

## The Biparental Care System of the California Mouse, *Peromyscus californicus*

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Most knowledge of parent-offspring relations in mammals is derived from studies of mother-infant interactions. Male parental care has been less well studied. We explored maternal and paternal behavior of the California mouse, *Peromyscus californicus*. Six pairs of parents and their young were videotaped continuously for 12 hours/day, on alternate days from Days 1 to 31 postpartum. Males exhibit all parental activities and to the same extent as displayed by mothers, except lactation. Male parental behavior begins on the day of birth. Mothers and fathers spend substantial and equivalent amounts of time in the nest and in physical contact with pups throughout lactation. Males devote more time than females to licking pups, although females engage in more pup anogenital licking. Mothers nurse for at least 4 weeks, and fathers and mothers both build nests and carry young. The biparental care system of *Peromyscus californicus* affords an opportunity to develop a broader, more complete view of parent-offspring relations.

Most of our knowledge of parent-young relations in mammals is based upon studies of mother-infant interactions. It is possible that emphasis on maternal-filial interactions has given us a limited view of parent-offspring relations. The allocation of parental care in mammals is not restricted to the mother (Hrdy, 1976; Spencer-Booth, 1970; Wilson, 1975). There is a new awareness of the mammalian father as an important participant and contributor to the care and development of the young (Kleiman & Malcolm, 1981; Lamb, 1981; Wuensch, 1985).

Male parental care is relatively uncommon in mammals and is found predominantly among rodents, carnivores, and primates (Elwood, 1983b; Hrdy, 1976; Kleiman, 1977; Kleiman & Malcolm, 1981; Mitchell & Brandt, 1972; for reviews of paternal care in other taxa, see Blumer, 1979; McDiarmid, 1978; Ridley, 1978). Although the evolution of paternal investment has been a lively area of debate (Dawkins & Carlisle, 1976; Grafen & Sibley, 1978; Maynard Smith, 1977; Trivers, 1972; Wittenberger, 1979), the quantity and quality of systematic empirical data pertinent to such issues often has not kept pace with theoretical developments (Brown, 1985). We know relatively little about proximate mechanisms underlying paternal behavior in any mammal (Daly & Wilson, 1978). In contrast, there is a vast amount of information about the proximate causation of maternal behavior in mammals, based primarily upon studies of rodents (Elwood, 1983a; Noirot, 1972; Rosenblatt & Siegel, 1981).

Paternal care can be observed in approximately 6% of rodent genera, but most instances are poorly documented (Dewsbury, 1985; Elwood, 1983b; Kleiman & Malcolm, 1981). Early descriptions of paternal behavior in rodents were

based on incidental laboratory observations of only one or two males (e.g., Horner, 1947; Horner & Taylor, 1969; Layne, 1959). More recent studies have provided systematic, quantitative analyses. Laboratory studies of paternal care of the young have been reported for the southern grasshopper mouse, *Onychomys torridus*, white-footed mouse, *Peromyscus leucopus* (McCarty & Southwick, 1977b); cactus mouse, *P. eremicus* (Hatton & Meyer, 1973); Mongolian gerbil, *Meriones unguiculatus* (Elwood, 1975); house mouse, *Mus musculus* (Priestnall & Young, 1978); Egyptian spiny mouse, *Acomys cahirinus* (Makin & Porter, 1984); hamster, *Mesocricetus auratus* (Marques & Valenstein, 1976); prairie vole, *Microtus ochrogaster* (Gruder-Adams & Getz, 1985; Hartung & Dewsbury, 1979; Oliveras & Novak, 1986; Thomas & Birney, 1979); and pine vole, *M. pinetorum* (Oliveras & Novak, 1986). (For reviews of paternal care in other mammals, see Kleiman, 1977; Kleiman & Malcolm, 1981; Spencer-Booth, 1970.)

Although male rodents may exhibit parental behavior similar to that of females, the mechanisms underlying paternal behavior may be different from those underlying maternal behavior. The relatively few studies on male parental behavior in rodents are largely descriptive. We need a broader data base on the proximate causation of paternal behavior that will contribute to both our basic understanding of the relations between fathers and offspring and to theories of the evolution of paternal investment and parent-offspring relations.

We have initiated a program of research on male parental behavior and its proximate causation through investigation of the biparental care system of the California mouse, *Peromyscus californicus*. Our first objective has been to gather basic normative data about their paternal and maternal behavior. We present these data here to provide a necessary foundation for future exploration of the proximate causation of paternal care.

The California mouse (see Figure 1) is a member of the family Cricetidae (genus: *Peromyscus*; subgenus: *Haplomys*) and is found predominantly in chaparral and sage scrub regions of coastal California, from San Francisco to the

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Figure 1. A male California mouse, *Peromyscus californicus*, in a typical, arched "nursing" posture huddled over his 5-day-old pup. (The dorsal surface of one pup and the hind foot of another pup can be seen under the male.)

Baja peninsula (Cranford, 1982; MacMillen, 1964; MacCabe & Blanchard, 1950; M'Closkey, 1972; Merritt, 1974; Meserve, 1974). It is the largest *Peromyscus* in the United States; adults weigh 40–70 g (data from our lab). Their natural diet consists of seeds, vegetation, invertebrates, and larvae (Merritt, 1978).

Adult *P. californicus* are fairly sedentary, with low but stable population sizes and low reproductive potential (Chandler, 1979; McCabe & Blanchard, 1950). Their activity in the field peaks within a few hours of nightfall and predawn (Marten, 1973). Life expectancy in the field is approximately 9–18 months (Chandler, 1979; McCabe & Blanchard, 1950). Breeding occurs throughout the year in both the laboratory and field (Drickamer & Vestal, 1973; McCabe & Blanchard, 1950). After a 31–32 day gestation period (Gubernick, 1987c), females give birth to 1–4 altricial young; the average litter size is 2 (Drickamer & Vestal, 1973; Rood, 1966).

Field and laboratory data are consistent with the idea that the California mouse forms pair bonds and lives in small, semipermanent family groups (Dewsbury, 1981). High recapture rates (70%) of the same male and female in the same or adjacent traps (Chandler, 1979) suggest nest site fidelity and persistent association of a male and female. This is corroborated by laboratory studies in which male–female pairs of *P. californicus* remained paired rather than exchanging mates with other pairs that were inhabiting the same enclosure (Eisenberg, 1962, 1963). Lactating females allow the male and previous young to remain in the nest with her new litter (Eisenberg, 1962). The California mouse tolerates conspecifics although adults may exhibit brief and transient bouts of aggression towards strangers (Eisenberg, 1962, 1963). Intromission latencies are long in *P. californicus* in the laboratory (Dewsbury, 1974), which is a copulatory pattern typical of species that tend to form mating pairs in their natural habitat (Dewsbury, 1981).

Thus *Peromyscus californicus* appears to be a social species, which is characterized by at least persistent, if not a monogamous, association between male and female. The limited available data indicate that male California mice would provide care for the young. Dudley (1974b) observed animals for 2 hr on Days 1, 2, 8, and 9 postpartum and reported a single

composite score for the amount of time males and females spent in the nest when the mate was present or absent. In retrieval tests, males retrieve pups, huddle over them, and reportedly groom pups (Dudley, 1974b), but no data are available on the extent of such caregiving by males.

## Method

### Subjects

Six pairs of male and female *Peromyscus californicus* and their litters served as subjects. Animals were descendants of mice originally captured in the Santa Monica mountains, northeast of Los Angeles, California. On the day of birth (Day 0), the mother, father, and litter were placed in observation cages. Each established pair had lived together continuously and had previously reared at least one successful litter. Number of pups in a litter ranged from 2 to 4. Purina Mouse Chow and water were provided ad lib, and cages were cleaned once a week. The observation room was kept at 23 °C and was maintained on a 16:08-hr light/dark cycle initiated at 0700.

### Procedure

Fathers, mothers, and their litters were kept in partitioned cages (35.8 × 20.3 × 16.5 cm) made of Plexiglas and stainless steel (see Figure 2). One end of the cage (11.4 × 20.3 × 16.5 cm) was designated as the nest area. The nest area was bounded by a metal partition 19.1 cm high, with a hole (2.54 cm diameter) at the bottom of the partition for access in and out of the nest area. By providing bedding and by placing an opaque cover on the hardware-cloth lid over this portion of the cage, parents were induced to use the nest area. The nonnesting compartment contained food, water, and a small amount of scattered bedding. Observation cages were arranged end-to-end, so that the two nest areas were juxtaposed, with pairs of parents visually isolated from each other. The parents' behavior was recorded by a time-lapse video cassette recorder (Gyr Model TLC 2001) with a 12/1 record/playback ratio. A 12.5-mm lens was used to view, simultaneously, the two nest areas. Mirrors were angled against the back wall of each cage to allow viewing when the animals' backs were turned towards the video camera. To identify the male during rapid playback, a small patch of fur was removed from the male's dorsal rump region. The parents' behavior was recorded for 12 hr/day, every other day, from Day 1 to 31 postpartum for a total of 1,152 hr. At each age, three families were videotaped during daylight hours, and the other three families were videotaped during the dark cycle under red-light (25 W) illumination.

With a 12:1 record/playback ratio, it was possible to distinguish fathers and mothers and the various behaviors listed below. The

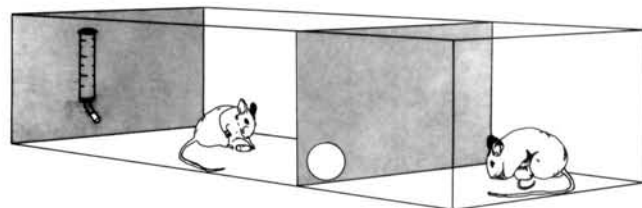


Figure 2. A sketch of the observation cage used for videotaping parental behavior of the California mouse. (The male is in the nest compartment and huddled over his young, while the female is out of the nest obtaining food. The nest compartment contained bedding; food and water were located in the nonnesting chamber.)

videotapes were scored during rapid playback (12× record speed) with the aid of a customized keyboard that interfaced directly with a LSI-11 computer. Data were entered directly onto file for later analysis. Standard videotapes were used to train observers to criterion of  $\geq .85$  interrater reliability for each recorded behavior.

### Behavior Recorded

Unless otherwise noted, each behavior was recorded separately for fathers and mothers. Behaviors which occurred at the same time were recorded simultaneously; for example, female in nest, simultaneously nursing and licking a pup and, at the same time, the male in nest and in contact with another pup. The frequency and duration of each behavior were measured.

*In nest.* An animal in the designated nest area.

*Male in sole contact with pups.* Male in physical contact with at least one pup and not in contact with the female. Physical contact involved touching with any body part except with tail and whiskers. Male contact with pups was typically characterized by males assuming a "nursing" posture (arched back while huddled over pups; see Figure 1).

*Female in nonnursing contact with pups.* Female in physical contact with at least one pup and not nursing and not in contact with the male.

*Anogenital licking of pups.* Licking the anogenital region of a pup. Parental licking of the pups' anogenital regions was distinguished from licking other body regions by the orientation of the parent's head (i.e., between the pup's hind legs) and, during rapid playback, a distinct "vibration" of the parent's head and snout. Maternal anogenital licking of pups usually occurred when the female was nursing pups. Paternal anogenital licking of pups typically occurred when only the male was in contact with pups, although such anogenital licking by the male occasionally occurred while pups were suckling.

*Nonanogenital licking of pups.* Licking any part of a pup's body except the anogenital region.

*All-in-contact.* Father, mother, and young collectively together in physical contact. This included cases in which the male was huddled with the female, or over her, and the pups were under the female and not in direct contact with the male.

*Nursing.* Female huddled over at least one pup in a nursing posture, or female lying on her side with a pup attached to her nipple.

*Carry pup.* Pup in mouth of parent and transported in or out of nest.

*Nest building.* Gathering existing bedding and making into nest or modifying nest. No additional bedding, other than that provided during cage maintenance, was available for nest building.

*Pup alone (or not in contact) in nest.* Pup in nest without its parents or with parent(s) in nest but not in physical contact.

### Statistical Analyses

Because of variability in anogenital licking, nonanogenital licking, and contact, a square root transformation was applied to these data. Data for each behavior per 12-hr observation session were averaged into 2-day blocks prior to analysis with a two-way analysis of variance (Sex of Parent  $\times$  Days) with repeated measures on one factor (days). Although parental behavior outside the nest represented a small proportion of the total time devoted to parental activities, the same behavior in and out of the nest were combined for statistical analysis. The figures presented later display the amount of time during the 12-hr observation period devoted to parental activities while parents were in the nest area.

## Results

### Behavior Recorded

*In nest.* As summarized in Figure 3, fathers and mothers spent equivalent amounts of time in the nest throughout the lactational cycle,  $F(1, 10) = 1.11, p > .10$ . Parents' time in nest decreased significantly,  $F(7, 70) = 10.42, p < .01$ . On Days 1/3, fathers were in the nest area on average of 10 hr 35 min. Nest attendance declined to 6 hr 51 min by Days 29/31. On Days 1/3, mothers averaged 10 hr 29 min in nest, and by Days 29/31 they spent an average of 6 hr 5 min in the nest area. Males and females were simultaneously in the nest for large proportions of their nest time (67%–96%) throughout lactation. Mothers and fathers spent similar amounts of time in the nest when their partner was out of the nest (range, 28–120 min),  $F(1, 10) = 1.58$ .

*In contact with pups.* Figure 4 presents the total amount of time parents were in physical contact with a pup while in the nest. Contact for mothers included time spent in nursing, nonnursing contact, and all-in-contact (but not nursing). Contact for fathers included all-in-contact time and male in sole contact with a pup. Mothers and fathers spent equivalent amounts of time in contact with pups while in the nest,  $F(1, 10) = 1.05$ . The amount of time in contact decreased significantly over the course of lactation,  $F(7, 70) = 9.53, p < .01$ . Contact time out of the nest was negligible.

On Days 1/3, mothers spent an average of 10 hr 12 min in contact with pups. Pup contact decreased to 4 hr 5 min by Days 29/31. During the first 2 weeks postpartum, 99% of the mothers' contact time in the nest was devoted to nursing. By Days 29/31 mothers were still spending 90% of their pup contact time nursing their young. Mothers spent relatively little time in nonnursing contact (2–17 min) throughout the

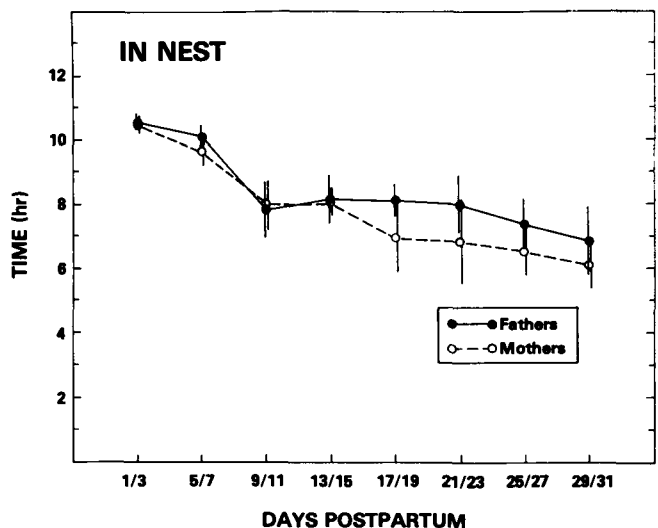


Figure 3. The amount of time during a 12-hr observation period mothers and fathers spent in the nest throughout lactation. (Each data point represents the mean ( $\pm$ SE) for 6 fathers and 6 mothers averaged over 2 days. Parents were videotaped continuously for 12 hr/day, on alternate days from Days 1 to 31 postpartum.)

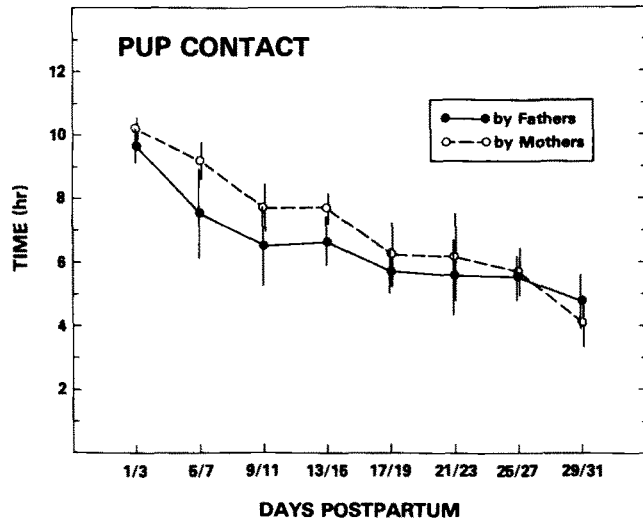


Figure 4. The amount of time in the nest mothers and fathers were in physical contact with a pup. (Pup contact for mothers included nursing and nonnursing contact. See Figure 3 for other details.)

lactational cycle. Fathers were in contact with pups an average of 9 hr 40 min on Days 1/3. Pup contact declined to 4 hr 47 min per observation period by the end of the study. Approximately 50% to 80% of fathers' pup contact over the course of the lactational cycle consisted of the male in contact with the female and pups collectively (all-in-contact). During simultaneous nest attendance (67% to 96% of the male's nest time), fathers were in sole contact with pups for 16–22 min. When fathers were the only parent in the nest (4% to 33% of the male's nest time), males were in sole contact with their young for 29–79 min.

**Licking pups.** Figure 5 summarizes the total time spent licking pups. Fathers devoted significantly more time than mothers to licking their young,  $F(1, 10) = 6.22, p < .05$ . On Days 1/3, fathers spent an average of 10 min 44 s licking pups. Paternal licking of young increased to 20 min 21 s by Days 17/19, then decreased to 8 min 7 s by Days 29/31. Mothers engaged in pup licking an average of 6 min 51 s on Days 1/3. Maternal pup licking increased to 12 min 30 s by Days 17/19, then decreased to 3 min 52 s by the end of the study. Both parents spent more time in nonanogenital licking of pups than in anogenital licking. Total licking consisted predominantly of nonanogenital licking and exhibited a similar time-course pattern as can be seen by comparison of Figures 5 and 6.

**Nonanogenital licking of pups.** The difference between fathers and mothers in total time spent licking their young was owing to fathers devoting significantly more time than mothers to licking other body regions of pups,  $F(1, 10) = 14.71, p < .01$ . Figure 6 presents the time parents devoted to nonanogenital licking. Nonanogenital licking increased significantly over the lactational cycle,  $F(7, 70) = 7.27, p < .01$ . On Days 1/3 fathers spent an average of 7 min 39 s licking other body regions of pups. Nonanogenital licking increased to 19 min 8 s by Days 17/19, then decreased to 7 min 48 s by Days 29/31. Mothers engaged in nonanogenital licking of pups an

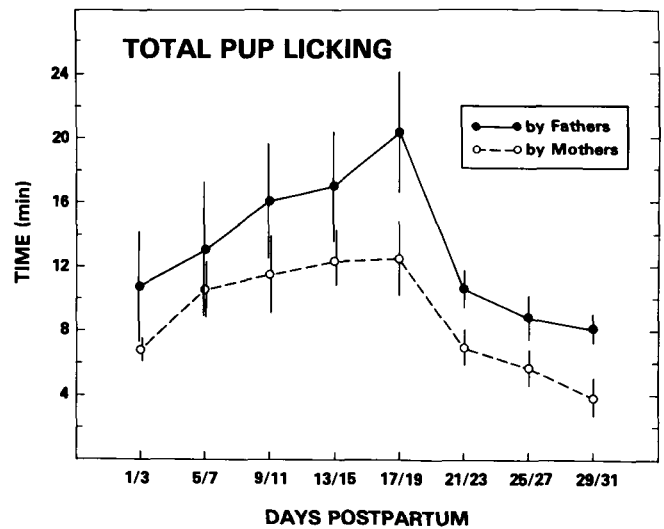


Figure 5. The amount of time in the nest mothers and fathers spent licking a pup. (Pup licking included anogenital and nonanogenital licking. See Figure 3 for other details.)

average of 3 min 27 s on Days 1/3. Maternal nonanogenital licking increased to 10 min on Days 17/19, then declined to 3 min 25 s by Days 29/31.

**Anogenital licking of pups.** Figure 7 shows the total time parents spent in anogenital licking of pups. In contrast to nonanogenital licking, mothers devoted significantly more time than fathers to licking the anogenital areas of pups,  $F(1, 10) = 6.40, p < .05$ . Both parents displayed a significant decrement in pup anogenital licking,  $F(7, 70) = 14.41, p < .01$ . On Days 1/3, mothers spent an average of 3 min 24 s licking pup anogenital areas. Anogenital licking increased to 4 min 26 s by Days 5/7, then decreased after Days 13/15, reaching a low of 27 s by Days 29/31. Fathers engaged in pup

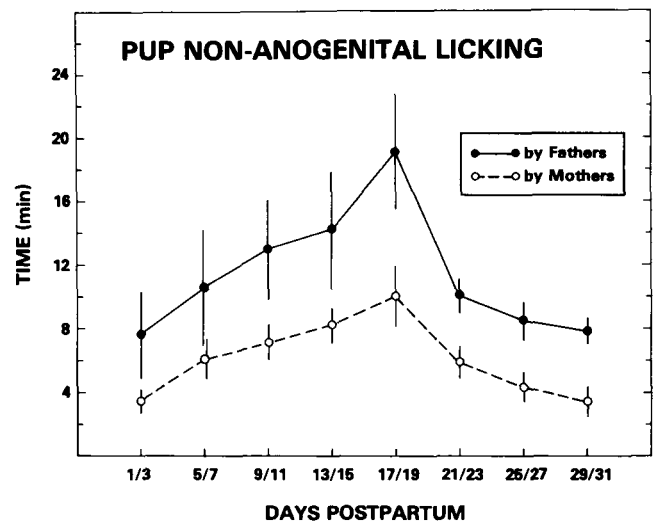


Figure 6. The amount of time in the nest mothers and fathers spent licking nonanogenital body regions of a pup. (See Figure 3 for other details.)

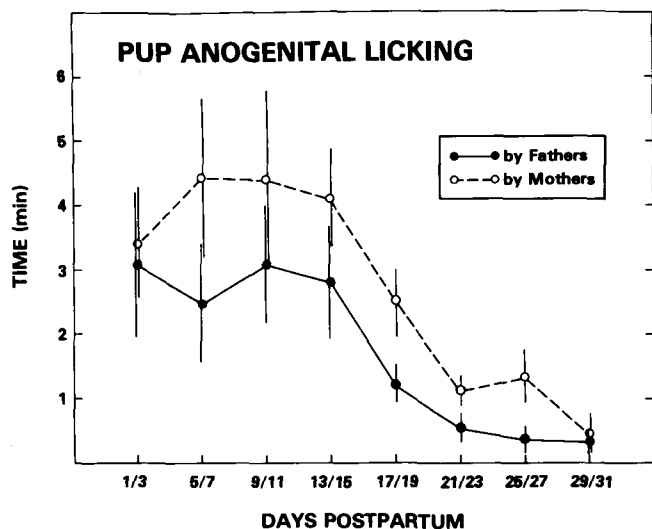


Figure 7. The amount of time in the nest mothers and fathers spent licking the anogenital area of a pup. (See Figure 3 for other details.)

anogenital licking an average of 3 min 5 s on Days 1/3. Paternal anogenital licking of young also declined after Days 13/15 to a low of 19 s by Days 29/31. The diminution in pup anogenital licking after the second week postpartum is likely related to increased spontaneous urination by pups (Gubernick, 1987a).

**Nursing.** The amount of time mothers spent nursing in the nest is summarized in Figure 8. On Days 1/3, nursing averaged 10 hr 6 min. Nursing steadily declined to 3 hr 48 min by Days 29/31.

**Pup alone or no contact in nest.** The amount of time a pup was alone or not in contact with a parent while in the nest gradually increased over the lactational period (see Figure 9). On Days 1/3, pups were without parental contact an average of 12 min 16 s. Noncontact time increased to 80 min 41 s by Days 17/19, decreased, and then increased again to 79 min 40 s by Days 29/31. Pups were without contact with parents for longer periods of time when only one parent was in the nest than when both parents were in the nest area.

**Carry pups and nest build.** In five out of six pairs, both parents built nests. Nest construction was observed occasionally throughout the 31-day period and during that time occurred on average of only 4.6 days by fathers and 4.6 days by mothers. Only 3 out of 6 males and 4 out of 6 females were noted to carry pups. Pup retrieval and nest construction were relatively infrequent events and not suitable for analysis.

## Discussion

The present results document the extensive biparental care of the young exhibited by *Peromyscus californicus*. Mother and father are intimately involved and actively participate in rearing their offspring. Fathers exhibit all parental activities displayed by mothers, except nursing.

In contrast to several other rodent species [e.g., *P. leucopus* and *Onychomys torridus* (McCarty & Southwick, 1977b);

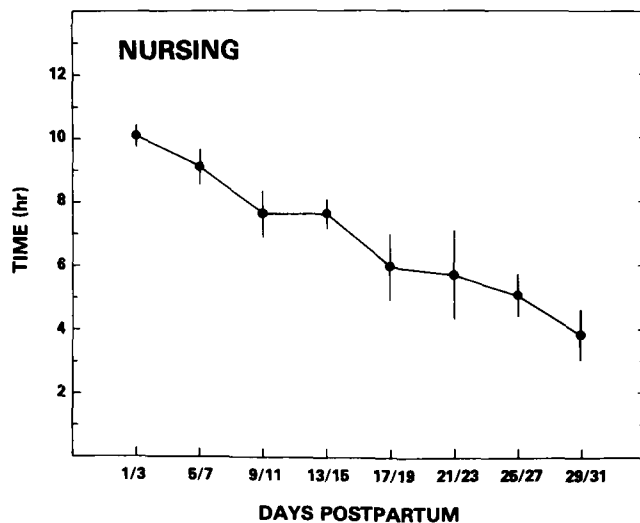


Figure 8. The amount of time in the nest mothers spent nursing their young. (See Figure 3 for other details.)

*Meriones unguiculatus* (Elwood, 1975)], the California mouse father is rarely excluded from the nest by the female. We have consistently observed that new fathers sniff and lick a pup at the moment of birth or immediately thereafter. Fathers often retrieve a newborn pup, lick, and huddle over it, while the mother gives birth to another young. After parturition is completed, the father, mother, and their young collectively remain together in physical contact in the nest.

Nest attendance by the parents and contact with pups remained substantial throughout the 31 days postpartum. Mothers and fathers were equivalent in the extent of nest occupancy. Dudley (1974b) also found nest occupancy to be

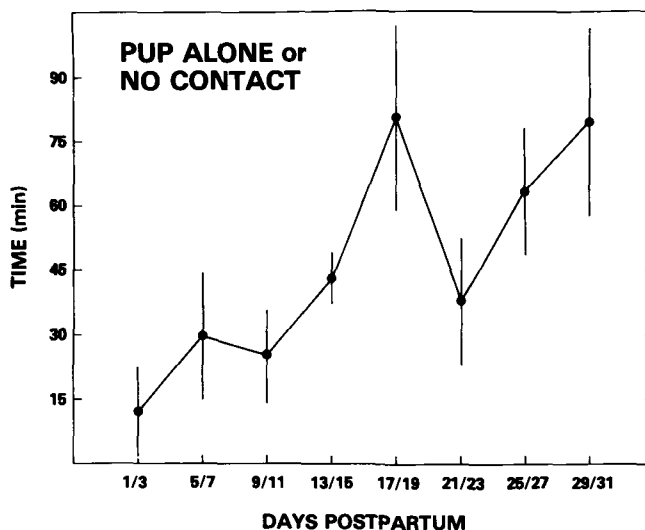


Figure 9. The amount of time a pup was in the nest without its parents or with a parent in the nest but not in physical contact. (Each data point represents the mean ( $\pm$ SE) for six litters averaged over 2 days. See Figure 3 for other details.)

the same in parental California mice during a 1-hr period. In the laboratory, the southern grasshopper mouse, *Onychomys torridus*, displays a similar pattern of nest attendance, except for the first few days postpartum when the father is excluded from the nest by the female (McCarty & Southwick, 1977b). In other species, fathers may spend either more time than mothers in the nest [laboratory *Mus musculus* (Priestnall & Young, 1978); *Meriones unguiculatus* (Elwood, 1975)] or less time than mothers [*P. leucopus* (McCarty & Southwick, 1977b); *Microtus pinetorum* and *M. ochrogaster* (McGuire & Novak, 1984; Oliveras & Novak, 1986; but see Hartung & Dewsbury, 1979)].

As a result of the high rates of nest occupancy, *P. californicus* pups were rarely left unattended, particularly during the first week postpartum (Figures 3 and 9). Fathers spent as much time in physical contact with pups in the nest as did mothers (Figure 4). In several rodent species, mothers engage in more pup contact than did fathers (McCarty & Southwick, 1977b; McGuire & Novak, 1984; Oliveras & Novak, 1986; Porter, Cavallaro, & Moore, 1980; Wilson, 1982); and in gerbils, mothers and fathers are equivalent in pup contact time (Elwood, 1975). *Peromyscus californicus* family members were together collectively in physical contact throughout the 31-day observation period. On Days 1/3 all-in-contact time averaged 8 hr 50 min and declined to 3 hr 45 min by Days 29/31. The substantial amount of contact time between parents and young reflects the cohesiveness within family units of California mice. It is possible that the male's nest occupancy and contact with pups reflected, in part, the male's attempt to remain close to his mate in addition to providing offspring care.

The extent of time a pup was in the nest and not in contact with either parent increased over days (Figure 9). During the first 2 weeks postpartum, parents were responsible for initiating and maintaining contact with pups in the nest. As pups advanced in age, they actively participated in making contact with parents and in remaining away from parents while in the nest. Pups were observed to first leave the nest area at 16 days of age (range, 13–19 days), usually when both parents were out of the nest.

Nest attendance and pup contact by the parents probably has substantial thermoregulatory effects because individual California mice pups are ectothermic prior to Day 15 postpartum (Gubernick, 1987b). Thus more of the pup's energy could be allocated to growth and development rather than to maintenance of body temperature. The presence of a father reportedly increases pup growth and survivorship in *P. californicus*, presumably through the thermal energy fathers provide pups via huddling (Dudley, 1974a). Physical contact may also affect parent–infant bonding and subsequent social interactions. We are currently examining effects of the father on pup growth and development.

Licking of young is a nearly ubiquitous feature of maternal behavior in mammals. At birth, parental licking of young removes fetal membranes, dries the newborn, and stimulates peripheral blood circulation in the offspring (Ewer, 1968). Licking activates infants and stimulates their suckling behavior (Alexander & Williams, 1964; Rheingold, 1963).

Parental California mice avidly lick their offspring. Fathers engage in more pup licking than do mothers (Figure 5). In most other rodent species in which male parental care has been quantified, mothers spend more time than fathers grooming pups (Elwood, 1975; Hartung & Dewsbury, 1979; McCarty & Southwick, 1977b; McGuire & Novak, 1984; Oliveras & Novak, 1986), except in the case of degus, *Octodon degus*, in which fathers lick their semiprecocial young more than do mothers (Wilson, 1982).

*Peromyscus californicus* parents distribute differentially their licking of pups' body regions. Parents spend more time licking nonanogenital areas than anogenital regions of pups. Furthermore, fathers devote more time than mothers to licking nonanogenital regions. In contrast, mothers spend more time than fathers in pup anogenital licking (Figure 7). Anogenital licking of young stimulates reflexive urination (Ewer, 1968) and facilitates urine production in infant rats (Capek & Jelinek, 1956). Maternal anogenital licking of young is accompanied by maternal ingestion of the infant's excreta, which serves the function of cleaning the young's body surface and nest and reducing conspicuousness to predators (Lent, 1974). Anogenital licking of young affects development of male sexual behavior in rats (Moore, 1984).

Maternal anogenital licking of young also has important consequences for the mother. Mothers provide pups with water, electrolytes, and other dietary requirements in the form of milk (Jenness, 1974). By licking pups' anogenital areas, the rat dam stimulates pup urination and it then consumes physiologically significant quantities of pup urine (Friedman & Bruno, 1976; Friedman, Bruno, & Alberts, 1981). This recycling of water and electrolytes between the rat dam and its young occurs throughout lactation (Gubernick & Alberts, 1983) and contributes significantly to the mother's total body water balance (Friedman et al., 1981).

Water recycling also occurs between *P. californicus* mothers and their young throughout lactation (Gubernick & Alberts, in press). Although fathers do not provide pups with milk, fathers do obtain measurable quantities of pup urine via pup anogenital licking (Gubernick & Alberts, in press). Mothers, however, recover more pup urine than do fathers, which probably reduces water loss associated with lactation and reduces costs to mothers of foraging for food and water.

Mothers continue to nurse during the first 31 days postpartum. Nursing declined steadily with advancing age of pups (Figure 8). Nursing was the predominant mode of contact with pups. By Days 29/31, mothers were still spending 90% of their contact time nursing their young. Mother's milk is the sole source of food and water for pups for the first 2 weeks postpartum. Weanling California mice begin to eat solid food about Day 20. Visual inspection of stomach contents of 30-day-old weanlings used in another study (Gubernick & Alberts, in press) revealed no traces of milk, which suggests that suckling by older pups in the present study may serve functions other than obtaining nutrients (see also Kleiman, 1972; Porter et al., 1980).

Although not shown in the figures, there was diurnal and nocturnal variation in some parental behavior patterns. *Peromyscus californicus* are most active in their natural habitat

shortly after nightfall and before dawn (Marten, 1973). A similar pattern of activity was apparent in our laboratory and was reflected in several behaviors. Nest attendance occurred predominantly during daylight hours and, as a consequence, nursing and all-in-contact occurred more frequently and pups were left alone for shorter periods than at night. During the night, fathers often remained with the pups while the mother was out of the nest and fathers engaged in more pup licking than during the day. In contrast, there were no day/night differences in maternal licking of pups.

The occurrence of male parental care under laboratory conditions may be induced by confinement to small cages (Dewsbury, 1985; Hartung & Dewsbury, 1979; Oliveras & Novak, 1986). To investigate the possibility that a heterosexual pair of *Peromyscus californicus* would be less tolerant of each other and that a male would fail to exhibit parental care in a larger, less restrictive living space, we housed a father, mother, and their 1-day-old young in a cage (152 × 31 × 31 cm) that was partitioned into four compartments (two 51 × 31 × 31 cm, and two 25 × 31 × 31 cm) suitable for viewing. A bolt hole in each partition allowed access to each compartment. On Day 5 postpartum, the pair and their litter were videotaped continuously for 12 hr, and their parental behavior was scored as described earlier. We replicated this procedure 4 times ( $n = 4$  pairs of parents and their young). Pertinent data on paternal and maternal behavior shown in the large cage is presented in Table 1. Corresponding parental behavior displayed in the smaller cage used in the present study is included in Table 1 for comparison. On Day 5 postpartum, fathers in less confined space exhibited a significant diminution only in time in nest. All of the other parental behaviors exhibited in large and small cages were equivalent, supporting the conclusion that the extent of paternal (and maternal) care described earlier was not because of limited space.

Our results reveal that infant *Peromyscus californicus* receive extensive tactile and olfactory stimulation, important influences in ontogeny of rodents (Russell, 1971; Vandenberg, 1967). Behavioral and sexual development of young rodents is also affected by father's presence. Fathers affect

development of locomotor activity (Csermely, 1980; Elwood & Broom, 1978), open-field activity (McCarty & Southwick, 1977a; Mugford & Nowell, 1972), aggression (McCarty & Southwick, 1977a; Mugford & Nowell, 1972; Smith & Simmel, 1977; Wuensch & Cooper, 1981; see Gerling & Yahr, 1979; Priestnall & Young, 1978, for exceptions), mating preferences (Mugford & Nowell, 1972), and reproductive inhibition (Haigh, 1983; Skryja, 1978). The extent of the father's affect on infant sexual maturation in *P. californicus* is currently under investigation.

Paternal California mice appear to invest extensively in the care of their young. The evolution of paternal investment is often associated with monogamy (Kleiman, 1977; Kleiman & Malcolm, 1981; Wittenberger & Tilson, 1980), production of altricial offspring (Zeloff & Boyce, 1980), low reproductive potential and occupying a stable habitat (Eisenberg, 1966; Kleiman, 1977), certainty of paternity (Alexander, 1974; Dawkins & Carlisle, 1976; Maynard Smith, 1978; Trivers, 1972; but see Werren, Gross, & Shine, 1980), and monopolization of resources and mates (Barash, 1975, 1976; Emlen & Oring, 1977; Orians, 1969). Our observations of extensive paternal behavior in *Peromyscus californicus* are consistent with the limited information available on this species in its natural habitat. More field research on the mating system, social structure, and parental behavior of *Peromyscus californicus* is needed to further address questions of the evolution of paternal care. The biparental care system of *Peromyscus californicus* affords an opportunity to test and to integrate questions of ultimate and proximate causation into a broader, more complete view of parent-offspring relations.

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Table 1

*Amount of Paternal and Maternal Behavior (in hr:min:s) Displayed in Different Sized Cages on Day 5 Postpartum*

	Small cage <sup>a</sup>		Large cage <sup>b</sup>	
	Fathers	Mothers	Fathers	Mothers
In nest	9:33:17 <sup>c</sup>	8:37:26	5:24:20 <sup>c</sup>	7:44:15
Pup contact	7:36:56	7:47:47	5:08:28	7:22:00
Anogenital licking	3:29	4:17	5:08	6:21
Nonanogenital licking	15:59	6:26	24:24	10:23
Nursing	—	7:42:37	—	7:21:23
Pup alone (or no contact)	59:34		1:20:35	

<sup>a</sup> Cage used in present study to obtain normative data, dimensions of 35.8 × 20.3 × 16.5 cm.

<sup>b</sup> Dimensions: 152 × 31 × 31 cm

<sup>c</sup> Significantly different from each other,  $U = 1$ ,  $p < .02$ , two-tailed.

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