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Milk Availability Modulates Weaning in the Norway Rat (*Rattus norvegicus*)

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Two experiments were conducted to investigate the role of milk availability in the development of independent feeding and drinking in the Norway rat pup. Beginning on Day 14 postnatally, pups were exposed to different levels of milk supply by (a) changing litter size from 8 to 4 versus 12 pups (Experiment 1) or (b) limiting temporally the pups' access to a lactating dam to 8, 14, or 24 hr daily (Experiment 2). Both manipulations accelerated weaning in milk-poor pups in comparison with same-age pups with relatively greater milk supplies. By adding solid food and water to their diet, early weaning pups compensated for the negative energy consequences of milk reduction and achieved premanipulation growth rates. Milk availability thus appears to affect weaning, and it is suggested that the developmental changes in the nutritive energy balance between mother and offspring contribute to the emergence of independent ingestion.

Weaning in mammals can be characterized as the transitional process by which an offspring achieves independent feeding and drinking, thus separating itself irreversibly from obligatory dependence on the mother's resources. Although much has been learned about the bases of suckling (e.g., Blass & Teicher, 1980; Pedersen & Blass, 1981) and independent ingestion (e.g., Blass, Hall, & Teicher, 1979; Hall & Williams, 1983) in mammals, little is known about the developmental transition from the one mode of ingestion to the other.

One obstacle to rigorous analyses of weaning is that it is embedded in a complex web of correlated changes that occur simultaneously in the mother and offspring. Nevertheless, with the current data base on infant development and maternal behavior, it is possible to begin to investigate the process of weaning with well-controlled studies of nonhuman species. The present report is concerned with weaning in the Norway rat (*Rattus norvegicus*).

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The infant Norway rat ingests no solid food or water during the first 2 postnatal weeks (Babicky, Ostadalova, Parizek, Kolar, & Bibr, 1970; Babicky, Pavlik, Parizek, Ostadalova, & Kolar, 1972). Weaning appears to begin during the third week. Suckling declines while independent feeding and drinking gradually increase (Redman & Sweney, 1976). After the fourth week, weaning is usually complete; the pups no longer suckle, and they subsist entirely on nutrients ingested independently.

This transitional process of weaning involves changes in the mother rat and offspring that alter the quantity and quality of their behavioral interactions. Milk production begins to decrease after Day 15 (Babicky et al., 1970), and changes in the caloric and mineral content of the dam's milk may reduce its nutritional utility (Keen, Lonnerdal, Clegg, & Hurley, 1981). At the same time, the pup's teeth erupt, locomotion and distal senses improve, suckling becomes influenced by nutritive and hydrational factors (Blass, Hall, & Teicher, 1979), and the gastrointestinal system reorganizes in ways that favor the utilization of solid food and render milk less useful (Rozin, 1976; Yeh & Moog, 1974). In addition, nursing episodes initiated by the mother decline, and she begins to evade the pup's advances during the third week (Reisbick, Rosenblatt, & Mayer, 1975; Rosenblatt, 1965, 1969).

One of the consequences of these weaning-associated changes is a net deficit between milk energy provided by the dam and the nutritional and hydromineral needs of her litter. This deficit progressively increases as the offspring grow older. When weanling-age pups are denied access to solid food and water, their body growth is impaired relative to pups that can supplement their diet with these alternative resources (Alberts & Gubernick, 1983). Transition to solid food and water could thus be viewed as an adaptive response by the infant to rising energy stress.

In the present article, we describe investigations of the development of independent ingestion. We focus specifically on the hypothesis that the sufficiency of maternal milk as sole nutritional resource functions as an instigating or regulating factor in the weaning process. To test this possibility, we employed two methods to manipulate milk supply and measured the onset and course of early feeding and drinking in rat pups.

Experiment 1

It is possible to create conditions of differential milk supply per pup by altering the size of the litter (Smart, 1983). Babicky, Ostadalova, Parizek, Kolar, and Bibr (1973) culled and added pups to litters on Day 2, thereby creating nests of 3, 8, or 15 infants. Onset and duration of weaning were equivalent in these different-sized litters, which led to the conclusion that neither volume nor content of milk affects weaning (Babicky, Parizek, Ostadalova, & Kolar, 1973).

Across the lactational cycle, however, total amount of milk production by the dam correlates positively with the amount of sucking stimulation she receives, which is usually a function of litter size. Moreover, the average body size of pups and, to some extent, the energy requirements of individual pups are negatively correlated with litter size (Babicky, Ostadalova, et al., 1973; Edwardson & Eayrs, 1967; Leon & Woodside, 1983). Differences in milk yield related to litter size may partially compensate for the specific demands of different-sized litters and thereby preserve the relative growth rates of offspring (Drewett, 1983).

By manipulating litter sizes early in development, it is possible that Babicky, Ostadalova et al. (1973) and Babicky, Parizek, et al. (1973) allowed the dams to make compensatory adjustments in milk production, which might have masked the effects in individual pups. In the present experiment we minimized this potential confound by deferring alteration in litter size until a point just prior to the expected onset of feeding, as established by pilot studies. Lactational output of dams and energy requirements of offspring do not adjust rapidly (Fleming, 1976a, 1976b), so we could expect that our manipulation of litter size, delayed until the end of the sucking phase, would create contrasting conditions of milk availability to offspring in large versus small litters.

Method

Subjects. A total of 10 multiparous Sprague-Dawley female rats and their litters (80 pups) served in this experiment. All mothers were outbred from stock originally obtained from Charles River (Portage, Michigan) and were born in the Animal Behavior Laboratory colony at Indiana University. Litters were matched by birth date to form five age-matched pairs. We deleted one pair due to dermatological symptoms in one mother. Three days after birth (Day 0) litters were reduced to 8 pups (4 males and 4 females) each. Until experimentation began (evening of Day 9), litters were housed in standard polypropylene maternity cages (48 × 20 × 26 cm). Purina Rat Chow and water were available ad lib. Throughout the experiment a 16:8 hr light/dark cycle (lights on at 0700 daily) was in effect, and litters were left undisturbed except during data collection.

Apparatus. The experimental cage (see Figure 1) was designed to provide separation of the mothers' and pups' food and water intake. It consisted of a large nesting area (30 × 32 × 35.5 cm) and two separate feeding compartments, one for the pups (24 × 12 × 35.5 cm) and one for the mother (24 × 20 × 35.5 cm). An opening (12 × 2.5 cm) at the base of the aluminum wall between the nesting area and the pups' feeding compartment permitted passage to pups only, and an indentation (20 × 5 cm) at the top of the wall between the nesting area and the mother's feeding compartment allowed only mothers to cross from one side to the other. A Plexiglas wall (24 × 35.5 cm) separated the two feeding compartments. The pups' feeding compartment contained a food tray covered by an aluminum lid with five holes (2 cm in diameter), which prevented food spillage, and a water spout. Similarly, the mother's feeding compartment contained a feeder specially designed to prevent spillage, and a water spout.

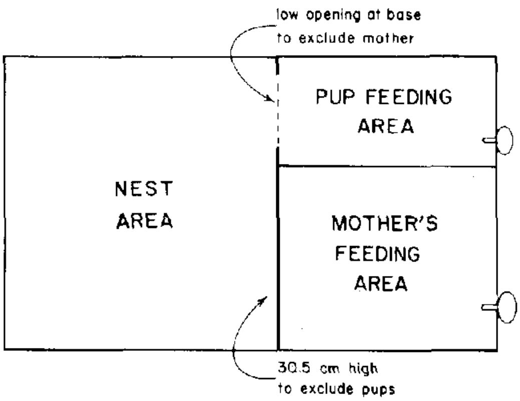

Figure 1. Floor plan of experimental cage that provided adjacent but exclusive feeding areas for mother and offspring. (The partition separating the two feeding areas was Plexiglas, permitting visual contact.)

We measured food intake (accurate to 0.01 g) and pup's body weight (accurate to 0.1 g) with an analytical balance (Fisher Ainsworth, Model MX-200) and mothers' body weight with a balance accurate to 0.5 g (Ohaus, Autogram 1000).

Procedure. On the evening of Day 9, we transferred mothers and their litters to experimental cages. The next morning (Day 10), we marked pups and, at 1030 hours, recorded body weights of mothers and their pups. Every 12 hr thereafter (1030 and 2230 daily), we measured body weights as well as food and water intake of the respective parties. Any food or water removed was replaced at those times.

On the morning of Day 14, we removed 4 pups from one litter and added them to the corresponding age-matched litter, thereby creating one 4-pup (milk-rich) and one 12-pup (milk-poor) litter. We repeated the procedure with the remaining two pairs on the evening of Day 14. The pups removed from a litter were matched for body weight to pups that remained with the natural mother. We recorded body weights and food and water intake daily at 1030 and 2230. The experiment lasted until the evening of Day 21.

Data analysis. There were no differences in body weight across age as a function of time on Day 14 at which litter sizes were changed—main effect of time, $F(1, 6) = 1.35$, $p > .25$; interaction of Time × Age, $F < 1$—and we therefore combined the data. We compared the onset of solid food and water intake between milk-rich and milk-poor pups with two separate, directional t tests for independent groups. Onsets of independent feeding and drinking were designated by the first occasions on which at least 1.00 g of powdered chow or 2.00 ml of water was consumed (by one or more pups). Because there emerged significant differences in body weight between milk-rich and milk-poor pups subsequent to the change in litter size (see below), we analyzed food and water intake relative to pups' body weights. For each set of milk-rich pups and their milk-poor siblings, we computed daily average food and water intake, and body weight. From these data we then calculated food and water consumption per pup as a percentage of body weight. We conducted two separate 2 × 4 × 7 analyses of variance (ANOVAs; Litter Size × Litter within Litter Size × Age; Winer, 1971) for food and water intake, respectively. To compare average body weights across age of milk-rich pups and their milk-poor siblings, we carried out two additional ANOVAs, one for the days prior to and one for the days following change in litter size (a 2 × 4 × 5 and a 2 × 4 × 7 ANOVA, respectively).

Results

Pups that entered weaning in large and small litters differed in onset of both independent feeding and drinking, $t(6) = 2.40$, $p < .03$, one-tailed, in both cases. On the average, milk-poor pups began to ingest solid food at 17.9 days and water at 18.4 days of age, whereas milk-rich pups did not initiate feeding and drinking until 19.3 and 19.8 days of age, respectively.

Figure 2 shows the average amount of food ingested per pup, expressed as percentage of body weight, in the milk-rich and milk-poor groups across age. Figure 3 shows the corresponding data for water intake.

As can be seen in Figures 2 and 3, the difference in onset of weaning was paralleled by differences in amount of food and, to a lesser extent, amount of water consumed. Litter size had a significant effect on food intake per pup, $F(1, 6) = 17.85$, $p < .01$, but affected water consumption only marginally, $F(1, 6) = 5.12$, $p < .065$. Pups clearly increased both food and water intake over the course of the third week, $F(6, 36) = 88.75$, $p < .01$ and $F(6, 36) = 35.15$, $p < .01$, respectively, and the magnitude of

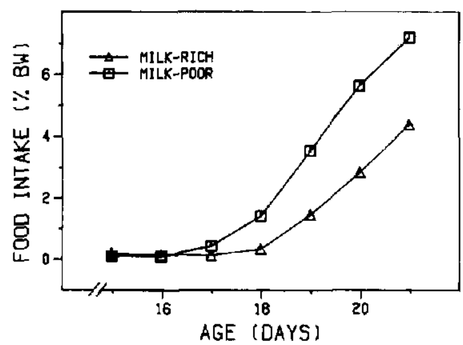

Figure 2. Mean food intake per pup, expressed as percentage of body weight, across age for the milk-rich (triangles) and milk-poor (squares) groups.

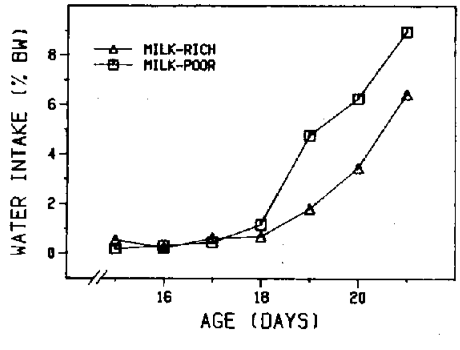

Figure 3. Mean water intake per pup, expressed as percentage of body weight, across age for the milk-rich (triangles) and milk-poor (squares) groups.

this increase was found to depend on litter size, $F(6, 36) = 7.13, p < .01$ and $F(6, 36) = 2.39, p < .05$ for food and water, respectively. Once milk-poor pups began to feed on alternate resources, they tended to consume greater amounts than milk-rich pups, at least until the end of the third week. A 21-day-old milk-poor pup ingested, on the average, 7.2% of its body weight in food and 9.0% in water; a same-age milk-rich pup consumed, on the average, only 4.4% and 6.4% of its body weight in food and water, respectively.

Figure 4 shows average body weight across age for milk-rich pups and their siblings in the 12-pup litters. The two groups did not differ from each other during the first 4 days of measurement (for both litter size and Litter Size × Age, $F < 1$). However, following litter-size manipulation milk-rich pups were reliably heavier than their milk-

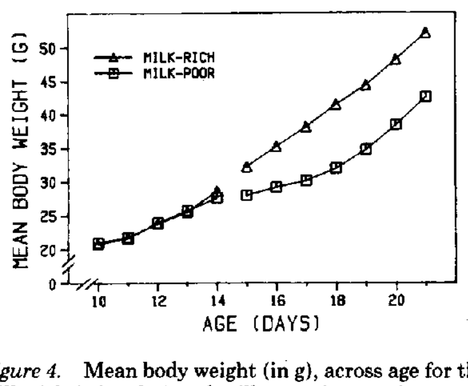

Figure 4. Mean body weight (in g), across age for the milk-rich (triangles) and milk-poor (squares) groups.

poor siblings, but both groups significantly increased body weight from Day 15 to Day 21: litter size, $F(1, 6) = 8.56, p < .03$; age, $F(6, 36) = 201.26, p < .01$; and Litter Size × Age, $F(6, 36) = 6.19, p < .01$.

The depressed weight gain by milk-poor pups (1.4% of their body weight) concurrent with the drastic increase in body weight by milk-rich pups (12.9% of their body weight) immediately following the change in litter size supports our assumption that the present procedure effectively established different levels of relative milk supply. Milk-poor pups rapidly returned to their original rate of body weight gain upon initiation of feeding (above 6.0% of their body weight from Day 18 on), which reflects the regulatory aspect of early transition to solid food under energy stress.

Discussion

The results of Experiment 1 suggest that initiation of solid food and water intake is sensitive to variations in maternal milk availability. Pups that experienced a sudden milk deficit incorporated solid food into their diet earlier than pups that had access to relatively more mother's milk (Figure 2). Scarcity of mother's milk also tended to accelerate ingestion of water (Figure 3); this effect, however, was less pronounced.

Regardless of litter size, pups initiated solid food intake prior to water intake. A temporal lag between onset of feeding and onset of drinking is characteristic for the development of independent feeding and drinking in rat pups (Babicky et al., 1972; Cheng, Rozin, & Teitelbaum, 1971; control groups in Experiment 2 below).

The results of Experiment 1 were in the direction predicted by our hypothesis that deficits in nutritive energy during infancy can accelerate weaning. It appears that Babicky, Ostadalova, et al. (1973) and Babicky, Parizek, et al. (1973) failed to obtain similar results because they manipulated litter size on Day 2 and thereby provided the dams at least 2 weeks to adapt to the various levels of suckling stimulation associated with different litter sizes. In contrast, our manipulation was performed on Day 14.

Nevertheless, it remains premature to conclude from Experiment 1 that milk availability regulates weaning. It is possible, for instance, that litter-size manipulation affected behavioral interactions between mother and offspring that facilitated weaning.

The amount of time mothers spend with their litters is inversely related to litter size (Ader & Grota, 1970; Grota, 1973). In addition to magnifying differences in milk availability, differences in maternal presence per se may have affected the outcome. Although maternal presence in the nest increases pups' likelihood to egress out of the nest, her presence in the vicinity outside the nest stimulates excursions to an even greater degree (Alberts & Leimbach, 1980; Galef, 1971; Galef & Clark, 1971a, 1971b, 1972).

In the present study, maternal absence from the nest was directly associated with her presence in her feeding compartment. Through migration into their feeding compartment, however, pups could reestablish visual contact with the dam, an important factor in initial nest egression and food intake (Alberts & Leimbach, 1980; Galef & Clark, 1971a). Milk-poor pups thus may have had more exposure to their feeding compartment as well as to the presence of an adult near their food source than milk-rich pups. Both of these factors might have facilitated transition to solid food.

In addition, the probability of a pup's entry into the feeding compartment is greater in a litter of 12 than in one of 4 pups. Given the importance of social facilitation effects in initial solid food intake (Galef, 1971; Galef & Clark, 1971b, 1972), this difference between litters might also have contributed to the observed effects. To determine the role of milk availability in weaning unconfounded by such factors, we conducted a second experiment.

Experiment 2

Experiment 2 was designed to measure onset and rate of weaning in pups sustaining different levels of milk availability, under equivalent conditions of maternal and littermates' behavior. One way to alter milk transfer without affecting maternal behavior is to remove surgically some of the dam's nipples (Codo & Carlini, 1979). This procedure, however, reduces pup's opportunity to suckle and thus introduces a change in mother–offspring contact in addition to that of milk availability. A related procedure that circumvents this problem, but retains the desired effects of mammectomy, is nipple ligation. Dams whose mammary ducts have been ligated are virtually indistinguishable from lactating mothers except that they provide no milk (Lynch, 1976). By presenting ligated mothers in place of lactating mothers for different amounts of time each day, we could thus effectively vary milk availability while meeting the criteria that total amount of maternal contact and litter size were equivalent but milk supply was not.

Method

Subjects. We used a total of 40 multiparous Sprague-Dawley female rats and their litters (320 pups) in this experiment. Litters were matched on the basis of birth date to form 20 pairs. We had to delete 2 pairs (4 mothers and 32 pups) due to death of 2 mothers, each from a different condition, which left a final number of 18 pairs of litters (36 mothers and 288 pups).

One member (mother plus litter) of each pair was randomly chosen to serve in one of the experimental groups and was maintained under the same conditions as described in Experiment 1. The other member of each pair served as foster mother and litter. They were housed in the same room as experimental litters but remained in standard maternity cages, as described above, throughout the entire experiment unless specified otherwise.

Surgical procedure. By surgically ligating the nipples of postparturient dams, we created caretakers that displayed behavioral, physical, and physiological characteristics typical of rat mothers but did not provide milk. Pups readily attached to the ligated nipples of these dams, and both the female and pups appeared to actively maintain the nursing relationship. Body weight measures confirmed that milk transfer was prevented. On Day 14, at least 8 hr prior to the evening data collection, we anesthetized foster mothers with chloral hydrate (400 mg/kg), made a small incision at the base of each nipple, ligated the collecting duct with surgical silk (Ethicon Type B, Size 5-0), and sutured closed the incision. Sham-ligated mothers were treated identically, but no incision was made. We merely pulled a threaded surgical needle through the base of each nipple. The entire procedure lasted 30–60 min.

Procedure. Until Day 14, experimental litters were treated as described in Experiment 1 except that we obtained daily measurements of body weights and food and water intake at 0930 and 2130 hours. Starting on the evening of Day 14, we replaced experimental mothers each day with the appropriate foster mothers for 10 or 16 hr. Experimental litters thus spent either 14 or 8 hr per day with their own mother and 10 or 16 hr, respectively, with a foster mother. For 12 litters the foster dam did not lactate, and pups thus had access to milk for only 8 (8-hr group; 6 litters) or 14 hr (14-hr group; 6 litters) daily. The remaining 6 litters always had a lactating mother available (24-hr group), but half of them spent 10 and the other half 16 hr each day with a sham-ligated, lactating dam. Thus, in the present experiment, litter size was constant (8 pups), and all litters were continuously attended by a maternally responsive rat. There were three levels of milk availability, beginning on the evening of Day 14. Pups resided with a lactating rat for either 8, 14, or 24 hr per day. Assignments to the four conditions were random, with the restriction that experimental litters were balanced across conditions with regard to average pup body weight as determined on the evening of Day 14.

We continued to record experimental pups' body weights as well as their food and water intake daily at 0930 and 2130 hours. No data were available for foster pups. Mothers were weighed when exchanged between experimental and foster litters, that is, at 0730 and 2130 in the 14-hr and half of the 24-hr group, and at 1330 and 2130 in the 8-hr and the remaining half of the 24-hr group. We recorded food and water intake of experimental mothers at 2130, but no intake data were available for foster mothers because they never entered the feeding compartment. As with Experiment 1, this experiment lasted until the evening of Day 21.

Data analysis. As before, we designated independent feeding and drinking at the first measurement in which at least 1.0 g of powdered chow or 2.0 ml of water was removed. A 2 × 3 × 12 ANOVA (Hours × Litters within Hours × Age; Winer, 1971) revealed no differences in body weight between the two conditions comprising the 24-hr control group (for both hours and Hours × Age, $F < 1$), and we therefore combined their data.

We used two one-way ANOVAs (Winer, 1971) to compare onset of feeding and drinking between the three groups, a 3 × 6 × 5 ANOVA (Hours × Litters within Hours × Age) to compare body weights prior to manipulation, and three 3 × 6 × 7 ANOVAs to compare food and water intake relative to body weight, and body weights following introduction of foster dams between groups.

Results

Different levels of milk availability were associated with significant differences in the onset of independent feeding and drinking in the three groups, $F(2, 15) = 3.875$, $p < .05$ and $F(2, 15) = 35.323$, $p < .01$, respectively. Subsequent orthogonal comparisons on treatment means (Edwards, 1972) revealed that the 14-hr group initiated neither solid food nor water intake significantly earlier than the 24-hr group, $t(15) < 1$ and $t(15) = 1.205$, $p > .10$, one-tailed. However, 8-hr pups differed significantly from the average of the 14- and 24-hr groups on both dependent measures, $t(15) = 2.750$, $p < .01$, one-tailed, and $t(15) = 8.362$, $p < .01$, one-tailed, for food and water intake, respectively. On the average, 8-hr pups initiated feeding at 17.2 and drinking at 17.0 days of age compared with 18.2 (food) and 19.0 (water) days of age in the 14-hr group and 18.0 (food) and 19.3 (water) days of age in the 24-hr group.

The course of initial feeding presented in Figure 5 shows the average amount of food ingested per pup, expressed as a percentage of body weight, in the three groups. Beginning on Day 17, 8-hr pups consistently consumed greater amounts than 14- or 24-hr pups, which did not differ from one another. On Day 21, solid food consumption of 8-hr pups was 10.0% of their body weight compared with 7.3% and 5.7% in the 14- and 24-hr groups, respectively. The Hours × Age interaction, $F(12, 90) = 5.91$, $p < .01$, as well as both main effects proved to be significant, hours, $F(2, 15) = 14.43$, $p < .01$, and age, $F(6, 90) = 204.80$, $p < .01$.

Average water intake per pup, relative to body weight, is shown in Figure 6 for all three groups across age. Comparison with Figure 3 shows that, in contrast to the results of Experiment 1, the present manipulation produced greater differences in the

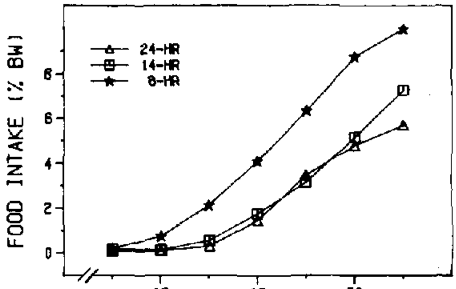

Figure 5. Mean food intake per pup, expressed as percentage of body weight, across age for the 24-hr (triangles), 14-hr (squares), and 8-hr (stars) groups.

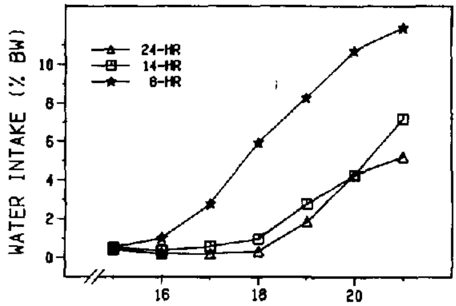

Figure 6. Mean water intake per pup, expressed as percentage of body weight, across age for the 24-hr (triangles), 14-hr (squares), and 8-hr (stars) groups.

transition to drinking than in the transition to independent feeding. Beginning on Day 18, 8-hr pups drank considerably more water than 14-hr pups, which consumed slightly more water than 24-hr pups. The mean amounts of water consumed on Day 21 were 11.9%, 7.2%, and 5.2% of body weight in the 8-, 14-, and 24-hr groups, respectively. ANOVAs revealed a significant Hours × Age interaction, $F(12, 90) = 9.20$, $p < .01$, as well as a significant hours, $F(2, 15) = 43.09$, $p < .01$, and age, $F(6, 90) = 101.09$, $p < .01$, effect.

Average daily body weights for the three groups are shown in Figure 7. The groups did not differ from one another prior to the introduction of foster dams: hours, $F < 1$; Hours × Age, $F(8, 60) = 1.11$, $p > .35$. However, differential restriction to a lactating dam produced significant differences

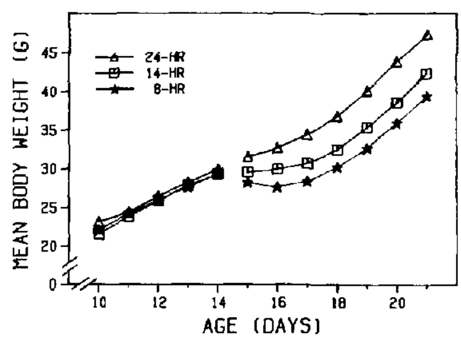

Figure 7. Mean body weight (in g), across age for the 24-hr (triangles), 14-hr (squares), and 8-hr (stars) groups.

in body weight between the groups, $F(2, 15) = 8.21$, $p < .01$, and this effect depended on age: Hours × Age, $F(12, 90) = 3.75$, $p < .01$. Pups in all three groups showed significant increases in body weight during the period of manipulation, $F(6, 90) = 373.43$, $p < .01$.

Introduction of nonlactating mothers resulted in an initial loss of body weight in 8-hr pups (4.0%), whereas body weights of 14-hr pups merely ceased to increase (0.9%). By supplementing their diet with solid food and water, however, 8-hr pups prevented any further weight losses. After 3 days they achieved the same levels of relative weight gain shown prior to experimental reduction of milk supply, that is, 6.2% on Day 18. Pups in the 14-hr condition also required 3 days to reach original levels of weight gain despite the milder effect of milk deprivation on their growth. Change in caretaker also slightly affected weight gain of 24-hr pups; on the average, their body weights increased only 3.6% on Day 15 compared with 6.0% which was common among all three groups prior to rotation of the mothers.

Discussion

The results of the present experiment corroborate those of Experiment 1, indicating that onset of weaning is affected by milk availability. In both experiments, relatively greater energy deficits were associated with earlier initiation of independent feeding and drinking. Experiment 2 was designed to eliminate behavioral differences, observed in Experiment 1, associated with litters of different sizes. With this potential confound eliminated, weaning was nevertheless accelerated in pups for which milk availability was most restricted, that is, to 8 compared with 14 or 24 hr daily. This finding is consistent with the view that weaning is an energy-dependent phenomenon.

Limiting pups' access to a lactating dam to 14 hr per day, however, did not produce more rapid transition to solid food and water than in pups with continuous access to a lactating dam. This outcome was unexpected, especially because the 14-hr arrangement produced sufficient energy stress to result in a transient attenuation of pups' growth. It appears that levels of energy constraint between nests must be relatively discrepant for onset of independent feeding and drinking to differ significantly.

In the present experiment, pups that repeatedly experienced prolonged periods of milk deprivation (16 hr daily) began to ingest water as early as solid food, which differs from the transitional profile seen in other situations (e.g., Babicky et al., 1972; Babicky, Ostadalova, et al., 1973; Babicky, Parizek, et al., 1973; Cheng et al., 1971; Experiment 1). The reasons for this discrepancy are unclear and cannot be resolved on the basis of the present data. In any event, the results of the present experiment show that 17-day-old pups can compensate for hydrational and nutritional deficits.

General Discussion

The results of the present series of investigations indicate that decreased milk availability is associated with earlier emergence of weaning in the infant Norway rat. We do not believe that milk availability per se is a stimulus for weaning. Rather, we interpret the present results as suggesting that the transition from suckling to independent feeding and drinking is mediated by the pup's sensitivity to its own energy balance or some correlated cue. Both manipulations used in the present studies, increasing the number of competitors for mother's milk (Experiment 1) or decreasing the temporal availability of a lactating dam (Experiment 2), resulted in a net energy deficit in the growing pup. Both manipulations accelerated weaning relative to same-age groups of pups with relatively greater supplies of milk. In both experiments, milk-poor pups demonstrated the capacity to respond to the imposed energy deficit by adding independent feeding and drinking to their previously exclusive suckling habit.

In the normal course of postnatal events, around Day 15 there are quantitative and qualitative changes in the mother's milk that result in overall reduction in energy provision to the litter (Babicky et al., 1970). In fact, due to the pups rapid growth, increased thermogenesis, and locomotor maturation around this time, the actual deficit realized by the offspring is even greater than would be estimated from the age-related changes in maternal milk. Nevertheless, under normal circumstances, the weanling rat displays a steady, positive growth trajectory during the transition from an exclusive diet of mother's milk to one of solid food. In contrast, experimental reductions in milk supply negatively affected growth rates, which suggests that pups did not compensate for the abrupt, induced energy deficits by immediately altering their ingestive behavior. However, by incorporating food energy into their diet, pups in these studies counteracted early weight loss and regained their original growth rates.

Weaning can be viewed as an adaptive reaction of the infant rat to the emergence of insufficient energy support from the mother for normal development. Whereas we interpret the findings of the present two experiments as supporting an energy mediation of weaning, the results may also be amenable with the view that the transition to independent intake is secondary to a decline in suckling produced by changes in milk availability. Whether our manipulations affected the pup's energy balance directly, or indirectly by altering its tendency to suckle, we have not conclusively determined. We doubt, however, that changes in time spent suckling per se significantly influenced our findings. We noticed in Experiment 2 that ligated mothers spent slightly more time in the nest than lactating dams, thereby providing the milk-poorer pups with more time to suckle than the milk-richer pups. These observations, together with the relations between changes in pups' body weights and the onset of food intake, suggest to us a direct contribution of energy factors to weaning. The precise underlying mechanisms remain to be identified.

Developmental changes in the sensory and neural controls of suckling (Almli, 1978; Williams, Hall, & Rosenblatt, 1980) may also be important variables in the regulation of weaning. Furthermore, other, nonenergy factors, including social cues provided by adult conspecifics, are known to affect early intake of solid food (Galef, 1971; Galef & Clark, 1971a, 1971b, 1972).

It should be noted that some investigators have reported ingestion of solid food by pups at earlier ages than those reported here (e.g., Babicky, Ostadalova, Parizek, & Kolar, 1971; Babicky, Ostadalova, et al., 1973; Galef, 1971; Redman & Sweney, 1976). Such variations can be explained by the investigators' use of different diets, smaller cages with different internal arrangements, and less stringent criteria for determining onset of ingestion. The purpose of the present studies, however, was not to specify the age at which weaning begins. Our goal was to investigate the role of nutritive energy factors in modulating weaning. Moreover, the weaning process involves both a decrease of suckling as well as an increase of independent feeding and drinking; the present investigations addressed only the development of solid food and water intake.

Current analyses of the control of suckling versus those of feeding have led to conclusions that emphasize independent controls of these modes of ingestion. Hall and Williams (1983), for example, delineated instances in which the sensory, hormonal, physiological, and anatomical substrates of suckling are distinct and separate from those of feeding, particularly in the young pup. In contrast to this "separatist" perspective, we must also acknowledge the linkage of suckling and feeding in relation to the common denominator of nutritive energy. Beginning in the third week postnatally, the pup shows sensitivity to nutritive and hydrational properties of the diet consumed from the nipple (Hall, Cramer, & Blass, 1977; Hall & Rosenblatt, 1977, 1978; Kenny, Stoloff, Bruno, & Blass, 1979). In addition, its suckling patterns become increasingly controlled by its internal milieu (Blass, Kenny, Stoloff, Bruno, & Teicher, 1979; Bruno, Craigmyle, & Blass, 1982) and thus reflect characteristics of energy-regulated ingestive behavior.

In summary, the results of the present investigations demonstrate that, in contrast to the conclusion of Babicky, Ostadalova, et al. (1973) and Babicky, Parizek, et al. (1973), the dynamics of the nutritive energy relationship between mother and offspring play an active, modulating role in weaning. When this relationship no longer favors uninterrupted growth of the young, the pups seek alternate dietary sources outside the nest, thereby emancipating themselves from direct dependence on maternal resources.

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