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SOCIAL FACTORS IN THE POISON AVOIDANCE AND FEEDING BEHAVIOR OF WILD AND DOMESTICATED RAT PUPS[1]

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When a colony of adult wild rats learned to avoid one of two palatable diets as a result of that diet's previous association with poison, rat pups born to colony members did not eat any of the diet the adults were avoiding and continued to avoid that diet following their removal to a new enclosure isolated from the adults. This finding is interpreted as resulting from a three-stage process in which the pups first follow the adults to food, then learn cues associated with that food, and thereafter avoid alternative diets as a result of their neophobia. The phenomenon is discussed as an adaptation facilitating food location by weanling rats rather than as a primary poison-avoidance mechanism.

Attempts by men to eradicate colonies of wild rats (*Rattus norvegicus*) through the use of poisons are believed to represent a major selective pressure on the rat (Barnett, 1963), especially since commensality with man has greatly reduced the number of natural predators (weasels, owls, ferrets, etc.) which have access to wild rat populations. Research conducted in both laboratory and field has provided an understanding of a number of behavioral mechanisms which have enabled wild rats to adapt to an environment in which they are faced with repeated threats to survival in the form of introduced poison baits.

Most important of the response tendencies resulting in poison avoidance by wild rats is their "neophobic" response (Barnett, 1958) or "new object reaction" (Shorten, 1954). This neophobia, which has been described as a tendency to avoid any new food or other novel object introduced into a familiar environment and to show extreme hesitancy in approaching such an object or ingesting such a food (Galef, 1970), leads rats to feed on familiar and, therefore, probably safe diets and avoid novel and, therefore, potentially noxious ones. A second and closely related behavior pattern of wild rats (Rozin, 1969) is their tendency to take small samples of new foods rather than make large meals of them (Rzóska, 1953), thus reducing their initial intake of potentially toxic substances. As a further refinement of their response to novel foods, wild rats tend to increase their neophobia following ingestion of sublethal doses of poison (Richter, 1953; Rozin, 1968), thereby increasing their caution in an environment in which toxic foods have been experienced.

The second major category of behavioral response which would appear to be of use to wild rats in avoiding repeated ingestions of noxious substances is their tendency to associate aversive gastrointestinal states with recent gustatory and olfactory stimuli (Garcia & Koelling, 1967), particularly novel ones (Revusky & Bedarf, 1967), and to tend to avoid ingesting substances providing similar cues (Rzóska, 1953) once an aversive gastrointestinal state has been experienced.

Thus, the adult wild rat has available a

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variety of behavioral responses which tend to reduce the probability of its ingesting lethal amounts of toxic agents introduced into an environment with which it is familiar. These responses markedly lower the rat's probability of eating new, potentially poisoned foods, minimize its initial intake of such substances, increase its caution in hazardous environments, and result in the avoidance of repeated intakes should aversive interoceptive consequences follow initial ingestion.

Two general observations concerning the behavioral mechanisms briefly described above are relevant to the investigations to be reported here. First, all the known poison-avoidance mechanisms of the wild rat depend on the response repertories of individual animals. Each individual rat must ascertain for itself the novelty and probable safety of any new food source and thereafter behave appropriately with respect to it. Second, all of the behavior patterns described above, believed to result in poison avoidance, depend to a greater or lesser extent on the recognition of an introduced food as novel. It is only to novel objects that neophobic responses are shown and novel foods are more readily associated with aversive gastrointestinal states than familiar ones.

With regard to the first of these two observations it is important to note that wild rats are highly social animals, living and defending territories in groups, sharing burrow systems, and communally nursing their young (Barnett, 1963; Calhoun, 1962). It is at least possible that the same selection pressures which have produced individual adaptations leading to successful poison avoidance have also produced group behaviors which could act to facilitate poison avoidance by individual group members. The second observation suggests that such facilitatory group mechanisms would be especially helpful to recently weaned pups. Rat pups emerge from the nest site into a totally unknown environment without any information as to the familiarity or novelty and, therefore, potential danger of any object or food in it. Clearly, it would be to the advantage of the pups, and therefore to the reproductive advantage of their parents, if the pups could be informed by their parents as to the safety of foods to be found in the environment.

The series of studies described below demonstrates the existence of socially mediated poison-avoidance behaviors resulting from the interaction between rat pups and their adult conspecifics and examines the mechanisms by which feeding preferences are transmitted between and within generations of wild *Rattus norvegicus*.

EXPERIMENT 1

The first experiment demonstrates the presence of parent-offspring influences determining the initial diet selection of weanling rat pups.

Method

A colony of two male and four female sexually mature wild Norway rats captured on a farm in Maine was established in a $3 \times 6 \times 1$ ft. enclosure constructed of slotted angle iron and hardware cloth. The sheet-metal floor of the enclosure was kept covered with food shavings and four wooden nest boxes were provided. The adults were maintained on a 3-hr. light and feeding schedule, the light-on period coinciding with food availability. Water was available ad lib (see Figure 1a). Following each feeding period, all spilled food was removed from the vicinity of each food bowl and the cage and nest boxes were checked for hoarded food. Any food caches were removed.

Food was presented to the colony in two ceramic food bowls (5¾ in. diam., 2½ in. deep) placed approximately 2½ ft. apart. Each of the food 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, the Turtox diet being highly preferred by the rats to the Purina.) Crystalline lithium chloride, a nonlethal toxic agent in the concentrations used, was added (4% by weight) to Diet A. The adult colony members rapidly learned to avoid feeding on Diet A and continued to avoid it even when offered new Diet A free from contamination with lithium chloride. Thus, a colony of wild rats was established having available 3 hr/day two unpoisoned, palatable, and nutritionally adequate diets, one of which was avoided as a result of its previous association with poison. Because the adults tended to spill small amounts of food around the bowl containing the diet on which they were feeding and thereby facilitated access to this diet, the experimenter spilled 3–5 gm. of the alternative diet around the other food bowl at the start of each feeding session to equate diet accessibility.

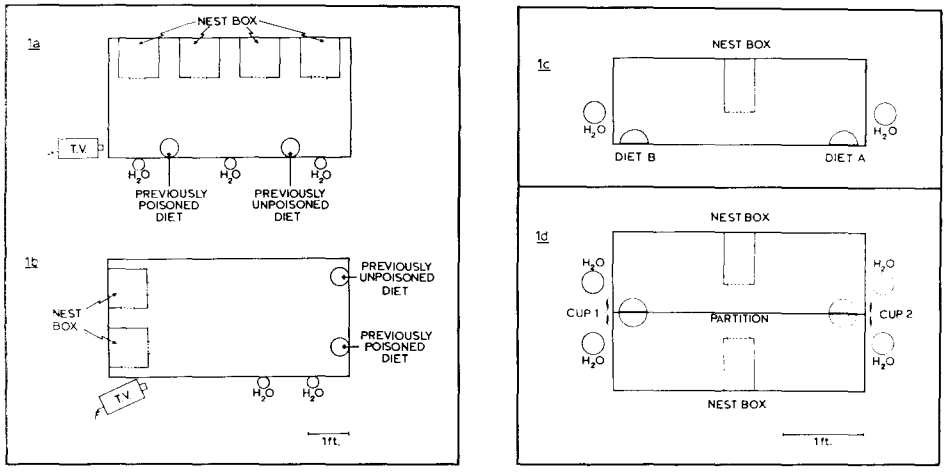

FIG. 1. Enclosures in which wild rat pups were observed prior to (a) and after (b) removal from their adult clan in Experiment 1. ([c] Enclosure to which individual pups were removed following 10 days of feeding with adults in Experiment 2 and [d] to which pairs of pups were removed following 10 days of feeding with adults in Experiment 10.)

This spillage was, of course, removed at the end of each feeding period.

The experiment proper began when a litter of six pups born to the colony began to eat solid food. 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.

Fourteen days following the first instance of feeding on solid food, the pups were transferred to a new enclosure (see Figure 1b). The pups were offered, on the original 3-hr. feeding schedule, new samples in new bowls of the unpoisoned Diets A and B which they had had available in their original enclosure. Observation of the feeding behavior of the pups was continued and, in addition, the amount of each diet eaten by the pups during each feeding period was recorded for the 3 wk. following transfer.

In order to control for effects of food preference, the adult colony was then poisoned on Diet B and taught to eat Diet A (Procedure 1b) and the entire experiment repeated on the next litter born to the colony (this litter was reduced to six pups at 10 days of age). These pups could only be left 10 days in the enclosure with their parents following their initial observed feeding because one of the female adult members of the colony began to exhibit considerable aggression toward the pups, and there was reason to fear for their survival if they remained with the adults.

Results and Discussion

Figure 2a and 2b shows both the number of approaches made by the pups to within 4 in. of the food bowls containing Diets A and B and the number of times the pups were observed feeding at each bowl during the days they spent with the parent colony. Comparison of the two figures demonstrates very clearly the effects of differences in the feeding behavior of the adults on the food preferences of the young. Both groups of young fed exclusively on the diet their parents were eating and both approached the alternative feeding site only rarely.

Figure 3 gives similar data for five other litters (31 pups) treated identically to Procedure 1b, born to colonies trained to feed on the nonpreferred Diet A. These pups were not observed to eat a single bite of Diet B during the 10 days they remained with the adults, while feeding thousands of times on Diet A.

Figure 4 indicates the amount of Diet A as a percentage of the total amount eaten by the first two litters of pups on the days following their removal to a new enclosure isolated from the adults. The data indicate that the dietary preferences learned in the presence of the adults had continued effects for 8–9 days following the pups' removal from the adults.

The results of this first experiment demonstrate that adult wild rats can, in some fashion, lead their offspring to feed solely on a safe diet in an environment containing food known to the adults to have been poi-

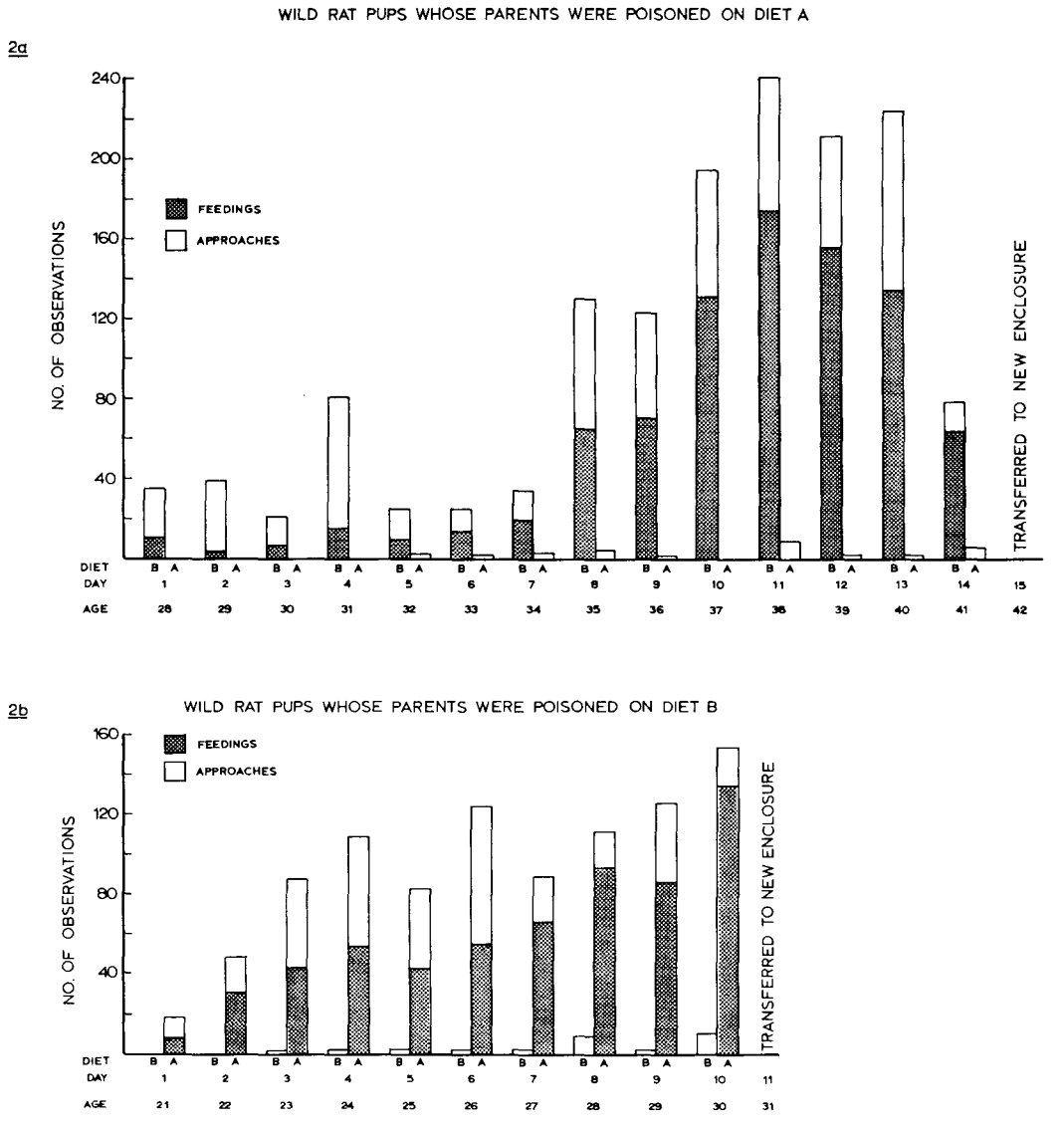

FIG. 2. Number of observed approaches to and feedings from Diets A and B by wild rat pups whose parents had been poisoned on Diets A(a) and B(b).

soned, thereby enhancing the avoidance of potentially noxious foods by the young. The data also show that the food preference learned in the presence of the adults continues to affect the feeding behavior of the pups for some time following their removal from intergenerational influences.

The present experiment does not indicate whether the young rats learned to eat what their parents were eating or to avoid what their parents were avoiding, nor does it demonstrate the way in which the behavior of the young was influenced by that of the adult generation. Experiment 2 deals with the first of these questions.

EXPERIMENT 2

It was demonstrated in Experiment 1 that wild rat pups feed exclusively on a diet which adult members of their parent colony

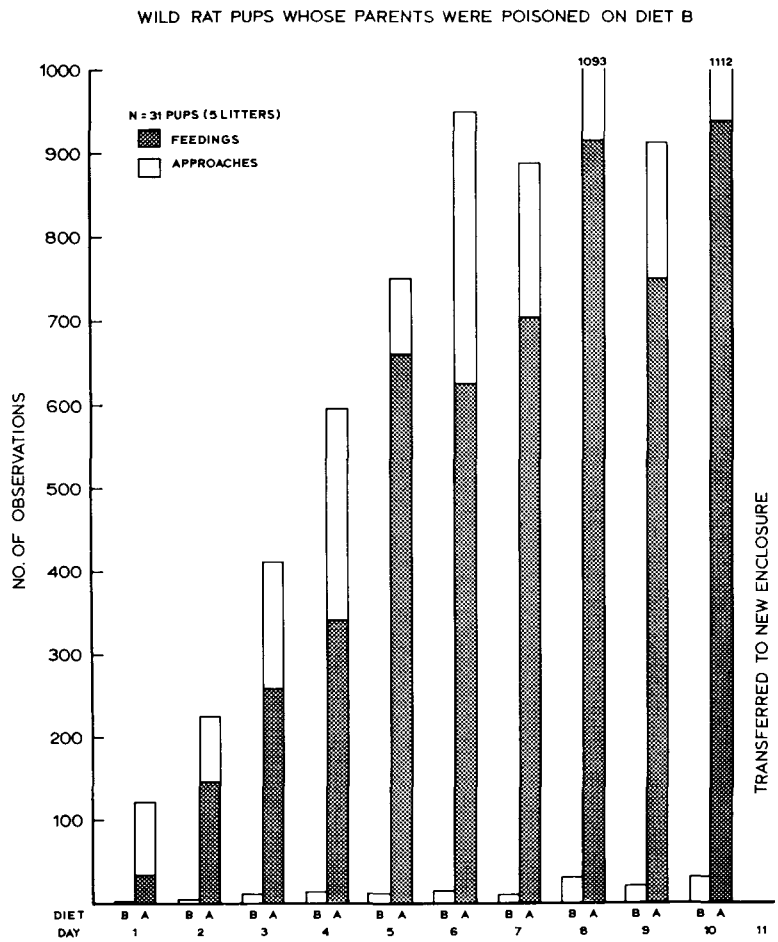

FIG. 3. Number of observed approaches to and feedings from Diets A and B by wild rat pups whose parents had been poisoned on Diet B.

are eating, and avoid an alternative diet which these adults are avoiding. It was also demonstrated that the pups continue to avoid the diet which their parents were avoiding for some time following transfer to a new enclosure in which no adults were present. The present experiment was designed to determine whether, for example, the pups in Experiment 1 (Procedure 1b) that ate Diet A exclusively had learned only to eat Diet A or had also learned to avoid Diet B. The basic supposition of the present experiment is that if the pups in Experiment 1 (Procedure 1b) had learned to avoid Diet B, they would take longer to begin feeding on Diet B (the preferred diet) following their transfer from the adult enclosure than other pups that had also fed exclusively on Diet A while with the adults but which had had no experience of Diet B.

Method

The procedure of Experiment 2 was essentially the same as that in Experiment 1 (Procedure 1b). Four adult colonies of first-generation laboratory-bred wild rats were trained to eat Diet A from a food bowl. Half the colonies were trained to avoid Diet B as in Experiment 1. The other two colonies were presented with an empty food bowl in place of Diet B during each feeding period. The colonies were observed during feeding periods via closed-circuit television and the pups were removed to new enclosures following 10 days of feeding on solid food. In the present experiment each pup

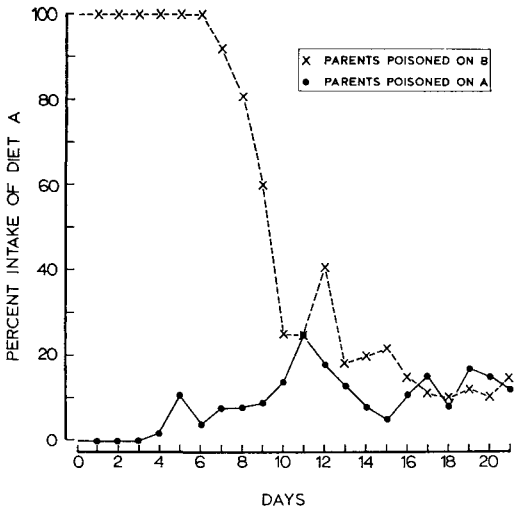

FIG. 4. Percentage of intake of Diet A by pups following removal to a new enclosure isolated from adults.

was moved to an individual enclosure (see Figure 1c) in which unpoisoned samples of Diets A and B were available and placed on a 9 hr/day feeding and light cycle. The experimenter weighed all food cups at the end of each feeding period.

Results and Discussion

Observation of the four litters in the experiment during the 10 days they spent with their respective parent clans revealed no instances of feeding on Diet B on the part of the pups in the group having Diet B available.

The main results of Experiment 2 are presented in Figure 5 which indicates the mean amount of Diet A as a percentage of total intake of the two groups in the experiment during their first 9 days in individual enclosures. Unfortunately, limitations in available space did not permit the continuation of the experiment with all subjects until such time as the last subject had reached a stable base line of Diet B intake. However, all subjects were left in the testing apparatus for at least 4 days after they began eating Diet B. Examination of Figure 5 reveals no appreciable difference between the two groups in their rate of transfer to feeding on Diet B.

The mean day-to-first ingestion of Diet B was 11.3 days ($\sigma_{\bar{x}} = 4.0$) for the Diet A empty-bowl group, and 11.9 days ($\sigma_{\bar{x}} = 4.8$) or the Diet A–Diet B group. The median delay to first ingestion of Diet B was 7 days for both groups.

The results of the present experiment strongly suggest that the presence of Diet B in an enclosure during the time the pups are feeding with the adults has no important effect on their observed feeding preference. The interpretation of the phenomenon most consistent with the data described in this experiment is that the pups are learning to eat what the adults of their colony are eating but not to avoid what the adults are avoiding. This result is not at all surprising in view of the extremely limited experience of the pups in the Diet A–Diet B group with the previously poisoned diet.

EXPERIMENT 3

The second major question left unanswered by Experiments 1 and 2 concerns the way in which adult colony members induce the pups to feed on the nonpoisoned diet. Several possible explanations suggest themselves. First, it is possible that the adults are introducing samples of the diet they are eating into the nest box, either purposely as hoardage or accidentally as particles clinging to their fur and vibrissae. The young could eat this introduced material, become

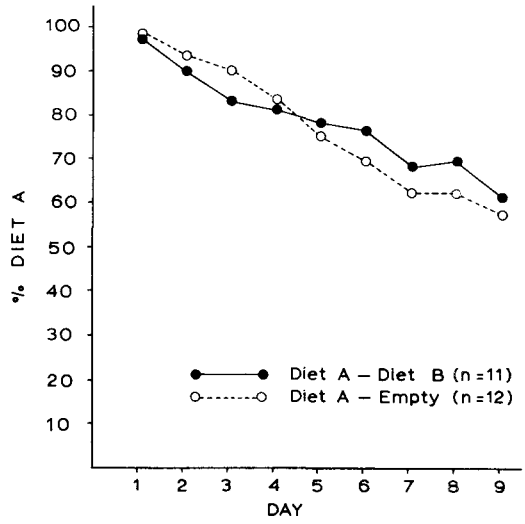

FIG. 5. Amount of Diet A as a percentage of total intake of pups following their transfer to individual enclosures.

familiar with it, and then seek similar substances in the larger environment. However, if the pups were in fact matching to sample, one would expect to see equal numbers of approaches to the previously poisoned and unpoisoned diets during the first few instances of feeding, gradually reducing in number as the pups became more familiar with the location of the diet they were seeking to match. Inspection of Figures 2 and 3 reveals that this is the opposite of the observed result. Thus, the matching-to-sample explanation is not adequate to explain the observed behavior of the rat pups.

Second, it is possible that the adult organisms have marked the previously poisoned bowl with some warning pheromone which serves to dissuade the young from approaching or eating at it. Von Steiniger (1950) has reported that adult wild rats urinate and defecate on poisoned foods and thereby dissuade their fellow adult colony members from feeding at that food source. In the experiments reported above, both continuous observation of the once poisoned food bowl and careful weighings revealed no urination or defecation in the bowl and no observable scent marking behavior on the part of the adults. The present experiment was designed to ascertain the possible role of pheromones in leading pups to approach or avoid the appropriate diets.

Method

The procedure was essentially the same as that in Experiment 1, Procedure 1b, and involved two litters of six pups each. Once again the adults were trained to eat Diet A and avoid the preferred Diet B. The food bowls containing the two diets were, in the present experiment, placed in their usual positions on top of two sheet-metal trays 18 × 24 × 1 in. covered with sawdust. After the pups were observed to have fed 20 times on Diet A on the first day of feeding, the positions of the trays and food bowls were reversed and new samples of Diets A and B placed in their original positions in the cage. Thus, the positions of the trays and shavings surrounding the two food bowls and the food bowls themselves were reversed, while the position of the new samples of the two diets remained constant.

Results and Discussion

The results are presented in Table 1 which shows the number of approaches to the bowls containing Diets A and B by the 12 pups prior to and following the change in position of the trays and bowls. It is quite clear that the pups are not following pheromone trails to the foods; if they were, the position reversals should have resulted in approaches to Diet B. This deduction is particularly compelling in view of the fact that six of the observed feedings by the pups on Diet A following reversal were made prior to any adults approaching that bowl (further interpretation of these six approaches is to be found in Experiment 6). The use of pheromones by the pups is not a necessary condition for the occurrence of the observed phenomenon.

TABLE 1

NUMBER OF OBSERVED APPROACHES AND FEEDINGS ON DIETS A AND B PRIOR TO AND FOLLOWING A REVERSAL OF THE SUBSTRATE OF THE TWO FOOD BOWLS

Reversal	Approach		Feeding	
	Diet A	Diet B	Diet A	Diet B
Prior				
Litter 1	25	0	20	0
Litter 2	36	1	20	0
Postreversal				
Litter 1	82	0	68	0
Litter 2	120	2	86	0

EXPERIMENT 4

Given that neither matching to sample nor the use of scent trails or warning pheromones is an adequate explanation of the fact that the pups eat only what their parents are eating, the question remains as to the cause of the observed feeding preference. If one observes the wild rat pups during their first few days of feeding on solid food, one thing becomes quite evident. The pups tend to follow the adults around the enclosure. Especially during the first few days of feeding on solid food, they tend to hide beneath the adults and move about under them. Their initial few bouts of feeding are often on food spilled by the adults as they eat. Calhoun (1962), observing wild rats in a seminatural 10,000-sq.-ft. enclosure, reported similar observations of what

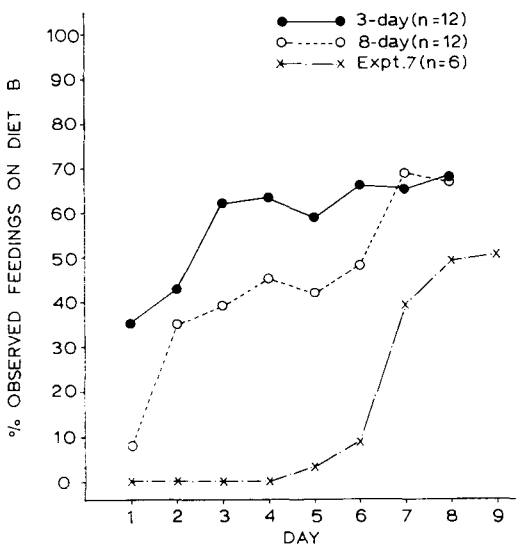

FIG. 6. Percentage of feeding responses directed toward Diet B by pups whose parents transferred feeding to Diet B.

he called close "trailing" of adults by pups. Barnett (1956), observing a female wild rat and her 21-day-old litter in a cage a little over a foot square, reported that the pups tended to orient toward the mother and that if the mother moved to food, the pups did also. The above observations suggest that adults are capable of leading the young to a location and perhaps thereby influencing their food preferences. The present experiment was designed to test the hypothesis that the pups follow the adults and feed on those diets with which the adults bring them in contact.

Method

The apparatus and method were similar to those used in Experiment 1, and the subjects were four litters of pups born to two adult first-generation laboratory-bred wild rat colonies. The adults in both colonies were first trained to eat both Diets A and B. They were then placed on a schedule in which on 2 out of every 3 days they were offered Diet A and an empty bowl during the 3-hr. feeding period. On the third day the empty bowl was replaced with a bowl containing the highly preferred Diet B. The colonies rapidly learned to switch their feeding to Diet B whenever it was made available. Once the pups in each litter reached 20 days of age the adult colonies were offered only Diet A, except as described below. Starting on the third day after the pups of the first two litters, and on the eighth day after the pups of the third and fourth litters began to eat solid food, the empty bowl in each colony was replaced with a bowl filled with Diet B.

Results

The results of Experiment 4 are presented in Figure 6 which indicates the percentage of observed feedings directed to Diet B by the pups on the day of introduction of Diet B and on succeeding days. It is clear from examination of Figure 6 that the pups begin feeding on Diet B when their parents transfer feeding to it, and that pups which have been feeding on Diet A for 8 days prior to the introduction of Diet B transfer feeding more slowly than those which have been feeding on Diet A for 3 days. Examination of the proportion of Diet B eaten by adults on the day of introduction of Diet B and subsequent days indicates that a difference in rate of transfer on the part of the adults was not responsible for the observed difference between the 8-day and 3-day groups. The rate of transfer of feeding site was roughly equivalent for the adults of all four litters.

Discussion

First, the results of the present experiment strongly support the hypothesis that the young actively follow the adults to food and that it is this following response which leads the pups to feed on the same diet which the adults are eating and to avoid alternative diets. When adult colony members shift their feeding site on the third day of pup feeding, the pups shift their feeding site immediately. The fact that the change in the feeding habits of the young is far slower when the adults shift their feeding site on the eighth day of pup feeding is also informative. It suggests that during the intervening 5 days a factor beyond simple following of adults is making itself felt in the food preferences of the pups. It would seem likely that during these 5 days the pups are increasing their familiarity with Diet A and, because of their general neophobia, thereby increasing their reluctance to approach alternative diets.

It is, however, possible that the difference between the 8-day and 3-day groups in rate

of transfer of feeding to Diet B could reflect a waning of the following response of the pups with increasing age. However, the results of Experiment 1 indicate that even if waning of following is partially responsible for the observed effect, the learning of cues associated with the diet fed upon also plays a major role.

In Experiment 1, once the pups were transferred to an enclosure separate from the adults, they continued to eat the food their parents had been eating and to avoid the available alternative. Clearly the pups have learned something about the food they have been introduced to by their parents and this, combined with their general neophobia, could lead to the observed continued avoidance of the preferred diet by the pups in isolation. An experiment by Church (1957) demonstrating that adult albino rats, when trained to follow a leader rat through a T maze, learned an incidental cue introduced midway through the experiment and were thus able to continue to perform correctly when the leader rat was removed offers support for the preceding interpretation. However, it remains to be demonstrated that neophobia actually plays a role in maintaining the pups' avoidance of the diet on which the adults of their colony were poisoned. The results of Experiment 2 indicated that the pups are actually only learning to eat the diet on which they and their parent colony are feeding. However, the pups avoid the previously poisoned diet. Experiment 5 explores the possible role of neophobia in maintaining this avoidance.

Experiment 5

As mentioned in the introduction, wild rats are highly neophobic animals (Barnett, 1958; Galef, 1970), tending to avoid any novel foods or objects in an environment with which they are familiar. The domesticated hooded conspecifics of the wild rat are, in contrast, only slightly neophobic (Barnett, 1958; Revusky & Bedarf, 1967; Rozin, 1968). If the observed feeding preferences of the wild pups are a result of three processes (first, an initial tendency to follow the adults, leading to ingestion of food the parents are eating; second, a learning of cues associated with that food; and third, a tendency to avoid other foods because they are novel, following learned familiarity with the initial diet), then the relatively "nonneophobic" domesticated pups should be expected to show initial following of the adults followed by a breakdown in feeding discrimination on the part of the domesticated young at the time when neophobia becomes responsible for the continued avoidance behavior of the wild pups. This prediction, of course, depends on the assumption that the following response of rat pups has remained intact through the process of domestication. Both the results of the present experiment and data to be reported separately (Galef, 1971) support this assumption.

Method

The subjects were five litters of pups (reduced to six pups per litter at 10 days of age) born to a colony of one male and five female hooded rats obtained from the Quebec Breeding Farm. The procedure was identical to that described in Experiment 1, Procedure 1b, except that it proved necessary to inject 6 cc of .12 M lithium chloride intraperitoneally into two of the adults following their observed ingestion of Diet B in order to maintain their continued avoidance of Diet B over periods of several weeks.

Results and Discussion

Figure 7a and 7b presents both the number of approaches made by two litters of domestic pups to within 4 in. of the food bowls containing Diets A and B and the number of times the pups were observed feeding at each bowl. The data from the other three litters were essentially identical and are not presented.

Comparison of these figures with Figures 2b and 3 reveals the considerable difference in behavior between the wild and domesticated rat pups in the experimental situation. These differences are in accord with the hypothesized mechanism underlying the phenomenon under discussion outlined in the introduction to the present experiment. Whereas none of the wild litters ever ate a single bite of the preferred diet which their parents were avoiding, all five litters of hooded pups began, after an initial period of avoiding Diet B, to feed on Diet B on

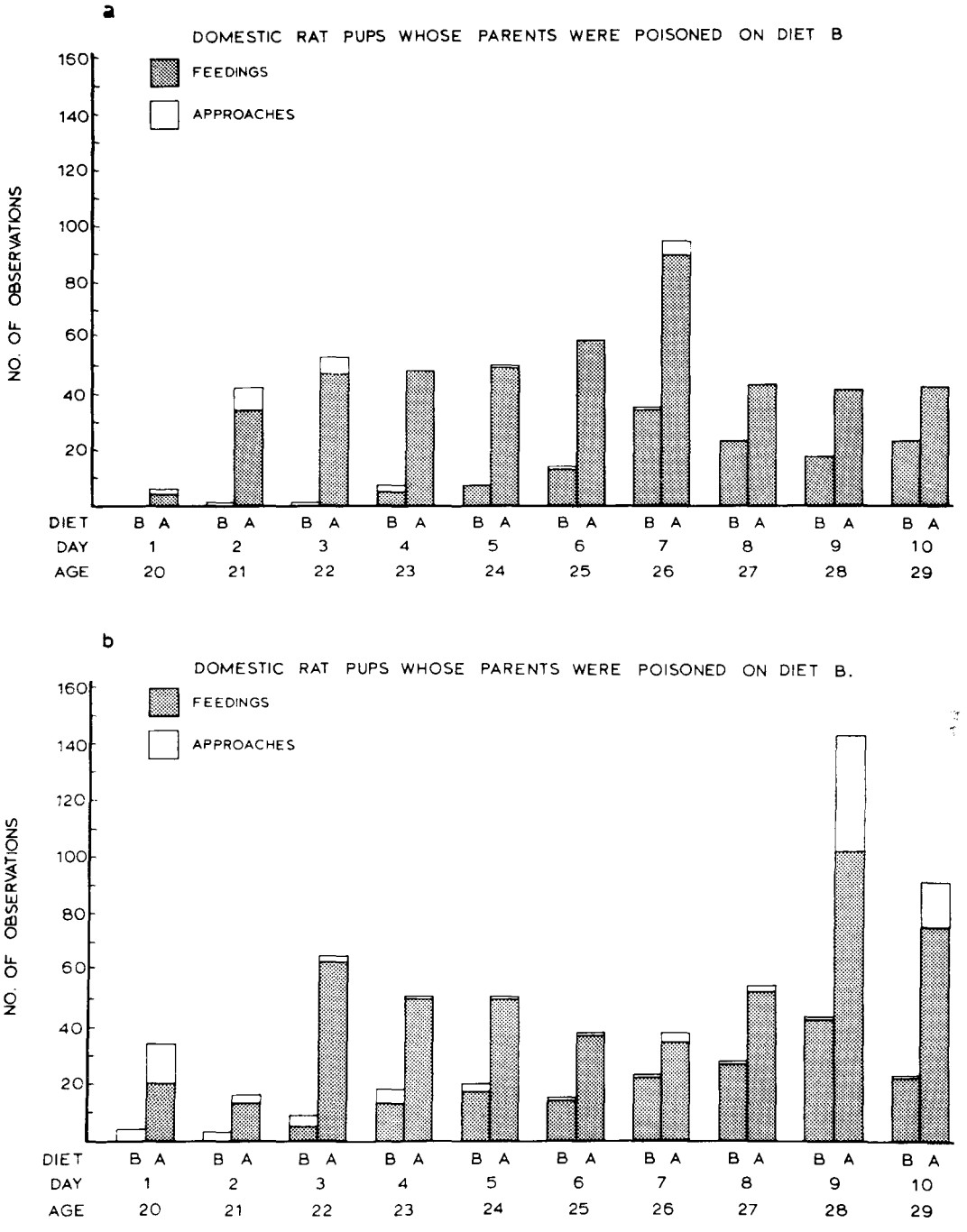

FIG. 7. Number of observed approaches to and feedings upon Diets A and B by domestic rat pups whose parents had been poisoned on Diet B.

either the third or fourth days of feeding on solid food. It would thus appear probable that the continued avoidance of the once poisoned diet by wild rat pups is the result of their neophobic response following learning of cues associated with the original diet. This interpretation is further supported by comparison of the rate of transfer of feed-

ing from Diet A to Diet B in the two groups in Experiment 4. The increased latency of transfer by the 8-day group as compared with the 3-day group suggests the learning of cues associated with the diet being eaten and a subsequent hesitancy to begin eating a new diet as a result of neophobia.

Two additional observations concerning the animals in the present experiment are of importance. First, it is clear that although the pups begin feeding on Diet B, they do not fully transfer their feeding to this diet. It is possible that this failure to eat more Diet B is due to a difference in taste preferences between wild and domesticated rats. However, when the pups in the present experiment were transferred to individual enclosures (see Figure 1c) following their 10 days with the adults and offered a choice of unpoisoned Diets A and B, their intake of Diet B was 63% of their total intake on the day following transfer and rose to 82% the next day. Diet B is clearly the preferred diet. The explanation for the pups' failure to feed more often on Diet B in the enclosure with the adults is probably to be found in the fact that, although the pups partially transferred their feeding to Diet B, the adults continued to feed exclusively on Diet A. It thus seems probable that the continued preference for Diet A on the part of the pups resulted from their demonstrated tendency to feed at the same location as the adults of their clan.

Experiment 6

The results of Experiment 4 demonstrated that wild rat pups will transfer their feeding from one food to another in response to a change in the feeding pattern of the adults of their colony. However, it is clear that the pups show some hesitancy in doing so. As discussed above, this hesitancy in transferring feeding from one diet to another is probably attributable in large measure to the learning by the pups of cues directly associated with the diet on which their parents are feeding, and to their inherent neophobia. In addition, observation of the pups in earlier experiments suggested that simple learning of a location in which food is to be found also plays a role in the diet selection of the pups. In Experiment 3, for example, following the change in position of sawdust, trays, and food bowls, six of the approaches and observed feedings by the pups at the bowl containing Diet A were made before any adults had approached that diet. The use of pheromone trails or of direct following of the adults is not a possible explanation of these observations. However, it is possible that the pups had learned the location of their usual food and were simply returning to that location in the absence of other cues. The present experiment was designed to ascertain the role of the learning of feeding-place location in the learned food preference of the pups.

Method

The method was identical to that of Experiment 1, Procedure 1b, except that with each of the two litters used, the location of the two food bowls was reversed. For one litter the position reversal was carried out on their fifth day of feeding on solid food (5-day group) and for the other on the tenth day of feeding (10-day group).

Results and Discussion

The results of the present experiment support the hypothesis that the pups learn the location of the diet on which they are feeding. In both litters the adults emerged from the nest boxes following the reversal and began feeding on Diet A before any pups emerged from the nest site. Two of the six pups in the 5-day group and one of the six in the 10-day group went directly to the food bowl containing Diet A at which the adults were eating. The other nine pups all went first to the bowl containing Diet B, sniffed at the bowl and/or its contents for from 3 to 24 sec., and then proceeded to the bowl containing Diet A where they fed. Following their initial exploratory approaches to the bowl containing Diet B one pup in the 5-day group and two in the 10-day group returned to sniff once at the bowl containing Diet B.

These data indicate that the pups do learn the position in which food is to be found and will respond to position cues alone. However, the effect is a relatively small one. The pups will not eat a novel food at the familiar feeding location and will readily transfer their feeding to a new

site at which the familiar food is to be found and adults are feeding.

EXPERIMENT 7

The results of Experiment 5 have indicated the existence of a mechanism by which adult wild rats can transmit learned food preference to weanling members of their clan. The present experiment was designed to ascertain the precision with which such information is transferred. In all the preceding experiments the two food bowls were 2½ ft. apart. It is unlikely that in nature various food items are so carefully spaced out that a behavioral mechanism allowing only such broad discrimination would be of any use, and it should be possible to demonstrate the ability of the observed mechanism to lead to much finer discriminations.

Method

The method was identical to that in Experiment 1, Procedure 1b, except that the two food bowls containing Diets A and B were only 2 in. apart. Subjects were a single litter of six pups.

Results and Discussion

The results of Experiment 7 are presented in Figure 8. The data indicate that the pups initially avoided Diet B and then very gradually transferred their feeding to that diet. Additional data recorded by the experimenter indicated that the shift to Diet B by the young did not cause the adults to begin eating Diet B. During the 10 days while the pups were in the adult enclosure only one adult switched its feeding to Diet B and it ate only a few bites.

At first glance, the contention that the pups could be induced to feed differentially on two food sources only 2 in. apart as a result of simple following of the adults would appear to be unrealistic. However, observation of the behavior of the pups strongly supports such an interpretation. When the pups moved from the nest box to the adults during the first 3 or 4 days of feeding on solid food they showed a singular approach pattern to the adults. The pups would in all but a few instances run beneath an adult immediately anterior to the adult's rear legs and move from there to the head of the adult, emerging right at the food bowl. Pups showing such behavior could clearly be directed to a very precise location indeed.

Comparison between the rate of transfer from Diet A to B of the pups in the present experiment with those in the 3-day group of Experiment 4 (Figure 6) indicates the hesitancy the pups show in eating a diet which the parents are avoiding and their readiness to feed on any diet the adults are eating.

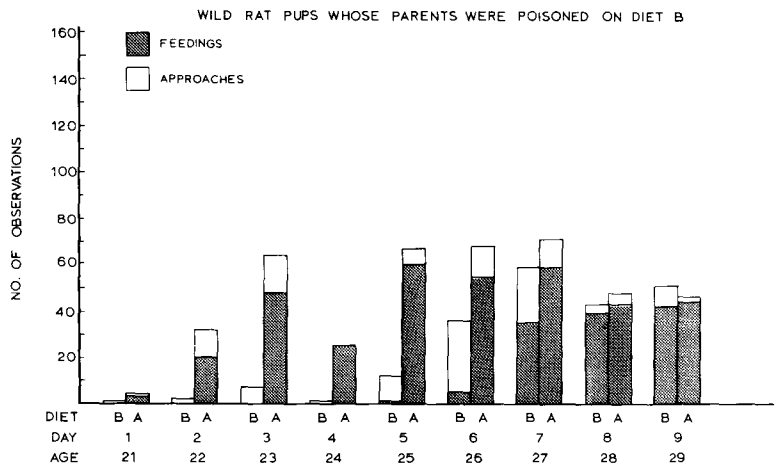

FIG. 8. Number of observed approaches to and feedings upon Diets A and B by wild rat pups when the two diets were placed 2 in. apart.

Experiment 8

The previous experiments provide strong evidence that the pups follow the adults to food. The present experiment was designed to determine if the pups followed a particular adult, their mother for example, or if the adults were equipotential in their ability to elicit following.

Method

The method was identical to that used in Experiment 1, Procedure 1b, except that the adult colony was reduced to three individuals (the mother of the pups, and one additional male and female) each marked by shaving so as to be individually identifiable. The experimenters, in addition to recording the usual data, kept track of the location of all adults throughout the feeding period. The subjects were a single litter of six pups.

Results and Discussion

A ratio was computed by dividing the number of approaches made by the pups to a food bowl when a particular adult or combination of adults was present at that bowl by the number of minutes that an adult or combination of adults was present at that food bowl during the feeding period. This ratio provides a measure of the probability of the pups approaching the bowl when any adult or combination of adults was present at the bowl. In order for this experiment to have been entirely successful it was necessary that each adult cooperate by appearing fairly frequently at the food bowl, both alone and in combination with the other adults, so that observations could be made under appropriate conditions for the computation of the ratios described above. This type of cooperation was particularly important during the first 3 or 4 days when the pups were feeding on solid food, as it is during this period that following behavior is believed to be especially important (see Experiment 5) in determining the food preference of the young. Unfortunately, the adults did not distribute their feeding times in such a way as to allow precise comparison of the pups' tendency to follow individual adults. Two generalizations, however, appear to be supported by the data. First, there was no pronounced tendency for the young to follow one adult rather than another; all adults elicited movement to the food cup during the first day of feeding, the male (2.1 approaches/min) more than either female, and the other female (1.6 approaches/min) more than the mother (.7 approaches/min). Second, the greater the number of adults at the food bowl, the greater the number of approaches by the young. For the most part during the 10 days when the pups were with the adults, three adults present at the food bowl elicited a higher frequency of approaches to the bowl (3.0 approaches/min) than two, and two adults (1.3 approaches/min) a higher frequency of approaches than any single adult (.8 approaches/min). In summary, there was no indication of a marked preference by the pups to follow one adult rather than another.

Experiment 9

In all the preceding experiments the assumption has been made that the pups behave relatively independently of one another. Barnett (1956) has stated that although "there is some orientation of one juvenile on another . . . specific acts such as feeding and feeding from a particular food are carried out independently [p. 35]." However, because the method employed in the present experiment seems particularly suited to disclosing social interactions with regard to feeding, it was decided to reinvestigate Barnett's observation.

Method

The method was identical to that employed in Experiment 1, Procedure 1b, except that following the transfer of the litter of pups to the new enclosure, in isolation from adults, the experimenter recorded the number of pups present at each food bowl when any pup ate from it. The subjects were three litters of six pups.

Results and Discussion

The results are presented in Figure 9a, 9b, and 9c. Unfortunately, we had not devised a method for marking individual pups in such a way as to distinguish them on television at the time this experiment was carried out so the data simply represent the number of pups simultaneously present at the bowl containing Diet B in the minutes following

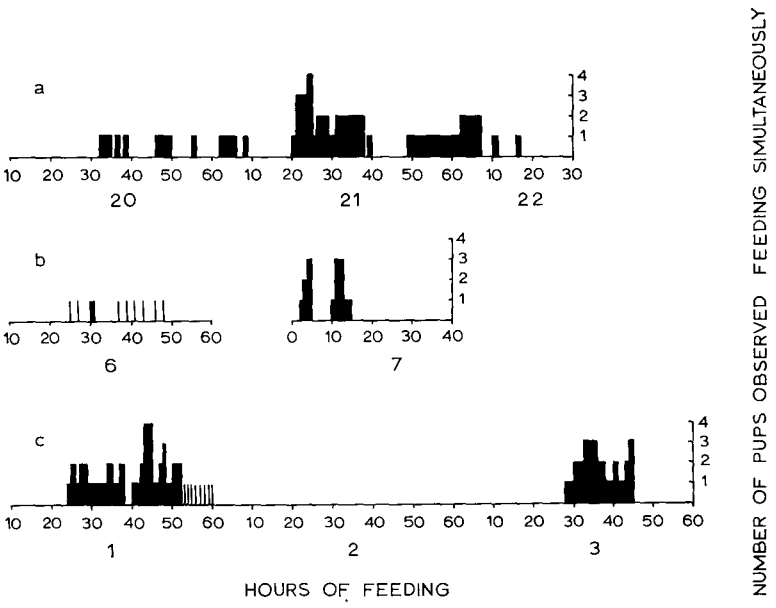

FIG. 9. Number of pups observed feeding simultaneously on Diet B.

the first observed intake of Diet B by any pup. It is clear that the presence of a pup at Food Bowl B has a strong recruiting effect on other pups. Figure 9a, for example, presents data from a litter none of whose members began eating Diet B for 20 hr. (six feeding periods) following their removal to the new enclosure, yet within 60 min. of the first pup's beginning to feed on Diet B, four pups were observed simultaneously feeding on that diet. The recruiting effect is clear.

Figure 10 presents a comparison of the percentage intake of Diet A for these three litters and two litters of pups reared under identical conditions and then transferred to individual new enclosures (the latter group are the Diet A–Diet B groups of Experiment 2). Although spatial arrangements and length of feeding periods are not identical for the two groups, comparison of the rate of transfer from feeding on Diet A to Diet B provides an indication of the size of the social effect among pups on feeding.

EXPERIMENT 10

The interpretation of the mechanism underlying the strong tendency of the pups to eat only what the adults eat offered in the introduction to Experiment 5 states that an active following response on the part of the pups directed toward the adults is responsible for the initial feeding preference shown by the pups. Such an interpretation implies the importance of visual, auditory, olfactory, or tactile cues in the observed social interaction. Practical difficulties have precluded the examination of the role of these cues in the interaction between adults and pups but the existence of analogous interaction among the pups allows the ready investigation of the cues important in the observed behavior. In the present experiment the effects of visual interaction on feeding-site preference of the pups were assessed, the hypothesis being that if visual cues are important in feeding-site selection then pups which can see each other should tend to feed at the same site more frequently than pups which cannot see one another.

Method

The method was identical to that used in Experiment 1, Procedure 1b, except that the pups were transferred to the enclosures shown in Figure 1d following their 10 days of feeding with the adult colony, and Diet A was presented in all food bowls following transfer. For half the subjects (three litters of six wild rat pups each) the partition shown in Figure 1d was opaque sheet metal and for the other half, clear Plexiglas. The pups

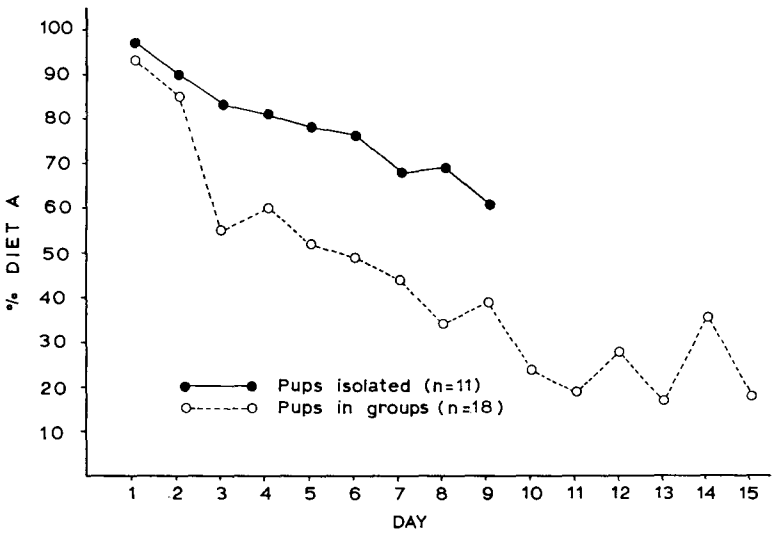

FIG. 10. Amount of Diet A as a percentage of total intake of pups following transfer to new enclosures either in groups or in isolation.

were left in the enclosures shown in Figure 1d for 8 days on a 3 hr/day feeding schedule and the experimenter weighed all food cups at the end of each feeding period. As can be seen from examination of Figure 1d, each pup had the option of eating Diet A either from a cup adjacent to, or at some distance from, its enclosure mate. For example, if the pup in one half of the enclosure was eating Diet A predominantly from Cup 1, the pup in the other half of the enclosure could eat Diet A from either the adjacent Cup 1 or the distant Cup 2.

Results and Discussion

A χ^2 analysis of the number of times enclosure mates in the two groups took the majority of their food from adjacent and distant cups revealed that pups with an opaque partition between them did not differ significantly from a chance distribution of feeding-site selections ($\chi^2 = .84$, $df = 1$, $.5 > p > .3$). Comparison of the distribution of food-selection sites of pups with clear partitions with those of pups with opaque partitions yielded a χ^2 of 15.8 ($df = 1, p < .001$), resulting from the tendency of pups which could see one another to eat predominantly at adjacent cups.

The results of the present study indicate that visual cues play an important role in the interaction among pups and, by implication, in the interaction between adults and young colony members. The data showing that pups do not eat at adjacent locations when separated by an opaque barrier suggest that auditory cues are not sufficient to produce significant effects on feeding-site selection, while the data given by pups separated by a transparent partition demonstrate a sufficiency of visual cues to produce the observed effects. The present study gives no information on the role of olfactory or tactile cues in producing changes in feeding-site selection and it remains possible that olfactory and tactile information also plays an important role in the observations reported in the preceding experiments.

GENERAL DISCUSSION

Scott (1958) has stated that wild rat pups in the process of weaning "have to go out and find their own food once the nursing period is over [p. 117]." The results of the present experiments indicate that the adult members of a wild rat colony play a far more active role in the direction of their young to desirable sources of solid food than Scott's statement implies. The data reported here demonstrate that the initial intake of solid food by the pups is determined by the learned feeding habits of the adult members of their colony and support the interpretation that the observed intergenerational influence is the result of an active

following of adults by pups. The existence of such trailing (Calhoun, 1962) or "caravaning" (Ewer, 1968) has been observed in a variety of mammalian species: house mouse (Crowcroft, 1966), shrew (Crowcroft, 1957; Meester, 1960), meer cat (Ewer, 1968), as well as wild rat (Calhoun, 1962), and has been interpreted (Ewer, 1968) as a means of reducing the trauma to young animals in making the transition from the safety of the nest site to the more threatening outside environment. That the same behavioral mechanism could provide for the introduction of young animals to a food source is not unlikely. Unfortunately, the present series of experiments, although indicating the importance of the behavior of adults in directing the young to feed from a particular food source, gives only circumstantial evidence as to the nature of the interaction between the animals. A question remains as to the actual interactive effect. Is the observed feeding response the result of actual imitation of the parents by the young, or is unintentional leading of the young by the parents into an area in which food is located all that is involved? Clearly the answer must await a more direct investigation of the nature of social effects in weaning and of the weaning process itself. The results of experiments dealing with these questions will be reported separately (Galef, 1971).

A second deficiency in the present study concerns its relation to the behavior of wild rats in natural environments. The rats in the present study were confined in an unnaturally small enclosure, food sources were located, possibly, abnormally close to nesting sites, and all hoardage was removed following feeding periods, so that young had to emerge from the nest site once their mother ceased lactating or starve to death. There is little to be said concerning the first two points; clearly they result in a distortion of the natural situation and require that a portion of the present studies be repeated using a free-living colony as subjects if the importance of the phenomena described above in the adaption of wild rat populations to their natural environment is to be properly evaluated. However, it is to be noted that the time course of the behavior observed in the present experiments was very similar to those reported by Calhoun (1962) in a 10,000-sq.-ft. enclosure. In the present experiments the initial observed feeding of the pups occurred when they were between 21 and 28 days of age. Calhoun observed initial explorations on the surface at between 23 and 28 days of age in his seminatural enclosure. Thus, the observed feeding behavior coincides with the period of initial exploration of the environment by the pups in a far more natural setting.

Further, von Steiniger (1950), in discussing what he calls the "local traditions" of colonies of wild rats, i.e., the location-bound peculiarities of behavior of groups of rats living in various areas, observed that if a certain poison (zinc phosphide) is used in rat control in one area over an extended period of time, despite initial success, later acceptance of the poison falls off radically and remains low. Von Steiniger attributes this "traditional" poison avoidance to the behavior of "older members of the clan," commenting that not even the offspring of such animals accept the poison so long as a few animals are present in the same pack which know and reject the poison. These observations on natural colonies of wild rats are readily explicable in terms of the results of the present experiments and support the hypothesis that similar processes operate in natural settings.

Some interesting observations are also available concerning the possible effects of hoarding by adult rats in natural situations on the development of food preferences in the young. Von Steiniger (1950) has reported that rats use separate burrows for nesting sites and food supplies. Observation of our captive colonies similarly revealed that food caches were, almost without exception, located in nest boxes not being used as nesting sites. These observations imply that even under conditions where hoarding occurs the pups must leave the nest site in order to transfer feeding to solid food. Hence, even in the wild, where large food caches are created by the rats, it is probably necessary for the pups to travel to them, and it is thus possible that intergener-

ational influences play an important role in the initial food selection of the pups even when hoarding is present.

A more fundamental question raised by the present experiments concerns the nature of the adaptation being studied. Williams (1966) has discussed the importance, when describing adaptations, of distinguishing between the forces that initiated the development of an adaptation and the secondary functions that the adaptation may acquire once it is developed. In the present study the observed behavior may be either a primary adaptation resulting from selective pressures on pups to avoid poisons, or the poison avoidance may be a secondary function resulting from a primary tendency on the part of the pups to follow adults and eat in their vicinity, combined with neophobia. If the latter interpretation is correct, the observed behavior could be a primary adaptation to pressures resulting from the need for pups to find alternative sources of nutrition rapidly once lactation of the mother ceases. The data from the present series of experiments tend to support this latter interpretation. First, the results of Experiment 2 indicate that the pups are only learning to eat what the adults are eating and not acquiring any information concerning the poisoned food. Second, the results of Experiment 4 indicate that following the parents to food is the initial response of the young responsible for the observed diet selection. It therefore seems likely that the observed behavior is primarily the result of the need for the pups to locate food in the external environment once the nursing period is over which has been modified to serve as a poison-avoidance mechanism during the relatively brief period when poison avoidance has played a major role in the survival of wild rat populations.

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