

PUP CANNIBALISM BY THE
MATERNAL GOLDEN HAMSTER

PUP CANNIBALISM: A DESCRIPTION
AND CAUSAL ANALYSIS OF ONE
ASPECT OF MATERNAL BEHAVIOUR OF THE
GOLDEN HAMSTER (MESOCRICETUS AURATUS)

By

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Abstract

Following parturition, the female golden hamster (Mesocricetus auratus, Waterhouse, 1839) exhibits a broad repertoire of maternal behaviours essential for the growth and protection of her developing offspring. In addition to engaging in obviously nurturant activities, the maternal hamster exhibits a behaviour infrequently observed in other species: she almost invariably cannibalizes some of her own live offspring.

Hamster pup cannibalism has been characterized in the literature as a breakdown of normal maternal behaviour, resulting from a variety of possibly stressful conditions imposed upon the mother (for example, disturbance following parturition). The influence of such factors on frequency of pup destruction, however, has not been empirically examined, and, in fact, no systematic observation of hamster pup cannibalism has been reported in the literature.*

The major purposes of this thesis were to provide normative data on the frequency, extent, and time course of cannibalism by hamsters rearing their litters under standard laboratory conditions, and to determine the proximal stimulation controlling the onset, maintenance, and cessation of this behaviour.

Systematic observations of 63 litters born to 21 mothers indicated that there is a high probability (.75) of a mother exhibiting

some cannibalism toward her young, but that each mother destroys only a few of her pups. Eighty percent of this destruction occurs within five days of parturition, and cannibalism is directed apparently randomly towards the pups present in the litter. While an individual hamster does not reliably cannibalize a certain number of pups, she does exhibit relative constancy in the number of pups she rears over successive litters.

Experimental results indicated that the pup cannibalism normally exhibited by the hamster is not dependent upon the presence of the possibly stressful conditions suggested in the literature. Instead, the results provided evidence that the initiation of pup cannibalism is systematically controlled by a variety of stimuli which reflect the size of the litter; including olfactory stimulation and stimulation received during nursing.

Each hamster apparently cannibalizes to regulate her litters at a particular size. If litter size is artificially reduced by removing pups from the litter, the mother reduces cannibalism proportionally. If litter size is increased on the day of parturition, by giving the mother newborn foster pups, she will exhibit a compensatory increase in cannibalism. The probability of observing this compensatory increase in cannibalism in response to artificial litter size increment decreases as a function of increasing time postpartum at which litter size is altered. The change in responsiveness to litter size was found to be a result of internal changes in the mother occurring as a function of time postpartum, rather than from changing stimuli received from pups increasing in age.

Variations between individual mothers in the number of pups they rear per litter probably results from long-term constancies in their relative capacity to conceive, deliver, and/or successfully maintain young. The observation that a hamster consistently gives birth to more pups than she will rear, and achieves a reduction in number of pups by an active culling of the litter, suggests that pup cannibalism enables the mother to alter the size of her litter to that size most compatible with her capacity to rear young under specific environmental conditions.

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INTRODUCTION

Following parturition, the female golden hamster (Mesocricetus auratus, Waterhouse, 1839) exhibits a broad repertoire of maternal behaviours essential for the growth and protection of her young. Like mothers of other altricial rodent species (e.g. Rosenblatt and Lehrman, 1963; Noirot, 1972) the parturient hamster cleans her pups, maintains a typical nursing posture over neonates in a carefully constructed nest, and retrieves stray pups back to this nest. Further, the pattern of maternal care exhibited by a hamster mother alters over time, as the physical, metabolic, and behavioural needs of her developing offspring change (Rowell, 1960; Scott, 1970). In addition to these obviously nurturant activities, the maternal hamster engages in a behaviour infrequently observed in other species: she almost invariably cannibalizes some of her own live offspring (Magalhaes, 1968; Porter, 1962).

Pup cannibalism by the golden hamster has been observed by virtually all breeders of the species, rearing their animals under a wide variety of conditions (e.g. Hindle and Magalhaes, 1957). In the literature concerned with the rearing and breeding of golden hamsters, this pup destruction has been characterized as an aberrant response, resulting from any of a variety of possibly stressful conditions imposed upon the mother. For example, it has been hypothesized that 1) disturbance of the mother after parturition (Bruce and Hindle, 1934; Hindle and Magalhaes, 1957; Poiley, 1950; Silvan, 1966; Summer, 1972; Whitney, 1963),

2) extreme litter size (Silvan, 1966; Whitney, 1963), and 3) immaturity of the mother (Dieterlin, 1959; Poiley, 1950) may be factors contributing to the observed high incidence of cannibalism. Further, it has been informally suggested that lack of maternal experience, hyperemotionality of particular females, and poor condition of pups may underlie cannibalism. Although readily testable, the role of these factors in increasing the incidence of pup cannibalism exhibited by hamsters has not been examined.

Implicit in the causal factors suggested above is the assumption that pup cannibalism is aberrant behaviour induced by factors acting to disrupt normal patterns of mother-young interaction. There is both empirical and theoretical support for this view. Empirical support for the position that cannibalism may result from abnormal stresses on the mother which disrupt her normal behaviour towards her young, is provided by experiments on a number of species which indicate that factors which increase the incidence of pup destruction concurrently disrupt other aspects of normal maternal behaviour. For example, female rats fed diets either deficient in vitamin B₁₂ (Hankin, 1958, 1960) or containing an overabundance of vitamin B₁ (Perla and Sandberg, 1939) both cannibalized their own pups and exhibited abnormalities in retrieving and nestbuilding behaviour. Maternal behaviour of mice (Brown, 1953; Southwick, 1955 a and b) and hamsters (Goldman and Swanson, 1975) is also disrupted by the stress provided by high population densities at parturition. Under conditions of high density, parturient animals of these species both cannibalized their young and failed to defend the

nest site against conspecifics. Furthermore, it has been found that "emotional" strains of mice (Poley, 1974), rabbits (Denenberg, Petropoulos, Savin and Ross, 1959), and sows (Hodgson, 1935) exhibited a higher probability of destroying their young than less "emotional" strains, presumably because of greater susceptibility to external disturbance in the more emotional strains.

Theoretically, any pattern of behaviour which results in an individual's destruction of its own progeny can be interpreted in one of two ways. First, one can assume that such behaviour reduces the cannibalizing animal's contribution of offspring to subsequent generations and thus reduces that individual's potential reproductive success. Given this assumption, the view would be taken that parent-induced mortality of young should be actively selected against, since, within the context of the synthetic theory of evolution, natural selection acts to maximize reproductive success (see: Williams, 1966). According to this view, the destruction of one's direct descendents in observed laboratory populations would reflect a situation-induced breakdown of normal adaptive patterns of parental behaviour. The alternative view is that elimination of some of one's own progeny might, under specific circumstances, maximize an animal's contribution of offspring to future generations, and thus act as an adaptive aspect of parental behaviour. For example, under conditions in which each member of a large litter has a significantly lower probability of survival than each member of a small one, a mother's destruction of a portion of her litter might increase the number of her young surviving beyond weaning (Lack, 1954). According to this position, pup cannibalism by the golden hamster may be

hypothesized to be a potentially adaptive behaviour, enabling the parturient female to adjust her litter to a size which maximizes her reproductive success under suboptimal conditions.

The position that pup cannibalism may serve an adaptive function in mammals is reflected in suggestions that mice cannibalize to reduce their litters to sizes compatible with their capacity to provide milk (Crozier and Enzmann, 1935; Falconer, 1947), and that cannibalism by mice living under severely crowded conditions is a mechanism for the regulation of population density (Southwick, 1955 a and b). A similar explanation has been offered for the parent-induced mortality of young in wild populations of white storks. Lack (1958) and Wynne-Edwards (1962) have suggested that parental destruction of stork young could be adaptive, allowing parents both to rear their entire brood when food was abundant, and to compensate for insufficient food by reducing the number of offspring they attempt to rear in times of scarcity. Cannibalism by white storks was discussed by Lack (1954, 1958) as a special instance of adaptive variability in clutch size in birds. Lack hypothesized that the ability to modify clutch size is an adaptive strategy, permitting birds to lay a number of eggs consistent with the food supply available either at time of egg laying or of egg hatching. According to Lack's hypothesis, stork cannibalism is a reproductive strategy functionally equivalent to production of the clutch size most compatible with prevailing environmental conditions, but cannibalism is a temporally delayed strategy, permitting modification of number of young to be made contiguously with the appearance of live young.

Lack drew a parallel between variability in clutch size in birds and the varying litter size that has been observed to occur in response to food supply in several viviparous species, including, for example, guinea pigs, voles, and arctic fox (Lack, 1948). In Lack's words:

In all groups of animals and plants, there is the evolutionary alternative between producing more young, or fewer young which are better nourished and better protected. In all cases, natural selection may be expected to work towards maximum productivity, but the latter will be achieved in very different ways in different cases, depending on the environments to which the offspring are exposed. (1948, p. 50).

A similar parallel can be drawn between the hypothesized adaptive functions of cannibalism by white storks and by golden hamsters: however, direct evaluation of the possible adaptive function of cannibalism by the golden hamster requires observation, not yet undertaken (Murphy, 1971), of species members in their natural habitat of the Arabian peninsula (Harrison, 1972).

The present series of studies was directed towards analysis of the proximal factors controlling the onset, maintenance, and cessation of cannibalism by the golden hamster rearing her litter under standard laboratory conditions. The goal of the present experiments was to determine whether the pup cannibalism typically exhibited by golden hamsters is an aberrant response to stressful conditions or an organized element of maternal behaviour.

Part I:
Description and Causal Analysis
of Pup Cannibalism
by the Golden Hamster

CHAPTER I

Tests of Hypotheses and Normative Data

The initial investigation examined the influence on pup cannibalism of the six factors mentioned in the introduction: 1) disturbance of the mother after parturition; 2) litters of extreme size; 3) breeding soon after sexual maturity; 4) lack of maternal experience; 5) behavioural idiosyncracies of mothers; and 6) poor condition of young, which have been suggested to increase frequency and probability of pup destruction. Cannibalistic behaviour observed was also analyzed to provide normative data on probability of occurrence, amount, and time course of pup cannibalism exhibited by female golden hamsters rearing their litters under standard laboratory conditions.

General Methods

Standardized procedures of animal maintenance and handling were used throughout the course of the present series of experiments. Variations in the standard procedure will be described where appropriate.

Subjects

Subjects were nulliparous female golden hamsters (Mesocricetus auratus) obtained either at 7 1/2 weeks of age from High Oak Ranch, Ltd., Goodwood, Ontario, or from litters reared in the McMaster colony. Colony-born animals were weaned between 21 and 28 days of age, and housed with their female siblings until seven to eight weeks of age, at which time they were placed in individual cages. These procedures

are comparable to those followed at High Oak Ranch (Reference note 1). All sexually mature animals were allowed contact with other adults only for purposes of mating.

Housing

Subjects were housed individually in transparent 37.8 x 32.7 x 16.8 cm. polycarbonate plastic cages (Maryland Plastics, Federalsburg, Maryland), the floors of which were covered to a depth of approximately 3 cm. with wood shavings. Cages were cleaned every two weeks, and within two days prior to the expected date of parturition. While mother and litter were kept together in the same uncleaned cage until the pups were weaned, clean wood shavings were added to the cage after seven days postpartum.

Animals were maintained at 21-23° C. on either a 13-hour day - 11-hour night or 14-hour day - 10-hour night schedule, with light onset between 7 and 8 a.m. The maintenance diet of ad lib. Purina Laboratory Chow and water was supplemented with 1-2 grams of Purina pigeon grain whenever an animal was handled.

Handling

Animals were handled during evening hours (6-11 p.m.). In order to habituate prepartum experimental animals to handling procedures, each female was removed from her cage to a separate container, provided with 1-2 grams of pigeon grain, and weighed, on at least five occasions during gestation.

Breeding

A female to be bred was placed in the home cage of a sexually mature male and left there until copulation was completed, or the animals started fighting. Females failing to copulate upon first exposure to a male were reexposed on subsequent nights until successful copulation was observed.

Observations

For purposes of observation, each mother was removed to a separate container and provided with grain while her litter was examined to determine the number of pups present, litter weight, and the general condition of each pup (skin colour, presence of milk in the stomach, presence of injury). Finally, before the mother was returned to her cage, the woodshavings were examined for the presence of dead pups. Mothers and litters were observed on the evening of the day of parturition (designated as Day 0 of lactation) and daily for at least the first 10 days thereafter.

Measures

Litters could not be observed continuously; therefore, a pup was considered cannibalized on Day n postpartum if it was alive on Day $n-1$ and absent on Day n . Because hamsters will devour dead pups, this measure of cannibalism was necessarily inflated by the number of pups dying from causes other than cannibalism and subsequently consumed by the mother. That cannibalism of dead pups was not a major cause of disappearance of young, is suggested by the infrequent direct observation

of mothers eating dead pups, and the frequent direct observation of mothers ingesting live young under five days of age.

Differential mortality of sickly pups over six days of age was observed in the course of pilot studies. Both mothers and young older than six days of age will consume dead pups. The problem of distinguishing cannibalized pups from those dying and subsequently ingested, therefore, becomes more acute as litter age increases. For this reason, whenever possible, statistical analyses were performed only on data of number of pups missing during the first five days postpartum. Analyses of results during this time period excluded minimal amounts of data, since there were relatively few instances of disappearance of young after Day 5.

Exclusion of Experimental Animals

A mother and litter were excluded from a study if, on the day of parturition and before any experimental manipulations were performed, most pups in that litter were found to be abnormal in any one of the following ways: no milk was present in the stomachs of the pups, the pups were runty, injured, or dark in colour. The probability of survival of pups in these litters was quite low, and the inclusion of these animals in a study would have assured an artificial inflation of the measure of amount of cannibalism. The number of mothers and litters discarded for these reasons was variable over experiments, but averaged 9.5% of the total number of births.

In addition, during the course of the entire series of studies, one mother was excluded when she cannibalized her entire litter by Day 1

postpartum, and three were excluded when they exhibited abnormal, aggressive behaviour towards their pups shortly after being handled on the day of parturition.

Experiment 1

The six factors suggested as contributing to the normal incidence of pup cannibalism by the hamster, together with their predicted effects, are described below.

1. Effects of "disturbance" of the mother. If handling of the puerperal mother and litter disturbs the mother and thus elicits cannibalism, then one would expect a lower rate of survival of pups reared by newly parturient mothers disturbed by daily handling than of pups reared by mothers left completely undisturbed.
2. Effects of litters of extreme size. If cannibalism is a response of mothers to litters of extreme size, highest levels of cannibalism should be present in litters larger or smaller than the average litter size observed in the population under study.
3. Effects of breeding soon after sexual maturity. If cannibalism is exhibited only in relatively immature females, then amount of cannibalism should decrease systematically as a function of increase in the age at which a female is bred.
4. Effects of lack of maternal experience. If there is a tendency for mothers to cannibalize pups in their first litters, then there should be a reduction in cannibalism over successive litters.
5. Effects of behavioural idiosyncracies of mothers. If particular

mothers tend to cannibalize to a greater or lesser degree than others, individual females should exhibit consistency, relative to other females, in the amount of cannibalism they direct towards their successive litters.

6. Effects of individual differences among pups. If cannibalism is a behaviour of "weeding out" particular pups, then cannibalized pups should exhibit some observable physical or behavioural characteristics distinguishing them from their non-eliminated siblings. Practical considerations limited evaluation of selective destruction to physiological differences among pups.

The effects of the first five factors were examined in Experiment 1(a), and the sixth factor, in Experiment 1(b). Measures taken in Experiment 1 also provided data requisite for describing the normal occurrence of cannibalism in the laboratory.

Methods

Subjects: Experiment 1(a)

The subjects were 42 female golden hamsters born in the McMaster colony, maintained under the conditions described in the General Methods section.

Subjects: Experiment 1(b)

The subjects were 243 pups reared by 25, 10-12 week old mothers obtained from both the McMaster colony and from High Oak Breeding Ranch. The mothers were bred in two groups, several months apart. Two mothers from an initial group of 27 were excluded from the experiment when,

after examination on the day of parturition, they exhibited abnormal aggressive behaviour toward their young.

Procedure: Experiment 1(a)

Age of onset of puberty was established in each of the 42 subjects by testing them on successive evenings, beginning at 35 days of age, for first incidence of estrus behaviour in the presence of a sexually mature male hamster. Onset of puberty was defined as occurring on the first night a female responded with lordosis to male approach.

Pubescent females were randomly assigned to one of three groups differing in the day post-puberty at which group members were first bred. Animals in the 0-Delay Group (n=14) were first bred on the night of first estrus, and animals in the 4-Week Delay (n=14) and 8-Week Delay (n=14) Groups were first bred, respectively, 4 or 8 weeks thereafter. All animals were bred to rear three successive litters, at intervals of approximately 7 weeks between successive impregnations. Mean ages at breeding of each group are presented in Table I.

Half the animals in each of the three groups were assigned to a Handled, and half, to a Not Handled condition. The 21 mothers in the Handled condition received the daily handling described in the General Methods section, from the day of parturition throughout the period of lactation. The 21 mothers in the Not Handled condition were left completely undisturbed from the day of parturition to Day 10 postpartum, at which time standard daily handling was resumed.

Table 1
 MEAN AGES (IN WEEKS) AT BREEDING OF MOTHERS
 IN EXPERIMENT 1(a)

	0-Delay Group			4-Week Delay Group			8-Week Delay Group		
	Litter No.			Litter No.			Litter No.		
	1	2	3	1	2	3	1	2	3
Handled	7.3	13.9	20.4	12.0	19.3	27.1	16.0	25.0	34.5
Not Handled	7.4	14.0	20.7	12.4	20.6	27.6	16.2	25.2	33.2

Procedure: Experiment 1(b)

On the day of parturition, pups were individually marked by toe clipping while under local anaesthetic (2% solution of Xylocaine Hydrochloride, Astra Pharmaceutical Division, Mississauga, Ontario), after which they were weighed, and the presence of bites, subcutaneous haemorrhages, and abnormalities in colour were recorded. Each mother was removed to a separate cage during the 10 to 20 minutes needed to mark, weigh, and examine her litter. Individual surviving pups were examined daily for changes in physical condition.

Results and Conclusions:

Tests of Hypotheses

1. Effects of "disturbance" of the mother. If "disturbance", operationally defined as daily handling, elicits cannibalism in puerperal females, then more pups should survive in litters reared by mothers left undisturbed during lactation than in litters reared by mothers handled daily. Assuming that the two groups of 21 randomly assigned animals in the Handled and the Not Handled conditions (Experiment 1(a)) gave birth to the same mean number of pups, the hypothesis predicts that the mean number of pups per litter surviving to Day 10 postpartum should be higher in the Not Handled than in the Handled Group.

The mean numbers of pups per litter surviving to Day 10 postpartum were 5.4 and 5.3 in Handled and Not Handled Groups, respectively. These data indicate no effect on pup survival of disturbance by handling. Presumably, therefore, disturbance by handling did not affect amount

of cannibalism.

2. Effects of litters of extreme size. The data from the 88 litters born to mothers in Experiments 1(a) and (b) were used to evaluate the hypothesis that cannibalism is most frequently directed towards litters of extreme size. It is clear from Figure 1, which presents percentages of litters of different initial size which suffered any cannibalism by Day 5 postpartum, that cannibalism was present in litters of all sizes, not just in litters of extreme size.

It is possible that the amount of cannibalism rather than the probability of occurrence of cannibalism is related to initial litter size. Figure 2 presents one measure of amount of cannibalism, the mean number of pups cannibalized by Day 5, as a function of initial litter size. In Figure 2a, a small relationship is apparent between mean number of pups cannibalized by Day 5 and initial litter size. Because these data included repeated measures from 21 mothers, statistical analyses of the strength of this relationship could not be performed on the entire set of data; therefore, analyses were performed only on the number of pups cannibalized in the first litters born to the 46 mothers observed in both studies, presented in Figure 2b. A Chi-square analysis performed on amount of cannibalism below, equal to, or greater than the mean amount, as a function of litter size at parturition below, equal to, or greater than the mean initial litter size (Table 2: Bruning and Kintz, 1968), did not indicate the existence of a significant relationship between these two variables ($\chi^2 = 3.4, p > .05$). In addition, the Pearson product-moment correlation (Bruning and Kintz, 1968)

Figure 1

Percentage of 88 litters suffering any cannibalism by Day 5 postpartum, as a function of initial litter size (Experiment 1(a) and (b)). Numbers above each data point refer to numbers of litters observed of each initial size.

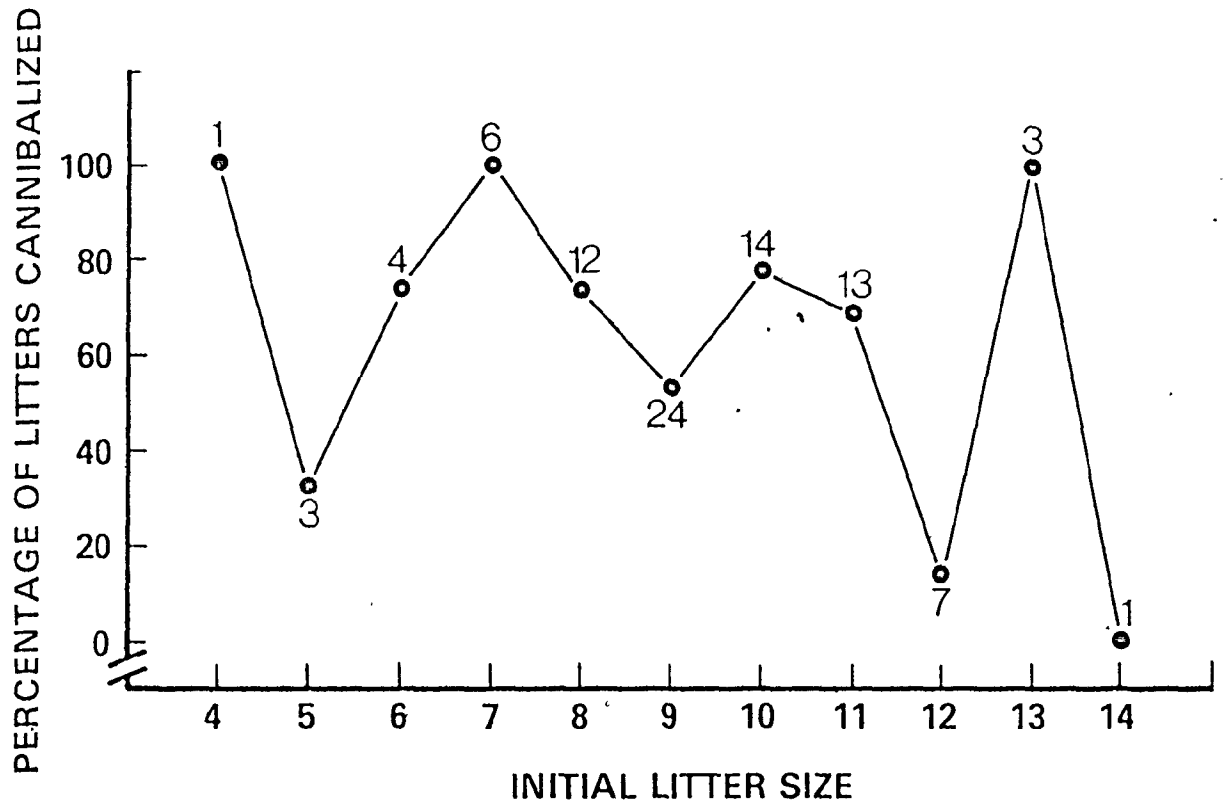


Figure 2

Mean number of pups cannibalized per litter by Day 5 postpartum as a function of initial litter size (Experiment 1(a) and (b)): (a) data from all 88 litters, and (b) data from 46 first litters. Numbers above each data point refer to numbers of litters observed of each initial litter size.

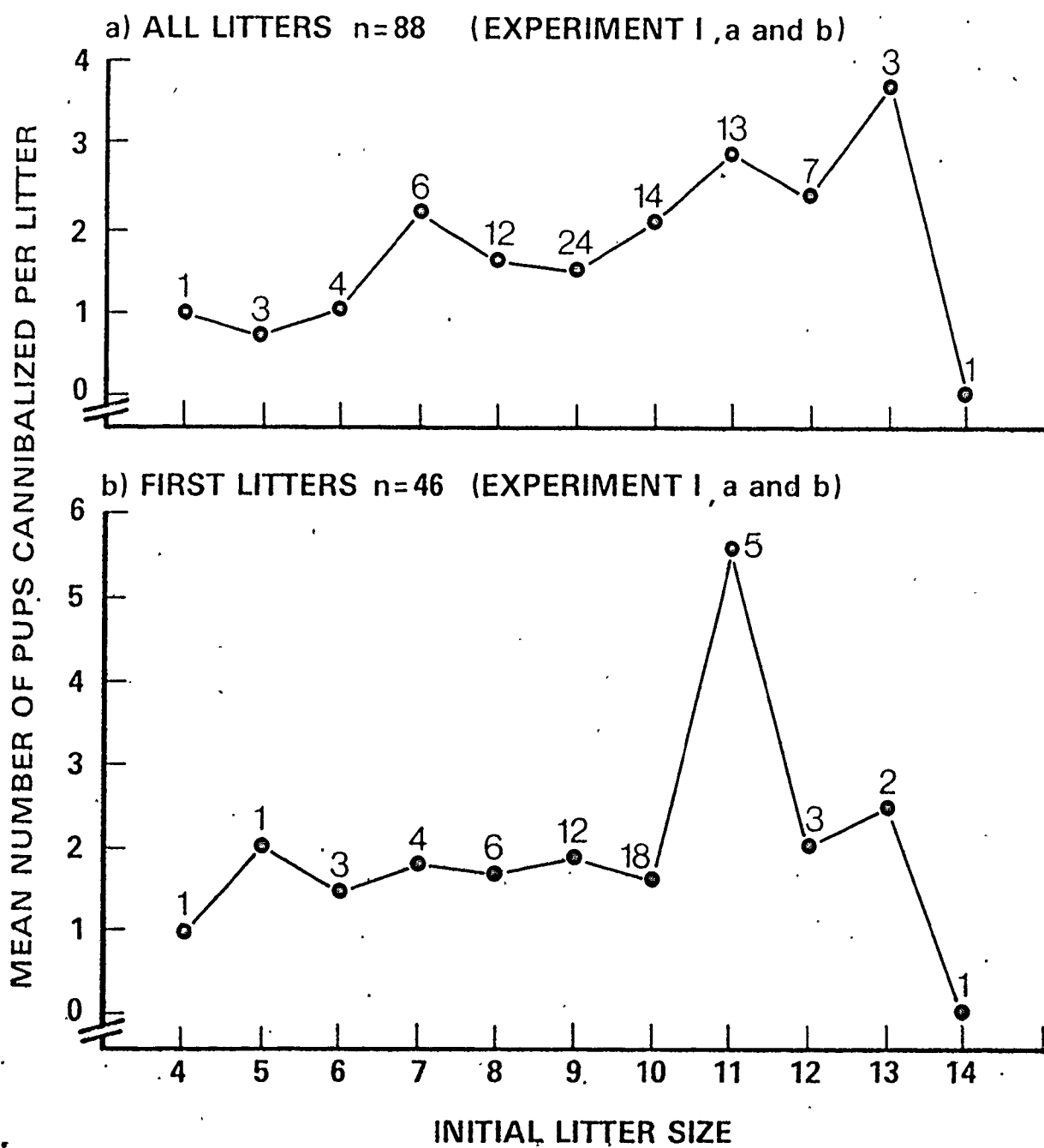


Table 2
 AMOUNT OF CANNIBALISM BY DAY 5
 POSTPARTUM AS A FUNCTION OF
 LITTER SIZE AT PARTURITION

Observed Frequencies

		Initial Litter Size		
		<9	9	>9
Number of Pups Cannibalized Per Litter by Day 5 Post- partum	<2	8	5	5
	2	4	3	5
	>2	3	4	9
				46

Expected Frequencies

		Initial Litter Size		
		<9	9	>9
Amount of Cannibalism	<2	5.9	4.7	7.4
	2	4.0	3.1	4.9
	>2	5.3	4.2	6.6

coefficient calculated from these data, was small and not statistically significant ($r = .22$, $p > .05$). From these results, it can be concluded that initial litter size is not a significant factor influencing the incidence of cannibalism.

The tendency for amount of cannibalism to be related to initial litter size (Figure 1) could be an artifact of the upper limit imposed on the number of pups cannibalized, by the number available to be destroyed. The use of percentage of litter destroyed as the measure of amount of cannibalism permits evaluation of this possibility. Figure 3, which presents median percentage of litter cannibalized by Day 5 postpartum as a function of initial litter size, does not indicate the presence of any relationship between this measure of amount of cannibalism and number of pups born per litter.

3. Effects of breeding soon after sexual maturity. If exhibition of cannibalism is dependent upon physical immaturity of the mother, females bred immediately upon reaching puberty should cannibalize more pups than animals bred after some delay. The effect of the delay can be studied by an examination of the amount of cannibalism in the first litters of the 21 Handled mothers bred either 0, 4, or 8 weeks after reaching sexual maturity (Experiment 1(a)), presented in Figure 4.

The one-way analysis of variance (Lindquist, 1953) performed on number of pups cannibalized by females bred 0, 4, and 8 weeks after reaching puberty, indicated that length of delay to breeding did not significantly influence amount of cannibalism ($F_{2,18} = 1.01$ Between Delay Groups, $p > .05$). That the 0-Delay Group had the lowest mean

Figure 3

Median percentage of litters cannibalized by Day 5 postpartum as a function of initial litter size (Experiment 1(a) and (b)): (a) data from all 88 litters, and (b) data from 46 first litters. Numbers above each data point refer to number of litters observed of each initial litter size.

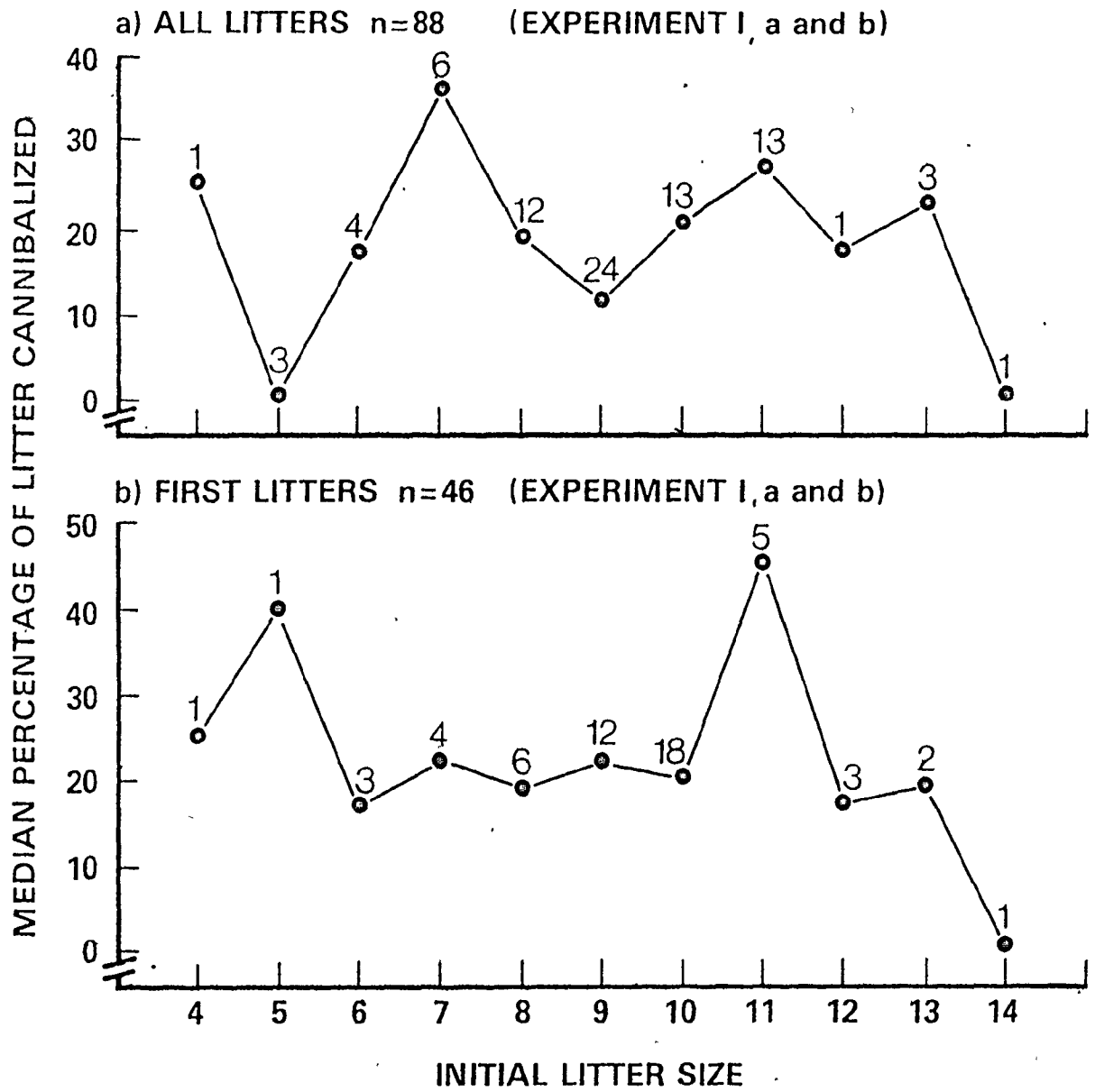
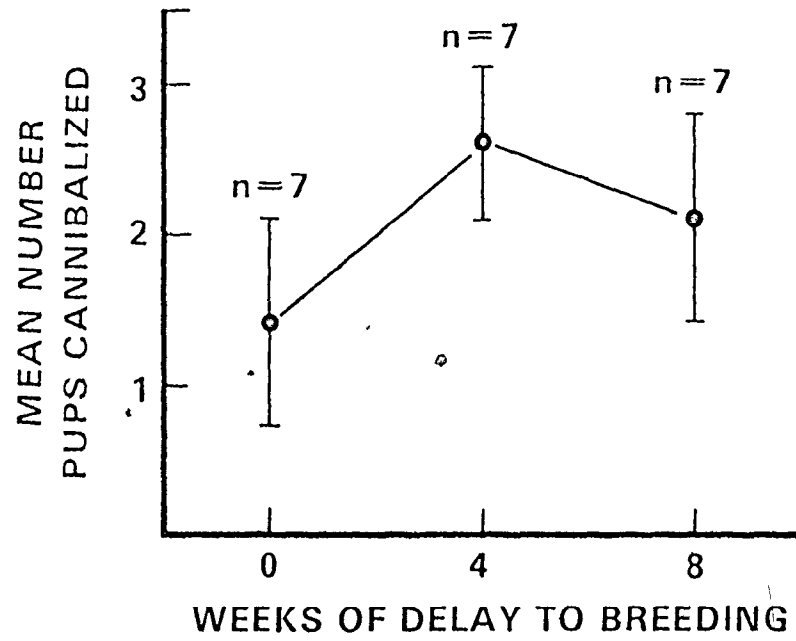


Figure 4

Mean number of pups per litter
cannibalized by Day 5 postpartum,
as a function of delay between
first estrus and breeding (Experi-
ment 1(a)). Flags indicate
 ± 1 S.E.M.



amount of cannibalism further contradicts the hypothesis that breeding soon after sexual maturity is responsible for cannibalism.

4) Effects of lack of maternal experience. If amount of maternal experience influences cannibalism, amount of cannibalism should vary systematically across successive litters. The data used to test this hypothesis were obtained from the 21 Handled mothers. (Experiment 1(a)).

In Figure 5a, which presents the mean number of pups per litter cannibalized by Day 5 postpartum as a function of successive parturitions, there is a slight tendency for cannibalism to decrease with increasing amount of maternal experience, but the Successive Litters effect did not approach statistical significance in a Trials X Subjects analysis of variance ($F_{2,40} = .74, p > .05$, Lindquist, 1953).

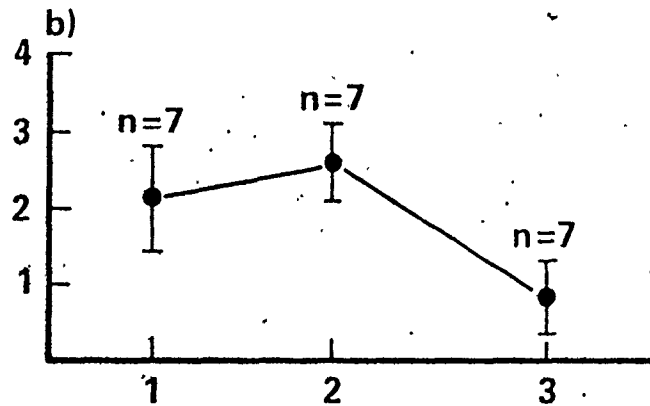
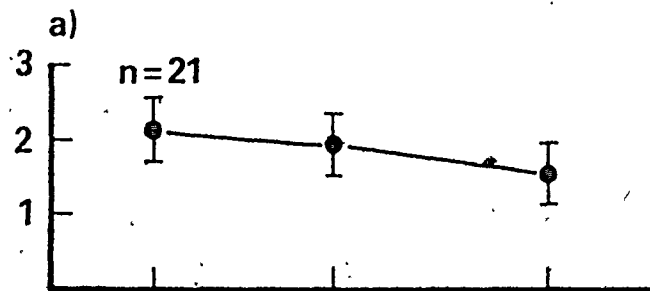
The small decrease in cannibalism over successive litters may have resulted from the confounding of age at parturition with amount of maternal experience. The role of experience relatively unconfounded with maternal age can be examined by a consideration of data from the following sources: first litters born to 3-Week Delay Group mothers, bred at 16.1 weeks of age; second litters born to the 4-Week Delay Group mothers, bred at 19.3 weeks of age; and third litters born to the 0-Delay Group mothers, bred at 20.4 weeks of age. The mean number of pups per litter cannibalized by Day 5 postpartum by these three groups of mothers, presented in Figure 5b, does not reveal an orderly effect of maternal age on cannibalism.

5) Effects of behavioural idiosyncracies of mothers. If particular mothers are consistent in the amount of cannibalism they direct towards

Figure 5

Mean number of pups cannibalized per litter by Day 5 postpartum over successive litters (Experiment 1(a)): (a) within-group data from 21 mothers, (b) between-group data, n=7 per group. Flags indicate ± 1 S.E.M.

MEAN NUMBER PUPS CANNIBALIZED



SUCCESSIVE LITTERS

their litters relative to other mothers, this consistency should be apparent in correlations between amounts of cannibalism exhibited by the 21 Handled mothers (Experiment 1(a)) over successive litters. The Pearson product-moment correlations (Bruning and Kintz, 1968) performed on number of pups cannibalized by Day 5, indicated that individual mothers did not exhibit significant consistency in number of pups cannibalized over successive litters ($r = .13$, litter 1 vs. 2, and $r = .42$, litter 2 vs. 3, p 's $> .05$). Correlations between percent of litter cannibalized in successive litters indicated a significant relationship between the amount of cannibalism in litters 2 and 3 ($r = .49$, $p < .05$), but not in litters 1 and 2 ($r = .19$, $p > .05$).

Further, visual examination of the scatterplots of these data did not reveal consistent deviations from linearity. These data indicate that individual mothers cannot be easily characterized as consistently cannibalizing to a greater or lesser degree than their counterparts.

6) Effect of individual differences among pups. Three Chi-square analyses (Bruning and Kintz, 1968) were performed on cannibalism by or survival to Day 5 postpartum of individual pups in Experiment 1(b), as a function of their classification within each of the following categories of physical characteristics observed on the day of birth:

a. Obvious physical abnormalities. The analysis was performed on the relationship between survival vs. cannibalism and the presence or absence of any combination of bites, subcutaneous haemorrhages, or obvious abnormalities in skin colour (either very pale or dark). These characteristics were taken as indicating general poor health (Table 3).

Table 3

OBSERVED AND EXPECTED FREQUENCIES
OF PUP CANNIBALISM BY OR SURVIVAL
TO DAY 5 VS. PRESENCE OR ABSENCE
OF INJURY, HAEMORRHAGES, OR AB-
NORMALITY IN COLOUR ON DAY 0
(EXPERIMENT 1(a)).

Observed Frequencies

	"Healthy"	"Not Healthy"	
Cannibalized by Day 5	37	18	
Survived to Day 5	122	66	243

Expected Frequencies

	"Healthy"	"Not Healthy"	
Cannibalized by Day 5	35.8	19.3	
Survived to Day 5	122.2	65.8	

b. Absolute birth weight. The analysis was performed on the relationship between survival vs. cannibalism and birth weight within the lowest (1.8 - 2.3 grams), middle (2.4 - 2.5 grams), or highest (2.6 - 3.0 grams) third of the distribution of weights of all pups observed (Table 4).

c. Relative birth weight. The analysis was performed on the relationship between survival vs. cannibalism and extremeness in birth weight relative to an individual pup's littermates. Data were collected only from the pups in each of the 25 litters having the lowest, median, or highest birth weights (Table 5) in each litter.

None of the χ^2 values approached statistical significance:

a) $\chi^2_1 = .12$, $n = 243$; b) $\chi^2_2 = 3.04$, $n = 243$; c) $\chi^2_2 = .57$, $n = 136$;

all p 's $> .05$. These analyses indicate that individual pup survival is not differentially dependent either on the presence or absence of specific physical characteristics, or on absolute or relative birth weights. While only the most obvious physical characteristics were considered, these data suggest that cannibalism may be randomly directed towards pups in a litter.

Discussion: Tests of Hypotheses

Failure to find significant effects on cannibalism of the six causal factors suggested in the literature indicates that these variables are not important influences on the behaviour. That is not to say that they may not, under particular circumstances, alter either the probability of occurrence or the extent of cannibalism. On the contrary, it is

Table 4

OBSERVED AND EXPECTED FREQUENCIES
OF PUP CANNIBALISM BY OR SURVIVAL
TO DAY 5 VS. ABSOLUTE BIRTH WEIGHT
(EXPERIMENT 1(a)).

	Observed Frequencies		
	Low Third	Middle Third	High Third
	1.8 - 2.3 g.	2.4 - 2.5 g.	2.5 - 3.0 g.
Cannibalized by Day 5	21	20	14
Surviving to Day 5	55	62	71
			243

	Expected Frequencies		
	Low Third	Middle Third	High Third
	1.8 - 2.3 g.	2.4 - 2.5 g.	2.5 - 3.0 g.
Cannibalized by Day 5	17.1	18.7	19.3
Surviving to Day 5	58.3	63.9	65.8

Table 5

OBSERVED AND EXPECTED FREQUENCIES
OF PUP CANNIBALISM BY OR SURVIVAL
TO DAY 5 VS. RELATIVE BIRTH WEIGHT
(EXPERIMENT 1(a)).

Observed Frequencies			
	Smallest	Median	Largest
Cannibalized by Day 5	9	14	6
Survived to Day 5	28	50	29
			136

Expected Frequencies			
	Smallest	Median	Largest
Cannibalized by Day 5	7.8	13.6	7.5
Survived to Day 5	28.9	50.3	27.8

plausible that disturbance by means other than handling can increase pup mortality (as demonstrated by the effect of high density on cannibalism, Goldman and Swanson, 1975), or that a strain of females more responsive to external disturbance can be selectively bred. Such endeavours appear fruitless, however, since cannibalism by the hamster rearing her litter under standard laboratory conditions occurs regardless of systematic manipulations of these variables.

Results: Normative Data

Amount of Cannibalism

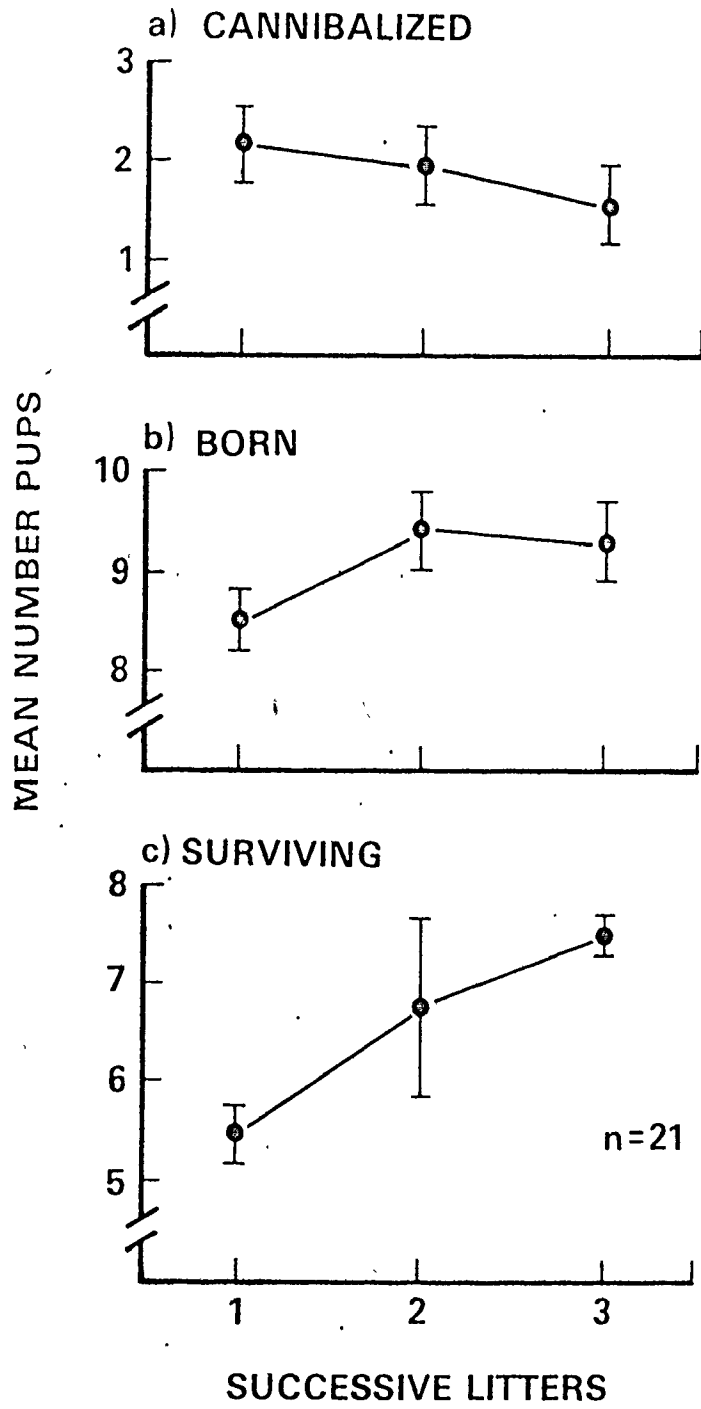
Seventy-six percent (48) of the 63 litters born to the Handled mothers in Experiment 1(a) suffered some degree of cannibalism during the three weeks between the birth and weaning of the pups. In litters which ranged in size from 5 to 13 pups mothers cannibalized a median of 2 pups. All 21 mothers cannibalized 1 or more pups before Day 21 postpartum in at least 1 of their 3 successive litters, and 19 mothers cannibalized 1 or more pups in at least 1 of their litters by Day 5 postpartum. While the probability was, therefore, considerable that a particular litter would suffer some degree of cannibalism, in no instance did a mother destroy her entire litter.

Changes in reproductive parameters over successive litters.

Figures 6a-c present means of, respectively, number of pups cannibalized by Day 5, number of pups born per litter, and number of pups surviving to Day 5, as a function of successive litters born to mothers in Experiment 1(a).

Figure 6

(a) Mean number of pups cannibalized per litter by Day 5; (b) mean number of pups born per litter; and (c) mean number of pups surviving per litter to Day 5 as a function of successive litters (Experiment 1(a)). Flags indicate ± 1 S.E.M.



A Trials X Subject analysis of variance (Lindquist, 1958) indicated that the mean number of pups cannibalized (Figure 6a) decreased slightly, but not significantly, over successive litters ($F_{2,40} = .74$, Number of Pups X Litter Number; $p > .05$). The slight increase over litters in mean number of pups born per litter (Figure 6b), concomitant with the small regular decrease over litters in mean number of pups cannibalized, resulted in the analysis of the increase in the mean number of pups surviving over successive litters reaching statistical significance ($F_{2,40} = 7.79$, Number of Pups X Litter Number, $p < .05$, Figure 6c).

The consistency in the behaviour of individual mothers across successive litters was examined by performing between-litter correlations on the number of pups cannibalized by Day 5, percentage of litter cannibalized by Day 5, number of pups reared to Day 5, and number of pups born per litter. These Pearson product-moment correlations are presented in Table 6.

As was noted above, individual mothers did not consistently cannibalize a greater or fewer number of pups than other mothers. Between-litter correlations of number of pups cannibalized by Day 5 were not statistically significant ($r = .13$, litter 1 vs. 2, and $r = .42$, litter 2 vs. 3, both p 's $> .05$). Between-litter correlations of percent of litter cannibalized by Day 5 indicated the existence of a significant relationship between litters 2 and 3 but not between litters 1 and 2 ($r = .49$, $p < .05$; and $r = .19$, $p > .05$, respectively).

An examination of the correlations between successive litters

Table 6

BETWEEN-LITTER PEARSON PRODUCT-
MOMENT CORRELATIONS ON DATA FROM
21 MOTHERS (EXPERIMENT 1(a)).

	Litters 1 vs. 2	Litters 2 vs. 3
Number of Pups Cannibalized By Day 5	.13	.42
Proportion of Litters Cannibalized by Day 5	.19	.49*
Number of Pups Born	.41	.43
Number of Pups Surviving to Day 5	.54*	.61**

*p < .05

**p < .01

in number of pups surviving to Day 5 revealed significant relationships between litters 1 and 2, and litters 2 and 3 (\underline{r} 's = .54 and .61, respectively, both \underline{p} 's $<.05$). These relationships resulted in part from the consistency, not statistically significant, present in the number of pups born to particular females over their three litters (\underline{r} = .41, litter 1 vs. 2, \underline{r} = .43, litter 2 vs. 3; both \underline{p} 's $>.05$). Examination of scatterplots of the data discussed above did not reveal consistent deviations from linearity in any instance.

Change in cannibalism as a function of day postpartum.

An examination of amount of cannibalism as a function of day postpartum indicated that most cannibalism occurred within the first few days after the birth of the pups. This was a highly reliable phenomenon: in 29 of the 48 litters (60%) in which cannibalism was observed, it terminated by Day 5 postpartum.

The relationship between cannibalism and time postpartum is clearly indicated in Figure 7, which presents the cumulative percentage of the cannibalism occurring by Day 21 postpartum in the 63 litters, as a function of day postpartum. Mortality of over 80% of the pups cannibalized between Day 0 and Day 21 occurred by Day 5. The high probability of cannibalism within a few days of parturition is also apparent in Figures 8 and 9, which present, respectively, the number of litters suffering any cannibalism, and the mean numbers of pups cannibalized per litter as a function of day postpartum.

Figure 7

Cumulative percentage of total cannibalism occurring by Day 21, as a function of day postpartum (Experiment 1(a)).

CUMULATIVE PERCENTAGE
TOTAL CANNIBALISM

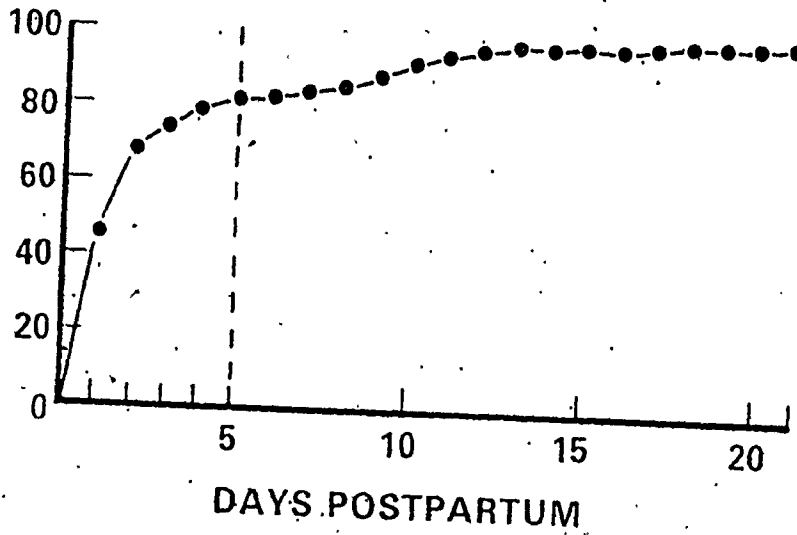


Figure 8

Number of litters suffering any cannibalism as a function of day postpartum (Experiment 1(a)).

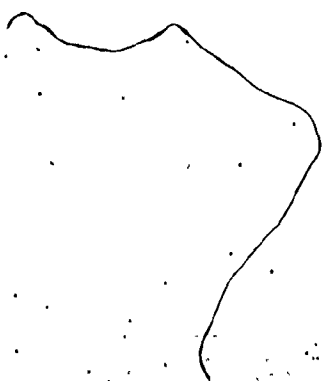
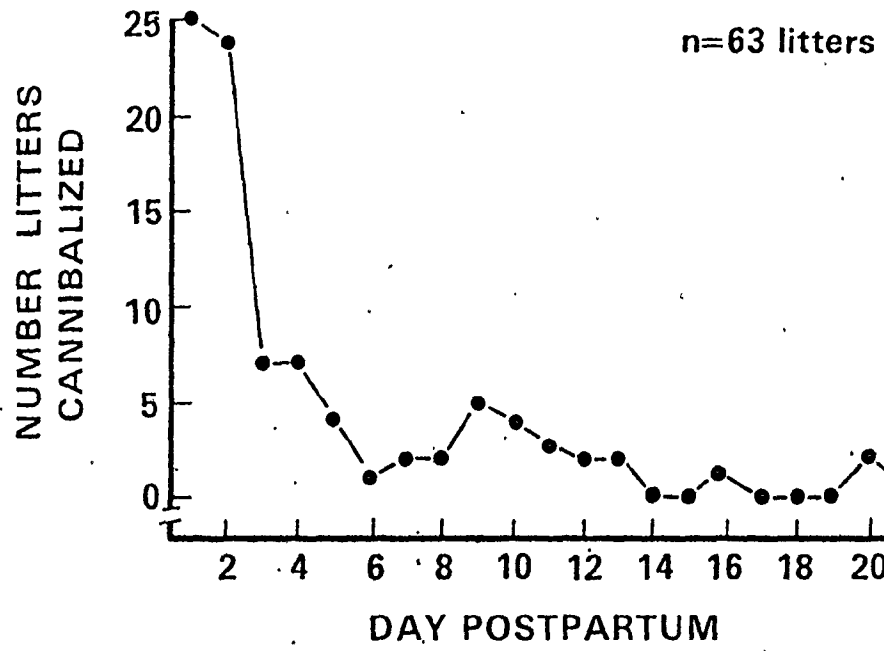
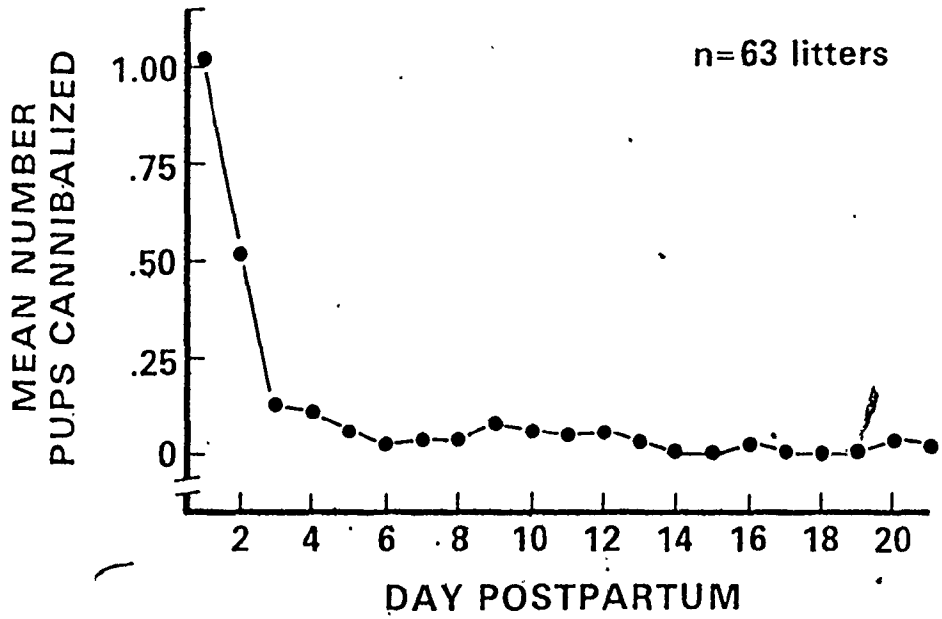


Figure 9

Mean number of pups cannibalized
per litter as a function of day
postpartum (Experiment 1(a)).



Discussion: Normative Data

While tests of the six hypothesized factors failed to illuminate proximal causes of cannibalism, examination of the normative data did provide some insight into the factors that may be important in influencing hamster cannibalism. The significant between-litter correlations in the number of pups surviving to Day 5 postpartum indicated some consistency in the relative number of pups reared by an individual mother. This consistency most probably results from long-term constancies in each mother's relative capacity to conceive, deliver, and/or successfully maintain her young. The observation that a female hamster consistently gives birth to more pups than she will rear, and reduces litter size by actively culling her litter, suggests that cannibalism may serve to reduce the litter to a size which is more compatible with her capacity to rear young. This hypothesis would account both for the fact that only a few pups, rather than an entire litter, are cannibalized, and that cannibalism virutally ceases within a few days of parturition, after some litter size reduction has been achieved. The hypothesis is also consistent with the apparently random selection of pups from a litter, since litter size reduction is effectively accomplished by the elimination of any pup.

General Discussion

In general, the results of Experiment 1 suggest that analysis of litter cannibalism in the hamster in terms of the types of causal factors posed in the literature, is not likely to be productive. Although the data reported above offer limited support for hypotheses implicating

unusually large litter size at birth or individual behavioural idiosyncrasy in high levels of litter cannibalism, the treatment of cannibalism as resulting from a stress-induced disruption of normal maternal behaviour does not seem a particularly appropriate one. Analysis of the behaviour in such terms could not account either for the observation that cannibalism was directed toward litters of small size at birth, or that the great majority of females cannibalized following one or more of their parturitions. Neither would such an orientation be useful in interpreting the observations of a high degree of constancy in the relative number of pups maintained by individual females or the observed decrease in cannibalism as a function of time postpartum.

It was, therefore, decided to undertake further studies treating litter cannibalism as an organized and possibly adaptive aspect of maternal behaviour in hamsters, by examining the factors responsible for the consistently observed marked reduction in probability of cannibalism after Day 5 postpartum. It was hoped that a study of the factors leading to cessation of cannibalism would provide some insight into the causes of its initiation.

Chapter II:

Cessation of Cannibalism

One of the most consistent phenomena observed in Experiment 1 was the dramatic decrease in incidence of cannibalism as a function of increasing time postpartum. Pup cannibalism was reliably observed only during the five days following parturition, and was infrequent thereafter. It seems reasonable to assume that either decreases in the size of the litter as a result of cannibalism of pups, alteration in the stimulus configuration of maturing pups, or changes in the internal state of the mother are responsible for the observed decrease in incidence of pup destruction as a function of time after birth.

Experiment 2

In the present experiment, the possibility was examined that the reduction in litter size resulting from cannibalism during the first days postpartum in itself decreases the probability of future occurrence of pup destruction. If dams continue to cannibalize until their litters are reduced to a size which no longer elicits pup destruction, then predictable alterations in behaviour should be observed in response to the following experimental manipulations:

1. If litter size is artificially maintained by replacing missing pups with foster young, culling of the litter should continue for an indefinite

period of time.

2. If litter size is artificially increased or decreased, the mother should exhibit compensatory increases or decreases in cannibalism appropriate to the maintenance of a specific litter size.

Experiment 2(a)

In the first study, the hypothesis that a hamster stops cannibalizing when she has reduced her litter to a certain size was tested by artificially maintaining original litter size. This was accomplished by daily replacement of missing or dead pups with foster pups of the same age. If reduction in litter size is the only factor controlling the cessation of cannibalism, so long as initial litter size is maintained, the female should continue to cull her litter. The experimental manipulation of litter size maintenance should thus indefinitely extend the duration of cannibalism, and should also result in an increase in the total number of young consumed.

Method

Subjects

The subjects were 15 nulliparous golden hamsters born in the McMaster colony, and bred at 14 weeks of age. Because the experimental procedure required the presence of some level of cannibalism, data from two mothers, one from the Experimental Group and one from the Control Group, were eliminated after the mothers failed to cannibalize.

Procedure

Litters reared by mothers in the Litter Size Maintained Group (n = 7) were artificially maintained at the size observed at parturition, by replacing pups found missing or dead on Day n, with foster pups n days of age. The Foster Control Group (n = 6) provided a yoked control for fostering. Each Foster Control mother received daily, a number of foster pups equal to that received by her randomly assigned partner in the Litter Size Maintained Group. The pups received by each Foster Control mother were the same age as her own pups, and were exchanged for an equal number of pups already present. Thus, the Foster Control litters were not artificially altered in size, and instead showed the normal decline in size over time, as a result of cannibalism and death of ill pups.

Foster pups were obtained from litters born to 17 multiparous colony females. Pilot studies had indicated no differential cannibalism of foster pups of the same age as a mother's own litter.¹

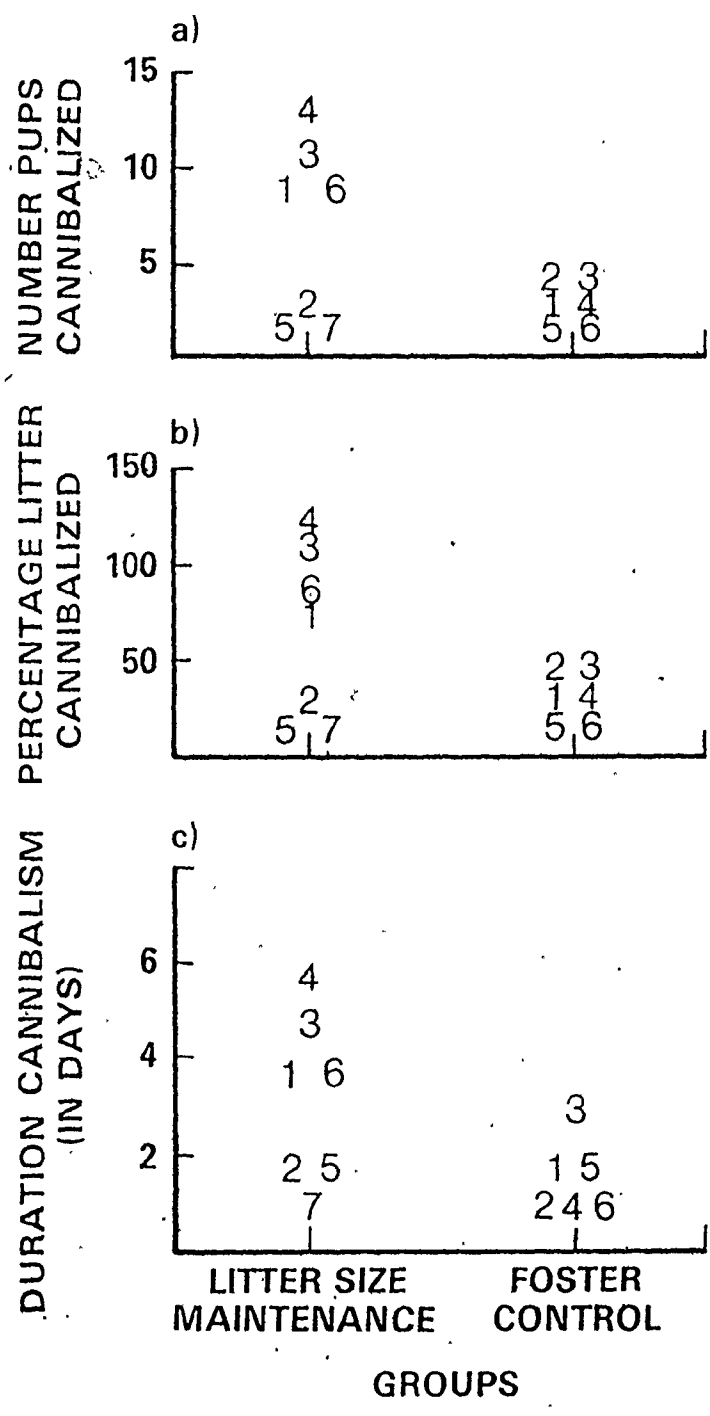
Results

In four of the seven Litter Size Maintained mothers, the duration of cannibalism was extended, although not indefinitely, and the amount of cannibalism was extreme. The variability in the responses of individual mothers in the Litter Size Maintained Group is apparent in Figure 10,

¹Ten pilot mothers reared litters unaltered in size, containing three or four foster newborn pups provided on the day of parturition. These mothers cannibalized a median of 25% of both their foster and their natural pups by Day 5 postpartum.

Figure 10

(a) Number of pups cannibalized,
(b) percentage of litter cannibalized, and
(c) duration of cannibalism (in days) by
individual mothers in Experiment 2(a).
Numbers identify individual subjects in
each group.



which presents the total number of pups cannibalized, percentage of litter cannibalized, and number of days of cannibalism by individual mothers.

Largely as a consequence of bimodality of results in the Litter Size Maintained Group, statistical analyses (Mann-Whitney U tests, Siegel, 1956) performed on between-group differences in number of pups cannibalized and percentage of litter cannibalized did not reach statistical significance ($U = 13$, $p > .05$, 1-tailed, for both measures). The between-groups difference in duration of cannibalism (in days) was, however, statistically significant ($U = 9.50$, $p < .05$, 1-tailed).

As Figure 10a indicates, the four experimental animals responsive to litter size maintenance cannibalized an average of more than twice the number of pups destroyed by control animals. An examination of percentage of original litter cannibalized, presented in Figure 10b, reveals that this was equivalent to destruction of between 70% and 120% of original litter size as compared to the range of 10% to 40% in Foster Control litters. Further, the temporal duration of cannibalism in these responsive experimental mothers was over twice the Foster Control Group's average duration (Figure 10c).

Discussion

The results suggest that reduction in litter size is one factor influencing termination of cannibalism. If it is the only factor, then as long as initial litter size was maintained by external manipulation, Litter Size Maintained mothers should have continued to cannibalize.

Failure of cannibalism to be extended beyond Day 6 even in the responsive experimental mothers indicates that another factor must also be involved in the cessation of cannibalism.

A problem in interpreting the data is presented by the fact that maintaining litter size obviously had a powerful effect on some, but not all of the experimental mothers. An examination of initial levels of cannibalism exhibited by experimental mothers provides one possible explanation of these results. Responsive mothers in the Litter Size Maintained Group destroyed two or three pups (mode = 3 pups) within 24 hours of parturition; while during the same period, unresponsive experimental mothers either had not cannibalized at all or had cannibalized only one pup (mode = 1 pup). Perhaps the four responsive experimental mothers were responding to the degree of alteration in litter size which was, by virtue of the size maintenance procedure, greater than that experienced by the non-responsive mothers. This possibility indicated the necessity of modifying the experimental design so that litter size is altered by a predetermined number of pups rather than by a number dependent upon observed levels of cannibalism.

Experiment 2(b)

The results of Experiment 2(a) suggest that reduction in litter size to a preferred number may be one factor responsible for the cessation of cannibalism. Experiment 2(b) provided a second test of this hypothesis by using the procedure of altering litter size by a predetermined number of pups.

According to the hypothesis that mothers cannibalize to decrease their litters to a certain size, artificial litter reduction of or increase in litter size on the day of parturition should result in compensatory changes in amount of cannibalism consistent with the magnitude of experimenter-induced alteration in litter size. The graphical representation of the predicted relationship between mean amount of cannibalism by Day 5 postpartum and magnitude of litter size alteration is a straight line with a slope of 1.0, and passing through the point representing the mean amount of cannibalism exhibited by Control Group mothers whose litters are unaltered in size. Figure 11 illustrates this predicted relationship given a normal Control Group mean level of cannibalism of about two pups per litter.

Method

Subjects

The subjects were 42 nulliparous golden hamsters obtained from High Oak Breeding Ranch Ltd., at 7.5 weeks of age, and bred at about 9-10 weeks. Foster pups were obtained from an additional 40 multiparous females.

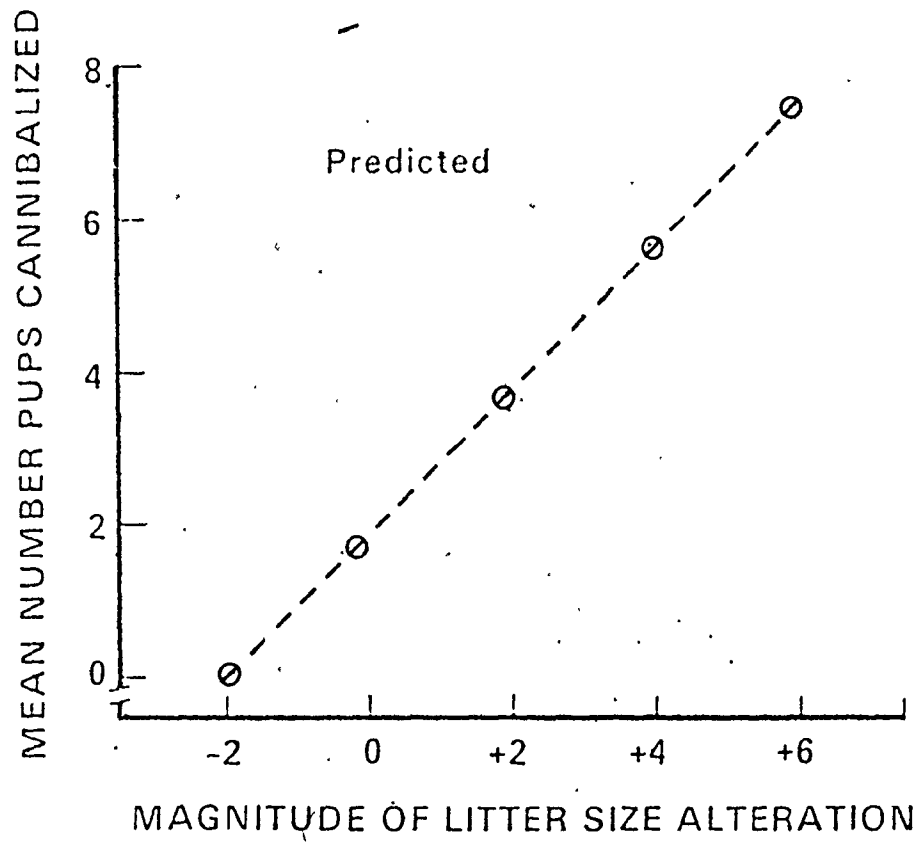
Procedure

On the day of parturition, a predetermined number of newborn foster pups were provided to each female. Control Group mothers (Group 0, $n = 9$) received four foster pups in exchange for four of their own offspring, leaving litter size unaltered. Group -2 females ($n = 9$) had four pups removed, and two foster pups replaced, so that their litters were reduced in size by two pups. Mothers in Groups +2, +4, and +6

Figure 11

Predicted mean number of pups cannibalized per litter by Day 5 as a function of magnitude of litter size alteration (Experiment 2(b)).

50



($n = 8$ per group) received, respectively, an addition of two, four, or six foster pups.

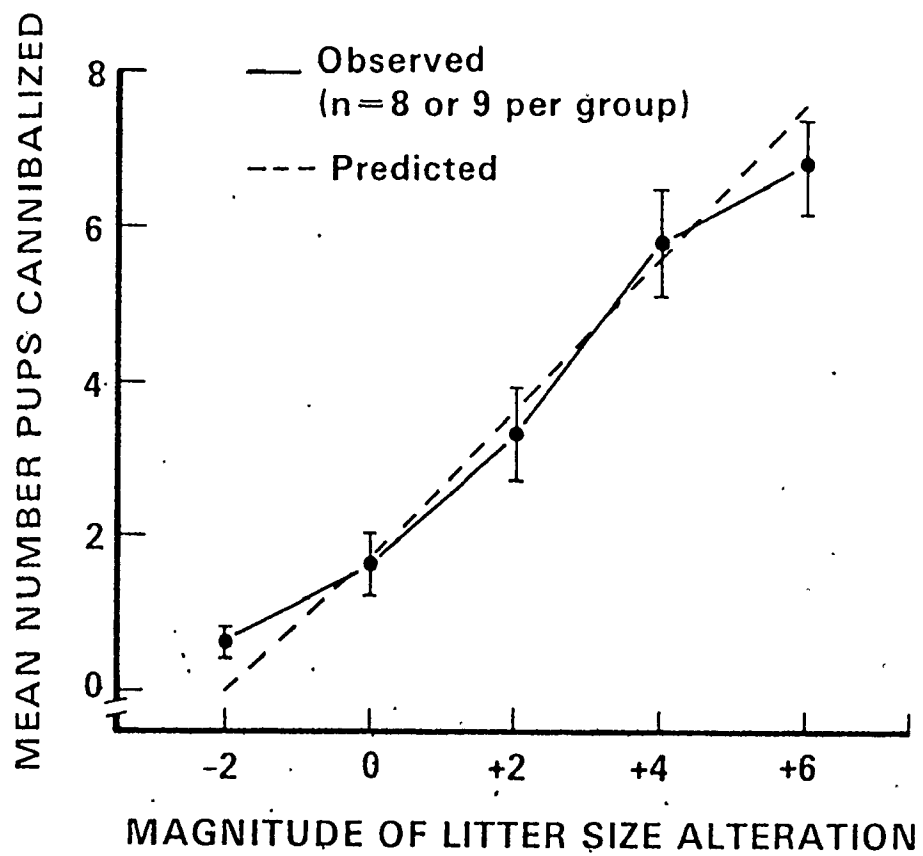
Results

Mean amounts of cannibalism by Day 5 postpartum are presented in Figure 12. These data indicate that mothers are extremely responsive to the degree of alteration in litter size. Reduction or increment in litter size resulted in mean changes in amount of cannibalism from the Control Group level, almost directly proportional to the number of pups subtracted from, or added to, the litters.

As predicted by the hypothesis, a decrease in the number of pups per litter (Group -2) reduced cannibalism from the level exhibited in litters unaltered in size (Group 0). Five of the nine Group -2 mothers, but only two of the nine Group 0 mothers did not cannibalize at all. The comparison between amounts of cannibalism by Group -2 and Group 0 mothers did not, however, reach statistical significance, probably because of the floor effect on number of pups cannibalized by Group -2 mothers (Dunnett's $t = 1.42$, $df = 37,5$, $p > .05$, 1-tailed; Winer, 1971). Each of the three litter size increases did result in significant increases in cannibalism over the Control Group's level (Dunnett's $t = 2.38$, Groups +2 vs. 0; $t = 5.90$, Groups +4 vs. 0; $t = 7.31$, Groups +6 vs. 0; p 's $< .05$, 1-tailed, df 's = 37,5). In addition, the mean numbers of pups cannibalized by females in Groups +2, +4, and +6 were quite close to the predicted means, i.e., the mean number cannibalized by Group 0 mothers, plus the number of pups added.

Figure 12

Observed and predicted mean number of pups cannibalized per litter by Day 5 as a function of magnitude of litter size alteration (Experiment 2(b)). Flags indicate ± 1 S.E.M.



Discussion

These results support the predictions from the model that a female hamster is sensitive to the number of pups in her litter and that individual mothers cannibalize to reduce the litter to a set size. Reduction in litter size is thus one factor responsible for the cessation of cannibalism. Further, the results from Group -2, indicating that mothers do not necessarily exhibit any cannibalism if litter size is artificially reduced, suggest that litter size is also a factor in the initiation of cannibalism.

It is possible, however, to attribute increased cannibalism in Groups +2, +4, and +6 to destruction of added foster pups as well as normal cannibalism of natural offspring in the litter. This explanation is unlikely for two reasons. First, no differential cannibalism of foster pups was found in any other study. Second, if females cannibalize foster pups, at least four pups should have been destroyed in Group 0 and Group -2 litters. Because of the great sensitivity of the response of the mothers in the present study, however, this alternative explanation was tested in the study to follow:

Experiment 2(c)

The present study replicated Groups 0 and +4 of Experiment 2(b). In this study, however, individual pups were marked in order to determine whether the observation of extreme sensitivity of mothers' responses to litter size increase is merely an artifact of the fate of added foster pups.

Method

Subjects

The subjects were 27, 7.5-week old nulliparous golden hamsters obtained from High Oak Breeding Ranch, bred at approximately 10 weeks of age.

Procedure

On the day of parturition, each mother was removed from her home cage, her pups were individually marked by toe clipping under Xylocaine Hydrochloride anaesthetic, and their weights and physical appearance were noted. In litters assigned to the Control Group ($n = 13$), four marked newborn pups were placed in the nest in exchange for four of the original pups. In litters assigned to the Experimental Group ($n = 14$), litter size was increased by four by the addition of four marked newborn pups.

The entire litter of one Control Group mother was missing on Day 1 postpartum. Because total litter cannibalism is exceptional, data from this mother was discarded, leaving a total of 12 mothers in the Control Group.

Results and Discussion

Adding four pups to Experimental Group litters significantly increased cannibalism by Day 5 postpartum over the Control Group level, by a mean of 3.7 pups per litter ($t_{24} = 3.84, p < .05$). Thus, the results of Experiment 2(b) were essentially replicated.

In order to examine the hypothesis that the increased cannibalism in Experimental Group litters resulted from differential mortality of foster pups, the observed frequency of cannibalism in each litter was compared to the frequency expected if cannibalism had been directed randomly. The expected frequency, which is dependent upon both litter size and observed amounts of cannibalism, was calculated using the following equation (Reference note 2):

$$\frac{E_c}{O_c} = \frac{N_f}{N_T}$$

E_c = expected number of foster pups cannibalized

O_c = total number of pups cannibalized per litter

N_f = number of foster pups per litter, always equal to 4

N_T = total number of pups per litter.

A comparison of differences between observed and expected frequencies of foster pup cannibalism by Experimental Group mothers indicated that in nine of the 14 litters, cannibalism of foster pups was slightly lower than expected (average difference between observed and expected frequencies = -.9), while in the remaining five litters, cannibalism was slightly higher than expected (average difference between observed and expected frequencies = .7). Thus, experimental mothers did not show any tendency to selectively cannibalize the added foster pups.

From these data it can be concluded that: (1) hamster mothers

do not differentially direct cannibalism towards foster pups; and (2) the increases in mean levels of cannibalism proportional to increased litter size found in this and the preceding study are not artifacts of selective cannibalism of foster pups.

Experiment 3

The evidence from Experiment 2 indicating that reduction in litter size is an important factor controlling the cessation of cannibalism does not exclude the possibility that other factors, such as increasing age of the pups and changes in the mother as a function of time postpartum, also play a role in controlling the course of litter cannibalism. In fact, the finding in Experiment 2(a) that even "responsive" mothers rearing litters maintained in size stop cannibalizing within a week of parturition, implies that either one or both of these factors act in conjunction with decreased litter size to terminate cannibalism.

The present experiment was designed to examine the role of changes in behaviour or morphology of maturing pups in the termination of cannibalism. One method of examining the influence of age-dependent characteristics of pups on cannibalism is to provide newly parturient females with litters of older pups, and mothers at a later stage in lactation with litters of newborn pups. Though theoretically valuable, such a procedure is, in fact, impracticable with hamster mothers. Unlike rats and mice, which will provide maternal care for foster pups differing in age from their own (Wiesner and Sheard, 1933; Noirot, 1972),

female hamsters respond to older or younger foster pups with cannibalism, and the probability of cannibalism increases with the discrepancy in age between the natural and the foster pups (Rowell, 1960, and personal observation). An alternative procedure was, therefore, used.

Five mothers were supplied daily with foster litters of newborn pups in exchange for their own young. If the stimulation from older pups either fails to elicit or actively inhibits cannibalism, then mothers rearing litters containing only newborn pups should continue to cannibalize indefinitely. Because reduction in litter size had been found to be effective in stopping cannibalism, initial litter size was maintained by providing each mother with a number of newborn foster pups equal to that which she had originally delivered. Thus, the experimental procedure essentially replicated the Litter Size Maintained Group of Experiment 2(a), but with foster litters of newborn pups.

Method

Subjects

The subjects were five nulliparous golden hamsters born in the McMaster colony, and bred at 10-12 weeks of age. Foster pups were obtained from over 45 other hamsters, including multiparous colony mothers, and primiparous mothers purchased from High Oak Breeding Ranch.

Procedure

During the week following parturition, each experimental mother received daily a new litter containing newborn pups, in exchange for her one-day-old litter. The number of foster pups provided was such as to

maintain original litter size. The experiment was discontinued on Day 7 postpartum due to an insufficient number of foster pups.

Results and Discussion

If older pups inhibit or do not elicit cannibalism, then cannibalism should have extended over the seven days of the experiment. The observed durations and amounts of cannibalism exhibited by the five mothers, presented in Figure 13, failed to support the predictions. Four of the five mothers stopped cannibalizing within the first week postpartum. The modal day of last incidence of cannibalism was Day 3. The fifth mother was still cannibalizing at the conclusion of the experiment, and, in fact, continued to destroy pups in her last litter over the abnormally long period of two weeks.

The observation that four of these five experimental mothers ceased cannibalizing both contradicts the hypothesis that increasing pup age causes cessation of cannibalism, and provides support for the influence on the termination of cannibalism of changes in the internal state of the mother occurring as a function of time postpartum.

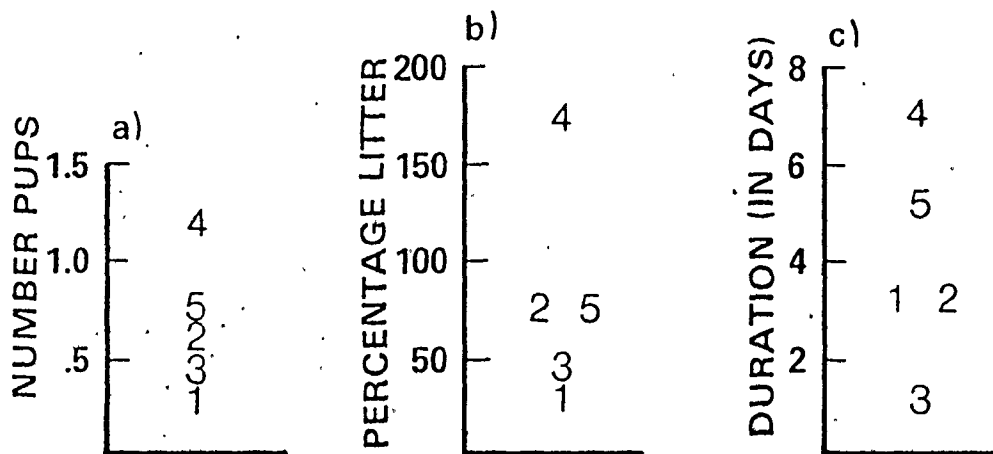
Experiment 4

Since mothers in Experiment 3 stopped cannibalizing when both pup age and litter size were kept constant, the termination of cannibalism must have resulted from the only aspect of the situation which did not remain constant; i.e., the internal state of the mother.

The cessation of cannibalism by mothers rearing litters

Figure 13

(a) Number of pups cannibalized;
(b) percentage of litter cannibalized;
and (c) duration of cannibalism (in
days) by individual mothers in Experi-
ment 3. Numbers identify individual
subjects.



LITTER SIZE MAINTENANCE MOTHERS:
NEWBORN PUPS ONLY

maintained in size could be a direct result of the continuous presence of large numbers of pups; that is, this procedure could provide conditions under which the mother habituates to large litter size. Alternatively, the decreased probability of cannibalism over time could occur independently of continuous experience with a large litter; instead, internal changes in the mother occurring as a function of time postpartum could reduce her predisposition to respond to large litter size with cannibalism.

Experiment 4(a)

The experimental procedure involved restoration on Day 10 postpartum of litter size at parturition, by replacement of pups cannibalized to that time with 10-day-old foster pups. If an increase in litter size on Day 10 elicits cannibalism, cessation of cannibalism by mothers rearing litters maintained in size would be attributable to habituation to a large number of pups. If, on the other hand, pup replacement does not increase cannibalism, then it could be concluded that these mothers cease cannibalizing because changes in their internal state reduce their predisposition to respond with cannibalism to a large litter.

Method

Subjects

The subjects were 20 nulliparous golden hamsters born in the McMaster colony and bred at 11-12 weeks of age. Because the experimental manipulation necessitated the presence of some cannibalism,

seven females failing to cannibalize were eliminated from the experiment. Foster pups were provided by litters born to colony females.

Procedure

On Day 10 postpartum, each of six Experimental Group mothers received a number of 10-day-old foster pups equal to that lost by cannibalism or illness during the first 10 days postpartum. At the same time, each of seven Control Group mothers received foster pups equal in number to those they had lost, in exchange for the same number of their own offspring, so that litter size remained at its Day 10 level.

Results and Discussion

A median of two foster pups (range from 2 to 4) had to be added to Experimental Group litters to restore original litter size. The same median number (range from 1 to 5) of foster pups were exchanged in Control Group litters. By Day 15 postpartum, i.e., within five days of the experimental manipulation, one pup had been cannibalized in each of two Control Group litters, and in each of three Experimental Group litters. The remaining litters suffered no cannibalism in the five days following the experimental manipulation. Pup replacement on Day 10 postpartum thus did not significantly increase cannibalism over the extremely low levels normally observed in litters over 10 days of age. That litter size increase on Day 10 did not significantly increase cannibalism provides support for the hypothesis that internal changes in the mother occurring as a function of time postpartum, rather than

habituation to litter size, is a second factor influencing cessation of cannibalism.

Experiment 4(b)

While the data of Experiment 4(a) suggest the influence on cessation of cannibalism of internal changes occurring in the mother as a function of time postpartum, it is possible that the results were due, in part, to the small litter size increments necessary to restore original size of litters in the Experimental Group. Therefore, in the present study, a constant large number of pups was added to each experimental litter regardless of amount of cannibalism present. In addition, the experimental procedure was modified by presenting the foster pups to different groups of mothers at various points in time postpartum. If predisposition to respond with cannibalism to a large litter wanes as a function of time postpartum, then a maximal response to litter size enlargement should be observed when litter size is increased soon after parturition, and litter size enlargement should be decreasingly effective in eliciting cannibalism the later during lactation that it is effected.

Method

Subjects

The 39 subjects were nulliparous golden hamsters obtained from High Oak Breeding Ranch at about 7 1/2 weeks of age, and bred 4 1/2 weeks later. Foster pups were obtained from the experimental mothers and from multiparous colony females.

Procedure

In four Experimental Groups, litter size was increased by four pups on either Day 0 (n = 8), Day 2 (n = 8), Day 5 (n = 8), or Day 9 (n = 7) postpartum. Added pups were the same age as the natural pups, and all pups were marked with waterproof ink to enable examination of possible differential cannibalism of foster pups. In order to control for possible between-group differences in the reaction of mothers to foster pups introduced at varying points in time, all mothers received four foster pups in exchange for four offspring already present in their litters on each, except the critical day defining group assignment. Control Group mothers (n = 8) daily received four appropriately aged foster pups in exchange for four pups remaining in their litters, so that litter size was never artificially altered.

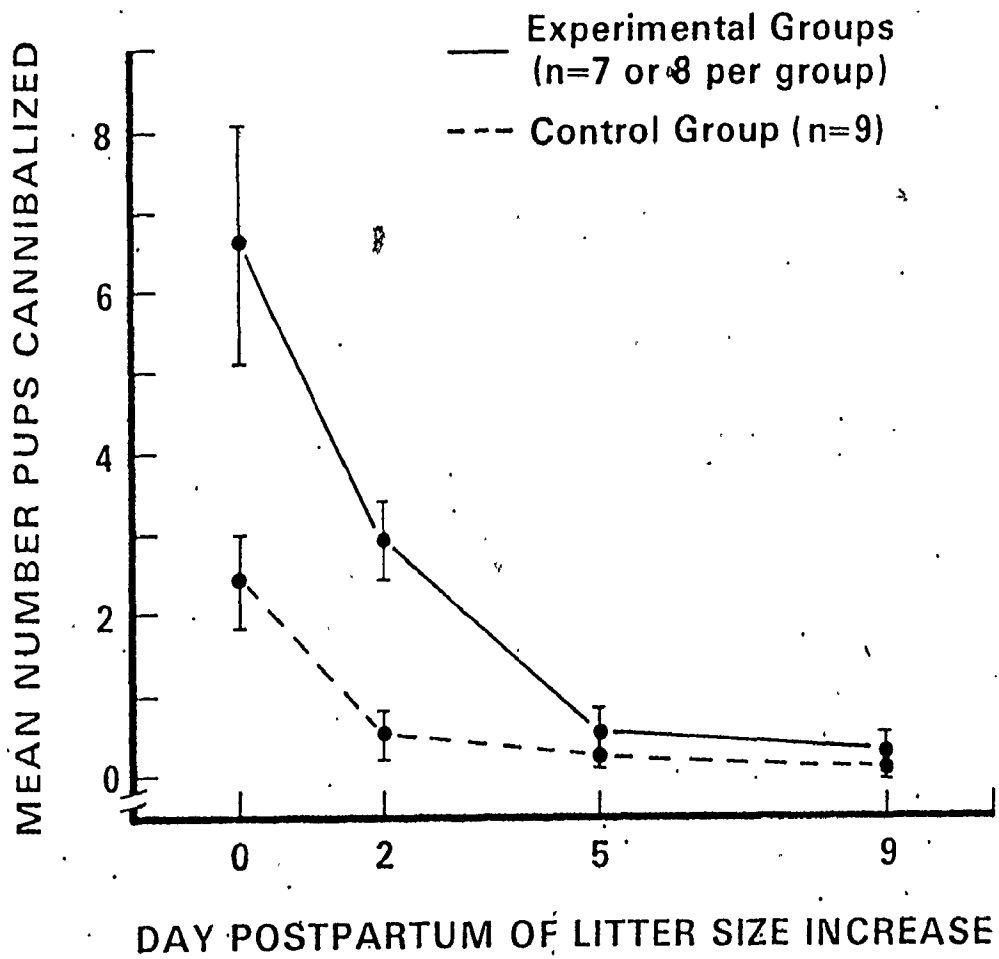
Results and Discussion

Figure 14 presents the mean number of pups cannibalized by females in each Experimental Group during five days following litter size increase. Data from each Experimental Group were contrasted with those from the Control Group for the comparable time period, both in the figure and for purposes of statistical analysis.

Enlargement of litter size significantly increased amount of cannibalism over normal control levels only when this increase was made on Day 0 ($t_{14} = 2.58, p < .05$) or on Day 2 postpartum ($t_{14} = 4.33, p < .05$). An increase in litter size by four pups did not elicit cannibalism on either Day 5 or Day 9. Examination of individual pups did not reveal differential mortality between foster pups and natural pups.

Figure 14

Mean number of pups cannibalized per litter within five days of the experimental manipulation (Experiment 4(b)). Flags indicate ± 1 S.E.M.



These results provide support for the hypothesis that mothers stop cannibalizing large litters because internal changes in the mother occurring as a function of time since parturition reduce her predisposition to respond with cannibalism to large litters.

General Discussion

The pup cannibalism typically exhibited by the maternal laboratory golden hamster has generally been conceived as an aberrant behaviour resulting from stressful conditions. The results of the present series of studies suggest that cannibalism by the parturient hamster is not the result of a breakdown in normal maternal behaviour occurring in response to the stressful factors suggested in the literature; instead, the data suggest that pup cannibalism is a highly regulated behaviour. It is systematically controlled by stimuli received from the litter, and the probability of occurrence of cannibalism is dependent upon changes in the internal state of the mother, occurring as a function of time postpartum.

Given the systematic expression of cannibalism, it appears that the most useful approach to the analysis of this behaviour is one that views it not as a breakdown of normal mother-young interactions, but, rather, as a behaviour that serves some adaptive function for the mother. The hypothesis consistent with all the data is that pup cannibalism serves as a means by which the newly parturient female can control the number of pups for which she must provide nutrition and care. This number is presumably one that is compatible with the capacity of a

female to rear her young under a given set of environmental conditions.

This conception of pup cannibalism raises at least three major questions. The first concerns the stimulus control of the behaviour. As it is the issue most amenable to empirical investigation, it is this problem with which the remainder of the thesis is concerned. The second question concerns the determination of the number of pups that a female will rear. If this number reflects some capacity of the mother to rear her young, it should vary in accord with changes in the availability of the resources limiting reproductive capacity in the natural environment. The third question concerns how such a system permitting control of litter size could serve an adaptive function for the animal in its natural environment. As there has been, to my knowledge, no study of the behaviour of the golden hamster in its natural habitat of the Arabian Peninsula, it is only possible to provide a speculative interpretation of the function of the behaviour.

The area of Aleppo, Syria, in which hamsters were first captured (Harrison, 1972) is an arable steppe (Beckingham, 1960), and while wheat and cereals are cultivated there (Seltzer, 1961) it provides only "irregular rainfall and food supply" (Richards, 1966, p.308). If capacity to successfully raise offspring is dependent upon availability of food, then pup cannibalism could serve the adaptive function of permitting the mother to rapidly respond to unpredictable changes in the environment by altering the number of pups she must rear. If, at the time of parturition, food were plentiful, the mother would have a greater capacity to rear pups, and would, therefore, cannibalize few, if any,

young. If, on the other hand, food were scarce, the mother would eat more pups in response to her lowered capacity to rear young. In the latter situation, the mother would more effectively divide the limited amount of food among a fewer number of offspring, thus probably maximizing the number of young surviving beyond weaning (Lack, 1948, 1958).

If alteration in litter size can be viewed as adaptive behaviour permitting the decision to produce a set number of live young to be delayed until the young actually appear, then the differential reproductive success must outweigh the disadvantage to the mother resulting from the energy wasted in maintaining to parturition a larger number of embryos than she would attempt to rear. Compatible with this position is the fact that hamster females have an exceptionally short gestation period (16 days) in comparison with other rodents (Richards, 1966). Thus, there may be less energy investment in each foetus in the hamster than in other rodents.

Part II:
Stimulus Control of Litter Cannibalism by
the Golden Hamster

The fact that cannibalism by an individual female is affected by litter size must result from the response of the mother to specific cues from the pups. The experiments presented below are directed towards an examination of some of the possible cues arising from the pups to which the mother could be responding.

Litter size affects a variety of variables. In mice and rats, litter size alters frequency and duration of time mothers spend in the nest (Ader and Grota, 1970; Grota, 1973; Grota and Ader, 1969), as well as altering pup retrieval and nest building (Priestnall, 1972; Seitz, 1954). Litter size also affects rat milk yield (Kumareson, Anderson, and Turner, 1967; Moon, 1969) and rat and hamster mammary gland development as indicated by gland RNA and DNA content (Moon, 1965; Tucker, 1964, and 1966; Yu and Anderson, 1972). Perhaps the maternal hamster uses one of these factors to respond to the number of pups in her litter. The studies to be presented examined the role of olfactory cues and of stimulation received during nursing upon alteration of litter size by the maternal hamster.

Two general approaches are available to determine the modality of stimulus control over the maternal hamster's response to litter size. One, is reducing stimulation of a particular modality which should result in a decrease in cannibalism by mimicking a decrease in litter size. The other is augmenting a particular class of stimulation which should imitate litter size increase, and thus increase cannibalism. The former method was used in the experiments to follow.

CHAPTER III

The Role of Olfactory cues

The studies in the present experiment were designed to investigate the role of olfactory stimulation from pups in the control of hamster cannibalism. In order to mimic litter size decrease, olfactory information was decreased by eliminating the mother's capacity to detect odour.

In the two experiments to be presented, anosmia in the mother was produced peripherally or centrally. Each method has advantages and disadvantages in terms both of technical difficulty and possible side-effects on behaviour (Alberts, 1974). When studying the effects of anosmia on maternal behaviour, it is critical to make use of both methods since peripheral and central anosmia have been found to have differential effects on maternal behaviour depending upon the species studied, parity of the mother, and whether the female has had previous exposure to pups (Benuck and Rowe, 1975; Gandelman, Zarrow, Denenberg, and Johnson, 1971; Fleming and Rosenblatt, 1974, a, b; Seegal and Denenberg, 1974; Schlein, Zarrow, Cohen, Denenberg and Johnson, 1972; Vandenbergh, 1973).

Experiment 5(a)

In the first experiment, temporary anosmia was created in the mothers by bathing the nasal mucosa with a solution of zinc sulfate (Alberts and Galef, 1971; Powers and Winans, 1973). This procedure, involving primarily peripheral rather than central interference, has the advantage that it does not normally result in the side effects on behaviour, such as increased aggression, frequently observed as a result of centrally-produced anosmia (e.g., Alberts and Friedman, 1972; Alberts, 1974). It does, however, have two disadvantages. First, ingestion of zinc sulfate during the operation producing anosmia may produce illness in the subject (Alberts, 1974), and second, the duration of anosmia is highly variable.

Method

Subjects

The subjects were 12 nulliparous golden hamsters from the McMaster colony, bred at 11-13 weeks of age.

Procedure

Subjects were operated upon on the evening of the 14th day of pregnancy, two days before each animal was due to deliver. After being placed under ether anaesthesia (Mallinckrodt Canada, Ltd., Toronto, Ontario), the animal was held head downwards, its jaws propped open, and the end of a blunted and hooked 18 gauge hypodermic needle placed in the nasopharyngeal meatus. When the needle was in place, 0.5 cc. of solution was forced through the nasal passage and out the external

nares. The animal was then aspirated for about 15 seconds at each nostril and at the rear of the throat. The animal was held head downward until consciousness was regained to facilitate drainage of any remaining liquid. The entire operation, from anesthesia to recovery, took less than five minutes.

Experimental subjects (n=6) received a solution of 5% weight/volume zinc sulfate. Control animals (n=6) were administered a solution of 0.9% physiological saline. Saline control animals showed a more rapid recovery from the procedure than zinc sulfate animals. The former group behaved normally within 10 minutes of completion of the procedure, while experimental animals sneezed frequently, pushed their noses through the sawdust in their cages, face washed, and kept their eyes half closed for some time. Differences in behaviour were still apparent even 24 hours after the operations.

Test for Anosmia

A simple test for reduction in olfactory capacity was given daily, beginning at least two days before the operation and for approximately a week thereafter. The test involved a three-minute period during which the behaviour of the animal was observed in its home cage, after pigeon grain had been scattered on the wood shavings in the cage. Normal hamsters are ordinarily quite adept at finding and gathering this highly preferred food, while pilot study indicated that following zinc sulfate administration, hamsters fail to gather most of the seeds. Although this test does not discriminate between lack of food gathering due to anosmia or to motivational deficits, the fact that zinc sulfate

treated animals spend a considerable portion of the three-minute interval nosing through the sawdust after the grain is scattered, and will pick up and either eat or food-pouch large, clearly visible seeds, suggests that these animals are unable to collect the grain because of their sensory deficit. A reduction in cannibalism by anosmic hamsters may be interpreted as the hamster failing to recognize pups as a novel food source. This seems unlikely, however, because anosmic hamsters hoard or eat a completely novel food, such as carrots.

Results

The six animals undergoing the zinc sulfate procedure were unable to gather grain from one to five days following the operation. It was, therefore, assumed that these subjects had severe olfactory deficits from the time of the operation, on the day of parturition, and on at least the first day of lactation. An examination of the cannibalism exhibited by these mothers reveals that no mother having undergone the zinc sulfate operation cannibalized any pups, either during the time the animals exhibited an olfactory deficit or thereafter. In contrast, the Control mothers exhibited normal levels of cannibalism. By Day 5 postpartum, five of the six Control animals had cannibalized to some degree (mean = 3.3 pups).

Discussion

Because the anosmic mothers did not initiate pup cannibalism, the results of the present study provide support for the hypothesis that pup odour is a cue used by the mother to respond to litter size with

cannibalism. There are, however, two alternative explanations of these data.

First, it is possible that the anosmia resulted in elimination of cannibalism because sudden elimination of any sensory capacity may reduce or eliminate cannibalism. This explanation was rejected after performing an experiment (described in Appendix A) which investigated the effect of sudden elimination of visual stimulation. A group of mothers delivering and rearing their litters in a 24-hour dark room cannibalized slightly more than Control Group mothers rearing their litters under a normal day-night cycle.

The second alternative explanation is that post-operative illness observed in the experimental mothers reduced motivation to ingest any food, including pups. Although these mothers did search through the sawdust, presumably for grain, during the test for anosmia, it is critical to observe the effects on cannibalism of anosmia produced by a method which does not produce illness.

Experiment 5(b)

The decreased levels of cannibalism found in the previous study may have been an artifact of illness caused by the zinc sulfate preparation. It is necessary, therefore, to test the role of olfactory stimulation in normal cannibalism by an alternative procedure. In the present experiment olfactory deficits were produced centrally. The most straightforward method of producing central anosmia is to ablate both olfactory bulbs. Unfortunately, bilateral bulbectomy, in addition to producing anosmia, has been found to have highly deleterious side effects

on maternal behaviour. In one study, five out of 15 hamsters bilaterally bulbectomized as neonates cannibalized their entire litters (Leonard, 1972), and personal observation has shown that females operated upon as adults destroy their entire litters. Removal of both olfactory bulbs eliminated maternal behaviour in the mouse (Gandelman, Zarrow, Denenberg, and Myers, 1971), and this operation has resulted in pup cannibalism by normally non-cannibalistic rats (Benuck and Rowe, 1975; Schlein, Zarrow, Cohen, Denenberg, and Johnson, 1972).

In the present study an alternative method of producing central anosmia was used. This procedure, developed by Devor and Murphy (1973), involves removal of one olfactory bulb combined with suturing of the nostril contralateral to the removed bulb. The preparation of unilateral bulbectomy combined with suturing relies upon the existence of unilateral connections between peripheral olfactory structures and the two olfactory bulbs. Depending upon which nostril is closed, the animal is either left with free air passage to the intact bulb or not. If the nostril contralateral to the removed bulb is sutured, the animal is left functionally anosmic, and if the nostril ipsilateral to the removed bulb is sutured, the animal retains olfactory capacity. Of critical importance is the fact that use of this preparation involves equal brain damage to experimental and control animals. Any behavioural side effects resulting from tissue damage will be present in all animals. Since the only procedural difference separating control and experimental animals is which nostril is sutured, behavioural differences between groups can be attributed to decreased olfactory capacity.

The operation of unilateral bulbectomy was not found in the

present study to have any unexpected effects on behaviour. It did, however, share a drawback with the zinc sulfate method. It too was a temporary procedure, with its effective duration depending upon the time the sutured nostril remained closed. The suture frequently tore through the delicate nostril tissues within only a few days.

Method

Subjects

The subjects were 32 nulliparous golden hamsters obtained from High Oak Breeding Ranch at about 7.5 weeks of age. The animals were obtained in two shipments, four months apart.

Procedure

Operations were performed within one week following the arrival of the animals. While under Nembutal anesthesia (Abbot Laboratories, Ltd., Montreal, Canada; the dosage of 90 mg./kg. was supplemented with injections of .02 cc.), the animals' head was secured in a stereotaxic apparatus with blunted ear bars, preventing damage to the ear drums. After exposing the skull by a 1 cm. incision made over the sagittal suture, a dental burr was used to drill a small opening over either the right or left olfactory bulb. Once the dura was broken, the bulb was aspirated, and the resulting space packed with "Gelfoam" (The Upjohn Co. of Canada, Don Mills, Ontario). The wound was closed with sutures. Recovery was rapid, and the animals were bred within a week of the operations.

For the first series of operations, mothers (n=16) were placed under ether anesthesia on the evening before the day of parturition to

suture the nostril. In the second series, mothers (n=16) were placed under Nembutal anesthetic, on the evening of the day of parturition.

As no differences in behaviour were observed to result from the varying procedures, animals were combined from the two series.

The nostril contralateral to the removed bulb was closed in a total of 21 Experimental Group animals (10 with left bulb removed, 11 with right bulb removed), and the ipsilateral nostril was sutured in the remaining 11 Control Group animals (6 with left bulbs removed, 5 with right). In most cases, only one suture was used to close the nostril, and "Collodion" glue (McArthur Chemical Co., Ltd., Montreal) was placed on the suture thread to further secure it.

Contralateral nostrils were sutured in a larger proportion of animals to insure the existence of a large enough pool of anosmic animals, as pilot study had indicated that some animals undergoing this procedure did not exhibit olfactory deficit. Failure to produce a deficit could result either from incomplete closure of the nostril, permitting air to travel to the unoperated bulb, or from insufficient damage to the lesioned bulb. Data from six operated animals were eliminated (two from the first series and four from the second) when, on the day of parturition, their litters were found to be abnormal with respect to general appearance (poor skin colour, absence of milk in the stomach, etc.). This left a total of 17 mothers in the Experimental Group, the possibly anosmic group, and 9 in the Control Group.

On the day following suturing, animals were presented the test for anosmia described in Experiment 5(a) to determine whether they were

able to gather the scattered grain. The test was continued until an individual mother was clearly gathering the food normally.

Histology

Approximately three months after the conclusion of the experiment, the animals were sacrificed with an overdose of Nembutal anesthesia and were perfused intracardially with solutions of physiological saline followed by 10% formalin. Gross histological examination of brains was made to observe the extent of the damage to the lesioned and the unoperated bulbs.

Results

Seven of the 17 experimental mothers, whose preparation should have left them with a marked decrease in sensory capacity, were not anosmic according to the seed gathering test. Gross histological examination of six of these unimpaired experimental animals (the seventh was not examined after its death from illness) revealed that more than half of the dorsal portion of the damaged bulb remained intact. In contrast, less than half of the bulb remained intact in anosmic experimental animals. Only data from the 10 mothers operationally defined as anosmic will be discussed further.

These 10 experimental mothers were anosmic for periods ranging from one to four days postpartum. In all but one animal, the reappearance of normal food gathering behaviour was contiguous with opening of the suture. All nine control sutured animals exhibited normal capacity to gather grain during all tests.

Figure 15 presents the percentage of mothers cannibalizing in each group, as a function of day postpartum. Between Day 0 and Day 1 postpartum, when all Experimental Group animals were anosmic, two of the 10 mothers exhibited some cannibalism as opposed to five of the nine Control Group mothers exhibiting some cannibalism. This difference between proportions of animals cannibalizing is statistically significant ($Z = 2.14$, $p < .05$, Bruning and Kintz, 1968).

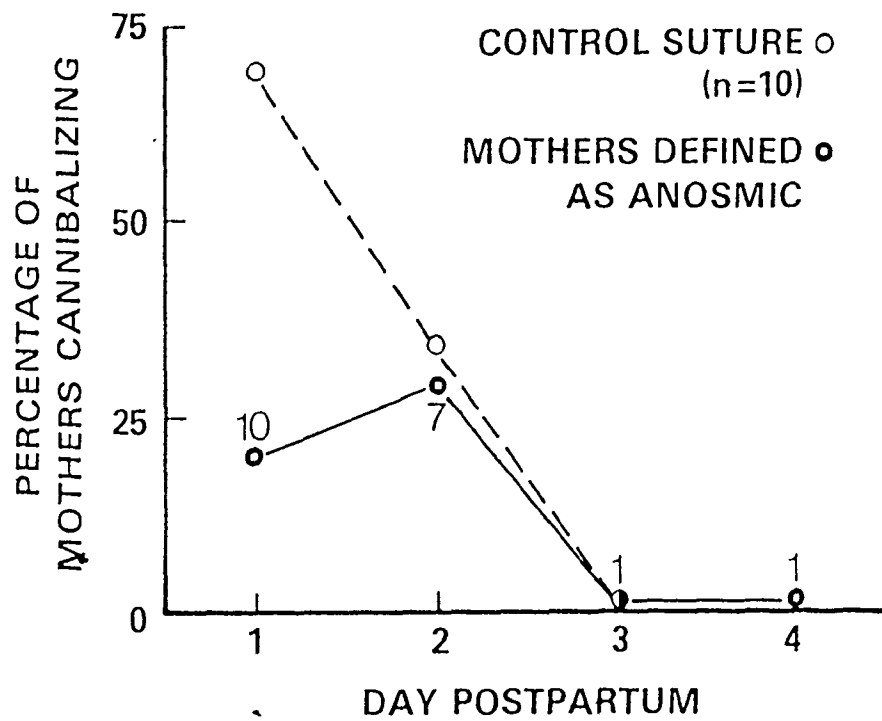
Discussion

While the peripheral anosmia produced by zinc sulfate eliminated pup cannibalism completely, anosmia produced centrally merely delayed the initiation of the behaviour. The causes of the unequal effects of the two procedures cannot be determined from the present data. The results of both studies, however, lead to the conclusion that normal olfactory capacity plays an important role in the exhibition of pup cannibalism by the maternal hamster.

If amount of pup odour is the stimulus to which the female hamster responds when altering her litter size, then one would predict that increases in amount of pup odour should increase cannibalism. Several methods were used in pilot studies to examine this possibility. In one procedure, normal mothers reared litters in cages with mesh floors and large numbers of pups were placed beneath the mesh, under the nest site. In a second, mothers reared litters in large air-tight containers. Air flow to the containers passed through a small air-tight container holding a large number of pups. In a third procedure, pups were placed in

Figure 15

Percentage of mothers cannibalizing in the Control and Experimental Groups, on each of the four days following parturition. Numbers refer to the number of experimental mothers operationally defined as anosmic on each day (Experiment 5(b)).



a wire mesh container in a standard home cage, near the nest site. All procedures presumably increased the quantity of pup odour received by the mother, but none resulted in the expected increase in cannibalism. Because of the inability of increased olfactory stimulation to increase cannibalism, it cannot be concluded that quantity of pup odour provides the stimulus allowing the mother to determine the number of pups in her litter; instead, it appears that sensitivity to odour is necessary only for the normal initiation of the behaviour.

CHAPTER IV

The Role of Nursing Stimulation

Experiment 6

The role of stimulation from nursing on litter size alteration by hamsters was investigated in the present experiment. During the normal course of caring for her offspring, the rodent mother spends a large portion of time nursing her young. Rats, for example, spend about 85% of the day in the nest with their pups immediately after parturition (Grota and Ader, 1969). During this time, the pups normally are attached to the nipples, suckling and receiving milk (Croskerry, Smith, Leon, and Mitchell, 1976). Thus, for a large portion of the day, the newly parturient female receives tactile stimulation on the ventral surface and the teats, and undergoes vast hormonal and physiological changes as a result of nursing-induced stimulation.

One or more of the various facets of normal lactation may provide the requisite stimulation for the response of cannibalism to litter size in hamsters. Milk yield and/or development of mammary tissue have been found to vary systematically with variations in litter size in hamsters (Yu and Anderson, 1972), rats (e.g., Kumaresan, Anderson and Turner, 1967), and mice (e.g., Falconer, 1947). While

these studies examined the relationships between those factors and litter size after the mothers had suckled their litters of a set size for a minimum of 10 days postpartum, it is probable that the varying nutritional demands of litters of different sizes effect some changes in milk production beginning from the initial period of nursing.

In the present study, the hypothesis that the maternal hamster uses some stimulation from nursing pups to respond with cannibalism to litter size was tested by eliminating normal stimulation obtained during nursing. Stimulus decrement was effected by thelectomizing the mothers. Removal of the teats prevents stimulation from physical attachment of the pups and milk removal, and prevents normal development of mammary tissue. If the mothers use any of these cues in responding to litter size with cannibalism, removal of the stimulation should eliminate cannibalism.

Because thelectomized mothers cannot nutritionally sustain their pups, it is necessary to continually foster pups between intact and operated mothers. Pilot study indicated that fostering had to occur at relatively short intervals. Although pups left at room temperature without any maternal care at all survive over a 12-hour period, there is a high death rate in pups in contact with thelectomized mothers for a 12-hour period, perhaps as a result of a higher rate of metabolism.

Method

Subjects

The subjects were 32, 7.5 week old nulliparous golden hamsters obtained in two shipments, about one month apart, from High Oak Ranch,

Ltd. Foster mothers were obtained from the same source and from multiparous colony stock.

One mother was excluded from the experiment after she exhibited highly abnormal aggressive behaviour toward her pups when she was returned to her cage on Day 2 postpartum.

Surgical Procedure

Operations were performed on the animals, under Nembutal anesthetic, approximately one week after their arrival in the laboratory. In the Thelectomy Group (n=13), teats were removed surgically. In the Control Group (n=18), similar small wounds, about 2 mm. in diameter, were made along the nipple line, between teats. The number of teats varied between five to eight per side, with a median and mode equal to seven. The wounds were bathed with Xylocaine anesthetic, and left open to heal. Healing and recovery were quite rapid, and the animals were bred within 10 days of the surgery.

Fostering Procedure

The 10-hour night period under which animals were maintained was interrupted by periods of less than an hour of normal light to permit unimpaired data collection and pup fostering. At 6-hour intervals, a mother was removed from her cage, her litter weighed and checked for general health and the presence of milk bands, and the litter exchanged for new foster pups.

The first time a mother and litter were checked, at 6 p.m. on the evening of the day of parturition, she was provided with a foster litter of newborn pups containing four more pups than were present in

her original litter. The addition of four pups was made to insure high enough levels of cannibalism to enable between-group comparisons. On each occasion thereafter, mothers received a number of appropriately aged foster pups, equal to the number of pups present in her foster litter at the time when the fostering procedure was executed.

Thelectomy Group mothers always received foster pups that had been nursed for at least the previous 6-hour period. These pups came from either Control Group and colony foster mothers, or when necessary, from the very few pups observed to have milk in their stomachs in the litters reared by other Thelectomy Group mothers (a result of incomplete thelectomy). Control Group mothers received both pups that had been nursed and those that had not received milk during the previous 6-hour period. The former pups were provided by other Control Group and colony foster mothers, and the latter, by Thelectomy Group mothers. The source of the foster pups was thus variable within litters, and between 6-hour intervals.

Results

In spite of fostering pups every six hours, the number of pups dying from factors other than cannibalism remained significantly higher than normal. The result was a continually decreasing supply of healthy and nursed foster pups, which prevented observations from being continued beyond two days postpartum. Data from one thelectomized mother was collected only during the 24-hour period of survival of any of her pups.

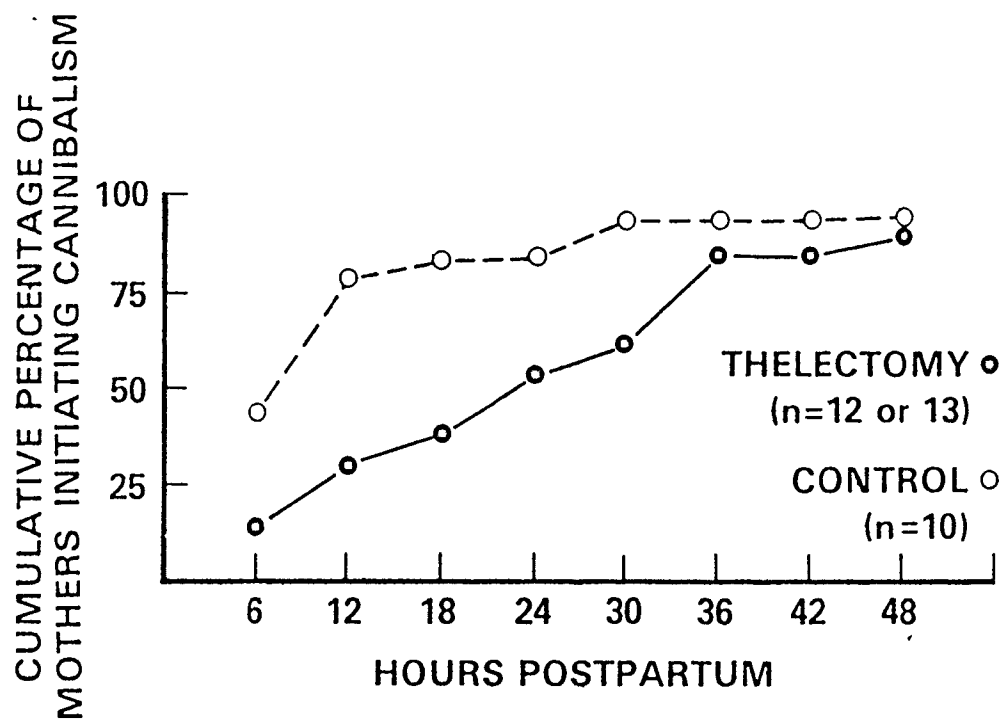
Examination of changes in average pup weight over 6-hour periods

indicated that the thelectomies were successful in severely reducing milk yield. Between Days 0 and 2, 100 measures were taken of average weight change of litters kept with thelectomized mothers, and of these, there were eight instances (8%) of gains in average litter weight. This is in contrast to 121 (84%) measures of weight gain in the 144 average litter weight change measures taken on litters cared for by Control Group mothers. The few cases of average weight increases observed in litters cared for by thelectomized mothers are probably indicative of some errors in the surgical procedure. A teat could have been missed during surgery, since the teats are variable in number (a range of 12-16 were observed), unequally spaced, and appear only as tiny imperfections in the surface of the skin.

The crucial measure of the effect on cannibalism of decreased stimulation from nursing is the proportion of mothers initiating cannibalism in each group. If stimulation obtained in nursing provides the critical cue of litter size to which the maternal hamster responds, then the thelectomies should have resulted in a drastic decrease in the number of mothers cannibalizing. Figure 16 presents the cumulative proportion of mothers in each group initiating cannibalism, as a function of successive 6-hour intervals postpartum. Tests of significance were performed on between-group proportions (Bruning and Kintz, 1968, Chapter 5) at each interval. As can be seen in the figure, fewer thelectomized than Control Group mothers initiated cannibalism over the 48 hours after parturition, but differences between proportions were statistically significant (all p 's $\leq .05$) only at 12, 18 and 30 hours postpartum.

Figure 16

Cumulative proportion of mothers
initiating cannibalism, as a function
of time postpartum (Experiment 6).



An examination of Figure 17, which presents mean number of pups cannibalized within each 6-hour period postpartum, indicates lower levels of cannibalism were exhibited by thelectomized mothers within the first 24 hours postpartum, but, thereafter, little difference was present between groups.

Discussion

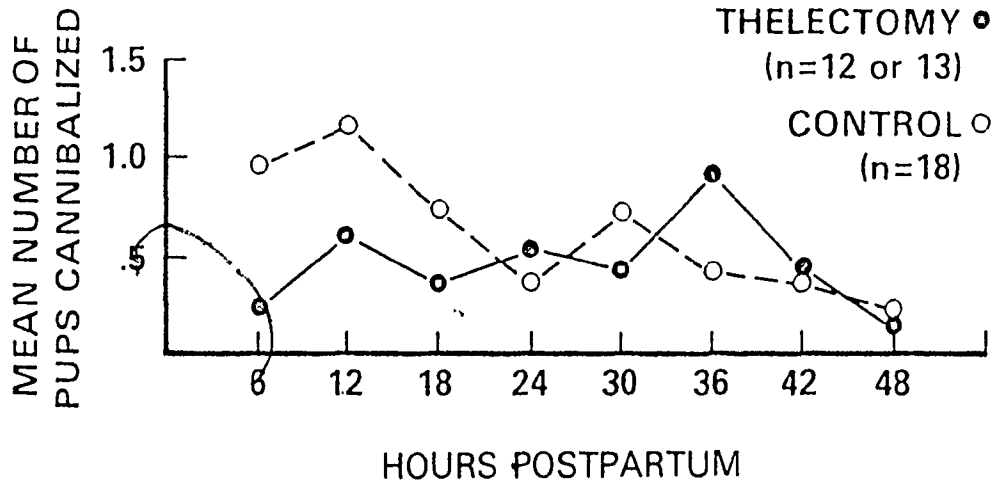
Reduction in stimulation normally received in nursing significantly altered the normal pattern of cannibalism exhibited by the golden hamster. The effect of removal of this class of stimulation was to delay the time of the onset of normal cannibalism. Once cannibalism was initiated, however, thelectomized mothers cannibalized to the same degree as control operated mothers.

It will be recalled that a similar delay in initiation of cannibalism was effected by central anosmia. The fact that both reduction in olfactory stimuli and in stimulation received in nursing had similar effects on cannibalism, implies that it is under multiple stimulus control. That is, while olfactory and nursing cues coming from large litters are definitely contributory factors to the normal initiation of cannibalism, neither source of stimulation is a necessary, or even a sufficient, source of stimulation, so that its removal could eliminate the behaviour.

The apparently multi-modal nature of the stimulus control of initiation of cannibalism by the hamster is thus similar to other mammalian behaviour patterns, such as maternal behaviour (Beach and Jaynes, 1956) and sexual behaviour in rats (Stone, 1922; Beach, 1942), neither of which is dependent on a single mode of sensory stimulation.

Figure 17

Mean number of pups cannibalized per litter as a function of time postpartum (Experiment 6).



CONCLUSION

Results of the preceding experiments indicate that a female hamster cannibalizes her pups so as to obtain a particular size litter, and that an individual mother shows some consistency, relative to other mothers, in the number of pups she will rear. These observations suggest that pup cannibalism may serve an adaptive function by providing the hamster mother with the potential to alter the size of her litter to that which is most compatible with her individual capacity to rear young in the environmental conditions prevailing at the time of her parturition. Given this orientation to pup cannibalism, further investigations of this behaviour can be approached at three levels of analysis: ecological, physiological, and psychological.

The critical issue from an ecological perspective is a determination of those aspects of the environment which act as the stimulus to the mother's response of altering the number of pups she will rear. Under Lack's hypothesis that variability in litter size is an adaptive modification enabling the animal to maximize reproductive success under any given set of environmental conditions, the problem is to specify those resources which limit reproductive capacity. Ecological information, which is necessary for specification of the critical factors in the natural habitat, is not available for the golden hamster. It may be possible, however, to determine at least those variables that can

influence reproductive capacity in the laboratory. If any factor, such as amount or quality of food, or availability of secluded nesting areas, changes the capacity of the laboratory hamster to successfully rear young, this would be reflected in changes in the intercept of the linear function relating amount of cannibalism to magnitude of artificial alteration in litter size. Females would presumably compensate for experimenter-induced changes in litter size, but would regulate about different values as a function of changes in availability of limiting resources.

Second, there must exist some physiological system which provides the substrate which allows the mother to regulate her litter size. If, as proposed above, this set point of the regulatory system is affected by the availability of resources in the external environment, or by the monitoring of internal states which reflect changes in the external environment, then study of the physiology of this regulatory system should prove of some interest. The experimental result that mothers are responsive to litter size only for a relatively short duration after parturition suggests that the control of this system is also of limited duration.

Finally, the mother is obviously capable of responding, with some precision, to the number of offspring present in her litter at parturition. The third level of analysis thus involves an understanding of the psychological mechanisms through which the mother responds to litter size. While the experiments in Chapter II indicate that the initiation of cannibalism is under multiple stimulus control, the proximal

factors controlling the maintenance of cannibalism were not identified. The solution of this problem requires demonstration that increases in sensory input of a specific modality result in appropriate increments in amount of cannibalism.

Investigation of the phenomenon of pup cannibalism by the golden hamster as an organized part of maternal behaviour, seems to offer an excellent opportunity for integrating ecological, physiological, and psychological approaches to the study of one aspect of reproductive behaviour.

Appendix A

The present experiment was performed to determine whether a deficit in sensory stimulation in any modality is sufficient to reduce cannibalism. To this end, visual stimulation was reduced in one group of mothers by having them rear their litters in continual darkness.

MethodSubjects

The subjects were 18 nulliparous female hamsters obtained at about 7.5 weeks of age from High Oak Breeding Ranch, Ltd., and bred within 10 days of arrival.

Procedure

On the evening before parturition, one group of females (n=9) was shifted to a small room kept in continual darkness. These animals received standard handling thereafter, under temporary red light illumination. A Control Group (n=9) also was shifted to a new room of approximately equal size, on the evening before parturition. This room was illuminated with a normal light cycle of 14 hours of daylight and 10 hours of night.

Results and Discussion

Both groups of mothers exhibited normal levels of cannibalism, with the light-deprived group cannibalizing a mean of 3.2 pups per litter, and the Control Group cannibalizing a mean of 2.3 pups per litter. These results indicate that any decrease in sensory stimulation

does not provide a sufficient condition for reduction in cannibalism. The lowered levels of cannibalism found in mothers having an olfactory deficit were specific to that sensory modality.

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