REGURGITATION FEEDING OF YOUNG IN HARVEST MICE, *MICROMYS MINUTUS* (RODENTIA: MURIDAE)

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Regurgitation feeding of young is regarded as a behavior specific to the Canidae among mammals. In this study, we document regurgitation feeding by female harvest mice, *Micromys minutus*. We gave a composite ball made from sunflower seeds and small pieces of blue plastic to lactating females. Subsequently, some pieces of plastic were found in the digestive tracts of young with whom the mother had displayed regurgitation-like behavior. Regurgitation feeding started on the day of parturition and continued through weaning, but a switch existed in quality and quantity of behaviors related to regurgitation at ca. 9 days postpartum in this species.

Key words: *Micromys minutus*, harvest mice, regurgitation, maternal care, suckling young

Regurgitation of partially digested food is occasionally used as a way of feeding the young (Malm, 1995; Malm and Jensen, 1993). Among mammals, this has been observed exclusively in some species of canids (Biben, 1982; Johnsingh, 1982; Lamprecht, 1979; Malcolm, 1980, 1985; Malcom and Marten, 1982; Martins, 1949; Moehlman, 1979; Packard et al., 1992; Rasmussen and Tilson, 1984; Rheingold, 1963; Ryden, 1974; Ryon, 1986) and is regarded as a behavior specific to the Canidae (Malm and Jensen, 1993). However, we observed regurgitation feeding of young in the harvest mouse (*Micromys minutus*). Female harvest mice regurgitate food directly to their young throughout the period of lactation and beyond. Here we report details of maternal care in *M. minutus*, with particular focus on the possible ecological significance of regurgitation feeding in this species.

MATERIALS AND METHODS

We studied harvest mice from a colony established in 1992 from wild individuals captured in Saga Kyushu, Japan. Mice were housed as breeding pairs in 27 by 16 by 20 cm plastic cages. Cage floors were covered with wood chips and rice straw was provided as nest material. Harvest mice were maintained at 23 ± 1°C on a 14L:10D photoperiod with lights on at 0830 h. Water and food were available ad libitum, the diet consisting of canary seeds, Chinese, foxtail, and Japanese millet seeds, flax seeds, sunflower seeds, and commercial laboratory chow (Oriental Yeast Co., Ltd., Tokyo). Breeding females were selected for behavioral observation based on obvious evidence of pregnancy, and evidence that the female had successfully raised at least one previous litter to weaning.

Experiments to demonstrate regurgitation feeding.—During observations of mothers and young in their nests, we noted young sticking their noses into and licking the inside of their mother's mouth. The mother then appeared to give the young food from her mouth in response to this behavior. To examine if this exchange involved regurgitation, we made a composite ball of ca. 8 mm in diameter from sunflower seeds and many small pieces of blue plastic (ca. ≤1 by 1 mm). The ball was given to a female that was rearing 7-day-old pups. The female consumed the sunflower seed ball while we watched and thus ingested pieces of blue plastic. The female was then removed from the cage, and we examined her oral cavity. We sedated the female, washed the inside of her oral cavity with water, and examined the oral cavity using a dissecting microscope. Neither food nor blue plastic pieces were detected in the female's mouth. The female was then returned to the nest. Four hours and 36 min later, we took from the nest a young with whom, in that interim, the mother

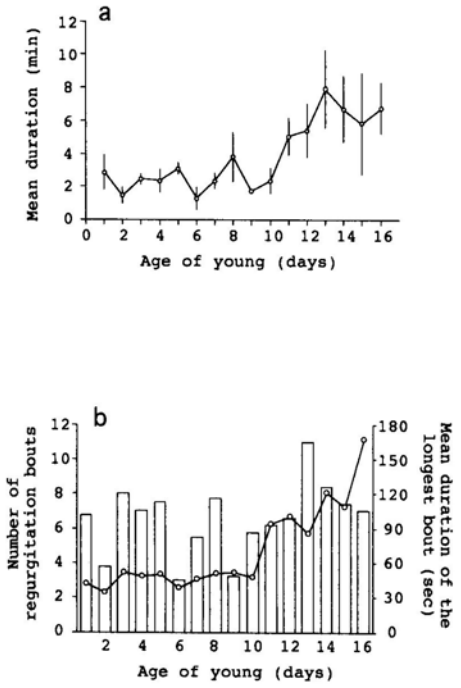

FIG. 1.—a) Changes in mean duration of regurgitation behavior relative to age of young; vertical bars indicate *SE*. b) Changes in mean number of regurgitation bouts and duration of the longest regurgitation bout during each observation period relative to age of young; columns and circles show mean number and duration of bouts, respectively.

had displayed regurgitation-like behavior. We sacrificed the young by using ether, and removed and examined its esophagus and stomach under a dissecting microscope. We repeated this experiment three times with three different mothers and their litters, with each female given a composite ball once. In addition, we examined the upper alimentary tract of a lactating harvest mouse when it returned to the nest after eating a sunflower seed ball to determine if the mother kept ingested food somewhere anterior to the stomach.

Behavioral observation.—To observe maternal behavior, we housed a female and her young in a transparent plastic cage (27 by 16 by 20 cm). Wood chips and rice straw to a depth of 15 cm were provided as bedding. Because pregnant females were likely to select dark areas as nest sites in cages, one wall of the cage was covered with paper (12 by 12 cm), so that pregnant females built their natal nests in contact with this part of the wall. Some females made a small window in the paper where the nest was in contact with the wall. To prevent light from entering the window opening, we attached a 6- by 6- by 15-cm squared pipe (made from a milk carton) with tape at the window outside the wall at a 90° angle. Behavior in the nest was then observed through this pipe. Behavior outside of the nest was recorded by direct observation.

We observed maternal care for five female harvest mice. Each female in the observational cage was maintained under the same feeding, lighting, and temperature conditions as those in the colony rooms. Although data were collected as continuously as possible from 1 day to 16 days postpartum, some observations could not be carried out because the window to the nest was occasionally obstructed with nest materials or substrate. Thus samples obtained for each day were as follows: day 1 and 2, $n = 4$; day 3 and 4, $n = 3$; day 5–10, $n = 4$; day 11–15, $n = 5$; day 16, $n = 4$. Litter size ranged from three to five.

Each female was observed in a 4-h session beginning at 0830 h every morning. During each observation period, we recorded frequency and duration of nursing (female covering pups with her body), grooming young, brooding young (female covering pups with thin pieces of straw, and sitting on them for a while before leaving nest), and regurgitating food to young. We recorded the interval from the time that the female finished eating until regurgitation, or, when feeding was not seen before regurgitation, simply from the beginning of the observation until regurgitation. We included intervals from the beginning of observation to regurgitation because only a few feeding bouts were observed before regurgitation in the earlier days of lactation. No adult males were included in the study because male *M. minutus* are not tolerated near the nest and take no part in caring for the young.

Neonatal young of *M. minutus* often kept their mouths open when taken out of their nest, whereas mouths of neonatal young of *Mus musculus* remained closed. In addition, harvest mouse young taken out of their nest tended to lick objects such as a hand of the observer, and it was clearly unlike either grooming behavior

toward themselves or other individuals. We examined the extent and duration of this behavior in an additional 42 young from 14 litters. Each day, we removed young from their nest and noted if the young kept its mouth open and displayed non-specific licking behavior at least once within 10 min after being taken from the nest. To reduce stress for young and their mothers, litters were divided into an even-day group (22 pups from seven litters) first observed on the day of birth, and an odd-day group (20 pups from seven litters) first observed on day 1 postpartum. Thus young were removed from the nest only every other day.

RESULTS

Experiments to demonstrate regurgitation feeding.—Pieces of blue plastic were found in both the esophagus and stomach of young *M. minutus*. All pieces of plastic found in the young's digestive tract were broken into much smaller ones. Because the female and her young were observed continuously from the time the sunflower seed ball was eaten until exchange of regurgitation, this established that the mother had transferred ingested food to its young. The same result was obtained in all three repetitions of the experiment.

Food and pieces of blue plastic were found in the stomach of the female that was sacrificed after eating a sunflower seed ball, but no food or plastic pieces were evident in the oral cavity, pharynx, larynx, or esophagus. Morphology of the oral cavity, pharynx, larynx, and esophagus of the dissected harvest mouse was similar to that of other Murid rodents. There were no morphological adaptations of the upper alimentary tract of *M. minutus* for storage of food, such as the cheek pouch of squirrels (*Sciurus*) and hamsters (*Mesocricetus*) or the crop sacs of some birds. Thus, food material transferred to young actually comes from the stomach of the mother.

Behavioral observation.—We did not observe any aggressive behavior of the mother toward pups or any insistent nipple attachment by the young. Young opened their eyes and achieved skillful self-grooming by day 13.

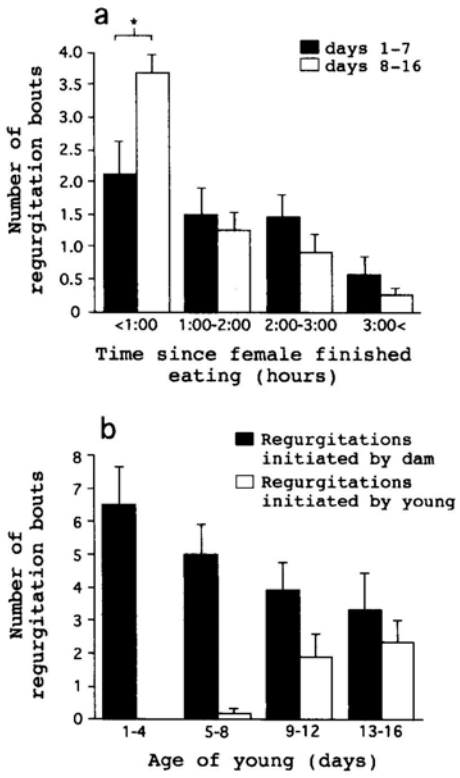

FIG. 2.—a) Comparison of number of regurgitation bouts at days 1–7 and days 8–16 relative to eating-regurgitation intervals (Mann-Whitney test, the asterisk indicates $P < 0.05$; bars indicate *SE*). b) Changes in mean number of regurgitation bouts initiated by lactating females and by young in each observation period relative to age divided into four age classes of young; vertical bars indicate *SE*.

The amount of time that the lactating female spent in regurgitation behavior in each observation period rose significantly after day 10 (mean duration of regurgitation behavior in days 1–10, 143.2 ± 14.5 *SE*; mean duration of regurgitation behavior in days 11–16, 376.9 ± 47.4; Mann Whitney $U = 201$, $d.f. = 1$, $P < 0.0001$; Fig. 1a). The length of the longest regurgitation bout

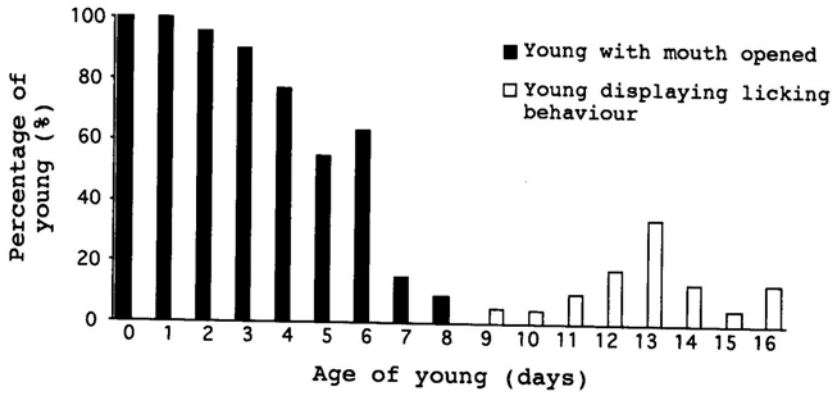

FIG. 3.—Changes in percentage of young with mouth opened and displaying licking behavior relative to their age.

in the first 10 days postpartum was generally 40–50 s but increased dramatically thereafter, lasting nearly 180 s on day 16 (Fig. 1b). The number of regurgitation bouts per observation period remained similar or increased in the later days of lactation (days 10–16 postpartum) when length of the longest regurgitation bout was increasing.

Number of regurgitation bouts per hour decreased gradually as length of time since the female had finished eating increased during days 1–7, whereas during days 8–16 more than one-half of the regurgitation bouts were observed within 1 h after eating (Fig. 2a). There were more regurgitation bouts within 1 h of the time the female finished eating during days 8–16 postpartum than during days 1–7 (Mann-Whitney U = 356, $d.f.$ = 1, P = 0.03).

Some regurgitation bouts appeared to be initiated by dams, preceded by licking of the mouth of the young or placing its nose against the young's mouth in a way that resembled sniffing. Other regurgitations appeared to be initiated by the young licking around their mother's mouth (begging behavior). Number of regurgitations initiated by dams was greatest on days 1–4 and declined thereafter (Fig. 2b). In contrast, regurgitation initiated by young first appeared on days 5–8 and became more common thereafter.

All young kept their mouths open when removed from the nest on the day of parturition and day 1, but the proportion of young doing so declined to zero by day 8 (Fig. 3). A few young first displayed licking behavior on day 9, and some continued to do so until day 16.

The time that females spent nursing, grooming, or brooding young tended to decrease with increasing age of the young (Fig. 4). Mean duration of nursing behavior during each observation period began to decrease after 8 days postpartum. Similarly, mean duration of grooming behavior toward young gradually declined from day 5 and grooming of young by females was observed rarely after 13 days postpartum. Until day 4, each female harvest mouse often completely covered young with thin pieces of straw and brooded them for a short while before leaving the nest. Young covered with straw made little movement until their mother returned. Mean duration of this brooding behavior during observation periods had almost disappeared by day 9.

DISCUSSION

Our study demonstrates that regurgitation feeding of young, thought to be confined to

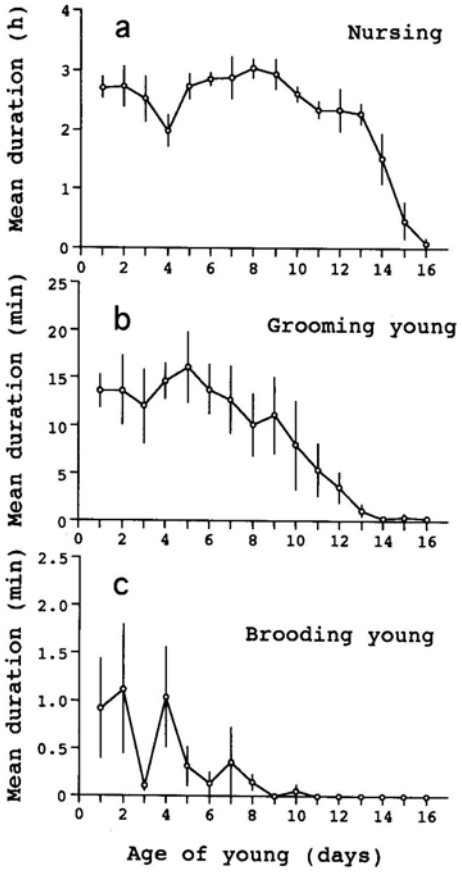

FIG. 4.—Changes in mean duration of a) nursing, b) grooming young, and c) brooding young by female harvest mice relative to age of their young; vertical bars indicate *SE*.

the Canidae among mammals (Malm and Jensen, 1993), is also carried out by *M. minutus*, a rodent. Regurgitation feeding in the harvest mouse begins on the day of birth and continues for a short while after lactation has ceased. Throughout lactation, the mother licked or placed her nose against the young's mouths in a way that resembled sniffing prior to regurgitation. A young whose mouth was licked or sniffed responded by moving its mouth. To this response, a regurgitation then followed. Early

TABLE 1.—*Comparison of reproductive traits of the smallest rodents.*

Species	Characters									Authority
	ABW	WB	PG	MLS	MLW	LA	AW	WW	SMM	SMF	
Mus musculoides	6	0.8	22	3.4	2.7	0.45	24	3.5			Anadu, 1976
Reithrodontomys humulis	6	1.2	24	2.2	2.6	0.44	21–28	4.3	49	77	Layne, 1959
Mus minutoides	7.5	0.8	19	4.0	3.2	0.43	17	3.7	42	42	Willan and Meester, 1978
Micromys minutus	8.5	1.1	17	3.9	4.3	0.50	15–16	4.0	30	35	Present study
Baiomys taylori subater	9	1.1	20	2.7	3.0	0.33	18–22	3.0	66	64	Blair, 1941
Perognathus longimembris	9	1.3		3.2	4.2	0.46	21	5.5	150	60	Hayden and Gambino, 1966

[a] ABW, adult body weight (g); WB, weight at birth (g); PG, period of gestation (days) as minimum interval between litters; MLS, mean litter size; MLW, mean litter weight at birth (g); LA, mean litter weight at birth/adult body weight; AW, age at weaning (days); WW, weight at weaning (g); SMM, sexual maturity in male (days); and SMF, sexual maturity in females (days).

regurgitations tended to be accompanied by the support of a young's head by the mother's forelimbs. In contrast to this passive behavior early in the lactation period, young later begged actively for food, as do young canids (Malm, 1995). Facilitation of regurgitation with begging behavior by the young and more frequent eating by females coincides with increasing energy requirements of the young later in lactation. Frequency of regurgitation bouts within 1 h of eating by the female also was greater later in the period of lactation. Because regurgitated materials might be degraded into more simple form and contain more gastric juice as more time passes after ingestion, length of the interval between eating and regurgitation, and thus the possibility for pre-digestion, should be associated inversely with development of the digestive system of young.

Mouth-opening behavior performed by the young until 8 days postpartum seemed to facilitate regurgitation while young were very immature. On the other hand, some of the young who were ≥9 days old tended to lick inanimate objects and the appearance of licking behavior by young on day 9 generally coincided with onset of begging behavior. Young began active movement inside the nest, which involved more skillful self-grooming and playing with nest materials, from then on. The transition from mouth opening to licking by young might be related to an increasing consumption of energy by young.

As predicted, mean duration of each of three maternal behaviors displayed by female *M. minutus,* namely nursing, grooming of young, and brooding, tended to decrease with age of the litter. Because brooding was performed immediately before females left the nest and was not observed after day 9 when young were covered completely with fur, it might function for maintenance of the young's body temperature when their ability to thermoregulate was not yet well developed. Similarly, grooming of young disappeared after day 13 when young were capable of skillful self-grooming. These results are in partial agreement with reports in rats (*Rattus rattus*—Cramer et al., 1990; Thiels et al., 1990) in which maternal care and development of young are coordinated.

Young harvest mice facilitated regurgitations with begging behavior after 9 days postpartum, and mean duration of regurgitation behavior drastically increased after day 11. Therefore, at least after day 9, partially digested food provided by lactating female *M. minutus* appears to play a role as 'baby food' for the young as suggested for canids (Malm and Jensen, 1993) and supplements milk. This also is supported by the fact that no young displayed tenacious nipple attachment. Moreover, extremely large energy requirements have been reported for lactating females in some rodents, for example, *Sigmodon hispidus* (Randolph et al., 1977), *Peromyscus maniculatus* (Millar, 1979), and *Microtus pinetorum* (Lochmiller et al., 1982). A comparison of some parameters concerning reproduction shows that *M. minutus* has a shorter gestation and lactation period, larger ratio of litter weight at birth to adult body weight, and earlier sexual maturity than many of the smallest rodents (Table 1). In *M. minutus,* regurgitation feeding may help reduce energy demand on the female during lactation and thus indirectly compensate for some of the constraints of small body size. This type of maternal care may be of particular benefit to species such as *M. minutus* in which males take no part in care of young. Our results also raise questions about the age-related digestive capacity of neonatal pups.

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