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Differences in Affiliative Behavior of Weanling Rats Selecting Eating and Drinking Sites

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The presence of an adult rat at a feeding site profoundly influenced a conspecific weanling's probability of eating there. Presence of an adult rat at a drinking site did not have a comparable effect. This result is interpreted as indicating that the influence of adult presence at a feeding site on pup feeding site selection, reported in previous studies, is not simply an epiphenomenon reflecting a general affiliative tendency of rat pups. Rather, social affiliation appears to be a factor of special importance in the feeding site selection of young rats.

Weanling rats exhibit a marked preference for a diet that the adults of their colony have been trained to eat, even if that diet is the normally less palatable of available alternatives (Galef & Clark, 1971b).

One way in which juvenile rats can come to exhibit a pattern of food preference similar to that of the adults of their colony results from the tendency of pups, when seeking their first meals of solid food, to approach adult conspecifics at a distance from the nest site, (Galef, 1971; Galef & Clark, 1971a, 1971b). The young initiate ingestion in the immediate vicinity of an adult rather than at alternative feeding sites and, as a result, ingest the same food that the adults of their colony are eating (Galef, 1977a; Galef & Clark, 1971b).

There are two contradictory interpretations of the tendency of rat pups to approach conspecific adults when selecting a feeding site. First, it is possible that young rats are motivated to spend much of their time in the vicinity of adults of their species and it is purely fortuitous that this affiliation leads juveniles to food. Alternatively, it is possible that when young rats are seeking food, they orient to adults more consistently than when they are engaged in other activities. If the first interpretation should prove to be correct, then the fact that pups feed in the presence of adults would be an epiphenomenon simply reflecting general affiliative behavior on the part of young rats. Conversely, if young rats should exhibit enhanced affiliation with adults when seeking food, then the tendency of pups to feed in the vicinity of adults of their species would be more adequately viewed as an aspect of feeding behavior itself rather than as a consequence of general affiliative motivation.

Informal observations in the course of our previous studies suggest that although rat pups, both wild and domesticated, exhibit a strong tendency to eat in the presence of conspecifics, they are relatively indifferent to the presence of conspecifics when selecting a site for ingestion of water. If this observation should be confirmed under controlled conditions, it would demonstrate at the least that the level of affiliative behavior exhibited by rat pups varies as a function of pup activity. Such evidence would not be compatible with the view that the influence of adult rats on the orientation of pup behavior is explicable in terms of a general affiliative motivation of young rats. Rather, observation of greater adult influence on pup selection of a feeding as compared with a drinking site would suggest that affiliation with conspecifics is of particular importance in the orientation of pup feeding behavior.

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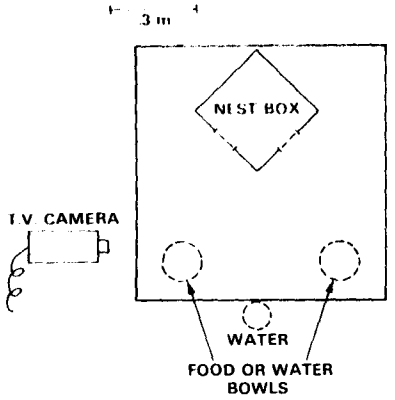

Figure 1. Overhead schematic view of the enclosure used in Experiment 1. (Water was present only when the enclosure contained food-deprived pups, and appropriately filled bowls were presented for 2 hr/day.)

Experiment 1

The present experiment was undertaken to determine the relative influence of the presence of an adult rat on pup choice of site for food ingestion compared with pup choice of site for water ingestion.

Method

Subjects. Subjects were 14 virgin female adult (14–20 wk old) and 14 juvenile (22–26 day old) Long-Evans rats, each from a separate litter. All juvenile subjects were maintained in 36 × 31 × 16 cm cages with their littermates and dam on ad lib Purina Laboratory Chow and water until 22 hr prior to the initiation of testing procedures.

Procedure. Twenty-two hours prior to initiation of testing, one adult and one juvenile rat were placed in the enclosure illustrated in Figure 1. For half of the subject pairs, the enclosure contained ad lib food (pellets of Purina Laboratory Chow) scattered on the floor of the enclosure and no water. For the remainder of subjects the enclosure contained water in the location indicated as WATER in Figure 1 but no food. At the commencement of testing, two ceramic bowls were placed in the positions indicated in the figure. Food-deprived subjects received bowls containing powdered Purina Laboratory Chow, and water-deprived subjects received bowls containing tap water. For the next 2 hr the experimenter observed the ingestive behavior of the subjects by closed-circuit television, recording the location, time of initiation, and time of termination of each ingestive bout at each bowl. At the end of the 2-hr test period the ceramic bowls were removed, and 22 hr later the test procedure was repeated.

Data analysis. To determine whether the subjects in a given pair were influencing one another's choice of ingestion site, I examined those instances in which one animal of a pair initiated ingestion while the other pair member was eating or drinking from one of the ceramic bowls. The former animal could, of course, choose to eat or drink together with its pair-mate (T) or separate (S) from it. The ratio of the number of times each member of a pair chose to ingest together with its pair mate divided by the total number of instances of initiation of ingestion when a pair mate was active at a bowl ($T/(S + T)$) provides one measure of the extent of social influence on each individual when choosing a location for ingestion. The $T/(S + T)$ ratios were calculated separately for the adult and juvenile members of each pair.

Such measures of social influence on ingestion site selection could obviously be distorted by strong position bias on the part of subjects. If, for example, all subjects had an individual bias to ingest only at the right-hand bowl, each would exhibit a ratio of $T/(S + T) = 1$, even though no social influence existed. To provide a control for such individual position bias, I calculated the ratio $T/(S + T)$ from the data of randomly composed pairs of animals. The data collected from each adult animal, indicating the location, time of initiation, and time of termination of each of its ingestive bouts, were randomly paired with those of a juvenile in the same deprivation condition, and the ratio $T/(S + T)$ was calculated for these randomly constituted pairs.

All probability values reported are two-tailed.

Results and Discussion

The main results of Experiment 1 are presented in Figure 2, which indicates the mean $T/(S + T)$ values for food- and water-seeking adults and juveniles and their random controls. Examination of the figure reveals, and statistical analyses confirm, that only juvenile food-seeking rats exhibited $T/(S + T)$ ratios greater than those of their random controls (food-seeking pups, Mann-Whitney $U = 0$, $p < .001$; water-seeking pups, Mann-Whitney $U = 19$, $p < .534$) and that food-seeking pups were more socially influenced in their choice of site for ingestion than water-seeking ones (Mann-Whitney $U = 7$, $p < .052$). The differences in affiliative tendency of food- and water-seeking pups were apparent on both Day 1 and Day 2 of testing (food-seeking pups, $T/(S + T)$, Day 1 = .91, Day 2 = .92; water-seeking pups, $T/(S + T)$, Day 1 = .69, Day 2 = .55), but they were not statistically reliable on Day 1.

The finding that a food-seeking pup is more likely to eat together with an adult than a food-seeking adult is with a pup (Mann-Whitney $U = 0$, $p < .001$) confirms an earlier finding (Galef, 1977b). This last

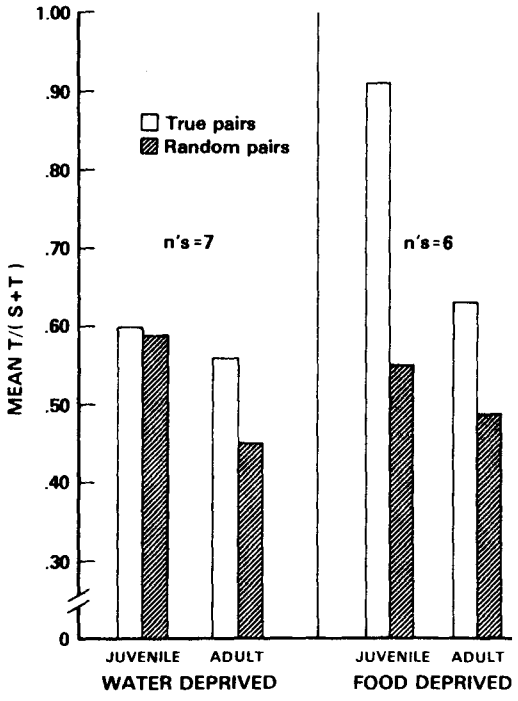

Figure 2. Mean amount of eating together as a proportion of total instances of eating together and separately. (See Data Analysis of Experiment 1 for an explanation of Groups and $T/(S + T)$ ratios.)

result is particularly convincing given that juveniles spent more time per testing period (M = 39.8 min) than adults (M = 23.2 min) at the food bowls and, thus, had greater opportunity to influence adult feeding site choices than adults had to influence juvenile feeding site choices.

Although offering support for the hypothesis that food-seeking pups approaching a food source are more readily influenced by social factors in selecting a site for ingestion than water-seeking pups approaching a water source, the present data are open to several interpretations. First, it is possible that while eating, adult rats emit signals (chewing noises, etc.) that attract pups but that while drinking, adult rats do not do so. Second, the fact that adult food-deprived rats spent considerably more of the 2-hr test periods eating (M = 23.4 min) than water-deprived adult rats spent drinking (M = 9.0 min) and that food-deprived adults made many more trips to the food bowls (M = 10.1 trips/day) than water-deprived adults made to the water bowls (M = 4.8 trips/day) leaves open the possibility that the difference in relative influence of adults on food- and water-seeking young reflects the difference in the amount of time they are present at an ingestion site to influence pup behavior. The second experiment examines the social influence of the presence of an adult on the ingestion site selection of pups in the absence of these confounding variables.

Experiment 2

In the present experiment individual pups were habituated to a strange adult conspecific (Days 1 and 2), habituated to a 16-hr deprivation schedule and accustomed to eating and drinking in a test apparatus (Days 3 and 4), exposed to the presence of the adult in the test apparatus and accustomed to a discrete trials procedure in the test apparatus (Day 5), and finally tested to determine the influence of adult presence on pup choice of feeding and drinking sites in the test apparatus (Days 6 and 7). Adults in the test situation were confined in the vicinity of one food and water source without access to food or water throughout the testing procedure, thus controlling the variables confounding Experiment 1.

Method

Subjects. Subjects were 16 adult virgin female Long-Evans rats and 16 pups of the same strain, each from a separate litter; the pups were weaned immediately prior to initiation of the test procedure at 22 days postnatally. Each subject was randomly assigned to either the food or water deprivation group at weaning, but all subjects were treated identically for the first 4 days of the experiment.

Procedure. Days 1 and 2. Each 22-day-old juvenile subject was placed in a 36 × 31 × 16 cm cage with one of the adult subjects and left undisturbed for 48 hr on ad lib Purina Laboratory Chow and water.

Days 3 and 4. All pairs of subjects were food and water deprived for 16 hr. At the end of the deprivation period the juvenile subject was removed from the cage it shared with its adult and left for 2 hr in the apparatus illustrated in Figure 3. Food and water intakes at each of the indicated locations were determined by weighing, and any subject that had not ingested more than .5 g at each of the four ingestion sites on Day 3 or 4 was excluded from further study. Following each 2-hr exposure period in the apparatus, all pups were returned to their cagemates and allowed free access to food and water for 6 hr.

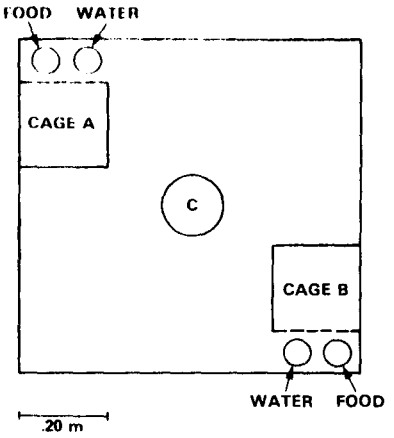

Figure 3. Overhead schematic view of enclosure used in Experiment 2. (Dashed lines indicate the wire mesh portion of Cages A and B through which pups could see and smell confined adults.)

Day 5. Those juvenile subjects originally assigned to the food deprivation group (n = 7) and their adult cagemates were food deprived for 16 hr, and those subjects originally assigned to the water deprivation group (n = 7) and their adult cagemates were water deprived for 16 hr. Each juvenile subject was then placed in the apparatus, with its cagemate confined in one of the two small cages (labeled Cages A and B in Figure 3) and allowed to eat and drink ad lib for 1 hr. Half of the adults in each deprivation condition were confined in Cage A and half in Cage B. At the end of the 1-hr feeding and drinking period, each pup was given 20 discrete trials in which to eat or drink. At the beginning of each trial the pup was restrained under an opaque container (C in Figure 3) for 30 sec. The container was then removed, and the pup was allowed 90 sec to initiate ingestion and 20 sec to eat or drink at the food or water bowl of its choice. A trial was terminated and the pup was returned to C for 30 sec if the pup failed to initiate ingestion within 90 sec of release or 20 sec following initiation of ingestion, whichever occurred first. Following 20 trials, pup and cagemate were turned to their home cage for 6 hr of ad lib food and water.

Days 6 and 7. On Day 6, each pup and its cagemate were again either food or water deprived, in accordance with group assignment, for 16 hr. Following deprivation, the adult pair member was returned to the same small cage (A or B) it had occupied on Day 5, and the pup was given 40 discrete ingestion trials as described above. Pup and cagemate were then returned to the home cage for 6 hr of free access to food and water. The entire Day 6 procedure was repeated on Day 7.

The experimenter recorded the location at which ingestion occurred and the substance ingested during each of the 80 trials on Days 6 and 7.

Results and Discussion

On Days 6 and 7, water-deprived pups chose to drink on 80.1% of test trials on which they initiated ingestion within 90 sec of release (M = 52 trials) and food-deprived subjects chose to eat on 83.1% of trials on which they initiated ingestion (M = 74 trials). Generally, food-deprived pups spent most of the first 20 trials of each test day eating (91.2% of trials) and increased their frequency of drinking during the last 20 trials (26.2%), and water-deprived pups spent the majority of their first 20 trials on each test day drinking (84.0%) and increased eating during the last 20 trials (39.0%).

Data describing ingestive behavior during the hour preceding discrete trials on Day 3 unfortunately had to be discarded because of the frequency of spillage of both food and water.

The main results of Experiment 2 are presented in Figure 4, which indicates the mean percentage of trials on which ingestion occurred that food- and water-deprived juveniles ate, drank, or both ate and drank at the location nearer the adult. As can be seen in Figure 4, and as would be expected on the hypothesis that pups seeking a feeding site affiliate with adults more reliably than pups seeking a drinking site, the food-deprived pups ate and drank more frequently in the vicinity of an adult than did the water-deprived pups (Mann-Whitney U = 8, p < .038).

It might also be argued that, for example, on those individual trials on which water-deprived pups ate rather than drank, they were less interested in seeking food than on those trials on which they drank. Hence, one might predict on the hypothesis under ex-

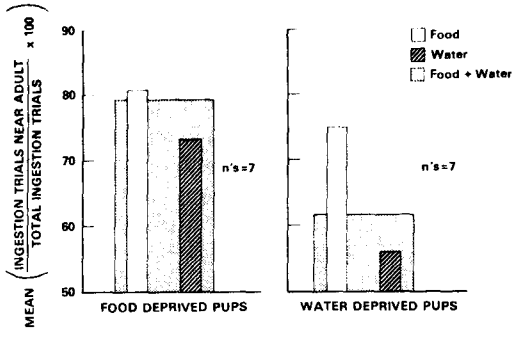

Figure 4. Mean percentage of discrete trials on which food- and water-deprived pups chose to eat or drink or both eat and drink in the vicinity of adult cagemates.

amination that all pups, regardless of experimentally induced deprivation state, should exhibit a higher probability of eating than of drinking in the presence of its adult pair-mate. In fact, 12 of the 14 subjects in the present experiment, considered independent of experimentally induced deprivation state, ate in the vicinity of the caged adult with higher probability than they drank there (sign test, $N = 14$, $x = 2$, $p = .012$).

It might be argued that the tendency of pups to eat rather than drink near adults is a result not of differences in pup internal state but rather of the deprivation state of the target adults that the pups were approaching. That is to say, both members of pup–adult pairs in both the present experiment and Experiment 1 were in similar deprivation states during testing, and it is possible that pups are for some reason more likely to affiliate with hungry adults than thirsty ones. However, the finding in the present experiment that juvenile members of both food- and water-deprived pairs were more likely to eat then drink in the presence of their adult pair-mate, independent of that adult's deprivation state, renders the explanation of differences in pup behavior in terms of differences in adult deprivation state difficult to maintain.

On the hypothesis under investigation, one would further expect that the highest probability of ingesting in the presence of an adult would be exhibited by food-deprived pups on those trials on which they ingested food and the lowest by water-deprived pups on those trials on which they ingested water, a prediction borne out by examination of Figure 4. Thus, analysis of both the main effects and fine grain of the data suggests that pups selecting a feeding site are, as suggested by the results of Experiment 1, more likely to exhibit affiliative behavior than those seeking a drinking site.

Experiment 3

The results of Experiments 1 and 2 offer confirmation of the hypothesis that pups seeking food exhibit enhanced affiliative behavior in comparison with pups seeking water. One obvious explanation of such an outcome is that food-deprived pups, independent of their ongoing activity, are more socially motivated than water-deprived or nondeprived ones. In both of the preceding experiments deprivation state and ingestive behavior were confounded, which prevents assessment of the contribution of deprivation state itself to the observed differences in affiliative behavior of food- and water-seeking subjects. The present experiment examines the affiliative tendency of food-, water-, and nondeprived rat pups in a noningestive situation to determine whether deprivation state, independent of ingestive behavior, influences levels of affiliation.

Method

Subjects. Subjects were eight litters (8 pups/litter) of 24-day-old Long-Evans rat pups born in the McMaster colony. Sixteen adult virgin female rats of the same strain were used as stimuli in the test situation.

Procedure. Each litter of pups and its dam were maintained in a 35 × 30 × 16 cm polycarbonate cage on ad lib Purina Laboratory Chow and water until the pups were weaned at 23 days of age. At weaning, the pups in each litter were randomly assigned for 24 hr to 35 × 30 × 16 cm cages providing ad lib access to Purina Laboratory Chow (water-deprived group), water (food-deprived group), or both Purina Laboratory Chow and water (nondeprived group).

Immediately following the 24-hr treatment each pup was individually tested in the apparatus illustrated in Figure 5 for its tendency to affiliate with an adult virgin female rat.

The apparatus consisted of a 1-m alley with a guillotine door at its midpoint and a hardware-cloth-covered window (15 × 8 cm) 1 cm from each end. The floor of

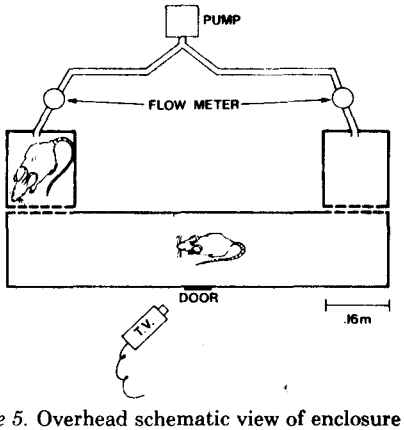

Figure 5. Overhead schematic view of enclosure used in Experiment 3. (Dashed lines indicate the hardware cloth windows through which pups could observe adults.)

Table 1
Affiliative Behavior and Activity of Food-Deprived, Water-Deprived and Nondeprived Pups in Experiment 3

		0–5 min			5–10 min			10–15 min		
Group	*n*	%	*M* rank	*M* crossings	%	*M* rank	*M* crossings	%	*M* rank	*M* crossings
Food deprived	8	72.0	1.4*	9.38	80.7	1.4*	6.39	79.2	1.75	5.93
Water deprived	8	65.8	2.5	9.59	74.3	2.5	5.78	79.8	1.88	4.25
Nondeprived	8	66.8	2.1	9.29	75.1	2.1	6.11	73.1	2.38	4.93

* $.025 < p < .05$, two-tailed binomial tests.

apparatus was covered with paper toweling which was changed after the testing of each pup. Visual, olfactory, and auditory cues from an adult virgin female rat, restrained in a 23 × 16 × 11 cm Plexiglas box through which a 1.4 l/min air stream was passed, were presented at one end of the alley, and an identical empty box through which a clean air stream passed was presented at the other. Pups in the various deprivation groups within a litter were tested in the apparatus in counterbalanced order; the two virgin females assigned to a given litter as stimulus objects were alternately confined for 15-min periods in the Plexiglas box presented at one window.

At the beginning of a trial the experimenter placed an adult rat in one restraining box, introduced a pup into the alley through the door, and left both animals undisturbed in the apparatus for 15 min. The experimenter observed the alley by closed-circuit television and recorded the amount of time the pup spent in the half of the alley nearer to the adult and the number of times the pup crossed the midline of the apparatus during the first, second, and third 5 min of testing.

Data Analysis

As a control for litter effects, the mean percentage of each of the three successive 5-min periods spent by food-deprived pups on the side of the apparatus containing the adult was compared with the mean percentage of time spent there during the same 5-min periods by water deprived and nondeprived pups from the same litter. The rank order of these means across litters was compared by a two-tailed binomial test with $p = 1/3$.

Results and Discussion

The main results of Experiment 3 are presented in Table 1 which shows the mean percentage of time spent by food-deprived, water-deprived, and nondeprived groups of pups on the side of the apparatus from which the adult could be viewed, and the mean rank order within litters of those percentages. Also shown are the mean number of midline crossings made by individual subjects in each group. As is evident from inspection of the table, there is a small, transitory, but reliable tendency for food-deprived pups, in comparison with water-deprived and nondeprived ones, to spend a greater proportion of the test period with the adult. The difference in mean percentage time spent with the adult was significant during the first and second 5 min of testing (binomial test, $ps = 1/3$, $rs = 6$, $.02 < ps < .05$) but disappeared during Minutes 10–15. These data suggest that even in noningestive situations, food-deprived pups exhibit slight enhancement of affiliative tendencies.

The absence of differences in the number of midline crossing made by subjects in the three treatment conditions during the first two 5-min periods spent in the apparatus indicates that differences in activity, as a function of deprivation state, are not sufficient to account for the observed outcome.

Unfortunately, both the brief duration and the small size of the effects of deprivation state on affiliation found in the present experiment limit the usefulness of these data in interpreting the large and long-lasting effects of treatment on behavior found in Experiments 1 and 2. Either the procedures used in the present experiment were such as to minimize the observable effects of food deprivation on affiliative tendency or food-deprived pups engaged in food-seeking behavior are far more likely to affiliate with adults than are hungry pups simply exploring a novel enclosure. The data are not sufficient to decide between these two alternatives.

General Discussion

The results of previous studies in our laboratory have demonstrated a profound influence of adult rats on both the time course and orientation of the weaning of juveniles. The presence of adult rats at a food source can both accelerate the weaning process (Galef & Clark, 1972) and orient weanlings to specific feeding locations and specific foods. Such affects of adults on the behavior of weaning pups have been previously shown to depend in part on a tendency of rat pups to approach conspecific adults at a feeding site (Galef, 1971, 1977a; Galef & Clark, 1971a, 1971b, 1972).

The results of the present experiments, undertaken to determine whether the tendency of weaning rat pups to approach adults at a feeding site simply reflects a general affiliative tendency on the part of young rats or is specifically related to food-seeking behavior, suggest several conclusions. First, rat pups, regardless of deprivation state, tend to affiliate with adults. All groups of pups in Experiments 1, 2, and 3 preferred sites close to an adult female to those distant from her. Second, pups selecting a feeding site are more likely to affiliate with an adult than are pups seeking a drinking site. Third, the finding of a small but statistically reliable enhancement of affiliative tendencies in food-deprived pups, compared with water-deprived or nondeprived ones, in noningestive situations suggests that deprivation state itself may play a role in determining the degree of affiliative behavior that pups exhibit.

Taken together, these results indicate that the ability of adult rats to influence pups' diet selection as a result of their presence at a feeding site is a phenomenon not totally explicable in terms of general affiliative behavior on the part of pups. Rather, the tendency of pups to approach adults when seeking solid food should be viewed as directly related to juvenile feeding behavior.

It remains to be determined whether experience either of suckling from the dam or of feeding and drinking with conspecifics contributes to the development of the enhanced affiliative tendencies to be observed in pups seeking food.

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