

Pup Cannibalism: One Aspect of Maternal Behavior in Golden Hamsters

Corinne S. D. Day and Bennett G. Galef, Jr.
McMaster University, Hamilton
Ontario, Canada

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-

This research was supported by National Research Council of Canada Grant AP307 and a McMaster University Research Grant to the second author. The experiments reported here formed part of a dissertation submitted by the first author to McMaster University in partial fulfillment of the requirements of the PhD degree. Material from this paper was presented at a meeting of the Eastern Psychological Association, New York, April 1976.

Requests for reprints should be sent to Corinne S. D. Day, who is now at the Department of Psychology, Carleton University, Ottawa, Ontario, Canada K1S 5B6.

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 1. Colony-born female age, housed in old, and subsequent 30.5 × 16.5 cm (Taconic, Inc.). All animals on a 14:10 hr Purina Laboratory animal was housed

Handling

To habituate to cages and place on at least Identical handling parturition.

Measures

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

A pup was counted as alive on Day 0. Because maternal measure of cannibalism, by the mother other than cannibalism by the mother, not a major concern suggested by the rarely observed cannibalism frequently seen in

Differential mortality more days of age course of pilot study days of age control of distinguishing pupping and subsequent as litter age in possible, data on appearance of pup

Exclusions of

A mother animal if, on the day of bands, was seen collected in a litter color. It was determined litters were used numbers of dead females consumed the high death

ductive strate-
low females to
oung they pro-
nmental varia-
alts of extensive
emales of many
clutch size to
s in food availa-
imilarly, labora-
guinea pigs tend
a food-rich envi-
or ones (Lack,

uggest that pup
a hamsters may
to the cases of
oung delivered
response would
e size to a value
mental circum-
ung are to be
sm, rather than
embryos devel-
a mechanism for
fort, it would be
age in reproduc-
he female ham-
er after parturi-
antage resulting
eveloping to the
rger number of
tained. The fact
nales exhibit a
Daly, 1976; Rich-
may have less
bryos at birth—
of cannibalism
patible with such

series of experi-
s of a variety of
pup destruction.
nts examine the
requency, dura-
cannibalism by
tters under stan-
ds.

thod

female golden ham-
obtained 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.

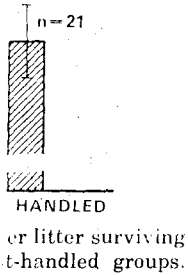
Experiment 1

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

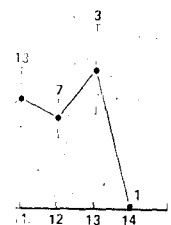


er litter surviving
t-handled groups.

able levels of
.22, $p > .05$).
Figure 3 pre-
pups per litter
he first litters
bred 0, 4, or 8
ty. As is clear
ure, there is
immature fe-
pups than do

itions. Figure
e mean num-
alized by Day
in Study 1 in
though there
annibalism to
parturitions, the
t analysis of
did not ap-
significance,

ences: *Moth-*
n product-mo-
ormed on the
nnibalized by
dled mothers



annibalized per
er size at birth.
ates the number
ags indicate ± 1

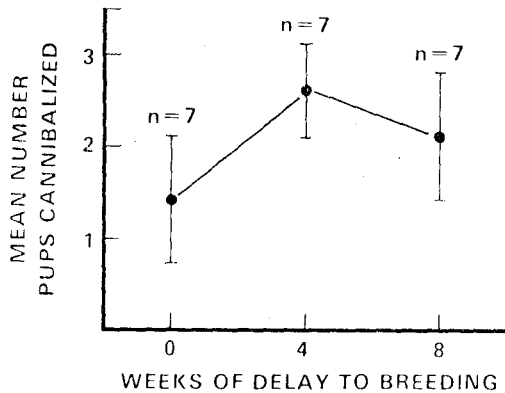


Figure 3. Mean number of pups per litter cannibalized by Day 5 in the first litters of mothers bred 0, 4, or 8 wk after first estrus. (Flags indicate ± 1 SE.)

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

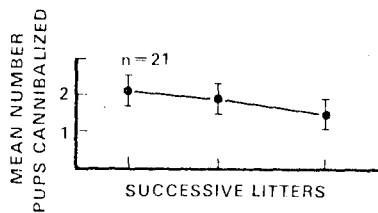


Figure 4. Mean number of pups per litter cannibalized in three successive litters. (Flags indicate ± 1 SE.)

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

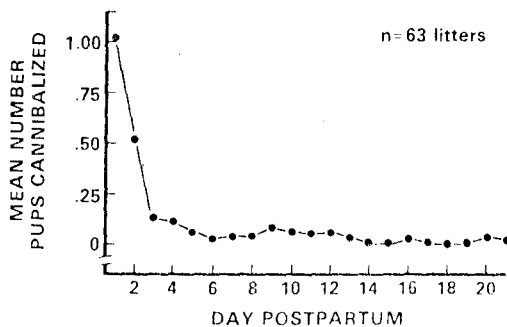


Figure 5. Mean number of pups per litter cannibalized as a function of time postpartum.

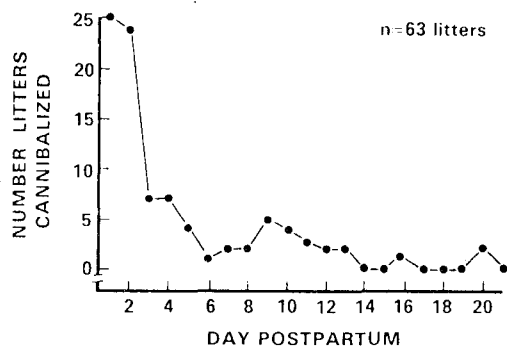


Figure 6. Total number of litters in which cannibalism occurred as a function of time postpartum.

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

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 |

* $p < .05$.

** $p < .01$.

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

no longer mothers were increased in should exhibit of can whose litter day replac ing the pro exhibit nor indefinite

Method

Subjects.

born in the M of age, were groups.

Procedure.

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

Maintenan described in C

Results and

The mai given in Fi number of females in Reduced, at 10 days foll from exami maintenance amount of s ductio ma and amount to controls

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.

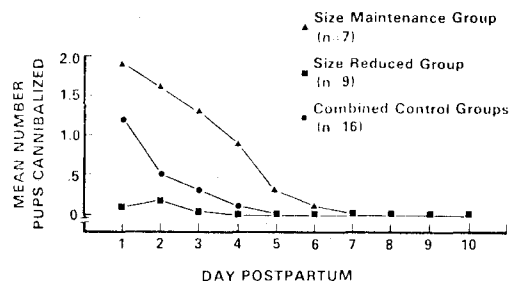


Figure 7. Mean number of pups per litter cannibalized as a function of time postpartum.

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

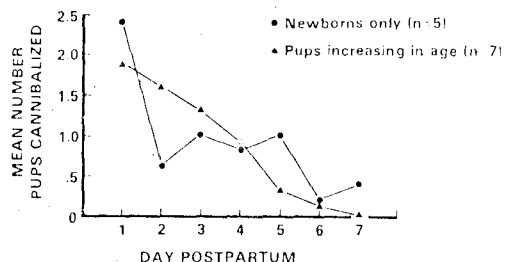


Figure 8. Mean number of pups per litter cannibalized as a function of time postpartum.

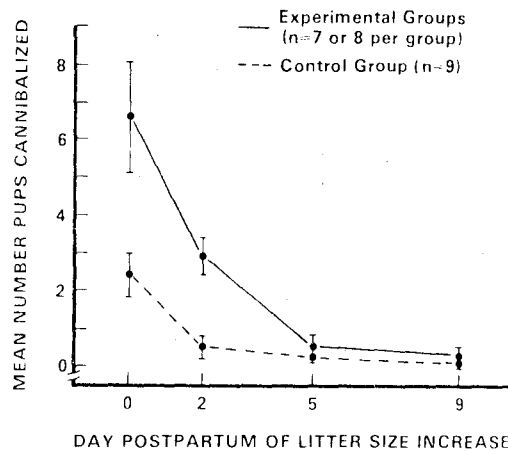


Figure 9. Mean number of pups per litter cannibalized within 5 days of increment in litter size. (Flags indicate ± 1 SE.)

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 10, respectively, are 2.5 and 0.2. The purposes of comparing the two groups is to examine the effect of increasing litter size on increasing cannibalism. The data 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 present in the laboratory hamster and are clearly not sufficient to support the conclusion suggested by other workers that pup cannibalism is an adaptive behavior that permits females to reduce the number of pups that they are maintaining in the environment at the time of the increase in litter size. The hypothesis that cannibalism requires three or more female hamsters per litter. Second, it was determined that the amount of cannibalism was regulated by changes in the environment. The limiting reproductive environment necessary to maintain litter sizes maintained under a range of conditions. The hamsters reared in each laboratory environment.

The present experiment was undertaken to examine the effect of increasing litter size on cannibalism in laboratory hamsters reared in each

