The effects of forced nest-site feeding on the food preferences of wild rat pups at weaning*

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The experiment reported below examined the role of the ingestion of food samples at the nest site on the feeding preferences of wild rat pups during weaning. The results indicated that although food preferences during the first few days of feeding on solid food were not affected by ingestion at the nest site, later preferences were. These data were interpreted as providing additional evidence of the insufficiency of the ingestion of food samples in the nest site to determine pups' choice of diet for early ingestion and of the role of neophobia in maintaining adult-initiated food preferences.

Observation of the behavior of a number of mammalian species indicates that the food preferences of juveniles may be influenced by interaction with adult conspecifics. Examination of the literature suggests that adult feeding patterns can affect those of juveniles in at least three readily discriminable ways. First, the taste of a lactating female's milk can reflect the flavor of the diet she eats during the nursing period, and her young may show strong preferences for diets of that flavor while in the process of weaning (Galef & Clark, 1972; Galef & Henderson, 1972; LeMangen & Tallon, 1968). Second, the young of many species are reported to take food directly from adult conspecifics, and it is probable that ingestion of these purloined food samples affects food preferences at weaning (cf. Harper, 1970). Third, there is evidence in at least a few species of what might be called "behavioral transmission" of learned feeding patterns from adults to juveniles (Kawamura, 1959; Steiniger, 1950). Recent experiments in our laboratory have demonstrated the existence of a mechanism which seems to be of this third type, enabling adult members of a wild rat colony to affect the feeding preferences of their offspring at weaning.

Laboratory-maintained colonies of adult wild rats were trained to avoid a palatable diet (because of its previous association with poison) and to eat a less palatable diet located nearby. Pups born to colonies trained in this way did not eat the diet which the adults of their colony were avoiding and, for the 10 days of the experiment, ingested only the relatively

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There is, however, an alternative explanation for the observation that pups initiate feeding on the diet the adults of their colony are eating and ignore a normally preferred alternative. While the young are still in the nest, the adults may introduce samples of the diet they are eating into the nesting quarters, either purposely as hoardage or accidentally as particles clinging to their fur and vibrissae. The young could eat this introduced

material, become familiar with it, and then seek similar substances for ingestion in the larger environment. Although observation of the behavior of wild rat pups does not support this alternative interpretation (Galef & Clark, 1971a), the experiment reported here was undertaken to examine directly the possibility that food ingested in the nest site could affect the observed feeding preferences of wild rat pups during weaning. If the ingestion of food samples at the nest site determines the pups' observed preference for the diet which the adults of their colony are eating, then one would expect pups to eat the diet that the adults of their colony are avoiding, if they had ingested samples of that diet while in the nest site.

SUBJECTS

The Ss were four litters of wild rat pups (reduced to six pups per litter 10 days postpartum) born to colonies of fourth-generation laboratory-bred wild rats.

APPARATUS

Colonies of one male and five female sexually mature wild rats were established in $6 \ge 3 \ge 1\frac{1}{2}$ ft enclosures constructed of slotted angle iron and hardware cloth. The galvanized sheet metal floor of each enclosure was covered with $2\frac{1}{2}$ in. of wood shavings. Four wooden nest boxes $(1 \ge 1 \ge \frac{1}{2}$ ft) with two entrance holes were provided, and water was available ad lib (see Fig. 1).

Food was presented to the colonies in two aluminum food bowls (5³/₄ in. diam x 2¹/₄ in. deep). Each bowl was mounted on a 5³/₄-in.-diam plastic disk that was attached to the center of a sheet metal plate 18 x 18 in. The sheet metal plate 18 x 18 in. The sheet metal plates were, in turn, placed in Plexiglas trays, 18 x 18 in., with a 1-in.-high Plexiglas edge. The aluminum bowl and metal plate of one



Fig. 1. Enclosure in which wild rats were observed during daily 3-h colony feeding periods.

Table 1 Grams of Diet Eaten by Pups During Their 3-H Periods of Restraint

Litter	Days Postpartum										
	16	17	18	19	20	21	22	23	24	25	26
Experimental											
J-28	0	0	0	0	1.0	2.8*	5.5	5.5	11.0	10.0	4.6
J-30	0	0	0	0	2.0	1.8*	1.9	1.9	1.6	1.6	2.8
Control											
J-31	0	1.4	1.1	1.3*	2.4	2.1	1.7	2.7	1.4		
J-32	0	0	0	0	2.1*	1.9	3.2	3.8	4.4	3.0	

feeding apparatus was connected through a Grason-Stadler Model E1065GS shock generator modified so as to bypass the scrambler and set at 1.6 mA. The arrangement was such that any animal attempting to eat from this bowl would close the circuit and receive a shock.

PROCEDURE

Each colony was established on a 3 h/day feeding and light schedule, with light onset coinciding with food availability. Food was presented to the colony in the two food bowls described above, placed approximately 2¹/₂ ft apart. Each of the bowls contained a different nutritionally adequate powdered diet, referred to below as Diets A and B (Diet A was powdered Purina Rat Chow, and Diet B, Turtox "fat sufficient diet" composed mainly of sucrose and casein). The diets differed in color, texture, taste, and smell, Diet B normally being highly preferred by rats to Diet A. The application of a 1.6-mA shock to adults trying to eat Diet B resulted in their rapidly learning to avoid the bowl containing Diet B and to concentrate their feeding exclusively on Diet A. The adults continued to avoid the bowl containing Diet B when shock contingent on touching that bowl was terminated as each litter of pups born to a colony reached 14 days of age.

The experiment proper began when pups reached 16 days of age. Following the 3-h colony feeding period on the day on which each litter reached 16 days of age, it was restrained for 3 h/day in its nest box with a foodcup (3¼ in. diam x 3 in. deep). Two of the litters of pups (experimental group) were offered Diet B, the preferred diet the adults of their colony were avoiding, and two litters (control group) were offered Diet A, the diet the adults of their colony were eating, during the 3-h period of restrained feeding.

Each litter continued to receive 3-h restrained feedings of the appropriate diet daily until members of that litter were observed to have eaten during the colony feeding period for 6 consecutive days. Intakes during the restrained feeding periods were determined by weighing. The Es observed the colony throughout each colony feeding period via closed circuit television and recorded the number of times pups ate from either food bowl. Observation of each litter was continued until members of that litter began to eat Diet B or until its members had been observed to eat only Diet A during colony feeding periods for 16 consecutive days. All spillage and hoardage were removed following each colony feeding period.

RESULTS

Table 1 indicates the grams of diet eaten by each litter during its daily 3-h period of restraint. The asterisks indicate the day on which each litter was first observed to eat in the large enclosure.

The main results of the experiment are presented in Fig. 2 which indicates the percent of observed feedings directed to Diet A by the pups in the two experimental and two control litters during colony feeding periods. Dayl for each litter in Fig. 2 is the day on which that litter was observed to

begin to eat solid food during the colony feeding period and corresponds to the day postpartum marked with an asterisk in Table 1. Inspection of Fig. 2 reveals that, whereas pups in control litters ate only Diet A during their first 16 days of feeding during colony feeding periods, those in experimental litters ate Diet A for varying lengths of time before starting to feed on Diet B. Pups in Experimental Litters J-28 and J-30 were observed, respectively, to feed on Diet A 208 and 889 times before ingesting their first bite of Diet B in the colony feeding situation.

DISCUSSION

There are three aspects of the data reported above which deserve discussion. First, it is apparent that when pups ingest a normally preferred diet in their nest box which the adult members of their colony are avoiding, they still initiate feeding on the nonpreferred diet that the adults of their colony are eating. This result supports the conclusion of Galef & Clark (1971a) that the ingestion of samples of diet in the nest site is not responsible for the determination of pups' choice of diet for early ingestion in the colony feeding situation.

Second, the data also indicate that pups in experimental litters transfer feeding to the normally preferred but adult-avoided diet more rapidly than do pups in control litters. This result is readily interpretable in terms of the three-stage analysis of weaning briefly described in the introduction to the present paper. It supports the proposal



Fig. 2. Percentage of observed feeding responses directed to Diet A by litters of pups in experimental and control conditions.

that neophobia is responsible, at least in part, for the maintenance of avoidance of adult-avoided diets by pups. The experience of ingesting Diet B in the nest site should have made pups in experimental litters more familiar with Diet B than were controls and, therefore, should have reduced their tendency to delay ingestion of Diet B as a result of its novelty. Of course, in order for such a reduction in latency of transfer of feeding to Diet B by experimental pups to be observable as weaning progressed, there would have to be a waning of the pups' tendency to feed only in the immediate vicinity of adults. Further data indicating both the importance of the novelty of the adult-avoided diet in maintaining avoidance of that diet by pups and of the waning of the pups' tendency to feed only in the vicinity of adults is to be found in Galef & Clark (1972).

Third, the data reported in Table 1 and Fig. 2 indicate that a correspondence may exist between the day on which nest site feeding of experimental litters was terminated and the day on which experimental pups began feeding on Diet B in the large enclosure. If such a relationship were reliable, it would require a different interpretation of our results than that suggested above. However, two additional litters of wild rat pups, which were fed Diet B, one litter for 1 and one litter for 3 days following initiation of feeding in the large enclosure (7 and 3 days of nestbox feeding, respectively), did not begin eating Diet B during colony feeding periods for 8 and 5 days, respectively, following termination of nestbox feeding. Thus, the correspondence in the data presented above between termination of nestbox feeding on Diet B and initiation of feeding on Diet B in the large enclosure would appear to be coincidental and require no alternative interpretation.

REFERENCES

- GALEF, B. G., JR. Social effects in the weaning of domestic rat pups. Journal of Comparative & Physiological Psychology, 1971, 75, 358-362.
- GALEF, B. G., JR., & CLARK, M. M. Social factors in the poison avoidance and feeding behavior of wild and domestic rat

pups. Journal of Comparative & Physiological Psychology, 1971a, 75, 341-357.

- GALEF, B. G., JR., & CLARK, M. M. Parent-offspring interactions determine time and place of first ingestion of solid food by wild rat pups. Psychonomic Science, 1971b, 25, 15-16.
- 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 & Physiological Psychology, 1972, 78, 220-225.
- GALEF, B. G., JR., & HENDERSON, P. W. Mother's milk: A determinant of the feeding preferences of weaning rat pups. Journal of Comparative & Physiological Psychology, 1972, 78, 213-219.
- Psychology, 1972, 78, 213-219.
 HARPER, L. V. Ontogenetic and phylogenetic functions of the parent-offspring relationship in mammals. In D. S. Lehrman, R. A. Hinde, and S. E. Shaw (Eds.), Advances in the study of behavior. Vol. 3. New York: Academic Press, 1970.
- KAWAMURA, S. The process of sub-culture propagation among Japanese macaques. Primates, 1959, 2, 43-54.
- LeMANGEN, J., & TALLON, S. Préference alimentaire du jeune rat induite par l'allaitement maternel. Comptes Rendus des Séances de la Societé de Biologie, 1968, 162, 387-390.
- STEINIGER, F. von. Beiträge zur Soziologie und sonstigen Biologie der Wanderratte. Zeitschrift für Tierpsychologie, 1950, 7, 356-379.