

# Adaptive significance of male parental care in a monogamous mammal

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Paternal behaviour presumably evolved because male care of young was critical for offspring survival. We report field evidence indicating that paternal behaviour enhances offspring survival in a monogamous mammal, the biparental California mouse, *Peromyscus californicus*. Male removal resulted in lower offspring survival in father-absent than in father-present families. New males took up residence with widowed females, but usually after females had stopped lactating, suggesting that the importance of the father is not primarily protection against infanticidal intruders but rather direct care of young.

**Keywords:** male parental care; monogamy; California mouse; offspring survival

## 1. INTRODUCTION

Male parental care is relatively rare among mammals (Kleiman 1977; Kleiman & Malcolm 1981), in part because males typically are 'emancipated' from care of young during gestation and lactation and often have the first opportunity to desert and seek additional mates (Orians 1969; Trivers 1972; Maynard Smith 1977; Clutton-Brock 1991). Furthermore, males would forfeit potential reproductive success (RS) if they increased their parental effort in any one female's young at the expense of lost mating opportunities (Kurland & Gaulin 1984). Nevertheless, male care of young does exist in mammals and presumably evolved, in part, because male care sometimes improves offspring survivorship to such an extent that the benefits of paternal investment outweigh the costs of lost mating opportunities. However, the adaptive significance of male care has not been documented previously in mammals, so assumptions concerning its benefits to offspring remain untested. Here we provide field evidence for the fitness benefits of male care in a monogamous mammal.

Most empirical studies have examined the importance of male care in birds rather than in mammals (Bart & Tornes 1989; Mock & Fujioka 1990). Male birds are equally capable as females to incubate, brood and feed young, and hence a reproductively viable alternative to desertion for male birds is to stay and invest in young rather than seeking additional mates. In some cases, male presence is important for offspring survival in birds, whereas in other cases, male presence has little or no effect on offspring survival (Bart & Tornes 1989).

The California mouse, *Peromyscus californicus*, is exclusively monogamous in the wild. DNA-fingerprinting and paternity exclusion analyses indicate that in every case only the paired male sires his mate's offspring; there are no extra-pair fertilizations (Ribble 1991). *P. californicus* is also socially monogamous: males and females form long-term pair bonds, remain together permanently unless the mate dies, and are found in association only with

their partner (Ribble & Salvioni 1990). Males exhibit extensive care of the young both in the field (Teferi & Gubernick 2000) and in the laboratory (Gubernick & Alberts 1987), and in the field males (and females) spend between 65 and 85% of the time in the nest with their young (Ribble & Salvioni 1990; Teferi & Gubernick 2000). Males display all the components of parental behaviour shown by mothers (huddling, licking, carrying) and to the same extent, except lactation (Dudley 1974b; Gubernick & Alberts 1987). In both the field and the laboratory, young suckle until about 30–40 days of age, and continue to occupy the nest with their parents after first emergence (D. J. Gubernick and T. Teferi, unpublished data). In the laboratory, and in the absence of any maternal care, direct male care of young, in the form of huddling over pups and keeping them warm, enhances offspring survival (Dudley 1974a). Hence, *P. californicus* provides an excellent opportunity to examine the adaptive significance of male care in a mammal.

The main breeding season for *P. californicus* at our study site extends from October to May, which coincides with the rainy season and the coldest times of the year (Ribble & Salvioni 1990; D. J. Gubernick and T. Teferi, unpublished data). Females average ( $\pm$ s.e.)  $2.35 \pm 0.18$  litters per season (range one to four), and average lifetime reproductive success (LRS) is similar for males ( $4.4 \pm 0.9$  young) and females ( $4.7 \pm 0.7$ ) (Ribble 1992b). They live for 9–11 months or more in the wild (Ribble 1992b; D. J. Gubernick and T. Teferi, unpublished data). Interbirth intervals are longer for mate switches (e.g. after death of a mate) than for those continuously paired (Ribble 1992b), suggesting a potential cost to LRS if either partner deserts.

## 2. METHODS

In order to determine the fitness effects of male care in *P. californicus*, we manipulated male presence and compared offspring survival in father-present and father-absent families. We used live trapping on three permanently marked study grids at Hastings Natural History Reservation, Monterey County, California, from July 1994 to May 1996 to assess the effects of male presence on offspring survivorship.

The study grids consisted of either a  $6 \times 14$ ,  $6 \times 11$  or  $4 \times 32$  trap-station configuration with trap stations spaced 10 m apart.

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Each trap station consisted of two Sherman live traps provided with rolled oats and cotton bedding. Traps were opened and baited during the late afternoon, checked twice, once in the night and again before dawn. Each grid was trapped for three consecutive nights once a week at seven-day intervals. In addition to this standard trapping protocol, intensive live trapping was used at other appropriate times to target specific individuals (e.g. late pregnant and early post-partum females, males with newborn young and juveniles at emergence). This intensive live trapping allowed us to obtain all the critical measurements in this study (see below). Each mouse was given a uniquely numbered ear tag, weighed to the nearest 0.5 g, and sexed. At each capture, we identified females as nulliparous, pregnant, parous but not pregnant or lactating. Adult females were dusted at least once a week with one of six uniquely coloured fluorescent pigment powders that transfers to their young and to their mates (Ribble 1991). The powder remains on the fur for at least two weeks. At each capture, males were checked for the presence and colour of fluorescent pigment with a hand-held long-wave ultraviolet light. Because the presence of the female-specific pigment on a male correlates perfectly in all cases with the identity of the genetic father (Ribble 1991), we considered a male that showed the female-specific colour for three or more trapping weeks to have paired with the female. In all cases, such pairs remained together unless the mate died or was experimentally removed.

We removed males within three days (mean  $\pm$  s.e. =  $1.8 \pm 0.3$  days; range = 0–3) following the birth of their first litter, and compared the RS of females without partners ( $n=11$ ) with that of the RS of females with partners ( $n=14$ ). In the first year of the study, all males immigrated onto the study grids and presumably had no previous breeding experience because established breeders do not disperse (Ribble 1992a,b). As best we could, we alternated assignment of males to the male-present or male-absent treatment. Removed males were kept in captivity and later released. RS was defined as the number of young that emerged from the nest. We controlled for the number of young born into each group by estimating the number of young born based upon the weight loss of females from the last days of pregnancy to the first three days post-partum. A pup weighs approximately 2.5–3 g at birth (based upon extensive laboratory data and late pregnant females caught in the field and brought into captivity), which allowed us to estimate the number of young born. In no case did more young emerge from a nest than was estimated at birth. Young emerge about 30–35 days post-partum and disperse around 65–70 days of age (Ribble 1992a). We saturation trapped extensively around known nest areas before and after young would typically emerge and continued to trap the entire grid site until ten days after juveniles would normally disperse (65–70 days of age); thus we were confident of not missing any juveniles. Nest areas were located primarily by radio-telemetry for another study and by following powder tracks of dusted females.

Some females from the male-removal group produced a second litter with a new male. We monitored the number of young born and the number that emerged from these second litters as described above and compared survival of their first litters without male assistance with survival of their second litters with male assistance.

### 3. RESULTS

There was no difference in the number of young born to father-present (mean  $\pm$  s.e. =  $1.9 \pm 0.2$ ;  $n=14$ ) and father-

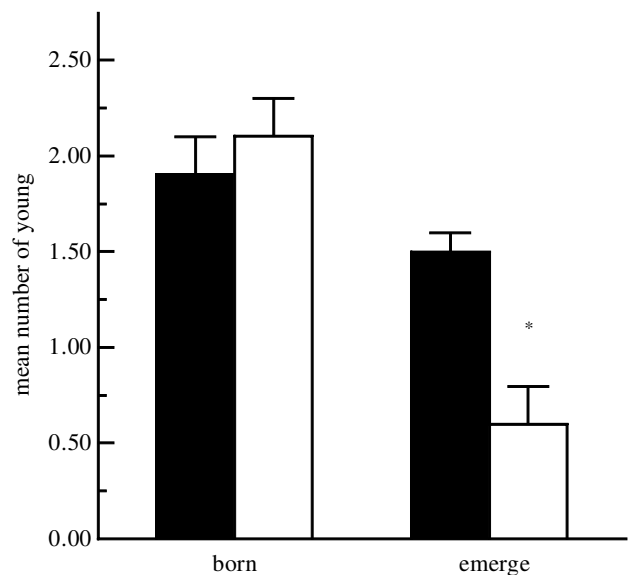


Figure 1. The mean ( $\pm$  s.e.) RS of female *P. californicus* as a consequence of the presence or absence of the male. Filled bars, male present, open bars, male absent.

absent ( $2.1 \pm 0.2$ ;  $n=11$ ) families, unpaired  $t$ -test =  $-0.95$ , d.f. = 23 (figure 1). However, significantly more young emerged from father-present ( $1.5 \pm 0.1$ ) than from father-absent ( $0.6 \pm 0.2$ ) families, unpaired  $t$ -test =  $3.25$ , d.f. = 23,  $p < 0.01$ , two-tailed (figure 1). Furthermore, there was no significant difference between the number of young that emerged compared with the number of young born in father-present families (paired  $t$ -test =  $2.11$ , d.f. = 13), whereas significantly fewer young emerged than were born in father-absent families (paired  $t$ -test =  $7.46$ , d.f. = 10,  $p < 0.001$ , two-tailed).

Almost 81% of young born into father-present families emerged, whereas only 26% of young born into father-absent families survived to emergence (figure 1). Every female with a partner (14 out of 14) raised young, whereas only three out of 11 (27.3%) females without partners weaned any offspring (table 1;  $G_{adj} = 7.30$ , d.f. = 1,  $p < 0.001$ ). Six females without partners subsequently raised a second litter with a new male. RS of these females was significantly greater for their second litter with male assistance ( $1.5 \pm 0.4$  young emerged) than for their first litter without male assistance ( $0.3 \pm 0.4$  young emerged; paired  $t$ -test =  $2.91$ , d.f. = 5,  $p < 0.05$ , two-tailed). This demonstrates that the female's inability to raise young was not something inherent in the female, but rather was the result of male absence.

The evolution of paternal behaviour may be favoured by direct male care of young or through indirect paternal investment in the form of male protection against infanticidal intruders (Van Schaik & Dunbar 1990). Evidence for male deterrence of infanticide would include loss of the female's litter (female no longer lactates) following replacement by or presence of a new male. We determined when a female stopped lactating by examining the female's nipples (when young are suckling, the fur around the nipples is matted and the nipples are distended; based on our laboratory observations, it takes 24–48 h after suckling cessation for nipples to retract). In 11 out of 11 cases,

Table 1. *The percentage of females successful at raising young under father-present and father-absent conditions*

(Litter success is based upon the number of young that emerged from the nest compared with the number of young that were born.)

litter success	father present	father absent
whole litter	71.4% (10/14)	9% (1/11)
partial litter	28.6% (4/14)	18% (2/11)
none	0% (0/14)	73% (8/11)

a new, previously unpaired male (tagged and resident on the trapping grids) took up residence with the 'deserted' female (i.e. new male had the female-specific pigment and resided in the same home range) within  $17.4 \pm 3.8$  days (range 2–38) after male removal. Inspection of female nipples indicated that the eight females that did not raise any young had already stopped lactating either before (six out of eight females) or on the day (two out of eight females) the replacement male took up residence, contrary to the infanticide protection hypothesis. Because we dusted females with powder at least once a week during lactation and we frequently and extensively live trapped, it is unlikely that a new male could have entered a female's nest and killed her young prior to taking up residence with the female without pigment transferring to the new male and without our detecting his presence in the female's home range. Moreover, the other three 'deserted' females continued to lactate even after the arrival of the replacement male and still weaned young. In one case, the replacement male arrived shortly after we removed the resident male, in the other two cases the replacement male arrived either 14 or 30 days after removal of the resident male. Thus, two out of the three females may have been assisted by the replacement male. The young of these three females grew normally and survived to disperse. Although it was a small sample size, these three females did not differ in body mass from the eight 'deserted' females that did not raise any young. In the laboratory, pup mortality after male removal in *P. californicus* was primarily the result of maternal cannibalism of whole litters (Gubernick *et al.* 1993). There were no replacement males in our laboratory study, so pup loss could not be attributed to infanticidal intruders. Thus, male protection against infanticide apparently is insufficient to account for the evolution of paternal care in this species.

#### 4. DISCUSSION

In the absence of any maternal care, direct male care of young enhances infant survival in *P. californicus* in the laboratory primarily through heat transfer from males huddling over pups (Dudley 1974a), but the effects of male absence on pup mortality may be mediated in part by the mother's response to mate loss (Gubernick *et al.* 1993; Gubernick 1994; Cantoni & Brown 1997). Three females weaned young without their mate, suggesting that under certain circumstances some females will attempt and succeed in raising offspring without male assistance. Females that did not raise any young ( $n=8$ ) stopped

lactating on average  $13.3 \pm 3.3$  days after male removal (range 5–28 days), suggesting that these females also attempted to raise young but either they were unsuccessful or it was too costly to continue and they terminated investment. Such curtailment of maternal investment also increases the potential costs to males of mate desertion and pursuit of additional mating opportunities (Maynard Smith 1977). This may help to explain why only unpaired males filled vacancies left by male removal, even though paired males also were neighbours.

Our results indicate that for the vast majority of female *P. californicus*, male care is crucial for offspring survival. Some females were able to raise young without male assistance, but male investment in young significantly enhanced offspring survival compared with 'non-investing, absent' males. The California mouse is unusual among *Peromyscus* species in exhibiting paternal behaviour (for reviews of rodents, see Elwood (1983) and Dewsbury (1985)). The relatively few *Peromyscus* species that exhibit male care in the wild also appear to be monogamous (e.g. *Peromyscus polionotus*, Foltz 1981), suggesting that the importance of male care for offspring survival may have favoured the evolution of monogamy in *Peromyscus*. In a recent phylogenetic analysis, Komers & Brotherton (1997) found that male care of young did not, as a general rule, favour the evolution of monogamy in mammals, except perhaps among *Peromyscus*. However, it is not yet clear why male care is critical for offspring survival in the California mouse, whereas males of other *Peromyscus* species inhabiting the same grid sites show no care of young (M. Kalcounis, unpublished data).

Hypotheses about the evolution of male care in humans and other mammals are based upon the untested assumption that male care is important for infant survival (Trivers 1972; Maynard Smith 1977; Alexander & Noonan 1979; Lazarus 1989), and educated guesses as to the likely costs and benefits of care to males and females (Clutton-Brock 1991). Our findings support the male care hypothesis for the evolution of paternal investment in mammals and indicate that, although male care may not be indispensable for offspring survival, it is sufficiently important to outweigh the benefits of alternative mating strategies. Thus, it will be important to determine why the evolution of paternal investment was favoured in some mammalian species and not others (Smuts & Gubernick 1992; Komers & Brotherton 1997).

We thank Charles Land, Siri Ibarquien, William Funk, Karen Ritchie and Matthew Daugherty for help with field data collection. We thank Dr Janis Dickinson, Dr Tim Halliday, Dr Walt Koenig and Dr Mark Stromberg for their helpful comments on an earlier version of the manuscript. This research was supported by grants from the US National Institutes of Mental Health to D.J.G.

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