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The results of the present experiments indicate that adult rats are capable of influencing their pups' choice of diet during weaning in two ways. First, cues transmitted from a mother to her pups during the nursing period are sufficient to determine the dietary preference of the young at weaning. Second, the presence of adult rats at a feeding site is sufficient to determine the choice of feeding site by the pups independent of cues transmitted during the nursing period.

The results of recent investigations (Galef, 1971; Galef & Clark, 1971) indicate that weaning wild and domesticated rat pups are strongly influenced in their choice of diet for initial ingestion by the learned dietary preferences of the adult members of their colony. When a colony of adult rats learned to avoid one of two adequate diets as a result of that diet's previous association with poison, rat pups born to colony members and feeding with them ate only the diet that adult members of their colony were eating and did not eat any of the diet the adults were avoiding for varying amounts of time depending on subject strain and experimental conditions. The behavior observed was interpreted as demonstrating a three-stage process in which rat pups first approach adults at a feeding site and eat there, then learn cues associated with the diet they ingest, and, in the case of wild rats, thereafter avoid alternative diets as a result of their inherent neophobia. This interpretation im-

PLICITLY assumes that the influence of adult rats on the food choice of their young commences at the time of initiation of feeding on solid food by the pups. However, the results of more recent experiments (Galef & Henderson, 1972) suggest that cues contained in the milk of lactating female rats are capable of influencing the food choices of their young at weaning. It seems that odors or flavors associated with the mother's diet are transmitted via her milk to nursing pups and that these cues influence the young's choice of diet for early ingestion. The first experiment presented here was designed to determine whether or not the cues received by pups during nursing would be sufficient to produce a preference for the diet the adults of the colony were eating under the experimental conditions used by Galef and Clark (1971).

EXPERIMENT 1

If, as was proposed in Galef and Clark (1971), the adults of a colony only begin to influence the dietary preferences of their young when the pups begin feeding on solid food by inducing them to approach one diet rather than another, then pups who are offered a choice of diets only in the absence of adults should not show any systematic difference in their choice of diets for first ingestion as a consequence of differences in the feeding habits of the adults of their colony. Alternatively, if lactating female rats can influence the dietary preferences of their young at wean-

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ing, as a result of olfactory or gustatory cues transmitted to the young during nursing, then one should observe regular differences in the food preference of pups as a function of the dietary history of the adults of their colony even if the pups feed only in the absence of adults.

Method

Two colonies each composed of five female sexually mature hooded rats obtained from the Quebec Breeding Farm were established in enclosures $3 \times 6 \times 1$ ft. constructed of slotted angle iron and hardware cloth. The sheet metal floor of each enclosure was covered with wood shavings and four wooden nest boxes were provided (see Figure 1). Male hooded rats (Quebec Breeding Farm) were introduced for 72 hr. to impregnate the females. Water was available ad lib and the females were removed from their enclosures for 3 hr/day for feeding in separate cages. Females from one enclosure (Diet A group) were fed powdered Purina Rat Chow (to be referred to below as Diet A) and females from the other enclosure (Diet B group) were fed Turtlox "fat sufficient diet" (a sucrose and casein based powdered diet, highly preferred to Diet A, to be referred to below as Diet B). During the 3 hr. in which adults were being fed in separate cages, two ceramic food bowls ($5\frac{3}{4}$ in. diam., $2\frac{1}{2}$ in. deep) were placed approximately $2\frac{1}{2}$ ft. apart in each test enclosure. One of the bowls contained Diet A and the other Diet B.

The experiment proper began when a litter of pups (reduced to six pups/litter at 10 days of age), born to each of the colonies, began to eat solid food. The experimenter observed the feeding behavior of the pups in the test enclosures throughout the 3-hr. feeding periods via closed-circuit television, recording the number of approaches the

pups made to within 4 in. of each food bowl and the number of times pups were observed to eat from each bowl. Bowls were also weighed at the beginning and end of each feeding period to ascertain the amount of each diet ingested by the pups.

A third group of two litters of hooded rat pups (control group) were treated identically to the Diet A group but were offered Diet A in both food bowls during the experimental period in order to determine the extent of position preferences.

Results

The main results of Experiment 1 are presented in Figure 2a which indicates the proportion of Diet A eaten by pups whose mothers were fed either Diet A or Diet B. It is apparent that pups whose adult colony members have eaten Diet A prefer Diet A while those whose adult colony members have eaten Diet B prefer Diet B even though the adults and pups in this experiment never had the opportunity to interact in a feeding situation. Similar results were obtained from an analysis of the number of observed feedings at each food bowl.

The data from the control group is of some interest in itself and is presented separately in Figure 2b. There are two important aspects of the data, first, the pups' day-to-day variability in feeding-site selection and, second, the closeness of their means over the 10 days of the experiment to an equal distribution of food intakes from the two food bowls ($\bar{X} = 50.6\%$ of total intake in the Diet A position over 10 days for Control Litter 1 and

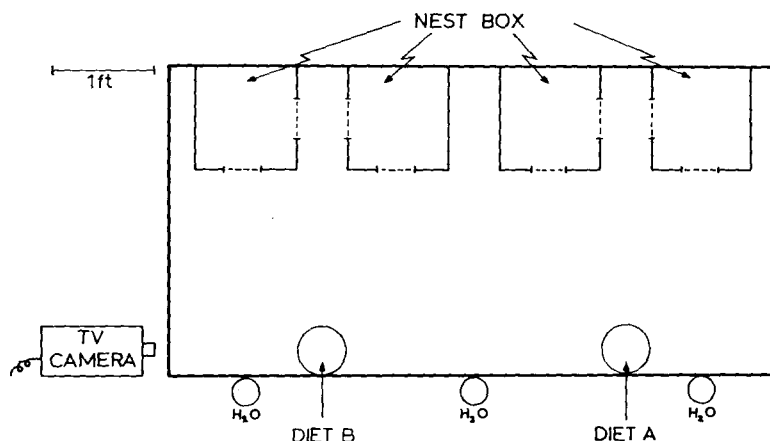


FIG. 1. Enclosure in which pups were observed feeding.

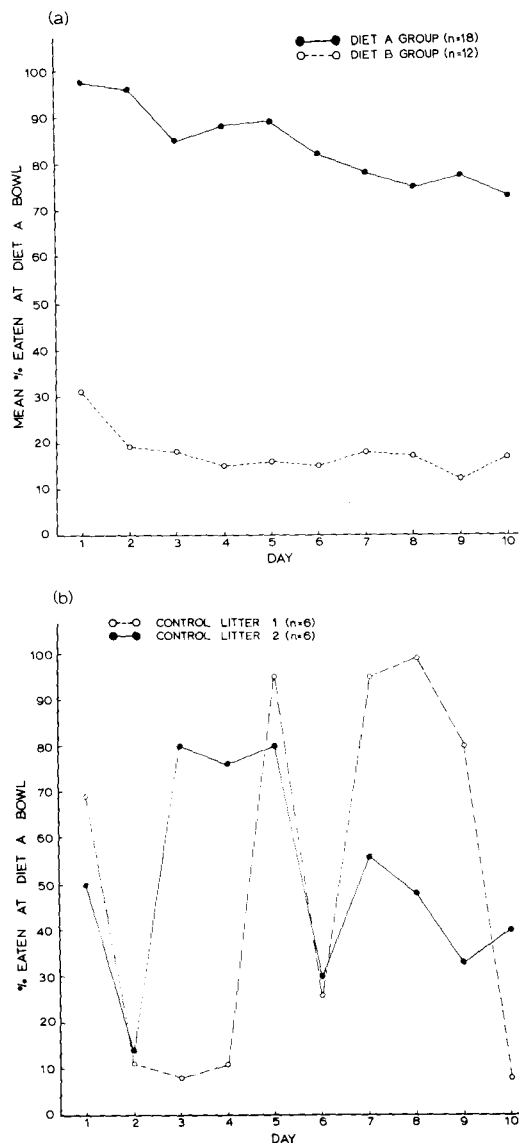


FIG. 2. Percentage of food eaten from the food bowl in the Diet A position by pups in (a) experimental and (b) control groups in Experiment 1.

$\bar{X} = 49.8\%$ for Control Litter 2). The first aspect is not unexpected in view of the previously demonstrated tendency of pups to influence one another's choice of feeding site (Galef & Clark, 1971). The equal distribution of intakes from the two bowls over the 10 days of the experiment suggests that observations taken on successive

days are independent of each other. In fact, a chi-square analysis of the predictability of preferred feeding site on Day $n + 1$ on the basis of site preference on Day n revealed independence of successive observations ($\chi^2 = .35$, $df = 1$, $.70 > p > .50$).

The seven litters in the present experiment began to eat at a mean age postpartum of 25.4 days ($SD = 4.7$).

Discussion

The results of the present experiment have several implications. First, as was found in Galef and Henderson (1972), it would seem that adult colony members can influence the dietary selection of pups without the opportunity to interact with them in the presence of food. Second, the data presented here indicate that a crucial control was lacking in several of the investigations reported in Galef and Clark (1971). In this earlier work it was assumed that dietary selection by the pups in the presence of adults was determined by the presence of the adults at the food bowl at which the pups chose to eat. The present investigation indicates that the pups would have shown similar preferences even if the adults had been absent. The importance of an approach response elicited by the adults and influencing dietary selection by the pups, thus, becomes open to question. Experiment 2 was designed to examine the influence of adults in determining the feeding site selection of pups under conditions in which information as to the diet the parents were eating could not influence the pups' choice.

It is interesting to note that pups in the present experiment, who were only offered food when the adults of their colony were absent, did not begin eating solid food until they reached a mean age of 25.4 days. In our earlier work with rats of the same strain, offered a choice of the same diets in the same enclosures in the presence of the adults of their colony (Galef & Clark, 1971), it was observed that litters of pups began to eat solid food at a mean age of 19.9 days postpartum ($n = 7$, $SD = 2.20$; unpublished observation). This marked difference in age of initiation of feeding on

solid food on the part of pups feeding in isolation in comparison with those feeding with the adults of their colony supports the conclusion of Galef (1971) that adults play a role in initiating feeding on the part of the young, and indicates that the presence of adults at the time of initiation of feeding on solid food is an important variable in the weaning process.

EXPERIMENT 2

In our previous experiments involving the observation of colonies of rats, weaning rats have been offered two distinct diets in separate locations. The dietary preference shown by the pups under these conditions can be interpreted as the result either of a tendency of the pups to approach the adults and begin eating in their vicinity (Galef, 1971; Galef & Clark, 1971) or, on the basis of the results of Experiment 1 and Galef and Henderson (1972), as a learned food preference resulting from the interaction of the nursing mother and her young outside the feeding situation. In the present experiment pups were offered the same diet in two locations after the adults of their colony were trained to eat at only one of them. Cues as to the nature of the mother's diet received by the pups during nursing could not, in this case, influence the pups' choice of site

for ingestion of food. Any observed preference of the pups for one feeding site as opposed to the other would have to be attributed to the direct influence of the adults' presence on the pups' selection of feeding site.

Method

Subjects. The subjects were a colony of four female and one male third-generation laboratory-bred wild rats (*Rattus norvegicus*) and two litters of pups born to colony members (reduced to six pups/litter at 10 days of age).

Procedure. The colony was established in the enclosure illustrated in Figure 1 and placed on a 3 hr/day feeding and light schedule. Food (Diet A) was made available to the colony in two aluminium food bowls (5¾ in. diam., 2½ in. deep) located approximately 2½ ft. apart. Each of the bowls was mounted on a 5¾-in.-diam. plastic disc which was attached to the center of a sheet metal plate 18 × 18 in. These sheet metal plates were, in turn, placed in Plexiglas trays 18 × 18 in. with a 1-in.-high edge. The aluminium bowl and metal plate of each feeding apparatus could be connected through a Grason-Stadler Model E1064GS shock generator modified so as to bypass the shock scrambler and set at 1.6 ma. The arrangement was such that any animal attempting to eat from a charged bowl would close the circuit and receive a shock. The position of the two feeding bowls was reversed daily and the bowl located in the position indicated as Diet B in Figure 1 was charged throughout each 3-hr. feeding period prior to the first emergence of the pups from the nest site. The adult rats rapidly learned to feed only from the food bowl located in the position indicated as Diet

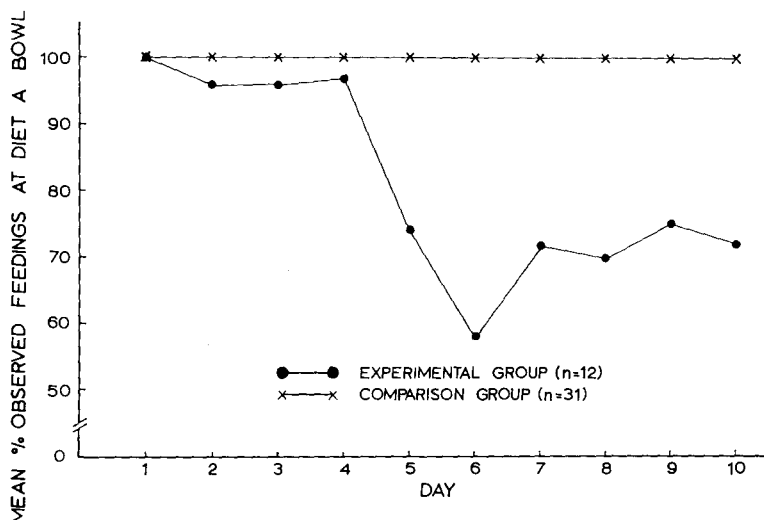


FIG. 3. Mean percentage of feedings by pups observed at Diet A bowl in Experiment 2.

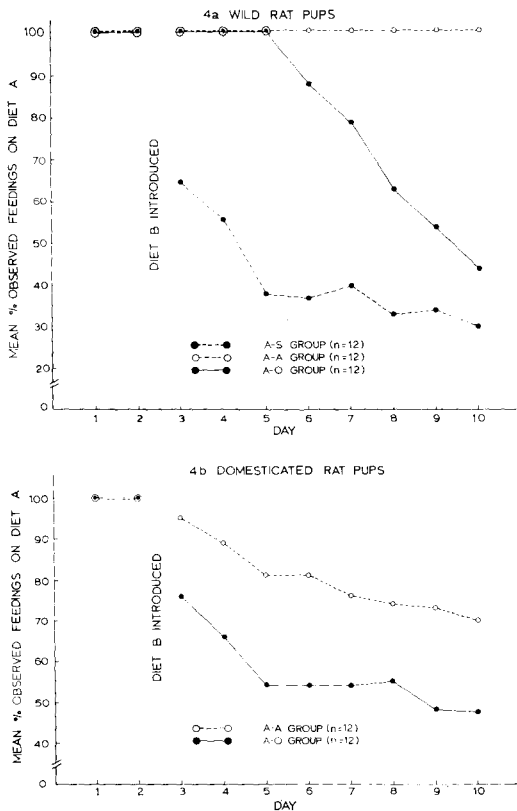


FIG. 4. Mean percentage observed feedings at Diet A bowl by (a) wild and (b) domesticated rat pups in Experiment 3.

A in Figure 1 and continued to do so following termination of shock presentation prior to the first pup's beginning to feed.

The experiment proper began when pups born to colony members began to eat solid food. As in Experiment 1, the experimenter observed the feeding behavior of the pups throughout the 3-hr. feeding periods via closed circuit television, recording the number of approaches the pups made to within 4 in. of each food bowl and the number of times pups were observed to feed from each bowl.

Results

The results of Experiment 2 are presented in Figure 3 which indicates the proportion of feeding responses on the part of the pups directed toward the bowl at which the adults were feeding. Data from five litters of wild rat pups whose parents were eating Diet A and avoiding Diet B, and who were offered the choice of Diets A and B in the enclosure (Galef & Clark, 1971) are included for purposes of com-

parison. There are two important aspects of the data. First, the pups showed a strong preference for the feeding site at which the adults were eating throughout the 10 days they spent in the enclosure with them. Second, although the pups did the majority of their feeding at the same bowl as the adults of their colony throughout the 10 days of observation, they also ate at the location avoided by the adults. This distribution of feeding contrasts markedly with that observed in the comparison group which had Diet B available at the location which the adults were avoiding and failed to ingest any of it. Both of these findings support the interpretation of the dietary preferences of wild rats reported in Galef and Clark (1971) and outlined above. Wild rat pups are directly influenced in their choice of site for ingestion of food by the position in which the adults of their colony are eating and the presence of a novel diet at the alternative feeding site would appear to be partly responsible for the pups' continued avoidance of food in that location.

EXPERIMENT 3

The present experiment provides additional evidence of the effects of the adults' presence at a feeding site on the feeding site selection of their young.

When adult members of a rat colony and their pups are feeding on a nonpreferred diet and are then offered a choice between that diet and a preferred diet in a separate location, opportunities are provided for the observation of a variety of types of interaction between parent populations and their offspring. If, as suggested in Experiment 2 above and in Galef and Clark (1971), the pups' selection of feeding site is influenced by the presence of the adults at a food site, then, should the adults rapidly transfer their feeding to the preferred diet following its introduction, their presence at the site of the preferred diet should facilitate transfer of feeding to that diet on the part of the young. On the other hand, adults trained to avoid the new diet and to continue to eat the nonpreferred one should inhibit transfer to the new diet by the pups. Last, pups whose parent clan has been removed prior to introduc-

tion of the preferred diet should provide an indication of the rate of transfer of feeding by the young independent of adult influence. The present experiment examines the role of parent-offspring interaction on the rate of transfer of feeding of the pups to a new diet in the situations outlined above.

Method

Animals in the present experiment were maintained in the enclosure shown in Figure 1 on a 3 hr/day feeding and light schedule. A single ceramic food bowl containing Diet A was presented to each colony during the feeding periods in the position indicated as Diet A in Figure 1 and an empty ceramic bowl was presented in the location indicated as Diet B in the same figure during each feeding period. Experimental manipulations were begun after the pups had been observed to feed on Diet A for 2 days. On the third and subsequent days of pup feeding the pups were offered both Diets A and B during 3-hr. feeding periods in their appropriate positions as indicated in Figure 1.

Three experimental groups were used.

Adult-switch (A-S) group (two litters of wild rat pups). Prior to the birth of the young, colonies of this group had been trained to eat Diet B (using the method described in Galef & Clark, 1971) whenever it was offered to the colony.

Adult-avoid (A-A) group (two litters of hooded rat pups and two litters of wild rat pups). Prior to the birth of the young, colonies of this group were trained (using the method of Galef & Clark, 1971) to avoid ingesting Diet B by associating it with poison.

Adult-out (A-O) (two litters of hooded rat pups and two litters of wild rat pups). Adult colony members of this group were removed 3 hr. prior to the introduction of Diet B on the third day of pup feeding on solid food and not returned for the remainder of the experiment.

The experimenter again observed the colonies via closed circuit television throughout the 3-hr. feeding periods, recording the number of approaches to, and feedings from, each food bowl by the pups.

Results and Discussion

The results of Experiment 3 are presented in Figures 4a and 4b which show for wild and hooded pups, respectively, the percentage of observed feedings directed to Diet B by the various groups. In accordance with the predictions outlined above, the wild pups in the A-S group showed an accelerated rate of transfer to the new diet and those in the A-A group a reduced rate of transfer in comparison to the A-O group.

Similarly the hooded A-O group transferred feeding to Diet B more rapidly than the hooded A-A group.

Data collected on Day 3, during the feeding period in which Diet B was first introduced, provides the strongest evidence of the effects of the presence of adults at a feeding site on the feeding behavior of the pups independent of effects attributable to cues received by the pups during nursing. Observations made on Days 4-10 could reflect both the influence of adults' presence at the new food and differences in preference resulting from changes in the cues associated with the pups' mothers' milk as a consequence of differences in the diet of mothers in the various groups following Day 3. The absence of nursing during feeding periods (authors' observation) prohibits this interpretation of data gathered on Day 3.

GENERAL DISCUSSION

The result of the present series of experiments indicate that adult rats are capable of influencing the choice of diet by their young in two ways. First, cues associated with the mother's milk (Galef & Henderson, 1972) appear to influence the young to preferentially ingest a substance their mother has been eating. Second, the physical presence of the adults in the vicinity of a food site attracts the pups to that site, and consequently affects their choice of diet. The data strongly indicate that both the quality of mother's milk, as a result of mother's diet, and the physical presence of adults at a feeding site serve to direct young rats' early ingestions of solid food.

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