

Differential Influence of Adult and Juvenile Conspecifics on Feeding by Weanling Rats (*Rattus norvegicus*): A Size-Related Explanation

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Weanling Sprague Dawley rat pups (*Rattus norvegicus*) selected between 2 safe palatable diets in concordance with the preferences of either an adult or a juvenile conspecific model (Experiment 1). Nevertheless, weanlings chose to feed more in the vicinity of an adult than in the vicinity of a juvenile, thus fulfilling the prediction of an adaptive feeding strategy (Experiment 2). The weanlings' bias for feeding in the vicinity of an adult was eliminated by increasing the magnitude of pup stimulus to 3 pups (Experiment 3). Thus, weanlings do not possess a specialization rendering them more sensitive to adults than to pups as models for diet selection. By responding to stimulus magnitude, weanlings are more likely to feed with adult conspecifics, choose foods used by them, and derive the benefits correlated with the adults' successful feeding habits.

When a wild Norway rat (*Rattus norvegicus*) weans from mother's milk, it becomes an opportunistic omnivore, living by the selection and ingestion of a variety of safe, nutritious substances. Because the species is known to humans as a destructive pest, the Norway rat is frequently threatened by palatable but toxic substances, which it must avoid ingesting in order to survive. Thus, the weanling rat faces a complex world of ingestive challenges to which it must quickly and unerringly adapt.

Galef and Clark's (1971a, 1971b) seminal studies showed that the presence of conspecifics are a powerful determinant of the site at which the pups feed and the substances which they initially ingest at weaning. Pups observed in various seminatural settings consumed only the diet eaten by adult colony members and never sampled an alternative, safe substance that adults completely avoided (because it had been previously paired with a toxic substance). It is reasonable to assume that weanling rats that respond to the appropriate cues and contingencies for such social learning have survival and reproductive advantages over those that do not.

Additional studies of the cues that attract weanlings to feeding sites and enable them to recognize foods have explored the stimuli and responses that combine to create a flexible, responsive process of behavioral development. Movement cues and odors can attract pups over distances (Alberts & Leimbach, 1980; Leon & Moltz, 1971); residual chemical cues can identify a feeding site and facilitate pup

food sampling (Galef & Heiber, 1976). Weanling-age pups can use postingestional stimuli to recognize the nutritional value of novel substances after a single, brief encounter (Melcer & Alberts, 1989). To some extent, milk-borne flavors derived from the mother's diet can assist pups' recognition or initial acceptance of diet (Galef & Henderson, 1972; Galef & Sherry, 1973).

In contrast to the available literature on the adults' influences on weanlings' feeding behavior, there are rather few data concerning similar influences among weanling animals. Some studies suggest that weanlings can facilitate feeding among peers. Galef and Clark (1971b) described evidence for recruitment effects between feeding rat pups. For example, Galef and Clark (1971b) more often observed multiple pups or no pups feeding from a bowl than a single pup feeding from the bowl. Group-housed weanlings required less time to begin consuming a safe, unfamiliar diet than did pups housed individually. Thiels, Cramer, and Alberts (1988) showed that pups can influence the suckling behavior of weanlings. Twenty-day-old pups mixed among a litter of 15-day-olds attached to the nipples of an anesthetized dam more readily than did 20-day-olds tested withagemates, which suggests that social regulation of ingestive behavior applies to suckling as well as to feeding.

Thus, the early feeding behavior of weanling rat pups can be influenced by adults as well as by young conspecifics, although the specific cues involved and the strength of these effects remain poorly defined. In this investigation we established a method for observing such social effects on weanlings' feeding and for comparing the influences on food preferences exerted by adult and juvenile conspecifics. Our inquiry was motivated, in part, by the apparent adaptive significance of the social learning involved in these effects. In particular, we hypothesized that weanlings are differentially responsive to cues from an adult versus those from a younger animal, because the adult, by virtue of its longevity, presents a priori evidence of the success of its feeding habits, whereas the younger conspecific cannot demonstrate

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comparable success. Weanling pups may display differential responsivity to diet-relevant information from adult and juvenile conspecifics. Such a result and the identification of the underlying mechanisms will further enhance our understanding of this developmental transition from suckling to independent feeding as well as social learning processes.

Experiment 1: Diet Selection by Weanlings Can be Determined by Feeding Patterns of Adult or Juvenile Conspecifics

There are numerous means by which adult rats affect the weaning of offspring within the colony: The presence of adults attracts pups to feeding sites, facilitates onset of independent ingestion, and contributes to the formation of taste preferences (see Galef, 1977a, 1981, for review). Agemates, on the other hand, have rarely been examined as potential sources of induction or canalization of weaning. Galef (1977b), however, provided evidence to suggest that weanlings' choice of feeding site is influenced by agemates as well as adults. Juvenile pups given a choice of two food bowls with the same diet were more likely to feed from a bowl when an adult or juvenile conspecific was eating rather than feed alone at the alternative bowl. Paired adults, on the other hand, were less likely to attract one another to a food site.

Experiment 1 was designed to confirm that weanling pups could influence each other's choice of feeding site (Galef, 1977b) and, moreover, influence each other's choice of diet. These observations provided basic data on the feeding patterns in pairs of adult and weanling rats or of two agemate, weanling rats. Hence, pairs were observed in a standard environment in which they had free access to two safe, distinct, palatable diets. We measured the time spent feeding from each of two food bowls by the weanling subject and by the adult or the agemate demonstrators. (We use the terms *demonstrator* and *model* interchangeably but emphasize that neither term is meant to imply that we are observing imitation; see Galef & Wigmore, 1983.) Our methods differ subtly, but significantly, from those used in previous studies by Galef and Clark (1971b), in which adult models presented with two distinctly flavored diets, one of which had been previously poisoned, ate only the safe diet. In our study the diets were uniquely flavored, yet both were safe and acceptable, and this enabled us to observe a variety of possible outcomes for diet selection by the animals. Such data are not available from studies that involve poison avoidance because such methods generally encourage exclusive acceptance of only one of two available foods.

Method

Subjects

The subjects were 24 female Sprague Dawley rat pups, 18 days old. They were bred and born in the Animal Behavior Laboratory colony at Indiana University, from original stock obtained from Charles River Laboratories (Wilmington, MA). The subjects came

from litters that had been culled to 8 pups (4 males and 4 females). In addition, 8 females, 18 days old at the start of the study, served as pup models. Weanling-age pups weighed 35 ± 10 g. All pups were housed with their mother and littermates in standard maternity cages (26 cm wide \times 21 cm high \times 47 cm long) and were maintained on a 16:8-hr light-dark cycle at an ambient temperature of 22–24 °C.

Four adult females were used as adult models. They were housed alone in tubs and kept under the same lighting and temperature conditions as the pups. These females were approximately 1 year old and had given birth 5–6 times before the start of this experiment. Thus, the adult models were experienced with pups. None of the females were, however, lactating at the time of the study. To reinstate maternal responsivity (Rosenblatt, 1967) and eliminate variable responses to weanlings (Alberts & Leimbach, 1980), the females were continually housed with 3-day-old rats (replaced every 24 hr) and 20- to 22-day-old rats (replaced every other day) for 1 week before the first test.

Apparatus

Test cages built previously for other experiments measured $33.7 \times 13.0 \times 77.5$ cm or $33.7 \times 36.0 \times 57.0$ cm (there were no discernible effects of cage size) and contained two food troughs ($7.6 \times 3.8 \times 12.7$ cm) set 15.2 cm apart. The troughs were placed in the corners at one end of the cage. Each trough contained 35 g of powdered Purina Rat Chow (Ralston-Purina, St. Louis, MO). The food in one dish was mixed with a liquid peanut flavoring, and the food in the other dish was mixed with a liquid bread flavoring (100 μ l per 25 g rat food). Location of the dishes was constant throughout the study. The flavorants were generously provided by International Flavors and Fragrances (Union Beach, NJ).

Procedure

On each experimental day a single subject was separated from its lactating dam as well as from food and water for 6 hr before the start of an experimental session. The pup was then placed into the test cage for 4 hr on 2 consecutive days. Pups tested with models were paired with the same model on each day of testing.

Pup and adult models were food deprived to ensure that they would feed reliably during the test and fulfill their role as demonstrators. The subjects were assigned to one of three experimental conditions.

Adult model. Each pup subject in this condition was paired for 4 hr with an adult that was previously trained on a 20-hr daily food-deprivation schedule.

Pup model. Each pup subject in this condition was paired for 4 hr with a pup model whose food had been removed the night before the test.

No model. This group served as a control for social effects on food preference. These subjects were put in the test environment for 4 hr by themselves.

Test sessions were recorded with a time-lapse videorecorder (Model No. TLC1400, Gyr, Anaheim, CA 6:1 record-playback ratio). During playback, an observer used a computer-based encoding program to quantify the duration of time spent in oral contact with each food (feeding). The program provided a printout that showed (a) the total number of seconds that the model and weanling subject spent eating from each food dish and (b) the total number of seconds that the paired animals spent simultaneously eating from the same food dish or from separate food dishes.

Data Analysis

Analysis of the total time that the pups and models spent feeding in the different social conditions was obtained by averaging across Days 1 and 2 for each subject.

Food flavor preferences were defined as time spent eating peanut-flavored diet divided by the total time spent eating peanut-flavored diet and bread-flavored diet. The use of such proportions corrected for differences in total time spent feeding, particularly those likely to arise in comparisons of the feeding behavior of adults and pups. Tests in which total time spent feeding by either the model or subject was less than 60 s were omitted from the analysis.

Correlations were calculated between the percentages of time spent eating peanut-flavored food by test pups and their models from scores averaged across Days 1 and 2. Furthermore, three types of feeding arrangements were encoded and quantified (again, data for Days 1 and 2 were averaged): *Matched feeding* occurred when the pup and model simultaneously fed from the same food trough; *nonmatched feeding* occurred when the pup ate from one food trough while the model ate from the other trough; and *solitary feeding* occurred when the pup fed alone (i.e., the model was not feeding).

Reliability and Validity

Mean intraobserver reliability was 96%, based on scoring numerous videotapes two times each. To ensure that duration of time spent feeding was a valid measure of food intake, 8 individual pups were recorded with a time-lapse videorecorder (6:1 record-playback ratio) during a 4-hr feeding test. There was a positive correlation between duration of time spent feeding and grams of food eaten, Pearson's $r(8) = .93$, $t(6) = 6.18$, $p < .05$.

Results and Discussion

The different social conditions resulted in different durations of pup feeding time, one-way analysis of variance (ANOVA), $F(2, 21) = 10.11$, $p = .0009$. Weanling subjects tested alone spent an average of 479 s (± 117 s) feeding, whereas those tested in the presence of an adult model ($M = 1,258 \pm 98$ s), $t(14) = 5.09$, $p = .0002$, or a pup model ($M = 1,146 \pm 172$ s), $t(14) = 3.20$, $p = .006$, spent more than twice as much time feeding. Feeding by the weanling subjects was equivalent whether they were with an adult ($M = 1,258 \pm 98$ s) or a pup model ($M = 1,146 \pm 172$ s), $t(14) = 0.57$, *ns*. Thus, social stimulation clearly affects time engaged in feeding.

As expected, adult demonstrators ($M = 4,601 \pm 343$ s) spent more time feeding than did agemate demonstrators ($M = 3,102 \pm 372$ s), $t(14) = 2.96$, $p = .01$, and thus provided differential social stimulation at the food troughs. Despite differences in feeding time between pup and adult models, weanling subjects fed for equivalent durations of time in both social conditions, as we note earlier.

The two flavored diets used in this study were palatable and acceptable to both subjects and models, as determined from a repeated measures ANOVA on the time spent eating at each bowl: main effect for flavor, $F(1, 35) = 1.17$, *ns*; Flavor \times Group (subjects and models together) interaction, $F(4, 35) = 0.10$, *ns*.

By examining the proportion of time spent feeding from each diet source separately by individual weanlings and their models, we can determine each animal's feeding pattern as well as the extent to which there was concordance between the paired animals in the intake of each diet. Figure 1 (top panel) shows the proportion of time spent by each weanling eating peanut-flavored diet as a function of the peanut-flavored diet preference of its adult model. The preferences for peanut-flavored diet of the weanlings and their adult models were significantly correlated, Pearson's $r(8) = .88$, $t(6) = 4.60$, $p < .005$. Figure 1 (bottom panel) shows the results for weanlings paired with agemate models, and again, there was a significant positive correlation of preference displayed by the weanling subject and its juve-

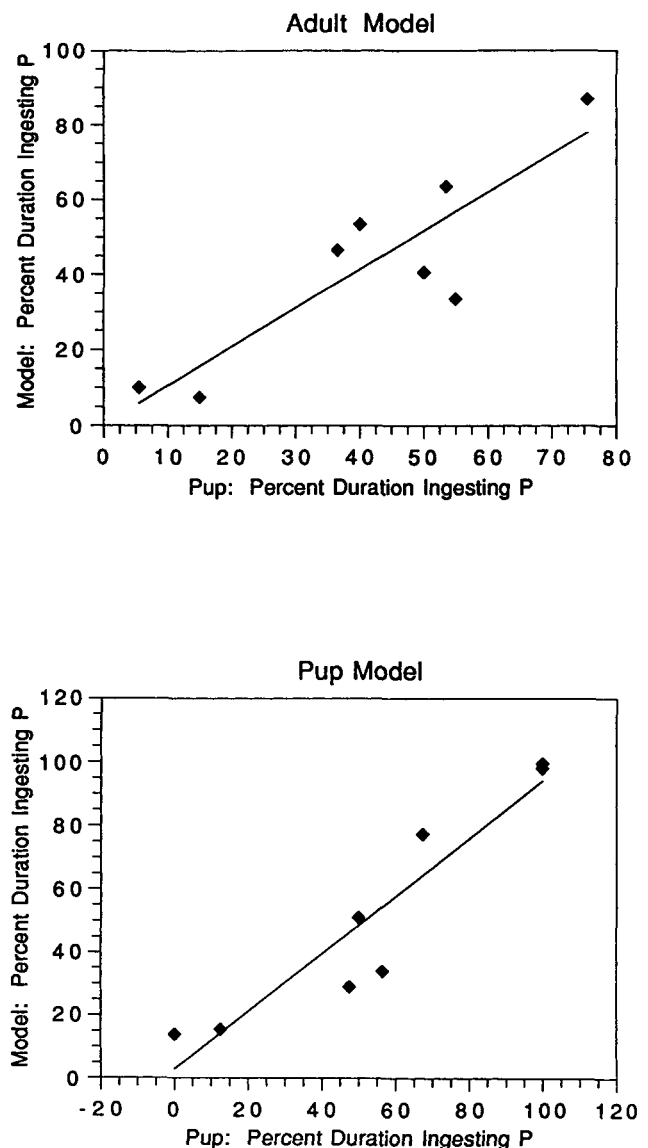


Figure 1. Scatterplot showing the percentage of time that the pups and models spent eating peanut-flavored diet (P) in the adult model (top panel) and in the pup model (bottom panel) conditions.

nile demonstrator, Pearson's $r(8) = .94$, $t(6) = 6.77$, $p < .0005$. Differences between the two correlations were not significant, $z(8) = 0.57$.

Figure 2 shows in histogram form the percentage of feeding time spent by weanling subjects engaged in the three types of feeding, in the presence of an adult or juvenile conspecific. A repeated measures ANOVA suggests that there were no model-related differences in these forms of feeding: main effect for social condition, $F(1, 14) = 1.00$, *ns*, and Social Condition \times Feeding Type interaction, $F(2, 28) = 2.22$, *ns*. There was, however, a difference in the overall proportion of time that the subjects engaged in matched, nonmatched, and solitary feeding, repeated measures ANOVA, main effect for form of feeding, $F(2, 28) = 23.42$, $p = .0001$. Newman-Keuls analysis was used for post hoc comparisons.

About half of the time spent feeding by the weanling subjects paired with either a pup or adult model was matched feeding. Pups in both social conditions spent as much time engaged in solitary feeding ($M = 46\%$ of total feeding time) as they did in matched feeding ($M = 44\%$; Newman-Keuls, *ns*). Duration of time in nonmatched feeding ($M = 8\%$) was significantly lower than solitary and matched feeding (Newman-Keuls, $p < .05$).

There is a potential for reciprocal effects in the feeding dyads. *Subjects* and *models* are designations that serve our experimental design but do not necessarily reflect all the activities of the rats. It is likely that the models' feeding not only influenced that of the subjects, but that the subjects' feeding influenced the models' as well. Such reciprocal effects are implied by the elevation in time spent feeding observed in the social versus the nonsocial conditions. The models, however, ate more than did the subjects and therefore provided more stimuli for pup feeding behavior than the subjects provided for the models.

As in past research, adult rats affected the amount of time spent feeding by the more food-naïve weanlings. In addition, a juvenile conspecific was also found to be an effective

influence on another weanling's feeding. The results of Experiment 1 showed that the presence at a food site of an adult or an agemate are both sufficient conditions to attract a weanling pup to the vicinity of the food, stimulate feeding, and bias the weanling's subsequent food selection. Adult and juvenile conspecifics both led to significant concordance in diet choices of weanlings. Furthermore, pup and adult models stimulated a similar pattern of matched, non-matched, and solitary feeding.

Experiment 2: Weanlings' Diet Selection Is More Strongly Influenced by an Adult Than by a Juvenile

The design of Experiment 1 was not adequate for comparing a weanling rat's attraction to an adult with its attraction to an agemate. We designed Experiment 2 to make such a comparison.

To achieve conditions appropriate for comparing directly the weanling's attraction to different conspecifics, we gave pups in Experiment 2 a simultaneous choice between an adult and a juvenile model located at different food sites. We measured approach frequencies and feeding durations at food bowls associated with each model. More attractive models ought to elicit more approaches to and more feeding at associated food sites than less attractive models at different food sites.

Method

Subjects

The subjects were 10 female Sprague Dawley rats, 21 days old; 10 female Sprague Dawley rats, 22–23 days old, served as juvenile models. In addition, 6 adult multiparous female Sprague Dawley females housed in pairs were used as models. The subjects and models were bred and maintained as described in Experiment 1. From 10 days before testing, the adults were continuously housed with two 22- to 30-day-old pups to refamiliarize them with weanlings (Alberts & Leimbach, 1980). Pups and models were unrelated and unfamiliar to each other.

Procedure

At the beginning of each test, a subject was placed in the center of a clear glass cage ($26.0 \times 30.4 \times 50.8$ cm, as depicted in Figure 3). An adult model was placed behind a mesh and Plexiglas barrier 10.8 cm from one end of the cage, and a pup model was placed behind an identical barrier 7.6 cm from the other end of the cage; the difference provided the models with similar areas of space in which to move. Visual, olfactory, and acoustic cues could be exchanged through the barriers. The remaining region of the cage was evenly divided into three 10×26 cm areas. The middle, neutral area contained a water bottle. The areas on either side of the neutral area each contained a food dish (7.6 cm in diameter) with 24 g of powdered chow; the dishes were placed against the barriers as shown in Figure 3. Only the subjects had access to the food.

Food was removed from the subject's cage 7 hr before the test. Testing began approximately $\frac{1}{2}$ hr before lights off (2300 hr) to ensure that the subjects and models were relatively active. During

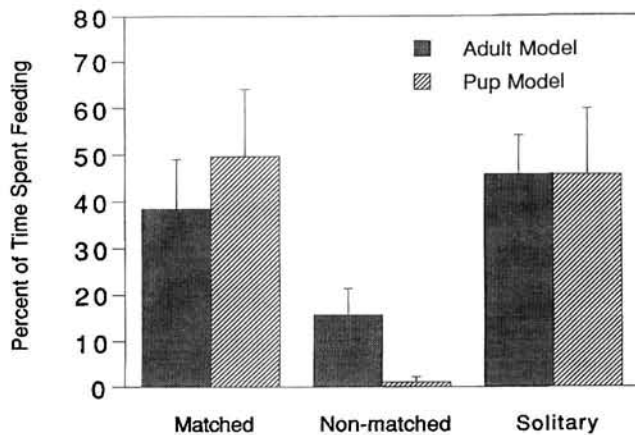


Figure 2. Percentage of time that the subjects spent in matched, nonmatched, and solitary feeding in the adult model and in the pup model conditions.

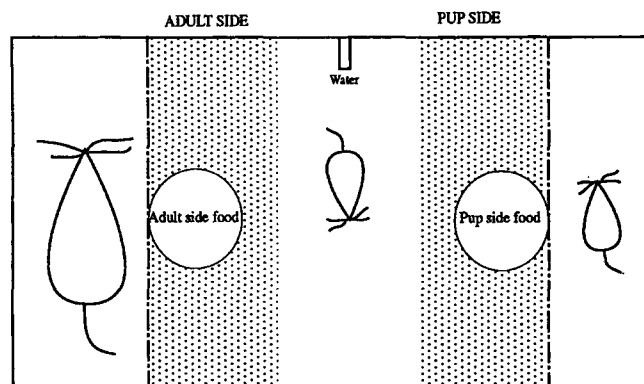


Figure 3. Diagram of test apparatus used for simultaneous choice test (not drawn to scale).

the dark phase (2300–0700 hr), red light bulbs illuminated the cages so that the animals could be videorecorded. To verify that the models and subjects were generally awake during the test session, we made notes from the videotape on the animal's overall activity level during the test period.

Test sessions were recorded with a time-lapse videorecorder (6:1 record–playback ratio). During rapid playback an observer used a computer to quantify the frequency and duration (in seconds) that each subject spent in oral contact (eating) with the food on the pup side or on the adult side and the frequency and duration that each rat spent on the pup side or on the adult side (more than half of the subject's body in either side was scored as an approach to that particular area). Frequency of a particular behavior was tallied each time a button was depressed to initiate a measure of the duration of the behavior. Thus, the program provided a printout of the following: duration of time spent eating by the subject from each food dish, frequency of approaches made by the subject to each food dish, duration of time that the subject spent on the pup side and the adult side, and frequency of approaches made by the subject to the pup side and the adult side.

Data Analysis

One-tailed sign tests were used to analyze the data. Hence, each pup was given a positive sign if the frequency or duration measure for a particular behavior was greater on the adult side than on the pup side.

Results and Discussion

All weanling pups showed more approaches to the food bowl associated with the adult than to the food bowl associated with the juvenile (sign test), $N(10)$, $X(0)$, $p = .001$. Likewise, most pups ate more from the food bowl associated with the adult than they ate from the bowl associated with a juvenile, $N(10)$, $X(1)$, $p = .011$. For the 4-hr test, the average frequency of approaches was 13.0 ± 0.8 to the adult-associated food and 4.5 ± 1.0 to the pup-associated food. Correspondingly, the average time spent feeding was 859 ± 80 s on the adult side and 262 ± 116 s on the pup side.

All weanlings entered the adult side more than the pup side, $N(10)$, $X(0)$, $p = .001$. However, descriptive statistics

indicate that the mean difference was only slightly greater for the adult side ($M = 114.0 \pm 11.0$) than for the pup side ($M = 96.6 \pm 8.6$). Pups showed no preference in duration of time spent on the adult side versus the pup side, $N(10)$, $X(3)$, *ns*. The mean durations of time spent on either side were $7,665 \pm 718$ s on the adult side and $5,576 \pm 705$ s on the pup side.

These data indicate a bias of weanlings to approach the food and feed in the vicinity of the adult relative to an agemate. There was a slight overall tendency to approach the adult side more than the pup side. Differences in the proportion of time spent on the adult side as compared with the pup side were not significant. Thus, the weanlings bias is apparent in its feeding behavior but not in its overall movement or spatial affiliation. Clearly the role of the model is to attract approaches to the direct vicinity of the food. The model need not demonstrate active feeding (see also Galef, 1971).

Notes made on the overall activity levels of the animals indicated that both the models and the subjects were active for the majority of the test session. The adults were more active, sleeping for only about 15 min of the 4-hr experiment. The subjects appeared more active than the pup models. Approximations of the duration that the weanlings spent sleeping indicated that, in general, the subjects slept slightly less than one quarter of the test period and the pup models slept slightly more than one quarter of the test period.

The main finding of Experiment 2 is that a weanling pup given a choice between a food bowl in the vicinity of an adult conspecific and one near an agemate spends more time feeding from the adult-associated food. This finding is consistent with the hypothesized adaptive benefits of using adult-associated cues over those from younger, less experienced conspecifics.

Experiment 3: A Quantitative Basis for Biased Responses to Conspecific Cues

Experiment 3 was designed to test the hypothesis that the basis of the adult rats' superior influence for controlling weanlings' feeding, in comparison with juveniles' influence, is related to quantitative rather than qualitative differences in the stimuli adults and juveniles present. To this end, we repeated the procedures used in Experiment 2, except that the pup side of the apparatus was occupied by 3 juvenile conspecifics, rather than by 1, in order to better equilibrate the total sizes of the adult and juvenile stimuli.

Method

Subjects

The subjects were 10 female 21-day-old Sprague Dawley rats bred and maintained as described earlier. Their average body weight was 55 g. The pup models were 10 female Sprague Dawley rats, 22–23 days old. Six adult models were used. They were Sprague Dawley rats with an average body weight of 300 g that were housed in pairs and had given birth to at least one litter before

the start of this experiment. From 10 days before testing, the adults were continuously housed with two 22- to 30-day-old pups to refamiliarize them with weanlings. The subjects were unrelated and unfamiliar with the pup and adult models. Likewise, pup and adult models were unfamiliar with each other.

The size (weight) of the adult stimulus was about 1.8 times that of the total pup biomass when 3 pups were used. An adult model was about 5.5 times greater in mass than a single pup.

Procedure

The test began when a subject was placed in the center of the cage described in Experiment 2 (see Figure 3). A single adult model was behind one of the Plexiglas barriers and 3 pup models (rather than 1 pup model as in Experiment 2) were behind the other barrier. The procedure was otherwise the same as described in Experiment 2.

Data Analysis

One-tailed sign tests were used to analyze the data. For each measured behavior the subjects were assigned the appropriate sign based on the direction of the difference between the adult and the pup sides.

Results and Discussion

During the 4-hr test, we observed an average of 10.5 ± 1.3 approaches to the food dish associated with the adult rat and 9.4 ± 1.6 approaches to the dish associated with the 3 juveniles. The mean total duration of time spent feeding was 665 ± 130 s for the adult-associated food and 804 ± 186 s for the pups-associated food, and more generally, time spent in the vicinity of the adult conspecific was $5,035 \pm 752$ s and in the vicinity of the pup conspecifics, $7,954 \pm 837$ s. Sign tests indicated that when 3 pups were used, the subjects distributed approaches to each food dish, feeding duration, and time on a model's side equally between pups and adults: approaches to adult-associated food, $N(8) X(4)$, *ns*; duration of eating from adult-associated food, $N(10) X(5)$, *ns*; and duration spent on pup side, $N(10) X(2)$, *ns*. The only difference that emerged from the various statistical comparisons was that most weanlings approached the side of the apparatus that contained the adult ($M = 96.6 \pm 7.4$) more than they approached the side of the apparatus that contained the pups ($M = 86.6 \pm 6.4$), $N(9) X(1)$, $p = .02$. The overall pattern of responding indicates that weanlings were equally attracted to the adult and to the trio of agemates and that they consumed food in equivalent amounts in the presence of each.

Notes made on activity levels of the pups and models showed that all animals were active for the majority of the 4-hr test session. Similar to reports discussed in Experiment 2, the adults were most active, followed by the pup subjects, and lastly the pup models. However, the overall amount of activity for all animals showed a slight difference; the pups and models slept less in Experiment 3 than in Experiment 2. We also observed that awake pup models in Experiment 3 were highly active and frequently engaged in rough-and-tumble play.

The results of Experiment 3 thus support the hypothesis that an aggregate of rat pups, similar in size to an adult rat, exerts an influence on weanling rats' attraction to a food site and stimulation of its ingestive behavior equivalent to that of an adult. We found no evidence that the adult presents a qualitatively specialized stimulus, and the adult is not perceived in a special manner by the weanling, beyond the implication that the adult is bigger and may be more salient because of its size or some correlated dimension.

General Discussion

Both adult and juvenile Norway rats can augment rate of food intake and determine diet selection by a weanling conspecific (Experiment 1). Though adults and other pups both exert these effects, an adult attracts weanlings more often to its vicinity and stimulates more food intake from a nearby food dish than does an agemate similarly confined to an area adjacent to a different dish of food (Experiment 2). We therefore predicted that if weanlings use an adaptive approach to the dual challenge of omnivory and poison avoidance, they will be more influenced by the adult than by another pup. The prediction was confirmed.

We conducted Experiment 3 to examine the specificity of the presumed adaptive mechanism that enhances the adult's effects on the weanling. The results suggested that the critical difference between an adult and a pup model may be simply size related. Cues from the adult are more influential because more of them are present in or are presented by a larger body.

It appears unnecessary to postulate the existence of distinct adult cues or even specialized receptivity in the weanling. Simple and general mechanisms can result in the expression of rather complex and specific behavior patterns. This theme pervades much of the research into social learning in Norway rats and is echoed in our results.

Precise identification of the stimuli that mediate the social transmissions involved in the control of ingestive behavior will be an asset for future studies. It is likely that multiple cues from a variety of sensory modalities may mediate this size-related attraction to adults in the vicinity of solid food. There are numerous possible roles for the pups' olfaction, some of which have been identified in other research (see Alberts, 1981, 1984). Other cues ought not to be overlooked. We noted that the juvenile models were more active when they were grouped as a cohort than when they served as single pup models. Perhaps the enhanced activity levels of the pup models in social groups (Experiment 3) may have increased the visual or acoustic cues present and thus contributed to the juveniles' efficacy. In fact, Galef and Clark (1971b) suggested that visual stimuli can influence diet selection by weanlings. Alberts and Leimbach (1980) found evidence that cues emanating from an adult's movement outside the nest stimulates approach by pups. Interestingly, Galef and Clark (1971b) noted that approaches to a food site are a function of the number of adult conspecifics at the site; this observation is consistent with our finding that more massive stimuli are more effective.

Our experiments successfully demonstrate proximate influences on food selection by weanlings, but they were not designed to assess the longevity of the effects. Similarly, these investigations do not address how much or how rapidly the weanlings acquired information about the diets and whether there are differences in learning mediated by adults and juveniles. The major contribution of these experiments is the demonstration that an adaptive benefit of adult experience may be gained by weanlings through a simple, general, magnitude-based mechanism of responsivity. Weanlings respond to adults over juveniles because the adult is larger; the presumed benefits can be gained because certain critical characteristics (e.g., survival in the face of poison predation) covary with the attainment of larger size. Classical ethology is replete with examples of magnitude-related responsivity. Supernormal stimuli, such as giant eggs preferred by gulls over their own, natural eggs (Tinbergen, 1953), is one such example. Our analysis, however, is unusual in positing a role for such response modulation in a functional, developmental context.

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