

## Pup Cannibalism: One Aspect of Maternal Behavior in Golden Hamsters

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Examination of the role of six factors generally held to affect incidence of litter cannibalism in the golden hamster revealed little influence of any of them on frequency of pup destruction. More than 75% of mothers in all conditions examined cannibalized a portion of their litters during the first few days postpartum. Termination of cannibalism was found to result both from reduction in litter size, consequent upon destruction of young, and from changes in the internal state of the mother following parturition. The outcome of additional studies indicated that mothers maintain litter size at an individually determined value, behaviorally compensating for experimental alterations in pup number. The results are interpreted as indicating that pup cannibalism in hamsters is an organized part of normal maternal behavior which allows an individual female to adjust her litter size in accord with her capacity to rear young in the environmental conditions prevailing at the time of her parturition.

After parturition the female golden hamster (*Mesocricetus auratus*; Waterhouse, 1839) exhibits a broad repertoire of maternal behaviors important for the growth and protection of her young. The maternal hamster, like other postpartum rodents, maintains a nest, nurses and grooms her offspring, and retrieves strays to the nest site. In addition to these obviously "nurturant" activities, the hamster dam typically exhibits a behavior directed toward her young that is less frequently observed in other species. She almost invariably cannibalizes some of her own live offspring. Virtually all breeders of hamsters, rearing animals under a wide variety of laboratory conditions, have re-

ported loss of neonates as a result of such maternal destruction of pups.

Although we can find no systematic investigation of the causes of pup destruction by postpartum hamsters, those researchers who have informally observed the phenomenon have attributed cannibalism to a variety of factors. A number of workers have suggested that disturbance of the dam by the breeder results in destruction of young (Bruce & Hindle, 1934; Hindle & Magalhaes, 1957; Poiley, 1950; Silvan, 1966; Summer, 1972; Whitney, 1963). Others have proposed that extreme litter size at birth or immaturity of the mother at parturition increases the probability of cannibalism (Dieterlin, 1959; Poiley, 1950; Silvan, 1966; Whitney, 1963). Further, it has been informally suggested that illness of pups, lack of maternal experience in primiparous females, and hyperemotionality of particular females may underlie pup destruction.

These proposals concerning factors important in the induction of litter cannibalism have in common the assumption that pup destruction is aberrant behavior, induced by factors that disrupt patterns of "nurturant" maternal behavior normally exhibited by postpartum females. Empiri-

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cal support for considering litter cannibalism as a breakdown in adaptive behavior patterns is to be found in the results of experiments indicating that emotional strains of rabbits, mice, and pigs are more likely to cannibalize their offspring than less emotional ones (Denenberg, Petropoulos, Sawin, & Ross, 1959; Hodgson, 1935; Poley, 1974). Also consistent with this interpretation are observations suggesting that destruction of litters by maternal mice and hamsters attempting to rear their young in crowded cages results from failure of the mother to prevent the intrusion of conspecifics into the nest area and the consequent disruption of normal mother-young interaction (Brown, 1953; Goldman & Swanson, 1975; Southwick, 1955a, 1955b).

Theoretical considerations also lend some support to the hypothesis that pup destruction is the result of a disruption of normal patterns of maternal behavior. Within the context of the synthetic or neo-Darwinian theory of evolution, natural selection is viewed as acting on both morphology and behavior so as to maximize differential reproductive success. Because a female's cannibalism of her own young appears to directly reduce her potential relative contribution of descendants to subsequent generations, it can be argued that such behavior should be actively selected against. In this view, the presence of the apparently maladaptive behavior of pup destruction in hamsters can be treated only as the result of disruption of normal adaptive "nurturant" behavior of the dam with respect to her offspring.

Alternatively, it has been hypothesized that there are circumstances in which it would be adaptive for reproductively active females to develop fewer embryos than the maximum number that they are capable of producing (Lack, 1954, 1958); for example, in a period of food shortage a female that delivered a small, rather than a large, number of young might successfully wean more offspring. It would be consistent with this view for natural selection to act to allow females to modify their reproductive effort in accord with environmental circumstances. There is, in fact, consid-

erable evidence that reproductive strategies have evolved that allow females to regulate the number of young they produce in response to environmental variables; for example, the results of extensive field studies indicate that females of many avian species adjust their clutch size to compensate for fluctuations in food availability (Lack, 1954, 1958). Similarly, laboratory studies indicate that guinea pigs tend to produce larger litters in food-rich environments than in food-poor ones (Lack, 1954).

It seems reasonable to suggest that pup cannibalism by postpartum hamsters may be functionally analogous to the cases of reduction in number of young delivered described above. Either response would permit adjustment of litter size to a value appropriate to the environmental circumstances in which the young are to be reared. For pup cannibalism, rather than reduction in the number of embryos developed, to have evolved as a mechanism for regulating reproductive effort, it would be necessary that the advantage in reproductive success accruing to the female hamster from culling her litter after parturition outweigh the disadvantage resulting from energy wasted in developing to the time of parturition a larger number of embryos than will be maintained. The fact that golden hamster females exhibit a shorter gestation period (Daly, 1976; Richards, 1966)—and, hence, may have less energy investment in embryos at birth—and a greater incidence of cannibalism than other rodents is compatible with such a position.

The first of the present series of experiments assesses the effects of a variety of stresses on incidence of pup destruction. The remaining experiments examine the factors controlling the frequency, duration, and termination of cannibalism by hamsters rearing their litters under standard laboratory conditions.

### General Method

#### Subjects

Subjects were nulliparous female golden hamsters (*Mesocricetus auratus*) obtained either at 7.5

wk of age from tario, or from l. Colony-born fe age, housed in old, and subseq 30.5 × 16.5 cm tics, Inc.). All a on a 14:10 hr Purina Labora mented with 1 animal was hu

#### Handling

To habituate rition, we remo cages and place min on at lea. Identical handl parturition.

#### Measures

Litters were (termed Day 0 thereafter. The from her home pups present, p of pups (color, p of injury).

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#### Exclusions

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stained either at 7.5

wk of age from High Oak Ranch, Goodwood, Ont-  
ario, or from litters reared in the McMaster colony.  
Colony-born females were weaned at 21–28 days of  
age, housed in groups of three to six until 7.5 wk  
old, and subsequently individually housed in 35.6 ×  
30.5 × 16.5 cm polycarbonate cages (Maryland Plas-  
tics, Inc.). All animals were maintained at 21–23 °C,  
on a 14:10 hr light/dark cycle. Ad lib rations of  
Purina Laboratory Chow and water were supple-  
mented with 1–2 g of pigeon grain whenever an  
animal was handled.

### Handling

To habituate animals to handling prior to partu-  
rition, we removed all pregnant females from their  
cages and placed them in a separate enclosure for 5  
min on at least five occasions during gestation.  
Identical handling procedures were used following  
parturition.

### Measures

Litters were examined on the day of parturition  
(termed Day 0) and daily for at least 10 days  
thereafter. The experimenter removed the mother  
from her home cage and determined the number of  
pups present, pup weight, and the general condition  
of pups (color, presence of milk bands, and presence  
of injury).

A pup was considered cannibalized on Day *N* if it  
was alive on Day *N* – 1 and not present on Day *N*.  
Because maternal hamsters ingest dead pups, this  
measure of cannibalism was inflated, to some ex-  
tent, by the number of pups dying from causes  
other than cannibalism and subsequently consumed  
by the mother. That scavenging by the dam was  
not a major cause of disappearance of young is  
suggested by the observation that mothers were  
rarely observed eating dead pups but were fre-  
quently seen ingesting their live offspring.

Differential mortality of sick pups of seven or  
more days of age was, however, observed in the  
course of pilot studies. Because pups seven or more  
days of age consume dead littermates, the problem  
of distinguishing cannibalized pups from those dy-  
ing and subsequently ingested becomes more acute  
as litter age increases. For this reason, whenever  
possible, data analysis was restricted to the disap-  
pearance of pups during the first 5 days after birth.

### Exclusions of Litters

A mother and litter were excluded from a study  
if, on the day of parturition, a litter lacked milk  
bands, was scattered about the cage rather than  
collected in a nest, was runty, injured, or dark in  
color. It was observed in pilot studies that such  
litters were unlikely to survive and produced large  
numbers of dead and uneaten pups. The fact that  
females consume dead pups, taken together with  
the high death rate in such litters, suggested that

the inclusion of data from these litters would have  
ensured inflated estimates of the amount of cannib-  
alism. Of the 273 litters examined in the five  
experiments described below, 10.2% were excluded  
from analysis.

### Experiment 1

The two studies reported here examine  
the influence of the six variables, men-  
tioned in the introduction, that have pre-  
viously been assumed to affect the fre-  
quency of occurrence of litter cannibalism  
in postpartum golden hamsters. We pre-  
dicted that (a) if disturbance by the  
breeder of a dam and litter increases can-  
nibalism by the mother, then fewer pups  
should survive to weaning in litters reared  
by dams handled daily than in litters  
reared by dams left completely undis-  
turbed. (b) If pup cannibalism is a re-  
sponse by dams to litters of extreme size  
at the time of parturition, then more can-  
nibalism should be observed in very large  
and/or very small litters than in those of  
intermediate size. (c) If cannibalism is  
more frequently exhibited by relatively  
immature dams, then the amount of can-  
nibalism should decrease systematically  
as a function of increase in age of dams at  
the time of parturition. (d) If lack of pre-  
vious maternal experience increases can-  
nibalism, then incidence of cannibalism  
should decrease over successive litters. (e)  
If individual dams are more or less likely  
to cannibalize than others, then there  
should be a consistency in the amount of  
cannibalism that individual females, rela-  
tive to others, direct toward their succe-  
ssive litters. (f) If dams cannibalize to re-  
move unhealthy pups from their litters,  
then those pups destroyed should exhibit  
some physical features in common prior to  
their destruction.

The data were further analyzed to de-  
scribe the probability of occurrence and  
time course of litter cannibalism by female  
hamsters rearing their young under stan-  
dard laboratory conditions.

### Method

*Study 1.* Age of onset of puberty was estab-  
lished in 42 subjects from the McMaster colony by

observing their behavior when placed in the cages of individual sexually mature males on successive evenings, beginning at 35 days of age. Onset of puberty was defined as occurring on the first night a female responded with lordosis to male approach ( $M = 51.1$  days).

Fourteen pubescent females were randomly assigned to each of three groups differing in time postpuberty at which its members were first bred. Subjects in the 0-Delay group were bred on the night of first estrus, and those in the 4-wk- and 8-wk-Delay groups were bred, respectively, 4 and 8 wk thereafter. Each subject in all three groups was bred at approximately 7-wk intervals to rear three successive litters.

Half of the dams in each group were randomly assigned to a Handled and half to a Not-handled condition. The 21 dams in the Handled condition were removed from their home cages to a holding cage for 5 min/day from Day 0 to Day 10 postpartum. Dams in the Not-handled condition were left completely undisturbed from the time of parturition to Day 10 postpartum, at which time standard handling was resumed.

**Study 2.** To determine the fate of individual pups, we marked 243 pups born to 25 primiparous females, bred at 10-12 wk of age, on the day of birth by toe clipping under local anesthesia (Xylocaine, Abbott Laboratories, Montreal). The experimenter handled mothers and examined each surviving pup daily, recording its weight and physical condition.

## Results

**Effects of disturbance.** Figure 1 shows the mean number of pups per litter in Handled and Not-handled conditions surviving to Day 10. As is clear from examination of the figure, survival was unaffected by daily handling. If one assumes an equal mean number of pups born to the dams randomly assigned to each condition, daily handling did not affect incidence of cannibalism.

**Effects of litter size at parturition.** Figure 2 presents data from the 63 litters born to the 21 handled mothers in Study 1 and from the 25 litters born to the 25 females in Study 2, showing the mean number of pups cannibalized per litter by Day 5 as a function of litter size at birth. Examination of the figure reveals a trend toward increasing cannibalism with increasing litter size at birth. However a Pearson product-moment correlation performed on the amount of cannibalism as a function of litter size at birth for first litters born to each of 46 females in Studies

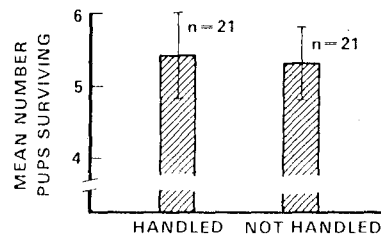


Figure 1. Mean number of pups per litter surviving to Day 10 in Handled and Not-handled groups. (Flags indicate  $\pm 1$  SE.)

1 and 2 did not reach acceptable levels of statistical significance ( $r = .22$ ,  $p > .05$ ).

**Effects of age of mother.** Figure 3 presents the mean number of pups per litter cannibalized by Day 5 in the first litters born to handled dams first bred 0, 4, or 8 wk following onset of puberty. As is clear from examination of the figure, there is no tendency for relatively immature females to cannibalize more pups than do older conspecifics.

**Effects of previous parturitions.** Figure 4 presents data describing the mean number of pups per litter cannibalized by Day 5 by the 21 handled mothers in Study 1 in successive parturitions. Although there was a slight tendency for cannibalism to decrease in successive parturitions, the results of a Trials  $\times$  Subject analysis of variance (Lindquist, 1953) did not approach acceptable levels of significance,  $F(2, 40) = .74$ ,  $p > .05$ .

**Effects of individual differences: Mothers.** Between-litters Pearson product-moment correlations were performed on the number of pups per litter cannibalized by Day 5 by each of the 21 handled mothers

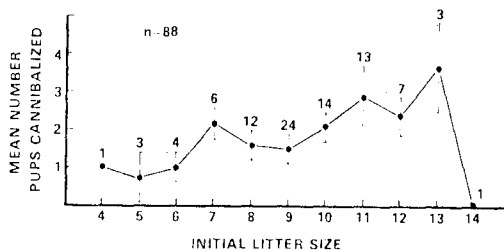


Figure 2. Mean number of pups cannibalized per litter by Day 5 as a function of litter size at birth. (The number above each point indicates the number of litters of that size observed; the flags indicate  $\pm 1$  SE.)

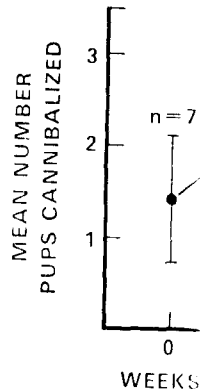


Figure 3. Mean number of pups cannibalized by Day 5 in the first litters born to handled dams first bred 0, 4, or 8 wk after first estrus.

in Study 1. The mean number of pups in Litter 1 was significantly higher than in Litter 2, but there was a no significant difference in the number of mothers exhibiting cannibalism toward Litter 1 versus Litter 2.

**Effects of successive parturitions.** Chi-square tests were performed on the data from the 243 pups born to the 25 handled dams in Study 2 as a function of condition of the dam at birth. Apparently, there was no difference in the frequency of cannibalism toward Litter 1 versus Litter 2. Similarly, pup

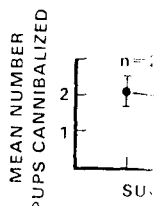
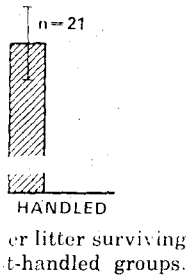


Figure 4. Mean number of pups cannibalized by Day 5 in three successive parturitions. (The flags indicate  $\pm 1$  SE.)



stable levels of .22,  $p > .05$ ).

Figure 3 presents the mean number of pups per litter cannibalized by Day 5 in the first litters of mothers bred 0, 4, or 8 weeks after first estrus. As is clear from the figure, there is no significant difference in the number of pups cannibalized between the three groups.

Figure 4 presents the mean number of pups per litter cannibalized by Day 5 in the first litters of mothers bred 0, 4, or 8 weeks after first estrus. As is clear from the figure, there is no significant difference in the number of pups cannibalized between the three groups.

Figure 5 presents the mean number of pups cannibalized per litter on each day by the 21 handled females in Study 1. As is clear from examination of the figure, cannibalism is most frequent during the 72 hr following parturition and is virtually complete by Day 5. Similarly, examination of the number of litters in which cannibalism occurred on each day (Figure 6) reveals a concentration of litter cannibalism in the days immediately following parturition.

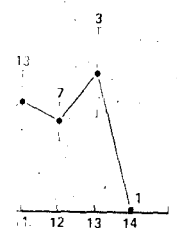


Figure 7 presents the mean number of pups per litter cannibalized by Day 5 in the first litters of mothers bred 0, 4, or 8 weeks after first estrus. As is clear from the figure, there is no significant difference in the number of pups cannibalized between the three groups.

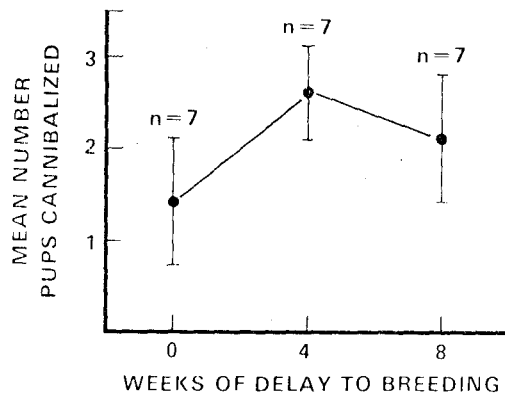


Figure 3. Mean number of pups per litter cannibalized by Day 5 in the first litters of mothers bred 0, 4, or 8 wk after first estrus. (Flags indicate  $\pm 1$  SE.)

in Study 1. There was no tendency for females that cannibalized a large number of pups in Litter 1 to cannibalize a large number in Litter 2 ( $r = .13$ ). However, there was a nonsignificant tendency for mothers exhibiting relatively more cannibalism toward Litter 2 to cannibalize relatively more in Litter 3 ( $r = .42$ ,  $p > .05$ ).

**Effects of individual differences:** *Pups.* Chi-square analyses were performed on the cannibalism or survival to Day 5 of the 243 individually marked pups born to the 25 mothers of Study 2 as a function of condition of the pups on day of birth. Apparently normal pups were destroyed as frequently as those exhibiting bites, subcutaneous hemorrhages, or color abnormalities,  $\chi^2 (1) = .12$ ,  $p > .05$ . Also, no difference in probability of survival to Day 5 was found to correlate with relative pup birth weight. The heaviest, lightest, and median weight pups within a litter did not differ significantly in their frequency of destruction,  $\chi^2 (2) = .57$ ,  $p > .05$ . Similarly, pup survival was not found

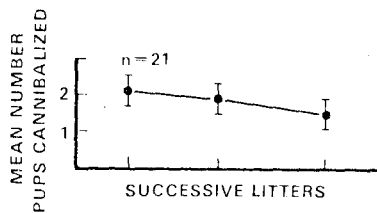


Figure 4. Mean number of pups per litter cannibalized in three successive litters. (Flags indicate  $\pm 1$  SE.)

to be related to absolute weight at birth. An equal proportion of pups in the lowest, middle, and upper third of the distribution of birth weights across litters survived to Day 5,  $\chi^2 (2) = 3.04$ ,  $p > .05$ .

**Descriptive data.** Seventy-six percent of the 63 litters born to the 21 handled mothers in Study 1 and 88% of the 25 litters in Study 2 suffered some degree of cannibalism between birth and Day 5. One of 88 mothers cannibalized her entire litter, and the remaining 87 destroyed a mean of 1.9 pups from litters varying in size from 4 to 14 pups at birth.

Figure 5 presents the mean number of pups cannibalized per litter on each day by the 21 handled females in Study 1. As is clear from examination of the figure, cannibalism is most frequent during the 72 hr following parturition and is virtually complete by Day 5. Similarly, examination of the number of litters in which cannibalism occurred on each day (Figure 6) reveals a concentration of litter cannibalism in the days immediately following parturition.

Table 1 presents between-litters Pearson product-moment correlations performed on the number of pups surviving to and cannibalized by Day 5 and on the number of pups born to individual handled females in Study 1. As can be seen in the table, individual females exhibited a relatively greater constancy in the number of pups they successfully maintained to Day 5 than in the number of pups to which they gave birth or which they cannibalized.

Further normative data describing litter

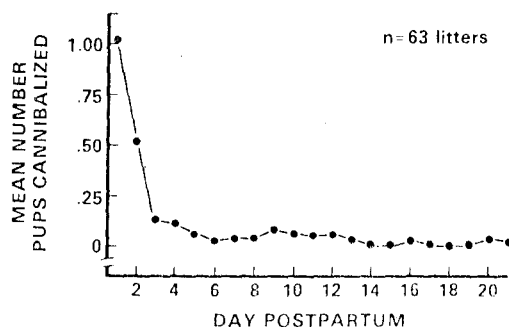


Figure 5. Mean number of pups per litter cannibalized as a function of time postpartum.

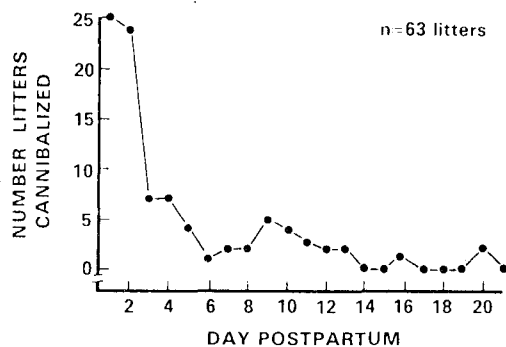


Figure 6. Total number of litters in which cannibalism occurred as a function of time postpartum.

sizes at birth as a function of age at breeding, successive parturitions, and other variables not directly relevant to the present experiments are to be found in Day (1976).

### Discussion

In general, the results of Experiment 1 suggest that analysis of litter cannibalism in the hamster in terms of variables previously hypothesized to be important in controlling its occurrence is unlikely to be fruitful. Although the data reported above offer limited support for hypotheses implicating unusually large litter size at birth or individual behavioral idiosyncrasy in high levels of litter cannibalism, the treatment of cannibalism as resulting from a stress-induced disruption of normal maternal behavior does not seem a particularly appropriate one.

Of course, it cannot be inferred from a failure to find an effect of some variable on incidence of cannibalism that similar manipulations could not be effective. In fact, we have little doubt that cannibalism

could be increased by, for example, selectively breeding highly emotional females or those giving birth to very large litters. However, such findings could not account either for the observation that cannibalism was directed toward litters of small size at birth or for the observation that the great majority of females cannibalized following one or more of their parturitions. Similarly, such findings would not be useful in interpreting the observation of a high degree of constancy in the relative number of pups maintained by individual females over successive litters or the observation of a decrease in cannibalism as a function of time postpartum.

We, therefore, decided to undertake further studies, treating litter cannibalism as an organized and possibly adaptive aspect of maternal behavior in hamsters, to examine the factors responsible for the consistently observed marked reduction of probability of cannibalism after Day 3 postpartum. It was hoped that study of the factors leading to cessation of cannibalism would provide some insight into the causes of its initiation.

### Experiment 2

Perhaps the most consistent phenomenon 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 72 hr following birth and was infrequent thereafter. It seems reasonable to assume that change in the stimulus configuration of individual pups which resulted from maturation, change in the internal state of the mother, or change in the size of the litter as a whole as the result of cannibalism of pups was responsible for the observed decrease in incidence of pup destruction as a function of time after birth.

The present experiment examines the possibility that 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 that

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### Method

**Subjects.** born in the M of age, were groups.

**Procedure.** Maintained p to Day 10. Th had disappea amination w subject's nate litters of sub to four pups with two of For control Size-Maintain control condition. Maintained foster pup of exchange for pup was added. Maintained subject the effects of each subject received two equal number differences w ism between data were con

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### Results and

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Table 1  
Between-Litters Pearson Product-Moment  
Correlations for Individual Females in Study 1

Measure	Litter 1 vs. Litter 2	Litter 2 vs. Litter 3
No. of pups surviving	.54*	.61**
No. of pups cannibalized	.13	.42
No. of pups born	.41	.43

\*  $p < .05$ .

\*\*  $p < .01$ .

no longer elicits pup destruction, then mothers whose litters are artificially decreased in size at the time of parturition should exhibit low levels and short durations of cannibalism. Conversely, mothers whose litters are maintained in size by each day replacing any pups cannibalized during the preceding 24 hr should continue to exhibit normal levels of cannibalism for an indefinite period.

### Method

**Subjects.** Thirty-two female golden hamsters, born in the McMaster colony and first bred at 14 wk of age, were randomly assigned to one of three groups.

**Procedure.** Subjects assigned to the Litter-Size-Maintained group were examined daily from Day 0 to Day 10. The experimenter replaced any pup that had disappeared during the 24 hr preceding an examination with a foster pup of the same age as a subject's natural litter. The experimenter culled the litters of subjects in the Litter-Reduced group ( $n = 9$ ) to four pups on Day 0 by providing each mother with two of her own and two newborn foster pups. For control of the effects of fostering in the Litter-Size-Maintained condition, each subject in one control condition ( $n = 7$ ) was yoked to a Litter-Size-Maintained subject. The control subject received a foster pup of the same age as her natural litter in exchange for one of her own pups whenever a foster pup was added to the litter of the Litter-Size-Maintained subject to which she was yoked. For control of the effects of fostering in the Litter-Reduced group, each subject in a second control condition ( $n = 9$ ) received two newborn foster pups in exchange for an equal number of her own pups on Day 0. Because no differences were observed in incidence of cannibalism between subjects in the two control groups, their data were combined for purposes of analysis.

Maintenance and handling procedures were those described in General Method.

### Results and Discussion

The main results of Experiment 2 are given in Figure 7 which presents the mean number of pups cannibalized per litter by females in Litter-Size-Maintained, Litter-Reduced, and control groups on each of the 10 days following parturition. As is clear from examination of the figure, litter size maintenance increased both duration and amount of cannibalism, and litter size reduction markedly decreased both duration and amount of cannibalism, with respect to controls.

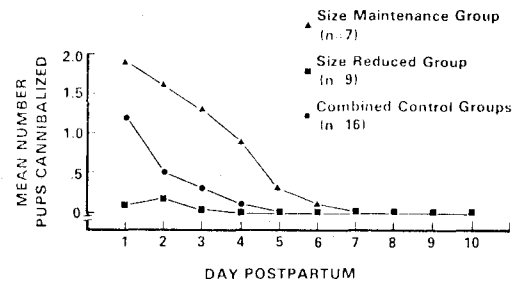


Figure 7. Mean number of pups per litter cannibalized as a function of time postpartum.

Comparison of the behavior of the control group in the present experiment with the normative data presented in Figure 5 reveals no increment in cannibalism as a result of the fostering manipulation, which indicates that the presence of foster young in a litter did not in itself increase cannibalism.

The data of the present experiment indicate that litter size reduction resulting from cannibalism soon after parturition plays a role in reducing future incidence of pup destruction.

### Experiment 3

The observation that even those females whose litters do not become steadily smaller as a consequence of cannibalism stop cannibalizing suggests that some factor other than litter size reduction plays a role in the termination of cannibalistic behavior. The present experiment examines the possibility that pup destruction ceases because of maturational changes in the morphology or behavior of maturing pups. If cannibalism terminates because older pups do not elicit destruction by the mother, then a female rearing only foster newborn pups given to her daily by the experimenter should exhibit substantial increases in duration and total amount of cannibalism.

### Method

**Subjects.** Subjects were five hamsters born in the McMaster colony and first bred at 10-12 wk of age. Foster pups were obtained from an additional 48 colony females.

**Procedure.** On each of the first 7 days postpartum,



tum each subject female received a number of newborn foster pups equal to the number of young to which she gave birth. Thus, the experimental procedure in large measure replicated the Litter-Size-Maintained group of Experiment 2 except that mothers received newborn foster pups rather than foster pups of the same age as their natural litters.

### Results and Discussion

The main results of Experiment 3 are presented in Figure 8 which shows the mean number of pups cannibalized per litter by the five females whose litter size was maintained with newborns. Data from the Litter-Size-Maintained group of Experiment 2 are presented for purposes of comparison. Although there was some tendency for the group of subjects maintained with newborn pups to cannibalize a greater mean number of pups on Days 5, 6, and 7 than subjects in the Litter-Size-Maintained group of Experiment 2, this difference is due entirely to the behavior of one subject in the group maintained with newborn young. Of the remaining 4 subjects in the group maintained with newborn young, 1 stopped cannibalizing on Day 1, 2 on Day 3, and 1 on Day 4. This failure to find differences in the amount or duration of cannibalism exhibited by mothers maintaining newborn or maturing young suggests that maturation of young is not an important factor in causing an end to pup destruction.

### Experiment 4

The present experiment was undertaken to determine whether internal changes in the mother, occurring over the course of lactation, are responsible in part for the

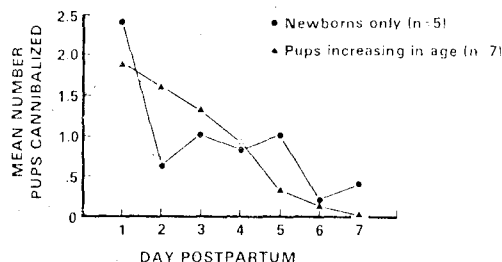


Figure 8. Mean number of pups per litter cannibalized as a function of time postpartum.

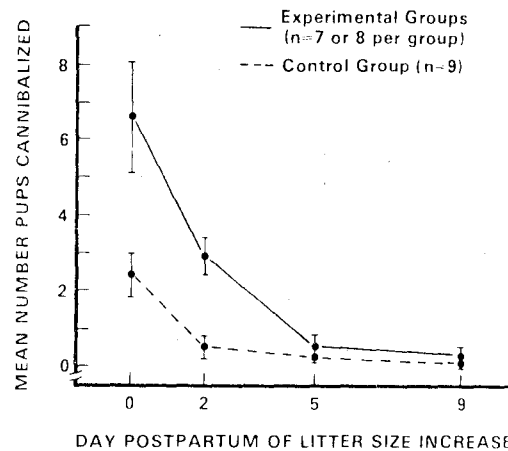


Figure 9. Mean number of pups per litter cannibalized within 5 days of increment in litter size. (Flags indicate  $\pm 1$  SE.)

cessation of cannibalism. The results of Experiment 2 indicate that recently parturient females respond to the addition of pups to their litters by increasing their levels of cannibalism. If the tendency of females to cannibalize wanes as a function of time postpartum, then one would expect that experimental litter size enlargement should become less effective in increasing cannibalism as a function of increasing time postpartum.

### Method

**Subjects.** The subjects were 39 nulliparous golden hamsters obtained from High Oak Ranch and bred at 12 wk of age. Foster pups were obtained from experimental mothers and from 12 additional colony females.

**Procedure.** Subjects were randomly assigned to one of four experimental groups or a control group. Females in experimental groups had four foster pups of the same age as their natural litter added to their litter on Day 0 ( $n = 8$ ), Day 2 ( $n = 8$ ), Day 5 ( $n = 8$ ), or Day 9 ( $n = 7$ ) postpartum, depending on the group to which they were assigned. All these subjects also received four foster pups of the same age as their natural pups in exchange for four of the pups they were maintaining on the remainder of the first 14 days postpartum. Control mothers ( $n = 8$ ) received daily four foster pups of appropriate age in exchange for four of the pups they were maintaining from Day 0 to Day 14.

### Results and Discussion

Figure 9 presents the mean number of pups cannibalized by females in each ex-

perimental group immediately following the increase in litter size. The mean number of pups cannibalized by control mothers from Day 0 to Day 10, and 9 to Day 14, respectively, were 2.5 and 0.2. The increase in litter size caused an increase in cannibalism, but the levels only on Day 0 indicate that cannibalism early in lactation is insufficient to cause a change in the litter size which leads to cannibalism.

The data presented here demonstrate that cannibalism is clearly not an adaptive behavior. The conclusion suggests that pup cannibalism is an adaptive behavior that permits females to maintain a certain number of pups in the litter with the environment. The hypothesis is that cannibalism is a function of litter size. Cannibalism requires three conditions: (1) the mother would be needed to maintain the litter size. Second, the mother must be regulated by changes in the environment. The limiting reproductive environment necessary to maintain the litter size under a range of conditions. The mother reared in each environment.

The present study was to examine the effect of laboratory studies on hamsters regu-



Experimental Groups  
(per group)  
Group (n=9)

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perimental group during the 5 days immediately following litter size increase. The mean number of pups cannibalized by control mothers from Day 0 to Day 5, 2 to 7, 5 to 10, and 9 to 14 are presented for purposes of comparison. As is clear from examination of the figure, experimental increase in litter size was effective in increasing cannibalism over control group levels only on Days 0 and 2. These results indicate that cues sufficient to elicit cannibalism early in the postpartum period are insufficient to do so at a later date, which suggests an important role of internal change in the mother occurring postpartum which leads to the cessation of cannibalism.

#### Experiment 5

The data presented above, although demonstrating a certain degree of organization present in cannibalistic behavior, are clearly not sufficient to justify the conclusion suggested in the introduction, that pup cannibalism in the golden hamster is an adaptive facet of maternal behavior that permits females to regulate the number of pups they attempt to rear in accord with the environmental conditions prevailing at the time of parturition. Confirmation of the utility of Lack's (1954, 1958) hypothesis to explain the adaptive function of litter cannibalism in the hamster requires three types of evidence. First, it would be necessary to demonstrate that female hamsters regulate the size of their litters. Second, it would have to be determined that the value at which litter size was regulated varied in accord with changes in the availability of resources limiting reproductive capacity in the natural environment. And, third, it would be necessary to show that the mean litter sizes maintained by parturient females under a range of conditions was such as to maximize the number of young a female reared in each set of conditions in the natural environment.

The present experiment was undertaken to examine that issue most amenable to laboratory study: whether parturient hamsters regulate the size of their litters

under constant conditions. If hamster dams do, in fact, regulate the number of pups that they attempt to rear, then one would expect them to compensate for experimental alterations in litter size with a directly proportional adjustment in the number of pups they remove from their litters.

#### Method

**Subjects.** Subjects were 67 nulliparous golden hamsters obtained from the High Oak Ranch and bred at 9-10 wk of age. Foster pups were obtained from an additional 40 colony females.

**Procedure.** On the day of parturition subjects were randomly assigned to one of four experimental conditions or a control condition. Mothers in Experimental Groups +2 (n = 8), +4 (n = 8), +6 (n = 8) received, respectively, an addition to their litters of 2, 4, or 6 newborn foster pups on the day of parturition, and mothers in Experimental Group -2 (n = 9) had four of their natural pups removed and two newborn foster pups added to their litters on the day of birth. Control mothers (Group 0, n = 8) received four newborn foster pups in exchange for four of their own newborn young on the day of parturition.

To be sure that any observed increase in cannibalism was not the result of differential destruction of foster pups and to provide a check on reliability of the outcome of the main experiment, we examined the behavior of two additional groups. On the day of parturition pups born to 25 additional subjects were marked by toe clipping under local anesthesia (Xyloraine, Abbott Laboratories, Montreal) to permit individual identification. Thirteen of these mothers (Group +4 Replicate) received four newborn toe-clipped pups in addition to their own newborn litter, and 12 mothers (Group 0 Replicate) received four newborn toe-clipped foster pups in exchange for four of their natural pups on the day of parturition.

#### Results and Discussion

Figure 10 shows the mean total number of pups destroyed by dams in Groups -2, 0, +2, +4, and +6. As is clear from examination of the figure, experimental reduction or increment in litter size resulted in mean changes in amount of cannibalism almost directly proportional to the extent and direction of experimental manipulation. The results strongly suggest that during the days immediately postpartum, female hamsters behaviorally regulate the number of pups in their litters, maintaining litter size at some individually determined preferred value.

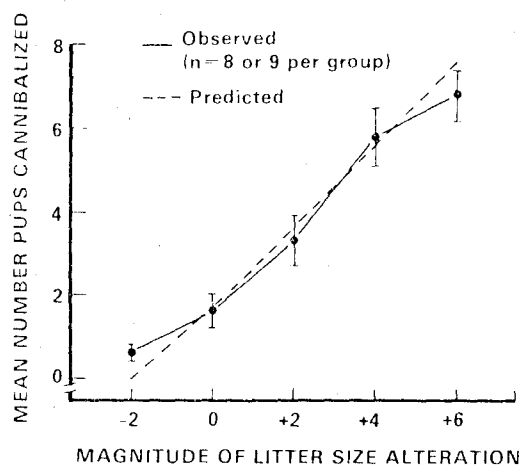


Figure 10. Observed and predicted mean number of pups per litter cannibalized by Day 5 as a function of magnitude of litter alteration. (Flags indicate  $\pm 1$  SE.)

Analysis of the cannibalism of foster and natural pups by mothers indicated a slightly lower proportion of foster pups cannibalized than would be expected if cannibalism were randomly directed toward natural and foster litter members. Group +4 Replicate cannibalized a mean total of 6.4 pups ( $SE = .7$  pup) by Day 5 and Group 0 Replicate a mean total of 2.7 ( $SE = .8$  pup) pups, which confirms the finding of the main study of an adjustment in amount of cannibalism directly proportional to the extent of experimental manipulation of litter size.

### General Discussion

The results of the studies reported here indicate that during the first few days postpartum the female hamster regulates her litter to a specific size. Such a finding is not consistent with the view that litter cannibalism represents a breakdown in normal maternal behavior. To the contrary, litter cannibalism appears to be a carefully organized and regulated aspect of maternal behavior in the golden hamster, which allows the parturient female to adjust the number of young which she must nurture.

Although the present experiments do not provide any evidence bearing directly

on the issue, it seems reasonable to hypothesize that the individual female hamster adjusts her litter size preference in response to alterations in her internal state that reflect changes in environmental conditions. Thus, pup cannibalism might permit the recently parturient hamster to adjust the demands made upon her by her litter in accord with environmental circumstances prevailing at the time of birth of her young. Delay of the decision about how many young to attempt to rear until after parturition might be particularly useful in the conditions of "irregular rainfall and food supply" (Richards, 1966, p. 308) that characterize the golden hamsters' natural habitat in the Arabian Peninsula.

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