavioral testing commenced, the number of subjects in each condition was as follows: RR male (n = 9), RR female (n = 11), C male (n = 16), C female (n = 11). One control female died before testing had been completed, reducing the number of subjects in that group to 10 for all tests except the open-field.

Apparatus. For open-field testing the apparatus was a white board, 1.22 m^2, marked off by black lines into 16 equal squares and having .3 m high white Masonite walls. A fine mesh screen covered the field during testing. A single lamp suspended above the field provided the only source of illumination which was set at 1.0 ft-c.

The apparatus used for territorial marking and fighting tests was a white open field, 60 cm^2 with walls 19 cm high and covered by a heavy mesh screen. The field was divided into 16 imaginary (ie. unmarked) squares and at the nine intersections removable plexiglass pegs were placed, all oriented in the same direction. The pegs were 2.6 cm in length, 1.2 cm in width, and 0.7 cm in height. The surface of each peg was roughened on the top by criss-crossed gouges. Illumination on the floor of the apparatus with the screen in place was 2.0 ft-c and was provided by a single lamp source.

Procedure. Preweaning treatment: All gerbil litters were left untouched with their natural mothers for 72 hrs. Each litter was then removed and placed in a box with paper shavings for 90 mins to allow any

odour to dissipate. Meanwhile, a female lactating rat which had given birth 48 - 120 hrs previously was removed from her own litter and placed in a cage with clean wood shavings. Half of the gerbil litter was then introduced to the rat and the other half returned to the original gerbil mother. Thirteen litters were treated in this manner. Table 1 shows the number of subjects in each litter, their assignment to conditions, and the number of subjects surviving in each condition. Of the rat-reared subjects some were raised in plastic cages, 20.5 cm x 33.0 cm x 17.0 cm with wood shavings and some were reared in metal cages 24.0 cm x 40.4 cm x 17.0 cm with plywood floors and wood shavings and paper as nest material. All control animals were raised in metal cages under identical conditions to the latter rat-reared group. It was originally intended that all subjects, both experimental and control, be reared in plastic cages. However, because the gerbil mothers failed to care for their young under these conditions they were moved to the metal cages. Gerbils which were reared by a rat mother in plastic cages were allowed to remain there until weaning. However, for further litters born, the cage condition was made constant across groups. Of the rat-reared subjects which survived to be tested, 12 were reared in plastic cages and 8 in metal cages. Cages were cleaned four times between fostering and weaning at 23 days. Purina Lab Chow and water were available ad libitum to mother and pups.

Postweaning maintenance: From weaning to 40 days the subjects were housed in metal cages similar to those used during the preweaning period in groups of 2 - 3 littermates per cage without regard to sex. At 40 days the subjects were regrouped according to sex, keeping littermates together where possible. When there was a single subject left over from one litter, it was regrouped with animals from another litter close in age. This procedure

TABLE 1

The Number of Subjects Born, Assignment to Conditions, and Survival Rate within each Litter

		Rat Mother					Gerbil Mother				
Litter no.	Total no. of pups at birth	No. of pups fostered	No. at weaning	No. at testing	Males	Females	No. of pups fostered	No. at weaning	No. at testing	Males	Females
1	9	5	0	0	0	0	4	4	1	1	0
2	5	3	0	0	0	0	2	2	2	2	0
3	9	3	1	1	0	1	3	3	3	2	1
4	9	5	4	2	2	0	4	4	3	2	1
5	8	3	2	2	1	1	5	3	3	1	2
6	7	4	0	0	0	0	3	3	3	1	2
7	6	3	0	0	0	0	3	3	3	2	1
8	5	3	2	1	1	0	2	0	0	0	0
9	8	4	4	3	1	2	4	3	3	3	0
10	9	6	5	3	0	3	3	2	2	0	2
11	6	*6	6	2	1	1	0	0	0	0	0
12	7	*4	3	3	1	2	3	2	2	1	1
13	6	*4	3	3	2	1	2	2	2	1	1
Totals	94	53	30	20	9	11	38	31	27	16	11
**Means	7.23	4.07	3.33	-	-	-	3.17	2.82	-	-	-

*Reared in metal cages

**Based only on litters with at least 1 subject

involved only 5 animals: a male and female from Group RR and one male and two females from Group C. In no case were experimental and control litters mixed. The subjects were given ad lib access to food (Purina Lab Chow and mixed grain) and water. In addition, subjects which developed a cough were administered Megacillin in wet ground chow until the infection appeared to subside. Cages were cleaned twice weekly at which time paper was put into the cages. One day before behavioral testing was begun, the subjects were separated and housed in individual cages, where they remained throughout the testing period. The subjects were weighed at 23 days, 60 days, and 100 days of age.

Because the subjects varied in age by as much as 70 days, they were tested in four separate blocks, each block containing subjects which did not differ in age by more than 10 days. The schedule for behavioral testing was based on the average age of the subjects within each age block. All ages given in subsequent sections of this paper will therefore refer to the average age of the subjects within a block.

Open-field test: Open-field testing began when the subjects were 128 days old. It consisted of 8 daily 5 min sessions conducted between 7:00 and 11:00 pm during the dark phase of the light cycle. Each subject was carried individually in a transporting cage from the animal colony to the testing room. It was tested then immediately returned to its home cage. Testing consisted of placing the animal in a designated square of the apparatus and observing and recording certain aspects of its behavior for a 5 min period. After each trial the field was washed with a mild vinegar solution and dried. The order of testing was systematically varied among the four groups over days, although the order within each group remained constant.

The following measures were obtained: (a) total number of squares entered, with entrance defined as placing at least both forepaws in a square,

(b) "thigmotactic ratio" - the number of central squares entered/total number of squares entered, (c) number of seconds spent in the four central squares, (d) number of rears, and (e) number of faecal pellets deposited.

Paper-shredding test: From day 135 - 137, the paper-shredding activity of the animals was assessed. The test was conducted from 1:30 - 4:30 pm during the light phase of the cycle. Each subject was removed from its home cage and placed in a temporary holding cage for 20 mins during which time the home cage was cleaned and all bedding material and food removed. Four folded sheets of paper, 28.8 cm x 15.1 cm, which together weighed 33.0 g $\pm$ 0.2 g were placed on the floor of the cage. Each subject was then returned to its respective home cage and left undisturbed for 2.5 hrs. To avoid the possibility of soiling the paper and thereby adding extraneous weight, food and water were not available during this time. At the end of the testing period, the gerbils were again removed from their home cages and placed in the holding cages. The plywood floors were turned over and the paper dumped into the mesh bottom of the home cage. Shredded paper was filtered through the metal grids and remaining paper weighed. Subjects were then returned to their home cages with the plywood floors replaced, and bedding material, food, and water available ad lib. The identical procedure was followed on the two following days.

Territorial marking test: From day 138 - 145, subjects were tested nightly between 7:00 - 11:00 pm for territorial marking. Each subject was treated in the same manner as for open-field testing. During a 5 min observation period the experimenter recorded the frequency of ventral marking responses with a hand tally. Noise from the instrument was muffled by wrapping a towel around the experimenter's hand. Only discreet responses directed over the pegs were scored. The number of faecal boli were also counted at the end of each trial. The pegs were then removed, soaked in

a mild vinegar solution for 5 mins and dried. The apparatus was also cleaned and dried between the testing of each subject. The order of testing was rotated between each of the four sex-treatment groups each day.

Fighting test: Fighting encounters between pairs of subjects were conducted on day 146. Within each sex-treatment group within each age block, subjects were randomly assigned to pairs. For groups with an odd number of subjects, one animal was randomly chosen to serve twice. Two subjects in each of the control groups and one subject in each of the rat-reared groups were used in two encounters. To identify each member of a pair their tails were marked with a felt pen, one at the base, one at the tip.

Testing was conducted in the same apparatus as that used to assess territorial marking. Illumination was 2.0 ft-c. The two members of a pair were carried to the testing room in separate cages and placed simultaneously in the apparatus. A stopwatch was used to record the latency to fight from the time the pair was introduced. The subjects were separated after 5 secs of fighting and the trial terminated. If a fight did not exceed 3 secs the subjects were not interrupted and the trial was continued. A maximum latency of 300 secs was allowed. If a fight did not occur within this time the trial was terminated and scored as negative. In such an instance a latency of 300 secs was assigned. A trial was scored as positive if a fight occurred within 5 mins. Only one trial per pair was given.

Gland measurement: At approximately 155 days the gerbils were sacrificed and their ventral sebaceous glands measured. This was done by clipping the hair surrounding the gland, measuring its length and width with a ruler, and computing the area.

RESULTS

An unweighted means analysis of variance procedure (Winer, 1962) was used in all cases where cell frequencies were unequal and there was more than one between-subjects variable. Such cases included the main analyses on all dependent measures with the exception of weight at 23 days. Although n's were unequal for this measure, only one variable (treatment) was involved since the weights for males and females had been combined within each treatment group. Thus, it was possible to apply a standard one-way analysis of variance to this measure.

Because Group RR included subjects which had been reared in two types of maternity cages, it was necessary to perform a subsidiary analysis on Group RR scores for each measure in order to assess the effect of the cage variable. The scores for males and females within each cage condition were combined in these analyses since further partitioning of groups would have reduced the n's to below an acceptable level. Sex was included as a variable in the subsidiary analyses of only the 60-day and 100-day weight measures, for which the n's were somewhat larger. Where repeated measures were obtained on subjects, these scores were added together and the analyses based on the total scores. It was not necessary to use an unweighted means solution for the subsidiary analyses where only one variable was involved.

Offspring Mortality. Of the pups fostered to rat mothers, 58.8 per cent survived to weaning at 23 days whereas the survival rate for pups which were left with their natural mothers was 81.6 per cent.

The survival rate of rat-reared pups from the time of fostering to testing at 128 days was only 37.8 per cent. In contrast, 71.1 per cent of the pups raised by gerbil mothers survived to be tested.

With reference to Group RR only, the pre-weaning survival rate of pups reared in plastic cages was 46.2 per cent compared to 85.7 per cent for pups reared in metal cages. The percentage of rat-reared animals surviving to 128 days was 30.8 per cent for subjects with plastic cage experience and 57.1 per cent for those with metal cage experience.

The cause of preweaning deaths was not determined, however killing by the mother did not appear to be a major cause since pups found dead were rarely mutilated. In only one case was a rat mother observed to kill a pup and in no case were gerbil mothers observed to do so.

The high mortality rate of rat-reared pups between weaning and testing was primarily due to an epidemic of a streptococcus lung infection. The cause of death was determined in only one animal but the symptoms were similar in others.

The four deaths which occurred in the control group between weaning and testing all involved animals which developed a skin infection and were eliminated by the experimenter. A fifth animal died before testing was completed, presumably from a respiratory ailment. Refer to Table 1 for a summary of survival rates of individual litters.

Body Weight. The means for body weight at 23, 60, and 100 days of age are summarized in Tables 2 to 4. At 23 days, gerbils reared by rat mothers weighed more than gerbils reared by gerbil mothers (F=9.81; df=1/59; $p<.01$). Analysis of cage type within Group RR indicated that gerbils reared in metal cages were heavier at weaning than gerbils reared in plastic cages (F=62.46; df=1/28; $p<.01$).

At 60 days, however, control gerbils weighed significantly more than their rat-reared counterparts (F=31.56; df=1/52; $p<.01$). A weight difference between males and females was also apparent at this age (F=15.01;

TABLE 2

Means of 23 Day Weight (grams)

Control	Rat-reared
19.13	22.28

Plastic	Metal
19.31	26.73

TABLE 3

Means of 60 Day Weight (grams)

Control		Rat-reared	
Male	Female	Male	Female
66.62	53.41	49.87	47.37

Plastic		Metal	
Male	Female	Male	Female
50.13	44.00	49.35	52.78

TABLE 4

Means of 100 Day Weight (grams)

Control		Rat-reared	
Male	Female	Male	Female
79.96	62.86	72.41	64.55

Plastic		Metal	
Male	Female	Male	Female
68.72	63.22	77.02	66.87

df=1/52; p<.01), and in addition, the interaction between treatment and sex was significant (F=6.97; df=1/52; p<.05). The weight difference between control males and females was greater than that between rat-reared males and females. The subsidiary analysis for this measure did not reveal any significant effects due to cage type, sex or cage x sex.

For weight at 100 days, the fostering treatment failed to differentiate between the subjects. On the other hand, sex was a highly significant source of variance at this age (F=26.87; df=1/44; p<.01). The treatment x sex interaction was no longer statistically reliable, as it was at 60 days, but the male - female weight difference was still less pronounced in Group RR than in Group C (F=3.69; df=1/44; p<.10). Sex was the only significant source of variance in the subsidiary analysis (F=5.09; df=1/16; p<.05). The analyses for the three weight measures are summarized in Tables 5 to 10.

Open-field Test. Fig. 1 shows the mean number of squares entered on each of the successive test days for males and females of each treatment group. Gerbil-reared gerbils locomoted significantly more than rat-reared gerbils (F=9.21; df=1/43; p<.01). There was no difference between the activity level of males and females and the interaction was also nonsignificant. There was a general decline in locomotion over the eight tests for all groups (F=34.97; df=7/301; p<.01) and a significant treatment x sex x days interaction (F=2.70; df=7/301; p<.05). This interaction apparently reflects the different ordering of the four groups on different days. The other interaction terms failed to attain significance. As Fig. 2 shows and analysis confirmed, there was no difference in activity between rat-reared subjects with plastic and metal cage experience. The data analysis is summarized in Tables 11 and 12.

TABLE 5

Summary of Analysis of Variance of 23 Day Weight: Treatment

Source	df	SS	MS	F	p
Total	60	1057.16	---	---	---
Treatment	1	150.75	150.75	9.81	<.01
Error	59	906.41	15.36	---	---

TABLE 6

Summary of Analysis of Variance of 23 Day Weight: Cage Type within Group RR

Source	df	SS	MS	F	p
Total	29	573.73	---	---	---
Cage	1	396.05	396.05	62.46	<.01
Error	28	177.68	6.34	---	---

TABLE 7

Summary of Analysis of Variance of 60 Day Weight: Treatment

Source	df	SS	MS	F	p
Treatment	1	1794.38	1794.38	31.56	<.01
Sex	1	852.69	852.69	15.01	<.01
T x Sex	1	396.08	396.08	6.97	<.05
Error	52	2953.26	56.79	---	---

TABLE 8

Summary of Analysis of Variance of 60 Day Weight: Cage Type within Group HR

Source	df	SS	MS	F	p
Sex	1	10.39	10.39	< 1	n.s.
Cage	1	91.36	91.36	1.60	n.s.
C x S	1	130.41	130.41	2.29	n.s.
Error	21	1194.71	56.89	---	---

TABLE 9

Summary of Analysis of Variance of 100 Day Weight: Treatment

Source	df	SS	MS	F	p
Treatment	1	98.67	98.67	1.48	n.s.
Sex	1	1791.01	1791.01	26.87	<.01
T x S	1	245.41	245.41	3.69	n.s. (<.10)
Error	44	2932.87	66.65	---	---

TABLE 10

Summary of Analysis of Variance of 100 Day Weight: Cage Type within Group RR

Source	df	SS	MS	F	p
Cage	1	169.93	169.93	3.30	n.s.
Sex	1	261.45	261.45	5.09	<.05
C x S	1	25.65	25.65	<1	n.s.
Error	16	821.80	51.36	----	----

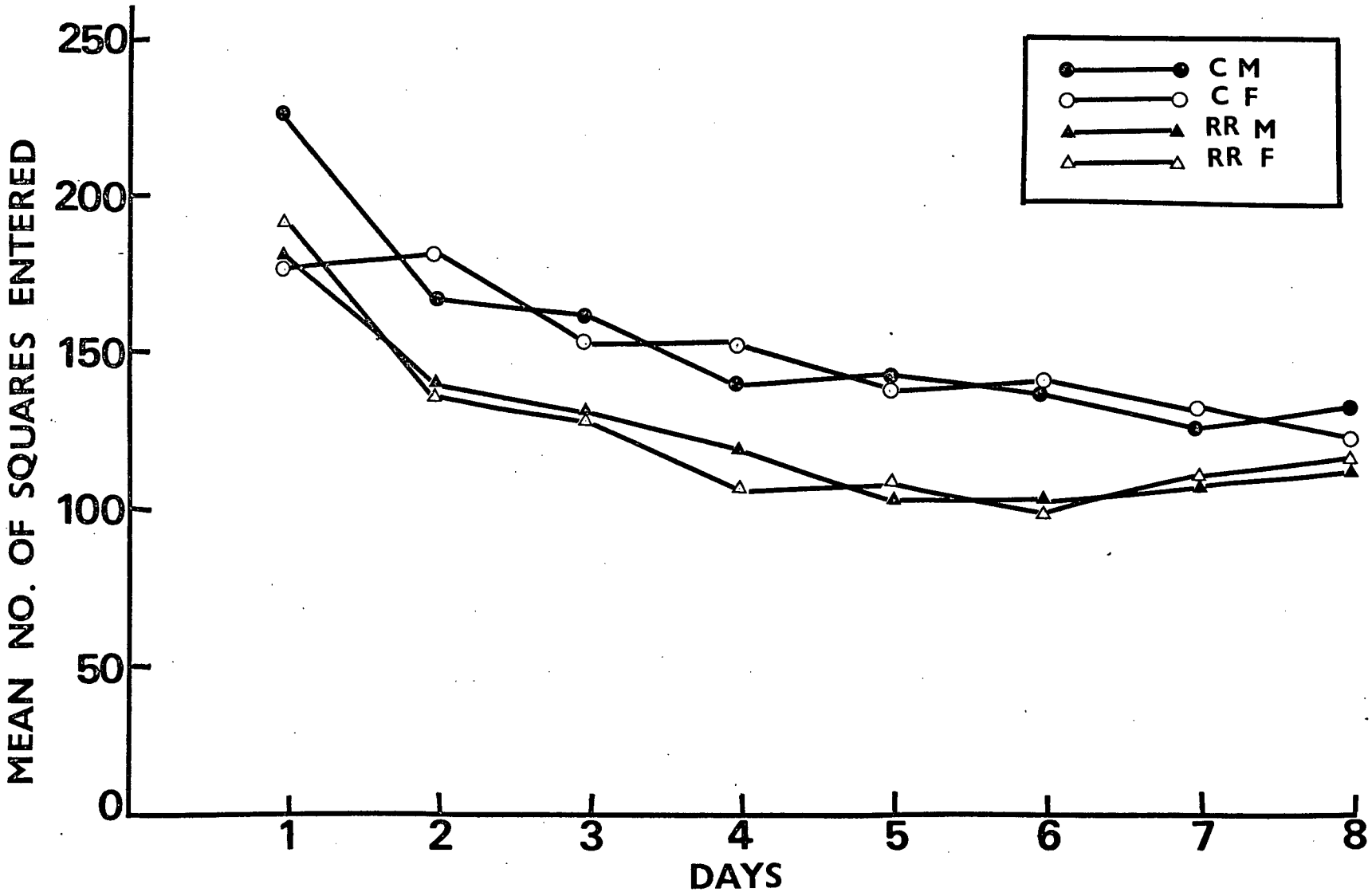

Figure 1. Mean number of squares entered during 5-min open-field tests by control males, control females, rat-reared males, and rat-reared females

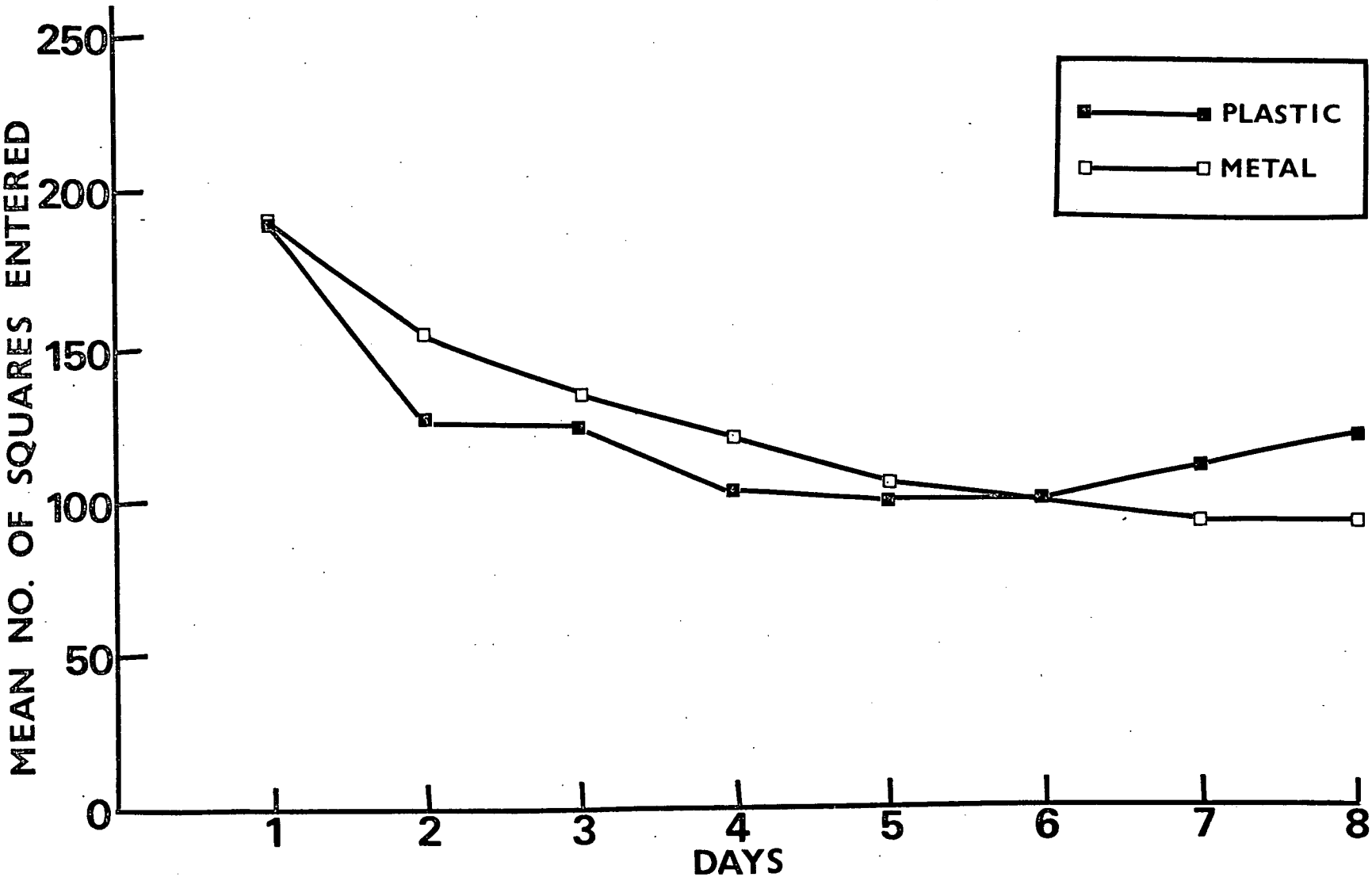

Figure 2. Mean number of squares entered during 5-min open-field tests by rat-reared gerbils raised in metal and plastic cages

TABLE 11

Summary of Analysis of Variance of Total Squares: Treatment

Source	df	SS	MS	F	p
Treatment	1	60746.785	60746.785	9.21	<.01
Sex	1	30.578	30.578	<1	n.s.
T x S	1	473.639	473.638	<1	n.s.
Error Between	43	283779.310	6599.519	---	---
Days	7	231901.160	33129.737	34.97	<.01
T x D	7	8069.086	1152.726	1.22	n.s.
S x D	7	2885.996	412.285	<1	n.s.
T x S x D	7	17884.418	2554.917	2.70	<.05
Error Within	301	285129.520	947.274	---	---

TABLE 12

Summary of Analysis of Variance of Total Squares: Cage Type within Group RR

Source	df	SS	MS	F	p
Total	19	1078653	---	---	---
Cage	1	65965	65965	1.17	n.s.
Error	18	1012688	56260	---	---

The mean rearing scores over days are presented in Fig. 3. It can be seen that both male and female control gerbils reared more than their rat-reared counterparts (F=8.86; df=1/43; $p < .01$). There was no difference in frequency of rearing between the two sexes and the treatment x sex interaction also failed to reach significance. A significant days effect in rearing primarily reflects the increase from Day 1 to Day 2, which all four groups exhibited (F=3.13; df=7/301; $p < .01$). For the remainder of tests rate of rearing showed no consistent trend. None of the interactions with the days variable was significant. As Fig. 4 indicates, there was no evidence that cage type experience influenced rearing frequency within Group RR. Analyses of rearing scores are summarized in Tables 13 and 14.

Fig. 5 indicates that time spent in the center squares was unaffected by either the sex of the subjects or the type of mother they had. Analysis of the results yielded a nonsignificant sex effect, a nonsignificant treatment effect, and a nonsignificant interaction between the two variables. A significant days effect reflects the tendency for center time to increase over days, reaching an asymptote at about Day 3 (F=4.73; df=1/301; $p < .01$). The only significant interaction was that of treatment with days (F=2.14; df=7/301; $p < .05$). Both treatment groups show a parallel increase in center time until Day 5 when Group RR exhibits a sharp decrease. On the other hand, Group C does not show a decline in center time until Day 8. Analysis of the cage variable within Group RR revealed a marginal but nonsignificant effect (F=4.06; df=1/18; $p < .10$). As Fig. 6 suggests, gerbils reared in metal cages showed a slight tendency to spend more time in the center than those reared in plastic cages. The analyses of center time data are summarized in Tables 15 and 16.

The thigmotactic ratio is a measure of the degree of wall-hugging

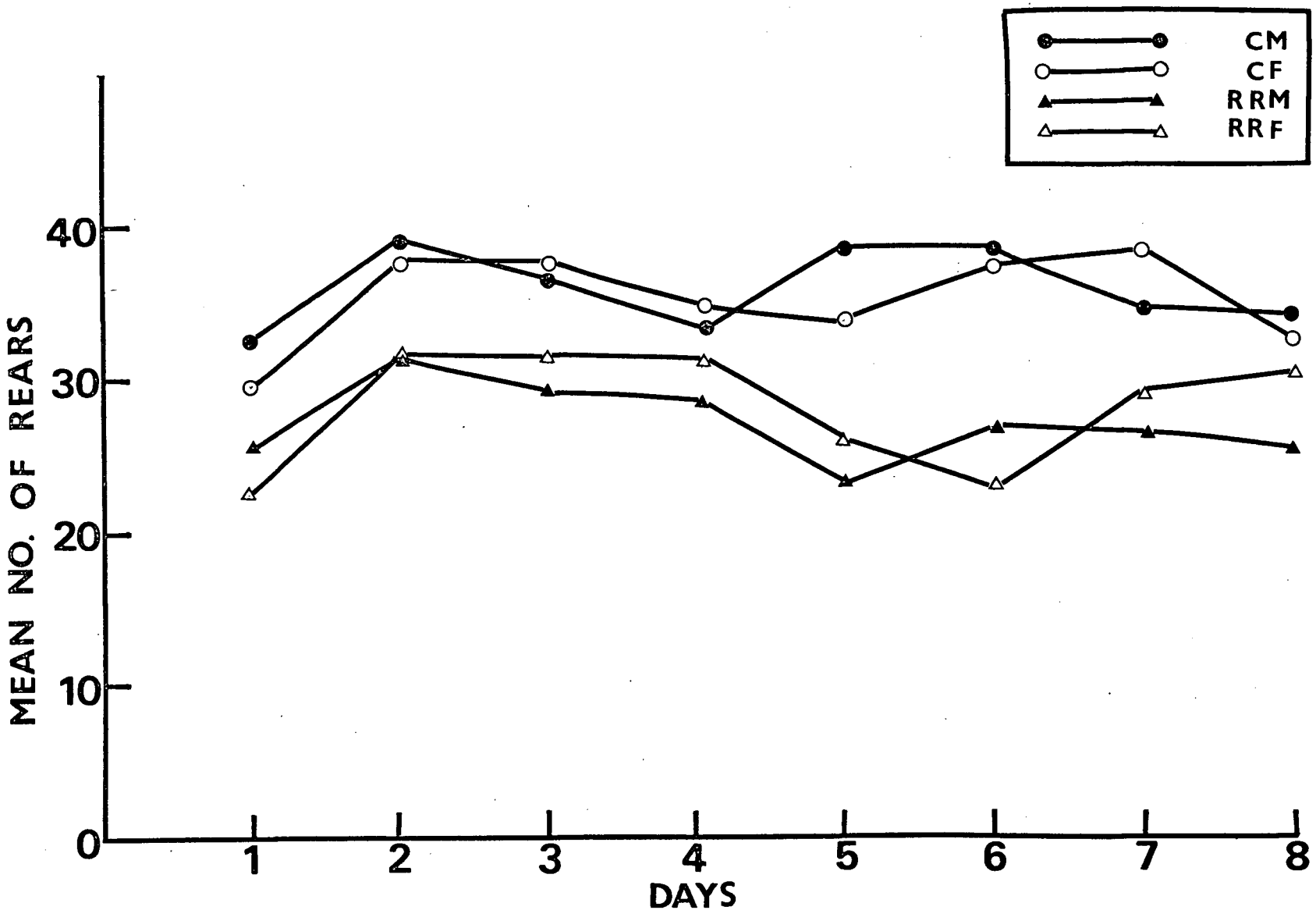

Figure 3. Mean number of rears during 5-min open-field tests by control males, control females, rat-reared males, and rat-reared females

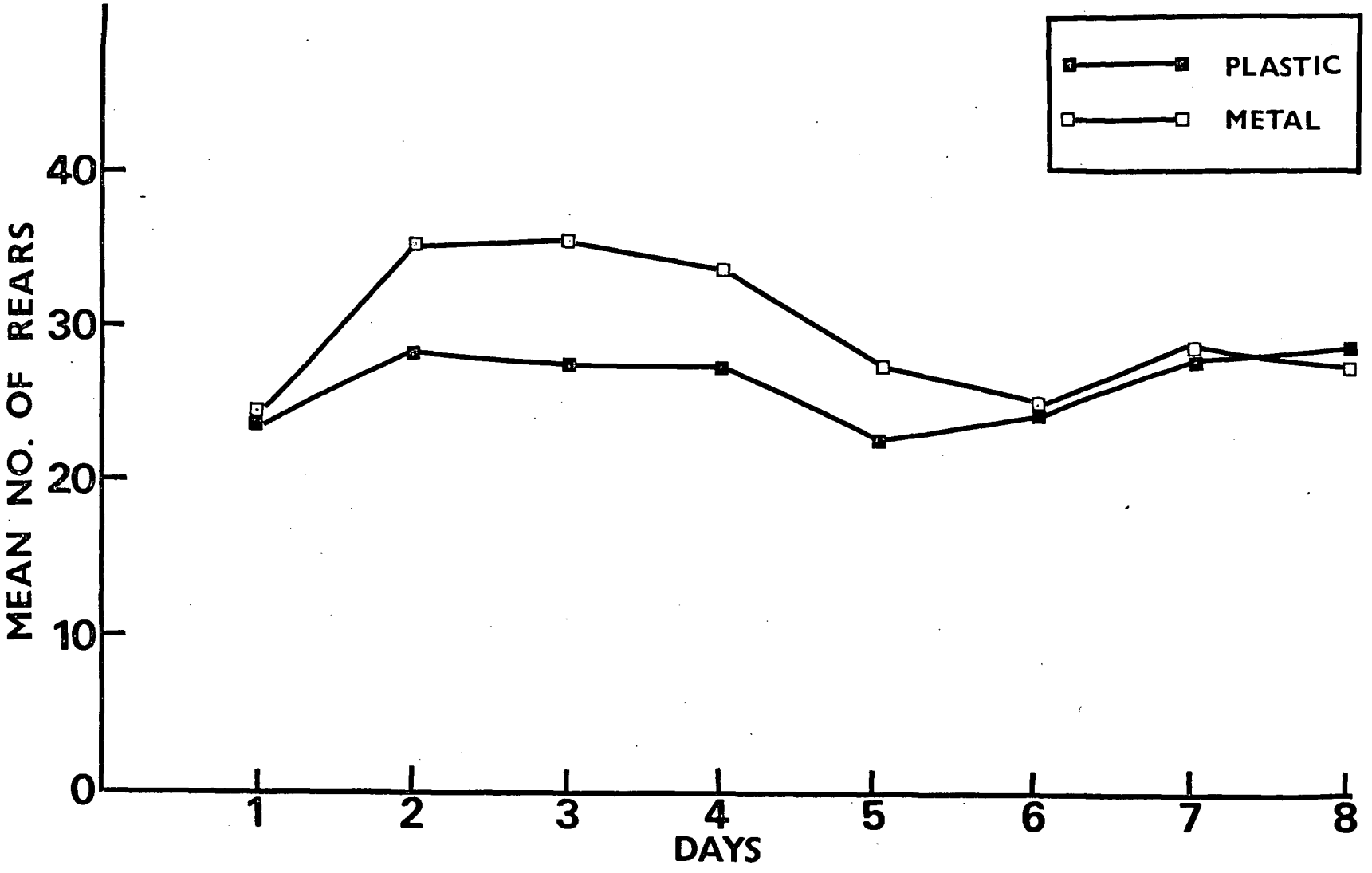

Figure 4. Mean number of rears during 5-min open-field tests by rat-reared gerbils raised in plastic and metal cages

TABLE 13

Summary of Analysis of Variance of Rears: Treatment

Source	df	SS	MS	F	p
Treatment	1	5880.012	5880.012	8.86	<.01
Sex	1	1.308	1.308	<1	n.s.
T x S	1	88.344	88.344	<1	n.s.
Error Between	43	28553.570	664.036	---	---
Days	7	1637.930	233.990	3.13	<.01
T x D	7	723.809	103.401	1.38	n.s.
S x D	7	376.311	53.759	<1	n.s.
T x S x D	7	256.175	36.596	<1	n.s.
Error Within	301	22534.600	74.864	---	---

TABLE 14

Summary of Analysis of Variance of Rears: Cage Effect within Group AR

Source	df	SS	MS	F	p
Total	19	49664.0	---	---	---
Cage	1	3255.2	3255.2	1.26	n.s.
Error	18	46408.8	2578.3	---	---

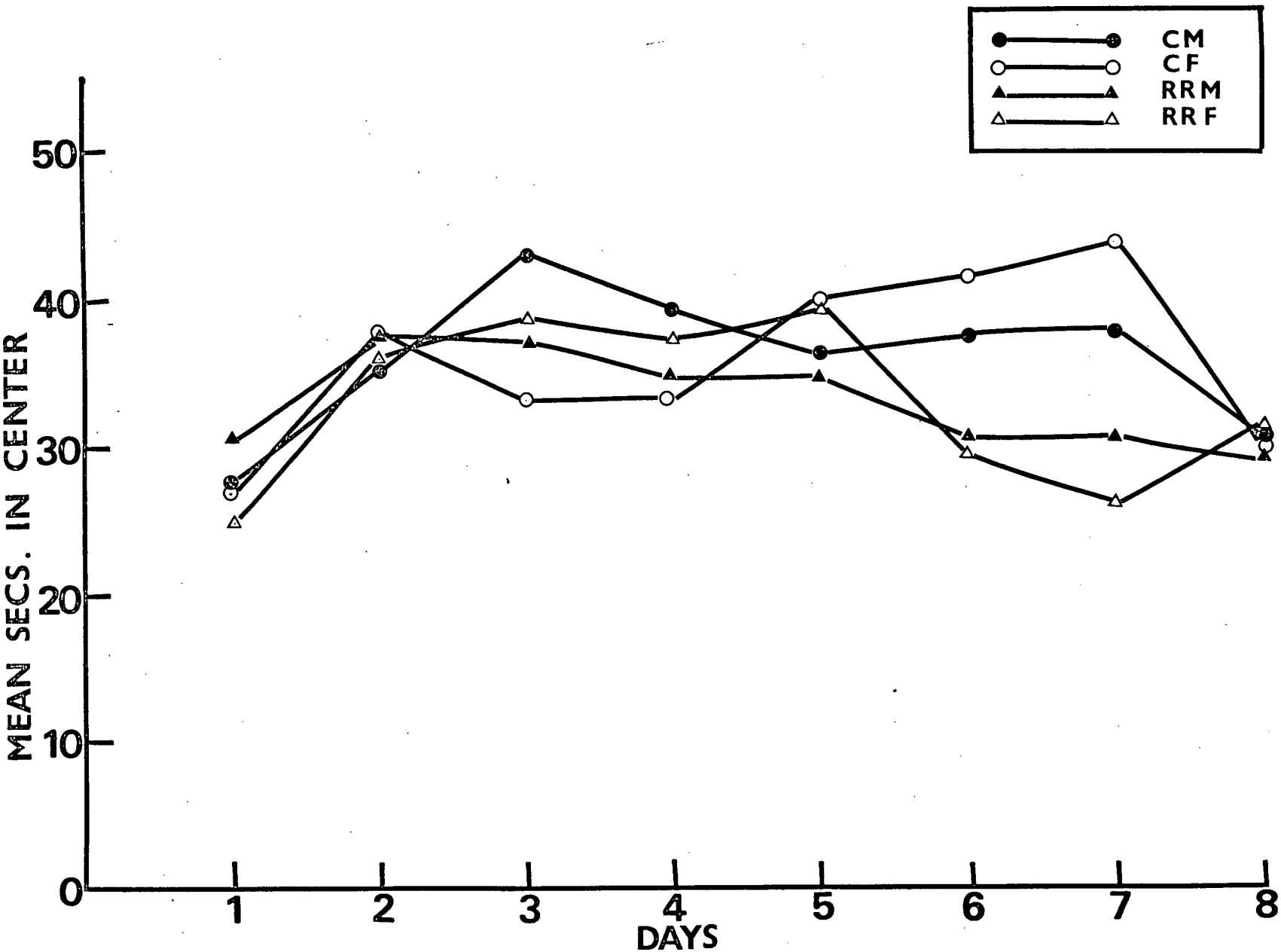

Figure 5. Mean number of seconds spent in the central area of the open-field on each 5-min test by control males, control females, rat-reared males, and rat-reared females

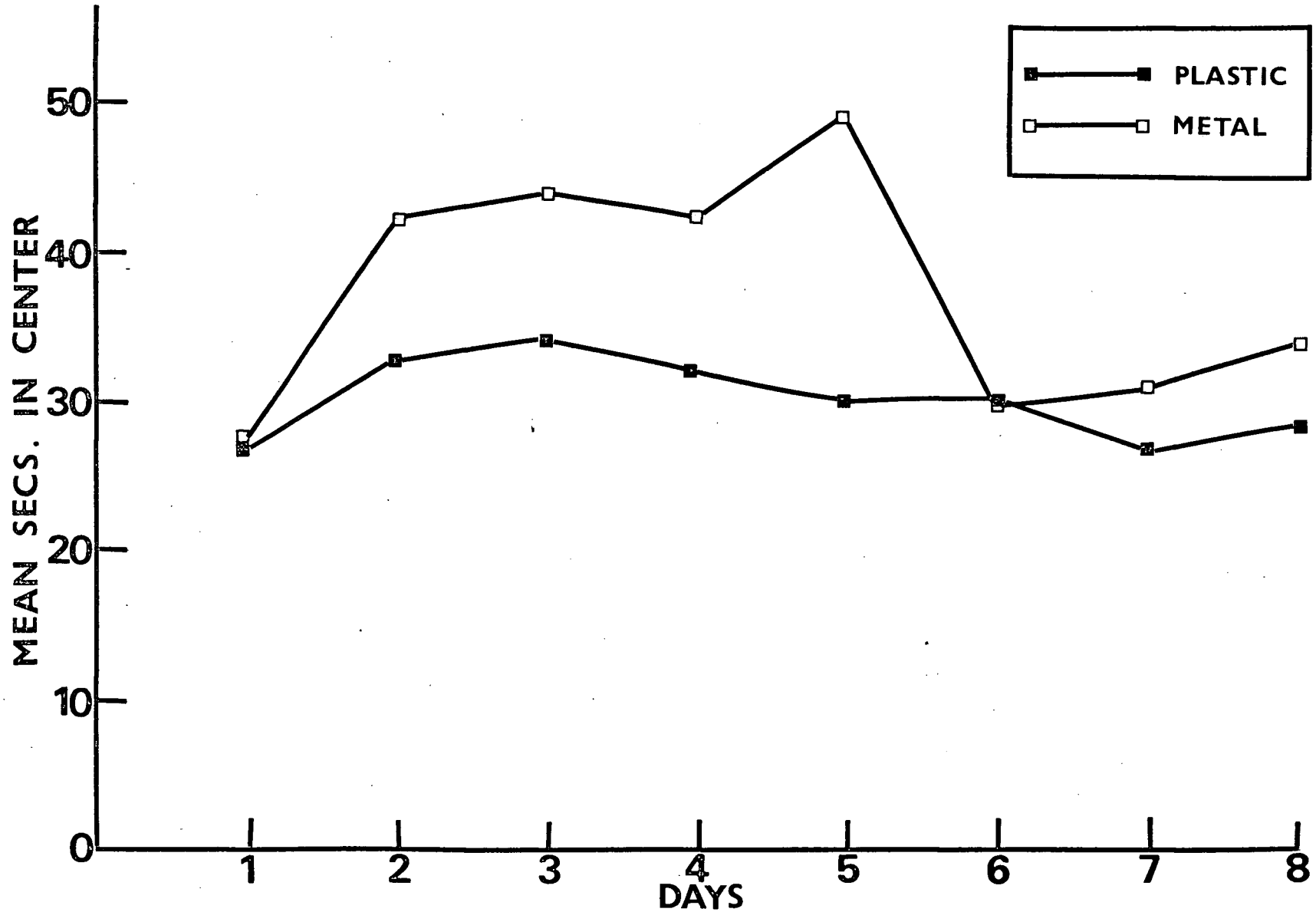

Figure 6. Mean number of seconds spent in the central area of the open-field on each 5-min test by rat-reared gerbils raised in metal and plastic cages

TABLE 15

Summary of Analysis of Variance of Center Time: Treatment

Source	df	SS	MS	F	p
Treatment	1	70304.076	70304.076	1.05	n.s.
Sex	1	108.342	108.342	<1	n.s.
T x S	1	1.699	1.699	<1	n.s.
Error Between	43	2871452.670	66777.969	---	---
Days	7	443341.539	63334.506	4.73	< .01
T x D	7	200451.521	28635.932	2.14	< .05
S x D	7	56963.516	8137.645	<1	n.s.
T x S x D	7	110975.806	15853.687	1.18	n.s.
Error Within	301	4027736.700	13381.185	---	---

TABLE 16

Summary of Analysis of Variance of Center Time: Cage Type within Group HR

Source	df	SS	MS	F	p
Total	19	89220.82	---	---	---
Cage	1	16426.80	16426.80	4.06	n.s. (<10)
Error	18	72794.02	4044.11	---	---

exhibited by an animal. Since the open-field contains 16 squares, 4 central and 12 peripheral, one would expect to obtain a thigmotactic ratio of .25 if the animal was entering the squares randomly. Thus a ratio of less than .25 indicates an avoidance of the center squares (or an attraction to the peripheral ones) while a ratio of greater than .25 indicates the reverse.

As Fig. 7 illustrates, there was little difference between the thigmotactic ratios of males and females or between those of rat-reared and control gerbils. Analysis of these data (summarized in Table 17) showed that sex, treatment, and the interaction between them were all nonsignificant sources of variance. Analysis further revealed a significant days effect (F=10.92; df=7/301; $p < .01$). and a barely significant interaction of treatment with days (F=2.20; df=7/301; $p < .05$). The remaining interactions were not significant. It can be seen from Fig. 7 that the thigmotactic ratio first increases, then decreases over days. Initially the rat-reared gerbils have a higher mean ratio than the control gerbils but the ratios of the two groups become more similar on later tests. The subsidiary analysis (summarized in Table 18) showed cage type to be a highly significant source of variance (F=21.36; df=1/18; $p < .01$). Subjects of Group RR that were reared in metal cages tended to have higher thigmotactic ratios than those reared in plastic cages. This relationship is shown in Fig. 8.

Fig. 9 presents the mean number of faecal boli deposited in the open-field by each of the four groups over the eight test days. As seen in Fig. 9, males defecated more than females. Analysis of variance gave a significant effect due to sex (F=24.77; df=1/43; $p < .01$), a nonsignificant treatment effect, and a significant days effect (F=5.09; df=7/301; $p < .01$). The only interaction to attain significance was sex x days (F=3.25; df=3.25; $p < .01$). While the frequency of defecation increased over days for all

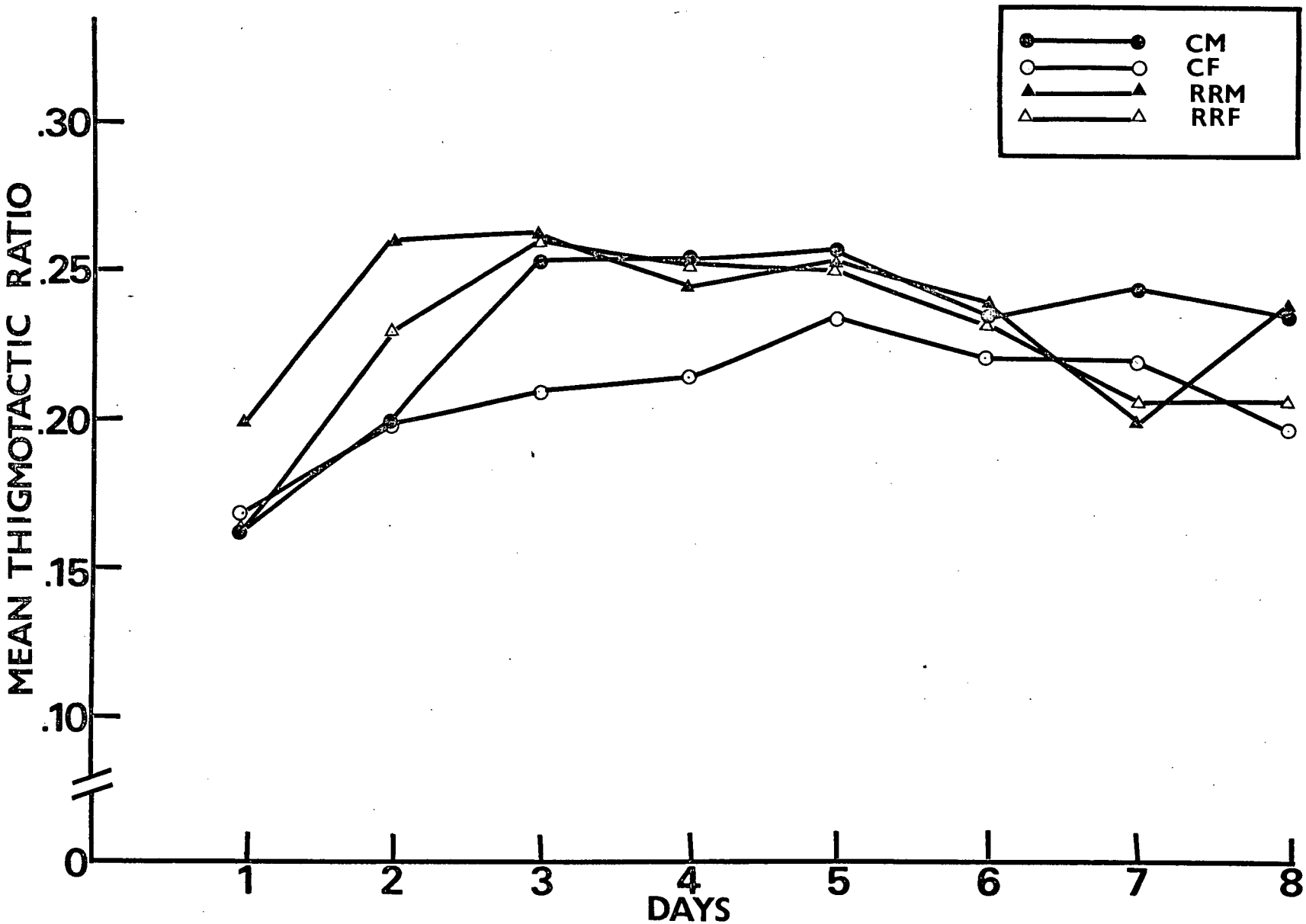

Figure 7. Mean thigmotactic ratio of control males, control females, rat-reared males, and rat-reared females during 5-min open-field tests

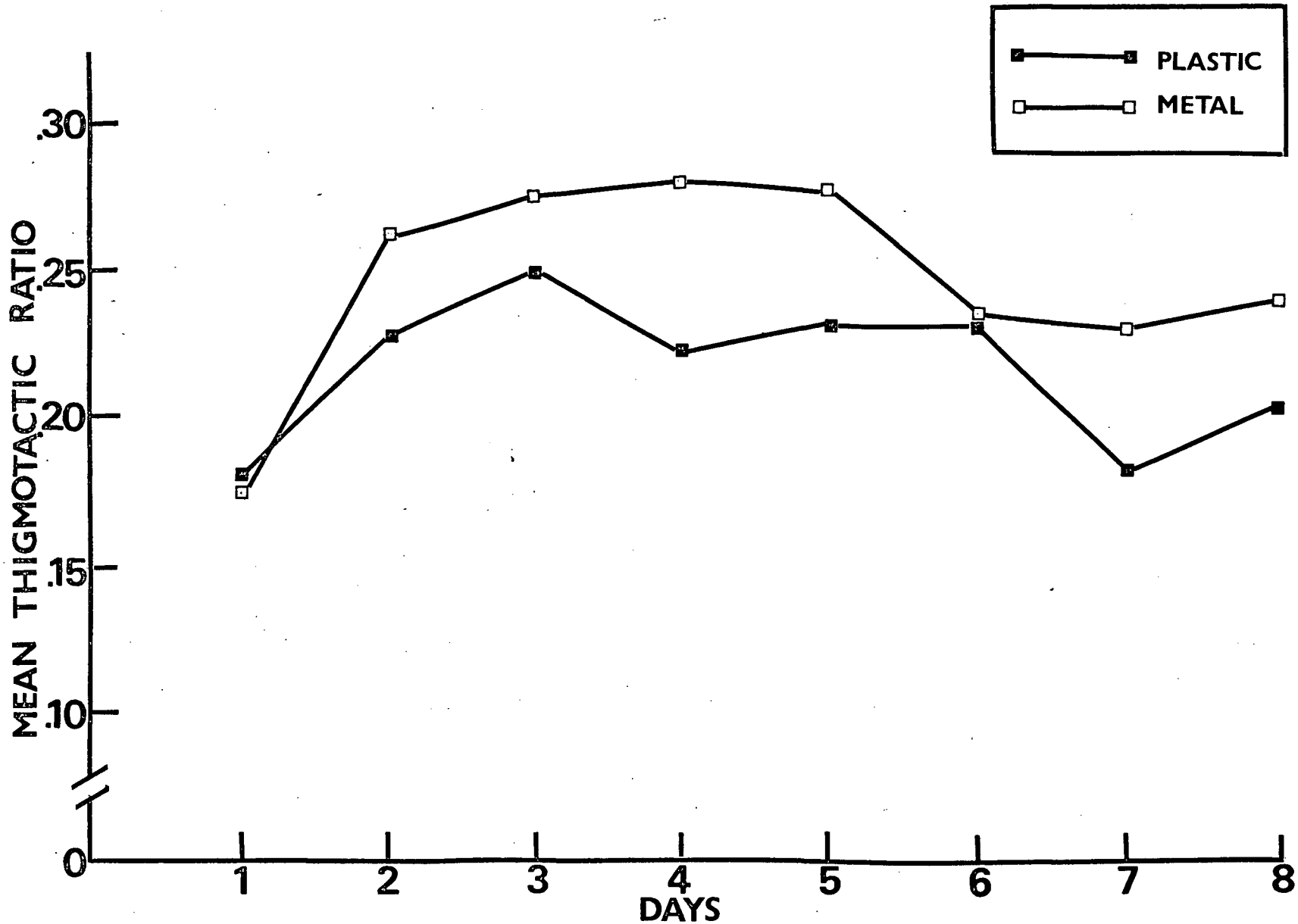

Figure 8. Mean thigmotactic ratio of rat-reared gerbils raised in metal and plastic cages during 5-min open-field tests

TABLE 17

Summary of Analysis of Variance of Thigmotactic Ratio: Treatment

Source	df	SS	MS	F	p
Treatment	1	121.05	121.05	1.32	n.s.
Sex	1	250.72	250.72	2.73	n.s.
T x S	1	25.64	25.64	<1	n.s.
Error Between	43	3953.29	91.94	---	---
Days	7	1849.04	264.15	10.92	<.01
T x D	7	372.81	53.26	2.20	<.05
S x D	7	54.53	7.79	<1	n.s.
T x S x D	7	216.88	30.98	1.28	n.s.
Error Within	301	7277.49	24.18	---	---

TABLE 18

Summary of Analysis of Variance of Thigmotactic Ratio: Cage Type within Group RR

Source	df	SS	MS	F	p
Total	19	.5791	---	---	---
Cage	1	.3141	.3141	21.36	<.01
Error	18	.2650	.0147	---	---

groups, males showed a much sharper initial increase than females did. Within Group RR, cage type experience also influenced defecation in the open-field (F=7·52; df=1/18; p<·01). Those subjects which had the metal cage preweaning environment defecated more than those with plastic cage experience. Fig. 10 illustrates this effect. The analyses of variance for open-field defecation are summarized in Tables 19 and 20.

Paper-shredding Test. Fig. 11 shows the amount of paper shredded on three consecutive test days for the four groups of subjects. No significant main effects or interactions were found when analysis of variance was applied to the data. Although males tended to shred more paper than females, this difference did not reach the criterion for significance (F=3.89; df=1/42; p<·10). The subsidiary analysis, on the other hand, produced a highly significant difference between the metal cage and plastic cage subjects (F=25.80; df=1/18; p<·01). Those subjects with early experience in the metal cages shredded more paper on the three tests than those subjects with early plastic cage experience. This difference in paper-shredding activity can be seen in Fig. 12. The analysis of variance summaries are presented in Tables 21 and 22.

Territorial Marking Test. Fig. 13 indicates an effect on frequency of territorial marking due to sex as well as an interaction between sex and treatment. Analysis of variance gave a nonsignificant treatment effect and a significant sex effect (F=12.08; df=1/42; p<·01), but showed the interaction between sex and treatment, which is indicated in Fig. 13, to be only marginal (F=3.01; df=1/42; p<·10). In addition, analysis revealed a significant days effect (F=11.76; df=7/294; p<·01), a nonsignificant treatment x days effect, a significant sex x days effect (F=2.06; df=7/294; p<·05), and a significant triple interaction (F=2.97; df=7/294; p<·01).

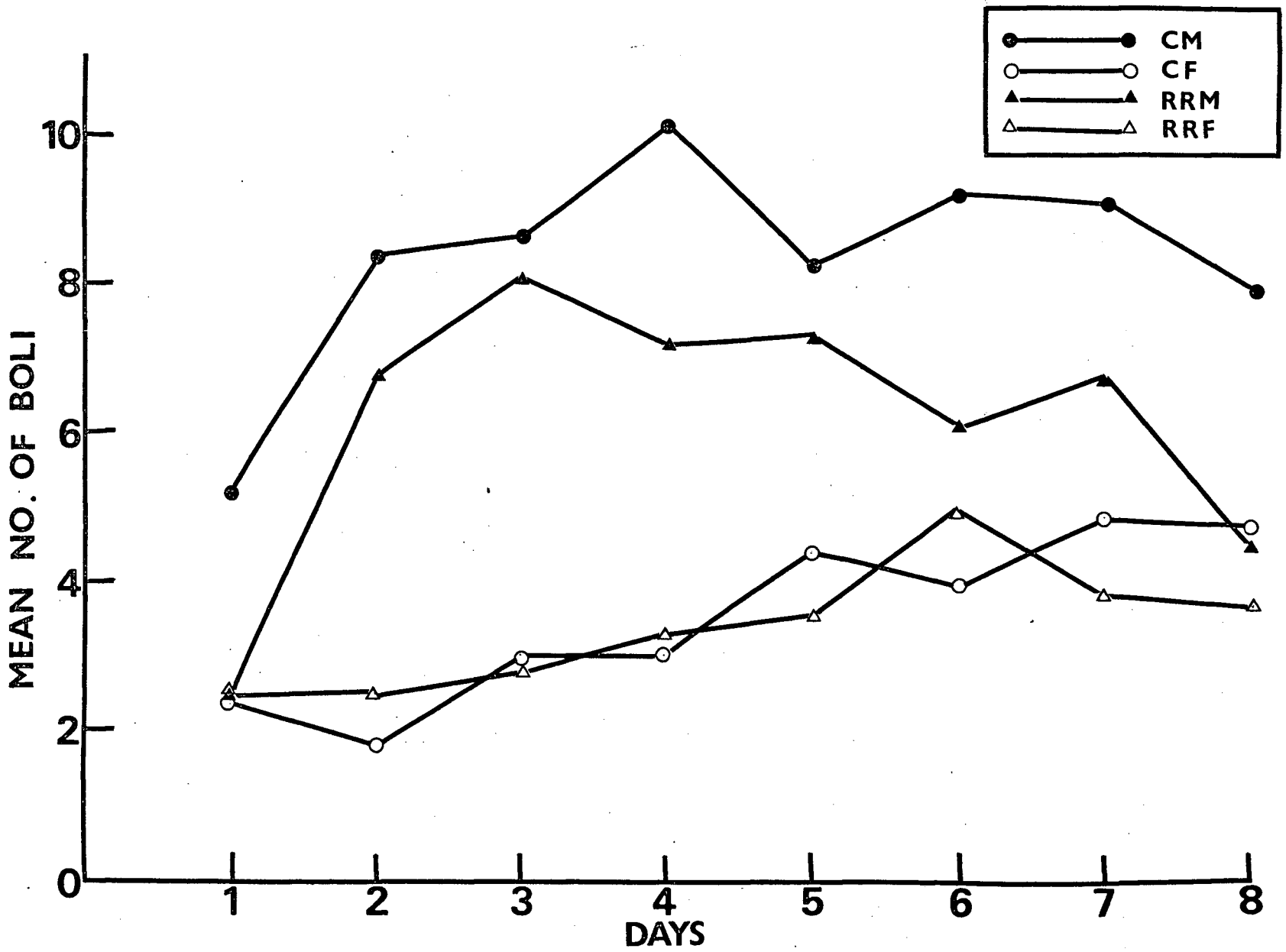

Figure 9. Mean number of boli deposited on each 5-min open-field test by control males, control females, rat-reared males, and rat-reared females

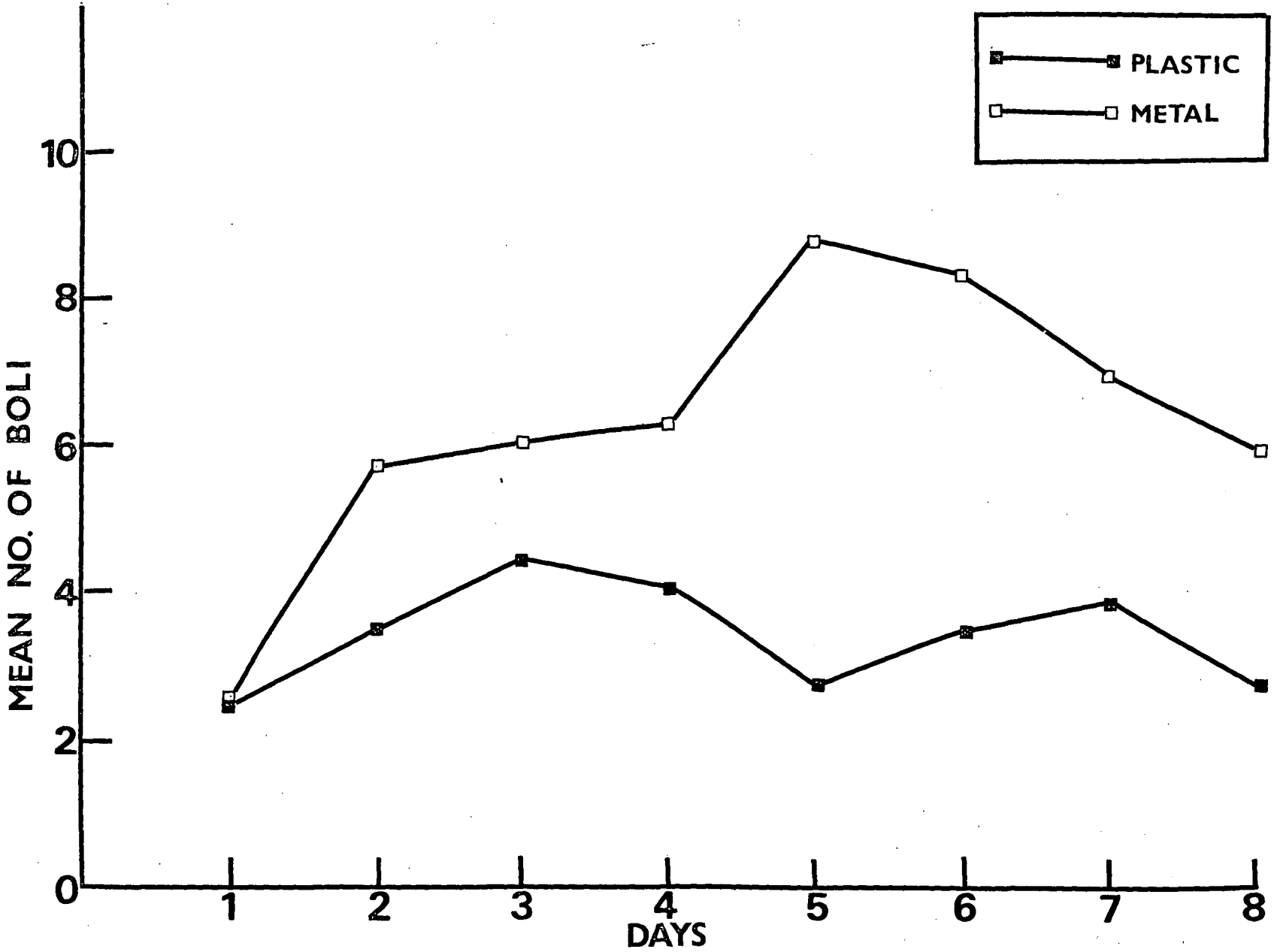

Figure 10. Mean number of boli deposited on each 5-min open-field test by rat-reared gerbils raised in metal and plastic cages

TABLE 19

Summary of Analysis of Variance of Open-field Boli: Treatment

Source	df	SS	MS	F	p
Treatment	1	115.072	115.072	2.25	n.s.
Sex	1	1268.108	1268.108	24.77	<.01
T x S	1	97.302	97.302	1.90	n.s.
Error Between	43	2201.305	51.193	---	---
Days	7	311.196	44.457	5.09	<.01
T x D	7	28.034	4.005	<1	n.s.
S x D	7	198.556	28.365	3.25	<.01
T x S x D	7	41.201	5.886	<1	n.s.
Error Within	301	2628.834	8.734	---	---

TABLE 20

Summary of Analysis of Variance of Open-field Boli: Cage Effect within Group RR

Source	df	SS	MS	F	p
Total	19	8924.95	---	---	---
Cage	1	2632.03	2632.03	7.52	<.05
Error	18	6292.92	349.60	---	---

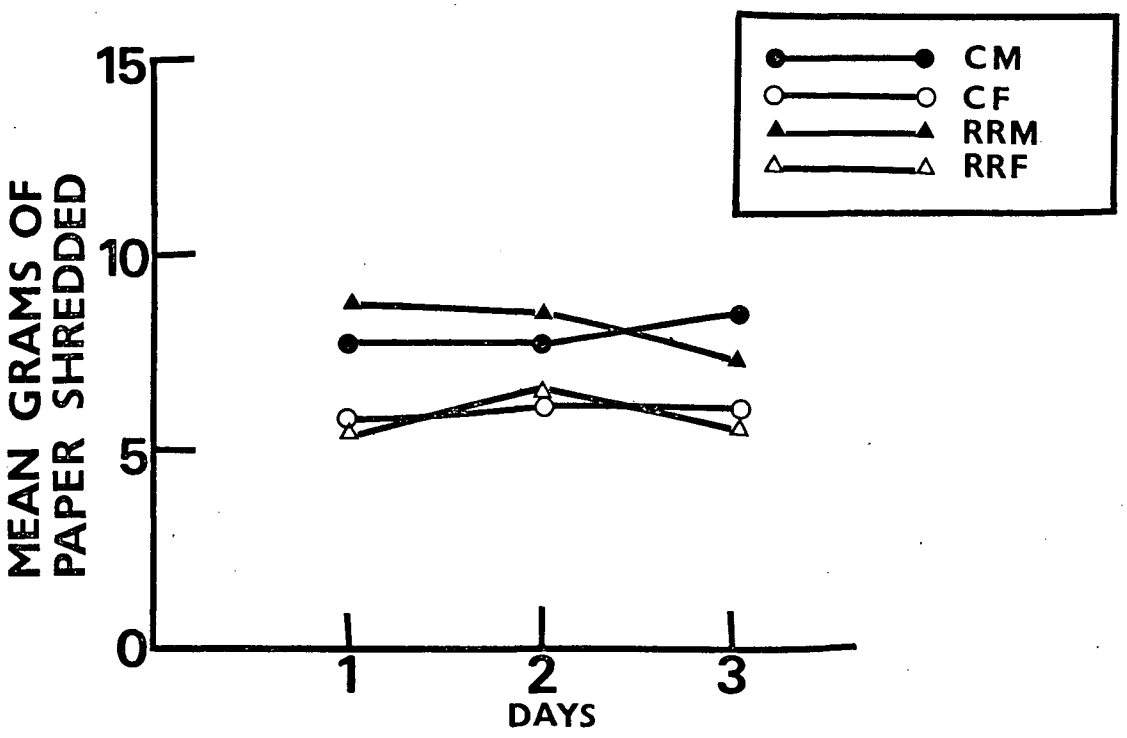

Figure 11. Mean number of grams of paper shredded during 2.5 hr tests by control males, control females, rat-reared males, and rat-reared females

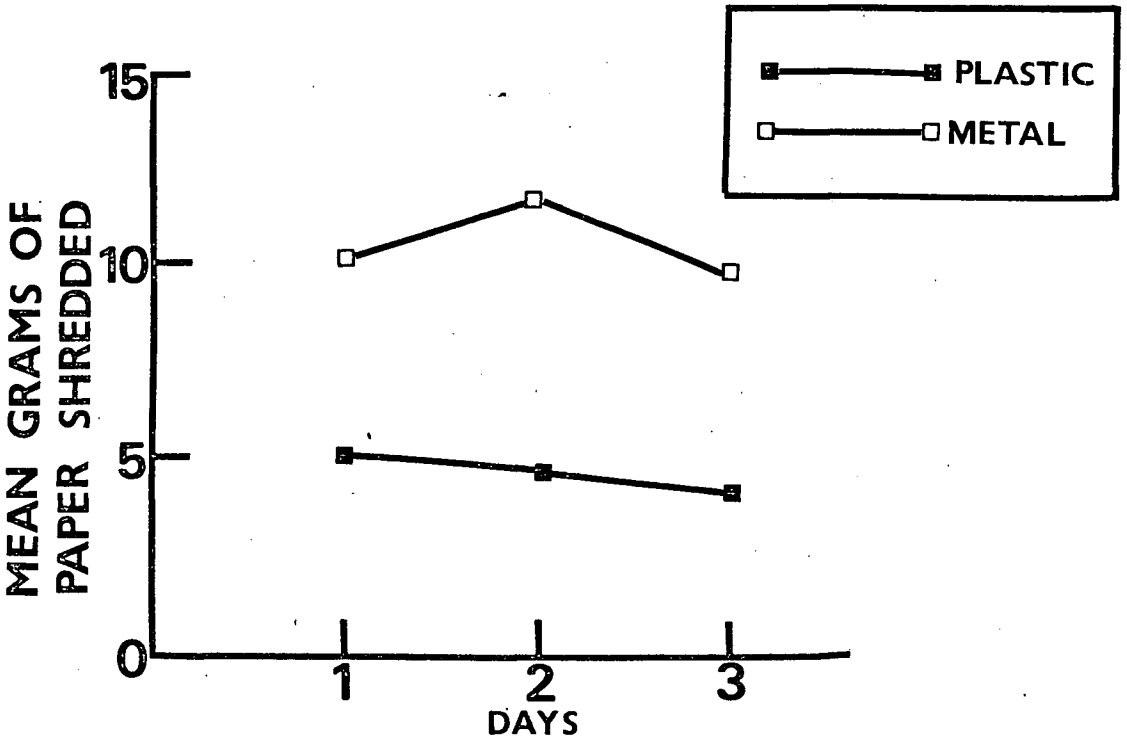

Figure 12. Mean number of grams of paper shredded during 2.5 hr tests by gerbils raised in metal and plastic cages

TABLE 21

Summary of Analysis of Variance of Paper Shredded: Treatment

Source	df	SS	MS	F	p
Treatment	1	30.16	30.16	<1	n.s.
Sex	1	15652.64	15652.64	3.89	n.s.(<10)
T x S	1	132.44	132.44	<1	n.s.
Error Between	42	169100.00	4026.19	---	---
Days	2	294.16	147.08	<1	n.s.
T x D	2	1244.54	622.27	<1	n.s.
S x D	2	507.26	253.63	<1	n.s.
T x S x D	2	461.15	230.58	<1	n.s.
Error Within	84	57676.96	686.63	---	---

TABLE 22

Summary of Analysis of Variance of Paper Shredded: Cage Type within Group RR

Source	df	SS	MS	F	p
Total	19	2587.43	---	---	---
Cage	1	1523.68	1523.68	25.80	<.01
Error	18	1063.75	59.05	---	---

It is apparent from Fig. 13 that frequency of territorial marking exhibits a steady increment from Day 1 to Day 8 and this increment is steeper for males than females. Of the four groups, RR males show the most rapid increase in marking scores while RR females display virtually no increment at all. For C males and females marking frequency rises at about the same rate. It is these differential rates of acceleration among the four groups that account for the significant triple interaction. Fig. 14 gives no evidence that early cage type experience influenced frequency of territorial marking. Analysis confirmed this lack of relationship. Analysis of variance summaries for territorial marking are presented in Tables 23 and 24.

The measure of defecation which was taken during territorial marking tests, in general parallels the open-field defecation scores. The relationship between sex, treatment, and defecation in the marking apparatus is illustrated in Fig. 15. Males defecated more than females (F=17.09; df=1/42; $p<.01$) and rat-reared subjects defecated less than controls but the latter difference did not attain significance (F=3.90; df=1/42; $p<.10$). All other main effects and interactions were nonsignificant. For this measure, defecation scores were at about the same level on Day 1 as they were on Day 8 of open-field testing. That this level is asymptotic is indicated by the lack of a significant days effect on the second boli measure. Analysis is summarized in Table 25.

The effect of cage type experience on defecation which was obtained for the open-field test is less apparent for the marking test, as Fig. 16 shows. Analysis of variance (summarized in Table 26) failed to yield a significant effect for cage type experience.

Gland Size. Table 27 shows the mean ventral gland size of each of the groups. Analysis of gland size (presented in Table 28) revealed a nonsignificant treatment effect, a significant sex effect (F=96.20; df=1/42; $p<.01$),

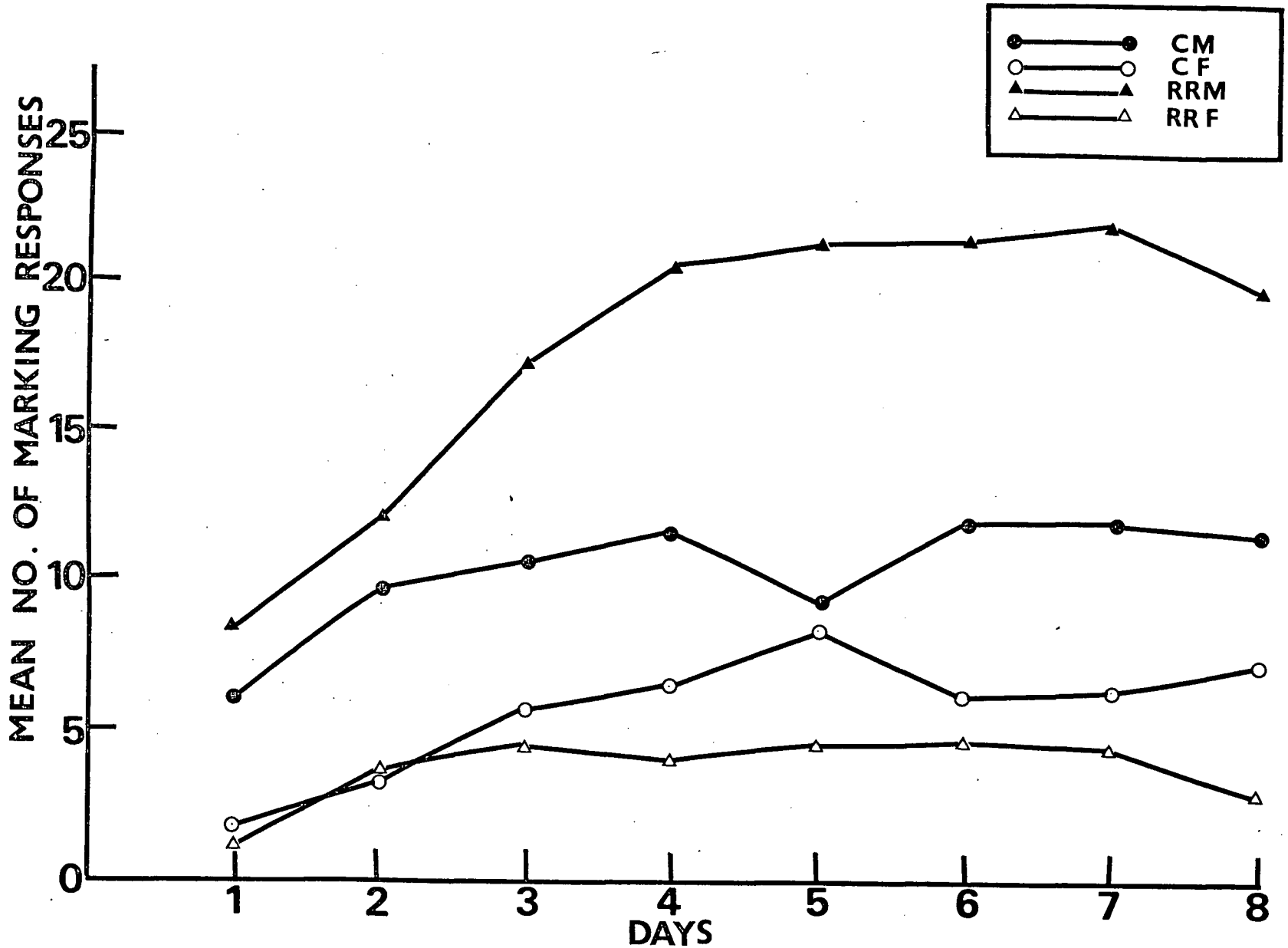

Figure 13. Mean number of ventral marking responses performed in apparatus on each 5-min test by control males, control females, rat-reared males, and rat-reared females

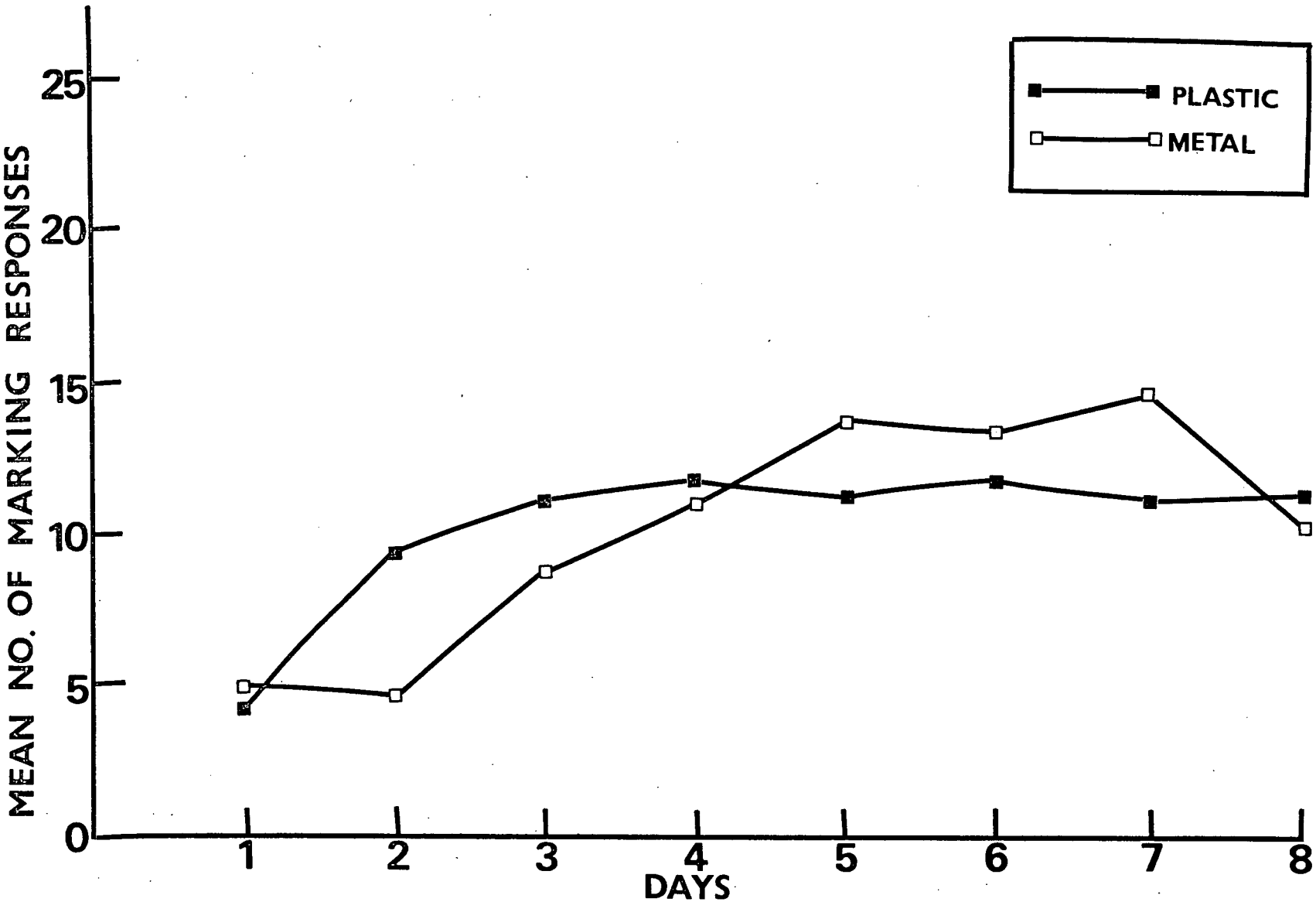

Figure 14. Mean number of ventral marking responses performed in apparatus on each 5-min test by rat-reared gerbils raised in metal and plastic cages

TABLE 23

Summary of Analysis of Variance of Territorial Marking: Treatment

Source	df	SS	MS	F	p
Treatment	1	707.177	707.177	1.11	n.s.
Sex	1	7691.239	7691.239	12.08	<.01
T x S	1	1915.502	1915.502	3.01	n.s.(<.10)
Error Between	42	26737.750	639.613	---	---
Days	7	1802.732	257.533	11.76	<.01
T x D	7	118.245	16.892	<1	n.s.
S x D	7	316.286	45.184	2.06	<.05
T x S x D	7	456.060	65.151	2.97	<.01
Error Within	294	6441.028	21.908	---	---

TABLE 24

Summary of Analysis of Variance of Territorial Marking: Cage Type within Group RR

Source	df	SS	MS	F	p
Total	19	124785	---	---	---
Cage	1	6923	6923	1.06	n.s.
Error	18	117862	6547	---	---

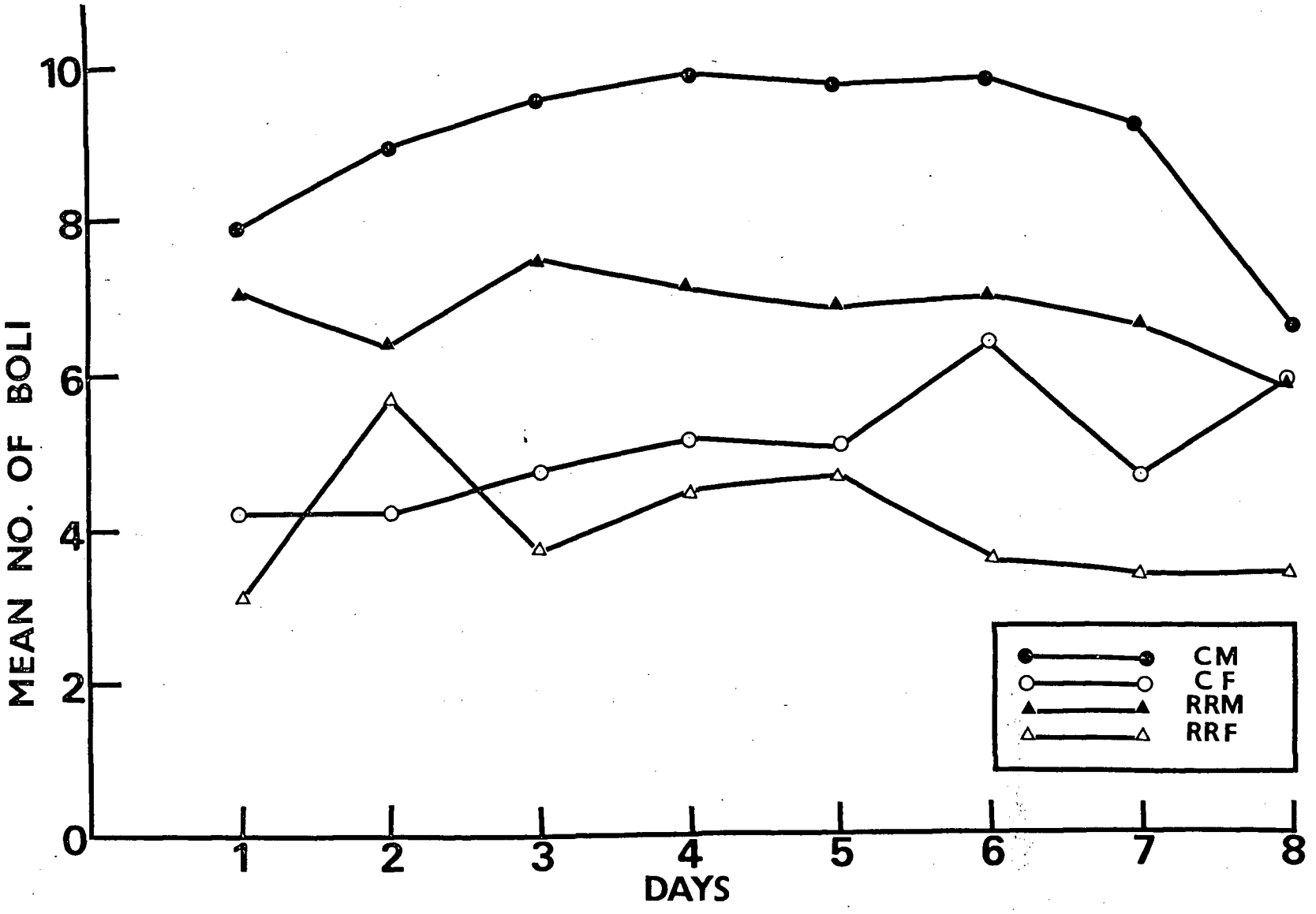

Figure 15. Mean number of boli deposited during 5-min tests in marking apparatus by control males, control females, rat-reared males, and rat-reared females

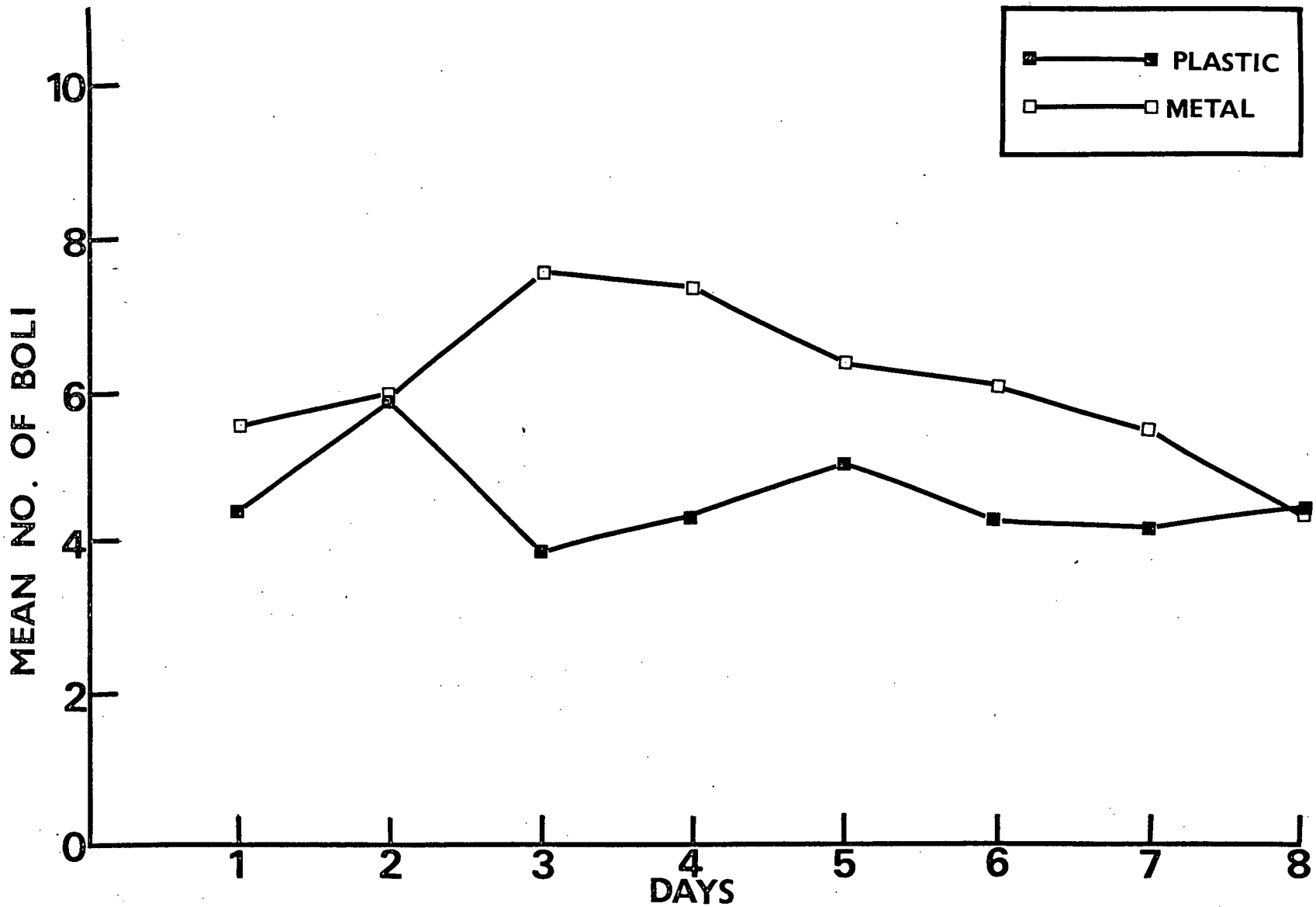

Figure 16. Mean number of boli deposited during 5-min tests in the marking apparatus by rat-reared gerbils raised in metal and plastic cages

TABLE 25

Summary of Analysis of Variance of Defecation in the Marking Apparatus: Treatment

Source	df	SS	MS	F	p
Treatment	1	221.238	221.238	3.90	n.s.(<.10)
Sex	1	968.905	968.905	17.09	<.01
T x S	1	30.417	30.417	<1	n.s.
Error Between	42	2381.720	56.708	---	---
Days	7	68.022	9.717	1.43	n.s.
T x D	7	33.215	4.745	<1	n.s.
S x D	7	53.120	7.589	1.12	n.s.
T x S x D	7	60.692	8.670	1.28	n.s.
Error Within	294	1992.551	6.777	---	---

TABLE 26

Summary of Analysis of Variance of Defecation in the Marking Apparatus: Cage Type within Group RR

Source	df	SS	MS	F	p
Total	19	9286	---	---	---
Cage	1	701	701	1.46	n.s.
Error	18	8585	477	---	---

and a nonsignificant interation. Early cage type experience also had no effect on the gland size of rat-reared gerbils. The subsidiary analysis is presented in Table 29.

Fighting Test. Table 30 shows the number of pairs of animals in each of the four groups which fought. A chi-square analysis which was applied to the male fighting frequencies failed to show a significant difference between Group RR and Group C males ($\underline{X}^2 = 1.98$; $\underline{df}=1$; $\underline{p}>.05$). Because fighting frequencies for the two female groups were identical, no statistical analysis was performed on these data.

The mean fighting latencies for each of the four groups are presented in Table 31. Raw scores for each pair of subjects were transformed to log $(x+1)$ sec. Analysis of variance, summarized in Table 32, failed to reveal any significant main effects or interactions. No subsidiary analysis was carried out on Group RR data because the group $\underline{n}$'s were too small (7 and 4 respectively for the plastic and metal cage conditions).

Relationships Among Dependent Measures. To obtain a representative score for each animal on the open-field and territorial marking measures, the scores for the last four tests (test days 5 through 8 of each test) were summed. The reason for using only the last four test scores was that behavior was presumably more stable later in testing than on initial tests. Thiessen et al.(1969) also used only data from the last four days in correlating various open-field behaviors of gerbils. Representative scores for paper shredding were obtained by summing each subject's scores over tests 1 through 3. Obviously only one measure of gland size for each subject could be used. On the basis of these scores all possible product moment correlation coefficients among the nine measures were computed. A separate coefficient was computed for each of the four sex-treatment groups. The intercorrelation matrix appears in Table 33.

TABLE 27

Means of Ventral Gland Size (square centimeters)

Control		Rat-reared	
Male	Female	Male	Female
1.48	0.60	1.68	0.65

Plastic		Metal	
Male	Female	Male	Female
1.50	0.86	1.90	0.29

TABLE 28

Summary of Analysis of Variance of Ventral Gland Size: Treatment

Source	df	SS	MS	F	p
Treatment	1	0.1711	0.1711	1.64	n.s.
Sex	1	10.0046	10.0046	96.20	$<.01$
T x S	1	0.0625	0.0625	<1	n.s.
Error	42	4.3717	0.1040	---	---

TABLE 29

Summary of Analysis of Variance of Ventral Gland Size: Cage Type within Group RR

Source	df	SS	MS	F	p
Total	19	7.5203	---	---	---
Cage	1	0.0052	0.0052	<1	n.s.
Error	18	7.5151	0.4175	---	---

TABLE 30

Number of Pairs Which Fought

	Control	Rat-reared
Male	5/9 (56%)	5/5 (100%)
Female	1/6 (17%)	1/6 (17%)

TABLE 31

Means of Fighting Latencies (seconds)

Control		Rat-reared	
Male	Female	Male	Female
177.3	286.5	115.2	293.7

TABLE 32

Summary of Analysis of Variance of Latency to Fight: Treatment

Source	df	SS	MS	F	p
Treatment	1	0.0114	0.0114	<1	n.s.
Sex	1	0.5471	0.5471	1.40	n.s.
T x Sex	1	0.0167	0.0167	<1	n.s.
Error	22	8.5906	0.3905	---	---

TABLE 33

Correlations between Behaviors

		O.F. Boli	Rears	Thig. Ratio	Center Time	Terr. Mark.	Mk. Boli	Paper	Gland Size
Total Sqs.	CM	.11	.76***	-.34	.28	-.32	.41	-.13	-.22
	CF	-.25	.68*	-.51	-.49	-.13	-.12	.48	-.27
	RRM	.15	.30	-.02	.59	-.47	.45	.10	.33
	RRF	-.12	.47	.04	.43	.19	.09	.21	-.22
Open-field Boli	CM		.10	-.02	-.08	-.07	.11	-.12	-.01
	CF		-.34	.54	.42	-.04	.32	.08	.74*
	RRM		.00	.65	.28	.52	.21	.94***	.72*
	RRF		.38	.47	.38	-.83**	.37	.62*	-.58
Rears	CM			-.22	.14	-.16	.28	-.08	-.30
	CF			-.29	-.17	-.47	.20	.44	-.53
	RRM			.21	.34	-.18	-.10	-.06	-.42
	RRF			.25	.37	-.47	-.02	.30	-.58
Thig. Ratio	CM				.68**	-.02	-.46	-.04	-.18
	CF				.88***	.28	.11	-.29	.46
	RRM				.28	.05	-.10	.56	.26
	RRF				.80**	-.63*	-.01	.47	-.77**
Center Time	CM					-.16	-.07	-.39	-.21
	CF					.42	-.15	-.05	.32
	RRM					-.19	-.22	.26	.13
	RRF					-.31	-.06	.69*	-.84**
Terr. Marking	CM						-.36	.21	.64**
	CF						-.61	.32	.00
	RRM						-.30	.44	.30
	RRF						-.32	-.37	.53
Marking Boli	CM							-.42	-.31
	CF							-.36	.04
	RRM							.35	.42
	RRF							.17	.07
Paper Shredded	CM								-.03
	CF								.29
	RRM								.72*
	RRF								-.81**

*$p < .05$
**$p < .01$
***$p < .001$

DISCUSSION

Offspring Mortality. During both the preweaning period and the period between weaning and testing, the rat-reared group had a lower incidence of survival than the control group. The cause of preweaning deaths was not determined, however killing by the mother did not appear to be a major cause since pups found dead were rarely mutilated. In only one case was a rat mother observed to kill a pup and in no instance were gerbil mothers observed to do so. Some rat mothers totally ignored their foster young and in such cases the entire litter was lost. Other factors which may have contributed to offspring mortality in the rat-reared group include the possibility that pups were inadvertently crushed by the rat mother's weight or that they had difficulty nursing because the nipples were larger and harder to reach. Hudgens, Denenberg and Zarrow (1968) and Paschke et al. (1971) also report higher mortality rates in rat-reared mice.

The high mortality rate in Group RR between weaning and testing was primarily due to an epidemic of a streptococcus lung infection. The cause of death was determined in only one animal but the symptoms were similar in others. None of the control subjects was afflicted. This fact suggests that rat-reared subjects were less resistant to the infection. However, it is also possible that the infection originated from a rat mother and following weaning spread to animals housed in adjacent cages. Since control subjects were housed in a separate cage rack from rat-reared subjects, they may have escaped exposure to the bacteria.

The four deaths which occurred in Group C between weaning and testing all involved animals which developed a skin infection and were eliminated by the experimenter. A fifth animal died before testing was completed, presumably from a respiratory ailment.

Within Group RR there was a lower percentage of preweaning deaths for

pups which were reared in metal cages than for pups reared in plastic cages. In fact, the survival rate of Group RR pups in metal cages was comparable to that of control pups, all of which were reared in metal cages. This fact suggests that some aspect of the plastic cage pre-weaning environment was detrimental to the survival of the pups. The plastic cages differed from the metal cages in a number of respects, most notably in volume and level of illumination. The plastic cages were somewhat smaller and had transparent walls. Whether or not the pups were directly affected by these variables is impossible to ascertain, but it is quite probable that the mothers' behavior was influenced by cage type. Although no attempt was made to record maternal behavior, it was noted that rat mothers in plastic cages often left their litters unattended while rat mothers in metal cages were observed to leave the nest only occasionally. The fact that some gerbil mothers failed to care for their young in the plastic cages also indicates that plastic cages of the type used in the present study do not provide an optimal maternal environment.

The differential rate of survival between Group RR and Group C introduces the problem that the results may have been influenced by a subject selection factor. In other words, Group RR may have included only very hardy individuals whereas Group C may have contained a more random assortment of subjects. There is no way of determining whether or not mortality in the rat-reared group was random with respect to individual. Furthermore, if a subject selection factor was operating, there is no way of knowing whether or not it influenced the results. Unfortunately differential mortality rate has been a characteristic of cross-fostering studies and one should bear this in mind when interpreting results.

Body Weight. Gerbils which were reared by rat mothers weighed more at weaning than control gerbils. Increased weaning weight has also been

reported for rat-reared mice (Denenberg, Hudgens and Zarrow, 1966; Hudgens et al., 1967; Hudgens et al., 1968; Paschke et al., 1971). However, the weaning weight was found not to differ from that of control mice when mice were tended by a rat aunt rather than a lactating rat (Denenberg, Rosenberg, Paschke, and Zarrow, 1969). This suggests that where weight differences at weaning are obtained, they may be due to the increased supply of milk provided by the rat mother. A second possibility is that the pups received more handling from the rat mother than they ordinarily would from their natural mother and that this increased handling stimulates growth. A study by Bessler (1962) suggests that body weight of pups is positively correlated with maternal handling. He found that pups of both the BALB/c strain and the C57BL/10 strain weighed more if they were reared by BALB/c mothers than if they were reared by C57BL/10 mothers. In addition BALB/c mothers were shown to handle both strains of pups more than the C57BL/10 mothers did.

Although a significant effect of treatment on weaning weight was obtained in the present study, the increased weight for Group RR was limited to subjects reared in metal cages, as Table 2 shows. Therefore, one can conclude that under similar cage conditions rat-reared gerbils weigh more at weaning than control gerbils. The mean weaning weight of Group RR subjects which were reared in plastic cages differed very little from that of control subjects. Since pups in plastic cages appeared to suffer greater neglect from the rat than the pups in the metal cages, a reduced body weight along with higher mortality rate in the former group is not surprising.

At 60 days the position of the two treatment groups with respect to body weight was reversed, rat-reared gerbils weighing less than the controls. This result was to be expected since many rat-reared subjects were suffering from an infection at this time. At 100 days of age there was no weight

difference between rat-reared and control gerbils.

Open-field Behavior. The assumptions which have come to underlie the use of the open-field are based almost entirely on work with rats. The two most commonly employed open-field measures are defecation and locomotory activity. High defecation and low activity have generally been assumed to reflect high emotionality; conversely low defecation and high activity have been associated with low emotionality (Broadhurst, 1958; Goldman, 1969; Hall, 1934; 1936). Such a conception of open-field behavior is probably an oversimplification and has been criticized by Ader (1969).

In order to account for the open-field behavior of rats over repeated testings, it is necessary to introduce at least one additional construct. Montgomery (1955) proposed that exploration or curiosity, as well as fear or emotionality, influenced open-field behavior and Valle (1971) has expanded this notion. In general, exploration and fear are conceived as opposing tendencies. While exploration presumably facilitates such behaviors as locomotion, rearing, and entering the central squares, fear inhibits these behaviors because it induces incompatible behaviors such as freezing and withdrawal. Defecation, however, is still considered a relatively pure measure of fear, being largely unaffected by exploratory tendencies.

The meaning of open-field behavior in rats is still a widely debated issue, despite the fact that a vast amount of research has been devoted to the subject. The meaning of open-field behavior in other species is even less clear. In mice, Rosenberg, et al. (1970) suggest that high open-field activity indicates increased rather than decreased emotionality since activity was positively correlated with plasma corticosterone level. Moreover, Candland and Nagy (1969) report that for mice defecation increases over repeated testings while for rats defecation decreases. These relationships are independent of sex. Bruell (1969), however, found that for male

mice exploratory behavior and defecation were positively correlated ($r = .124$) while for female mice a negative correlation existed between the two behaviors, ($r = -.159$). On the basis of these results he proposed that for males defecation serves a largely territorial function.

Very little work has been done on open-field behavior of gerbils (Nauman, 1963; Thiessen, Blum, and Lindzey, 1969). However these studies, as well as the present one, clearly indicate that gerbil open-field behavior is very different from that of rats and it would be premature, if not erroneous, to make similar assumptions regarding its meaning.

In the present study certain aspects of open-field behavior were affected by the nature of the pre-weaning environment. In order to understand how the fostering treatment (and cage type experience) exerted their effects, it is necessary to know something about the nature of open-field behavior. Because such information is largely unavailable, any statement regarding the mechanisms involved in cross-fostering will, of necessity, be highly speculative.

Fostering gerbils to rat mothers resulted in reduced adult open-field activity as measured by the total number of squares entered. Therefore the effect of the fostering treatment on the open-field activity of both gerbils and mice is similar.

The failure to obtain a sex difference for activity in the present study is consistent with the results of Thiessen, et al. (1969). Rodent species in which females engage in more open-field activity than do males include rats (Masur, 1972; Valle, 1970; Valle and Bols, 1973), hamsters (Swanson, 1969), and C57BL/6J mice (Nagy and Glaser, 1970). In mice a sex difference seems to be strain dependent, as Nagy and Holm (1970) failed to obtain one for C3H mice.

Rearing activity of gerbils in the open-field was depressed by the

fostering treatment, and as was the case with total squares, no sex difference was found. Rearing data is not available for other rodent species except the rat. Masur (1972), Valle (1970), and Valle and Bols (1973) found that female rats reared more than males.

The fact that in the present study both locomotion and rearing were similarly affected by the fostering treatment and sex suggests that these behaviors may be related. Furthermore, they were shown to be positively correlated although these correlations were considerably higher for the control groups than the rat-reared groups (see Table 33). It should be noted, however, that this relationship may hold only for the latter part of testing since scores were based on the last four of the eight days. Indeed locomotion and rearing do not follow similar patterns over days (see Figs 1 and 3). Whereas locomotion exhibits an initial sharp decline, rearing shows a sharp incline before stabilizing. It is possible that the meaning of a behavioral measure can change over the course of testing. Denenberg (1969) has postulated that high activity in rats on Day 1 of open-field testing indicates high emotionality whereas high activity on subsequent testing days is indicative of low emotionality. His hypothesis was based on the results of a factor analysis of rat open-field behavior (Whimbey and Denenberg, 1967). Day 1 activity was found to have a high positive loading on the "emotional reactivity" factor whereas activity on subsequent days had a high negative correlation with emotional reactivity.

Since center time and thigmotactic ratio both measure the tendency to enter the central squares, it is not surprising that these measures should yield similar results. For both measures the tendency to explore the central squares appeared to habituate more rapidly in the rat-reared subjects than controls but this effect was barely significant.

Whereas wall-hugging was little affected by the fostering treatment, it

was sensitive to cage type experience within the rat-reared group, "plastic-reared" subjects tending to exhibit more wall-hugging than "metal-reared" subjects. Visual and tactile factors may play an important role in the development of wall-hugging behavior and the two cage types differed in a number of physical properties which have been discussed previously (see page 56). These differences may account for the observed differences in thigmotactic behavior of the "metal-reared" and "plastic-reared" subjects.

Although "metal-reared" subjects in Group RR were less thigmotactic than "plastic-reared" subjects, they defecated more. In fact, defecation of rat-reared subjects raised in metal cages was comparable to that of the control subjects. The reduction in defecation for Group RR males apparent in Fig. 9 is therefore largely due to reduced defecation for "plastic-reared" subjects only. The fact that the sex x treatment interaction failed to reach significance also indicates that the variability within the rat-reared group was considerable. Thus the present study provides no evidence that the fostering treatment reduces defecation in gerbils as it does in mice.

The large sex difference for defecation is in agreement with the results of Thiessen et al. (1969) and is also in the same direction as the sex difference obtained for rats (Masur, 1972) and mice (Brusll, 1969).

The obtained increase in defecation scores over days is not consistent with an interpretation of defecation in terms of fear, since fear should decrease with repeated exposures to the situation. Moreover no significant negative correlations were obtained between open-field defecation and those behaviors which fear has been assumed to inhibit (total squares, rears, thigmotactic ratio, and center time). However, it may also be erroneous to assume that the latter behaviors are, in fact, inibited by fear.

The assumption that low activity indicates high emotionality is based on the observation that freezing (presumably an emotional response) inhibits locomotion. Freezing, however, is a rarely observed response of gerbils placed in an open-field and all gerbils exhibit high levels of activity (relative to rats). Therefore individual differences in open-field activity of gerbils probably reflect variations in running speed rather than differences in amount of freezing.

The fact that gerbils engage in far less wall-hugging than do rats may mean that for gerbils this behavior is not a sensitive index of the level of fear. It may also be a poor measure of exploratory tendencies in the gerbil since the animals enter the central squares at near chance frequencies. Perhaps it is for this reason that the wall-hugging measures showed no consistent relationship with total squares or rears, as indicated in Table 33.

Paper Shredding. Rearing gerbils with rat mothers appeared to have no effect on the amount of paper they shredded as adults. Despite the fact that rats do not engage in this behavior, rat-reared gerbils shredded paper as vigorously as did the control gerbils. This result indicates that paper shredding requires no learning from the mother. However, further conclusions regarding its development cannot be drawn until more is known about this behavior.

The present study indicates that males tend to shred more paper than females, although this difference was not significant and requires further investigation. Glickman, Fried, and Morrison (1967) failed to obtain a sex difference for paper shredding but their sample included only six animals of each sex.

While amount of paper shredding was highly resistant to any influence by the fostering treatment, it was clearly affected by early cage type

within Group RR, "metal-reared" subjects engaging in more paper-shredding than "plastic-reared" subjects. No explanation can be offered for this result at the present time. Equally puzzling are the significant positive correlations which were obtained for Group RR males between paper shredding and open-field defecation, and paper shredding and gland size. For Group RR females paper shredding correlated positively with open-field defecation but negatively with gland size. No comparable correlations were obtained for control animals (see Table 33). Whether or not these correlations were spurious, perhaps a result of a subject-selection factor within Group RR, is not possible to ascertain and remains to be determined by future replication.

Although it is not clear what paper shredding represents or what factors influence its occurrence, it does not appear to be related to locomotory activity or rearing since there were no significant positive correlations between paper shredding and these behaviors.

Territorial Marking and Gland Size. The effects of fostering on frequency of territorial marking were somewhat inconclusive. Fostering appeared to elevate marking in males while depressing it in females, yet this interaction of treatment x sex did not quite reach the .05 level of significance.

Fostering did, however, have a differential effect on the rate of acceleration of the marking response over days for males and females (indicated by a significant interaction of treatment x sex x days). An increase in marking frequency with repeated exposure to the test situation has been reported for both male and female gerbils (Thiessen et al., 1969) and was also found in the present study. Low marking scores on Day 1 of testing may be due to the predominance of exploratory responses which interfere with territorial responses. The habituation of exploratory

responses with repeated testing may then permit the expression of territorial tendencies. Fear may also inhibit marking on initial tests. Thus rat-reared males may adapt to the test situation at a more rapid rate than control males but why the fostering treatment should not have the same effect on females is unclear.

The measure of defecation which was recorded in the marking apparatus was primarily for comparison with the open-field defecation measure. The correlations between these two defecation measures were surprisingly small (see Table 33), indicating that either (a) defecation is not a very reliable measure or (b) subjects responded differently to the two apparatuses. Although both possibilities may be true, support for the former comes from the results of Thiessen et al. (1969). They reported fairly low reliability coefficients for defecation in a marking apparatus (.34 and .24 for males and females respectively).

Evidence that defecation in gerbils serves a territorial function was somewhat contradictory. Correlations between marking and both defecation measures were negative in seven out of eight cases although in only one instance was the coefficient reliable. Marking and open-field defecation correlated -.83 in Group RR females. Despite the lack of positive association between marking and defecation, there was an increase in defecation frequency with repeated exposure to the open-field. The latter result is consistent with a territorial interpretation of defecation. Clearly, further investigation is necessary to establish the function of defecation in gerbils.

The large sex difference obtained for marking frequency as well as gland size confirms earlier findings. Furthermore marking and gland size correlated positively (.64) for control males. The lack of relationship for other groups probably reflects the fact that marking is influenced by factors other than androgen titre, especially in females (Thiessen, Owen, and

Lindzey, 1971).

The fact that the fostering treatment had no influence on the sebaceous gland size of gerbils indicates that levels of circulating androgens were similar in rat-reared and control subjects, (assuming that gland size is a reliable index of androgen titre). Therefore, any differences in marking behavior between rat-reared and control subjects cannot be attributed to differences in androgen levels.

Fighting. The results of the fighting test are inconclusive because of the small number of pairs tested as well as the fact that a few subjects were tested twice while the majority were tested only once.

However, it is probably safe to conclude that fostering gerbils to rat mothers does not reduce incidence of fighting as is the case for fostered C57BL/10 J mice. One hundred per cent of the rat-reared male pairs fought compared to fifty-six per cent of control male pairs. Whether or not rat-reared males actually exhibit a significantly greater incidence of fighting than control males remains to be determined. The observed incidence of fighting for females was identical (seventeen per cent) for both groups.

The latency to fight revealed no additional information. Mean latencies were slightly shorter for rat-reared males but not significantly so. The failure of this measure to reveal a sex difference undoubtedly reflects the small sample size. Thiessen et al. (1971) report that females fight only occasionally, although no statistical data are given.

CONCLUSIONS

The only clear-cut effect of fostering gerbils to rat mothers was a reduction in activity as measured by both open-field locomotion and rearing. However the interpretation of this reduced activity must be largely speculative as very little additional data to the present results are available.

There are at least three possible explanations for reduced activity as

a result of fostering. The first is that fostering reduces emotionality. This interpretation is favoured by Denenberg (1970) to account for the effects of fostering mice to rat mothers. That high activity is associated with high emotionality in mice receives support from the finding that activity and corticosterone response to a novel stimulus are positively related (Rosenberg et al. 1970). It has been argued earlier in the present paper (p. 62) that for gerbils activity is not related to emotionality. Following this argument, it is unlikely that the observed reduction in activity for rat-reared gerbils was a result of either increased or decreased emotionality.

A second possible explanation is that fostering gerbils to rat mothers reduces their curiosity or "exploratory drive." Thompson and Lippman (1972) recently proposed that gerbils are more exploratory animals than rats. Using a Greek cross maze with black, white, striped, and checkered compartments, these authors found that on early trials gerbils had a greater tendency to explore all compartments whereas rats showed a marked preference for the black one. Thus if rat mothers cause their gerbil foster pups to become more rat-like in some respects, a reduction in exploration would be in the predicted direction.

It is also possible, however, that locomotion and rearing measure nothing more than a general activity factor. Activity level is to some extent genetic, and within a range of variability, fixed for a given species. For example, gerbils and rats differ with respect to activity level and this difference may depend to a large extent on biochemical and metabolic differences which have no relation to differences in emotionality or curiosity between the two species. Although the concept of a general activity factor may not be a particularly useful or meaningful one, it is introduced into the present context simply as a label for those variables which influence

activity but which are unrelated to the conceptual variables, emotionality and curiosity.

Because it is not possible to separate a curiosity factor from a general activity factor in the present study, either could have been affected by the fostering treatment. However it may be possible to separate them by comparing activity in a novel environment such as an open-field, with a familiar environment such as a home cage. If the animals differed in curiosity but not general activity, then presumably their home cage activity would be similar. Unfortunately such observations have not been made but they would aid interpretation of the present results considerably.

Since early cage type experience appeared to have no effect on locomotion or rearing frequency of rat-reared gerbils, it is very unlikely that cage type could account for the treatment effect on these measures.

Early cage type experience did, however, have definite effects on later behavior although these effects were quite different from those of cross-fostering. Rat-reared gerbils which were housed in plastic cages before weaning, as opposed to metal cages, had a greater tendency to wall-hug, defecated less, and shredded less paper.

Many types of stimulation when applied during infancy have been shown to be effective in altering later behavior. The effects of these various treatments are often quite diverse and there is no reason to assume that they are mediated by a similar mechanism. Clearly the preweaning period is a stage when young rodents are extremely vulnerable to many varieties of environmental influence.

To what extent these early experience effects are direct results of the treatment and to what extent they are maternally mediated is difficult to determine, especially where no observations of maternal behavior are made. With cage type, as with most early treatments, it is impossible to estimate

the relative role of maternal mediation. With fostering, however, the mother is the variable being manipulated; therefore any effects must be attributed solely to maternal influence. One can then attempt to isolate the critical aspects of the mother which are responsible for observed effects on the offspring. This approach has characterized Denenberg's work on rat-reared mice and differential handling by the two species of mother has been implicated as a crucial factor mediating the fostering effect, although no comparison of maternal handling of mouse pups by rats and mice has yet been made.

A similar comparison was not made in the present study either but an observation by Kaplan and Hyland (1972) indicates that differential maternal handling could be a factor mediating fostering effects in gerbils. They found that gerbil mothers rarely retrieved their pups, and pups which were out of the nest usually had to make their own way back. For rat mothers, however, pup-retrieving is a fairly dominant response. Since strong evidence has been presented to implicate maternal manipulation as a mediator of early handling phenomena (Bell et al., 1971; Bell et al., in press), there is good reason to suspect that it may also be important in other early experience effects, including fostering.

Now that it is established that fostering mice or gerbils to rat mothers alters their respective behavior, more attention can be paid to examining how these changes are mediated. In particular, detailed species comparisons of maternal behavior and its effects on the young would seem to be the most fruitful approach to understanding how fostering effects are mediated as well as how the mother of a given species shapes the behavior of her own offspring.

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