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Effects of the Presence of the Father on Pup Development in California Mice (*Peromyscus californicus*)

ABSTRACT: *Pup development and behavior in California mice were studied in litters housed with single mothers, or with fathers and mothers living together. Behavior of pups was recorded during a 15-min session every 2 days from 10 to 30 days of age. Physical contact, locomotion, grooming, and physical development indicators were recorded. It was found that the physical contact between siblings was greater and there was a tendency to have more contact between pup and either parent in the group in which the father was present. Finally, it was noted that the presence of the father did not affect either the first appearance of pup behavior during development or physical growth. In conclusion, the results indicate that the presence of the father had a greater influence on social contact between the different members of the litter than on pup behavioral development and physical growth.*
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Keywords: *parental behavior; pup development; rodent; California mouse*

There are some rodent species in which the father participates in the care of pups. The ultimate explanation for the evolution of paternal care is related to offspring survival. Studies with hamsters and mice have demonstrated that fathers have an influence on offspring survival. In the Djungarian hamster (*Phodopus campbelli*) 95% of pups were successfully raised to weaning at 21°C, when mother and father were present (Wynne-Edwards & Lisk, 1989). However, survival fell to 47% in the male-absent group. Furthermore, when the ambient temperature was 4°C and the father was absent, only 32% of pups survived to weaning. Paternal investment significantly increased pup survival in albino mice (*Mus musculus*) in both a cold environment (Barnett & Dickson, 1985) and when parents were required to run in a wheel to get food (Wright & Brown, 2000). In California mice (*Peromyscus californicus*), the presence of the father enhanced pup survival in cold temperatures and when parents had to forage for food (Gubernick, Wright, & Brown, 1993). In another experiment with California mice, females without a mate present that were required to forage for food by running in a wheel were able to raise litters of two but not four pups (Cantoni & Brown, 1997). When the mate was present, pups in litters of four pups also survived. Furthermore, mated pairs had four times as many pups survive over a 74-day period than single female mothers.

Another study, in which Djungarian hamsters were used as subjects, also provides evidence that the presence of the mate is essential for survival of the pups, even under the ideal climatic and nutritional conditions of the laboratory. Males and females had greater success in rearing pups than solitary females. Pairs reared 95% of pups and 100% of litters to weaning, while females alone reared only 47% of pups and 77% of the litters (Wynne-Edwards, 1987).

The advantage of the presence of the father for the pup can be related to his feeding them, defending them from predators or other infanticidal conspecifics, and keeping them warm (Wuensch, 1985). In California mice, when

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the mother was removed for 12 hr/day, from the first to the 18th postpartum day, but the father remained with the offspring, the pups had higher body temperatures than pups from an absent father group (Dudley, 1974a). In Mongolian gerbils (*Meriones unguiculatus*) it was found that pups reared with the mother and father together spent more time in the nest and in physical contact with adults than pups whose fathers were removed on the day of parturition (Elwood & Broom, 1978). In Djungarian hamsters, the presence of either the father or an aunt reduced the proportion of time that pups were left alone by about 50% (Wynne-Edwards, 1995).

It appears that the presence of the extra adult is important for temperature regulation to both mothers and pups. During lactation, the body temperature of paired females is lower than that of solitary females (Walton & Wynne-Edwards, 1998). Therefore, the alleviation of maternal hyperthermia, in paired females, improves the body contact between mother-offspring and reduces the demand for water to maintain thermoregulation (Wynne-Edwards, 1998). Thus, paired females should raise pups to weaning even with reduced water availability.

On the other hand, it remains to be determined exactly what is the influence of the father on behavioral and physical development and on social interactions in pups. When the father was present, Mongolian gerbils opened their eyes earlier and they were behaviorally more advanced (Elwood & Broom, 1978), California mice were heavier (Dudley, 1974a), and prairie voles (*Microtus ochrogaster*) began to ingest solid food and leave the nest earlier (Wang & Novak, 1992) than those reared by the mother alone. Nevertheless, several studies found no evidence that the father has an influence on the offspring. The presence of the male had no influence on pup weight in Djungarian hamsters (Wynne-Edwards, 1987), in California mice (Gubernick et al., 1993), and in Mongolian gerbils (Elwood & Broom, 1978).

We investigated whether the father has any influence on pup growth and behavior (individual and social) in California mice housed with an adequate food supply and at a warm temperature in the laboratory. One question that remains open in relation to the California mouse concerns the pup body mass because there are contradictory data in the literature. Dudley (1974a) noted that pups reared with their father gained significantly more weight in comparison to pups reared by the mother alone. On the other hand, Gubernick et al. (1993) found that pups raised without the father tended to be heavier than those pups raised by the mother and father together. The difference between groups approached significance ($p < .06$).

Another question in this experiment was whether California mouse pups have their behavioral development advanced and whether the physical contact with adults is greater as a function of the presence of the father, as was reported in Mongolian gerbils (Elwood & Broom, 1978). Furthermore, the impact of the father on the interactions between pups or between pups and parents in California mice also was investigated because there are few data on this subject.

SUBJECTS AND METHODS

Subjects

Eighteen mothers, nine fathers, and 36 pups of California mice (*P. californicus*) served as subjects (N = 63 mice). The adult animals were experienced parents. All the animals used in this research were originally captured in the Santa Monica mountains, northeast of Los Angeles, California, and were provided by Dr. D. J. Gubernick (University of Wisconsin, Madison, Wisconsin). Initially, male–female pairs were housed in Plexiglas cages (length 45 cm, width 22 cm, height 15 cm) containing a standardized amount (100 g) of wood shavings for bedding. Food (Laboratory Rodent Chow number 5001, Ralston-Purina) and water were available ad libitum. The colony room was kept at $21 \pm 2^{\circ}$C and on a 16:8 hr light:dark cycle, with the light phase starting at 11:00 h. The cages were cleaned once each week. Animals used in this experiment were cared for in accordance with principles and guidelines of the Canadian Council on Animal Care through a protocol approved by the Dalhousie University Animal Care Committee.

Procedure

Two groups were formed with multiparous adult mice ($n = 9$ for each group). In Group 1 mother, father and pups stayed together throughout the experiment. In Group 2, males were removed 3–4 days after the birth of the pups. The males were not removed earlier to avoid stressing the female at the beginning of the lactation period and to ensure that females became pregnant during the postpartum estrus. All litters used in the experiments were of the same size (two pups). When the litter had only one pup, it was not used. However, when the litter had more than two pups, the extra pups were removed 3–4 days after birth and cross-fostered with another litter. California mouse parents accept alien pups (Gubernick & Alberts, 1989).

Behavioral measurement began when pups reached 10 days of age (day of birth = Day 1). On Day 9, one pup was individually marked on the rear legs with a green non-toxic pen. This pup was designated FOCAL-PUP (FP). This animal was used for observations on development and growth. The record of behavior was made every 2 days from 10 to 30 days of pup age in a 15-min session during the light phase (between 15:00 and 19:00 h) The period from 10 to 30 days was chosen based on results obtained from pilot studies, which indicated that until 9–10 days of age, pups remained under their parents almost all the time. Furthermore, the first coordinated movements began only between days 12 and 16 (personal observation). During each observation session, the home cages were moved to a room near the colony room. A computerized event recorder program was used to calculate either the frequency or duration of each behavior.

Measures

Physical Contact. Involved mutual touching of any part of the partner's body (except tail and whiskers). This behavior was divided into three sub-categories: (1) physical contact between the FP, the sibling, and either parent; (2) physical contact between the FP and any parent only; and (3) physical contact between the FP and the sibling. The time that the FP spent in each kind of physical contact was recorded.

Locomotion Activity. This behavior was divided into two sub-categories: (1) walking or running, which included any spontaneous movement leading to a change in body location on the floor; and (2) rearing, which was positioned with the forepaws either against the wall or in the air, while the rear paws were on the floor. The frequency in each subcategory was recorded.

Self-Grooming. The animal, with rapid movements of the forepaws, stroked at its face and/or, with forepaws and mouth, licked any part of its own body. The duration of this behavior was recorded.

Social Grooming. This behavior occurs when an animal with its mouth licks any part of the body of a partner. The time spent by either parent grooming the FP was recorded.

Body Weight. The mass, in grams, of the FP was recorded every 5 days, from 10 to 30 days of age. The animal was placed on a Dial-O-Gram balance and its weight was measured.

Eye Opening. The day (age) at which the complete separation of the upper and lower eyelids of both eyes occurred for the first time was noted. Eye opening was assessed every day from 10 days of age until the age at which it first occurred.

Statistical Analysis

The data were analyzed using the ANOVA for repeated measures since the data were collected on various days.

RESULTS

Physical Contact and Social Grooming

There was a tendency in time spent by the FP in simultaneous contact with either parent and the sibling to be greater in the group in which the father was present [$F(1, 16) = 4.26$, $p < .06$] [Fig. 1]. From 10 to 20 days of age, the FP from the single mother group spent approximately 82% of total time in physical contact, while this time for animals from the mother and father group was about 91%. There was a tendency to the FP from this last group in spending greater time in physical contact [$F(1, 16) = 3.51$; $p < .08$]. In relation to the other period (from 22 to 30 days), the total time in physical contact decreased abruptly in both groups. When the father was present, approximately 26% of total time of the experimental session was spent in physical contact. In the other group, the percentage was around 41%. There was no significant difference between the groups in relation to these last values [$F(1, 16) = 2.56$; $p > .05$].

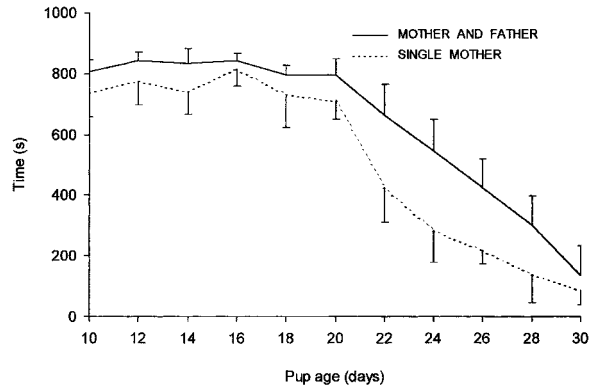

FIGURE 1 Mean time (*SEM*) spent by Focal-pup (FP) in physical contact with other pup and adult(s) together.

However, there was a significant difference between the groups when the time spent in contact between the FP and the sibling was analyzed [$F(1, 16) = 7.92$, $p < .05$] [Fig. 2]. When the father was absent, the FP spent significantly more time in physical contact with other pups than the FP of the other group. As can be seen in Figure 2, at 22 days of age, the FP of the single mother group showed a peak of physical contact with other pups, which was not noted in the other group.

On the other hand, there was no significant difference when physical contact between the FP and either parent was compared between groups [$F(1, 16) = .39$, $p > .05$] [Fig. 3]. In relation to analysis over time, a difference was noted, although this was not significant. The FP spent more time in physical contact with either parent during the second period of the experiment (from 22 to 30 days of age). The FP from the single mother group spent approximately 10% of the time in contact with any parent in that period, while this time was 16% in the other group. In the

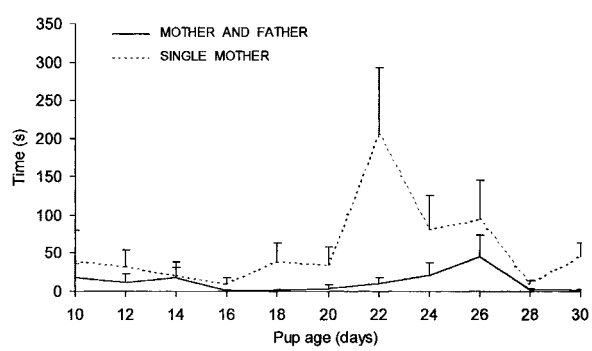

FIGURE 2 Mean time (*SEM*) spent by FP in physical contact with other pup only ($p < .05$).

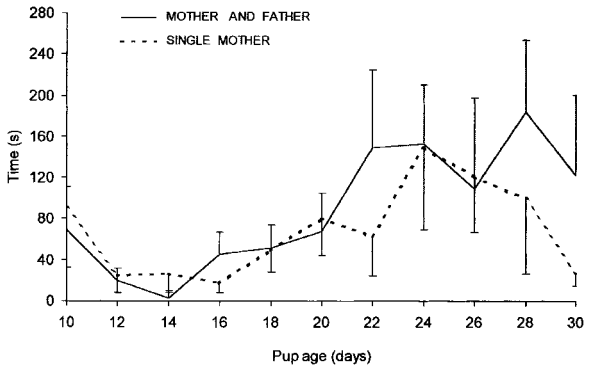

FIGURE 3 Mean time (*SEM*) spent by FP in physical contact with adult(s) only.

first period (from 10 to 20 days) the FP from both groups spent approximately 5% of the time engaged in that social activity. Likewise, the presence of the father did not affect the length of time that the FP was groomed by either parent [$F(1, 16) = .02$, $p > .05$] (Fig. 4).

Spontaneous movements and physical development of the pups. There was no significant difference between the groups in relation to FP spontaneous movements, which included (1) walking [$F(1, 16) = .47$, $p > .05$], (2) rearing [$F(1, 16) = .20$, $p > .05$], and (3) self-grooming [$F(1, 16) = 2.46$, $p > .05$].

Furthermore, it was noted that the presence of the father did not affect the first appearance of pup behavior during development (Table 1). However, as can be noted from the table, the FP in the single mother group began to show the first walking, rearing, and self-grooming behavior earlier than the FP from the other group, although the differences were not significant.

In relation to physical development, there was also no significant difference between groups in the body weight, when the comparison was made either by combining all days [$F(1, 16) = .50$, $p > .05$] or considering each day (10, 15, 20, 25, and 30) in separate analyses. The day at which FP opened its eyes also was not affected by the presence of the father (Table 1).

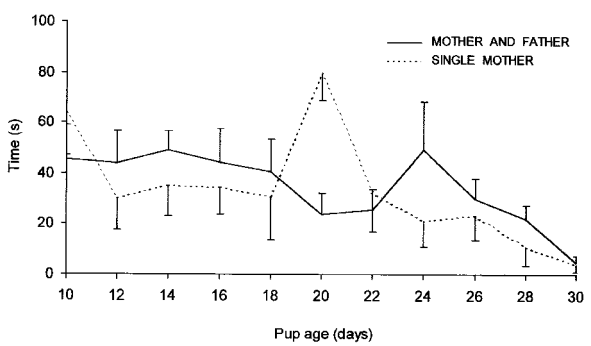

FIGURE 4 Mean time (*SEM*) spent by adult(s) grooming the FP.

Table 1. Mean Age, in Days, (±*SEM*) at Which Focal-Pup Showed Indicators Related to Behavioral and Physical Development for the First Time

	Group		
Measures	Mother and Father	Single Mother	*t* test
Walking	22 ± 1.83	18 ± 1.67	$t(16) = 1.62$*
Rearing	22.75 ± 1.16	20.9 ± 1.16	$t(15) = .90$*
Self-grooming	25 ± 1.20	21.22 ± 1.6	$t(14) = .24$*
Eye opening	$15 \pm .44$	$15.44 \pm .24$	$t(16) = .88$*

*$p > .05$.

DISCUSSION

Our results indicate that the presence of the father under adequate climatic conditions and with food freely available had a greater influence on physical contact between the FP and other members of the litter than on both behavioral and physical development in California mouse pups. Data from a previous study that used the same species as subject also indicated that the father is not a variable that affects development (Gubernick et al., 1993). In Djungarian hamsters (Wynne-Edwards, 1987), Mongolian gerbils (Elwood & Broom, 1978), and albino mice (Wright & Brown, 2000), it was observed that the weight gain by pups also was not influenced by the presence of the father. Only one study noted weight gain to be greater in the group in which the father was present (Dudley, 1974a). Nevertheless, in this study the presence of the father had an impact only until 21 days of age, after which the effect disappeared. In our experiment, no temporary or long term effect on body weight as a function of the presence of the father was identified.

One of the causes of these differences may be found in the experimental conditions to which animals were exposed. In one of the groups from Dudley's study, mothers were removed every day (from birth to 18 days pup age) for 12 hr. This situation is very traumatic to pups. The normal weight of a California mouse at 18 days, when pups from Dudley's study were weaned, was around 14 g. Dudley had pups 50% lighter at 18 days. Furthermore, several pups died in the group in which fathers were absent. In this way, the fathers' presence was important for weight gain and survival. In the study carried out by Gubernick et al. (1993), there was no difference in the weight of the pups that survived in groups, with or without the father present, at a cold temperature, and in which parents needed to forage for food. Although in both experiments animals were exposed to adverse conditions, it appears that in Dudley's study, the mother's removal was more critical

for pup weight gain than in Gubernick's study, in which the father was removed.

On the other hand, although the impact of the father's presence is greater in adverse situations, it has been demonstrated that offspring development was affected, even in favorable conditions. In prairie voles (Wang & Novak, 1992) and in Mongolian gerbils (Elwood & Broom, 1978), pups reared in the presence of the father developed more rapidly in comparison with those reared by the mother alone. The results of the present study are in conflict with these data because the presence of the father did not affect the first appearance of pup behavior, eye opening, and body weight.

In a general way, the paternal care can be important to offspring inasmuch as the father defends pups from predation or other infanticide, contributes to obtaining food, huddles and retrieves pup (Wuensch, 1985). However, the paternal presence may in fact be critical to offspring because it could be related to pup thermoregulation. Dudley (1974a) suggested that the contribution of the father to pup survival is due to the fathers' keeping them warm. The probability of pups remaining alone is smaller when they are reared by both parents (Dudley, 1974b; Elwood & Broom, 1978; Wynne-Edwards, 1995). Recent data confirm this hypothesis on pup thermoregulation and paternal behavior. Siberian hamster (*P. sungorus*) pups grow significantly faster than Djungarian hamster pups during the lactation phase, in which pups are entirely dependent on their mothers to get food and keep themselves warm (Wynne-Edwards & Lisk, 1989). In the Siberian hamster, the faster growth rate is not dependent on the father because it occurs even when mothers rear pups alone. In fact, it was confirmed that the incidence of acute maternal heating, when pups were 12 days old, was higher in the Siberian hamster than in the Djungarian hamster (Newkirk, Cheung, Scribner, & Wynne-Edwards, 1998). On the other hand, in this study, it has been found that at cool ambient temperature the biparental care improved early growth.

Although the father had no significant influence on pup development, in the present study there were changes in the social contact among members of the litter. Pups and any parent spent more time in physical contact when the father was present in the group. On the other hand, pups spent significantly more time together without the presence of either parent in the group in which the father was not present. However, this situation did not have any impact on pup development. It may be that the result is different when pups are reared in adverse climatic conditions. In sum, it appears that in adequate conditions of food and/or temperature, the influence of the father on offspring development in several species is sometimes positive and sometimes neutral.

In the present study, experienced adult animals were used. Further research must be done to explore the effects of parent parity on pups. The influence of the father on maternal behavior and pup development when the mother and/or the father is inexperienced remains to be determined. It is suggested that the fact of having pups for the first time is more adverse than when parents have experience in caring for pups. In this way, the father's role could have more impact on pup development in the first condition. However, this hypothesis needs to be more thoroughly investigated because data in the literature on this subject are scarce. Also, new studies should investigate biological and environmental factors that may explain why pup development in the California mouse is slower than in many other rodent species, such as *Peromyscus maniculatus*, *Peromyscus truei* (Layne, 1968), *Mesocricetus auratus*, and *Phodopus sungorus* (personal communication), which are uniparental. In mammals, it has been demonstrated that species with altricial young show a tendency to be monogamous and those with precocial young show a tendency to be polygynous (Zeveloff & Boyce, 1980). In evolutionary perspective, in species in which the descendents are slow in growth and behavioral development, the energetic cost of rearing offspring could be divided between mother and father, which would increase the reproductive fitness of the species. The comparative analysis between monogamous and polygynous species may show promise in answering what differences exist in the pup development when distinct mating systems are analyzed.

NOTES

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