

## Physiological and Behavioral Consequences in Rats of Water Recycling During Lactation

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Radioactive water injected into 10-day-old rats was recovered the following day from their mothers' blood. This transfer of water was nearly eliminated by ligating the injected pups' urethras, a result indicating that mother rats consume their offspring's urine. Preventing urine consumption by ligating urethras of all pups in a litter doubled the plasma volume deficit in dams produced by 24 hr of water deprivation alone and led to increased isotonic saline, but not water, intakes following water deprivation. Mother rats' daily water intakes increased after they were deprived of pup urine, and their pup-licking behavior increased following water deprivation. These findings indicate that urine consumption by mother rats has both physiological and behavioral consequences and suggest that pup licking is, in part, an ingestive behavior.

The first behavior a mother rat directs toward her young is licking. As each pup emerges, the mother licks it, and after she consumes the fetal membrane, placenta, and umbilical cord, she licks the newborn's body surface again, eventually concentrating this activity on its anogenital region. Subsequently, during the suckling period, nearly all the mother's licking is directed toward her infants' anogenital region (Rosenblatt & Lehrman, 1963). Because infant rats do not urinate spontaneously until 2-3 wk after birth, they normally depend on this licking to provoke micturition reflexly; in addition to stimulating urination, licking may also increase urine production (Capek & Jelinek, 1956).

Even without anogenital stimulation,

elimination of excess fluid derived from milk occurs relatively rapidly in infant rats. Four hours after a bout of nursing, 10-day-old rats produce a volume of urine that amounts to more than half of the volume of water obtained earlier by suckling (Friedman, 1979). On the basis of the volume of urine formed during this period, it has been estimated that a litter of rats of this age produces more than 20 ml of urine per day. This volume of urine is equivalent to approximately 5%-6% of the mother's body weight and nearly two thirds of the amount of water the dam provides to her young in milk (see Friedman, 1979; Friedman & Bruno, 1976). Considering the hydromineral demands of lactation, this is a substantial water loss for the mother to endure. However, in the experiments described below, we show that this water is not lost but rather recovered by the mother as she licks her pups and stimulates them to urinate. In addition, we find that the urine consumed by the mother may have both physiological and behavioral consequences for her and that it appears to provide an alternative source of fluid when none is otherwise available. Thus, not only does pup licking help to maintain body fluid balance in infant rats, but it also contributes to the mother's fluid homeostasis as well.

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## Experiment 1

In this experiment we sought to determine whether and to what extent mother rats consume their young's urine. To do this, we studied the transfer of radioactive water from rat pups to their mothers and their littermates.

### Method

**Subjects** Sprague-Dawley rats (Zivic-Miller; Camm Research) were bred in the laboratory, and 12 mothers and their offspring were used. Litters were culled to eight pups each 3 days after birth. Rats were maintained on a 12:12 hr light/dark cycle, and adults were given Purina Laboratory Chow and water ad lib.

**Procedure** Ten days after birth, two pups from each of six litters were injected sc with tritiated water (25  $\mu$ Ci per rat in .25 ml of .15 M NaCl; New England Nuclear) and then returned to their mother and littermates. After the bladders were emptied by stroking the perineum with a cotton swab, two pups from each of six other litters were anesthetized with ether, and their urethras were ligated through a small incision in the skin. The incision was closed with silk sutures, and the pups were injected as above. As described below, pups appeared to tolerate urethral ligation inasmuch as it did not interfere with subsequent milk intake.

Twenty-four hours later, all pups and their mothers were decapitated, and trunk blood was collected. Blood from both injected pups in each litter was pooled because of the small volume, as was that from their uninjected littermates. Samples were centrifuged to obtain serum. Urine was removed from bladders of the ligated, injected rats with a hypodermic needle and syringe, weighed, and pooled. Aliquots (.5 ml) of serum and urine were deproteinized with 2 ml of 3% perchloric acid and centrifuged, and 2.0 ml of the resulting supernatant were mixed with 10 ml of Scintiverse and counted in a liquid scintillation spectrophotometer. Background activity was approximately 12 counts per minute (CPM). In this and all other experiments described below, statistical analyses were performed with Student's *t* test, paired comparisons being used when appropriate.

### Results

At the time of sacrifice, the bladders of ligated pups were greatly distended, containing on the average 1.6 ml of urine. Bladders of pups without urethral ligation were typically empty or nearly so. Rats did not appear to be adversely affected by urethral ligation; they had suckled, as evidenced by the presence of milk in their stomachs, and had gained about 1.5 g more weight than their littermates (corrected for the weight of urine remaining in the bladder).

As shown in Table 1, substantial radioactivity was transferred from injected pups without urethral ligation (controls) to their mothers and littermates during the 24 hr following administration of tritiated water. Preventing micturition by urethral ligation greatly reduced this transfer of tritium. The specific activity of serum from mothers and from uninjected littermates of ligated, injected pups was, respectively, 7% and 44% of that found in their counterparts from control litters. Injected pups had the highest concentration of tritium in serum, and the blood of injected, ligated pups contained approximately 12% less radioactivity than that from injected controls. The specific activity of urine taken from the bladders of ligated pups (469,406  $\pm$  20,488 CPM/ml) was essentially the same as that in their serum, a result suggesting that the tritium had equilibrated in body fluids during the 24 hr following injection.

### Discussion

The results of this experiment show that by ingesting the urine excreted by their young, mother rats reclaim a large portion of the water they lose by providing milk to their pups. As shown in Table 1, substantial radioactivity was recovered from mothers 24 hr following injection of tritiated water into their pups. Transfer of tritium appeared to be almost entirely due to consumption of the injected pups' urine since, when micturition was prevented by urethral ligation, the exchange was nearly eliminated. The relatively small amount of radioactivity that was recovered from mothers of ligated pups given tritiated water may have been derived from ingesting their injected young's feces and their uninjected pups' excreta, from grooming radioactive saliva deposited on their nipples by suckling pups, or by inhaling tritiated water evaporated by the offspring.

On the basis of the specific activity of urine in the bladders of ligated pups and of the mothers' serum, and assuming the body water content of mothers to be two thirds of their body weight, the results indicate that on the 10th day of lactation, mother rats consume about 19 ml of urine from a litter of

Table 1  
*Effects of Urethral Ligation on the Transfer of Tritiated Water From Suckling Rats to Their Mother and Littermates*

Group	No. of litters	Tritium in serum (CPM/ml) from					
		Mother		Uninjected pups		Injected pups	
		<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>
Control	6	9,094	659	2,791	238	523,530	8544
Ligated	6	594**	55	1,504**	44	460,749*	26,878

\*  $p < .05$ ; \*\*  $p < .001$ ; compared with controls.

eight pups. This value approximates the estimate of daily urine formation in 10-day-old pups and suggests that mother rats consume nearly all the urine their pups produce. On the 10th day of lactation, rats produce 42–48 ml of milk (Hanwell & Linzell, 1972) which contains approximately 70% water (Luckey, Mende, & Pleasants, 1954). Thus, by consuming her offspring's urine, the mother reclaims nearly two thirds of the water she loses to her pups in milk. Although these estimates of urine consumption and water recycling do not account for loss of water by the mother to the environment or by other potential routes of recycling within the mother–litter group (see below), it is nevertheless clear that urine drinking is an important means of water conservation during lactation.

These findings and conclusions are consistent with those of Baverstock and Green (1975), who, using different methods, showed a transfer of tritiated water from offspring to mothers in several desert species, including rodents and canids. In addition to confirming fluid transfer between mothers and their young, the present experiment also demonstrated a direct exchange of water between littermates. Whereas urethral ligation reduced the concentration of tritium recovered from mothers by 93% (Table 1), ligation resulted in only a 46% reduction in the specific activity of serum from uninjected littermates. Thus, about half of the tritium found in uninjected pups appears to be derived directly from their injected littermates and not from the mothers' milk. How water is transferred between pups is not clear from the present experiment; it may result from pups licking one another, from pups inhaling tritiated

water evaporated by injected pups in the "huddle," or from pups consuming radioactive saliva left on the mother's nipples by other siblings. In any case, under the conditions of the present experiment, this exchange does not appear to contribute substantially to water conservation in the litter. Assuming total body water of pups to be equal to two thirds of body weight, each pup obtained approximately .15 ml of water from its seven littermates which amounts to a net conservation of a little more than 1.0 ml in 24 hr by the litter. If, however, the exchange between littermates is due to pulmonary uptake, such conservation may become more important in a closed, moist, stagnant atmosphere, such as a maternal burrow.

Both injected and uninjected pups from litters with ligated young had lower concentrations of tritium in serum than their counterparts from control litters. The reduction in serum specific activity in uninjected littermates of pups with urethral ligation was probably due, in large measure, to a greatly decreased intake of radioactive milk, since mothers of ligated pups also incorporated far less tritium than those in control litters. Compared with their counterparts in control litters, injected pups with urethral ligations also showed a much greater absolute decrease in serum radioactivity than their uninjected littermates. Thus, while a low specific activity of milk may have contributed to reduction in serum tritium of ligated pups, it apparently does not account for all of it. Because the amount of urine remaining in the bladders of ligated pups at sacrifice constituted only half of the estimated daily urine production of rats at this age (Friedman, 1979) and because ligated pups gained more weight than their injected

littermates beyond that due to the urine in their bladders, pups with ligatures may have retained in body fluids more of the water they consumed by ingesting milk. Since this water in milk apparently had a lower specific activity than their body fluids, it may have diluted the concentration of injected tritium and thus contributed to the observed decrease in serum specific activity.

## Experiment 2

The first experiment showed that mother rats consume their young's urine. In the next series of experiments, we examined whether ingestion of pup urine contributes to the maintenance of body fluid balance in the mother.

### Method

**Subjects** Sprague-Dawley rats (Zivic-Miller; Camm Research) were bred in the laboratory, and mothers and their offspring, culled to eight per litter, were used. Rats were maintained on a 12:12 hr light/dark cycle, and adults were given Purina chow and water ad lib except as noted.

**Procedure** Experiment 2A Ten days after birth, pups in each of 14 litters were weighed as a group after their bladders were emptied. In one group of five litters, infants were returned to their mothers and left undisturbed (controls). Pups in another four litters were returned, and their mothers were deprived of water (water deprived). In another group of five litters, all pups underwent urethral ligation as described above and were returned to their mothers which were then also deprived of water (water-plus-urine-deprived). Twenty-four hours later, mothers were killed by decapitation, and trunk blood was collected into heparinized tubes. Plasma obtained after centrifugation was analyzed for protein (by refractometry) and sodium (by flame photometry). Litters were killed with ether and weighed as a group after their bladders were emptied by puncture.

Experiment 2B. Fourteen litters were divided into three groups 10 days after birth. In this experiment, three control litters in which mothers had free access to water were used. In six litters, mothers were deprived of water after their pups underwent control surgery which entailed anesthetization, localization of the urethra, and suturing of the incision. Pups from five other litters were ligated, and their mothers were deprived of water. Twenty-four hours later, water bottles were returned to the deprived mothers, and water intakes of all mothers were measured by weighing bottles (to the nearest .1 g) 30, 60, 120, and 180 min later.

Experiment 2C: This experiment was identical to the last except that all mothers were given .15 M NaCl to drink 24 hr following water deprivation and that intakes were measured 30, 60, 120, 180, and 240 min later. In

this experiment, four, nine, and eight litters were used in control, water-deprived, and water-plus-urine-deprived groups, respectively.

### Results

**Experiment 2A.** All pups nursed during the 24 hr prior to sacrifice, as evidenced by the milk found in their stomachs and by weight gains for the litters, which averaged 13.9, 9.9, and 11.6 g for litters in the control, water-deprived, and water-plus-urine-deprived groups, respectively. The effects of water and urine deprivation on the mothers' body fluids are shown in Table 2. Plasma sodium concentrations in the two groups of deprived mothers were essentially the same and were significantly higher than in non-deprived controls. This elevation in plasma sodium represents approximately 9.3% increases in plasma osmolality and indicates a substantial intracellular dehydration. Plasma protein concentrations of water-deprived mothers were increased significantly over those of controls, while those of water-plus-urine-deprived mothers were higher than those of both controls and water-deprived rats. Compared with controls, the increases of plasma protein in water-deprived and water-plus-urine-deprived rats represent plasma volume deficits of approximately 9% and 18%, respectively.

**Experiment 2B** As shown in Figure 1, mothers in both deprived groups drank more water during the 3-hr drinking test compared with nondeprived controls. The in-

Table 2  
Mean ( $\pm$  SE) Plasma Protein and Sodium Concentrations in Mother Rats Deprived of Water and Prevented From Consuming Urine of Their 10-Day-Old Offspring

Group	n	Protein (in g/100 ml plasma)	Sodium (mEq/l water)
Control	5	5.94 $\pm$ .11	143.0 $\pm$ 1.5
Water deprived	4	6.53 $\pm$ .11**	155.5 $\pm$ .5***
Water + urine deprived	5	7.22 $\pm$ .20* .***	157.1 $\pm$ 2.6**

\*  $p < .05$ , compared with water-deprived group.

\*\*  $p < .01$ ; \*\*\*  $p < .001$ , compared with controls.

crease was apparent in the first 30-min access to water and continued until the end of testing. At no time did water intakes in the two deprived groups differ significantly.

**Experiment 2C.** The results of this experiment are displayed in Figure 2. Starting with the first 30-min access to fluid, both groups of deprived mothers showed markedly increased saline intakes during the 4-hr test compared with the nondeprived control group. Mothers deprived only of water drank steadily for the first 60 min of access to saline, and then intakes abated substantially for the next 3 hr. Mothers deprived of both water and urine tended to consume more saline in the first 30 min of the drinking test than those deprived of water, but this difference was not statistically reliable. However, saline consumption by mothers deprived of water plus urine did not decline as much after the first hour of access, and by the third and fourth hours of the drinking test they had consumed reliably more than mothers deprived only of water ( $ps < .02$  and  $.001$ , respectively).

### Discussion

Experiment 2A showed that lactating rats deprived of water become markedly dehy-

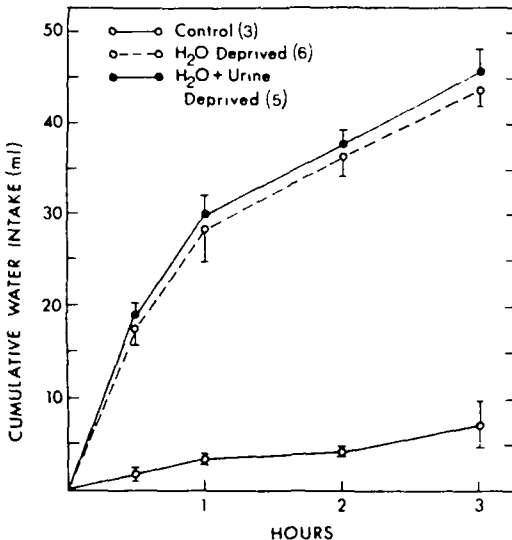


Figure 1. Cumulative water intake of lactating rats after 24-hr deprivation of water or water plus their offspring's urine. (Urine deprivation was accomplished by ligating the urethras of all pups in a litter. Controls were not deprived. Points show mean values per group [ $\pm$  SE], and numbers of mothers are given in parentheses.)

drated; fluid is lost from both intra- and extracellular compartments as evidenced by, respectively, increased plasma sodium and protein concentrations. Whereas additional fluid deprivation resulting from urethral ligation had no apparent effect on the mothers' intracellular fluid loss, it greatly compounded their plasma volume deficit produced by water deprivation alone; mothers without access to water or pup urine became twice as hypovolemic as those deprived only of water (Table 2). These findings indicate that the dam's consumption of urine produced by her young helps to maintain primarily extracellular rather than intracellular fluid balance. However, because infant rat's urine is hypotonic (e.g., Friedman, 1979; Heller, 1949), it is questionable whether urine consumption alone can help to maintain electrolyte concentrations; other mechanisms, such as enhanced secretion of antinatriuretic hormones, likely contribute to volume regulation as well.

Mothers deprived of both water and pup urine increased fluid intakes more than those deprived only of water when given access to isotonic saline, but not when given water to drink (Figures 1 and 2). The enhanced intake of saline by mothers denied access to pup urine may reflect the more pronounced plasma deficit found in similarly treated rats in Experiment 2A. Rats made hypovolemic by injections of polyethylene glycol increase consumption of both isotonic saline and water; however, whereas saline consumption continues unabated for many hours, water intake decelerates rapidly despite a continued plasma deficit (Stricker & Jaloweic, 1970). Previous research has attributed such constraints on water intake in hypovolemic rats to the inhibitory effects of overhydration, which are avoided when animals consume isotonic saline (Stricker, 1969). It is possible, therefore, that in Experiment 2B inhibition from osmotic dilution prevented mothers with ligated pups from further increasing water intake whereas in Experiment 2C overhydration was avoided by consumption of isotonic saline, which thereby allows the expression of a more intense hypovolemic thirst. On the other hand, it is possible that the response of rats to isotonic saline may reflect enhanced sodium appetite which has been observed previously in lactating rats (Richter &

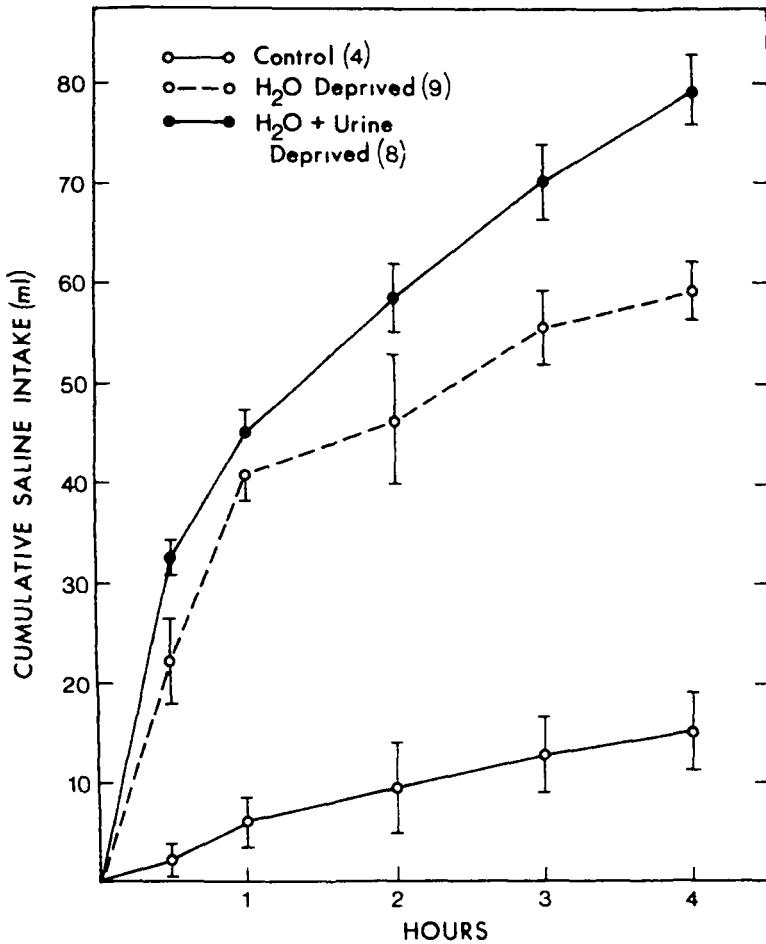


Figure 2 Cumulative .15 M saline intake of lactating rats after 24-hr deprivation of water or water plus their offspring's urine. (Urine deprivation was accomplished by ligating the urethras of all pups in a litter. Controls were not deprived. Points show mean values per group [ $\pm$  SE], and numbers of mothers are given in parentheses.)

Barelare, 1938) and which may stem from their greater plasma deficit (Wolf & Stricker, 1967) or some other cause.

### Experiment 3

The previous experiments showed that pup urine provides the mother with a source of fluid, in addition to water, that may help to maintain body fluid homeostasis. In the next studies, we examined whether mothers compensate the loss of one of these fluids by consuming more of the other.

### Method

**Subjects** Litters obtained by breeding Sprague-Dawley rats (Zivic-Miller; Camm Research; Laboratory Supply, Indianapolis) in the laboratory were used. Animals were maintained on a 12:12 hr light/dark cycle,

and adults were given Purina chow and water ad lib.

**Procedure** Experiment 3A: In this experiment we examined the effects on water intake of preventing mother rats from consuming their pups' urine. Ten days after birth, all pups in each of 11 litters underwent urethral ligation as described above. Pups in each of six additional litters underwent control surgery. Water intakes of the mothers in all litters were measured 24 hr before and 24 hr after surgery by weighing water bottles (to the nearest 1 g)

Experiment 3B: In this experiment we examined the effects of water deprivation on the dam's pup-licking behavior. On the eighth day after the pups' birth, two mothers and their litters were taken from the plastic cages in which they were housed and placed, along with their home-cage bedding, in separate 10-gal (37.8 l) glass aquaria that were positioned end to end. An opaque divider between the aquaria visually partitioned the two dams. Illumination was provided by an overhead incandescent bulb that maintained the light/dark cycle. We shaded about one third of each aquarium at their juxtaposed ends and thereby induced the mothers to establish their nests within the optimal range of the

video camera that recorded their behaviors. Mirrors were angled at the rear of the aquaria to allow observation when a mother's back was turned toward the camera and thus obscured the front view of the litter.

The next day, one mother was deprived of water at 6.00 p.m., and 16 hr later the 8-hr observation period began. Pilot studies showed that pups of water-deprived mothers gained less weight during the observation period than those with hydrated mothers. Presumably, dehydration due to water deprivation (Table 2) compromises milk production. Therefore, since one would expect reduced milk intake to also decrease urine production in pups (Friedman, 1979), the following procedure was used to equate the supply of urine available to water-deprived and control mothers.

At the start of the 8-hr observation period, pups in each litter were individually marked, and half of each litter (four pups) was given to the other mother. Two hours later, the other half of each litter was switched, and then, at 2-hr intervals, half of each litter, starting with those first exchanged, was switched again. At the end of the observation period, at which time mothers had all of their own pups, water was returned to the deprived mother and taken from the control mother. Sixteen hours later, another observation period began. A total of six mothers, in three pairs, were observed under control and water-deprived conditions.

The mothers' behavior during each of the four 2-hr periods after pups were switched was recorded on a time-lapse videotape recorder. The mothers' behavior was recorded continuously on videotape during each of the four 2-hr periods after pups were exchanged. The camera's lens subtended a field sufficient to keep the two nests in view. The video recordings were made with a time-lapse video recorder (Hitachi-Shibaden Model 512-U), with a 24/1 record/playback ratio. The mothers' pup-licking activities were observed during rapid playback and quantified with electromechanical counters and timers that provided the summated amount of time spent licking for each successive 15 min of each 2-hr observation period. Interobserver reliability was greater than .90.

## Results

*Experiment 3A* The effect of urethral ligation of rat pups on their mothers' water

Table 3  
Mean ( $\pm$  SE) Daily Water Intakes of Mother Rats Before and After Urethral Ligation of Their 10-Day-Old Offspring

Group	n	Before	After	Difference
Control				
operated	6	102.3 $\pm$ 4.5	98.7 $\pm$ 5.0	-3.57 $\pm$ .34
Ligated	11	97.4 $\pm$ 4.2	115.2 $\pm$ 4.5 <sup>*</sup> , <sup>**</sup>	17.8 $\pm$ 2.0

\*  $p < .05$ , compared with control operated.

\*\*  $p < .001$ , compared with baseline.

intake is shown in Table 3. Before surgery, daily water intakes of mother rats whose pups were control operated were not different from those whose pups had urethral ligatures. After pups were control operated, water intakes of their mothers did not change from this baseline. In contrast, mothers increased water intakes by an average of nearly 18.0 ml over baseline after their pups were prevented from micturating by urethral ligations, so that on the day after surgery mothers of ligated pups drank reliably more water than those with control operated pups.

*Experiment 3B.* The effects of depriving mother rats of water on their pup-licking behavior is displayed in Figure 3. The left side of the graph shows the median amount of time the mothers spent licking pups in consecutive 30-min periods throughout the 8-hr observation period. After pups were exchanged between dams (at 0, 2, 4, and 6 hr), licking increased markedly in the first 30 min and then gradually subsided thereafter. Although water-deprived and control mothers displayed similar patterns of behavior toward their pups, the amount of time spent licking was greatly potentiated when mothers were deprived of water. Accordingly, as shown in the right-hand side of Figure 3, the mean total time spent licking pups during the observation period increased significantly above control levels when mothers were deprived of water ( $t = 7.00$ ,  $p < .001$ ). Every mother licked pups more when water deprived; the average increase was about 90% above control levels.

## Discussion

The findings from these two experiments suggest that lactating rats can use water and pup urine interchangeably as sources of fluid. When deprived of the opportunity to ingest their pups' urine, mother rats ingested more water (Table 3). This result is consistent with that of Experiment 2 which indicated that the urine obtained from pups contributes to the mother's body fluid balance and that this contribution is sufficient to have impact on the mother's drinking behavior. Presumably, mothers increased water intake in order to compensate for the

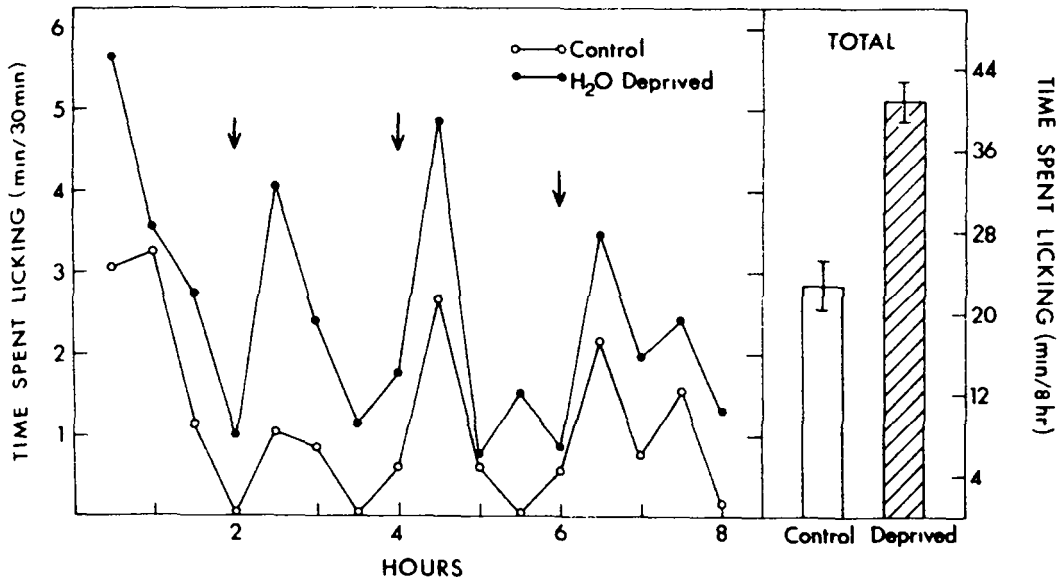


Figure 3 Effects of water deprivation on pup-licking behavior of six lactating rats (Median amount of time spent licking pups in 30-min intervals is shown on left. Half of the pups in each litter from control [nondeprived] and deprived mothers were exchanged at 0, 2, 4, and 6 hr [at arrows]. Mean time  $\pm$  SE spent licking pups for entire 8-hr observation period is shown on right.)

loss of fluid from their pups. In this regard, it is particularly interesting that the increase in water intake (about 18 ml) closely corresponds with the estimate of urine consumption (19 ml) based on the exchange of tritium from young to their mother (see above).

Whereas the results of Experiment 3A show that the availability of pup urine may affect the mother's water intake, the findings of Experiment 3B indicate that the availability of water may alter the mother's ingestion of urine. In this experiment, licking appeared to be focused on the pups' anogenital region regardless of the mothers' hydrational state. However, mothers spent nearly twice as much time licking pups when they were deprived of water than when they were not (Figure 3). Much of the licking behavior occurred soon after pups were exchanged and then gradually abated. Since this pattern was observed whether or not mothers were deprived of water, it may have been a response to disturbing the litter, which subsequently habituated. However, because this transient increase in licking was more pronounced when mothers were deprived of water, it is possible that the thirsty mothers were responding as well to a fresh

supply of fluids (urine) provided by pups that had recently nursed from a hydrated mother. Presumably, as the supply was exhausted, there was less cause to lick, and the behavior subsided.

### General Discussion

The results presented here describe some general features of the dynamics of fluid exchange and conservation in the mother-litter group. In addition to the usual routes of fluid loss, such as excretion and evaporation, the latter of which is likely to be magnified by the increased metabolic and thermal demands associated with caring for young (Leon, Croskerry, & Smith, 1978), the lactating dam also loses a significant amount of water by nursing young. Our measurements indicate that the mother loses to her pups more than 30 ml of water, through milk, on the 10th day of lactation. To help replace these substantial fluid losses as well as to satisfy the additional need for water created by the hyperphagia during lactation, the mother rat relies on two sources of fluid—water and her young's urine. By consuming her pups' urine, the mother offsets both the loss of body fluids (Table 2) and the need to

obtain fluids from the environment (Figures 1 and 2). That both sources of fluid available to the dam are relatively interchangeable and satisfy similar needs is suggested by the results of Experiment 3 showing that mother rats increase water intake when denied access to pup urine and increase pup licking, and presumably urine consumption, when deprived of water (Table 3 and Figure 3).

There also appears to be a second, related mechanism of conservation based on an exchange of water between pups. As discussed above, this mechanism may have minimal consequences in a laboratory setting but may contribute more substantially under natural conditions in which there is relatively low evaporative water loss to the environment. Similarly, the source of fluids provided by the young to their mothers may be more important in the wild since it would reduce the "costs" of seeking water at some distance from a nest or burrow. In arid climates, water recycling may be an even more critical mechanism for conservation and appears to account for the ability of desert mammals to sustain lactational performance and consequent growth of their young despite a limited water supply (Baverstock & Watts, 1975).

By licking her pups, the mother rat obtains fluid which has functional consequences for her hydrational balance as well as behavior. In addition, when she is thirsty, the mother appears to respond to young as a source of fluid by licking them more. These findings suggest that the act of pup licking operates, at least in part, in the service of body fluid homeostasis. In this sense, the present findings complement those of Leon et al. (1978) which show that the mother rat's contact with her young is influenced in part by their mutual thermoregulatory state. However, in contrast to the thermoregulatory control of maternal behavior, which acts to limit or terminate bouts of mother-young contact, the process of fluid exchanges, as described here, serves to maintain or augment contact. Collectively, such studies suggest that, in addition to hormonal and experiential factors, immediate physiological needs may motivate certain maternal behaviors (see also Wilson & Stricker, 1979).

It is unlikely that all aspects of pup licking

can be understood on the basis of changes in body fluid balance. The fact that mothers continue to lick pups when an unlimited supply of water is available, for example, indicates that other factors, besides hydrational state, maintain this behavior. The onset of pup licking also is not readily explained by consideration of the mother's fluid balance, although, in this case, it should be noted that one function of the mother rat's prepartum anogenital self-licking (Steinberg & Bindra, 1962) may be the conservation, through recycling, of water and electrolytes. Nevertheless, given the findings presented here, it may be worthwhile for future studies in which pup licking is used as an index of maternal responsiveness to consider licking as an ingestive as well as a maternal behavior.

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