Weaning in Rats: II. Pup Behavior Patterns

EDDA THIELS
JEFFREY R. ALBERTS
Department of Psychology
Indiana University
Bloomington, Indiana

CATHERINE P. CRAMER
Department of Psychology
Dartmouth College
Hanover, New Hampshire

In this study, litters of rat pups and their mothers were continuously video-monitored from Day 14 to Day 35 postpartum in order to describe the behavioral changes that occur during that period. Prior to the onset of solid food intake (Day 18), pups spent most of their active time suckling. During Days 18 to 26, feeding, drinking, grooming, and play-fighting rapidly became frequent daily activities, while suckling gradually began to decline. By Day 28, pups' food and water intake relative to body weight and time allocated to the new behaviors reached asymptote. Pups nevertheless continued to suckle until Day 34. These results suggest that (1) the transition from milk to solid food is embedded in a multitude of behavioral changes; (2) these behavioral changes have distinct temporal characteristics; and (3) the developmental period between Days 14 and 34 can be divided into three phases.

> Apart from the fascination and the self education of watching the developing of any form of life from its early protoplasmic simplicity into that complex maturity, there is solid scientific reason that . . . Psychology has much to hope from minute and accurate records of the developmental periods of young animals of all species (Small, 1899).

Weaning is an integral part of mammalian development. Infant mammals subsist entirely on mother's milk; as adults, however, they neither ingest milk nor depend on a conspecific for nutrition. Extensive research has been devoted to uncovering the dynamics that underlie the transition from nutritive dependence to independence, especially in rat pups (e.g., Babicky, Ostadolova, Parizek, Kolar, & Bibr, 1973; Babicky, Parizek, Ostadalova, & Kolar, 1973; Blake & Henning, 1983; Blake, Okuhara, & Henning, 1984; Galef, 1971; Galef & Clark, 1971, 1972;

Reprint requests should be sent to Dr. Catherine P. Cramer, Department of Psychology, Dartmouth College, Hanover, NH 03755.

Received for publication 31 July 1989
Revised for publication 26 April 1990
Accepted at Wiley 11 July 1990

Developmental Psychobiology 23(6):495–510 (1990)

CCC 0012-1630/90/060495-16$04.00

Henning, 1980; Lichtman & Cramer, in press; Thiels & Alberts, 1985; Thiels, Cramer, & Alberts, 1988; Williams, Hall, & Rosenblatt, 1980; Williams, Rosenblatt & Hall, 1979). Nevertheless, satisfying theories on the proximal (as well as ultimate) causes of this crucial developmental epoch remain to be advanced. Although lack of detailed description of a phenomenon is hardly the sole reason for our incomplete understanding, we share with Small the belief that gaining understanding has much to benefit from "minute and accurate records" of it. Accordingly, we present here the findings from comprehensive longitudinal observations of rat pups as they progress through the weaning period.

In contrast to previous reports (Bolles & Woods, 1964; Lee & Williams, 1977; Small, 1899), our findings are based on continuous observations of rat pups, beginning before the onset of solid food intake until the complete termination of suckling. Furthermore, we monitored a variety of behaviors, including pups' interactions with each other as well as with their mother during the weaning period. The companion paper (Cramer, Thiels, & Alberts, 1990) provides a detailed description of those mothers' behavior patterns during the same time period.

The pup behaviors we charted were: sleeping or resting, nipple attachment stretch response (postural reflex associated with milk receipt during nipple attachment), independent feeding, independent drinking, self-grooming, and play-fighting. Each of these behaviors is easily identifiable, and together they encompass a large portion of pups' daily activities. We monitored and encoded the behavior of one identified pup per litter, the same pup served as "focal" pup throughout the entire observation period (Day 14 to 32–35 postpartum). We also monitored pups' daily solid food and water intake and body weight gain.

Method

Subjects

Six multiparous and one primiparous female Sprague-Dawley rats and their litters (56 pups) served in this experiment. One dam died of unknown causes during the experiment, leaving a total of 6 mothers and 48 pups. Dams were outbred from stock originally obtained from Charles River (Portage, MI) and were born in the Animal Behavior Laboratory colony at Indiana University. The animals' housing conditions are described in the companion paper (Cramer et al., 1990).

Apparatus

Experimental habitats were identical to those described in Cramer et al. (1990). Pups' body weights and food intake were measured accurate to 0.1 g and 0.01 g, respectively, with an analytical balance (Mettler, Type PC 400). Continuous videographic records of the animals' behavior were obtained as described in the companion paper (Cramer et al., 1990).

Procedure

On the evening of Day 9 mothers and their litters were transferred to the experimental habitats. Around 2130 hr of Day 10, pups were earmarked for individ-

ual identification and daily measurements of their body weights begun. On the evening of Day 13 one pup from each litter (focal pup) was permanently marked with hair dye for recognition on videotape. Three of the focal pups were female and three of them male, and their body weights (M ± SEM = 28.1 ± 1.3 g) were representative of those of their littermates. Videography began that evening and continued until the end of experimentation, except for brief (30 to 50 min) daily interruptions to collect weight data and replace videocassettes. On the evening of Day 14, recording of pups' food and water intake every 12 hr (0930 and 2130 hr) daily commenced. Observations of a litter were terminated when, during a 24-hr day, more than 4 pups of a litter spent less than 11 consecutive min attached to their mother's nipples. Experiment duration therefore varied between 19 and 22 days of observation (M = 21 days, i.e., until Day 34 postpartum).

Data Analysis

A. *Behavior categories.* Each of the daily video records covered, on the average, 23.4 hr real time (*S.D.* = 0.2 hr); 12 hr real time were equivalent to approximately 1 hr videotape time. The first half of these records always included the day's 8-hr dark-period (room illumination off), and the second half consisted exclusively of light-period hours. To quantitatively code focal pups' behavior, daily video records were divided into successive 20-sec segments of real time (1.55 sec videotape playback time), and each segment was sampled for one of the following "target" behaviors in the focal pup:

(i) *Sleeping or resting*: The focal pup lies motionless, usually in a huddle with littermates.

(ii) *Nipple attachment*: The focal pup is attached to a nipple, or lying underneath the mother with its snout burrowed into her nipple region; both the pup's posture in relation to its mother's ventrum and occasional stretch responses (see below) helped to distinguish nipple attachment from huddling with the mother.

(iii) *Stretch response*: During a nipple attachment the focal pup extends its limbs and its body takes on a rigid, arching posture. This response occurs reliably upon milk release into the mammary ducts (Lincoln, Hill, & Wakerly, 1973) and is increasingly confined to the forelimbs and neck region in older pups (Hall, Cramer, & Blass, 1977).

(iv) *Independent feeding*: The focal pup has its snout burrowed into the food tray; food handling and/or chewing motions may be discernible.

(v) *Independent drinking*: The focal pup's mouth is in contact with the tip of the water spout; licking motions are often easily discernible. (We coded drinking in only 5 of the 6 focal pups).

(vi) *Self-grooming*: The focal pup licks or scratches itself, or moves its forepaws back and forth along its cheeks and/or around its snout.

(vii) *Play-fighting*: The focal pup wrestles with a littermate, lying on top or underneath the other pup, and engages in rapid exchanges of forepaw strikes with the other pup's face; the vividness of pups' movements helped distinguish play-fighting from social grooming.

(viii) *Other activities*: The focal pup engages in none of the above behaviors (i.e., default behavior category).

If a focal pup engaged in more than one of these behaviors during a 20-sec segment, the temporally dominant behavior was assigned to that segment. Sampling was carried out by a trained observer who maintained consistently a high intrarater reliability throughout the data transcription (91 to 95% bin-to-bin concordance between repeated viewing of 10 sample tapes). An index of interrater reliability was obtained by comparing sampling of the pup observer to that of a second observer who sampled the video records for the dams' behaviors. Specifically, for each record we determined the percent of 20-sec segments during which, according to the pup observer, the focal pup was attached to the nipple, whereas according to the dam observer, the mother was *not* nursing. This mother-pup behavior combination, of course, presents an impossible event, and the resultant index therefore reflects interrater *dis*agreement. The interrater disagreement never exceeded 5% for any of the records and averaged 1.8% across all litters on all days.

B. *Behavior parameters.* For all target behaviors except "Other Activities," we computed the following measures: (1) total daily percentage occurrence (i.e., the total daily proportion of 20-sec segments); (2) the percentage occurrence during the first 11.7 recordng hr of each day (i.e., the "nighttime" record); and (3) the percentage occurrence during the remaining 11.7 recording hr of each day (i.e., the "daytime" record).

For the various active behaviors (nipple attachment, independent feeding and drinking, self-grooming, and play-fighting) we also determined various "bout" parameters. Each "bout" was defined as a string of successive 20-sec segments of the same behavior. With regard to nipple attachment, bouts were at least 3 successive segments in duration (i.e., 1-min real time). A nipple attachment bout could be disrupted by a single 20-sec segment of another behavior (e.g., stretch response or brief nipple detachment) without disqualifying as one continuous bout.

Pups were differentially active during the 24-hr cycle (see Day-Night pattern in Results, below) and, depending on age, spent more time awake during the daytime or nighttime. Bout parameters were calculated for the more active half of the pups' day, i.e., the record containing less percentage of sleeping and resting. This approach reduced the enormous mass of data to be analyzed and allowed us to describe more accurately the changes in the pups' activity profiles, undiluted by the inactive portion of their day.

C. *Intake data.* The first occasion on which a litter consumed at least 1.0 g of chow, or 2.0 ml of water, was designated as the onset of independent feeding or drinking, respectively. To compare pups' food and water intake across age (i.e., changes in nutritive demand), the intakes were adjusted relative to body weight. Thus, for each litter and day, total food and water intake and litter weight were determined, and from these data daily food and water intake per pup, as a percentage of average body weight, computed.

D. *Statistical comparisons.* To determine trends in the various dependent measures, comparisons were conducted on data collected from Days 14 through 32, the last day of complete data from all focal pups. Repeated measures ANOVAs were used to assess overall age-dependent changes, and, if appropriate, Tukey's HSD (honestly significant difference, at the 0.5 level) method (Hays, 1981) was employed for pairwise comparisons between means to identify patterns of change. Matched *t*-tests (Hays, 1981) were used to determine day-night differences.

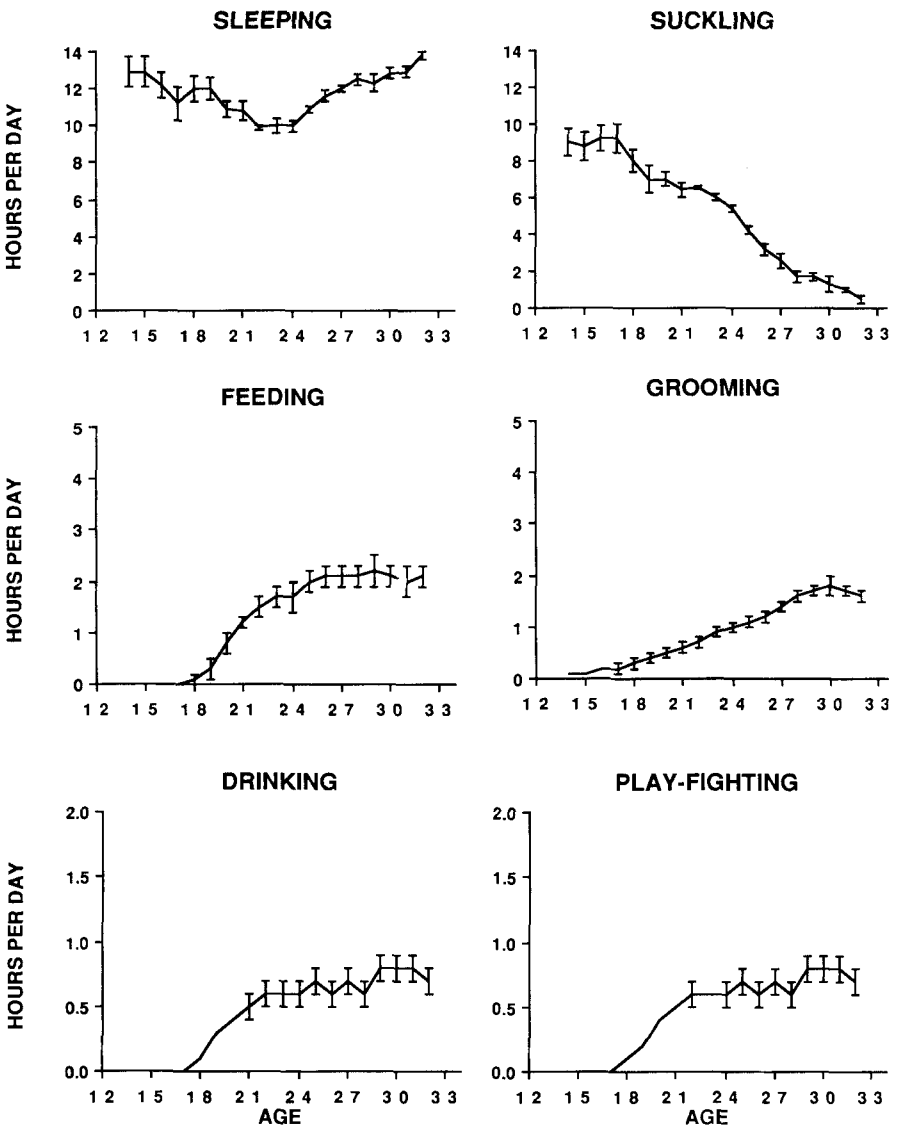

Fig. 1. Mean (±SEM) daily time focal pups spent sleeping or resting, suckling, independently feeding, independently drinking, self-grooming, or play-fighting across age. Note changes in scale of lower graphs.

Results

Daily Behavior Profiles

Figure 1 illustrates the average amount of daily time that focal pups spent in each activity across age. The observation period (Day 14 through 32)) was characterized by 3 distinctive phases: (1) Prior to the onset of solid food intake (M = Day 18), focal pups spent about half of the day sleeping and resting, and during most of their awake

time they were attached to their mother's nipples. (2) Days 18 through 24/25 were marked by the appearance and/or rapid increase of independent ingestion, grooming, and play-fighting. In contrast, the relative daily time that pups spent suckling began to decrease. (3) By about Day 25, pups' behavior profile had regained considerable stability, and only with regard to suckling and grooming their relative time allocation continued to change during the last 8 to 10 observation days.

This overall pattern of change evolved from the following specific trends: *Sleeping and resting* constituted at least 50% of the focal pups' day during the first and last few days of the observation period, whereas these behaviors constituted considerably less than 50% of the pups' daily time during the second phase; $F(18,90) = 6.05, p < .01$. Pairwise comparisons revealed that pups' sleep and rest time was significantly depressed during Days 20 through 25 relative to Days 14 and 15, as well as Days 30 to 32, and during Days 22 through 24 relative to Days 14 to 16 and 27 to 32 (critical difference = 1.87 hr).

As displayed in Figure 1, *nipple attachment* (with and without stretch response) was a stable and prominent component of pups' daily profile throughout the first phase. Beginning around Day 18, its relative occurrence began to decline in a stepwise fashion; $F(18,90) = 51.29, p, < .01$. One significant decrement in nipple attachment time was observed between Days 17 and 19, and a second one between Days 23 and 25 (critical difference = 1.76 hr). After Day 25 the decline proceeded more gradually, so that statistically significant decrements occurred only over three days combined throughout the last week of observation.

Some pups initiated *independent feeding* as early as Day 16; however, not all focal pups reliably fed until Day 18. Figure 1 shows that the amount of time focal pups allocated to solid food intake increased rapidly and steadily during the second phase of the observation period, this measure changed little and nonsystematically during the third phase; $F(18,90) = 52.66, p < .01$. Specifically, between Days 17 and 23 increments of 2 days combined consistently reached statistical significance (critical difference = 0.49 hr).

Pups initiated *independent drinking* 1 to 2 days after they began independent feeding. Similar to feeding, drinking rapidly became a stable component of focal pups' daily behavior profile and changed little during the third phase of the observation period; $F(18,72) = 42.48, p < .01$. Significant increments in the relative occurrence of drinking were noted between Days 19 and 20, and between Days 23 and 26 (critical difference = 0.12 hr).

Most focal pups displayed some *self-grooming* on Day 14 when we began observations. However, this behavior increased more than 20-fold between Days 14 and 28; $F(18,90) = 60.12, p < .01$. During that period increments of 3 to 4 days combined consistently reached statistical significance (critical difference = 0.33 hr), whereas no further increments were observed during the last few observation days.

Similar to feeding and drinking, *play-fighting* emerged as a new daily activity around Days 18/19. Figure 1 shows that the relative time allocation to play-fighting increased rapidly during the second phase and did not vary markedly from the attained asymptotic level during the third phase; $F(18,90) = 20.77, p < .01$.

Day-night pattern

Figure 2 illustrates that pups did not distribute their activities evenly across the 24-hr cycle. On Day 14, when the pups' day consisted almost entirely of

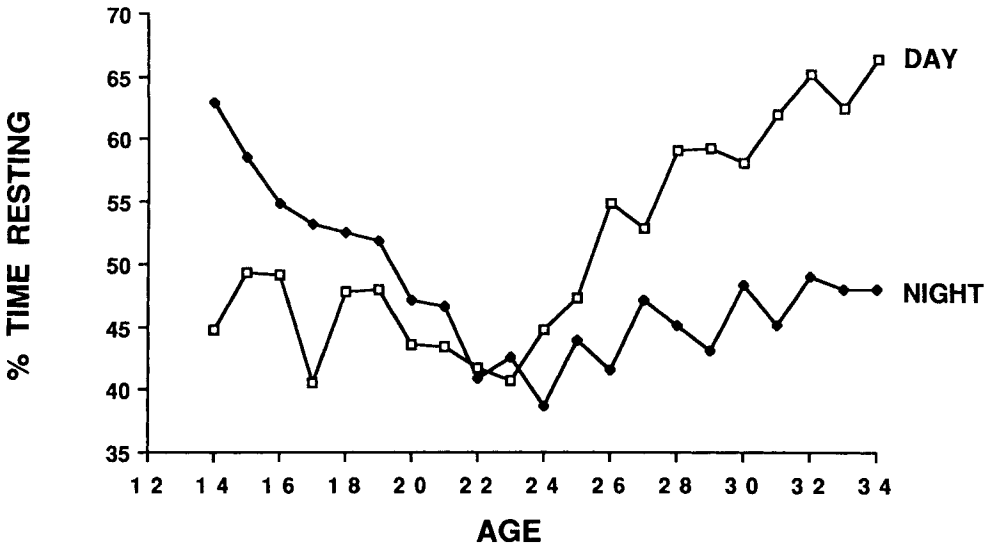

Fig. 2. Mean percentage time per nighttime record (solid symbol) and daytime record (open symbol) focal pups spent sleeping or resting across age.

sleeping and suckling, they rested significantly more during the nighttime than the daytime record, ($t(5) = 4.15$, $p < .01$, two-tailed), whereas they suckled more during the daytime than nighttime segment, $t(5) = 4.02$, $p < .01$, two-tailed.

The diurnal activity pattern disintegrated as pups' overall awake time increased and they began to engage in behaviors independent of the dam. During the second phase (Days 18 to 25) the focal pups displayed no reliable day-night differences with regard to any of the behaviors we sampled. Around Day 25 an apparent diurnal activity pattern reemerged. However, the reemergence of rhythmicity was coincident with a switch to greater nocturnal activity. On Day 32, the focal pups spent more time resting and sleeping during the daytime than nighttime records, ($t(5) = 5.21$, $p < .01$, two-tailed), whereas they engaged in more feeding and drinking at night than during the day, $t(5) = 3.59$, $p < .05$, two-tailed, and $t(4) = 4.45$, $p < .01$, two-tailed, respectively. No consistent, obvious diurnal patterns developed in any of the remaining behaviors during the second or third phase.

Bout parameters

Because we analyzed for each focal pup either the daytime or nighttime record (whichever record included relatively more awake time), the data presented below are mostly based on daytime records for Days 14 through 22 and nighttime records for the remaining observation days. Bout duration of a behavior was analyzed for only those days on which each focal pup displayed at least one bout of that behavior.

Figure 3 illustrates bout frequencies and durations for suckling (nipple attachment with and without stretch responses), independent feeding, independent drinking, and self-grooming across days. As can be seen in the top left panel, suckling time diminished as the pup grew older due to decreases in both frequency and duration of suckling bouts $F(18,90) = 11.80$, $p < .01$, and $F(17,85) = 7.30$, $p <$

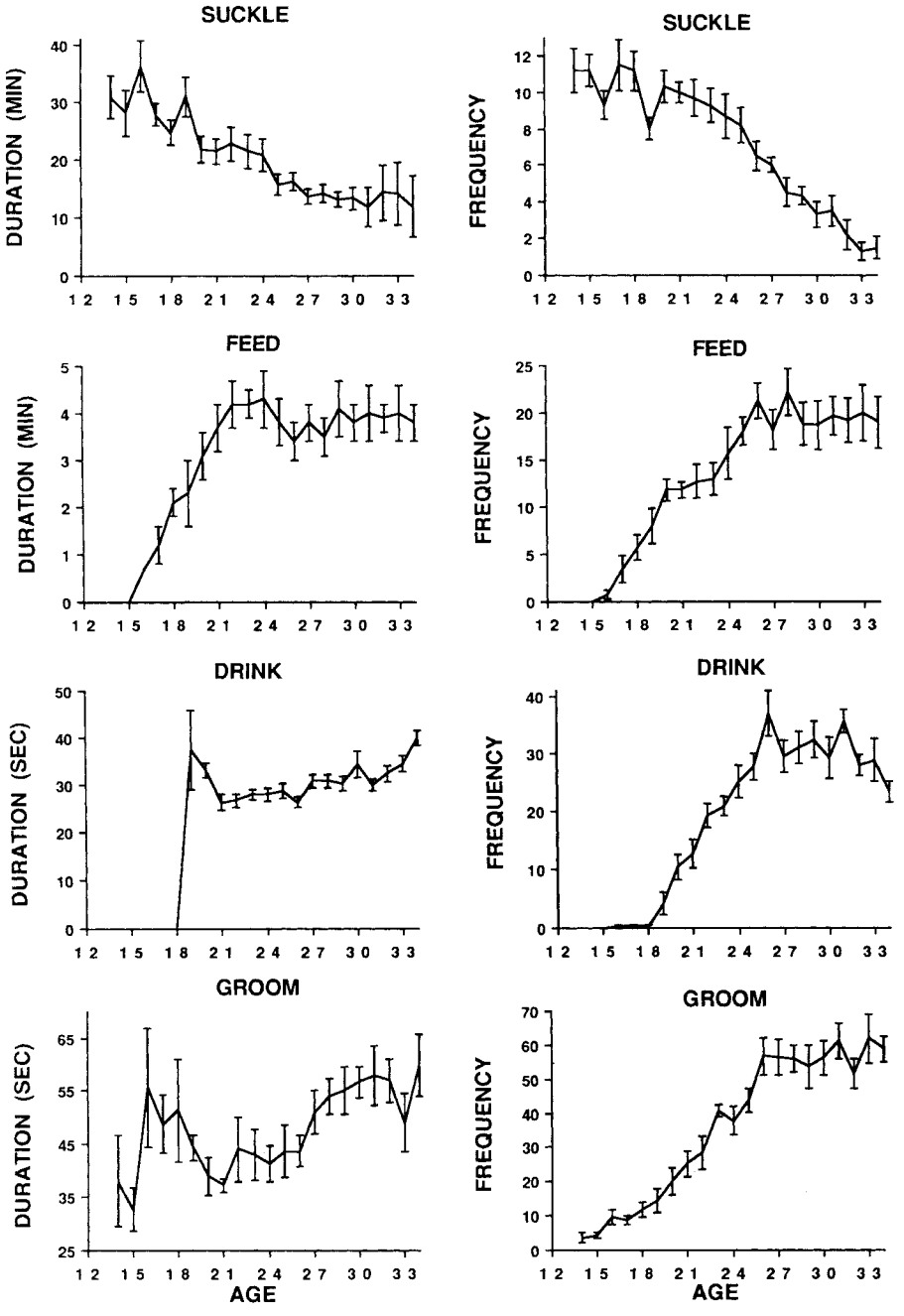

Fig. 3. Mean (±SEM) bout durations (left) and frequencies (right) during each day for the following behaviors: suckling, independent feeding, independent drinking, and self-grooming. Note different scales in each graph.

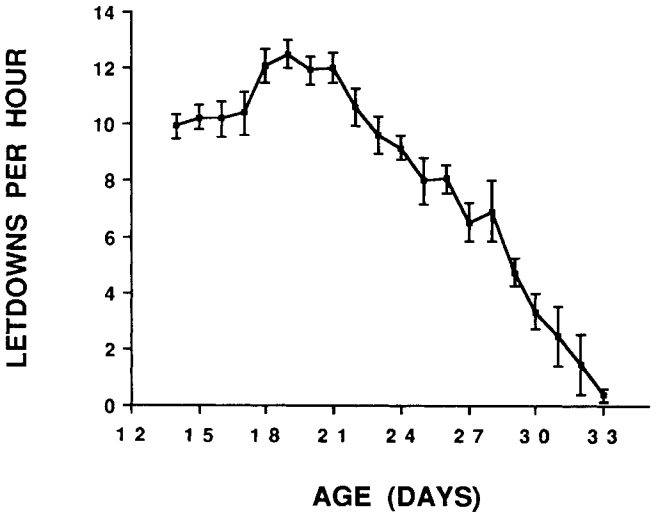

Fig. 4. Mean (±SEM) number of stretch responses per hour of nipple attachment.

.01, respectively. Pairwise comparisons revealed, however, that the change in suckling frequency did not reach statistical significance until the overall decline in suckling time was well underway on Day 26 (critical difference = 3.65 bouts/day). Suckling bout durations were variable both within and between pups, and the only systematic pattern that emerged was that bouts on Days 14 through 19 were significantly longer than those on Days 25 through 31 (critical difference = 33.52 min).

To gain some insight into changes in milk receipt coupled with these changes in suckling bout frequency and duration, we also analyzed the number of stretch responses, an index of milk letdown, during suckling. Figure 4 illustrates that from Days 14 to 26, pups received about 10 to 12 milk letdowns during each hour that they were attached to a nipple. The number of milk receipts per hour of attachment decreased markedly after Day 28 and reduced to about 2 milk letdowns per hour of attachment by Day 30 ($F(19,95) = 32.71$, $p < .01$; critical difference = 3.40).

As can be seen in the top right and bottom left panels of Figure 3, the rapid increases in the relative amounts of time that focal pups allocated to feeding and to drinking stemmed largely from pups engaging in more, rather than longer, feeding and drinking bouts as they grew older. However, both ingestive behaviors changed significantly across days in terms of both bout parameters, feeding frequency: $F(18,90) = 21.21$, $p < .01$, feeding bout duration $F(14,70) = 4.21$, $p < .01$, drinking frequency: $F(18,72) = 36.30$, $p < .01$, and drinking bout duration: $F(12,48) = 2.79$, $p < .01$. With regard to independent feeding, reliable increments in bout frequency and duration occurred primarily during the second phase of the observation period (i.e., Days 18 through 25) (critical difference = 6.63 for frequency, and critical difference = 4.07 min for duration). With regard to independent drinking, reliable frequency increments were also concentrated during the second phase (critical difference = 9.04), whereas bout durations did not vary systematically, except that bouts on Day 30 were significantly longer compared to

those on most other days (critical difference = .31 min). (Note that the temporal resolution of our behavior sampling was constrained to 20-sec segments. Therefore, the results may be biased against variation, especially of short-duration behaviors such as drinking).

Age-dependent increases in self-grooming (bottom right panel of Figure 3) and play-fighting originated primarily from changes in bout frequency rather than duration across age, grooming frequency: $F(18,90) = 46.38$, $p < .01$, grooming bout duration: $p > .05$, play-fighting frequency: $F(18,90) = 29.39$, $p < .01$, play-fighting bout duration: $p > .05$. Grooming frequencies increased continuously from the beginning of the observation period until Day 26 (critical difference = 12.62), and remained relatively stable thereafter. Significant increments in play-fighting frequency were observed between Days 19 and 20 and between Days 22 and 26 (critical difference = 8.86). Although significant day-to-day variations in play-fighting frequency were also noted during the final observation week, no systematic directional trend emerged.

Food and water intake

Figure 5 depicts pups' average solid food and water consumption, both in absolute amount and relative to body weight, across age. In parallel with the amounts of time they spent feeding and drinking, pups' relative food and water intakes increased significantly with age, $F(17,85) = 134.75$ and $F(17,85) = 100.93$, both $ps < .01$, for food and water intake respectively. Post-hoc comparisons revealed that there was a series of significant increments in food intake between Days 17 and 25, (critical difference = 2.04), all $ps < .05$. Relative food intake reached asymptote on Days 24 to 25 and did not change systematically thereafter.

Steep increments in relative water intake were concentrated between Days 18 and 26 (critical difference = 3.55). Although *relative* food and water intakes ceased their incline around Days 24 to 26, their *absolute* daily intakes never stabilized during the observation period.

Summary and General Discussion

The results of the present study of rat pups' behavior patterns during weaning are consistent with reports by earlier observers, but, due to our ability to monitor continuously for 20 days and nights the behavior of the focal pups within their family groups, we have extracted patterns and events that were not discernible in previous studies. A time distribution summary is presented in Figure 6. Taken together with the companion study of maternal behavior patterns (Cramer et al., 1990), we have a broader and richer view of behavioral dynamics during the weaning period—and of the weaning process.

Our analysis involved a spectrum of pup behavior including, but not limited to, suckling, feeding, and drinking. Weaning is typically considered to be the transition from the one form of ingestion to the other. Nevertheless, we feel that an important implication of our results is that an appreciation of the mechanisms of weaning requires the inclusion of other, noningestive behaviors.

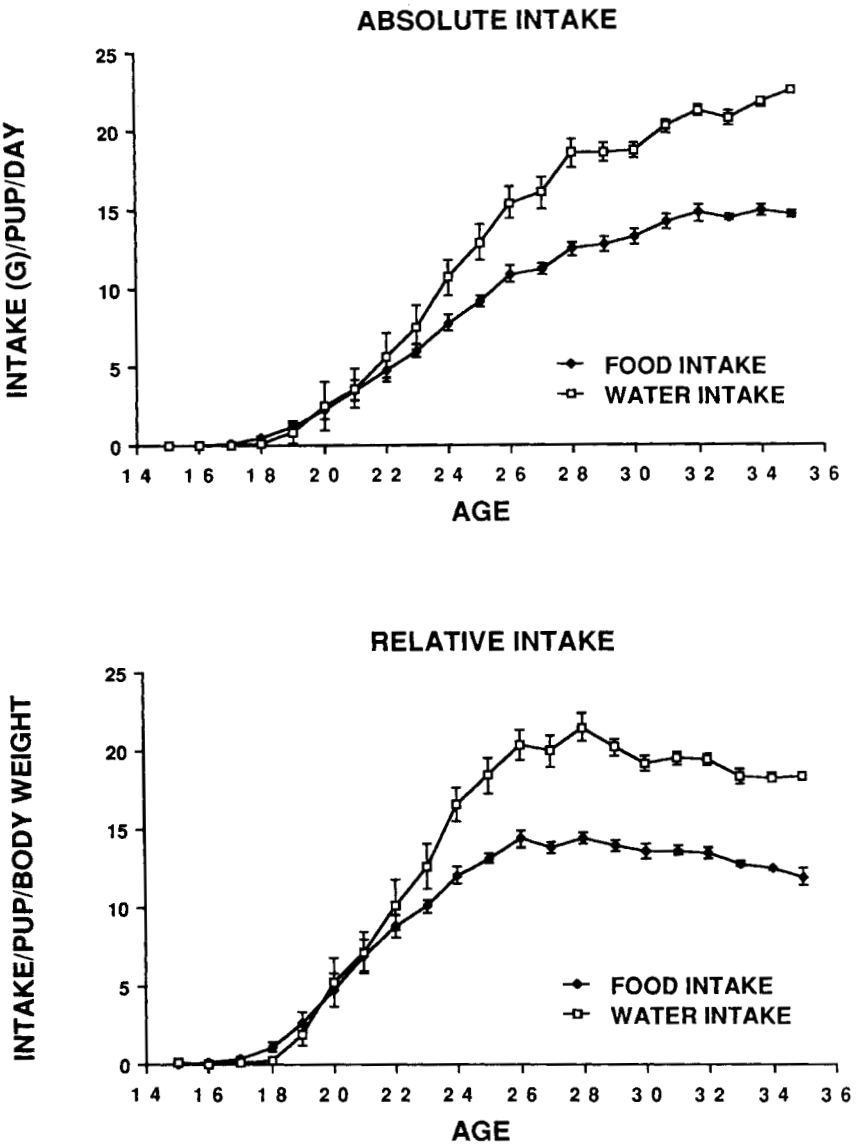

Fig. 5. Mean daily food (triangles) and water (open squares) intake per pup (upper graph) and expressed as percentage of body weight (lower graph).

Relations Between Suckling and Feeding During Weaning

Conventional wisdom holds that feeding somehow "replaces" suckling in the pups' repertoire and, perhaps, in the pups' daily time budget of activity. Our observations fail to support this idea. Although suckling diminished during the developmental period that feeding increased, the temporal relation between the two activities was poorly correlated. Significant daily changes in suckling time occurred in the face of a stable temporal structure of the pups' feeding behavior.

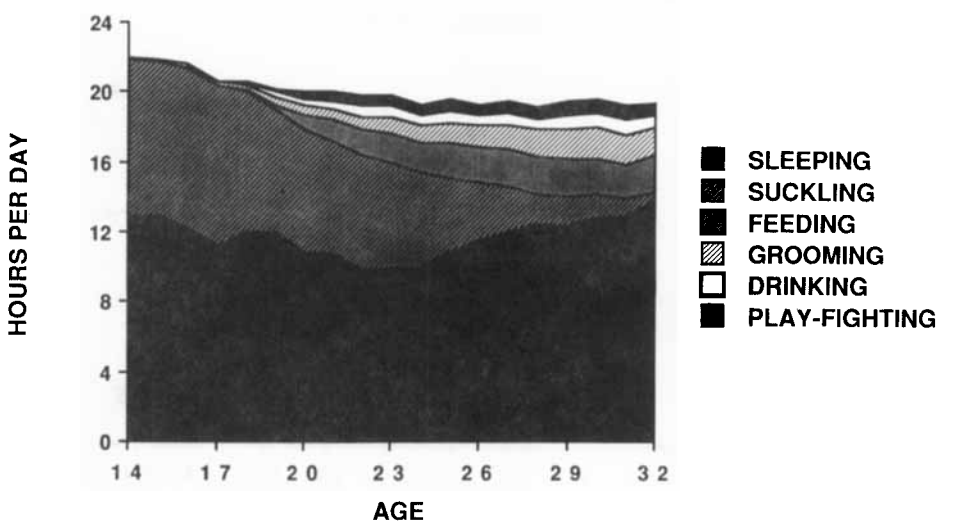

Fig. 6. Time distribution analysis of pups from Days 14 to 34.

Food intake increased most notably between Days 18 and 25 and continued to rise more gradually throughout the remainder of our observations. The largest increases in feeding time were due to more frequent, rather than longer, intake bouts. After Day 25, augmented energy intake was accomplished through more efficient rates of intake, rather than through increased time spent feeding, as indicated by continued increase in absolute amount of food intake (Fig. 5) without comparable increase in the amount of time allocated to feeding (Fig. 1).

A decrease in suckling was first discernible on Day 18 and was manifested as a decrease in average suckling bout duration. Suckling was a diminishing, unstable parameter throughout the next 10 days. Decreases in bout frequency did not contribute to this change in suckling behavior until after the overall decline was well in progress.

A Call for a Broader View of the Weaning Process, and Recognition of Three Transitional Periods During Weaning

Although the concept of weaning is usually centered around ingestive behavior, many of our observations and interpretations point to the need for a considerably broader view of the weaning process, one that necessarily includes the development of other, noningestive activities.

We now suggest that: (a) the transition from milk to solid food, i.e., the decline in suckling and the onset of independent feeding, are functionally embedded in a multitude of behavioral changes; (b) these behavioral changes can be characterized by their distinct temporal characteristics; and (c) the developmental period between postpartum Days 14 and 34 can be divided into three phases that differ in terms of both behavioral stability and behavior content.

Days 14 to 18. Between Days 14 and 18, pups' daily activities varied little within as well as between days and were largely confined to the nest. Basically,

pups either rested (slept) or, when the dam made herself accessible, they suckled. Activities such as grooming and exploration constituted only a small proportion of pups' daily time. Because dams nursed predominantly during the daytime, pups spent more time awake and active during the light phase than during nighttime. This stable, behaviorally limited, diurnal activity profile changed after Day 18, when pups began to explore the environment outside the nest.

Days 18 to 25. The second phase is characterized by a breakdown in the previous order and its replacement by sustained irregularities in previously patterned activities. Between Days 18 and 25 pups were very active throughout the entire 24-hr cycle, and their activity profile changed continuously from one day to the next. In agreement with previous reports, pups initiated food intake around Day 18 and water intake 1 to 2 days later (Babicky, Ostadalova, Parizek, & Kolar, 1971; Babicky, Pavlik, Parizek, Ostadalova, & Kolar, 1972; Redman & Sweney, 1976; Thiels & Alberts, 1985). Concurrent with the onset of feeding and drinking, pups also began to play-fight and increase markedly the amount of self-grooming. Pups engaged in all 4 of these behaviors almost exclusively outside the nest and physically independent of their mother, either in some other area within the common nest compartment or in their own feeding compartment.

Many other independent behaviors that were not specifically sampled, such as digging, social grooming, and so on, also emerged and/or became more prominent beginning around Day 18. Thus, pups' overall level of activity was greatly elevated during this phase. Previous investigators have described appropriately pups of that age as very "restless," "hyperactive," and "curious" to explore the world outside the nest (Bolles & Woods, 1964; Small, 1899). In short, the initiation of independent ingestion occurred in the context of a general behavior eruption that involved the emergence of a large variety of independently performed activities. Concurrent with this behavior eruption pups' attachment to their mother's nipples began to decline.

Days 24 to 34 (when our observations ended). By around Day 25/26 the pups' behavior profile regained considerable stability and was no longer characterized by daily changes in temporal structure. As during the first phase, pups spent half or more than half of the day sleeping or resting, though not necessarily in contact with one another or the dam. Most of their awake time was occupied by feeding, drinking, grooming, nd play-fighting—activities they carried out mostly outside the nest and physically independent of the dam.

During this phase a daily rhythmicity reemerged: Pups began to spend more time awake and active during the nighttime than daytime. This reversal in pups' activity cycle from the diurnal pattern of the first phase was not due to changes in the dams' nursing rhythms (Cramer et al., 1990). Rather, the nocturnal pattern arose from pups' tendency to engage in the newly emerging, independent behaviors during the nighttime instead of daytime. Based on pups' body weight gain, other investigators also have noted a diurnal-to-nocturnal shift in pups' feeding cycle around the age of weaning (Levin & Stern, 1975; Stern & Levin, 1976).

Thus, by about Day 25 pups' behavior profiles reflected considerable self-sufficiency and emancipation from maternal influences. Nevertheless, pups continued to attach to their mother's nipples and rarely interrupted nipple attachment for more than 2 consecutive hrs. Until Day 28 pups allocated as much or *more* daily time to suckling than to independent ingestion (i.e., feeding and drinking

combined), and nipple attachment did not completely disappear until about Day 34. This fidning is in marked contrast with earlier reports on the decline and termination of milk intake during weaning (Babicky, Ostadalova et al., 1973; Babicky, Parizek et al., 1973; Henning et al., 1979; Redman & Sweney, 1976). These investigators found that milk intake completely ceased by around Day 26. Our records of pups' stretch responses, which occur only upon milk delivery (Lincoln et al., 1973; Wakerley & Drewett, 1975; but see Drewett, Statham, & Wakerley, 1974; Lau & Henning, 1985), suggest that pups occasionally received milk until shortly before they completely abandoned their mother's nipples. In any event, the results show that pups continued to attach to their mother's nipples for an extended period of time despite little or no milk yield. In the rat, the mammary glands eject milk in bursts during continuous nipple attachment by the young (Wakerley & Lincoln, 1971), which may have promoted persistence of nipple attachment under conditions of low or no milk delivery. Such resistance to extinction is commonly observed after intermittent reward (e.g., Burdette, Brake, Chen, & Amsel, 1976).

Concluding Remarks: The co-ordering of the decrease in suckling (i.e., nipple attachment) and the emergence of independent behaviors raises the interesting question of whether these two classes of changes reflect the transformation from one to another form of a single, common underlying dimension, or whether they are manifestations of separate processes that develop together. The emergence of environment/peer-oriented behaviors proceeded rapidly, whereas the decline in nipple attachment (a mother-oriented behavior) developed slowly and extended well beyond the age of obligatory dependence (Galef, 1971). Lack of dependence between the developmental profiles of suckling and independent ingestion was also demonstrated by the findings that; (1) Pups forced to cease nipple attachment on postpartum Day 15 do not begin feeding or drinking earlier than normally weaning pups (Thiels and Alberts, submitted); (2) pups that never had the opportunity to suckle develop normal feeding and drinking patterns around the age of weaning (Hall, 1975); and (3) nutritively independent pups continue to suckle until 70 days of age when continuously maintained with a preweaning-age litter (Pfister, Cramer, & Blass, 1986). Taken together, these findings and the present observation of different temporal patterns of change strongly favor the notion that weaning involves many separate developmental processes, rather than one unitary process of transition.

Notes

This work was supported by an Indiana University Predoctoral Research Fellowship to E.T., a grant from the National Institute of Mental Health (#MH-28355) to J.R.A., and a National Science Foundation Visiting Professorship for Women (#RII-850387) and a Junior Faculty Fellowship from Dartmouth College to C.P.C. We thank Curt Matlock for assistance with both programming and data collection, and Thomas Blaine and Allen Fear for assistance in data collection. E.T. is now at the Department of Behavioral Neuroscience, University of Pittsburgh, Pittsburgh, PA 15260.

References

Babicky, A., Ostadalova, I., Parizek, J., & Kolar, J. (1971). Intake of 131_{BaSO4} labelled food by lactating rats and young during the weaning period. *Physiologia Bohemoslovaca, 20,* 358.

Babicky, A., Ostadalova, I., Parizek, J., Kolar, J., & Bibr, B. (1973). Onset and duration of the physiological weaning period for infant rats reared in nests of different sizes. *Physiologia Bohemoslovaca, 22,* 449–456.

Babicky, A., Parizek, J., Ostadalova, I., & Kolar, J. (1973). Initial solid food intake and growth of young rats in nests of different sizes. *Physiologia Bohemoslovaca, 22,* 557–566.

Babicky, A., Pavlik, L., Parizek, J., Ostadalova, I., & Kolar, J. (1972). Determination of the onset of spontaneous water intake in infant rats. *Physiologia Bohemoslovaca, 21,* 467–471.

Blake, H. H., & Henning, S. J. (1983). Weaning in the rat: A study of hormonal influences. *American Journal of Physiology, 244,* R537–R543.

Blake, H. H., Okuhara, C. T., & Henning, S. J. (1984). Role of dietary preferences in the weaning pattern of the rat. *American Journal of Physiology, 246,* R96–R101.

Bolles, R. C., & Woods, P. J. (1964). The ontogeny of behavior in the albino rat. *Animal Behaviour, 12,* 427–441.

Burdette, D. R., Brake, S., Chen, F. S., & Amsel, A. (1976). Ontogeny of persistence: Immediate extinction effects in pre-weanling and weanling rats. *Animal Learning and Behaviour, 4,* 131–138.

Cramer, C. P., Thiels, E., & Alberts, J. R. (1990). Weaning in rats: I. Maternal behavior patterns. *Developmental Psychobiology.*

Drewett, R. F., Statham, C., & Wakerley, J. B. (1974). A quantitative analysis of the feeding behaviour of suckling rats. *Animal Behaviour, 22,* 907–913.

Galef, B. G., Jr. (1971). Social effects in the weaning of domestic rat pups. *Journal of Comparative and Physiological Psychology, 75,* 358–362.

Galef, B. J., Jr., & Clark, M. M. (1971). Parent-offspring interactions determine the time and place of first ingestion of solid food by wild rat pups. *Psychonomic Science, 25,* 15–16.

Galef, B. J., Jr., & Clark, M. M. (1972). Mother's milk and adult presence: Two factors determining initial dietary selection by weanling rats. *Journal of Comparative and Physiological Psychology, 78,* 220–225.

Hall, W. G. (1975). Weaning and growth of artificially reared rats. *Science, 190,* 1313–1315.

Hall, W. G., Cramer, C. P., & Blass, E. M. (1977). Ontogeny of suckling in rats: Transitions toward adult ingestion. *Journal of Comparative and Physiological Psychology, 91,* 1141–1155.

Hays, W. L. (1981). *Statistics* (3rd ed.). New York: Holt, Rinehart and Winston.

Henning S. J. (1980). Maternal factors as determinants of food intake during the suckling period. *International Journal of Obesity, 4,* 329–332.

Lau, C., & Henning, S. J. (1985). The nature of the "stretch response" in suckling rats. *Physiology and Behavior, 34,* 649–651.

Lee, M. H. S., & Williams, D. I. (1977). A longitudinal study of mother-young interaction in the rat: The effects of infantile stimulation, diurnal rhythms, and pup maturation. *Behaviour, 63,* 241–261.

Levin, R., & Stern, J. M. (1975). Maternal influences on ontogeny of suckling and feeding rhythms in the rat. *Journal of Comparative and Physiological Psychology, 89,* 711–721.

Lichtman, A. H., & Cramer, C. P. (in press). Experience and availability of milk maintain suckling in juvenile rats. *Developmental Psychobiology.*

Lincoln, D. W., Hill, A., & Wakerley, J. B. (1973). The milk-ejection reflex of the rat: An intermittent function not abolished by surgical levels of anaesthesia. *Journal of Endocrinology, 57,* 459–476.

Pfister, J. P., Cramer, C. P. C., & Blass, E. M. (1986). Suckling in rats extended by continuous living with dams and their preweanling litters. *Animal Behaviour, 34,* 415–420.

Redman, R. S., & Sweney, L. R. (1976). Changes in diet patterns of feeding activity of developing rats. *Journal of Nutrition, 106,* 615–626.

Small, W. S. (1899). Notes on the psychic development of the young white rat. *American Journal of Psychology, 11,* 80–100.

Stern, J. M., & Levin, R. (1976). Food availability as a determinant of the rat's circadian rhythm in maternal behavior. *Developmental Psychobiology, 9,* 137–148.

Thiels, E., & Alberts, J. R. (1985). Milk availability modulates weaning in the norway rat (Rattus norvegicus). *Journal of Comparative Psychology, 99,* 447–456.

Thiels, E., & Alberts, J. R. (submitted). Weaning in the Norway rat: Relation between suckling and milk, and suckling and independent ingestion.

Thiels, E., Cramer, C. P., & Alberts, J. R. (1988). Behavioral interactions rather than milk availability determine decline in milk intake of weanling rats. *Physiology and Behavior, 42,* 507–515.

Wakerley, J. B., & Drewett, R. F. (1975). Pattern of sucking in the infant rat during spontaneous milk ejection. *Physiology & Behavior, 15,* 277–281.

Wakerley, J. B., & Lincoln, D. W. (1971). Intermittent release of oxytocin during suckling in the rat. *Nature New Biology, 233,* 180–181.

Williams, C. L., Hall, W. G., & Rosenblatt, J. S. (1980). Changing oral cues in suckling of weaning-age rats: Possible contributions to weaning. *Journal of Comparative and Phsyiological Psychology, 94,* 472–483.

Williams, C. L., Rosenblatt, J. S., & Hall, W. G. (1979). Inhibition of suckling in weaning-age rats:A possible serotonergic mechanism. *Journal of Comparative and Physiological Psychology, 93,* 414–429.