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Investigation of the Functions of Coprophagy in Juvenile Rats

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A series of experiments were undertaken to examine possible functions of the ingestion of maternal anal excreta by juvenile rats. No strong support was found for hypotheses suggesting (a) that maternal excreta serves as a major transition diet from mother's milk to solid food, (b) that ingestion of maternal excreta influences pup diet selection at weaning, or (c) that ingestion of maternal excreta is a necessary condition for inoculation of pups with enteric bacteria. Some support was found for the hypothesis that maternal excreta can serve as a short-term emergency food supply for rat pups after weaning. It is proposed that pup ingestion of maternal anal excreta may not be a functionally meaningful unit of behavior in preweaning rats. Allocoprophagy may be one facet of a broader pattern of oral exploration in which functional significance resides.

During the 17-day period when newborn rats are totally dependent on their dam's milk for sustenance (Babicky, Parizek, Ostadalova, & Kolar, 1973), they mouth and possibly ingest samples of most of the solid objects with which they come in contact. Under standard laboratory maintenance conditions the anal excreta of the dam are one of the substances samples of which are frequently contacted, chewed, and apparently swallowed by juvenile rats. Although there are reports in the literature of mouthing and chewing of maternal excreta by the young of numerous mammalian species (Ewer, 1968, p. 274), including the rat (see, e.g., Bolles & Woods, 1964). Leon (1974) was, to my knowledge, both the first to report stomach content analyses indicating that rat pups actually ingest maternal excreta and the first to consider systematically possible functions of coprophagy in the growth and development of young rats.

Leon suggested four possible functions of ingestion of maternal excreta by rat pups: (a) Ingestion of maternal excreta may inoculate young rats with maternal enteric bacteria which facilitate digestion of solid food at weaning (Ewer, 1968, p. 274). (b) Maternal excreta may be utilized by weanlings as a "baby food," an important transition diet from mother's milk to solid foods, as seems to be the case in koala (Minchin, cited in Gewalt, 1972, p. 125). (c) Excreta deposited in or near the nest site may serve as an emergency food supply which can sustain weanlings in the absence of their dam. (d) Ingestion of maternal excreta may serve to familiarize pups with the flavor of maternal diet and direct pups to their mother's diet at weaning (Galef, 1977; Galef & Henderson, 1972).

Although the role of autocoprophagy (the ingestion by an organism of its own excreta) in the maintenance of intestinal flora and the prevention of vitamin deficiencies in rats has been an area of active inquiry (see, e.g., Barnes, 1962; Gustafsson & Fitzgerald, 1960), little information is available on the significance of allocoprophagy (the ingestion of the excreta of conspecifics). Hence, the adequacy of the Leon (1974) hypotheses to account for the phenomenon of allocopro-

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phagy in juvenile rats remains open to question.

Experiment 1

In the present experiment systematic observation of the behavior of infant rats was undertaken to establish the age of initiation and the relative frequency of occurrence of mouthing and chewing episodes directed toward the various solid objects present in the environment. The collection of such descriptive data is a necessary first step in the investigation of hypotheses concerning the functions of allocoprophagy. If, for example, rat pups began to chew on solid food prior to initiating ingestion of maternal excreta, it would be difficult to maintain that allocoprophagy is a transitional stage between nursing and ingestion of more usual foods. Similarly, temporal precedence of ingestion of solid food over coprophagy would render difficult the maintenance of hypotheses proposing that pups use adult excreta as a supplementary diet when their dams are absent. Thus, a descriptive study of the time of onset of ingestion of the various solids available in the environment is a necessary precursor to any analytic investigations.

Method

Subjects. Subjects were eight recently parturient female Long-Evans rats obtained from Canadian Breeding Farms (St. Constant, Quebec), and their litters, culled to eight pups/litter on the day of birth.

Procedure. Each mother and litter was established in a 38 × 31 × 17 cm polycarbonate cage the floor of which was covered with wood chips (Betta-chip, Northeastern Products Corp., Warrensburg, New York) and given ad lib access to food (Purina Laboratory Chow pellets) and water. The eight litters were kept in a sound-attenuating room on a 12:12 hr light/dark cycle. Illumination during the dark period was provided by two 40-W red light bulbs suspended above the cages. Each of the eight litters was observed for .5 hr/day during each of the light and dark portions of the cycle, the observer recording every object mouthed by all eight litter members.

Results

The results of Experiment 1 are presented in Figure 1, which indicates the percentage of observation periods during which one or more members of each of the eight litters was seen to mouth various objects in its cage during 2 hr of observation on two consecutive days. As is clear from examination of the figures, prior to weaning, pups regularly mouth everything available in the environment—themselves, wood chips, other pups, their dam, food pellets, mother's fecal pellets, mother's cecotrophe, pup fecal pellets, and objects not reported in the figures (i.e., water spouts, cage walls, etc.). These descriptive categories are obviously somewhat arbitrary in that while chewing on a wood chip, its own foot, or its mother's tail, a pup may actually be tasting fecal material, urine, or cecotrophe. Further, the fact that pups mouth an object gives no indication of whether or not it is ingested.

In spite of their limitations, the present observations do indicate, for example, that (a) the range of objects mouthed by pups increases with increasing age, (b) there is a fair degree of consistency in the ages at

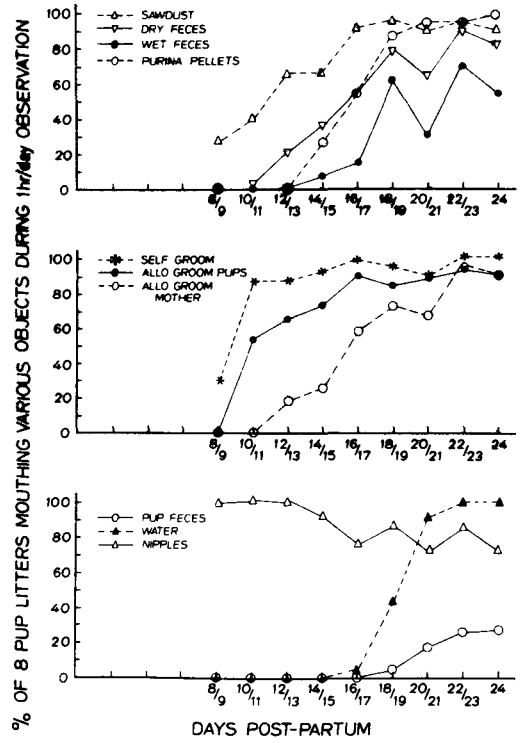

Figure 1. Percentage of eight pup litters in which mouthing of various objects was observed during four consecutive .5-hr observation periods.

which different items are first introduced by pups into their mouths (Day 1, nipples of mother and fur of mother's ventral surface; Days 9–11, own feet, fur of other pups, and substrate material; Days 13–15, feces of mother, nonventral surface of mother, and food pellets; Days 17–21, mother's cecotrophe, water, and pup feces), and (c) once mouthing of a class of objects begins it continues through the weaning period.

Discussion

The results of Experiment 1, though not conclusive because of the difficulty of determining by visual inspection whether or not chewed samples are ingested, suggest that ingestion of maternal excreta, particularly dried fecal pellets, is an extremely common pattern of behavior in laboratory-maintained juvenile rats. The data, though not sufficient to exclude any of the hypotheses briefly described above, cast serious doubt on interpretations of maternal fecal or cecal material as an important transition diet from mother's milk to solid food. Pups did not reliably initiate chewing on maternal excreta prior to chewing on Purina pellets, in spite of the fact that the former objects were far more common on the floor of the cage than the latter.

It is, however, clear that decisive tests of hypothesized functions of allocoprophagy require determination of the substances actually ingested by pups of various ages. Experiment 2 provides relevant data.

Experiment 2

To determine the substances actually ingested by rat pups of various ages, I directly examined their stomach contents. The results of a series of pilot studies revealed that pups 10 days of age were not sufficiently mature to ingest solid foods. When 10-day-old pups were force-fed a mash consisting either of ground Purina chow and water or ground dried excreta (deposited by a lactating female rat) and water, it was not possible to reliably discriminate excreta from chow in the stomachs of pups. However, lactating female rats fed a diet of powdered Purina Laboratory Chow adulterated with .2% by weight alcohol-soluble eosin (Telle, 1966) produced a bright orange anal excreta (both feces and cecotrophe) which, when dried, ground, sieved, and force-fed to pups, was readily discriminable from powdered Purina chow in pup stomachs. In blind experiments, as little as .01 g of ground, dyed powdered feces could be reliably detected in pup stomachs as long as 5 hr after force-feeding.

To determine the age of onset of ingestion by pups of both solid food and excreta, it was necessary to design an apparatus in which mothers ate eosin-dyed food at a location inaccessible to pups and pups had access to undyed food at a site inaccessible to their dam. Although the procedure described below was sufficient for this purpose, it has certain inevitable disadvantages which I consider in discussing the results of the present experiment.

Method

Subjects. One-hundred twenty Long-Evans rat pups from 15 litters, culled to eight pups/litter at birth, served as subjects.

Apparatus. A few days prior to parturition each female was established in a .9 × .9 × .9 m enclosure like that illustrated schematically in Figure 2. The enclosure was divided by a barrier, the height of which (12 in.; 30 cm) was such as to permit an adult rat, but not a juvenile, to cross from one side of the cage to the other. The juveniles were invariably delivered and maintained on the side containing a .3 × .3 × .15 m nest box, water bottle, and pup feeder. The pup feeder was a small box mounted on the cage wall with an entrance hole (1 in.

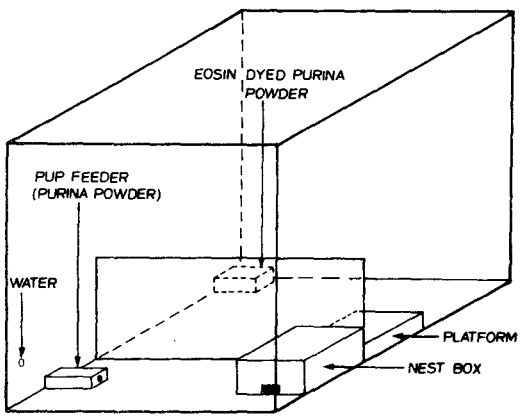

Figure 2. Enclosure for feeding dams eosin-dyed food separate from their young and young undyed food separate from their mothers (Experiments 2 and 3).

[2.54 cm] in diameter) sufficiently large to permit ready access by pups but too small for the mother to enter. The floor of the pup feeder was kept covered with powdered Purina chow. Daily inspection of the feeder revealed no disturbance of the food surface until pup footprints were found on it.

Food for the dam (powdered Purina Laboratory Chow, adulterated 2% by weight with alcohol-soluble eosin) was available ad lib on the far side of the barrier. Daily inspection of the enclosure revealed no transport of the bright orange food from one side of the enclosure to the other. Review of periodic time-lapse videotapes of the enclosure revealed no instance of a pup crossing the barrier.

Procedure. Each of six dams and litters were left undisturbed in one of six enclosures until the pups were 11 days of age. On Day 11 and every 2 days thereafter, two pups were taken from each litter and sacrificed, and their stomach contents were examined for the presence of food particles and orange maternal excreta. The remaining nine litters were treated identically to the first six except that sacrifice of litter members was initiated on Day 19.

Results

Pups 11 or 13 days of age invariably had stomachs containing a pure white milk curd of rubbery consistency which could be removed intact from the stomach. As can be seen in Figure 3, no particulate matter was found in the stomachs of either 11- or 13-day-olds, though the curds from the stomachs of the latter animals invariably exhibited a uniform very pale orange color, which I attributed to leakage of the eosin dye into maternal milk during the later stages of lactation for two reasons. First, if one pup in a litter had a pale orange stomach curd, all pups in that litter did, and, second, these curds contained no particulate matter at all.

Orange particles began to appear in the stomachs of pups at 15 days of age and were detectable thereafter in the stomachs of many animals. Although the present method did not provide a means of quantifying the amount of maternal excreta ingested by pups, the amounts found in pup stomachs throughout the study were invariably small. Comparison with the stomach contents of pups force-fed known amounts of ground, eosin-dyed feces indicated that voluntary feces intake rarely exceeded .1 g.

Greenish food particles (undyed Purina chow) were first detected in small quantities on Day 17, were invariable present in moderate or large quantity on Day 21, and virtually filled the stomach on Day 23.

In summary, our results indicated that pups initiated ingestion of excreta prior to feeding on Purina chow but that they in-

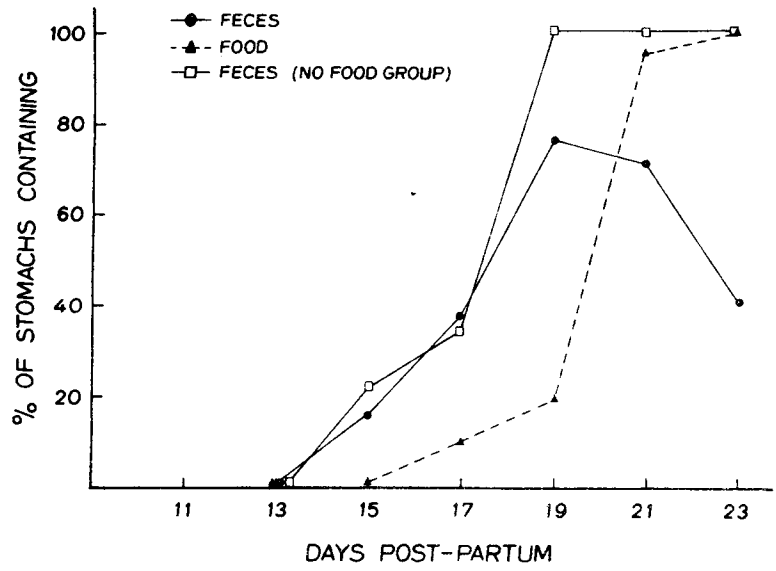

Figure 3. Percentage of pup stomachs observed to contain particles of Purina chow or maternal excreta as a function of pup age (Experiments 2 and 3).

gested very little of the former material and increasing amounts of the latter.

Discussion

The results of the present experiment do not provide support for the suggestion that in the rat, mothers' excreta serve as a major transition diet from milk to solid food. We could find no case in which a significant portion of a pup's stomach contents consisted of maternal excreta.

The data do offer limited support for the hypothesis that ingestion of maternal excreta is necessary to inoculate juveniles with enteric bacteria which facilitate digestion of solid food. Small quantities of excreta were observed in the stomachs of many pups in the absence of particles of Purina chow, but Purina chow was rarely observed in the absence of feces prior to Day 21 when the pups had weaned. These observations are consistent with the hypothesis that ingestion of small quantities of excreta precedes ingestion of solid food and that such ingestion of maternal excreta may be a necessary condition for the transmission of specific enteric bacteria to juveniles, facilitating their ingestion of solid food. It should, however, be kept in mind that the relative age of onset of allocoprophagy and ingestion of solid food found in the present experiment may well be specific to the experimental situation employed. My co-workers and I (Galef, 1971; Galef & Clark, 1972) have previously found that age of onset of weaning in rats is affected by such variables as distance from the nest to the feeding site and the presence or absence of conspecifics at the feeding site. In the present experiment, pups and dam were prevented from exploiting a common food source, and one would expect an artifactual delay in the weaning of the pups to solid food.

In addition, there are several reasons for questioning the necessity of explicit ingestion of maternal excreta for the development of a functional gastrointestinal flora in the rat. First, even pups reared artificially (without any direct contact with conspecifics or their excreta) exhibit normal growth following weaning to standard laboratory diets (Hall, 1975; Thoman & Arnold, 1968). Although it is impossible, in the absence of bacteriological examination of the gut flora of weaned, artificially reared pups, to know if such animals have a normal enteric population, they certainly possess an intestinal flora both acquired without direct contact with conspecifics or their excreta and adequate for normal growth in some environments.

Second, available evidence strongly suggests that although most of the organisms colonizing the alimentary tract of the neonate probably derive from the anal excreta of the dam (Smith, 1965a), active ingestion of feces is not a necessary condition for pup inoculation with a normal bacterial flora. The infant rat, sterile at birth, has a rich bacterial flora as early as 24 hr following birth, when the pup is insufficiently mature to locate and chew maternal feces. *Streptococci, lactobacilli,* and *E. coli* are all present in the gastrointestinal tract of young rats within 72 hr of birth (Raibaud, Dickinson, Sacquet, Charlier, & Mocquot, 1966; Smith, 1965a). *Bacteriodes* and *Clostridium welchii* are, respectively, first observed in the rat gut between Day 4 and Day 10 and at 18 days neonatally and might enter the gut as the result of allocoprophagy by pups. However, the fact that both *Bacteroides* and *C. welchii* invade the gut of a number of other altricial species (e.g., man and cat) on the day of birth (Smith & Crabb, 1961) suggests that these bacteria may also be transmitted from dam to young without explicit ingestion of excreta by the infant. The fact that *C. welchii* are not found in the excreta of the dam (Smith, 1965a) and that the ability of *C. welchii* to successfully colonize the rat alimentary tract is largely dependent on the diet of the host (Smith, 1965b) suggests that the appearance of *C. welchii* in the gut is the result of weaning from mother's milk to solid food on Day 18 and not pup ingestion of anal excreta. The evidence regarding the role of allocoprophagy in pup inoculation with *Bacteroides* is less clear, but the fact that some infant rats are colonized by *Bacteroides* as early as Day 4 (Smith, 1965a) again suggests that explicit coprophagy is not a critical factor in inoculation. In general, the literature does not provide strong support for the view that allocopro-

phagy functions to inoculate young rats with maternal enteric bacteria.

Experiment 3

In discussing the results of Experiment 2 with Leon, it became clear that the data which he collected on the ingestion of maternal excreta by weaning rat pups was at variance with our own. Leon (1974) found substantial quantities of maternal excreta in the guts of 93% of the 20-day-old pups he examined, whereas I found only traces of maternal excreta in less than 80% of the pups I examined at the same age (Day 21 in my system). Consideration of differences between Leon's experimental design and my own revealed that although they were very similar, there was a major difference in the access to food provided pups. In Leon's study, pups had no possible source of food other than maternal milk or excreta, whereas in Experiment 2 above they could ingest milk, maternal excreta, or Purina chow.

If the failure of pups in Experiment 2 to ingest large quantities of maternal excreta resulted from the availability of other solid food, then one would expect pups to ingest large quantities of maternal excreta if no other foods were available to them. The present experiment, which examines this possibility, bears directly on the hypothesis that maternal excreta may serve as an emergency food ration for weanlings.

Method

Subjects. Subjects were eight litters of Long-Evans rat pups born in the McMaster colony and culled to eight pups/litter on the day of birth.

Procedure. The procedure was identical to that of Experiment 2 except no food was present in the pup feeder and sacrifice of pups was initiated in half of the litters at Day 13 and in half at Day 23.

Results

As can be seen in Figure 3, pups without food available initiated ingestion of maternal excreta at about the same time as those with food available. Stomach content analyses revealed small quantities of orange granules in the stomachs of a steadily increasing proportion of pups on Days 13, 15, and 17. However, on Day 21 and thereafter, pups in Experiment 3, lacking access to solid food rations, invariably had stomachs filled with orange particles.

Discussion

The results of the present experiment strongly suggest that rat pups make use of maternal excreta as an emergency ration when mother's milk ceases to be a source of adequate nutrition and no other food is available to them. If, as was the case in Experiment 2, adequate food is available in the vicinity of the nest, pups ingest that food in preference to maternal excreta. These data support the hypothesis that maternal excreta is available to the young as an emergency ration in the event that no food is to be found in the environment at the time of compulsory weaning.

Experiment 4

The results of Experiments 1 and 2 indicate that pups initiate ingestion of maternal excreta well before weaning occurs. The results of Experiment 2 further indicate that so long as mother's milk or regular food is available to pups in adequate quantity, they ingest only small quantities of maternal excreta. In the present experiment, I examined the effects of removal of the dam and food on the ingestion of maternal excreta by pups of various ages to determine the range of ages at which pups are capable of utilizing maternal excreta as an emergency ration in the absence of alternative rations.

Method

Subjects. Subjects were 18 litters of Long-Evans rat pups, culled to eight pups/litter on the day of birth.

Procedure. Six litters of pups were examined at each of three ages (Days 16, 19, and 23) to determine the effects of both maternal and food deprivation on ingestion of maternal excreta. Each litter of pups was randomly divided into two groups of four pups/group, and each group was placed together in a polycarbonate cage (37 × 31 × 17 cm) with wood chip bedding and a water source. Pups assigned to the Excreta condition were given very large rations of fresh maternal excreta (both feces and cecotrophe) at the time they were removed from their dam and every 12 hr thereafter. Pups in the Deprivation condition were treated identically to those in the Excreta condition except that they were not given access to maternal excreta. Each pup was weighed at

the time of removal from its dam, and 24 and 48 hr thereafter. To assure independence of groups, I treated the mean weight loss of each group of four pups as a single data point in calculating means and standard errors.

Results and Discussion

The main results of Experiment 4 are presented in Figure 4 which shows the mean weight loss of pups in Excreta and Deprivation conditions following 24 and 48 hr of isolation from their dam. As is clear from examination of the figure, weight loss over a 48-hr period, but not a 24-hr one, was significantly reduced in 19- and 22-day-old pups by the presence of maternal excreta in their cages. The presence of maternal excreta had no comparable effect on pups 16 days of age at the onset of testing. Thus, pups of postweaning age are able to utilize maternal excreta as an emergency food supplement in the absence both of their dam and of other rations, but pups of preweaning age are not.

Of course, the fact that young rats ingest maternal excreta in the absence of their more usual sources of nutrition does not mean that such coprophagy provides a meaningful source of nutrients. However, in an experiment in which the longevity of seven 22-day-old rat pups left in a clean cage with ad lib water was compared with that of seven of their littermates left in cages provisioned with maternal excreta and water, it was found that although all pups succumbed within 24 hr of one another, the latter animals lived significantly longer than the former (Mann-Whitney $U = 1, p < .001$), which indicates that mothers' excreta is a partially adequate diet.

Although allocoprophagy may postpone death, its long-term value is not clear. The situation in which the pups in the present experiment were examined is, of course, far removed from that experienced in the natural environment. In particular, the pups in our study were prevented from dispersing from a location in which the only available food was inadequate for long-term survival. It might be argued that following prolonged absence of the dam, weanling pups in a nest site lacking food would be better advised to disperse from the nest site in search of adequate rations than to remain in the natal site

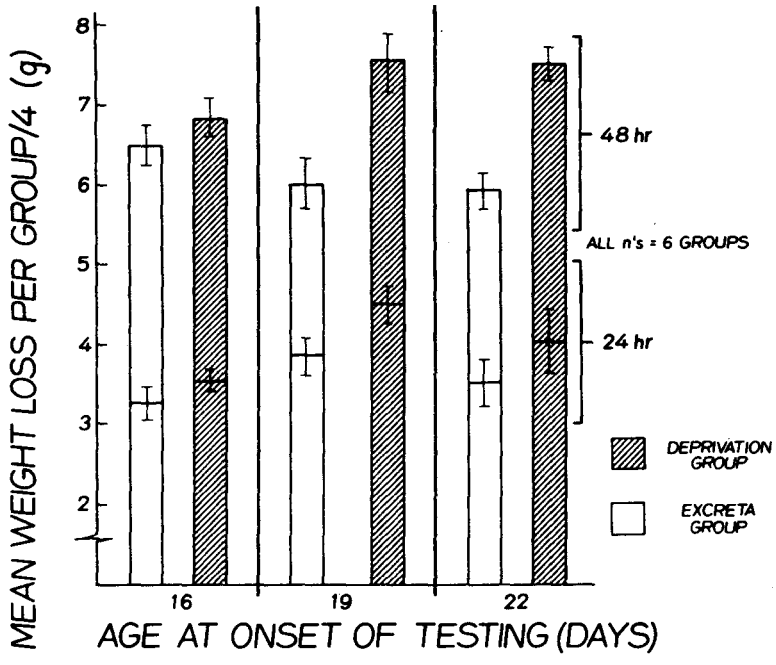

Figure 4. Mean weight loss by pups following 24 and 48 hr of isolation from the dam, in the presence or absence of maternal excreta.

feeding on an inadequate diet. Humans lost in the wilderness are advised not to linger in locals in which inadequate food is available in that further movement is necessary and the greater the period of subsistence on an inadequate diet the less the energy reserves available for further exploration (Angier, 1962, p. 52). By analogy, the utilization by rat pups of maternal excreta as an emergency ration, while providing some short-term benefit, might not, in the long run, be a useful strategy for weanling pups in the absence of both their dam and conventional foods.

Experiment 5

The final hypothesis to be examined suggests that the ingestion of maternal excreta by pups serves as a mechanism for the transmission of food preferences from a dam to her offspring. The results of studies in a number of laboratories (Bronstein, Levine, & Marcus, 1975; Capretta & Rawls, 1974; Galef & Clark, 1972; Galef & Henderson, 1972) indicate that at weaning, rat pups exhibit enhanced intake of the diet of their dam, and it is possible that allocoprophagy by the pups function to introduce the young to undigested particles of diet in the excreta of their dam. In a series of studies undertaken to determine the means by which pups become familiar with their mother's diet, Henderson and I (1972) found evidence of flavor cues in mothers' milk (see also Galef & Sherry, 1973) but found no evidence that pup ingestion of feces played a role in the transmission of food preferences from mother to young.

The results of studies published after Henderson and I completed our work (Leon, 1974) suggest that our experiments may not have been an adequate test of the hypothesis that maternal excreta is utilized by pups to determine their food choice at weaning (Galef, 1977). Leon presented data indicating the following: (a) Lactating female rats deposit two types of anal excreta, feces and cecotrophe, and virgin female rats reingest the latter and deposit only the former. (b) Feces is less attractive to rat pups of weaning age than cecotrophe. (c) Some maternal diets, among them one of the diets Henderson and I used, do not permit synthesis of attractive cecotrophe by lactating females of some strains (Galef & Heiber, 1976), and (d) food-deprived lactating females exhibit reduced cecotrophe deposition. All four of these findings cast some doubt on the adequacy of the experiments Henderson and I carried out to test the hypothesis that flavor cues in maternal excreta influence pup diet choice at weaning. The present experiment was undertaken to correct the methodological deficiencies of Galef and Henderson (1972).

Method.

Subjects. Subjects were 16 pregnant Long-Evans rats obtained from Canadian Breeding Farms. Eight females and their litters, culled to six pups/litter on the day of birth, were assigned to experimental groups, and eight were used as sources of excreta.

Maintenance apparatus. Each female assigned to serve as an experimental animal was placed in a standard plastic laboratory cage (37 × 31 × 17 cm) with ad lib access to water. Each female assigned to serve as a source of excreta was placed in a modified standard laboratory cage like that depicted in overhead schematic in Figure 5 and was maintained on ad lib food and water. A modified laboratory cage containing a source animal and her litter was suspended above each standard laboratory cage containing an experimental animal and her litter. Two thirds of the bottom of each modified cage was removed and replaced with hardware cloth (1.2 × 2.5 cm) to permit excreta to fall to the cage below it. The hardware-cloth-floored section of each source female's cage was separated from the remaining one third of her cage by a sealed transparent partition. Entrance to the third of the cage behind the partition was through a single 5-cm-diam. hole. A nesting area of aluminum sheet metal (10 × 10 × 17 cm) and a food source were located behind the partition.

Testing apparatus. The apparatus used to determine the food preferences of individual pups, described

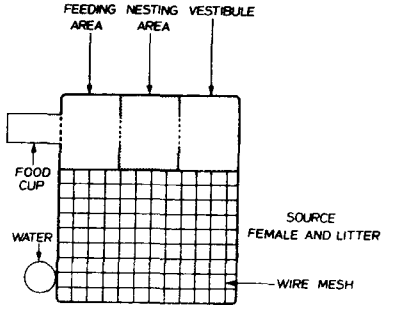

Figure 5. Overhead schematic view of the modified standard laboratory cage containing a source-group female and litter in Experiment 4. (This cage was suspended directly above a standard laboratory cage containing an experimental group female and litter.)

in detail in Galef and Henderson (1972), consisted of a plastic dish (22 cm in diameter, 6.6 cm deep) with two detachable food cups mounted 180° apart on its exterior. Water was available throughout testing in a shallow bowl placed in the center of the apparatus. Intake of diet from each food cup was determined by weighing.

Procedure. Three to four days prior to parturition, each female was assigned one of two maintenance diets and was given ad lib access to either powdered Purina Laboratory Chow (Diet P) or a powdered diet whose main constituents were potato starch and casein (Diet PSC).[1] Both diets are known to allow dams to synthesize cecotrophe highly attractive to young rats (Leon, 1974). On the day of parturition each female was assigned to either an experimental or a source cage. To ensure that pups born to experimental females ingested solid food for the first time when tested for their food preference in the test apparatus, each experimental female was fed for 3 hr/day (9–10 a.m., 3–4 p.m., 10–11 p.m.) in a cage separate from her young on the diet on which she had been maintained prior to parturition. Each female serving as a source of excreta was paired with an experimental female whose time of parturition was within 24 hr of her own and was provided ad lib access in her home cage to the diet on which she had been maintained prior to parturition.

Pups in experimental litters were reared in one of three conditions: (a) Both their dam and the dam overhead were eating Purina Laboratory Chow (P/P), (b) both dams were eating the potato-starch–casein diet (PSC/PSC), or (c) the dam overhead was eating Purina Laboratory Chow while the dam of experimental pups was eating the potato-starch–casein diet (P/PSC).

Cages containing source females were examined daily and were cleaned if any spillage was detected in the feeding area. Source mothers invariably kept their young in the nesting area and kept the area behind the partition relatively free of anal excreta, more than 90% of which fell to the cage below.

Testing was initiated when experimental pups were 21 days of age. Each experimental pup was placed individually in a test apparatus and was offered the choice of Diet P and Diet PSC. Intake of each diet was determined 3, 6, 12, and 24 hr following placement of a pup in the test apparatus.

Results and Discussion

I expected on the basis of previous work that pups in Groups P/P and PSC/PSC would exhibit a preference for the diet of their dam and the source female living above them. As can be seen in Figure 6, which indicates the amount of Diet PSC ingested by pups in Groups P/P and PSC/PSC as a percentage of total intake, my expectations were confirmed. Pups exposed to females eating Diet PSC ingested a considerably greater percentage of that diet during the test period than did pups exposed to females eating Diet P.

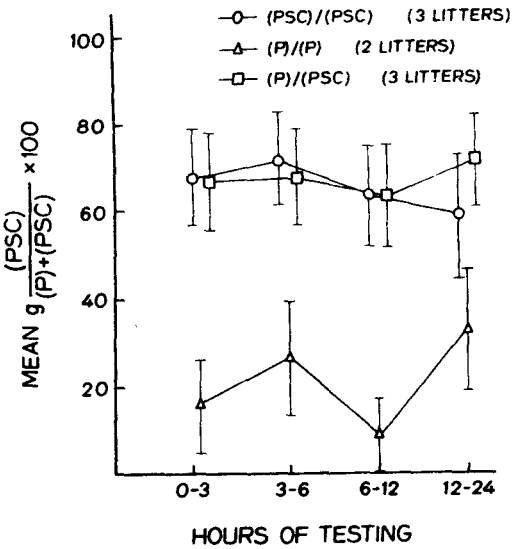

Figure 6. Amount of Diet PSC eaten by experimental group pups during 24-hr testing as a percentage of total intake.

I expected that if pups were influenced in their choice of diet at weaning by maternal excreta, then pups in Group P/PSC, which were exposed to the excreta of a lactating female eating Diet P during ontogeny, would exhibit less of a preference for Diet PSC during testing than pups in Group PSC/PSC which lacked such exposure. As can also be seen in Figure 6, pups in Group P/PSC did not exhibit any effect of exposure to the excreta of source females eating Diet P. The feeding preference of pups in Group P/PSC was not different from that of pups in Group PSC/PSC.

The results of the present experiment confirm those found previously (Galef & Henderson, 1972) and do not offer support for hypotheses implicating exposure to maternal excreta in the determination of pup feeding preferences at weaning. It might, of course, be argued that the reason why pups in Group P/PSC failed to exhibit any effect of exposure to the excreta of females eating Diet P is that pups in Group P/PSC did not ingest any of the excreta from the female eating Diet P and therefore the present ex-

[1] Diet PSC was compounded (in g/kg) of 584.5 g of potato starch, 211 g of casein, 104.5 g of cellulose, 50.0 g of corn oil, 40.0 g of salt mix VSP XIV, and 10.0 g of Vitamin Fortification Mix.

periment does not adequately test the hypothesis. It should be kept in mind that the question addressed in the present experiment was not whether pups could utilize information in maternal excreta if forced to do so but rather whether they would utilize such information if allowed to do so. The results of the present experiment suggest that the answer to the latter question is negative, but they provide no evidence bearing on the former.

General Discussion

The results of the present series of experiments are in a sense disappointing. The hypotheses under study concerning the function of allocoprophagy in young rats seemed at the outset readily testable and likely to be confirmed. However, the experiments and literature review presented above offer support only for the view that ingestion of mothers' excreta may serve as a short-term emergency diet when weaned pups are starving and no other food is available. Such data does little to explain the frequent gnawing of maternal feces to be observed in 12- to 18-day-old pups which are both adequately maintained by their dams and have access to an adequate diet of solid food.

There seem to me to remain two possible classes of answer to the question of the function of allocoprophagy in preweaning rats. First, future studies may reveal some as yet unknown benefits accruing to pups from the ingestion of their dam's excreta. In particular, it is possible that bacteriological investigations, beyond the capacity of our laboratory to perform, might reveal an impoverished intestinal flora in rats reared without access to maternal excreta, which would leave pups vulnerable to diets deficient in specific vitamins (Barnes, 1962). Alternatively, it is possible that the question What is the function of allocoprophagy in weanling rats? is unanswerable in that form. Nibbling on and ingestion of maternal excreta by young rats may not be the appropriate unit of behavior in which to seek functional significance. It is possible that allocoprophagy may simply be one expression of a general tendency of young rats to orally explore their environment and, perhaps, learn the adequacy of various substances as dietary constituents before serious weaning begins. In support of the latter view, the data presented in Figure 1 indicate that sawdust is the substance first and most frequently mouthed by pups 8 to 19 days of age. Perhaps sawdust chewing is in itself functional, perhaps not. Similarly, allocoprophagy by young rats may be a functional unit of behavior, or it may be one aspect of a broader pattern of oral exploration in which functional significance resides. The present studies fail to provide strong evidence supporting the former view.

References

Angier, B. *How to stay alive in the woods.* New York: Macmillan, 1962.

Babicky, A., Parizek, J., Ostadalova, I., & Kolar, J. Initial solid food intake and growth of young rats in nests of different sizes. *Physiologia Bohemoslovaca,* 1973, *22,* 557–566.

Barnes, R. H. Nutritional implications of coprophagy. *Nutrition Reviews,* 1962, *20,* 289–291.

Bolles, R. C., & Woods, P. J. The ontogeny of behaviour in the albino rat. *Animal Behaviour,* 1964, *12,* 427–441.

Bronstein, P. M., Levine, M. J. & Marcus, M. A rat's first bite: The nongenetic cross-generation transfer of information. *Journal of Comparative and Physiological Psychology,* 1975, *89,* 295–298.

Capretta, P. J., & Rawls, L. H. Establishment of a flavor preference in rats: Importance of nursing and weaning experience. *Journal of Comparative and Physiological Psychology,* 1974, *86,* 670–673.

Ewer, R. F. *Ethology of mammals.* New York: Plenum Press, 1968.

Galef, B. G., Jr. Social effects in the weaning of domestic rat pups. *Journal of Comparative and Physiological Psychology,* 1971, *75,* 358–362.

Galef, B. G., Jr. Mechanisms for the social transmission of food preferences from adult to weanling rats. In L. M. Barker, M. Best, & M. Domjan (Eds.), *Learning mechanisms in food selection.* Waco, Tex.: Baylor University Press, 1977.

Galef, B. G., Jr., & Clark, M. M. Mother's milk and adult presence: Two factors determining initial dietary selection by weanling rats. *Journal of Comparative and Physiological Psychology,* 1972, *78,* 220–225.

Galef, B. G., Jr., & Heiber, L. The role of residual olfactory cues in the determination of feeding site selection and exploration patterns of domestic rats. *Journal of Comparative and Physiological Psychology,* 1976, *90,* 727–739.

Galef, B. G., Jr., & Henderson, P. W. Mother's milk: A determinant of the feeding preferences of weaning

rat pups. *Journal of Comparative and Physiological Psychology*, 1972, *78*, 213–219.

Galef, B. G., Jr., & Sherry, D. F. Mother's milk: A medium for transmission of cues reflecting the flavor of mother's diet. *Journal of Comparative and Physiological Psychology*, 1973, *83*, 374–378.

Gewalt, W. Phalangers. In B. Grzimek (Ed.), *Grzimek's Animal Life Encyclopedia (Vol. 10)*. New York: Van Nostrand Reinhold, 1972.

Gustafsson, B. E., & Fitzgerald, R. J. Alteration in intestinal microbial flora of rats with tail caps to prevent coprophagy. *Proceedings of the Society for Experimental Biology and Medicine*, 1960, *104*, 319–322.

Hall, W. G. Weaning and growth of artificially reared rats. *Science*, 1975, *190*, 1313–1315.

Leon, M. Maternal pheromone. *Physiology and Behavior*, 1974, *13*, 441–453.

Raibaud, P., Dickinson, A. B., Sacquet, E., Charlier, H., & Mocquot, G. La microflore du tube digestif du rat: II. Dénombrement de différents genres microbiens dans l'estomac et l'intestin de rats conventionnels. Variations quantitatives individuelles et en function de l'âge. *Annales de l'Institut Pasteur*, 1966, *110*, 861–876.

Smith, H. W. The development of the flora of the alimentary tract in young animals. *Journal of Pathology and Bacteriology*, 1965, *90*, 495–513. (a)

Smith, H. W. Observations on the flora of the alimentary tract of animals and factors affecting its composition. *Journal of Pathology and Bacteriology*, 1965, *89*, 95–122. (b)

Smith, H. W., & Crabb, W. E. The faecal bacterial flora of animals and man: Its development in the young. *Journal of Pathology and Bacteriology*, 1961, *82*, 53–66.

Telle, H. J. Beitrag zur Kenntnis der Verhaltensweise von Ratten, vergleichend dargestellt bei, *Rattus norvegicus* und *Rattus rattus*. *Zeitschrift für Angewandte Zoologie*, 1966, *53*, 129–196.

Thoman, E. B., & Arnold, W. J. Effects of incubator rearing with social deprivation on maternal behavior in rats. *Journal of Comparative and Physiological Psychology*, 1968, *65*, 441–446.

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