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MECHANISMS FOR THE SOCIAL TRANSMISSION OF ACQUIRED FOOD PREFERENCES FROM ADULT TO WEANLING RATS

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This paper is concerned with the role of social interaction in the determination of diet selection by weanling wild rats (*Rattus norvegicus*). Discussion of the subject is presented in three parts: The first is intended to place the role of social factors in food preference determination within the context of other determinants of dietary selection. The second presents evidence concerning mechanisms by which adult rats may bias their young at weaning toward initiation of feeding on a particular food, and the third discusses neophobia as a factor in the maintenance of socially transmitted diet preferences in weanlings.

DETERMINANTS OF DIET SELECTION

INNATE TASTE FACTORS

It is a commonplace observation that the members of any species exhibit a tendency to select similar foods for ingestion. It seems reasonable to propose, as P. T. Young did many years ago, that such consistency in the pattern of food acceptance exhibited by conspecifics is determined, in part, by genetically encoded and transmitted propensities to experience some gustatory sensations as more pleasurable than others (Young, 1959, 1966, 1968). According to this hypothesis, primary responses to potential food items reflect the biological organization of sensory-affective processes and are assumed to have evolved as an adaptive response to constancies in the food resource base of the ecological niche of each species (Young, 1968).

Of course, the existence of genetically influenced consistencies in the flavor preference hierarchy of a species does not preclude the possibility that experiential factors may produce differences in the food preferences of conspecific individuals. It is, for example, well established that populations of laboratory animals which have experienced aversive gastro-intestinal events in association with the ingestion of normally preferred food will subsequently exhibit a profound aversion to that food. Conversely, there is preliminary evidence that groups of laboratory animals having a history in adolescence of prolonged ingestion of a normally nonpreferred food item may show a preference for that food or similar foods when subsequently offered such familiar but normally unpalatable items in a choice situation (Kuo, 1967).

Social Influences on Food Selection. Comparison, in the natural environment, of the feeding patterns of individuals belonging to distinct subpopulations reveals similar examples of within-species, intergroup differences in diet selection. In uncontrolled situations the causes of such between-group variability in resource exploitation are, of course, difficult to ascertain. However, a number of field workers have reported observations suggesting that to understand subpopulation differences in food selection in natural situations one has to take into account the social context within which feeding behavior occurs, as well as other food-related experiential variables more frequently considered by laboratory investigators. For example, it has been reported that a variety of species of British birds have acquired the habit of removing or puncturing the caps of milk bottles and eating cream from the surface of the milk. The fact that many birds in some localities, and none in other areas with similar milk bottles, have acquired the milk-bottle opening behavior strongly suggests a social transmission of this feeding habit from individual to individual in the localities where it is common (Fisher & Hinde, 1949; Hinde & Fisher, 1951, 1972. See also Galef, 1976, for other such examples). In laboratory situations, an observer normally will not see the effects of such social processes on diet selection, unless he intentionally looks for them, because most experimental paradigms are explicitly arranged so as to keep the behavior of individual subjects independent of one another. However, examples of feeding patterns which apparently require explanation in terms of the intraspecific social context in which the feeding occurs are not uncommon in the ethological literature.

The capacity of freely interacting natural subpopulations to socially transmit patterns of food resource utilization among themselves would be of obvious advantage. The mechanism of differential reproductive success responsible for the natural selection process [which, in turn, underlies the evolution of sensory affective processes of the type hypothesized by Young (1968)], is only sufficient to produce genetically coded and transmitted food preference patterns in a population adaptive with respect to the mean properties of that population's ecological niche (Williams, 1966). Adaptive behavior with respect to the special demands of an individual's particular home range can only develop as a result of individual behavioral plasticity in response to the demands and contingencies of a particular environment. In the natural situation, social transmission could function to facilitate individual acquisition of information concerning the exploitable resource base of a particular area (Mainardi, 1973), by reducing the cost to an individual organism, in both energy and risk, of the usual direct trial and error learning about a particular ecological situation (Galef, 1976). To the extent that an individual can utilize the experience of sympatric conspecifics in selecting or rejecting items for ingestion, it increases its probability of rapidly locating new sources of food already discovered by conspecifics and reduces its risk of ingesting noxious novel food items.

Importance of Social Influences During Weaning. If, as suggested above, the function of social transmission of information is to reduce the cost to the individual inherent in acquiring information about its individual ecological situation, then it seems reasonable to hypothesize that social influence would be particularly important in mammals during the weaning process. It is during the weaning stage that the demands on the individual to rapidly acquire appropriate behavior with respect to its individual ecological niche are most acute. With respect to dietary selection, it is weanling young which are ignorant of the location and identity of nutritious foodstuffs to be found in the vicinity of the nest-site and which have to seek out food at a stage of development during which they are particularly vulnerable to environmental stress. Adults rearing young have learned the identity and location of necessary foods during their own explorations in the area in which they reproduce, and it would clearly be advantageous to the young (and, hence, to the reproductive advantage of their parents) if the young could make use of the experience of adult conspecifics in locating solid foods.

In the case of wild rats, which have been the subject species in my own work on social transmission processes, the ability of weanlings to make use of the acquired feeding patterns of adult conspecifics might be particularly important because weanling rats not only have to locate and identify safe foods but also often need to avoid ingesting palatable poison baits introduced into their home ranges by humans seeking to exterminate commensal rodent populations. Because successful poison avoidance by rats depends in considerable measure on discrimination of familiar from unfamiliar foods (Galef & Clark, 1971), the weanling rat, to which all solid foods are unfamiliar, is in particular need of some source of information other than its personal experience if it is to avoid ingesting potentially lethal baits. There is, in fact, field data suggesting that adult rats can protect their young against the ingestion of toxic substances. Von Fritz Steiniger (1950), an ecologist working on problems of rat extermination, reported some years ago that if a given poison bait is used in one area for an extended period, despite initial success, later acceptance of that bait is very poor. He noted, in particular, that the offspring of animals surviving initial poisoning rejected the bait without sampling it themselves and continued to do so for so long as animals which had survived initial poison ingestion remained in the area. Steiniger attributed such avoidance of contact with potentially toxic baits by naive animals to the behavior of experienced individuals, which he believed, dissuaded the inexperienced young from ingesting poisoned food. For the past several years, my students and I have been examining the social interactions of both wild and domesticated rats under controlled conditions to determine the mechanisms by which such social transmission of feeding preferences might proceed.

MECHANISMS FOR THE SOCIAL TRANSMISSION OF FOOD PREFERENCES

BASIC EXPERIMENTAL PARADIGM

In our basic experimental paradigm (Galef & Clark, 1971), colonies consisting of two male and four female wild rats are established in enclosures like the one diagrammed in Figure 1a. Water is continuously available and food is presented to the colony for 3 hr daily in two ceramic food bowls located approximately 2.5 ft apart. Each of these bowls contains one of two nutritionally adequate diets, discriminable from one another in color, texture, taste, and smell. I will refer to these diets as Diets A and B. Diet A is powdered Purina Laboratory Chow, and Diet B, compounded by Teklad Mills, consists mainly of sucrose and casein and is highly preferred to Diet A by rats in a simple choice situation.

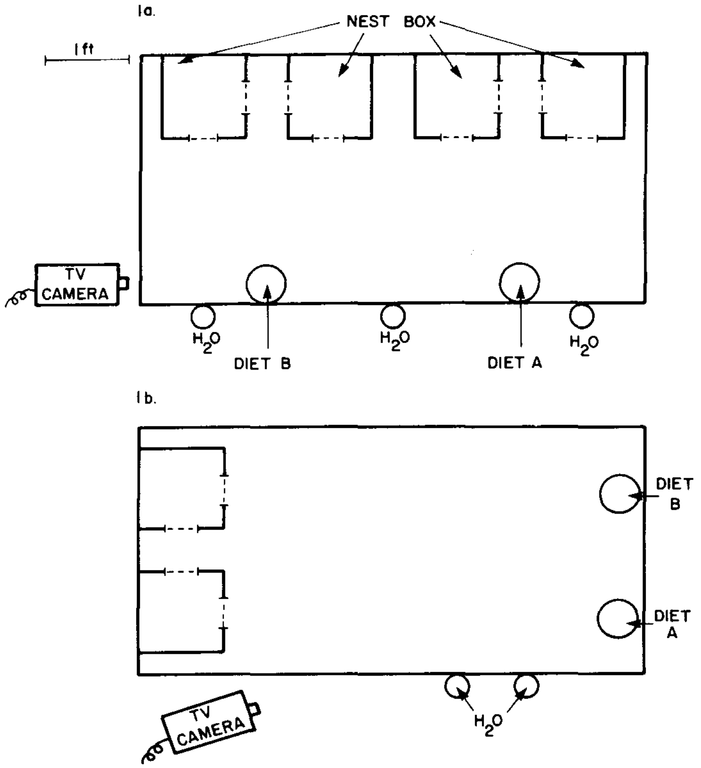

Figure 1
Enclosures in which rat pups were observed prior to (a) and after removal from (b) their adult clan in the "Basic Experimental Paradigm."

The adult members of the colony are trained to eat one diet and to avoid the other by introducing sub-lethal concentrations of a toxin, lithium chloride, into samples of one of the diets offered to the adult colony during daily 3-hr feeding periods. Under these conditions, members of our adult colonies rapidly learn to avoid ingesting the lithium-contaminated diet and continue to avoid it for some weeks even if subsequently offered samples of the once-poisoned diet free from contaminants.

The experiment proper begins when litters of pups born to trained adult colony members leave their nest site to feed on solid food for the first time. We observe both adults and pups throughout daily 3-hr feeding periods via closed circuit television and record the number of times the pups approach to within 4 in of each food bowl, each containing uncontaminated samples of diet, and the number of times they eat from each food bowl.

After the pups have been feeding on solid food for a number of days, they are transferred to new enclosures (illustrated in Figure 1b), where, without the adults of their colony, they are again offered the choice of uncontaminated samples of Diets A and B for 3 hr daily. The amount of each diet eaten by the pups in this situation is determined by weighing food bowls before and after each feeding session.

Typical results of such studies are presented in Figures 2a, 2b, and 3. Figure 2a presents data describing the food choices of a litter of

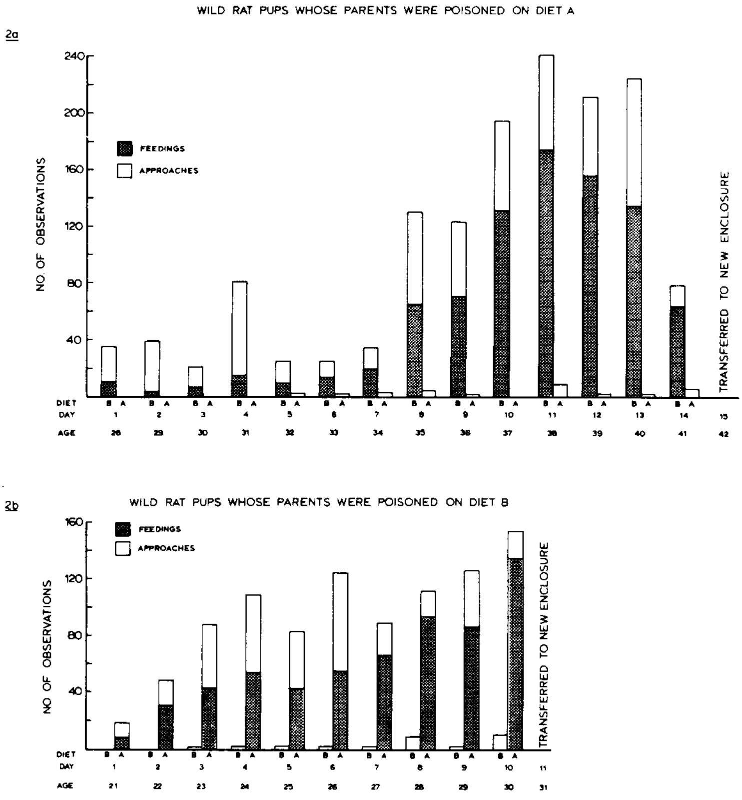

Figure 2
Number of observed approaches to and feedings from bowls containing Diets A and B by wild rat pups, the adults of whose colonies had been poisoned on Diet A (a) or Diet B (b). (From Galef & Clark, 1971.)

wild rat pups born to a colony of adults trained to avoid ingesting the normally non-preferred Diet A, while Figure 2b presents data describing the feeding behavior of a litter of pups born to a colony of adults trained to avoid ingesting the normally preferred Diet B. It is clear from comparison of the data presented in these figures that the learned feeding preferences of adult colony members profoundly affect the feeding preferences of their young. As Steiniger (1950) observed, in the presence of adult rats avoiding a diet, weanling colony members also avoid ingesting that diet. Furthermore, as illustrated in Figure 3, the learned dietary preferences of adults continue to affect the feeding preferences of their young for some 8 to 10 days following transfer of the pups to enclosures separate from the adult colony members.

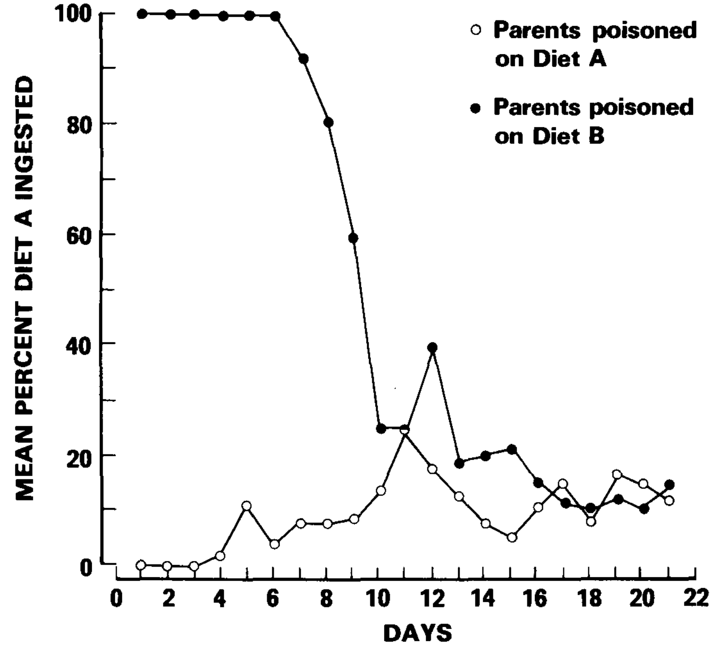

Figure 3
Percentage intake of Diet A by pups on the days following removal from adult influence. (Redrawn from Galef & Clark, 1971.)

WEANLINGS LEARN TO EAT WHAT ADULTS EAT

It is not possible to determine from the data described above whether the pups learn to ingest the diet consumed by the adults of their colony or to avoid the diet rejected by the adults. It is, however, important to determine the precise nature of the behavior being transmitted from adults to young before attempting an analysis of underlying mechanisms.

If pups learn to avoid the diet which the adults of their colony avoid, as a result of interaction with them, then it should be important that the pups experience that diet during the time they are with the adults. Conversely, if the pups learn only to eat what the adults of their colony eat, then the presence of the adult-avoided diet during the period of adult-young interaction should be of no importance.

The experimental design used to determine whether pups learn to eat the adult-ingested diet or to avoid the adult-avoided diet was

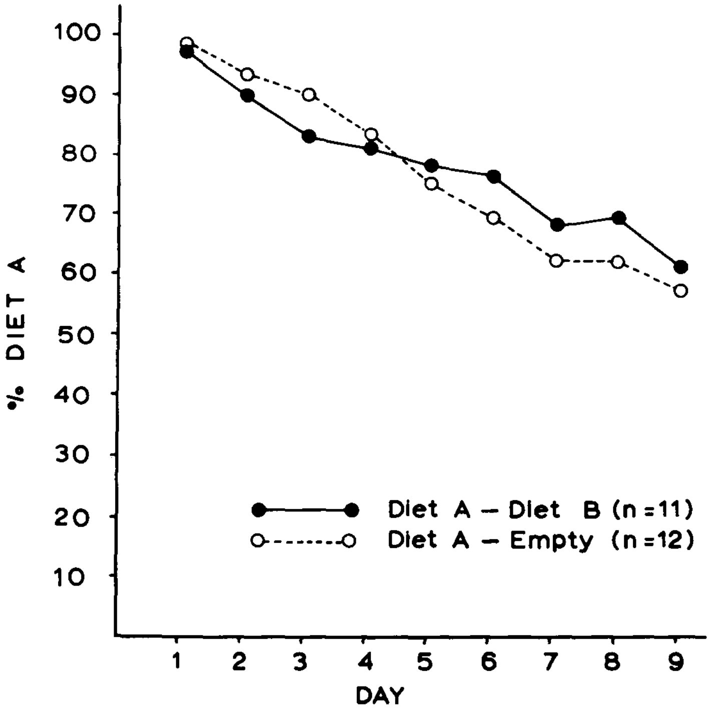

Figure 4
Mean percentage of Diet A eaten by pups following their transfer to individual enclosures. For one group the second food bowl contained Diet B; for the other group the second food bowl was empty. (From Galef & Clark, 1971.)

very similar to the "Basic Experimental Paradigm." Colonies of adults were again trained to avoid the normally preferred Diet B and to eat Diet A. Pups were allowed to feed with the adults for 10 days and were then moved to individual enclosures and offered the choice of uncontaminated samples of Diets A and B. While in the enclosure with the adults for 10 days of feeding, pups of one colony and their adults were offered the choice of Diets A and B (and ate only Diet A) while pups and adults in another colony were offered the choice between Diet A and an empty bowl placed in the location in which Diet B was usually available. If pups in the "Basic Experimental Paradigm" learned to avoid the diet that the adults of their colony avoided, then one would expect pups which had Diet B available while with the adults to show a more profound avoidance of Diet B, when offered the choice of Diets A and B in individual enclosures, than pups which had not previously seen Diet B.

Figure 4 illustrates the percentage of Diet A eaten by pups in the two groups when offered the choice of Diets A and B in individual enclosures. As is clear from examination of the figure, there is no difference between the two groups in their acceptance of Diet B. The simplest interpretation of these data is that pups learn to eat the diet that the adults eat rather than to avoid the diet the adults avoid.

POSSIBLE MECHANISMS FOR TRANSMISSION OF FOOD PREFERENCES

Any of a wide range of mechanisms might be responsible for the observed transfer of an acquired feeding preference from adult rats to pups. For example, adults may mark either the diet they are eating or the diet they are avoiding with residual chemical cues which attract or repel the pups and thereby influence their feeding site selection. Alternatively, adults may carry samples of the diet they ingest back to the nest site and ingestion of these samples may influence pups' subsequent choice of diet. Or, the physical presence of adults at a feeding site may attract pups to that site and influence their choice of diet for early ingestion. Each of these possibilities has been examined.

Effects of Chemical Cues on Feeding Site Selection. If adults deposit attractive chemicals in or near the food they are eating or mark the food they are avoiding, or its surrounding area, with some warning chemical and these residual chemicals are responsible for adult influence on pups' initial choice of diet, then it should be fairly easy to disrupt the apparent influence of the adults on the food choices of their young. All that would be needed would be to disturb the chemicals deposited by the adults. We have conducted the following experiment in order to determine the importance of such chemical cues for the behavior of the pups. The experimental situation was similar to the "Basic Experimental Paradigm" except that sheet metal trays (2 x 2 ft) covered with sawdust were placed under both food bowls during both the training of the adults (to eat Diet A) and the observation of the pups. When pups in each of the litters we used had been observed to eat solid food 20 times, we performed the following manipulations: (1) The two food bowls were emptied. (2) The food bowls and the trays of sawdust they were sitting on were reversed in position. (3) Finally, new samples of Diets A and B were placed in their initial positions in the now-reversed food bowls. Thus, all chemical cues located within 1 ft of the food bowls had been reversed in position within the experimental enclosure. These manipulations had absolutely no effect on the feeding behavior of the pups. Without exception, the pups continued to eat Diet A and avoid Diet B, as did the adults.

While the above result suggests that the deposition of residual chemical cues is not a necessary condition for the observed transmission of a preference for the diet of colony adults, more recent research indicates that such cues may be sufficient to influence pup choice of feeding site (Galef & Heiber, 1976). A lactating female rat and her litter were left undisturbed in the left-hand portion of the enclosure diagrammed in Figure 5 from Day 1 to Day 17 post-partum. Starting on Day 17, and for the subsequent 6 days, the female and her litter were removed from the enclosure for 3 hr daily. During the period when the enclosure was vacated, experimental pups of the

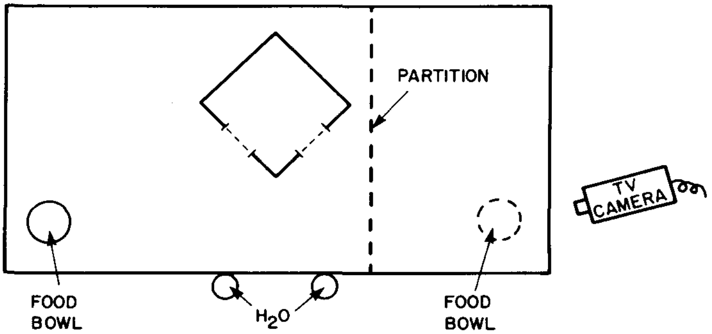

Figure 5
Enclosure in which effects of residual olfactory cues on pup behavior were ascertained.

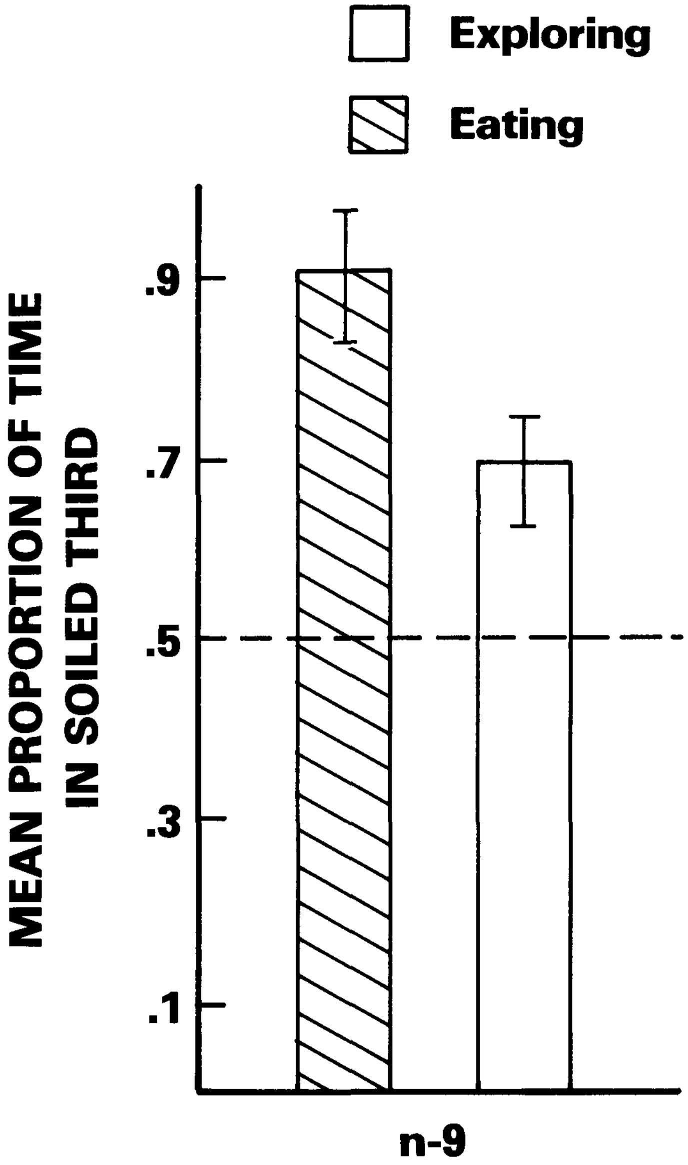

Figure 6
Mean proportion of time spent by individual pups exploring and feeding in the end of the enclosure previously occupied by a lactating female rat and her litter. (Redrawn from Galef & Heiber, 1976.)

same age as the pups just removed were placed individually in the enclosure and the partition indicated in Figure 5 was removed, allowing the experimental pups to choose between two food bowls containing Diet A. Each experimental pup was observed on closed circuit television for 50 min daily for 7 consecutive days. The observer recorded the amount of time each pup spent feeding from each food bowl and the amount of time each pup spent exploring in the previously occupied and unoccupied end thirds of the enclosure. The results are presented in Figure 6. It is clear from the figure that residual chemical cues deposited by a lactating rat are sufficient to affect the feeding locations selected by pups during weaning.

Taken together the results of the preceding two studies indicate that rat pups can utilize residual olfactory cues to select a feeding site previously visited by conspecifics. However, the data also indicate that the manipulation of such cues does not disrupt adult influence on pup food choice. Alternative mechanisms for the transmission of food selection must exist.

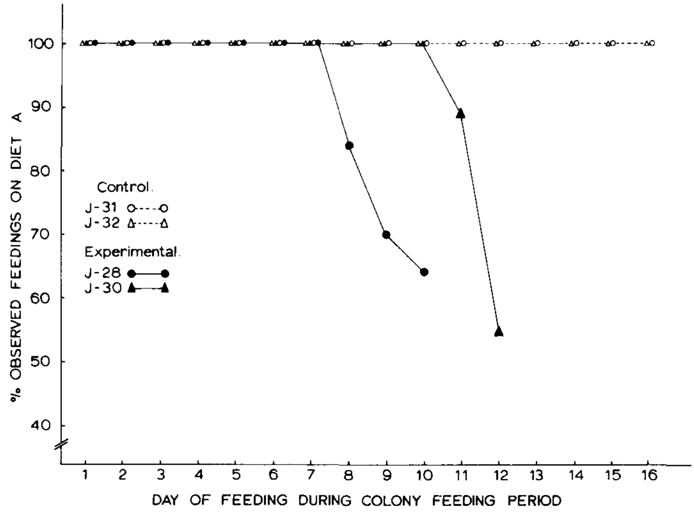

Figure 7
Percentage of observed feeding responses directed to the bowl containing Diet A during colony feeding periods by litters of pups offered in the nest site samples of Diet A eaten by adult colony members (Control) or samples of Diet B avoided by adult colony members (Experimental). (From Clark & Galef, 1972.)

Effects of Food Present in the Nest Site. To look at the effects of the ingestion of food stuffs at the nest site on subsequent food choices, one can offer the pups in the nest site, at some time other than the 3-hr colony feeding period, samples of the food the adults of their colony have been trained to avoid. The pups' food preferences during colony feeding periods can then be observed. The results of such an experiment (Clark & Galef, 1972) are presented in Figure 7. There are two interesting aspects of the data. First, sampling by the pups in the nest site of the adult-avoided diet did not produce an initial preference for that diet. Second, such sampling did affect the later rate of acceptance by pups of the adult-avoided diet. I will be returning to the second point later in discussion of the role of neophobia in the maintenance of socially transmitted feeding preferences in rats.

Effects of Physical Presence of Adults. If ingestion of food samples in the nest site is not sufficient to explain the pups' strong dietary preferences in the "Basic Experimental Paradigm," what is? The

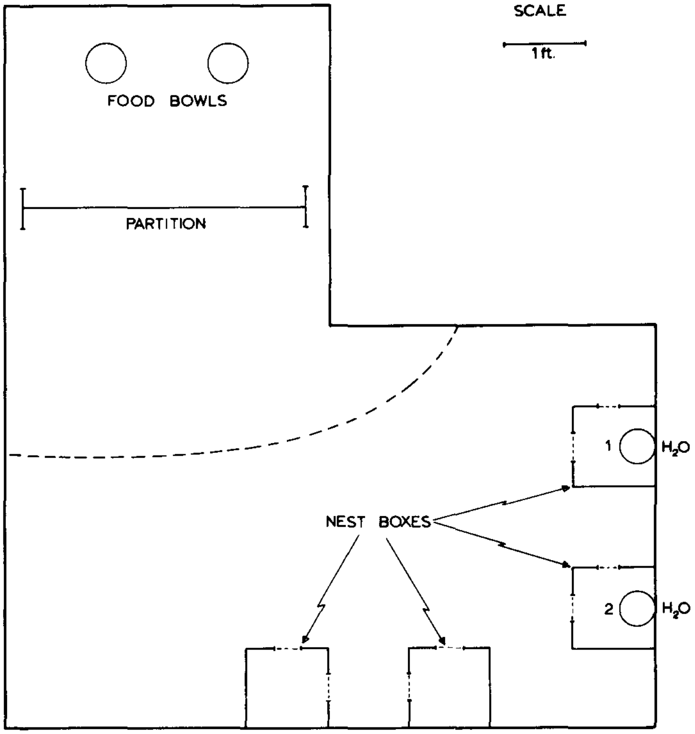

Figure 8
Enclosure for continuous observation of a wild rat colony.

evidence indicates that the most important factor influencing pups' choice of initial diet is the presence of adults at a food site at the time the pups are ready to begin feeding on solid food (Galef & Clark, 1971, 1971a). To examine this possibility, we established a colony of adult wild rats in the enclosure illustrated in Figure 8. Diet A was constantly available in the two food bowls located behind the partition (the adults ate at both bowls) and the area above the dotted line was continuously monitored via closed circuit television. We marked pups individually and looked to see under what conditions each pup ingested its first meal of solid food. We observed 9 pups in all, and all 9 ate their first meal under exactly the same circumstances: in the presence of a feeding adult and at the same food bowl as that feeding adult, not at the other bowl 1.5 ft away. Given the temporal distribution of adult meals, the probability of this occurring by chance was less than .001. The presence of an adult at a feeding site seems to attract pups to that site and to cause pups to initiate feeding on the diet present there. Our further observations and experiments within this enclosure indicated that the pups tend to approach adults outside the nest area rather than to follow them from the nest site to food, and that visual cues are necessary to guide this approach. Blinded pups showed no tendency to eat their first meal of solid food in the presence of a feeding adult (Galef & Clark, 1971a).

DIRECT ADULT INFLUENCE ON PUP FOOD SELECTION

The mechanisms by which adult rats may influence the food choice of their young discussed thus far are rather indirect. The adults bias their offspring to a feeding site rather than to a food. However, examination of the possibility of direct transfer of food preference from adults to young has revealed that this too can occur. We conducted an experiment which was similar to the "Basic Experimental Paradigm" except for one very important feature (Galef & Clark, 1972). Colonies of adult rats were again housed in 3 x 6 ft enclosures of the type illustrated in Figure 1a. However, in this experiment the adults were removed to a separate cage where they were fed either Diet A or Diet B for 3 hr daily, depending on the experimental condition to which their colony was assigned. While the adults were out of the colony enclosure, the pups were presented with two standard food bowls, one containing Diet A and the other Diet B. We weighed the food bowls before and after each 3-hr feeding session to determine the amount of each diet eaten by the pups. The results are presented in Figure 9. As is apparent from the figure, the diet eaten by the adults affects the food choices of the pups even though, under the conditions of the present experiment, the adults and young have no opportunity to interact directly in the feeding situation and the adults have no opportunity to influence pups' choice of feeding site. Similar results have been reported by Capretta and Rawls (1974) and Bronstein, Levine, and Marcus (1975).

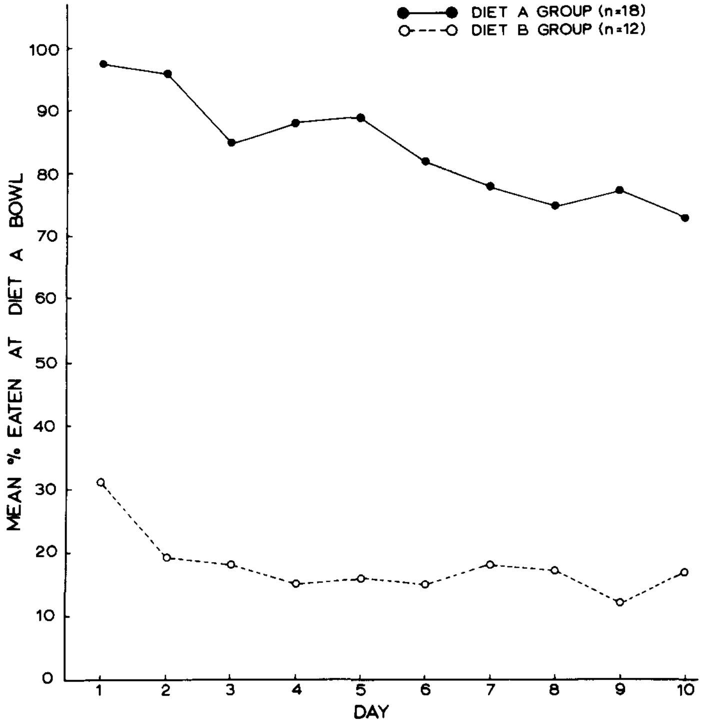

Figure 9
Mean percentage of Diet A eaten by pups, the adults of whose colony are eating Diet A or Diet B, when adults and pups have no opportunity to interact in a feeding situation. (From Galef & Clark, 1972.)

Again there are a number of possible explanations of the observed ability of the adults to influence pups' choice of diet. The flavor of the diet ingested by an adult rat may directly affect the flavor of its feces, and ingestion of adult feces may cause pups to preferentially ingest diets of a similar flavor during weaning. Alternatively, particles of food may cling to an adult's fur and vibrissae and pups could ingest these and become familiar with the adult's diet. Finally, the flavor of the diet ingested by a lactating female rat during the nursing period may directly affect the flavor of her milk and cause pups to prefer similar-tasting diets during weaning.

Effects of Mother's Milk on Pup Food Preference. The available evidence suggests that the most likely direct adult influence on pup food selection occurs through the flavor of the mother's milk (Galef & Henderson, 1972). The milk of a lactating female appears to contain gustatory cues reflecting the taste of her diet with sufficient accuracy to enable her pups to identify that diet during weaning. In one of our experiments which supports this conclusion (Galef & Sherry, 1973), rat pups nursing from a lactating female eating Diet A were force fed 0.5 ml of milk manually expressed from a second lactating female eating Diet B. Following this force feeding, the pups were poisoned by intraperitoneal injection of lithium chloride. A test session subsequently conducted at weaning revealed that this milk-lithium pairing conditioned an aversion to Diet B. Despite these results, however, we have not been entirely successful in producing a preference for a diet in pups at weaning by feeding the pups milk manually expressed from a female eating that diet. Although the outcome of such studies, involving a wide variety of parameters, have consistently been in the direction predicted by the milk-flavor hypothe is, we have not found a procedure which reliably produces acceptable levels of significance. The search continues. Thus, although there is reason to believe that there are cues present in maternal milk sufficient to enable pups to identify maternal diet, there is not yet sufficient evidence to justify the conclusion that such cues actually play a role in determining pups' diet preference at weaning.

Effects of Maternal Excreta on Pup Food Preference. Further work is also needed before firm conclusions may be reached concerning the adequacy of cues associated with the anal excreta of lactating female rats to influence weanling food choices. Leon (1974) presented data indicating that 20-day-old rat pups may ingest anal excreta produced by their mother. It is possible, as Leon has suggested, that cues influencing pup food choice may be transferred from mother to young via the smell or taste of the dam's excreta. This possibility has not, however, been directly tested. Data from my laboratory indicate that pup access, throughout the nursing period, to the anal excreta of a nulliparous female rat eating a diet different from that of their mother is not sufficient to modify pup food choice toward a preference for the diet of that nullipara (Galef & Henderson, 1972). However, given the known differences in the attractiveness of the anal excreta of nulliparous and lactating rats (Leon, 1974), such results are not adequate to permit conclusions concerning the importance of maternal excreta in the determination of weanling diet preference. Thus, the issue remains without satisfactory resolution at the present time.

Effects of Particles of Food Clinging to an Adult's Fur. Results of experiments in which lactating female rats were fed separately from their young, brushed clean, and then dusted with a diet other than the one they were eating following each feeding session and prior to being returned to their litters revealed no effect of this manipulation on initial pup food preferences. The pups continued to exhibit a normal preference at weaning for the diet their mother was eating (Galef & Henderson, 1972). Thus, explanations of the transfer of feeding preferences from adult to young rats via particles of food clinging to the fur of adults seem fairly well excluded.

SUMMARY

The results of our research to date indicate the existence of at least three mechanisms by which adult rats may bias the choice of diet by conspecific young at weaning. Both the physical presence of adults at a feeding site and residual olfactory cues deposited by adults in the vicinity of a food source influence pups' choice of place of weaning and thereby their choice of diet at weaning. There is very strong evidence that a further mechanism exists whereby adults can directly influence pup food choice as a result of interaction with them outside the feeding situation. Cues contained in maternal milk may play a role in this interaction.

ROLE OF NEOPHOBIA IN THE MAINTENANCE OF SOCIALLY TRANSMITTED DIET PREFERENCES

The ability of adults to influence the diet chosen for initiation of feeding is only part of the total phenomenon exhibited by wild rat pups in the "Basic Experimental Paradigm" described above. Young wild rat pups not only initiate feeding on an adult-exploited diet in preference to an adult-avoided one; they continue to ingest only that diet so long as they remain with the adults and for some 8-10 days following removal from interaction with adults. A question remains as to the cause of the wild pups' continued avoidance of the diet which the adults of their colony have learned to avoid. The results of our studies suggest a three-stage process adequate to account for the observed behavior of the weanling wild rats in our experiments.

First, as discussed in the preceding section, we have evidence that adult rats can bring their young to initiate feeding on one diet rather than another as a result of interaction with them. Second, it seems reasonable to suppose that, as a result of ingesting the diet to which the adults introduce them, the young become familiar with its taste and smell. Third, as we will see below, there is reason to believe that once wild rat pups become familiar with one diet, they avoid alternative diets because of the relative novelty of those alternatives. Wild rats are strongly neophobic organisms: they show a pronounced avoidance of novel foods or other novel objects in their environment (Barnett, 1958; Galef, 1970). It seems likely that this neophobia contributes to the tendency of wild rat pups to continue avoiding diets other than the one to which the adults of their colony introduce them.

Maintenance of Adult-Determined Food Selection in Wild and Domesticated Pups. If, in fact, neophobia is at least in part responsible for prolonged avoidance by wild rat pups of the adult-avoided diet, then one would expect domesticated rat pups, which are only mildly neophobic in comparison with their wild conspecifics (Barnett, 1958; Galef, 1970; Mitchell, 1976; Rozin, 1968), to behave quite differently from the wild pups in the "Basic Experimental Paradigm." Domesticated pups should follow adults to the diet which the adults were trained to eat (Galef, 1971), but the domesticated pups should then transfer feeding to the adult-avoided alternative diet at the time when neophobia becomes responsible for continued avoidance by wild rat pups (Galef & Clark, 1971). Figure 10 presents data describing the behavior of two typical litters of domestic rat pups tested in the "Basic Experimental Paradigm." Adult colony members were trained to eat the normally less preferred Diet A, and the food choices of their young were observed. As can be seen in Figure 10, although domesticated pups initially fed on the same diet as the adults of their colony, the pups began to ingest the adult-avoided alternative after some 3 to 5 days. In contrast, wild rat pups fail to ingest the adult-avoided alternative for at least 10 days (see Figures 2 and 3). These findings are consistent with an hypothesis implicating neophobia as an important factor in maintenance of wild rat pup ingestion of the diet to which the adults introduce them.

Novelty of Alternative Foods as a Factor in Pup Food Selection. If weanling wild rats do not ingest the adult-avoided diet because of its novelty, they should show less reluctance in feeding at the location avoided by the adults if the diet positioned there is familiar rather than novel. In a test of this prediction (Galef & Clark, 1972), we of-

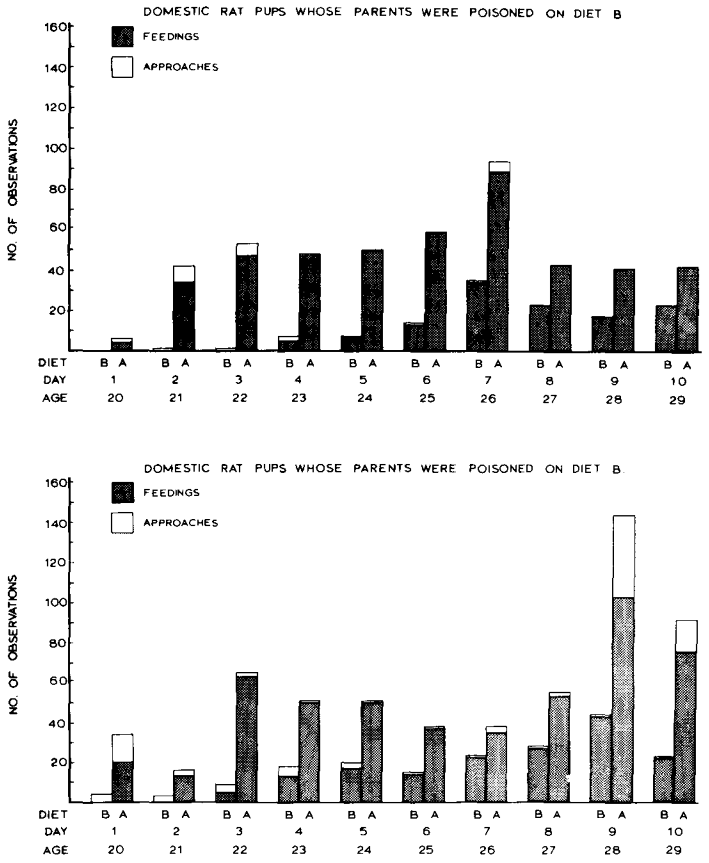

Figure 10
Number of observed approaches to and feedings from the bowls containing Diets A and B by domesticated rat pups, the adults of whose colony had been poisoned on Diet B. Each panel displays data for one litter of pups. (From Galef & Clark, 1971.)

fered adult colony members Diet A in two locations and trained them, using electric shock, to eat in one location but not the other. Independent litters of pups were then tested with samples of familiar Diet A or unfamiliar Diet B in the adult-avoided bowl. Figure 11 shows the proportion of pup feedings directed toward the adult-utilized food bowl (containing Diet A) by the two groups. Wild weanlings clearly transfer feeding to the adult-avoided site more rapidly if offered the same diet there that is available at the adult-utilized site. This finding provides additional evidence that the neophobia of wild rat pups in response to a novel food is, at least in part, responsible for prolonging avoidance of alternative diets once pups have become familiar with the diet to which the adults of their colony introduce them.

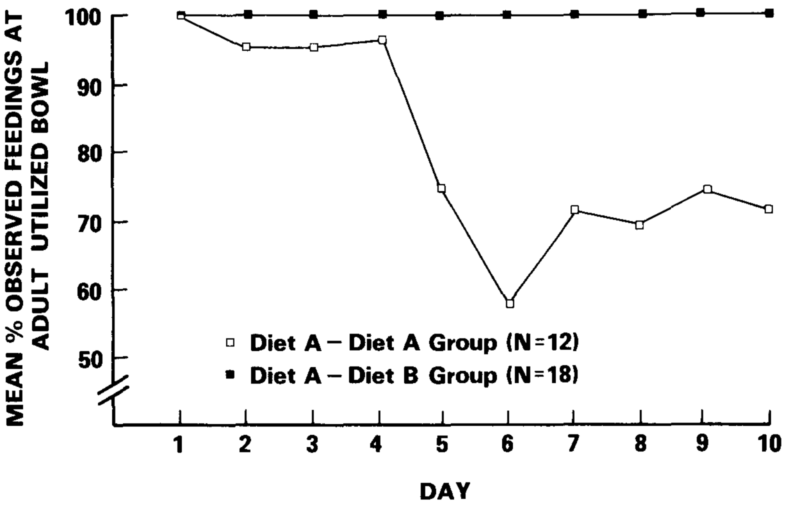

Figure 11
Mean percentage of observed feeding bouts by wild rat pups at the food bowl from which the adults of their colony were feeding when Diet A was present in both bowls (Diet A-Diet A group) and when Diet A was presented in the adult-utilized food bowl and Diet B in the adult-avoided food bowl (Diet A-Diet B Group). (Redrawn from Galef & Clark, 1972.)

Social Influence and Individual Experience in Determination of Pup Food Preference. A major effect of interaction between adults and young appears to be to familiarize the young with one diet rather than another, a result which can obviously be achieved experimentally by means other than social interaction. For example, Crockett (1975) has shown that exposure of pre-weanling rats to the smell of garlic in the general environment will produce an increased acceptance of garlic-adulterated food at weaning. Leon, Behse, and I are engaged in comparable studies, results of which indicate that exposure of pre-weanling rats to the smell of peppermint produces a tendency in the pups to approach the odor of peppermint as well as a preference for peppermint-flavored food. Our interpretation of these data, taken together with our findings on social transmission processes, is that rats will approach or ingest familiar-smelling objects in their environment regardless of whether this familiarity is achieved by social or other processes. Thus, the transmission of adult feeding preferences to the young wild rat depends, first, on an ability of adults to bias the young toward experience of a specific food, as a result of social interaction with them, and, second, on an independent predisposition on the part of the young to prefer an experienced food to unfamiliar ones.

Evidence of the independence of social influence and individual experience in the determination of pup food preference is provided by an experiment (Clark & Galef, 1972), the results of which are presented in Figure 7. The pups' experience of eating the adult-avoided diet in the nest site affected their choice of diet following 5-10 days of colony feeding, but not their choice of diet early in weaning. Thus, it seems reasonable to conclude that the response of wild rat pups seeking their first meals of solid food is initially a social one, with individual feeding history influencing later food selection.

DISCUSSION

If one looks across species at the role of social interaction in the development of feeding behavior, a similar pattern emerges with considerable regularity. Adult individuals introduce young ones to a subset of the class of potential food items to which the young might have been introduced and, for a limited time following exposure, the young exhibit a tendency to ingest the items experienced as a result of social interaction in preference to unfamiliar items (Galef, 1976).

The means of introduction clearly varies considerably from species to species. Mother hens, for example, use a specific food call to attract their young to a food source, and, as Hogan (1966) has shown, a food-calling hen can induce her chicks to ingest mealworms which they might otherwise avoid. A female meerkat (*Suricata suricatta*) with weaning young will run to and fro in front of her offspring, evoking a food snatching response in her kits and inducing them to ingest food such as banana, which they would normally ignore (Ewer, 1969). And, as discussed above, adult wild rats, as a result of their presence at a food site, can induce pups to feed there on a relatively unpalatable diet.

Although such social interaction may play a role in the initiation of a particular pattern of food selection at weaning, it is the response of the young animal to its early diet, in relation to other available foods, which is critical in determining whether or not the socially transmitted pattern of food selection is maintained to become a permanent feature of the recipient individual's feeding behavior. If it were the case that adult mammals showed an abiding preference for food items ingested at weaning, a sort of "food imprinting," then one might consistently observe relatively permanent effects of social influence at weaning on adult feeding patterns. However, young mammals tend to independently sample available foods in their environments and arrive at a stable pattern of food selection reflecting their species-typical palatability hierarchy (Figure 3; Bronson, 1966; Warren & Pfaffman, 1959). As a general rule, the observable effects of biases in food preference induced by social interaction occuring early in life appear transitory and become obscured as the maturing individual gains experience of the variety of foods available within its home range.

There are, however, important exceptions to this generalization, instances in which presumably socially transmitted feeding patterns (Galef, 1975, 1976) have permanent effects on the diet selection of individuals exposed to social transmission. It has been reported, for example, that many members of some colonies of wild rats (*R. norvegicus*) living along the banks of the Po river, dive for and feed on bivalve molluscs living on the river bottom, while members of neighboring colonies, which have molluscs available within their home ranges, do not exploit them as a food source (Gandolfi & Parisi, 1972, 1973). Similarly, members of some colonies of rats in Germany have been observed to stalk, kill, and eat sparrows, while most colonies do not, even though sparrows are present within their clan territories (Steiniger, 1950). Such examples, and there are numerous others, in which the effects of social interaction appear to be of sufficient duration to serve as the basis of distinctive feeding traditions in certain populations, require some explanation.

It seems reasonable to suppose that two necessary conditions must be met if the results of social interaction are to be observable in the feeding behavior of an individual or population over extended periods of time. First, the transmitted behavior must be one which any individual has a very low probability of acquiring independently. If the transmitted behavior is one which an individual has a high probability of acquiring on its own, the majority of species members will, by definition, acquire that behavior, even if not socially induced to do so. Although socially influenced individuals may acquire the transmitted behavior sooner than those acquiring it independently, differences between the observable feeding behavior of socially influenced and independent individuals will soon disappear. Second, in the absence of any "imprinting" on food ingested early in life, it would appear necessary that the transmitted food preference be for a relatively highly palatable food item, if it is to be maintained. As discussed above, the recipient of a transmitted preference for a relatively unpalatable food will soon find alternatives and abandon the diet to which it was socially introduced. In summary, it seems most consistent with available data to suggest that in the majority of cases the observable effects of biases in food preference induced by social interaction occurring early in life will be transitory and play their major role in vertebrates during thee weaning or fledging period. There are, however, special circumstances in which food preferences established as a result of social interaction may be maintained to maturity.

The importance attributed to the absolute duration of socially influenced patterns of food selection depends on one's theoretical position. Many of those who study the behavior of juvenile organisms do so with the view that the primary goal of such work is the understanding of the ontogenetic processes resulting in the development of an adult behavioral phenotype. The research program described here has proceeded from the view that to survive organisms must exhibit adaptive behavior with respect to their environment at each stage of development (Williams, 1966). Consequently, we have been more concerned with the role of social factors in diet selection as an adaptation during weaning than with the investigation of parameters affecting the duration of food preferences developed as the result of social interaction early in life. The particular case of social transmission of dietary selection we have investigated may well be of little importance in the determination of adult feeding patterns but it gives every indication of being an important adaptation of young mammals undergoing the transition from maintenance on mother's milk to independent acquisition of solid food in the general environment. Our data indicate that social interaction can facilitate the weaning process by reducing the time spent by weanlings in locating needed nutrients and reducing the probability that they will ingest toxic foods which the adults of their social group have learned to avoid. Study of the factors influencing the duration of socially influenced behaviors is clearly important, both from the developmental point of view and for the understanding of the maintenance of traditions in animal populations in natural situations, and we plan to turn our attention to these issues in the immediate future.

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REFERENCES

Barnett, S. A. Experiments on "neophobia" in wild and laboratory rats. **British Journal of Psychology,** 1958, **49,** 195-201.

Bronson, G. Evidence of the lack of influence of early diet on adult food preference in rats. **Journal of Comparative and Physiological Psychology,** 1966, **62,** 162-164.

Bronstein, P. M., Levine, M. J., & Marcus, M. A rat's first bite: The nongenetic, cross-generational 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.

Clark, M. M., & Galef, B. G., Jr. The effects of forced nest-site feeding on the food preferences of wild rat pups at weaning. **Psychonomic Science,** 1972, **28,** 173-175.

Crockett, D. P. Rats' food preferences are determined by maternal diet. Paper presented at meetings of the Eastern Psychological Association, New York, April, 1975.

Ewer, R. F. The "instinct to teach." **Nature** (London), 1969, **222,** 698.

Fisher, J., & Hinde, R. S. The opening of milk bottles by birds. **British Birds,** 1949, **42,** 347-357.

Galef, B. G., Jr. Aggression and timidity: Responses to novelty in feral Norway rats. **Journal of Comparative and Physiological Psychology,** 1970, **70,** 370-381.

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. The social transmission of acquired behavior. **Biological Psychiatry,** 1975, **10,** 155-160.

Galef, B. G. Jr. The social transmission of acquired behavior: A discussion of tradition and social learning in vertebrates. In J. S. Rosenblatt, R. A. Hinde, E. Shaw, & C. Beer (Eds.), **Advances in the study of behavior** (Vol. 6). New York: Academic Press, 1976.

Galef, B. G. Jr., & Clark, M. M. Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. **Journal of Comparative and Physiological Psychology,** 1971, **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,** 1971a, **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 and Physiological Psychology,** 1972, **78,** 220-225.

Galef, B. G., Jr., & Heiber, L. The role of residual olfactory cues in the determination of the 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 the transmission of cues reflecting the flavor of mother's diet. **Journal of Comparative and Physiological Psychology,** 1973, **83,** 374-378.

Gandolfi, G., & Parisi, V. Predazione su *Unoi pictorum* L. da parte del Ratto, *Rattus norvegicus* (Berkenhout). **Acta Naturalia,** 1972, **8,** 1-27.

Gandolfi, G., & Parisi, V. Ethological aspects of predation by rats, *Rattus norvegicus* (Berkenhout) on bivalves *Unio pictorum,* L. and *Cerastoderma lamarcki:* (Reeve). **Bollettino di Zoologia,** 1973, **40,** 69-74.

Hinde, R. A., & Fisher, J. Further observations on the opening of milk bottles by birds. **British Birds,** 1951, **44,** 392-396.

Hinde, R. A., & Fisher, J. Some comments on the republication of two papers on the opening of milk bottles by birds. In P. H. Klopfer & J. P. Hailman (Eds.), **Function and evolution of behavior.** Reading, Massachusetts: Addison-Wesley, 1972.

Hogan, J. A. An experimental study of conflict and fear: An analysis of behavior of young chicks toward a mealworm. Part II. The behavior of chicks which eat the mealworm. **Behaviour,** 1966, **27,** 273-289.

Kuo, Z. Y. **The dynamics of behavior development.** New York: Random House, 1967.

Leon, M. Maternal pheromone. **Physiology & Behavior,** 1974, **13,** 441-453.

Mainardi, D. Biological basis of cultural evolution. **Atti Academia Nazionale dei Lincei,** 1973, **182,** 177-188.

Mitchell, D. Experiments on neophobia in wild and laboratory rats: A re-evaluation. **Journal of Comparative and Physiological Psychology,** 1976, **90,** 190-197.

Rozin, P. Specific aversions and neophobia resulting from vitamin deficiency or poisoning in half-wild and domestic rats. **Journal of Comparative and Physiological Psychology,** 1968, **66,** 82-88.

Steiniger, von F. Beitrage zur Soziologie und sonstigen Biologie der Wanderratte. **Zeitschrift Fur Tierpsychologie,** 1950, **7,** 356-379.

Warren, R. P., & Pfaffman, C. Early experience and taste aversion. **Journal of Comparative and Physiological Psychology,** 1959, **52,** 263-266.

Williams, G. C. **Adaptation and natural selection: A critique of some current evolutionary thought.** Princeton: Princeton University Press, 1966.

Young, P. T. The role of affective processes in learning and motivation. **Psychological Review,** 1959, **66,** 104-125.

Young, P. T. Hedonic organization and regulation of behavior. **Psychological Review,** 1966, **73,** 59-86.

Young, P. T. Evaluation and preference in behavioral development. **Psychological Review,** 1968, **75,** 222-241.