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David O. Ribble

Trinity University, dribble@trinity.edu

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CHAPTER 5

The evolution of social and reproductive monogamy in *Peromyscus*: evidence from *Peromyscus californicus* (the California mouse)

David O. Ribble

INTRODUCTION

The genus *Peromyscus* (deer mice) is an attractive group in which to study the evolution of social and mating behaviours. This genus includes over 50 species (Carleton, 1989) that are widely distributed across North and Central America from coast to coast and from the northern subarctic to Panama (Kirkland & Layne, 1989). The diversity in body sizes among *Peromyscus* ranges from 13 to 77 g (Millar, 1989) and exceeds that of most other genera. Phylogenetic relationships among species of *Peromyscus* are relatively well understood (Stangl & Baker, 1984), although the systematics of *Peromyscus* is an active area of study (e.g., Rogers & Engstrom, 1992; Bradley *et al.*, 2000). Most relevant to this chapter, populations and species of *Peromyscus* exhibit a variety of social behaviours and mating systems (Wolff, 1989), with social monogamy, and particularly reproductive monogamy, being relatively rare. Since monogamy is rare among *Peromyscus*, those *Peromyscus* species that exhibit monogamous behaviours may reveal important factors in the evolution of the genus.

One of the best studied monogamous species within the genus is *P. californicus* (California mouse). Association patterns, biparental care, and mating exclusivity indicate that this species is socially and reproductively monogamous, and I will begin by reviewing these elements. Furthermore, recent field experiments demonstrate that male care is critical for offspring survival and is the salient feature of monogamy in this species. I will then review the ecology of female and male home range use and spatial organization and paternal care in other *Peromyscus* species. Finally, within a phylogenetic framework, I will examine the evolution of monogamy and paternal care in *Peromyscus* by mapping male and female spacing patterns as well as male paternal behaviour. This comparative look at monogamy in the

genus can provide clues to the maintenance and evolution of monogamy in *P. californicus*. My objective in this chapter is to explore the evolution of the reproductive strategies of *P. californicus* in the larger context of what is known about other *Peromyscus* species in order to gain a better understanding of the evolution of monogamous mating systems.

THE MONOGAMOUS MATING SYSTEM OF *PEROMYSCUS CALIFORNICUS*, THE CALIFORNIA MOUSE

Peromyscus californicus is one of the larger species of *Peromyscus* (ca. 40 g); it is distributed in California south of the San Francisco Bay down to northern Baja California along the coastal ranges and into the western foothills of the Sierra Nevada (Merritt, 1978). Within its range, *P. californicus* is associated with dense chaparral habitats in the south and broad-leaved forests in the north (Merritt, 1974). The breeding season typically begins with the onset of winter rains in November and extends until the dry summer months (Ribble, 1991). The average number of litters per female per breeding season is 2.35 (2SE = 0.38; Ribble, 1992b). Water availability, rather than photoperiod or food resources, regulates breeding activity in males (Nelson *et al.*, 1995), which is consistent with the species' relatively poor physiological capacities for maintaining internal water balance (MacMillen, 1964). Breeding males live on average 342.2 days (2SE = 97.2) and breeding females 280.9 days (2SE = 124.0), but it is not unusual for breeding males and females to live for more than one year (Ribble, 1992b).

Peromyscus californicus males tend to have larger ranges than females, but unlike most *Peromyscus* (Wolff, 1989), these males have very little intrasexual overlap,

resulting in mated pairs having largely overlapping home ranges that are statistically distinguishable from those of adjacent mated pairs (Ribble & Salvioni, 1990). These mated pairs remain together as long as both members of the pair are alive, with individuals switching to a new mate only after their first mate dies (Ribble, 1991). The amount of time fathers spend in the nest at night, presumably caring for offspring, is comparable to the amount of time spent by lactating mothers. Paternal care has been documented extensively in the laboratory (Gubernick & Alberts, 1987, 1989), and persists even when cages are enlarged or males are presented with other females (Gubernick & Addington, 1994). In natural populations, mated pairs mate exclusively with each other. All offspring from 28 families over a two-year period resulted from exclusive matings between single male and female pairs (Ribble, 1991). Extra-pair fertilizations were not detected using DNA fingerprinting, similar to the Malagasy giant rat (Sommer, chapter 7) but unlike the case for the fat-tailed lemur (Fietz, chapter 14). Thus, based on association patterns, biparental care, and mating exclusivity, *P. californicus* is monogamous, both socially and reproductively.

Survival of offspring to weaning age is high relative to other *Peromyscus* species (Ribble, 1992a). Litter size at weaning (mean = 1.73, 2SE = 0.22) in the field is close to the range of litter sizes at birth reported for female *P. californicus* (range 1.8–2.5). Parity (number of births) appears to have no effect on litter size, but interbirth interval does increase with parity. Interbirth intervals involving mate switches are significantly longer than intervals for pairs that remain together. Lifetime reproductive success (LRS; number of offspring weaned during lifetime) was similar between males (mean = 4.4, 2SE = 1.68) and females (mean = 4.7, 2SE = 1.41) during a three-year study (Ribble, 1992a), but the standardized variance in LRS for males was twice that of females. The number of days that individuals were mated was positively correlated with LRS for both sexes. Maximum weight was also correlated with female LRS. Time to first litter was negatively correlated with LRS in males, implying that stochastic demographic features do affect male LRS.

Unlike the socially monogamous fat-tailed lemur, in which offspring remain in their family group for one or more breeding seasons (Fietz, chapter 14), *P. californicus* offspring leave their natal home range prior to the birth of the next litter (Ribble, 1992b). Once offspring leave their natal home ranges, natal dispersal

patterns are sex-dependent, with females being more dispersive and males more philopatric (Ribble, 1992b). Female-biased dispersal is unusual for mammals, but it is more common among socially monogamous birds (Greenwood, 1980, 1983). In *P. californicus*, females that disperse tend to be from natal litters with significantly more females than from natal litters of those that remained philopatric, implying that females disperse due to competition. Male-biased philopatry is probably due to the monogamous mating system of this species (Ribble, 1992b).

Monogamy in *P. californicus* does not appear to be caused by female dispersion (Ribble & Salvioni, 1990; Ribble, 1991). Both male and female home range sizes are inversely correlated with population density, but even at high densities some males had territories large enough to encompass multiple females, yet they did not do so (Ribble, 1991). Mated males also failed to respond to unmated females in adjacent territories.

There is experimental evidence to indicate that male care in *P. californicus* enhances offspring survival, particularly under cold environmental conditions or when the parents must work for food. In the laboratory, under warm, ambient temperatures and with food provided *ad libitum*, *P. californicus* females can successfully rear offspring without any paternal care (Dudley, 1974a, b; Gubernick *et al.*, 1993). But Gubernick *et al.* (1993) and Cantoni and Brown (1997) have shown that the father's presence increases offspring survival in cold ambient temperatures and when parents must work for their food.

In the field under natural conditions, Gubernick and Teferi (2000) have experimentally demonstrated the critical importance of male care for offspring survival in the same populations that I studied. They removed 11 mated males within three days of the birth of their mated female's first litter, and compared the number of young that emerged to 14 females with their mated male present. There was no difference in the number of young born to the father-present pairs (mean = 1.9 ± 0.4 [2SE]) compared to the father-removed pairs (2.1 ± 0.4), but the number of young that emerged was significantly greater in the father-present pairs (1.5 ± 0.2 vs. 0.6 ± 0.4). Six of the females that had their partners removed went on to successfully reproduce with a new male partner, and their reproductive success was significantly greater with their new partner than their efforts without a male present (Gubernick & Teferi, 2000).

The social organization, mating system, and biparental care of *P. californicus* is strikingly similar to many monogamous birds that exhibit low extra-pair fertilizations (EPFs) and large contributions of paternal care by males (e.g., Black, 2001; Haggerty *et al.*, 2001; Quillfeldt *et al.*, 2001). For birds, it has been suggested that in species with low EPF rates, males should contribute to offspring care (Birkhead & Møller, 1996). Among mammals, female gestation and lactation typically emancipate males from care of the young (Kleiman, 1977; Barlow, 1988), and males usually maximize reproductive success by securing additional matings rather than investing in their offspring (Trivers, 1972). Paternal care, then, is an essential feature of male reproductive strategies in *P. californicus*, which is unusual compared with other *Peromyscus* species.

ECOLOGY OF SPATIAL ORGANIZATION IN *PEROMYSCUS*

Traditionally, most studies of *Peromyscus* have focused on the widespread *P. maniculatus* and *P. leucopus*. Wolff (1989) reviewed and summarized social behaviour of *Peromyscus*. Since Wolff's review, using modern techniques of radio telemetry and molecular biology, numerous studies of *P. maniculatus*, *P. leucopus*, and other species of *Peromyscus* have furthered our understanding of spatial organization and mating systems in *Peromyscus*. These advances are important because previously home ranges and spatial organization were largely determined by live-trapping individuals. We have demonstrated that for *Peromyscus*, live-trapping, compared to radio telemetry, significantly underestimates home range size, particularly at low densities (Ribble *et al.*, 2002). Thus, more and better information on home range use and spatial organization in *Peromyscus* has become available since Wolff's review.

Most studies of *Peromyscus* have indicated that females occupy home ranges that are mutually exclusive from adjacent females; hence females are solitary both spatially and socially (Table 5.1). In general, *Peromyscus* do not select home ranges that contain a *specific* food resource since they tend to be omnivorous (Kaufman & Kaufman, 1989). Females typically choose home ranges that contain a variety of resources, and compared with males, females tend to be more selective in their home ranges (Bowers & Smith, 1979). On the other hand, female selection of habitats may be limited by the avail-

ability of suitable nesting sites, and females may select habitats on that basis (Scheibe & O'Farrell, 1995). There are, however, documented cases of communal or group nesting by female *P. maniculatus* and *P. leucopus* (Howard, 1949; Hansen, 1957; Millar & Derrickson, 1992; Wolff, 1994). These cases appear to be due to the inclusion of female offspring in the nests of their mothers, and do not result in any noticeable decreases in the reproductive success of the reproductive females (Wolff, 1994). Furthermore, non-offspring nursing has been reported in *P. leucopus* (Jacquot & Vessey, 1994).

For females that are solitary and territorial, it is generally accepted that they defend their home ranges from other females in order to defend resources that are critical during the energetically demanding periods of gestation and lactation (Ostfeld, 1990). Females tend to demonstrate more aggressive territorial behaviours than males, particularly at higher densities (Wolff, 1989). Female home range size is typically inversely correlated with population density (Metzgar, 1971; Madison, 1977; Ribble & Salvioni, 1990; Ribble & Stanley, 1998), but not always (Wolff, 1985). Experimental studies of food addition usually indicate that addition of food results in smaller female home ranges (reviewed in Wolff, 1989). Wolff (1993) and Wolff and Peterson (1998) have suggested that female small mammals, including *Peromyscus*, may be territorial to protect young from infanticide, primarily by adjacent females (pup-defence hypothesis). Unfortunately, there are few experimental data that discriminate between the food-defence and pup-defence hypotheses of territoriality in *Peromyscus* or mammals in general (Wolff, 1993). Whatever the reason for mutually exclusive use of space by females, the spatial pattern of females is thought to select for spacing patterns among male *Peromyscus*.

Male home ranges are usually larger than female home ranges (Ribble & Stanley, 1998; but see Madison, 1977), and male spacing patterns are more variable than female spacing patterns across *Peromyscus* species (Table 5.1). Male spacing patterns vary from monogamy (one male overlaps one primary female with little intrasexual overlap), to roving (one male overlaps several females with extensive intrasexual overlap between males), to polygyny (one male overlaps several females with little intrasexual overlap between males) (Table 5.1). Male spacing in populations of *P. leucopus* and *P. maniculatus* has been shown to vary across subspecies and populations in different habitats. For example, male montane *P. maniculatus nubiterrae* tend to

Table 5.1. Documented spacing characteristics and paternal behaviour of *Peromyscus* species. *Onychomys* is included as an outgroup for comparative purposes

Taxon	Female spacing	Male spacing	Paternal care			References
			Laboratory	Field	Best evidence	
<i>Onychomys</i>	Solitary	Roving	Y	N	N	Horner & Taylor, 1968; Frank & Heske, 1992; Stapp, 1999
<i>Peromyscus crinitus</i>	Solitary	ND	N	ND	N	Eisenberg, 1963
<i>P. boylii</i>	Solitary	Roving	ND	N	N	Ribble & Stanley, 1998; Kalcounis-Rueppell, 2000
<i>P. eremicus</i>	Solitary	Roving	N	ND	N	Hatton & Meyer, 1973; Lewis, 1972; Eisenberg, 1968
<i>P. californicus</i>	Solitary	Monogamous	Y	Y	Y	This chapter
<i>P. melanocarpus</i>	ND	ND	Y	ND	Y	Rickart, 1977; Rickart & Robertson, 1985
<i>P. mexicanus</i>	Solitary	ND	Y	ND	Y	Rickart, 1977; Duquette & Millar, 1995
<i>P. truei</i>	Solitary	Roving	ND	N	N	Hall & Morrison, 1997; Ribble & Stanley, 1998
<i>P. leucopus</i>	Solitary & gregarious	Monogamous Roving Polygynous	Y	Y ^a	Y ^a	Wolff, 1989; Wolf & Cicirello, 1989, 1991; Schug <i>et al.</i> , 1992; Xia & Millar, 1988, 1989
<i>P. polionotus</i>	Solitary	Monogamous	Y	Y	Y	Blair, 1951; Smith, 1966; Foltz, 1981
<i>P. maniculatus</i>	Solitary & gregarious	Monogamous Roving Polygynous	Y	Y ^a	Y ^a	Horner, 1947; Howard, 1949; Xia & Millar, 1986; Wolff, 1989; Wolff & Cicirello, 1989, 1991; Ribble & Millar, 1996

^a Presence of paternal care in some populations but not others.
ND, no data.

be socially monogamous, while male *P. m. bairdii* tend to be polygynous or roving (Wolff & Cicirello, 1991). Wolff and Cicirello speculated that, because of the cooler breeding season of montane *P. m. nubiterrae*, there may be selection for males to invest in paternal care. Variability among different populations or subspecies may also be due to the density and dispersion of females. For example, Wolff and Cicirello (1990) have shown in *P. leucopus* that when females are at lower densities and widely dispersed, males adopt a non-territorial roving strategy. At higher female densities, males defend smaller home ranges that contain two to four females. Thus, the density of females largely determines the spatial organization and home range use of males. Exper-

imental food addition usually does not influence male spacing patterns (Wolff, 1989), although we have found in *P. boylii* that food addition results in greater reductions in male than in female home range size (Ribble, unpublished data).

In *Peromyscus* with solitary females and roving males, genetic evidence indicates that litters can be sired by multiple males (Birdsall & Nash, 1973; Xia & Millar, 1991; Ribble & Millar, 1996). Based on the reproductive patterns observed, the roving male spacing pattern is often referred to as a promiscuous mating system (e.g., Heske & Ostfeld, 1990). Rarely, however, do studies of promiscuous spacing patterns have genetic evidence on offspring paternity.

Male parental behaviour is poorly understood in most natural populations of *Peromyscus* due to the difficulty of studying this behaviour in nocturnal, secretive individuals. There have been many studies of *Peromyscus* in the laboratory demonstrating that males will care for offspring if the females will allow them (e.g., Horner, 1947; Eisenberg, 1963; Table 5.1). Some species, for example *P. leucopus*, will exhibit paternal care in the laboratory (Horner, 1947; Hartung & Dewsbury, 1979), but in larger enclosures or in the field, paternal care is not observed (Xia & Millar, 1988). Many of the species in Table 5.1 have been observed exhibiting paternal behaviour in the laboratory, but only three, *P. californicus*, *P. polionotus*, and *P. m. nubiterrae* have unequivocally been demonstrated to be paternal in the field. The evidence for paternal care includes long periods of occupation in a nest that contains offspring (Ribble & Salvioni, 1990) or sampling of nests that contain both male and females (Foltz, 1981). Two of these species, *P. polionotus* and *P. californicus*, have also been shown to exhibit mating exclusivity, that is to say the socially monogamous male is also the genetic partner (Foltz, 1981; Ribble, 1991).

The discrepancy between laboratory and field observations of paternal care at least indicates that males have the ability to care for offspring, but either female aggression or ecological situations prevent males from being paternal. For example, Schug *et al.* (1992) have shown that the genetic father in *P. leucopus* was found to be associated with pups in nest boxes only after their weaning, but not before. Also, Wolff and Cicirello (1991) observed *P. leucopus* fathers present in nest boxes with pups in 32% of litters. Thus, in some species of *Peromyscus* paternal care appears to be variable.

To conclude, female *Peromyscus* tend to have smaller, solitary home ranges and male associations can vary from monogamous to roving to polygynous. The density of females appears to be a determinant of whether males adopt a roving strategy rather than defending their home range, or defending a home range in a polygynous social organization. Paternal behaviour has been documented in many laboratory situations, but little is known about paternal behaviour in natural populations. Monogamous tendencies have been reported for *Peromyscus* (e.g., Hartung & Dewsbury, 1979; Dewsbury, 1981), but with the exception of *P. californicus* and *P. polionotus*, these are not very well understood.

COMPARATIVE VIEW OF MONOGAMY IN *PEROMYSCUS*

The most complete phylogeny to date of *Peromyscus* is that of Stangl and Baker (1984), and is based on karyotypic data. This phylogeny was also used by Langtimm and Dewsbury (1991) to examine variation in copulatory behaviour of *Peromyscus*. I used this phylogeny and included as the outgroup a commonly recognized one, *Onychomys* (grasshopper mice) (Carleton, 1989; Langtimm & Dewsbury, 1991). Character states from Table 5.1 were mapped on the phylogeny of *Peromyscus* using MacClade, Version 4.0 (Maddison & Maddison, 2000). I made no assumptions about the evolutionary sequence in which characters changed. Ambiguities in character tracings were resolved using the DELTRAN procedure, which delays changes away from the root of the phylogeny (Maddison & Maddison, 2000). Information that was not available (Table 5.1) was not scored. Female spacing patterns were scored as solitary (little or no overlap between home ranges) or gregarious (largely overlapping home ranges, usually accompanied with nest-sharing), based on spatial overlap during the breeding season. Species with both solitary and gregarious female spacing were scored as gregarious. Male spacing patterns were scored as monogamous, roving, polygynous, or variable if populations exhibited multiple patterns. No species has been documented as being solely polygynous; those species with polygyny have also been documented as being monogamous and roving. Paternal care was scored based on the best available evidence. If a species has exhibited male care in the laboratory but not in the field, then they were considered non-paternal. If a species has exhibited paternal behaviour in the laboratory, has other life history traits consistent with paternal care (e.g., Dewsbury, 1981), and there has been no conflicting information from the field, then they were considered paternal (Table 5.1).

Based on the phylogenetic patterns of female and male spacing patterns, it appears that the ancestral social organization of *Peromyscus* is one in which females are distributed in a solitary fashion and males rove across larger home ranges (Figure 5.1). The only cases of polygynous spacing by males are also in the species in which females have been documented as being gregarious, i.e., *P. maniculatus* and *P. leucopus*. The only two species of *Peromyscus* with well-documented, and exclusively male monogamous spacing patterns are

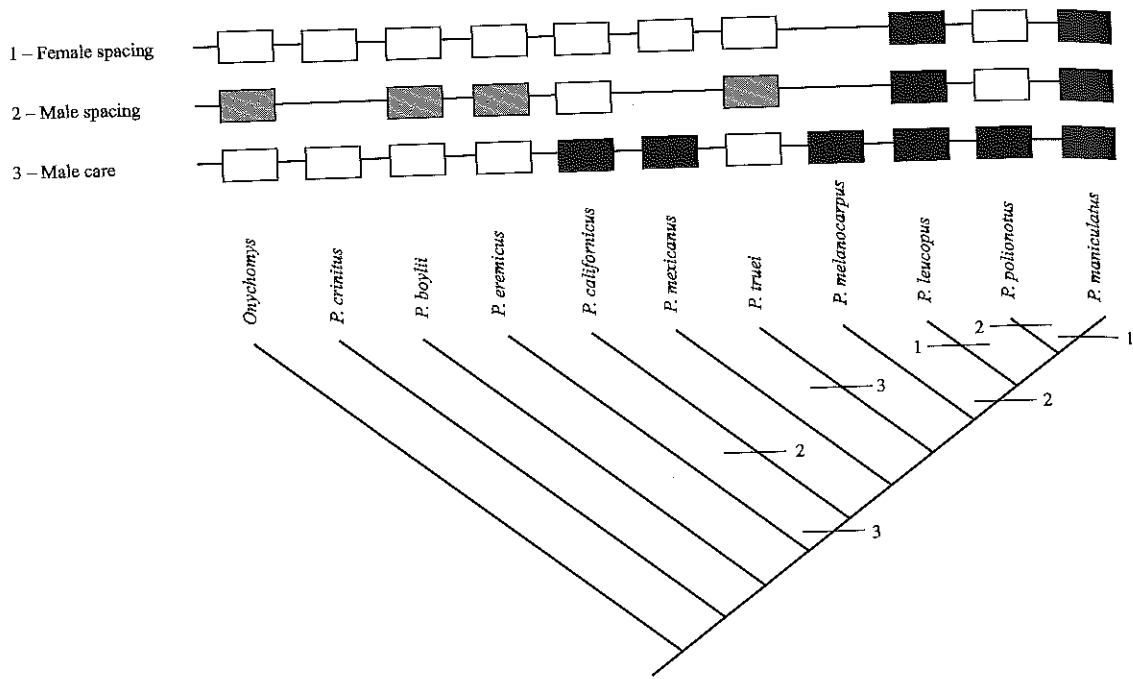


Figure 5.1. Spacing and paternal behaviours of *Peromyscus* overlaid on a cladogram modified from Stangl and Baker (1984). Character states (described in Table 5.1) are: female spacing: white – solitary, black – solitary and gregarious; male spacing: grey – roving, white – monogamous, black – monogamous, roving, and polygynous; male care: white – not present, black – present. Characters with no data are indicated without boxes. Branches in which the character state changes are indicated with horizontal bars and labelled with the character number.

P. californicus and *P. polionotus*. Based on the phylogenetic relationships, it appears that this feature is the result of homoplasy or convergent evolution. Based on limited information, and primarily from the laboratory, male care is potentially a relatively common feature of males. Thus, the presence of monogamous spacing and mating exclusivity in *P. californicus* and *P. polionotus* may be due to the paternal investment route suggested by Brotherton and Komers (chapter 3).

The only clear cases of male care in natural populations that appear to be fixed are, again, from *P. californicus* and *P. polionotus*. If male care has evolved twice in each of these lineages, then are there similarities in the ecologies and life histories of these two species? *P. polionotus* is one of the smallest *Peromyscus* species at an average weight of 14 g and *P. californicus* is one of the larger at 37 g (data from Millar, 1989). The average litter size of *P. polionotus* is 3.7, while that of *P. californicus* is around 2. Across *Peromyscus*, litter size tends to be inversely correlated with body size (Rickart, 1977), the smallest species producing larger litters. Part of this

correlation may be because the larger species tend to be tropical and more *K*-selected species than the smaller species, which exist in more variable temperate environments and are thus more *r*-selected (Rickart, 1977). However, *P. californicus* is not a tropical species and it has a very small litter size. Body size is positively correlated with both individual neonate weight and entire litter mass in *Peromyscus* (Millar, 1989). If neonate weight or litter weight are adjusted by adult weight, an interesting pattern appears relative to litter size (Figure 5.2). Litter size is not correlated with relative neonate weight, but it is positively correlated with relative litter mass. And thus, in the *Peromyscus* species, *P. californicus* has one of the smallest litter sizes, and one of the smallest relative neonate and litter weights (Figure 5.2).

Any investment by the male in parental care will decrease his chance to secure additional matings (Trivers, 1972; Maynard Smith, 1977; Kurland & Gaulin, 1984), so why should male *P. californicus* invest in his offspring and mate exclusively? Other species of *Peromyscus* (*P. boylii*, *P. truei*, and *P. maniculatus*) that are syntopic

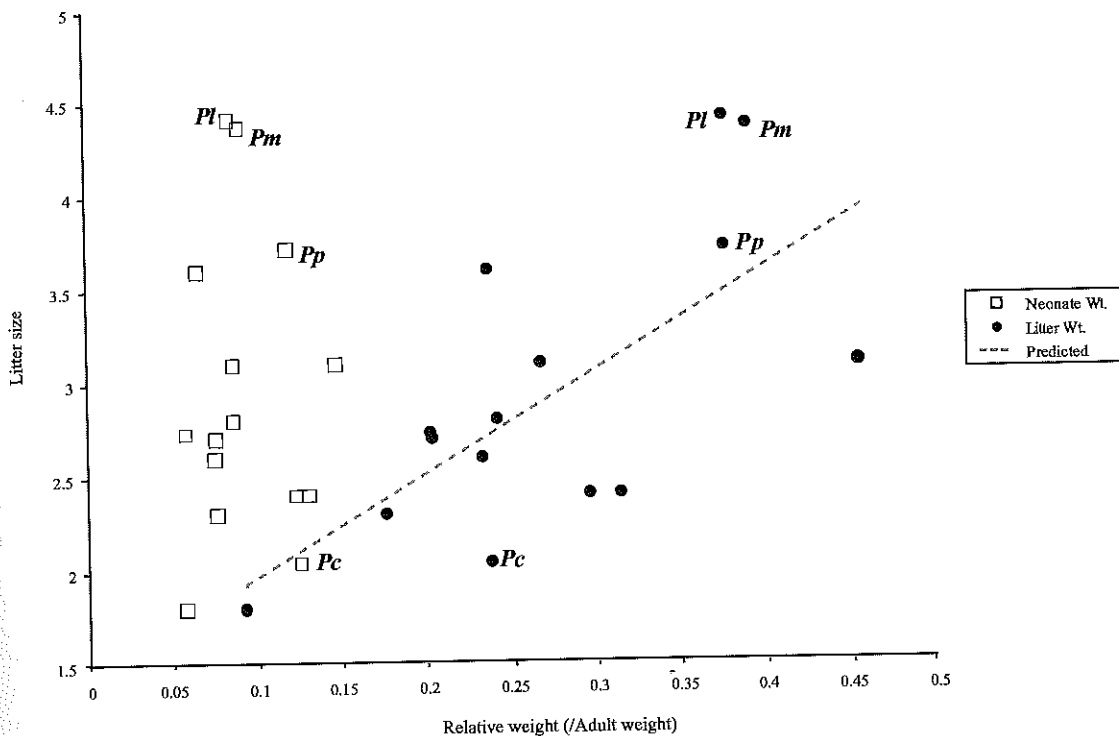
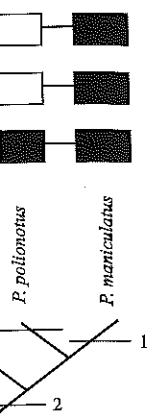


Figure 5.2. Relationships between relative weight (wt (g)/ adult weight (g)) of individual neonate mass and entire litter mass to litter size for *Peromyscus* species. Data were taken from Millar (1989). The predicted line was calculated from a regression analysis of all data. Select species discussed in the text are: *Pl*, *P. leucopus*; *Pm*, *P. maniculatus*; *Pp*, *P. polionotus*; *Pc*, *P. californicus*.

with *P. californicus* do not exhibit paternal care or monogamy (Ribble & Millar, 1996; Ribble & Stauley, 1998; Kalcounis-Rueppel, 2000). Furthermore, female *P. californicus* can raise at least some offspring without the male (Gubernick & Teferi, 2000). From the male's perspective, one can ask how many litters must a non-paternal male produce to equal the males that do engage in paternal care activities. Ribble (1992a) reported that average lifetime reproductive success for males was 4.5 weaned offspring. Assuming the average weaning success without paternal care is 0.6 offspring, then non-paternal males would have to mate and produce 7.5 litters to equal the average LRS for the average parental males (4.5/0.6). Since females produce an average of 2.5 litters in their lifetime, a non-parental male would have to mate with at least three females if each female produced 2.5 litters, to match the reproductive success of males that engage in paternal behaviours. The average lifespan of males in the field is almost one year (342 days), in which the breeding season is restricted from November to June (Ribble, 1992a). Thus,

it would appear that a male's best strategy is to mate and pair with only one female. Sommer (chapter 7) argued that for the Malagasy giant rat (*Hypogeomys antimena*), the male's contribution to offspring survival must outweigh the costs of lost mating opportunities due to the impact of predation. There is no evidence to suggest that male *P. californicus* provide protection from predators, but rather it is direct paternal care that increases offspring survival (Ribble, 1990; Gubernick & Teferi, 2000).

But why is male care critical for offspring survival in *P. californicus* compared with other *Peromyscus*? I would suggest that male reproductive success is maximized by investing in care of the offspring because of the small litter size and relative mass of the litter in this species. In *Mus musculus*, offspring from smaller litters are energetically less efficient at converting milk to body weight (König *et al.*, 1988) and mothers spend significantly more time caring for smaller litters (König & Markl, 1987). In both cases, the authors attributed these effects to greater heat loss of smaller litters simply due to the

number of bodies huddled in the nest. For *P. californicus*, it may be that with such small litters, fathers can contribute significantly to the growth of their offspring simply by huddling over them, providing warmth while the female is away from the nest foraging. *P. californicus* offspring are ectothermic up to 15 days postpartum (Gubernick & Alherts, 1987), and any warmth provided by parents would allow the offspring to invest their energy in growth. If litter size were larger, as is the case with most other *Peromyscus* (see review in Millar, 1989), the contribution of the male would be diminished by the thermal advantages of a larger litter and his reproductive success would then likely be maximized by securing other matings. Thus, I am suggesting that male *P. californicus* can contribute more to the growth of their offspring than most mammals due to the relatively (in terms of other *Peromyscus* species) small litter size of this species.

The thermal disadvantage of small litter size may be further exacerbated due to the timing of the breeding season. *P. californicus* begins breeding with the onset of winter rainfall in November and continues until the dry summer months (Ribble, 1992a). Consequently, many offspring are born during the coldest months of the year and the father's contributions to keeping the offspring warm may be critical during these months. Other *Peromyscus* species that coexist with *P. californicus* (*P. boylii*, *P. truei*, and *P. maniculatus*) do not initiate breeding until the warmer spring months (unpublished observation). Most *Peromyscus*, regardless of litter or body size, produce two or three litters per breeding season (Millar, 1989), and the earlier breeding by *P. californicus* is probably related to its longer interbirth intervals (Ribble, 1992a).

Females and their offspring are also likely to benefit indirectly from the presence of the male (Wittenberger & Tilson, 1980). Offspring are weaned at a heavier weight in the presence of the male in the laboratory (Dudley, 1974a), and fathers could provide protection from predators and conspecifics (Ribble & Salvioni, 1990). In laboratory experiments in which individuals must forage for food, the male's presence resulted in four times more offspring in a 74-day period compared with females without male help (Cantoni & Brown, 1997). In natural populations, survival from birth to emergence has been estimated at 30% in other *Peromyscus* species without paternal care (Millar & Innes, 1983; Ribble, unpublished data), which is similar to the survival rates

observed by Gubernick and Teferi (2000) in *P. californicus* where the father was not present. The high survival rate of offspring in *P. californicus* is no doubt due to biparental care. Furthermore, females who switch mates have longer interbirth intervals, possibly decreasing female lifetime reproductive success (Ribble, 1992a). In addition to the direct benefits of male care, males could also contribute in indirect ways to offspring survival by providing protection from infanticide (Agrell *et al.*, 1998). In the experiments by Gubernick and Teferi (2000), all 11 females that had their mates removed remated with a new male. In all 11 cases, the new male took up residence *after* the female had ceased lactating, suggesting that the new male was not responsible for loss of any offspring. Thus it appears that the evolution of male care in *P. californicus* is not due to the benefits of protection against infanticide (Gubernick & Teferi, 2000).

In contrast to *P. californicus*, *P. polionotus* has a litter size and litter mass similar to other species (e.g., *P. maniculatus* and *P. leucopus*, Figure 5.2) that do not exhibit monogamy. This species is confined to the southern USA, which is arguably warmer. This species does, however, build extensive burrows, and it has been suggested by Smith (1966) that it takes both sexes to maintain the burrow. Thus, it is likely that monogamy has evolved for different reasons among the genus *Peromyscus*.

SUMMARY

Komers and Brotherton (1997) examined male care and monogamy in mammals, concluding that the ancestral species of *Peromyscus* may have had a tendency towards monogamy and paternal behaviour. Their analyses depended primarily on secondary literature that has been contradicted by more recent primary sources. For example, most secondary literature sources describe the genus *Onychomys* as exhibiting a monogamous social organization, based on live-trapping studies. Recent field studies using radio telemetry demonstrate otherwise (Frank & Heske, 1992; Stapp, 1999). There are also problems, as indicated above, with interpreting male parental behaviours based solely on laboratory studies.

I have demonstrated that the likely ancestral social organization of *Peromyscus* is one of solitary females, with males adopting a roving strategy of home range use that can result in a promiscuous reproductive mating

system. And there are at least two species of *Peromyscus* (*P. californicus* and *P. polionotus*) with monogamous social and reproductive mating systems that appear to have evolved independently, and probably for different adaptive reasons.

Data from *P. californicus* suggest that the larger body size, smaller litter size, and relative litter mass may influence male reproductive strategies so that they mate exclusively and invest heavily in their offspring. Body size has long been recognized as important for various mammalian life history traits (see reviews of Clutton-Brock & Harvey, 1983; Sauer & Slade, 1987), but perhaps the importance of body size for mating systems has not been adequately appreciated in mammals. A notable exception is Jarman's (1974) analysis of mating systems among African antelope. He concluded that the interaction between body size and feeding ecology has influenced the evolution of mating systems between antelope species. Body size has also been recognized as an important trait in bird mating systems (Amadon, 1959; Wiley, 1974).

If the relationships between body size, litter size, and food resources are some of the principal factors accounting for monogamy in *P. californicus*, then other large-bodied, small litter size *Peromyscus* should provide important tests of this hypothesis. Based on reproductive tactics and behaviour observed in the laboratory, Rickart (1977) has suggested that *P. melanocarpus* (mean adult weight = 59 g; mean litter size = 1.8) and *P. mexicanus* (mean adult weight = 53.4 g; mean litter size = 2.1) may be monogamous. Unfortunately, little is known about the mating systems of other large-bodied *Peromyscus* in natural populations. There is obviously much to be learned about the evolution of monogamy from studies of *Peromyscus*. I hope this review will stimulate more work on the social ecology of lesser known species of *Peromyscus*.

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