

"Resource" Exchange in the Biparental California Mouse (*Peromyscus californicus*): Water Transfer From Pups to Parents

David J. Gubernick and Jeffrey R. Alberts
Indiana University

Mammalian mothers provide water to their young via milk. Rodent mothers reclaim much of this water by licking the anogenital areas of their pups, stimulating reflexive urination, and consuming the pups' urine. Male rodents do not provide milk (hence water) to the young, but in some species male parents may nevertheless lick their pups. We determined the amount of water transfer from pups to mothers and fathers in the biparental California mouse, *Peromyscus californicus*, by injecting 5-, 10-, 20-, and 30-day-old pups with tritiated water and measuring the radioactive label in maternal and paternal plasma after 24 hr of interaction with their litter. On Days 5 and 10 mothers obtained more pup urine than did fathers. Parents consumed equivalent amounts of pup urine on Days 20 and 30. Mothers engaged in more pup anogenital licking than did fathers, which accounted for the difference in pup urine consumption. Salt appetite controls, in part, pup anogenital licking in lactating rats (Gubernick & Alberts, 1983). Salt appetite was not implicated in the modulation of anogenital licking in the California mouse because the mice failed to display a salt appetite. Licking of young and urine consumption are not dependent solely on the bidirectional exchange of water between the dam and her offspring.

Mother-infant interactions in mammals involve bidirectional exchanges of metabolic resources that may be of mutual, though not necessarily equal, benefit to both mother and young (Alberts & Gubernick, 1983). For example, the relationship between a rat dam and her litter involves a behaviorally mediated, bidirectional transfer of two vital resources: water and electrolytes (Friedman & Bruno, 1976; Friedman, Bruno, & Alberts, 1981; Gubernick & Alberts, 1983, 1985). Water and electrolytes are delivered to the pups from the mother in the form of milk (Luckey, Mende, & Pleasants, 1954). Water and electrolytes are recovered by the mother when she licks the anogenital areas of her pups, stimulates urination, and then consumes the pups' urine (Friedman & Bruno, 1976; Friedman et al., 1981). Consumption of pup urine contributes significantly to the dam's extracellular fluid volume and total body water balance (Friedman et al., 1981). Mothers deprived of pup urine and water become twice as dehydrated (hypovolemic) as dams deprived only of water. Pup urine and water are used interchangeably as a source of fluids. Rat dams deprived only of pup urine significantly increase their consumption of water and electrolytes, whereas mothers deprived of water spend more time licking the ano-

genital area of their pups, presumably consuming more urine (Friedman et al., 1981).

The recycling of water and electrolytes between the rat dam and her young occurs throughout lactation (Gubernick & Alberts, 1983). The pattern of water transfer from pups to dams corresponds nicely to the pattern of milk transfer from mothers to young. Maternal anogenital licking of pups is controlled in part by the dam's hydrational state (Friedman et al., 1981) and the dam's salt appetite (Gubernick & Alberts, 1983).

The recycling of water between mothers and offspring occurs in other species (Baverstock & Green, 1975) and is probably of benefit to the water economy of lactating females and their young that live in dry, as well as moist, habitats. However, other species have not been studied as extensively as the laboratory rat. We extend our exploration of resource exchange between parents and offspring to include the California mouse, *Peromyscus californicus*, which inhabits chaparral and sage scrub areas of central and southern coastal California (Cranford, 1982; McCabe & Blanchard, 1950; M'Closkey, 1972; Merritt, 1974; Meserve, 1974). *Peromyscus californicus* form persistent, if not monogamous, associations between males and females (Dewsbury, 1981; Kleiman, 1977) and produce 1-4 altricial young per litter (Drickamer & Vestal, 1973; Rood, 1966).

Of particular interest to an analysis of resource exchange is that male *Peromyscus californicus* provide extensive care for their young from the day of birth to weaning (Gubernick & Alberts, 1987). We documented the biparental care system of the California mouse from Day 1 to Day 31 postpartum (Gubernick & Alberts, 1987). The male remains in the nest with the female and pups for 7 to 10 hr per 12-hr observation period. The male, female, and young collectively remain in contact for substantial periods of time throughout the course of lactation. Whereas female California mice spend fewer

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Correspondence concerning this article should be addressed to David J. Gubernick, Department of Psychology, Indiana University, Bloomington, Indiana, 47405.

than 20 min per 12 hr in nonnursing contact with their pups, males are in sole contact with pups an average of 1 hour or more per period. The male's being in sole contact with the pups occurs typically when the female leaves the nest. The male usually huddles over the pups in a "nursing" posture similar to that of the female. While in contact with the pups, the male often licks them. Transport of young occurs infrequently, although either parent will carry the pups in its mouth. Nursing gradually declines as the pups advance in age, but even at 31 days postpartum an appreciable amount of time (5 hr) is spent nursing. Paternal behavior in *Peromyscus californicus* appears equivalent in quantity and quality to maternal behavior except that the male does not lactate.

Because males do not provide water and electrolytes to the pups, they might not be motivated in the same manner as females to reclaim these resources, even though males otherwise provide extensive care for the young. In the present series of studies, we quantified the transfer of urinary water from pups to fathers and mothers by injecting pups with tritiated water and measuring the radioactive label in the parents' plasma (Experiment 1). Because salt appetite is known to modulate maternal anogenital licking of rat pups (hence urine consumption), we investigated whether *Peromyscus californicus* would display a salt appetite (Experiment 2).

Experiment 1: Transfer of Water From Offspring to Parents

In at least two other species of mice (*Mus musculus* and *Notomys alexis*), lactating females consume pup urine (Baverstock & Green, 1975). It is not known whether rodent fathers also ingest pup urine. The present experiment examined the transfer of water from *Peromyscus californicus* pups to their mothers and fathers throughout the lactational cycle of the dam.

Determination of Water Transfer

The amount of water obtained by fathers and mothers was estimated by labeling with tritium the body water (and hence the urine) of pups and measuring the amount of radioactivity found in both parents' body fluids after 24 hr of interaction with their litter. These values were used in combination with direct measures of body water, as described next.

Six adult, nonreproductive males and 6 females were killed by ether overdose. Each animal's stomach, intestine, and bladder were emptied, and the carcass and guts were weighed and freeze-dried under partial vacuum (Virtis Unitrap) to constant weight. The average water content of the male's body was 58% (volume/body weight), and that of the female's body was 60%. Because male and female body water content did not differ, $t(10) = 1.10$, $p > .10$, we used 59% of body weight as the best estimate of body water values.

We were well aware of potential insensible gain by nonurinary means (e.g., respiratory exchange with the litter) but deemed such measurements in this case to be inappropriate. Previously determined measures of insensible gain for lactating rats (Gubernick & Alberts, 1983) were low (0.11 ml/pup

for 5- to 20-day-olds and 0.56 ml/pup for 30-day-olds) and, given the size of our mouse colony, we did not wish to sacrifice other mice unnecessarily.

We measured the radioactivity in a sample of maternal plasma (P_M) and paternal plasma (P_P) and used P_M and P_P , in combination with total body water content of mothers and fathers, to estimate the total radioactivity in the parents' body fluids. This value, divided by the available radioactivity in pup urine (U ; as measured from the urine of ligated, injected pups), provided the measure of the amount of water transferred from a single pup to the mother or father. The amount of water transferred from litters of pups to parents was estimated by applying the following formula to data from each mother-father-litter triad:

$$\begin{aligned} \text{For mothers: } W_{PM} &= [(.59 B_{wt})(P_M)/U] \cdot 2 \\ \text{For fathers: } W_{PF} &= [(.59 B_{wt})(P_P)/U] \cdot 2 \end{aligned}$$

where W_{PM} and W_{PF} = the amount of water (ml) transferred from pups to mothers and fathers, respectively; B_{wt} = mother's or father's body weight, with $.59B_{wt}$ as an estimate of total body water content (ml); P_M and P_P = CPM/ml of plasma (CPM = counts per minute), a measure of radioactivity in mothers and fathers; U = CPM/ml of pup urine derived from ligated, injected pups, an estimate of the radioactivity available to the parents; and 2 = average number of pups/litter (Drickamer & Vestal, 1973; Rood, 1966; unpublished data), a standard litter size for comparison within and across ages.

Although parents ingest pup feces during some bouts of anogenital licking, and therefore obtain fecal water along with urine, we considered "urine ingestion" to include these two related sources of water.

Method

Subjects. A total of 24 male and 24 female *Peromyscus californicus* and their offspring served as subjects. Parents and their young were reared in standard polypropylene mouse maternity cages. Each pair had previously reared at least one litter successfully. Purina Mouse Chow and water were provided ad libitum. Until the day of injection, animals were housed in a colony room kept at 23 °C and maintained on a 16:8 hr light/dark cycle initiated at 0700.

Procedure. Animals were transported to another building where pups were injected sc at the nape of the neck with tritium (New England Nuclear) on either Day 5, 10, 20, or 30. Injected solutions contained 1 μ l of tritium (25 mCi) per ml of 0.15 M NaCl. Pups were administered either 0.5 ml (5- and 10-day-olds) or 1.0 ml (20- and 30-day olds) of the prepared solution, dosages that previously provided sufficient tritium in the urine of rat pups of similar body weights for reliable measurement of the radioactive label after further dilution in maternal plasma (Gubernick & Alberts, 1983).

On the day of injection, 1 pup (from litters of 2 or 3 pups) or 2 pups (from litters of 4 pups) were anesthetized with ether and their urethras ligated through a small midline incision in the skin approximately 0.2 cm above the urinary pore. The incisions were closed with silk sutures and the pups were returned to their parents 15 min later. Within 1 hr after surgery, the ligated pup(s) and a nonligated littermate(s) were injected with tritium as described earlier and were returned to their parents and littermates. Ligation had no apparent effects on pups or on parental behavior. Pups attached to nipples,

sucked and, by the next day, had gained weight. Six pairs of parents and their litters were used at each of four ages.

Twenty-four hr after pup injection, mothers and fathers were weighed and anesthetized. Approximately 0.5–2.0 ml of blood were collected by heart puncture. Blood samples were centrifuged at 3,000 rpm for 20 min at 4 °C to obtain plasma. Mouse pups were killed by ether overdose. Urine was collected from the bladders of ligated, injected pups with a hypodermic needle and syringe. Measured amounts of paternal plasma (0.06–0.40 ml), maternal plasma (0.11–0.58 ml), and pup urine (0.04–0.8 ml) were separately mixed with Aquasol (New England Nuclear) and counted in a Beckman LS-100 liquid scintillation counter for 10 min (background activity was approximately 28 CPM).

Results and Discussion

The results of the tritium transfer measures, adjusted for parents with a standard litter of 2 pups, are shown in Figure 1. These data indicate that the transfer of water from pups to parents occurs throughout the lactational cycle and that fathers ingest pup urine. On Days 5 and 10 postpartum, mothers obtained significantly more water than did fathers, $t(10) = 2.77$ and 3.68 , respectively, $p < .02$, two-tailed. There were no differences between fathers and mothers in the amount of water transferred on Days 20 and 30 ($t < 1.03$). The amount of water transferred changed in an orderly progression. On

Day 5, the earliest day of our measurements, fathers reclaimed an average of 0.58 ml of water from a litter of 2 pups, whereas mothers obtained 1.41 ml. The daily transfer of water to fathers and mothers increased to 3.26 and 4.69 ml by Day 20 and then declined to 0.33 and 0.58 ml, respectively, by Day 30.

The increased urine consumption by both parents was likely due to increased urine production by the growing litter. Similarly, the decline in water transfer after Day 20 may have been due to the maturation of spontaneous urination by the pups. We cannot judge conclusively the extent to which the decline in water transfer is related to diminished urine availability or to decreased anogenital licking by the parents.

Differences in the amount of water transferred to fathers and mothers may be due to differences in the amount or timing of anogenital licking by each parent. We previously documented the extent of pup anogenital licking by parents throughout the lactational cycle of *Peromyscus californicus* (Gubernick & Alberts, 1987), and here we present some of those data that are suitable for evaluating the differences in water transfer to fathers and mothers. We used a procedure similar to that used in the present Experiment 1 and videotaped parents interacting with their litters.

Figure 2, reproduced from Gubernick and Alberts (1987), shows the duration of pup anogenital licking by mothers and

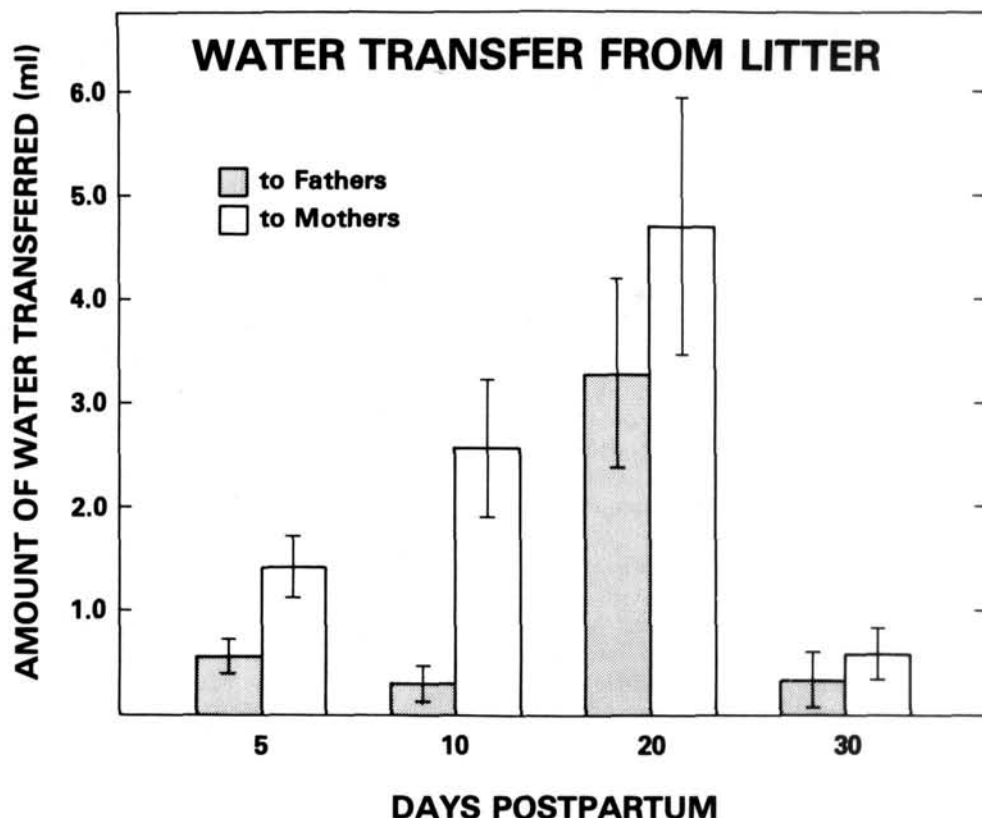


Figure 1. Amount of water transferred from a litter of 2 pups to their father and mother throughout lactation. (Each bar represents the mean and SE for 6 fathers and 6 mothers. Water transfer was estimated by injecting some pups with tritium and measuring the amount of radioactivity recovered in the father and mother 24 hr later [see text for details].)

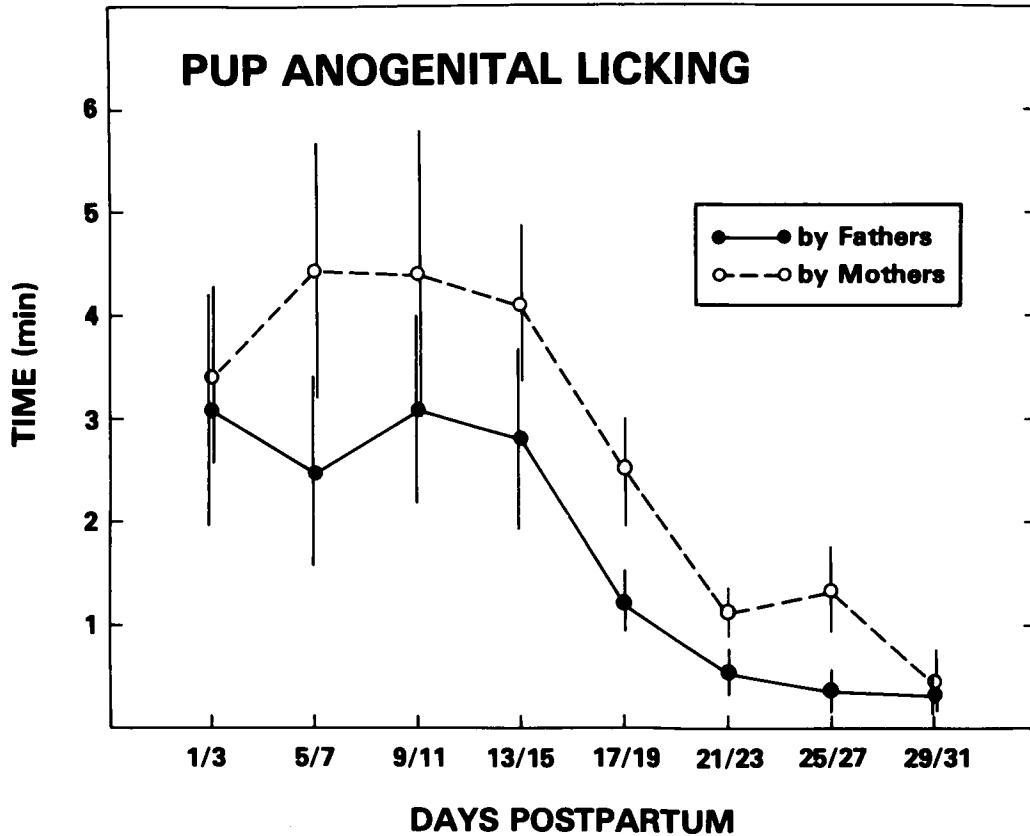


Figure 2. Duration of pup anogenital licking by fathers and mothers throughout lactation. (Each data point represents the mean and SE for 6 fathers and 6 mothers averaged over 2 days. Parents and their litters were videotaped continuously for 12 hr/day, on alternate days from Day 1 to Day 31 postpartum. From "The Biparental Care System of the California Mouse, *Peromyscus californicus*" by D. J. Gubernick and J. R. Alberts, 1987, *Journal of Comparative Psychology*, 101, p. 173. Copyright 1987 by the American Psychological Association. Reprinted by permission.)

fathers during 12-hr observation periods. Both parents licked the anogenital areas of their pups throughout the lactational cycle (see Gubernick & Alberts, 1987, for fuller treatment). Mothers engaged in significantly more pup anogenital licking than did fathers, $F(1, 10) = 6.40$, $p < .05$, which likely accounts for the greater consumption of pup urine by mothers in the present Experiment 1 (see Figure 1). Maternal anogenital licking typically occurred during bouts of nursing, but the amount of time mothers engaged in anogenital licking of their young represented a relatively small percentage of their total contact/nursing time (Gubernick & Alberts, 1987). Paternal anogenital licking of pups usually occurred when only the male was in the nest with the pups.

In contrast to pup anogenital licking, fathers devoted significantly more time than mothers to licking other body regions of pups (see Gubernick & Alberts, 1987, Figure 6). This differential distribution of pup licking by fathers and mothers may have important consequences for the developing young. Rat dams (*Rattus norvegicus*) spend more time licking the anogenital areas of their male pups than of their female pups (Moore & Morelli, 1979). Maternal anogenital licking

of male rat pups affects development of male sexual behavior (Moore, 1984). Whether maternal and paternal California mice lick male and female offspring differentially will be examined in subsequent studies.

In the present study, pup anogenital licking decreased significantly across days, $F(7, 70) = 14.41$, $p < .01$. The developmental decline in anogenital licking of the young occurred earlier than the diminution in water transfer to both parents. Anogenital licking decreased after Day 13, whereas the decrement in urine transfer occurred after Day 20 postpartum (Figure 1, Experiment 1), which suggests that pup anogenital licking is not rigidly or singularly controlled by receipt of pup urine.

Experiment 2: Salt Appetite in the California Mouse

In both the Norway rat (*Rattus norvegicus*) and in *Peromyscus californicus*, pup licking and the ingestion of pup urine are not entirely controlled by the water in urine because, in both species, licking and urine ingestion occur reliably in

the presence of abundant and ad libitum water. The rat dam's anogenital licking of pups appears to be modulated, in part, by a sodium-specific salt appetite. Lactating rats display an enhanced salt appetite (Alberts & Gubernick, 1983; Richter & Barelare, 1938) and ingest greater amounts of saline when prevented from consuming pup urine (Friedman et al., 1981). Rat dams provided with an additional source of salty fluids (NaCl) decrease anogenital licking of pups (Gubernick & Alberts, 1983). In Experiment 2 we investigated whether *Peromyscus californicus* parents would display an enhanced salt appetite compared to virgin males and females.

Method

Subjects. Ten adult virgin males, 10 nulliparous females, and 18 parents (nine pairs) served as subjects. Parents and their litters of 2 to 4 pups were housed in standard mouse maternity cages, whereas the virgin males and females were housed individually in stainless steel wire-mesh hanging cages. The colony room was kept at 23 °C and was maintained on a 16:8 hr light/dark cycle initiated at 0700.

Procedure. In previous investigations of salt appetite in virgin and lactating rats, we found variable and fluctuating salt appetites because of variations in the sodium content of normal Purina Rat Chow (Alberts & Gubernick, 1983, 1987). To obtain better control of salt appetite, we successfully used sodium-deficient diets. In the present experiment, mice were therefore given a sodium-deficient diet (0% Na salt; ICN Nutritional Biochemicals) as their only food, starting 2 days before testing and continuing throughout the experiment. Two fluids were continuously available in 25-ml, glass, graduated cylinders. One cylinder contained distilled water; 0.08 M NaCl was in the other. The position of the cylinders was alternated daily. Fluid consumption was monitored every 24 hr for 4 days. Traditionally, when an animal will ingest increased amounts of an aversively concentrated salt solution, it is considered to have an enhanced salt appetite (e.g., Richter & Barelare, 1938). For purposes of the present analysis, we modified the traditional approach so that it more closely approximated the parameters of the phenomena we were studying. Thus, our measure of salt appetite was based on preferences for dilute (0.08 M) saline. Our test solution was hypotonic, as is pup urine. Lactating rats on the sodium-deficient diet significantly preferred this concentration of sodium chloride to water (Alberts & Gubernick, 1987).

We wanted to evaluate the salt appetites of fathers and mothers separately, and we wanted both parents to receive pup stimulation (contact) during the tests. Parents were fed the sodium-deficient diet starting on Day 3 postpartum. On the evening of Day 4 and every evening thereafter parents were deprived of water for 16 hr. Each morning following deprivation the male and female were separated from each other by placing a wire mesh divider down the length of the home cage. The male and female were given 1 or 2 of their pups at the start of the test. Four hours later the pups were exchanged between the father and mother to allow pups to nurse. Both parents received distilled water and 0.08 M NaCl for 8 hr. After each daily test, the parents were placed back on water, and the cage divider was removed to allow parents and pups to nest together as usual. The percentage preference for the saline solution was calculated for each individual by the following formula: [amount of saline consumed / (amount of saline consumed + amount of water consumed)] × 100%.

Results and Discussion

Figure 3 shows the percentage intake of the saline solution averaged over 4 days for parents and nonparental males and

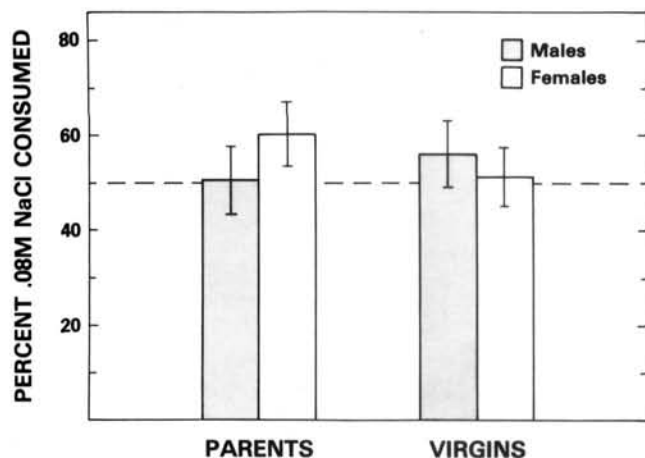


Figure 3. The preference of virgin and parental males and females for 0.08 M NaCl over water in a two-choice test. (Each bar represents the mean and SE percentage preference averaged over 4 days. The dashed horizontal line indicates the 50% chance level. Animals were maintained on a sodium-deficient diet [see text for details].)

females. There were no differences between parents and non-reproductives in their preference for sodium, $F(1, 34) = 0.6$. Males and females had similar saline preferences, $F(1, 34) = 1.3$, *ns*. Furthermore, parental males and females and virgin males and females failed to display an enhanced appetite for salt above the 50% chance level (all t s < 1.66, d fs = 8 and 9). It is unlikely that the mice were unable to detect the salt solution. Lactating rats show heightened intake of even more dilute (0.001 M) NaCl solutions (Alberts & Gubernick, 1987). Lack of a sodium preference has been reported for dogs (Fregly, 1980), cats (Kare, 1961), and numerous birds (Robinson, Kare, & Beauchamp, 1980).

The salt appetite of lactating rats regulates, in part, maternal anogenital licking of pups. The failure to find a salt appetite in California mice suggests that their parental anogenital licking is modulated differently from that of rats.

General Discussion

The results of the present series of studies indicate that water transfer from pups to parents occurs within the biparental care system of *Peromyscus californicus*. Although males of other rodent species reportedly lick their young (e.g., Elwood, 1975; Hartung & Dewsbury, 1979; McCarty & Southwick, 1977; Wilson, 1982), this is the first demonstration that fathers actually consume pup urine. Both mothers and fathers consume pup urine throughout the lactational cycle. Mothers, however, obtain more water from their young than do fathers during the first 2 weeks postpartum (Experiment 1), because mothers engage in more pup anogenital licking (Figure 2 and Gubernick & Alberts, 1987).

The bidirectional exchange of water between dam and offspring is now well established (Baverstock & Green, 1975; Friedman & Bruno, 1976; Friedman et al., 1981; Gubernick & Alberts, 1983), but it is apparently not essential to parental licking of young and consumption of urine (see also Guber-

nick & Alberts, 1985). The hormonal conditions of lactation are evidently not necessary to elicit anogenital licking of pups because fathers presumably do not show the same hormonal profile as the lactating female. The possibility that hormonal changes in the male associated with infant caregiving might mediate pup anogenital licking remains to be explored.

Urinary water is not the only stimulus that controls parental anogenital licking of pups. Fathers and mothers lick their young when food and water are freely available (Experiment 1), and anogenital licking declines (Gubernick & Alberts, 1987) prior to the decrement in water transfer to the parents (Experiment 1). The California mouse failed to exhibit a (sodium) salt appetite, which is known to modulate pup anogenital licking by rat dams (Gubernick & Alberts, 1983). Moore (1981) found that maternal anogenital licking in rats is influenced, in part, by an androgen-dependent odor cue in pup urine. The stimulus control of pup anogenital licking by *Peromyscus californicus* parents will be explored in subsequent studies.

Mammalian infants obtain water, electrolytes, and other dietary requirements from mother's milk (Jenness, 1974; Ling, Kon, & Porter, 1961), whereas mothers obtain water and electrolytes from pup urine (Friedman & Bruno, 1976). Lactation may have initially evolved as a means of providing water to the young, especially the young of terrestrial mammals (Chadwick, 1977). It is possible that consumption of offspring urine may have evolved, in part, as a means of reducing water loss associated with lactation. Recycling of water may also help reduce the costs to the mother of foraging for food and water.

The presence of the father and his licking of pups do not prevent the female from reclaiming water from her young. Given the importance of water recycling to the mother, why then would males obtain any urine? Although we do not have an answer to this question, several possibilities present themselves. The mother is probably not perfectly tuned to the time or amount of urine availability, thereby making it possible for the male to obtain some urine. The mother may also indirectly influence the male to continue caring for the young by allowing the father to consume pup urine, which implies that urine consumption may have some functional significance to the father. Perhaps males urine-mark territories more frequently as parents and reclaim lost water and electrolytes from ingestion of pup urine. Because fathers often remain with pups for substantial periods of time when the female is out of the nest (Gubernick & Alberts, 1987), urine consumption may compensate the male for reduction in foraging. The amount of urine obtained by fathers may not be costly to mothers, or the benefits to the mother may outweigh the costs. We need to further explore the costs and benefits of water recycling to understand better the nature of the biparental care system of *Peromyscus californicus*.

We have previously hypothesized that, initially, exchanges of resources help to establish and to maintain parent-infant interactions, providing a biological basis for those subsequent intimate interactions that constitute the bonds and attachments between parents and offspring (Alberts & Gubernick, 1983). The biparental care system of *Peromyscus californicus* affords an opportunity to investigate more complex family

relations that involve triadic interactions and resource transactions between fathers, mothers, and their young.

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The Publications and Communications Board of the American Psychological Association announces the appointment of Walter Kintsch, University of Colorado, as editor of *Psychological Review* for a 6-year term beginning in 1989. As of January 1, 1988, manuscripts should be directed to

Walter Kintsch
 Department of Psychology
 University of Colorado
 Campus Box 345
 Boulder, Colorado 80309

Manuscript submission patterns for *Psychological Review* make the precise date of completion of the 1988 volume uncertain. The current editor, Martin Hoffman, will receive and consider manuscripts until December 31, 1987. Should the 1988 volume be completed before that date, manuscripts will be redirected to Kintsch for consideration in the 1989 volume.
