

Environmental Temperature Modulates Onset of Independent Feeding: Warmer Is Sooner

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Individual dams and their litters were observed from Days 14–22 in a seminatural environment consisting of a nestbox attached to a larger, open field in which powdered chow was available. Ambient temperature in the field was either warm (30°C), moderate (21°C), or cold (10°C); nest temperature was always moderate. Behavior was monitored 12 hr/day by time-lapse video recording. The pups' egressions into the field and onset of independent feeding were temperature-related: Weaning was earliest in the warmth and increasingly late with decreasing ambient temperature. Among subjects in the cold condition, there was a positive correlation between duration in the field and duration feeding. Pup growth was unaffected by the temperature regimes. Environmental temperature has emerged as a determinant for early nest egressions and weaning onset. © 1996 John Wiley & Sons, Inc.

The drama and the universality of weaning reflects its fundamental significance in mammalian development. The transition from suckling to independent feeding is vital to offspring survival and growth. Adults also derive benefits from weaning because they can re-allocate their parental resources to subsequent propagules.

The weaning process consists of the disappearance of suckling and the development of solid food intake. Suckling by Norway rats (*Rattus norvegicus*) in the laboratory begins to decrease around Day 20 (Cramer, Thiels, & Alberts, 1990). Pups first ingest solid food around Day 16 and gradually increase daily intake, so that by Day 19, consumption of solid food augments their growth in comparison to pups that do not have access to solid food and only suckle (see Alberts & Gubernick, 1983, Figure 4). Weaning is complete by Day 34, when pups are self-sustaining on solid food and no longer suckle (Thiels, Alberts, & Cramer 1990).

Generally, past research on the weaning process has focused either on behavioral factors or on the offspring's nutritive requirements. Several kinds of behavioral interactions between adults and juveniles influence pups' initial feedings. For example, Galef

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(1971) found that pups' first ingestion of solid food was delayed if adults were absent during portions of the day when food was present. Adult movement cues and residual odors have been shown to increase the tendency of pups to leave their nest and make the excursions that bring them into contact with solid food (Alberts & Leimbach, 1980; Galef, 1981a; Galef & Heiber, 1976). Once pups are in the vicinity of food, chemical cues from mother's milk can influence the pups' initial dietary preferences (Galef & Henderson, 1972; Galef & Sherry, 1973).

There are various ways in which nutritive energy might regulate the weaning process. For example, Thiels and Alberts (1985) reduced milk availability to litters of pups and observed accelerated weaning onset, thus demonstrating that pups can respond to a deficit of milk energy by incorporating calories from solid food into their diet. This finding is consistent with the general hypothesis that weaning onset is a response to a net shortage of mother's milk. Presumably, such a deficit could arise because the mother's milk supply cannot meet the increasing nutritive requirements of the growing offspring, or because her milk supply is actually diminishing (Henning, 1980; Thiels & Alberts, 1985; see also Galef, 1981b). Thiels, Cramer, and Alberts (1988), however, found that maternal milk supply remains constant between Days 15–20. In fact, whereas Day-15 pups consumed virtually all the dam's available milk, Day-20 pups consumed only about 75% of the dam's supplies. Thus, while weanlings *can* respond to the nutritive challenge of milk shortage with an accelerated acceptance of solid foods, it seems unlikely that such shortages are normally part of weaning onset, at least under laboratory conditions.

Other experiments on physiological mechanisms involved in the utilization of nutrients and the maintenance of energy balance have further eliminated several possible explanations of weaning onset. For example, we can reject the hypothesis that decreases in intestinal lactase (the enzyme necessary to break down lactose, the principle sugar in milk) induces rat pups to discontinue suckling because: (a) lactase levels begin to decline around the 2nd postpartum week [Alvarez & Sas, 1961 (around Day 21); Koldovsky & Palmieri, 1971 (around Day 14)], but rat pups continue to suckle past the 4th postpartum week (Thiels, Alberts, & Cramer 1990); and (b) it is not until about Day 28 that pups demonstrate a preference for feeding over suckling (Stoloff & Blass, 1983), which is also considerably after lactase levels decline. Another popular notion was that the preweaning increase in thyroxine and corticosterone titers, which are important for gastrointestinal development and thus the utilization of solid food (for review see Henning, 1981), regulate the weaning transition (Blake & Henning, 1983). Yet, precocial treatment with these hormones failed to accelerate weaning onset (Blake & Henning, 1983).

Whereas behavioral factors are clearly important to the timing of weaning onset and pups' diet selection, the role of energetic factors in weaning onset remains poorly understood, and examined only in a limited way. In this study we consider a general, energetic parameter that has received little prior experimental analysis with respect to its influence on the initiation of independent feeding, namely, development of body temperature regulation. To maintain homeothermy, all mammals must balance heat production and heat loss. This is particularly difficult for newborn mammals because they are small and hence have a relatively large surface area to body mass, and many are born with poor insulation. Maturation of heat production mechanisms continues throughout the early weaning period (Conklin & Heggeness, 1971; Spiers & Adair, 1986). Even the larger, furred, weanling-aged pups are vulnerable to cool temperatures.

Under natural conditions, Norway rats often live in underground burrow systems where food is stored in an area separate from the nest (Calhoun, 1962; Von Steiniger, 1950). Captive colonies of wild rats reared in large, indoor seminatural habitats typically

stored food in locations separate from their nesting sites (Galef & Clark, 1971b). Thus, in order for a weanling to encounter food, it must leave the warmth and insulation of the nest and the littermates and venture to a new region of the burrow or some area outside the nest. Heat loss to the environment during such excursions might limit the pup's ability to spend time foraging or alter the likelihood that it will leave the nest to search for solid food. Limitations on the ability to maintain body temperature outside the huddle and nest can be viewed as a thermal constraint which affects weaning. Thus, it is not until pups develop sufficient thermoregulatory capabilities that they can leave the nest and ingest solid food.

In the present study, pups were tested with the dam and littermates to enable the complex of behavioral interactions important to weaning onset. Animals were observed in a seminatural habitat consisting of a nest connected via a tunnel to an adjacent field. The temperature of the field was manipulated to yield one of three experimental conditions: warm (30°C), moderate (21°C), or cold (10°C). The nest area was maintained at "room temperature" (21°C) to prevent differences in pups' growth and development that might affect their first egression and ingestion of solid food. Because solid food was present only in the field, pups were required to leave the nest to feed. This habitat provided pups with a challenge faced by many weanling mammals: to leave the warmth of the nest to ingest solid food.

The behavior of two focal pups per litter was recorded 12 hr/day from Days 14–22. We measured the duration that pups spent in the field and the duration pups spent feeding. By varying air temperature in the field, we sought to augment the limitations of the weanlings' immature thermoregulatory capabilities. We hypothesized that pups experiencing warmer field temperatures would leave the nest earlier and ingest solid food sooner than pups that had access to solid food in cooler environments. Because the presence of adult conspecifics can influence pups' first feedings (Galef & Clark, 1971a, 1971b), we also measured the duration of time that the dam spent in the field. Pups' weight gain, duration of time spent suckling, and day of eye opening were recorded. Finally, we expected that as the pups' thermoregulatory capabilities improved with age, they would remain in the field longer and therefore eat more. To address this hypothesis, we analyzed the correlation between duration in the field with duration spent feeding for animals in each condition.

Method

Subjects

Subjects were 18 Sprague-Dawley dams and their litters, bred and born in the Animal Behavior Laboratory at Indiana University. The original stock was obtained from Charles River (Wilmington, MA). Births were checked daily at 1700 hr (day of birth = Day 0). On Day 3, litters were culled to 8 pups, 4 males and 4 females. All pups were housed with their mother and littermates in standard maternity cages (47 cm long × 26 cm wide × 21 cm high) and were maintained on a 16 : 8 hr light : dark cycle (2300 hr lights off/0700 hr lights on).

Apparatus

The present experiment involved observations made on dams and litters that occupied a two-compartment "habitat," consisting of a nest that was connected by a short tunnel to a separate field area. Figure 1 depicts the habitat; its construction and operation are described below.

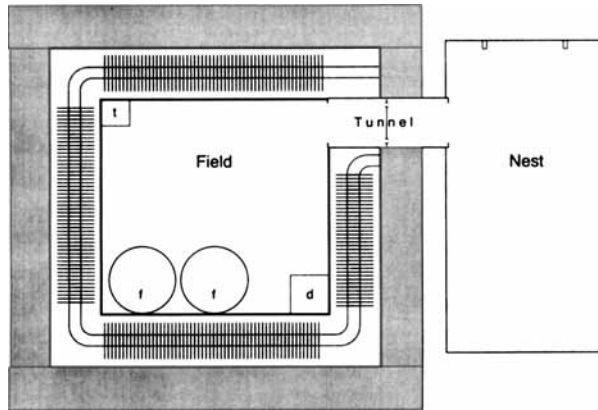


Fig. 1. Temperature regulated seminatural habitat; field (left), nest (right).

Animals were required to leave the nest to feed from either of two glass dishes (11 cm diameter \times 5 cm high) each filled daily with an abundance (60 g) of powdered raw chow. Powdered chow was used to prevent hoarding to the nest. Water was available ad libitum in the nest.

Air temperature in the field was thermostatically regulated to one of three temperature conditions: warm—30°C, moderate—21°C, or cold—10°C ambience. The nest area was maintained at room temperature (approximately 21°C). The field was a 33.5 \times 33 \times 12.5 cm area constructed of sheet metal. The walls of the field were surrounded by four connected lengths of slant-fin tubing, which served as a heating exchange apparatus. This commercially available assembly consisted of 2-cm copper pipe running through a series of 6 \times 4.5-cm aluminum fins. The pipe was connected to a temperature-regulated water circulator [Lauda RM6, Germany or Haake G (water bath) and Haake D1 (circulator), Germany]. The slant-fin system conducted heat into or out of the field and was bounded by an outer insulative shell of sheet metal followed by 5.1-cm-thick Styrofoam material (sides and bottom). A clear Plexiglas lid (48.5 \times 48 cm) covered the field. Approximately 16.5 cm above the field cover was a second layer of Plexiglas that covered the entirety of the field and surrounding heat exchanger (55.5 \times 55 cm). Both Plexiglas lids were perforated to allow sufficient ventilation within the habitat.

Field temperature was monitored by an air temperature probe (Yellow Springs Instrument Corporation #405, Yellow Springs, OH) located in one corner of the field, where it was protected from the rats by a hardware cloth barrier. To prevent condensation when the field temperature was cold, containers of desiccant were inserted within the apparatus; these were placed on the radiator fins and in a jar isolated from the rats by mesh within the field.

The nest and field were connected by a tunnel (19 \times 7.5 \times 6.5 cm) constructed of galvanized metal. To retard heat exchange between field and nest, a hinged door was inserted in the tunnel, as depicted in Figure 1. The metal surface of this tunnel conducted the field temperature. To avoid cold or warm surface temperatures affecting the rats' passage, a raised floor of Plexiglas was provided within the tunnel.

Field temperature was regulated around a setpoint maintained at the thermistor location depicted in Figure 1. There was, however, a gradient of air temperatures that extended across the field. In the cold condition, field ambience was 10°C around the probe and ranged to 18°C at the entrance to the tunnel. In the warm condition, field

ambience was 30°C around the probe and 22.5°C at the entrance to the tunnel. There was no measurable gradient in the moderate condition.

The nest area was adapted from a standard, polypropylene maternity tub (47 × 26 × 21 cm). Within the tub a rudimentary nestbox was provided (19 × 13 × 8 cm). The nestbox was constructed of wire mesh (approximately 1.3-cm squares), however, for support, the side of the nest compartment that was in the center of the maternity tub was constructed of Plexiglas.

Procedure

Acclimation to Dual Chambers

To familiarize the dam with a dual-chamber habitat, including the use of a tunnel with a swinging door, dams and their litters were placed in an acclimation apparatus at 6–8 days postpartum. This apparatus replicated the key features of the larger dual-chamber setting that would be used for the actual experiment, but it was less elaborate, occupied less overall space, and thus enabled us to work with more animals simultaneously than if we were limited solely to the test habitats. The acclimation apparatus consisted of two maternity tubs connected by a tunnel, identical to the type described earlier. Our maternity tub contained soiled bedding from the dam's home cage and was darkened by an opaque cover. Dams immediately and consistently used this portion of the habitat for the pups. The other tub, attached by the tunnel and door, was exposed to overhead illumination during the light portion of the day and contained ad libitum Rat Chow Pellets and water. Pups were no more than 12 days of age while the family group inhabited the acclimation apparatus, so only the dams were observed in the food site. The acclimation period was sufficient for all dams to utilize the tunnel and door, feed normally, and adapt to the dual-chamber structure of the environment.

Test Phase

On Day 11 or 12 postpartum, the nesting tub and tunnel of the acclimation apparatus were detached from the food-site tub and attached to the field area that would serve as the temperature-controlled feeding site outside the rats' nesting area. The nestbox was positioned in the nesting tub and the entire nesting tub was darkened by a metal lid. Each day for the next 2–3 days the lid was retracted incrementally so that by Day 14 only the nestbox was covered, thus providing a view of most of the nest tub. At the time of this restructuring of the environment, 1 male and 1 female pup with body weights average for their gender were selected as the focal pups and were marked for identification with Clairol black hair dye.

Behavioral Observations

During the test phase, (beginning on Day 11 or 12 postpartum) the animals' activities were recorded continuously with time-lapse videography (Gyyr #TLC1400, Anaheim, CA; 120 : 2 record : playback ratio), except for the time required for brief daily maintenance (see below). The nest area and the field area were monitored by separate cameras (Panasonic WV-BL90; Japan) that could accommodate to the illumination cycle. A screen-splitter permitted simultaneous recording of both areas on a single video record. The video records through Day 13 were for general surveillance and qualitative assess-

ment. We confirmed with these tapes that there were no premature egressions from the nest, and that the dam used the new habitat appropriately. On Day 14 data collection began. The animals' activities were video recorded for 12 hr/day (12 : 1 record : playback ratio). Recording started at approximately 2130 hr. Thus, most of the observation time was during lights off (2300 hr lights off/0700 hr lights on) because adult rats display a nocturnal activity pattern and the dam's activities are known to influence the pups' early feedings (Galef, 1971). Red lights (25 W) allowed viewing of the animals during the daily dark phase. Pilot studies indicated that these 12 hr of observation provided a reliable account of the animal's 24-hr behavioral profile.

Each day pups were weighed, remarked as needed, and checked for eye opening (day of eye opening = first day when both eyes were fully open). Before the animals were returned to the habitat, food and water were replenished, temperature of the field and nest were checked, and the field was vacuumed and filled with fresh bedding (if needed). As part of these daily operations, a sliding door was temporarily inserted into a slit at the top of the tunnel near the nest. We had noted that routine handling could activate the pups and lead to handling-associated excursions. The door in the tunnel prevented such excursions and was removed after the rats settled and resumed typical activity. Approximately 10–15 min was required for settling after handling. The entire procedure required about 40–50 min. Video recordings were made daily from Day 14 until Day 20 or until focal pups reached a criterion of feeding for at least five percent of the 12-hr observation period.

During playback an observer used a computer-based program to quantify the following:

1. *suckling*: duration that the focal pups spent attached to the nipples of the dam. Brief detachment from the nipple after milk-letdowns, that is, nipple shifts, were included in the total duration spent suckling.
2. *independent feeding*: duration that the focal pups spent in oral contact with the food.
3. *dam in field*: duration that the dam spent in the field. More than half of a body length entering the tunnel was scored as in the field.
4. *focal pups in the field*: duration that each focal pup spent in the field. More than half of a body length entering the tunnel was scored as in the field. Instances in which the dam carried the pups into the field were not included in the analysis (occurred once).

Reliability

Intrarater reliability scores for repeated viewing of two tapes were within 97.6%.

Data Analysis

For every measure (behavioral or physiological) values were averaged for each pair of focal pups to obtain a single mean value per day per litter. Temporal scores were converted to proportion of time active during the 12-hr test period. The behavioral data were analyzed using repeated measures ANOVAs (Field Temperature \times Day). Field temperature was the between subjects factor, while day was the within subjects factor. Fischers' LSDs were used for post-hoc analyses at the .05 level.

One-way ANOVAs were used to analyze day of weaning onset and day of first nest egression for pups in each experimental condition. A criterion was established for

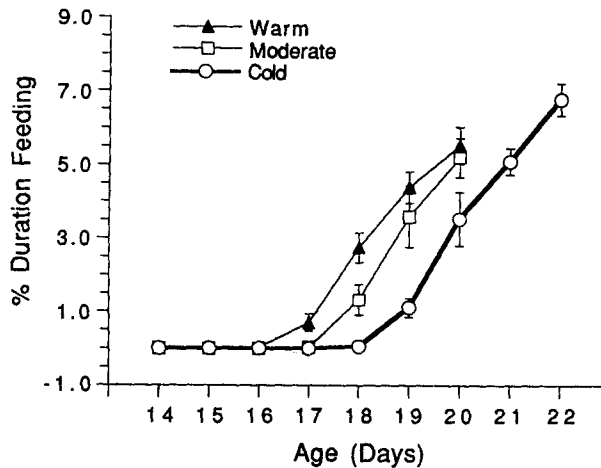


Fig. 2. Proportion of time that pups in the warm, moderate, and cold conditions spent feeding.

day of first egression. Behavioral observations from Day 11 or 12 to Day 13 revealed occasional brief excursions from the nest prior to first day of scoring (Day 14). However, these excursions were rare and erratic (i.e., typically occurring one day but not the next). Thus, criteria for 1st day of nest egression was 2 consecutive days in the field. Such a criterion was not needed for 1st day of feeding because weaning onset did not occur before data coding began.

Pup weight gain was calculated as the percent change from the weight on Day 12 (before first nest egression and thus before experience with the field temperature) versus Day 19 (after weaning onset had occurred). One-way ANOVAs were used to analyze weight data.

Correlations between duration spent feeding and duration in the field on each test day were calculated separately for each group. The correlation analysis was begun on the day that *all* pups in the particular temperature condition were feeding. Thus, values of zero were not included in the analysis. The last day of the correlation was the last day of testing for a given group.

Results

Figure 2 illustrates temperature-related differences in the onset and progression of weaning, reflected by the durations spent ingesting solid food by pups in the warm, moderate, and cold conditions. Mean proportion of time spent feeding, averaged across Day 18 (when the majority of the subjects had begun feeding) to Day 20, was $4.24 \pm 36\%$, $3.38 \pm 54\%$, and $1.58 \pm 32\%$ for pups in the warm, moderate, and cold groups, respectively. A repeated measures ANOVA indicated significant group differences, group main effect Days 18–20: $F(2,15) = 10.5$, $p = .0014$. Post-hoc analyses indicated that pups in the warm and moderate group spent more time feeding than did pups in the cold group ($LSD = 1.26$). There was also a main effect for day; animals increased the proportion of time spent feeding as they aged $F(2,30) = 66.6$, $p = .0001$. The interaction was not significant, $F(4,30) = 1.4$, $p = .25$.

First ingestion of solid food differed significantly between groups. First ingestion occurred on Day 17.12 ± 17 , 17.83 ± 10 , and 18.91 ± 15 for pups in the warm, moderate,

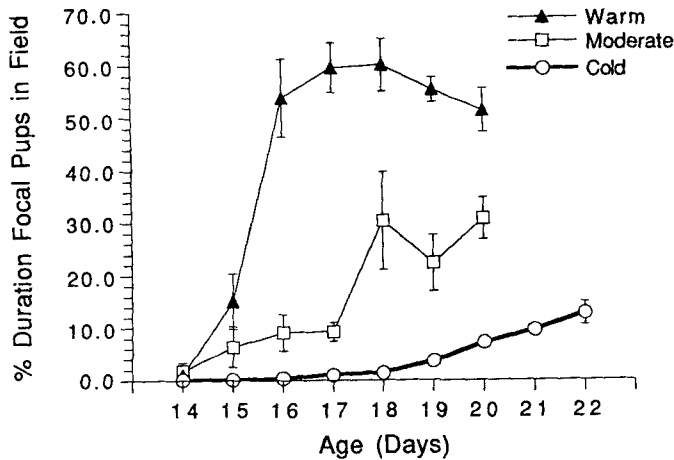


Fig. 3. Proportion of time that pups in the warm, moderate, and cold conditions spent in the field.

and cold conditions, one-way ANOVA: $F(2,15) = 37.4$, $p = .0001$. Post-hoc analyses indicated that independent feeding began earliest for pups in the warm condition, followed by pups in the moderate condition, and lastly followed by pups in the cold condition ($LSD = .435$).

Figure 3 shows that duration spent in the field by pups varied directly as a function of field temperature. Mean proportion of time in the field, averaged across Day 15 (when the majority of subjects had entered the field) to Day 20 was $49.03 \pm 2.36\%$ for pups in the warm condition, $17.96 \pm 3.41\%$ for pups in the moderate condition, and $2.22 \pm 27\%$ for pups in the cold condition. A repeated measures ANOVA indicated that there was a main effect for temperature condition, $F(2,15) = 98.7$, $p = .0001$. Post-hoc analyses indicated that pups in the warm group spent more time in the field than did pups in the moderate group, followed by pups in the cold group ($LSD = 7.23$). There was also a main effect for day; pups spent more time in the field as they aged, $F(5,75) = 15.7$, $p = .0001$. The Field Temperature \times Day interaction was significant, $F(10,75) = 6.9$, $p = .0001$, due to both the overlap between groups during early egression and to the onset of a slight decline in duration in the field by the warm pups starting around Day 18, while in contrast, pups in the moderate and cold conditions continued to increase daily duration spent in the field.

Day of first nest egression also varied as a function of field temperature, one-way ANOVA: $F(2,15) = 4.45$, $p = .03$. First egression was on Day $13.75 \pm .36$ for warm pups, $14.50 \pm .32$ for moderate pups, and $15.42 \pm .49$ for cold pups. Post-hoc analyses indicated that pups in the warm condition left the nest earlier than pups in the cold condition ($LSD = 1.19$).

Figure 4 (upper graph) illustrates differences in the daily durations in the field by the dams. Averaged across days, dams in the moderate and cold conditions spent $44.75 \pm 3.46\%$ and $38.24 \pm 16\%$ of the total test time in the field while dams in the warm condition spent an average of only $18.05 \pm 1.43\%$ of the total test time in the field, $F(2,15) = 18.5$, $p = .0001$. Post-hoc analyses indicated that dams in the moderate and cold conditions spent more time in the field than dams in the warm condition ($LSD = 9.75$). There were no differences in daily durations that the dams spent in the field, $F(6,90) = 1.37$, $p = .23$; the Field Temperature \times Day interaction was not significant, $F(12,90) = 1.07$, $p = .40$.

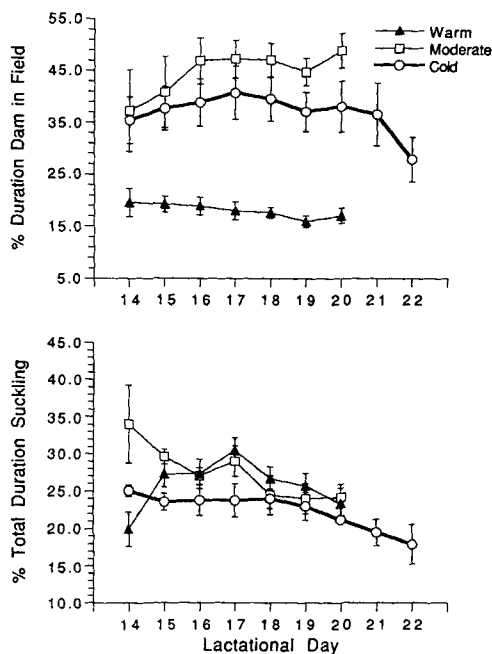


Fig. 4. Proportion of time that dams in the warm, moderate, and cold conditions spent in the field (upper graph). Proportion of time that pups in the warm, moderate, and cold conditions spent suckling (lower graph).

There were no differences between groups in percent weight gain (one-way ANOVA: $F(2,15) = 2.2$, $p = .14$). Percent weight gain was 65.40 ± 1.52 for pups in the warm group, 58.77 ± 2.31 for pups in the moderate group, and 58.40 ± 3.71 for pups in the cold group. Likewise, timing of eye-opening, which occurred on Day $14.00 \pm .29$, Day $13.83 \pm .28$, and Day $13.58 \pm .44$ for pups in the warm, moderate, and cold conditions, respectively, did not differ between groups, $F(2,15) = .38$, $p = .69$.

Figure 4 (lower graph) shows the suckling durations during the 12-hr observation period. Mean proportion of time spent suckling across Days 14–20 was $23.48 \pm 1.09\%$ for cold pups, $27.49 \pm .97\%$ for moderate pups, and $25.83 \pm .80\%$ for warm pups. A repeated measures ANOVA indicated a significant main effect for duration suckling, $F(2,15) = 4.39$, $p = .031$. Post-hoc analyses showed that pups in the moderate group spent a greater proportion of time suckling relative to pups in the cold group ($LSD = 2.89$). There was a trend toward a significant main effect for day, $F(6,90) = 2.09$, $p = .06$; pups spent less time suckling with age. The Field Temperature \times Day interaction was significant, $F(12,90) = 2.32$, $p = .012$, indicating differences between groups in duration suckled depending on the day. Inspection of Figure 4 suggests that the differences and trends that emerged from the statistical analyses were strongly affected by the highly variable data from Day 14. More important here is the inconsistent relation to temperature suggesting no relevant effect in this measure.

Figure 5 (upper graph) illustrates a positive correlation between duration in the field with duration spent feeding on Days 19–22 for cold pups. Pearson's r was $.80$ for this group, indicating that as cold pups spent more time in the field each day, they spent more time feeding, $t(22) = 6.3$, $p < .05$. There was no correlation between duration spent in the field and duration spent feeding for pups in the warm (Days

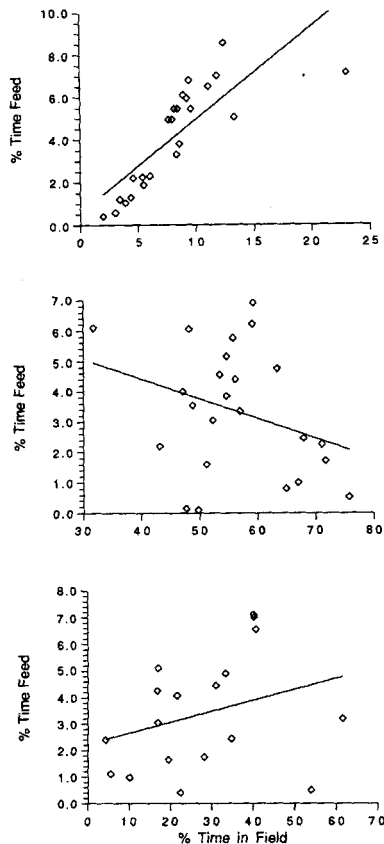


Fig. 5. Correlation between duration spent in the field with duration spent feeding for cold pups, Days 19–22 (upper graph), warm pups, Days 17–20 (middle graph), and moderate pups, Days 18–20 (lower graph).

17–20) and moderate (Days 18–20) conditions, see Figure 5 middle and lower graphs, respectively; Warm: Pearson's $r = -.32$, $t(22) = 1.5$, $p > .05$; Moderate: Pearson's $r = .30$, $t(16) = 1.3$, $p > .05$.

General Discussion

The main finding of the present study was that onset of independent feeding is modulated by environmental temperature. When solid food was located in a warm environment, pups began independent feeding sooner than when food was in a moderate environment and began feeding late when food was available in a cold ambience. Results for daily duration spent feeding showed a similar pattern: Throughout the observation period, pups in the warm and moderate groups spent a greater proportion of time feeding than did pups in the cold group.

Consistent with results for weaning onset, day of first nest egression and proportion of time in the field both varied with environmental temperature. First egression occurred earlier for pups in the warm compared to the cold condition. Proportion of time in the field varied directly with temperature. The warmer the temperature the greater the overall time spent in the field. Presumably, warmer temperatures present less of a thermal challenge to the young and hence permit earlier egression from the nest.

The pattern in the present results did not derive from the proportion of time that the dams were in the field. Dams in the cold and moderate groups spent more time in the field than did dams in the warm group. If dam presence in the vicinity of food contributed to weaning onset, pups in the warm group would have displayed a delay in weaning onset. Because these pups weaned *earlier*, the effect of temperature on weaning onset was independent of the time that the dam spent in the field.

Field temperatures did not affect pups' growth and development. Thus, we saw no evidence for a nutritive deficit as precursor to weaning onset. Differences in suckling durations did not result in differences in body weight. Furthermore, maturational rate as reflected by eye opening did not vary between groups. Together, these results further support the notion that environmental temperature had a direct, rather than indirect, effect on weaning onset.

Duration in the field was related positively to duration feeding for pups in the cold condition: As pups in the cold condition matured, they spent more time in the field and demonstrated a correlated increase in feeding. These results confirm earlier predictions and suggest that as the pups' thermoregulatory capabilities improved, they were able to leave the nest for longer periods and, for animals in the cold condition, spend more time feeding independently. Behavioral observations suggested that pups in the cold condition were in the field approximately long enough to feed and then returned to the nest. It appeared that pups in the warm and moderate conditions failed to show such a positive correlation between duration spent in the field and duration spent feeding because they engaged in additional behaviors while in the field. For example, they sometimes slept in the field and were more likely to engage in play and other activities in the field than were pups in the cold condition. There was, however, a clear effect of temperature on behavior; pups in the moderate condition spent less overall time in the field than did pups in the warm condition. Weaning onset occurred earlier for pups in the warm compared to those in the moderate temperature condition.

A common hypothesis regarding weaning is that pups must leave the nest because they need a nutritive supplement to mother's milk. Thiels et al. (1988) demonstrated, however, that weanling pups do not experience reduced maternal milk stores. In the present study, independent feeding occurred several days after first nest egressions, casting further doubt on the notion that pups leave the nest specifically to find an alternative to mother's milk. Furthermore, despite a difference of nearly 2 days in initial feeding by pups in the cold compared to the warm condition, there was no corresponding difference in body weights. These observations suggest that pups' early sampling of food is not significant to their energy balance. It is likely that egression and exploration, not a nutritive deficit, are the precursors to first ingestion.

Johanson and Hall (1980) found that ambient temperature can strongly influence independent feeding in *preweanling* rats. Young pups (Days 3 and 6) provided with infusions of milk or milk placed on the floor showed greater intake in warmer temperatures ($\geq 32^{\circ}\text{C}$). Furthermore, Hall and Bryan (1980) found that pups as young as 3 days of age provided with a wet mash diet and tested in a warm incubator ($\geq 32^{\circ}\text{C}$) licked and lapped for food, thus displaying regulated independent intake. Results from the present study further demonstrate a relation between temperature and independent feeding. We found that same-aged *weanling* pups began nest egression and independent feeding earlier when solid food was located in a warm rather than a cool environment. It appears that warmer temperatures can substitute for increased thermoregulatory capability, and thus allow earlier nest egression and first ingestion of solid food.

It is possible that proximity of food to the nest would allow earlier first feeding because reduced transit time would reduce the thermal challenge of being out of the

nest. Galef (1971), in fact, reported differences in first feeding by rats when food was located about 2.54 cm (1 in.) from the nest compared to a condition in which food was 27.94 cm (11 in.) from the nest.

Environmental temperature is important to weaning onset and its early progression. The present results are consistent with the view that the pups' developing thermoregulatory capabilities, which include both thermogenesis and heat conservation, are a key mediating element in the relation of ambient temperature and weaning. We have identified a nonnutritive, energetic factor that is important for weaning onset.

Notes

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