

Weaning in Rats:

I. Maternal Behavior

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Maternal behavior during the weaning period (postpartum Days 14–35) was described from continuous timelapse videorecordings of Norway rat dams and their litters. Time spent nursing declined steadily after Day 20 but persisted until Day 34, about a week longer than suggested by reports of milk transfer. Most of the decline in nursing was due to progressively fewer nursing bouts per day; milk letdowns per day were consequently diminished. Although a private feeding chamber was available to the dams, they did not use this chamber to spend more time away from the pups as weaning progressed. Instead, the dams remained with the pups in the nesting chamber but devoted increasingly less time to nursing. Subtle, progressive changes in maternal behavior are closely orchestrated and coordinated with pup development.

The unique bond between mammalian mothers and their infants, created and maintained by nursing, is irrevocable broken by weaning. In a strict sense, the weaning process involves a developmental reorganization of ingestive behavior. Infant altricial mammals subsist entirely on mother's milk; as adults they independently select and ingest solid foods. Weaning is the transition between these two forms of subsistence and constitutes an essential element in the progression to adult function in all mammals. In a general sense, weaning also represents a

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milestone in the achievement of more global forms of independence, a prominent and universal discontinuity in mammalian development that marks a significant change in life pattern.

Weaning has appeared in several theoretical treatments of mammalian development. For example, in Trivers' (1972, 1974) parental investment theory, conflicts of interest are viewed as integral features of parent-offspring relations. Weaning, in particular, is a phase of predictable conflict, during which it is in the parents to cease investing their resources in the young, whereas it is presumed that it remains in the young's selfish interests to continue obtaining the parental resources. Galef (1981) constructed a somewhat different characterization of weaning. He casts the infant mammal as a parasite on its mother and views weaning as a shift from obligate to facultative to commensal parasitism.

Despite its acknowledged significance, surprisingly few data exist on weaning. We have examined the literature on development in Norway rats for data on weaning in general and on maternal aspects in particular. Small (1899) pioneered this area with detailed descriptions of the behavioral characteristics of infant weanling rat pups, but paid little attention to the contributions of the dams. In contrast, Bolles and Woods (1964) reported comprehensive, longitudinal observations of behavioral change in both pups and mother. Unfortunately, their records offer only limited information on the weaning process because they separated dams and their litters on postpartum Day 21. In addition, their observation periods were too brief (30 min) and too infrequent (12-hr intervals) to capture integrated behavior patterns and sequences of interactions between mother and pups.

The literature on maternal behavior in rats is also a poor source of data relevant to weaning. Although Wiesner & Sheard's (1933) treatise contains a wealth of information on maternal behavior in rats, there is no direct consideration of the weaning process. Rosenblatt and Lehrman (1963) describe rat maternal behaviors and present an elegant series of experiments detailing the onset and maintenance of maternal responsiveness. Their focus, however, was on understanding the factors underlying maternal condition, so most of the work is based on maternal responses to standard-aged infant pups, thereby eliminating age-related interactions that might contribute to weaning. Finally, there are several studies in which partitioned cages equipped with mechanical sensors have been used to record mother-litter contact in a nest compartment (e.g., Grotta & Ader, 1969; Leon, Croskerry, & Smith, 1978; Plaut, 1974). Unfortunately, such methods are of little use after about Day 15, when pups can locomote and contact the mother outside the designated nest.

The phenomenon of weaning has yet to attract experimental attention commensurate with its importance in mammalian development. Nevertheless, from various behavioral studies, as well as more physiological analyses, a tentative, sketchy outline of changes during weaning in domesticated rats has emerged. During the first 2 weeks postpartum, rat pups feed exclusively on milk gained via suckling. During this time the mother is actively solicitous, spending much of her time licking, retrieving, and nursing the pups in the nest she has built and maintains (e.g., Rosenblatt & Lehrman, 1963; Bolles & Woods, 1964). Around Day 16, the pups begin to sample solid food; shortly thereafter milk intake gradually declines. Diminution of maternal responsiveness and milk transfer appear synchronized with increased intake of solid food. By about Day 26, milk consumption has

completely ceased, and the pups subsist entirely on solid food (Babicky, Ostadalova, Parizek, & Kolar, 1971; Babicky, Ostadalova, Parizek, Kolar, & Bibr, 1973; Redman & Sweney, 1976; Henning, Chang, & Gisel, 1979; Galef, 1979).

Although the term weaning is generally used in reference to the offspring, the parents also gain a form of independence when the young have weaned. This perspective, coupled with a general appreciation of the existence of reciprocal controls in mother-infant interaction, requires that an accurate and comprehensive picture of the weaning period must involve both qualitative and quantitative accounts of maternal behavior. The present report is, therefore, a description of the patterns of rat maternal behavior between Days 14 and 35 postpartum, that is, throughout the weaning period. We continuously observed mother rats and their litters in relatively spacious habitats composed of a common area with nest site and two separate feeding compartments. By using timelapse videorecording, we were able to collect continuous records of behavior with minimal disruption to the animals and without the time-based sampling errors inherent in more intermittent observational techniques. In combination with the companion paper (Thiels, Alberts, & Cramer, 1990) we can now more fully describe the behavior of the mother and the offspring during weaning.

Methods

Subjects:

Nine rat dams (8 multiparous and 1 primiparous) and their litters were subjects. Rats were bred from Sprague-Dawley stock originally obtained from Charles River (Portage, Michigan) and were born in the Animal Behavior Laboratory colony at Indiana University. One week prior to birth, females were housed in polypropylene tubs (48 × 20 × 26 cm) with stainless steel wire lids and Purina 5012 rat chow and tap water continuously available. Temperature in the colony rooms was maintained at 24–26°C. Illumination was on from 0700 to 2300 hr. Females were checked daily around 1700 hr for the birth of pups, and pups found at that time were considered born on that day (Day 0). Litters were reduced to 8 pups (4 males and 4 females) on Day 3. On the evening of Day 9, mothers and their litters were moved to a room maintained at 23–26°C, with the same L:D cycle as the colony rooms. For purposes of videography, a 25-watt red light bulb remained illuminated during the dark phase.

Apparatus

For the entirety of the observation period, each mother-litter group was housed in a relatively spacious, tri-compartment habitat, illustrated in Figure 1. Each habitat consisted of a larger nesting area (27 × 32 × 35.5 high cm) and two feeding compartments (27 × 16 × 35.5 high cm), one for the pups and one for the mother. An opening (4 × 2.5 high cm) at the base of the wall between the nesting area and the pups' feeding compartment permitted passage only to pups. An opening (16 × 5 high cm) at the top of the wall between the nesting area and the dam's feeding compartment was designed to permit only an adult to jump over it. Occasionally, older pups (beyond Day 30) jumped on top of that wall. Nevertheless, they never

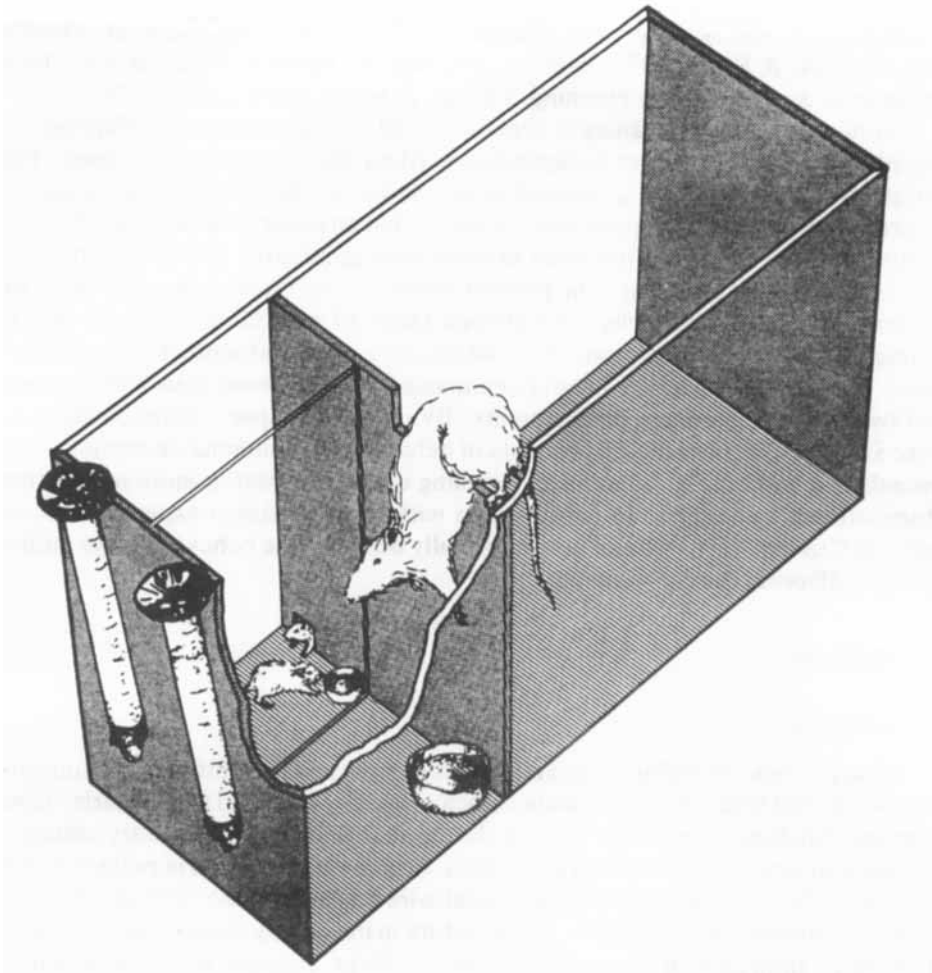


Fig. 1. A schematic drawing of the tricompartiment cage in which dams and their litters were housed during observation.

entered the dam's compartment. The wall separating the two feeding compartments and both wide external walls were constructed of Plexiglas; the two external end walls and the wall between the nesting area and the feeding compartments were constructed of galvanized steels. The cage lid was constructed of 1/4" hardware cloth.

The pups' feeding compartment contained a food tray, covered by an aluminum lid with 5 holes (2.5 cm diameter) and a 1-cm raised lip to prevent food spillage. A water spout protruded through one wall. A second water spout was added on Day 29 postpartum. Mothers' feeding compartment contained a food bowl and a water spout. During the entire experiment, powdered Purina rat chow and tap water were freely available in both feeding compartments. Hardwood chip bedding, replaced every 4–7 days, covered the galvanized floors of all compartments.

The observations used for behavioral coding were accomplished by timelapse videography. The cages were designed to permit surveillance of all three compart-

ments from one single side. Each of the two cages was monitored by a video camera aimed at the clear side. By appropriate framing of each video field, the images from the two cameras (Panasonic, Model V-1500X and V-1550; Cosmicar lenses) were combined through a screen splitter (RCA model 1470A), viewed simultaneously on a single television monitor and recorded by one timelapse videocassette recorder (GYR, model TLC 2001).

Video recording was made in a slow scan mode (2.5 fields/sec). The video records were reviewed for behavioral coding at normal, full speed (30 fields/sec), yielding a 12X acceleration of events on the screen. This form of timelapse recording allows continuous monitoring and quantification of slow or long-lasting events, which can be reliably captured and recognized during playback. The 12 : 1 record : playback ratio used for the present study was efficient, yet it permitted coding of key events in the dam's behavior, and, for some activities, it was possible to make reliable duration measures.

Procedure

On the evening of Day 9, mothers and their pups were placed in the experimental cages; videotaping began on the evening of Day 13, prior to the age at which rat pups begin to sample solid food (Galef, 1971; Rosenblatt & Lehrman, 1963; Thiels & Alberts, 1985). Videotaping was essentially continuous, only briefly (30–50 min) interrupted at about 2100 hr each day to replace videocassettes, collect weight data, replenish food and water, and clean cages when necessary. Videotaping was terminated when there were no full nursing bouts, defined as more than 3 pups simultaneously suckling for more than 1 min, for at least 24 hr, or at the end of Day 35, whichever came first.

Encoding of Behavior and Data Analysis

To encode the behavioral data from the videotapes, trained observers viewed the tapes at the normal playback speed and simultaneously operated a microcomputer keyboard (Radio Shack TRS-80, model 4P), by which the occurrence, onset and offset of various events were noted. The observer operated 6 keys that indicated whether the dam was:

- (a) in the common nest chamber or in her feeding compartment;
- (b) nursing pups;
- (c) nursing a small (1–3) or large (4–8) aggregate of pups;
- (d) holding her ventrum flat against the floor or wall of the cage (see Figure 6), thus interfering with pups attaching to her nipples.

Because the dam's posture and fur tended to obscure the view of pups' mouths, nursing was defined as 1 or more pups having their snouts nuzzled into her ventrum.

The computer program used to encode and quantify behavioral events divided the rats' 24-hr day into a series of 20-sec bins. Thus a full day would contain 4320 such bins. Excluding the daily interruptions, an average of 4211 bins were obtained for each dam per day in the present study.

Inter-rater reliability was determined from 8 sample tapes scored by at least two observers. Bin-by-bin concordance ranged from .92–.97. Reliabilities determined by correlating time distribution results all exceeded .99.

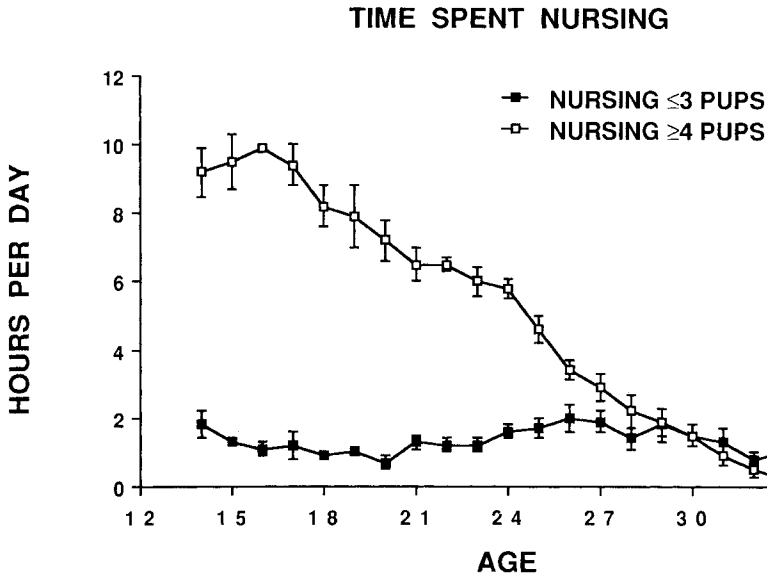


Fig. 2. Mean (\pm SEM) hours per day spent nursing by rat dams on Days 14–35 postpartum. Nursing both small (1–3) and large (4–8) aggregates of pups is shown.

For each of the target behaviors, we computed the total daily amount of time spent in the activity and the percentage of the day in which each dam engaged in that activity. We used repeated measures analysis of variance to assess changes in each behavior across age and conducted post-hoc comparisons with Tukey's HSD (honestly significant difference) test at the .05 level.

Results and Discussion

Nursing Behavior

On Day 14, when our observations began, dams spent nearly 10 hr/day nursing their pups. On Day 25, midway through the weaning period, daily nursing time had diminished to 7 hr/day. Nursing effectively ceased by Day 34. Figure 2 illustrates daily nursing time over the course of the observation period. Because milk letdown is unlikely to occur when fewer than 4 pups are attached (Grosvenor & Mena, 1974), Figure 2 shows separate categories of nursing behavior when only a few pups (1–3) versus many pups (4–8) were attached.

Nursing time was maintained at 9–10 hr/day through Day 19. The most dramatic behavioral change that we recorded was the decline, beginning on Day 20, in the amount of time the dam spent nursing 4 or more pups, $F(21, 147) = 73.14$, $p < .01$. This decline was gradual and very steady, resulting in a significant reduction in nursing time every 3–5 days until Day 31 (critical difference = 2.02 hr). The amount of time during which only a few pups attached changed somewhat over the course of the weaning period, $F(21, 147) = 2.48$, $p < .01$. Most of this difference was due to a slight increase in the time spent nursing a few pups on Days 24–29 and a significant decrease in this behavior after Day 33 (critical difference =

1.36 hr). Although we did not record the exact number of pups that were attached, casual observation suggested that much of the time the dams spent in nursing 3 or fewer pups, actually involved nipple attachment by only a single pup.

Frequency and Duration of Nursing

Nursing time, expressed as an average daily total, consists of a summation of discrete bouts of nursing contacts that vary in frequency and duration. Alteration (or stability) in nursing time could reflect differential contributions of number and length of bouts. Thus, to further characterize the decline in nursing behavior, we analyzed the frequency and duration of nursing bouts across the observation period. A bout was defined as 4 or more pups attached to the nipples for 3.3 or more consecutive, real time min (10 bins). These parameters were chosen on the basis of Slater & Lester's (1982) procedures derived from log survivorship analysis. These parameters also approximate the minimum time necessary for milk letdown (Grosvenor & Mena, 1974).

Nipple-shifting, in which pups briefly leave the nipple following a milk letdown (Cramer, Blass, & Hall, 1980) was the most common disruption during a nursing bout. Because dams nearly always remain stationary during nipple-shifting, we felt it appropriate to exclude these disruptions from an analysis of bout frequency and duration. Thus, a nursing bout could be disrupted by another behavior for 1 min or less without being disqualified as a continuous bout. Because bouts were so infrequent after Day 30, bout durations were not calculated after this point.

The lower graph in Figure 3 shows that the frequency of bouts declined steadily, accounting for most of the reduction in nursing time, $F(21, 147) = 38.46$, $p < .01$. The first significant reduction appeared on Day 25, and the number of bouts declined steadily every 3–4 days thereafter (critical difference = 4.57 bouts/day). The duration of suckling bouts also decreased over the course of the weaning period, $F(16, 112) = 8.57$, $p < .01$; however, these differences, however, were less dramatic. Again, the first significant effect was at Day 25, and bout duration remained steady after that point (critical difference = 14.67 min).

Milk Letdowns:

In our analysis of focal pup behavior (Thiels, Cramer, & Alberts, 1990), stretch responses were explicitly scored, providing an index of milk letdown frequencies (Lincoln, Hill, & Wakerly, 1974), for 6 of the dams. The results of this analysis are included in the present report, because the data pertain to the dams and the frequency with which they transferred milk (although in unknown quantities) to their pups. Dams released milk about 90 times/day when our observations began, and they maintained this rate of milk letdown through Days 19–20. As shown in Figure 4, the number of daily milk letdowns declined dramatically between Days 20–30, $F(19, 95) = 68.29$, $p < .01$; critical difference = 12.71 letdowns/day.

The lower graph in Figure 4 shows that the number of milk letdowns per bout also decreased, but somewhat later, $F(19, 95) = 34.12$, $p < .01$; critical difference = 1.0. As we expected, only very few milk letdowns (<2%) occurred when less than 4 pups were attached.

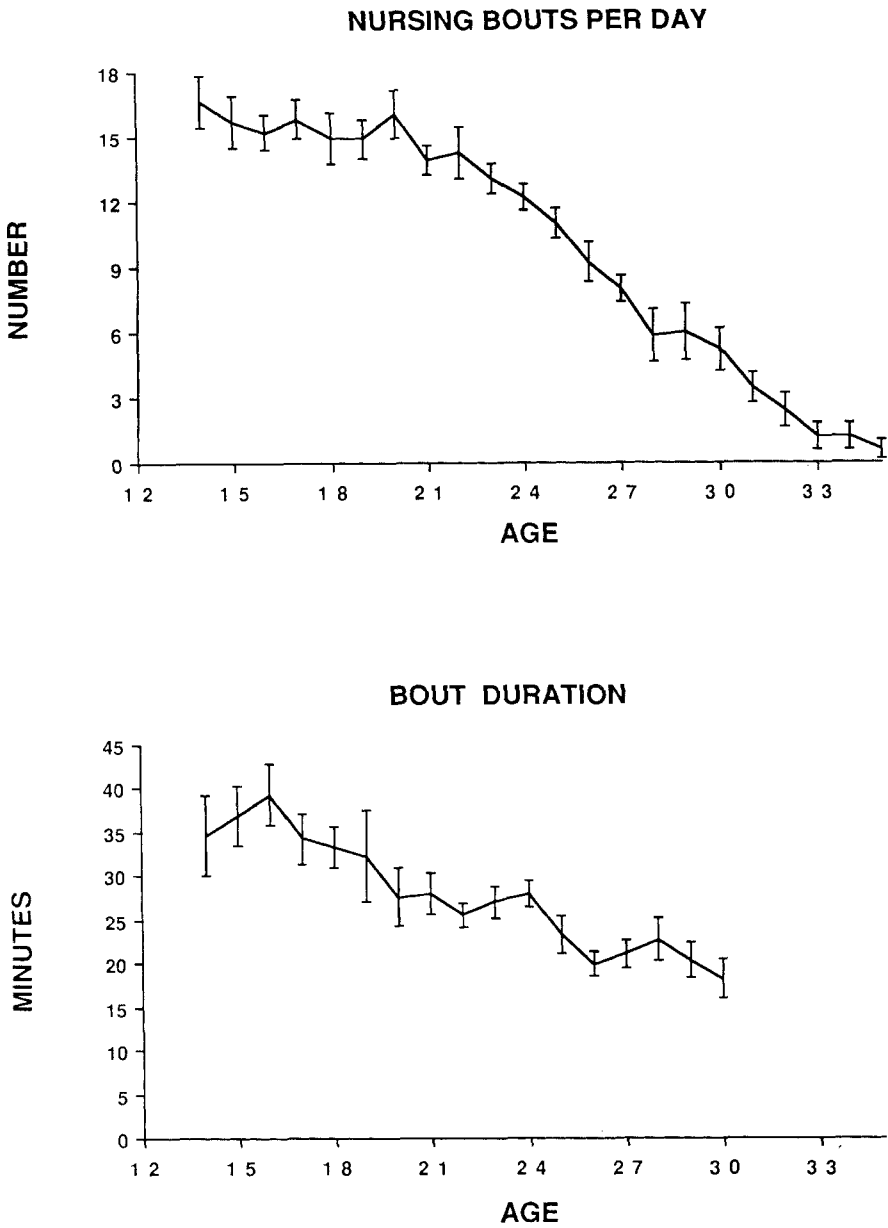


Fig. 3. Mean (\pm SEM) frequency (upper graph) and duration (lower graph, in min) of nursing bouts on Days 14–35 postpartum.

Avoidance and Proximity

One of the main goals of this study was to document changes in the dams' behavior that initiated, regulated, and/or culminated in weaning of the pups. We suspected that dams might use the private feeding chamber to escape from the pups and thus reduce nursing time. The upper graph in Figure 5 shows the amount of time dams spent in their private feeding compartment. Although there was an

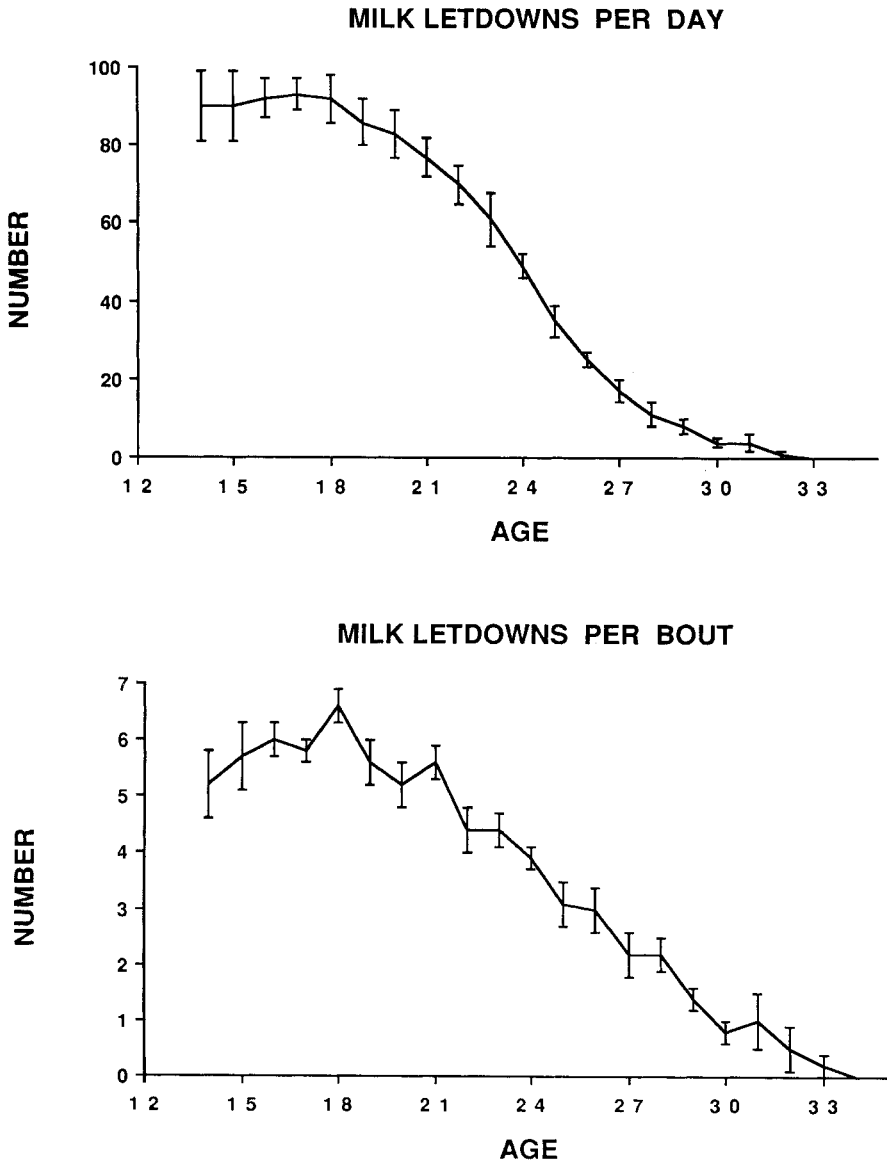


Fig. 4. Mean (\pm SEM) number of milk letdowns per day (upper graph and per nursing bout (lower graph) on Days 14–33 postpartum.

overall change in the time spent by dams in the private compartment, $F(21, 147) = 1.73$, $p < .05$, the pattern of change did not conform to our expectations of progressively more withdrawal from the pups. Instead, most of the difference was due to relatively little time spent in the private chamber on Day 14 compared to relatively longer times spent in the private chamber on Days 20 and 32 (critical difference = 4.78 hr).

A more pronounced change was apparent in the amount of time dams spent in the nest chamber with the pups but not nursing them, $F(21, 147) = 12.57$, $p <$

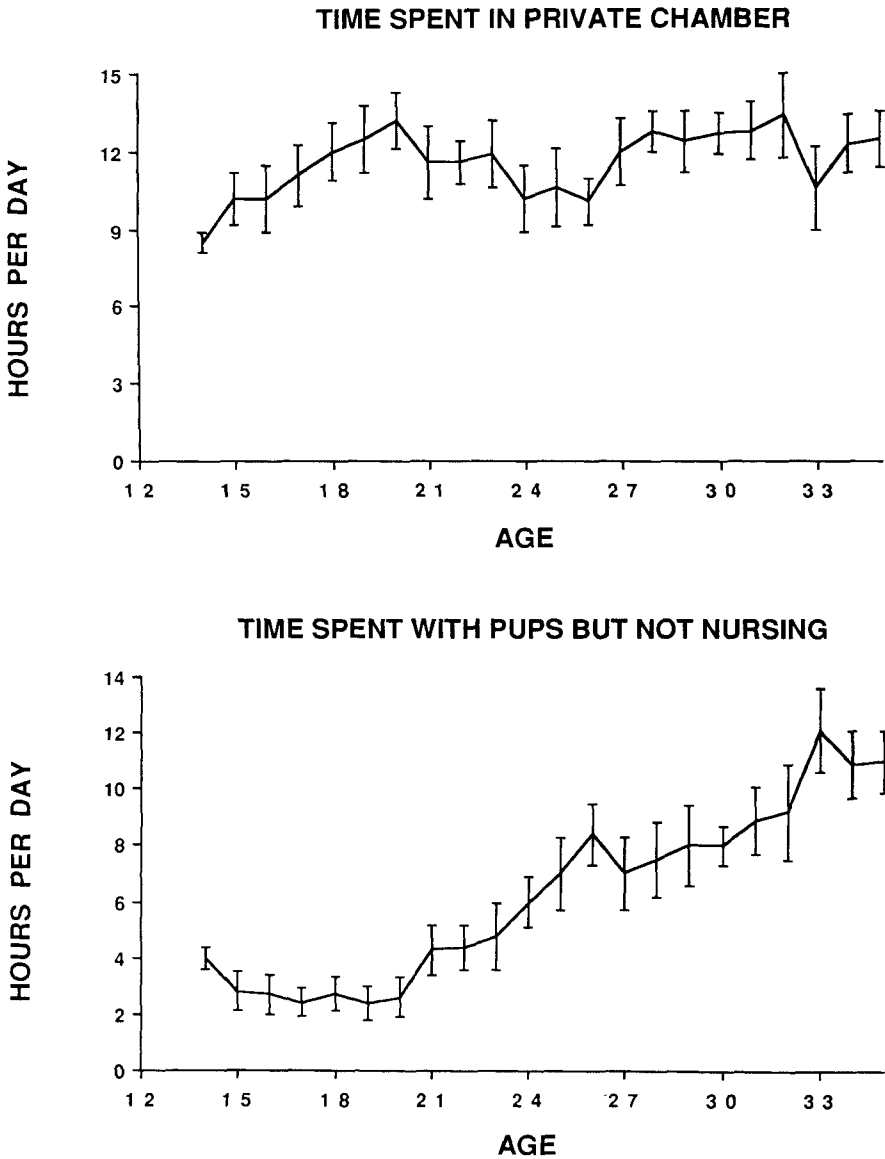


Fig. 5. Mean (\pm SEM) hours per day spent by dams in either their private feeding compartment (upper graph), or in the nest area without nursing (lower graph), on Days 14–35 postpartum.

.001. As shown in the lower graph of Figure 5, the amount of nonnursing time in the nest compartment was stable from Days 14–24, then rose significantly and stayed relatively stable from Days 25–32 before rising again (critical difference = 4.38 hr). It does not appear that the dams used the private feeding chamber to avoid the pups. That is, they did not spend more time in the private feeding chamber as nursing time declined. Rather, dams increase their time in the nest chamber but not in nursing the pups. It is, nonetheless, possible that the dams used the private chamber strategically to avoid the pups at specific times, without

actually spending more overall time there. Sequential analyses (in preparation) may shed light on this issue.

If dams spend more time with the pups but nurse less, the question arises whether they actively discourage the pups from suckling, and if so, how they do so. In contrast to reports of other species, we never observed a dam directly aggress against her pups by biting, pinning, or striking the. On the basis of previous observations (Cramer & Pfister, 1985) we noted instances in which the dam adopted a posture that held her ventral surface against either the floor or the walls of the cage. This "press posture" was also reported by Rosenblatt & Lehrman (1963). Figure 6 illustrates these postures and shows the incidence of this behavior over the observation period. The difference across age was significant, $F(21, 147) = 2.07$, $p < .01$; critical difference = 0.35 hr, primarily due to a relatively large amount of time spent in this behavior on Day 14 and the virtual absence of the behavior on Days 32–35. Analysis of the bout frequency indicated that dams averaged 2 bouts per day in this behavior during the 18 days sampled.

Adoption of the press posture could function in two ways (which are not mutually exclusive). As suggested earlier, the dams could be using the posture to prevent the pups from attaching to a nipple. Alternatively, they could be using the posture to conduct heat to the relatively cool wall or floor surfaces. The dams virtually never adopted the press posture in their private feeding chamber, suggesting the avoidance function, rather than simple dissipation of the heat. However, the feeding chamber, which contained the feeding bowl and water spout, may have interfered with or prevented the dams from adopting the posture, especially some of the horizontal variants. In addition, dams seem to display press postures more often when housed in tub cages (Cramer, Keenan, & Lichtman, 1988) or in larger glass cages (Cramer & Pfister, 1985), although such behaviors were not explicitly scored in those studies. These informal observations, if verified, would point toward the avoidance function; dams with access to a private chamber might have less need to use postural strategies to discourage the pups from attaching to her nipples.

Summary and Conclusions

The categories we used for behavioral encoding accounted for 99% of the dams' time throughout the weaning period, thereby providing an inclusive, albeit general, description of the mother's activities. A time distribution profile is shown in Figure 7. Several notable trends were apparent. The stippled areas at the top of the figure illustrate the overall reduction in time spent nursing across the weaning period; beginning at about Day 20 the decline was steady and steep. On Days 24–26, in the face of continued declines in time spent nursing, there was another apparent transition in the dams' activity, namely they spent *less* time in their private feeding compartments. At the same time, they spent *more* time in the nest chamber but not nursing, and more time nursing only a few pups. The frequency and duration of nursing bouts also began to decline significantly around Day 25. On Days 32 to 35, time spent in the nest chamber but not nursing again increased, time spent nursing a few pups declined, and time spent nursing the whole litter and milk ejections became relatively infrequent events (and in some litters disappeared entirely).

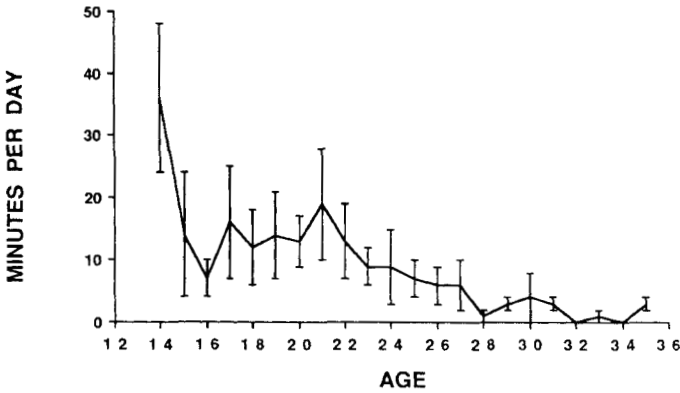
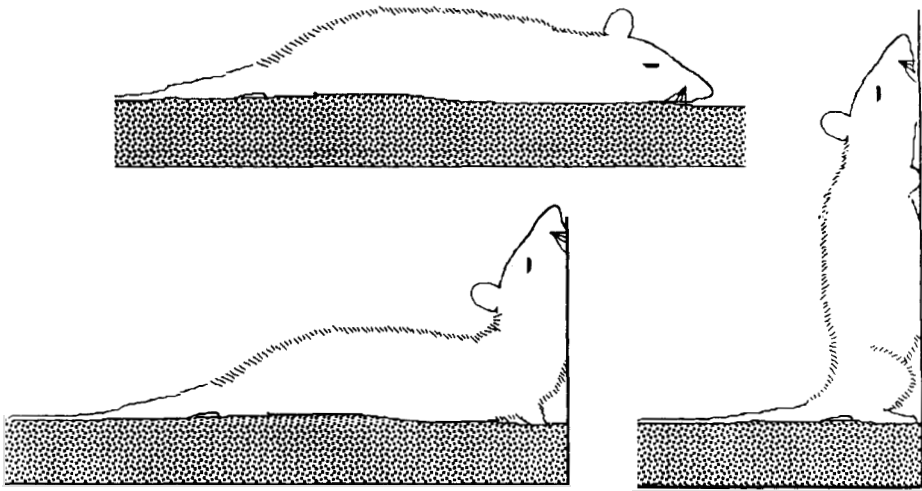


Fig. 6. Drawings of "press postures" and mean (\pm SEM) hours per day spent by dams in one of these postures on Days 14–35 postpartum.

These changes in maternal behavior coordinate nicely with transitions in the pups' development reported by Thiels et al. (1990). Dams' nursing time began to decline about 2 days after pups entered a phase characterized by high activity and rapidly changing behavioral profiles. Indeed, not only did nursing time decrease, but the dams reduced their proximity to the pups by retreating slightly more often to the private area. This sequence suggests the possibility, which we can now begin to test experimentally, that elements of the weaning process involve a response on the part of the mother to cues emanating from the pups.

As the pups settled into a third, more stable phase on Day 25 (see Thiels et al. 1990), the dam began to spend more time with them, although not nursing. By this

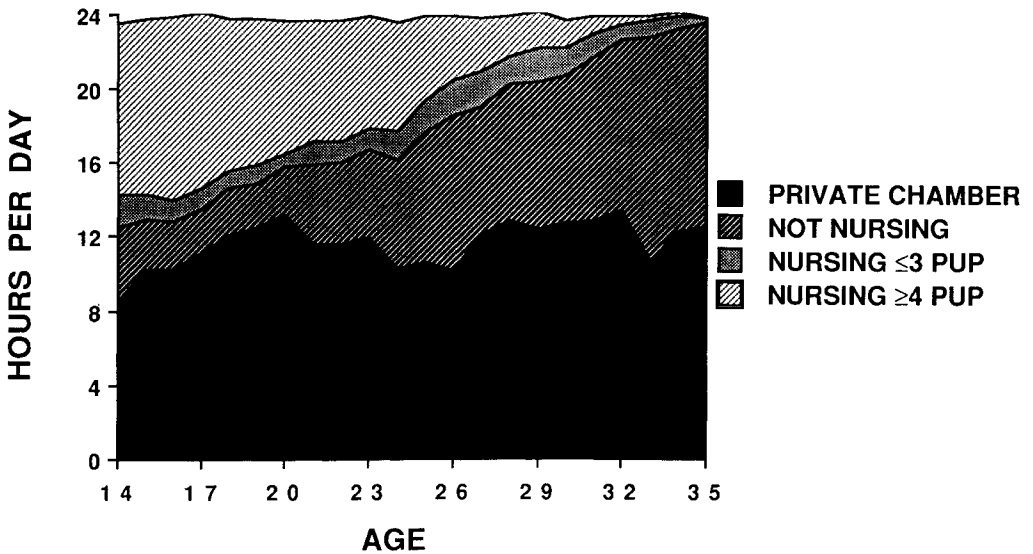


Fig. 7. Time budget summary of dams' principal behaviors on Days 14–35 postpartum.

time, the pups' feeding and drinking were well-established, and they no longer depended on her for nutritive support.

We noted a clear absence of reliable signs of parent-offspring conflict, such as dams fleeing from persistent advances of the pups or displaying overt punishment for attempted suckling. Nevertheless, it is possible that the dams were able to discourage suckling with only subtle cues, not readily apparent with the timelapse video observations. In addition, the pups may be increasingly prepared to respond to such cues, as independent feeding can now substitute for suckling (Williams, Hall, & Rosenblatt, 1980), and milk itself (rather than oral stimulation) has become the primary reinforcer for suckling (Stoloff & Blass, 1983; Cramer & Blass, 1985; Cramer, Keenan, & Lichtman, 1988; Lichtman & Cramer, 1989).

The temporal trends in mother-pup interaction fit well with the notions of synchrony and reciprocity (Rosenblatt, 1965; Alberts, 1985). Maternal behavior and pup development appear to be closely orchestrated and mutually interdependent. Although it is inappropriate to posit causal mechanisms on the basis of normative data such as those reported here, the tight temporal patterns appear to belie some active linkage between processes in mother and young.

Although weaning is generally viewed as a transition on the part of the young, as their emancipation from maternal dependence, the process can also be viewed from the mother's perspective in her independence from the demands of her young. A comprehensive view of weaning thus includes the process from the dam's perspective. During lactation, the rat dam contributes much energy in the form of milk and provides additional forms of energy as well (Alberts, 1985; Galef, 1981). Weaning reduces the mother's energy commitment to the young.

In addition to independence from proximate controls of offspring on maternal behavior and physiology, freedom to resume reproduction is often another conse-

quence of weaning. Ovarian cyclicity is halted during lactation in many species, so that weaning may return reproductive opportunities for the mother and thus be a partial determinant of lifetime reproductive success (Trivers, 1972, 1974). Similarly, in species such as rats which sometimes conceive during a postpartum estrus, weaning an older litter allows the mother to direct her resources to the next litter.

The data reported here lead to a fuller and somewhat different picture of weaning than that outlined in the introduction, particularly in regard to the duration of the weaning period. Studies that have measured pups' milk intake generally place the completion of what Babicky et al. (1971) called "physiological weaning," or the cessation of milk transfer, at about 27 days postpartum. Yet the break in nursing contact, which could be termed "behavioral weaning," occurs about a week later. One week is a lengthy period when considering that it constitutes 25% of the pups' previous postpartum life. Of all the descriptive studies published to date, only Calhoun (1962), based on field data of the physical condition of the dam, placed behavioral weaning in the same age range we have found here. The discrepancy may arise from any (or all) of three possible sources. First, the mothers in our study, like Calhoun's (1962), were not forced to remain in close proximity with their pups; most others have housed litters in standard laboratory cages. Second, our method of continuous recording, unlike previous work based on interval sampling, allowed us to detect relatively rare events. Finally, milk transfers offer only a partial reflection of weaning. The eventual separation of mother and young is clearly embedded within a complex network of behavioral change.

Notes

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