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THE IMPORTANCE OF PATERNAL CARE FOR PUP SURVIVAL AND DEVELOPMENT IN TWO SPECIES OF MICE
(*MUS MUSCULUS* AND *PEROMYSCUS CALIFORNICUS*)

by

SANDRA L. WRIGHT

Submitted in partial fulfillment of the requirements for
the degree of Doctorate of Philosophy
at

DALHOUSIE UNIVERSITY
HALIFAX, NOVA SCOTIA
NOVEMBER, 1994

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by Sandra Lea Wright

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Dated November 14, 1994

External Examiner [redacted]

Research Supervisor

Examining Committee

DALHOUSIE UNIVERSITY

DATE: 11 October 1994

AUTHOR: Sandra L. Wright

TITLE: The Importance of Paternal Care for Pup Survival and Development in Two Species of Mice (Mus musculus and Peromyscus californicus)

DEPARTMENT OR SCHOOL: Department of Psychology

DEGREE: Ph.D. CONVOCATION: May YEAR: 1995

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Abstract

Although males of monogamous species show more parental behavior than those of polygynous species, studies of parental behavior in rodents generally provide *ad lib* food and water in a warm environment and under these conditions the presence of the male has little or no effect on pup survival and development. I examined paternal care in a polygynous species, the house mouse and a monogamous species, the California mouse, when wheel running was necessary to obtain food. Single mothers (Father Absent) and paired mothers (Father Present) were compared under three different foraging requirements. In both species, Father Present groups weaned significantly more pups than Father Absent groups when wheel running was required for obtaining food (Wheel Contingent). There were no significant effects of the father's presence on pup survival in the No Wheel (standard laboratory housing with ad lib food) or Wheel Noncontingent groups (running wheel with ad lib food). Pup weight was lower in the Wheel Contingent group than in the other two groups but the father's presence had no significant affect on pup weight in either species. Mice in both the Father Absent and Father Present groups showed parental behavior in the light phase and wheel running in the dark phase of the LD cycle. Fathers directly facilitated pup survival by spending as much time in parental care as mothers and indirectly by running on the wheel to earn more food than they consumed in both species. *M. musculus* fathers may have engaged in parental behavior because they were paired with only one female and male parental behavior may not be observed if they were housed with several females. These results suggest that paternal care benefits pup survival more under conditions where the parents must forage to obtain food than in the standard laboratory environment where food is provided *ad lib.*

Acknowledgements

I would like to thank Richard Brown, for the opportunity to conduct research as a graduate student in his lab and for introducing me to a unique species, California mice. I would like to thank John Fentress and Ben Rusak for editing earlier versions of this thesis. For providing the California mice and the expertise necessary to handle and breed these animals, I wish to acknowledge David Gubernick of the University of Wisconsin. Gordon Troop and Russell Fenton were indispensable in building and maintaining the running wheels and I wish acknowledge their contribution as well. For helping me find solutions to several practical and technical problems I would like to thank, Richard Brown, Cathy Ryan, Heather Schellinck, Carolyn Graham and Thad Murdoch.

Finally, I am forever indebted to Patricia Wright, Alan Wright, Susan Wright, Bernice Campbell and Gloria Duffin for their emotional and financial support. A special thanks to Alan Wright for spending so many hours helping collate data and to my entire family for being there when I needed them.

Chapter 1

Introduction

Since internal fertilization and gestation in mammals allows the male to desert the offspring before the female and seek additional matings (Maynard Smith, 1977), parental behavior is usually associated with the female. However, males of many mammalian species exhibit parental behavior such as feeding offspring (carnivores, Frame et al., 1979) or carrying offspring (tamarins, Goldizen, 1987a). This thesis examines some of the factors involved in male parental investment in rodents, and asks the question "Does male parental behavior increase pup survival and development?, and if so, under what circumstances does this occur?" This chapter begins by defining parental investment and describing how it is measured (section 1.1), describing some male parental behaviors (section 1.2), describing three strategies for investigating the evolution of parental investment (section 1.3) and describing the relationship between male parental investment and species social organization and mating system (section 1.4). This chapter concludes by discussing the benefits of paternal care to offspring (section 1.5).

1.1 Definition and measurement of parental investment

The theory of parental investment was first developed by Trivers (1972, 1985), who defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring"

(Trivers, 1972, p. 139). Parental investment as defined by Trivers (1972) is an evolutionary concept measured in terms of cost to the parent and benefit to the offspring (Trivers, 1972, Maynard Smith, 1977). The costs of parental care are reduced fecundity, reduced survival, a reduced ability to invest in current offspring, a reduced ability to provide for offspring, reduced size of sex cells and a reduced ability to engage in anti-predator behavior (Clutton-Brock, 1991, Evans, 1990). Parental investment benefits offspring by increasing the likelihood that they will survive to reproduce (Trivers, 1972). The benefits of parental care are measured in terms of the increased number of offspring that survive to breed (Grafen & Sibly, 1978).

Wittenberger (1981) made a distinction between shareable and nonshareable parental investment. By shareable parental investment, he refers to investment that can be distributed among all current offspring equally, such as brooding eggs, while nonshareable parental investment refers to investment that is limited, to one offspring at a time, such as provisioning food. Direct shareable male parental care refers to behaviors that directly increase egg and offspring survival and can be distributed among several or hundreds of offspring with no reduction in the quality or quantity of parental care. Indirect, shareable parental care refers to behaviors that indirectly benefit the offspring such as territory maintenance (see section on territory) or protection with no reduction in the quality or quantity of parental care. In some birds, the desertion by the male of the nest could be a form of indirect, shareable parental care as many species are terrestrial breeders and emancipation of the male may make it easier to hide nests (several adults around a nest attract predators) and decrease the risk of predation (Lill, 1986). Direct unshareable male parental care refers to behaviors that, if performed for one offspring, are not available for other offspring, such as feeding and carrying offspring. Indirect unshareable parental care refers to behaviors that indirectly benefit the offspring but are not available to all offspring. Male swallows (*Hirundo rustica*) for example, feed only the primary female on their territory so, investment is available for only one brood (Moller, 1991).

Parental investment is currently measured in a less restrictive way than that proposed by Trivers (1972) and is more properly called parental input. Parental input is defined as the actual care or resources provided to the offspring by the parents, regardless of the cost to the parent (Evans, 1990). Parental input, as used by Evans (1990) to measure parental investment, may not always be highly correlated with parental investment. Trivers (1974) also realized this, so the use of parental input may be problematic when measuring parental investment. Trivers (1974) and Evans (1990) noted that when food is scarce, the increasing cost of parental investment will result in less food being delivered to the offspring and poorer survival of the offspring. On the other hand, when food is abundant, the cost of parental investment is lower (reduced foraging time) and the benefit to the offspring increases. So although it is practical to use parental input as a measure of parental investment, these two concepts are distinct (Evans, 1990).

The amount of parental care (parental behavior) is often used as an estimate of parental investment (Wittenberger, 1981) but this may also present problems. Parental care includes all nongametic investment in offspring following fertilization, such as aerating eggs (fish and amphibians), incubation of eggs, protection from predators and feeding young. Parental investment, however, includes investment in gametes as well as subsequent parental care (Wittenberger, 1981). Parental input and parental care appear to be similar measures of parental investment and in this thesis I use "parental care" as a measure of parental investment.

Parental care can be direct or indirect. Direct parental care is defined in terms of parental behavior toward eggs and offspring. Indirect parental care is defined as behavior which also may enhance offspring survival but does not involve direct contact with offspring. Indirect parental care may involve provisioning the female with food and providing protection from predators. In the next section I review some examples of direct and indirect parental care exhibited by fish, birds and mammals.

1.2 What do male parents do?

Male parental care can be direct or indirect and shareable or nonshareable. In this section, examples of the four possible categories of paternal care are given for fish, birds and mammals (rodents, carnivores and primates).

1.2 A. Fish

In fish, egg guarding is the most common form of direct shareable parental care in both males and females, but fish show a wide range of parental behaviors including: nest building and/or substrate cleaning, egg fanning (aerating the eggs by beating the fins above the eggs), removal of dead or diseased eggs, mouth brooding of eggs, retrieval of egg/fry (returning eggs or fry to the nest or school), cleaning eggs, external egg carrying (eggs are attached to the exterior of the parent and carried to hatching), moving nests (taking eggs or fry from one nest to another), brood-pouch egg-carrying (eggs are held in a special sac-like external structure during development), splashing eggs (eggs that are exposed to the air during low tide or eggs that are deposited out of the water are sprayed with water by the parent) and coiling (parent surrounds the egg mass with its own body while guarding them, Blumer 1979, Baylis, 1981).

A few species of cichlids such as the discus fish *Symphysodon* and *Cichlasoma citrinellum* exhibit direct nonshareable parental care in the form of ectodermal feeding (parent feeds young fry with mucus that forms on the parents exterior) (Perrone & Zaret, 1979, Noakes & Barlow, 1973). The feeding offspring is rare in fish, because of their small size, fry can forage more efficiently on tiny invertebrates than adults (Perrone & Zaret, 1979).

Male fish that exhibit indirect shareable parental care usually defend a territory to prevent rival males from fertilizing eggs on his territory. Species that guard territories often guard eggs, as occurs in sticklebacks (*Gasterosteus aculeatus*, DeFraipont et al., 1993, Perrone & Zaret, 1979), greenlings (*Oxylebius pictus*) and marine catfish (*Galeichthyes felis*). Male cichlids also guard fry (Perrone & Zaret, 1979). The literature does not mention whether fish exhibit indirect nonshareable paternal care, however it does not appear that males invest in their offspring by feeding the female. The data collected suggests that fish feeding their mate(s) is rare as adults can forage more effectively for themselves than for others (Perrone & Zaret, 1979).

1.2 B. Birds

Male parental care in birds is found in most monogamous (a male and female only mate with each other) species with altricial young. It involves shared incubation (direct shareable), feeding of young (direct nonshareable, Silver, Andrews & Ball, 1985, Muldal et al., 1986, Johnson & Kermott, 1993), territorial and predator defense (indirect shareable, Regelmann & Curio, 1986, Beletsky & Orians, 1990) and provisioning of the female (indirect, nonshareable, Silver, Andrews & Ball, 1985). The amount of care given by both sexes is not always equal as females often are more involved with care of the young than males and the two parents adopt different roles (Kendeigh, 1952, Lack 1968). For example, in many passerines, females incubate more than males and males spend more time in territory defense (Kendeigh, 1952). Some male swans and geese assist their mate in protecting the young, but most desert shortly after the beginning of incubation (Kear, 1970).

Males may feed their mates from the start of nest building, through incubation and up to the time that eggs hatch as in Marsh tits (*Parus palustris*). Males that feed their mate have clutches that hatch earlier, and the data suggests that the male's assistance may be important for clutch survival in cold weather (Nilsson & Smith, 1988). While both parents of the northern mockingbird (*Mimus polyglottos*) defend eggs and nestlings by mobbing humans that are visiting their nests, males show more frequent offspring defense than females (Breitwisch, 1988).

In some species of birds, males incubate the eggs and rear the young on their own. The mountain plover, *Chardrius montanus*, reproduces by double clutching. The male established a territory at the beginning of the breeding season and cares for the first brood. The female then lays a second clutch, with or without changing mates, which she rears herself (Gaul, 1975). Cassowaries such as *Casuarius casuarius* are solitary and each remains within their own territory for most of the year. In the breeding season, they are seen in pairs and may be monogamous (Lack, 1968). Once the eggs are laid, the male alone incubates the eggs, feeds and protects the offspring.

1.2 C. Mammals

As mammals have internal fertilization and gestation and only females lactate, no species has male-only parental care; however there is evidence of biparental care in some primates, carnivores and rodents. Male mammals assist in providing direct shareable parental care such as huddling with young, grooming young, retrieving young, defending young, and playing and socializing with young. Males also provide direct nonshareable parental care such as carrying and transporting young and feeding young; indirect shareable parental care, such as territory maintenance and shelter construction and maintenance and indirect nonshareable parental care, such as feeding the female (Kleiman & Malcolm,1981). The range of paternal behavior in primates, carnivores and rodents is described in the rest of this section.

In common marmosets (*Callithrix jaccus*) which are monogamous, males carry, feed and protect their offspring (Ingram, 1977, Goldizen, 1987b). Arruda et al. (1986) observed 11 families of common marmosets (mother, father and twins) from birth until the infants were 36 days of age. For the first three days the mother carried the infants 70% of the time, but by the fourth day, the male took over most of the carrying, and continued to carry the young until the end of the study. Carrying young is energetically expensive when engaged in for long periods of time; thus the male pays a high energetic cost for carrying the young (Arruda et al, 1986). Box (1975, 1977) found that for the first two days after birth of the young (*Callithrix jaccus*), the fathers carried both twins more than the female. In the pygmy marmoset (*Cebuella pygmaea*), adult females carried their offspring most often when they were less than three weeks old while adult and juvenile males were most likely to carry the offspring when they were more than three weeks old (Wamboldt, Gelhard & Insel, 1988).

In the night monkey (*Aotus trivirgatus*) and titi monkey (*Callicebus moloch*), fathers engage in extensive infant care. Fathers carry offspring on their backs for the fist 4 months, share food and guard offspring against predators, whereas mothers provide milk only.(Wright, 1984). In the titi monkey (*Callicebus moloch*) which is monogamous, the male is the primary carrier of infants and begins to carry infants in the first week of life. Mothers rarely share food with young while the father shares fruit and insects with offspring (Wright, 1984, Mendoza & Mason, 1986).

In both captivity and the wild, male saddleback (*Saguinus fuscicollis*) and cotton-top tamarins (*Saguinus oedipus*) carry infants as often and females (Tardif et al., 1992, Savage et al., 1990, Price, 1990). Vogt (1984) found that during the first two weeks of development, father saddleback tamarins predominate in infant carrying and after two weeks, carrying by males and females does not differ. Lone reproductive pairs of saddleback tamarins that have no helpers have little chance of successfully raising twins (Terborgh & Goldizen, 1985). Epple (1975) found that in seven different multimale groups of cotton-top tamarins, the dominant male carried infants the most frequently followed by mothers and by nonbreeding individuals; mostly juveniles of both sexes. When infant cotton-top tamarins are being harrassed, (other adults and juveniles are behaving aggressively toward the infant), they are usually retrieved by the father. However, when these infants are in no danger, mothers and fathers are equally likely to retrieve them (Tardif et al., 1990).

Heymann (1990) observed that all moustached tamarins (*Saguinus mystax*) in one group carried infants born to the group, but the most carrying was done by adult males and a young adult female while the least carrying was done by two juvenile males and one subadult male. The mother carried the infant an intermediate number of times. Likewise, Grieser (1992) observed that dominant males in two species of sifakas (*Propithecus diadema*, and *P. verreauxi*) carryied the infants that had been born into the group.

In monogamous species of gibbons (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) males show parental investment through territory maintenance and protection of infants. Male gibbons chase male intruders from their territory and females chase female intruders. Adult male gibbons are the principle protectors of the young against humans and other predators and are the more active aggressors in intergroup encounters. Male gibbons do not usually carry their offspring but have been seen to groom neonates, in the wild (Taub & Redican, 1984). Adult male gibbons spend more time than females playing with and grooming the young. The male siamang helps carry infants and is more active in socializing offspring (Robbins Leighton, 1987, Chivers, 1974). The male grooms and sleeps with juveniles while the female sleeps with and grooms infants. The males influence infant survival by engaging in riskier and more energetic defense of their offspring and territory (Robbins Leighton, 1987, Taub & Redican, 1984).

Several lines of evidence suggest that male rhesus macaques (*Macaca mulata*) interact with their own infants, and that males of greatest seniority in the groups are often found sitting next to infants (Smith, 1980, Berenstein et al., 1981). High ranking males intervene in fights on the infants' behalf and provide protection against humans (Vessey & Meikle, 1984). Adult rhesus macaque males have been observed to hold, groom, carry and protect infants (Makwana, 1977, Breuggeman, 1973) while some authors have argued that infant carrying is an example of "agonisitic buffering", in which the male holds the infant close to his ventral side to prevent the dominant male from attacking him (Hill, 1986, Taylor et al., 1978). This is defensive behavior rather than parental behavior. The presence of twins may influence male parental care in rhesus macaques. Twinning occurs at a low rate in rhesus macaques (0.25%) and places great physical demands on the female and the care of twins may induce the male to care for one member of a pair twins (Capitanio & Taub, 1992).

Ransom and Ransom (1971) found that male Olive baboons (*Papio anubis*) babysat, carried, and protected infants. Females left infants beside a male when they went to feed. In another study the resident males protected infants from immigrating males (Packer, 1980). Hamilton et al. (1982) concluded there was a tendency for male chacma baboons (*Papio ursinus*) to care for infants they probably sired. Male chacma baboons rarely carried their own offspring and when they did, it was only for short distances (Hamilton et al., 1982). Baboons seldom shared food items with other individuals including infants. When a concentration of food was available, the dominant males occupied the best foraging space. Since males tolerated the approach of some infants, the infants had an increased access to food. Adult males also opened fruit the juveniles could not and tolerance of proximity allowed juveniles access to this fruit. Males also intensively groomed infants (Altman, 1980). In chacma baboons, preadult males transported orphaned infants that they had adopted (Hamilton et al., 1982). The advantage to the infant was saved energy, although foster parents did not feed infants but, carried or walked with them to foraging places.

Evidence exists that infant carrying by males in baboons is a defense against other males, or an attempt to get close to the mother, rather than parental care. Adult olive male baboons established close proximity to an infant under conditions of stress and carried infants on their ventral or dorsal side when interacting with other males (Ransom & Ransom, 1971). Close contact with an infant inhibited aggression from the other male (agonistic buffering, Ransom & Ransom, 1971, Packer, 1980). Collins (1986) observed that subordinant yellow male baboons (*Papio cynocephalus*) carried infants in triadic interactions with other dominant males. Strum (1984) also found that males with a longer residency and lower social rank most often interacted with infants and used them against short term residents and new immigrants (usually of higher rank). The infant carried was not likely to be the male adult's own offspring, the father was likely to be a high ranking male. Therefore, carrying by subordinant males is a strategy to ward off attack by high ranking males. However, Busse and Hamilton (1981) provided some evidence that infant carrying was a form of parental behavior. They claimed that infanticide was infrequent and resident troop members protected infants from immigrant males.

Kummer (1967) reported that male hamadryas baboons (*Papio hamadryas*) adopted infants. Play groups formed around a subadult or young male who would babysit the infants. Adult males frequently carried infants on their backs while travelling (Redican & Taub, 1984). Male gelada baboons (*Theropithecus gelada*) used infants in the context of agonistic buffering, protection or soliciting support from other members in the group. The type of interaction between adult males and infants was usually restricted to grooming and carrying (Dunbar, 1984).

The most common paternal care among canids is feeding the young (by regurgitation in larger species and by carrying food to the den in smaller ones), defense, and care of the female by provisioning food (Kleiman & Eisenberg, 1973). In the African wild dog (*Lycaon pictus*), males groom pups, carry pups, retrieve pups, provide food, defend against predators, babysit and play with the young (Kleiman & Malcolm, 1981).

Female canids spend more time at the den than do males. The contribution of males and females in provisioning young is variable. In captive wolves (*Canis lupus*, Fentress and Ryon, 1982) and red foxes (*Vulpes vulpes* MacDonald, 1979), males provided twice as much food to the offspring as females. In African wild dogs, the dominant male provided a little more food to the pups than mothers. However, in golden and silver (black) backed jackals (*Canis aureus, Canis mesomelas*), females provided more food to the offspring than males (Malcolm, 1985).

Blandford's foxes (*Vulpes cana*) are monogamous, but males are never observed carrying food to the young. This could be due to the fact that they live on insects and do not regurgitate food to the young. Although, males were never observed provisioning the young or the female, males were observed grooming and accompanying the young (Geffen & Macdonald, 1992).

Male rodents engage in parental care that is direct and shareable, one example of which is keeping pups warm. Male Mongolian gerbils (*Meriones unguiculatus*) were in the nest more than females but both the male and female spent equal amounts of time in contact with the pups. When one parent was outside the nest, the other parent was in the nest so pups were not left unattended for long periods of time (Elwood, 1975, Waring & Perper, 1980). Females, however, built nests, sniffed pups and licked pups more than males and females were more likely to retrieve scattered pups than males (Elwood, 1979, Waring & Perper, 1979). Male and female Mongolian gerbils thus appear to work together to regulate pup temperature (Elwood, 1979).

Hartung and Dewsbury (1979) examined paternal behavior in meadow voles (*Microtus pennsylvanicus*), prairie voles (*M. ochrogaster*), California voles (*M. californicus*), montane voles (*M. montanus*), white-footed mice (*Peromyscus leucopus*) and deer mice (*P. maniculus bairdi*). Parents were observed together with pups and individually with pups (mate removed). In none of these species, was there a significant sex difference in the amount of time spent sitting on the nest in either the paired or single condition. Other measures that were used was the amount of time spent licking pups, retrieving pups, manipulating pups in the nest, and manipulating nest material. Hartung and Dewsbury (1979) concluded that all six species displayed substantial maternal and paternal behavior.

Under laboratory conditions, male prairie voles contributed to pup care as much as the female except for lactation (Thomas & Birney, 1979; Getz, Carter & Gavish, 1981). Father's built nests, groomed pups, retrieved pups and brooded the young (Thomas & Birney, 1979). Fathers also protected pups from predation by shrews (Getz & Snarski, 1992).

Gruder-Adams and Getz (1985) found no evidence that male meadow voles housed in large open pens contributed to nest building or pup care. Male prairie voles were, however, found with the pups in the natal nest. One member of the pair was always in the nest with the young. Hartung and Dewsbury (1979) may have observed pup contact in male meadow voles due to the limited space and lack of cover in the cages. When meadow voles were given adequate space in a lab setting, males contacted pups infrequently (Oliveras & Novak, 1986). Hartung and Dewsbury (1979) also reported that male and female montane voles both spent a considerable amount of time in the nest with the pups and males were observed to lick pups and manipulate pups in the nest. When placed in large pens, however, members of each pair occupied separate nests and males never interacted with offspring. (McGuire & Novak, 1986). Thus small changes in housing may have promoted or forced paternal behavior in these two species.

Meadow voles (*Microtus pennsylvanicus*) were observed in an enclosure for a minimum of 48 hours over the first 10 days postpartum. When fathers were housed with mothers and no other adults were present, fathers spent much of the observation time within the nest. Fathers also prevented unfamiliar males from entering the nest when the mother was removed (Storey, Bradbury & Joyce, 1994).

The main type of paternal care displayed by adult male spiny mice (*Acomys cahirinus*) is huddling with the pups. Males spent equal amounts of time huddling with the pups between 2 and 4 days of age regardless of whether the female was present. After 4 days of age, when the female was absent, males spent more time huddling with the pups than when the female was present. Coordination of pup attendance may be important under natural conditions when females are absent for long periods of time due to foraging (Makin & Porter, 1984).

McCarty and Southwick (1977) compared the patterns of paternal and maternal care in the southern grasshopper mouse (*Onychomys torridus*) and the white-footed mouse (*Peromyscus leucopus*). They found that mothers spent more time in the nest with the young than fathers in both species. However, male southern grasshopper mice spent more time in the nest than male white-footed mice. In addition, when *Peromyscus leucopus* were housed in large enclosures instead of laboratory cages, no direct or indirect paternal behavior was observed (Xia & Millar, 1987). Horner (1961) and Horner and Taylor (1968) found that in grasshopper mice, the male was excluded from the nest immediately after the birth of the pups, but when he was allowed to return, he huddled with the pups, groomed pups and retrieved pups back to the nest.

There is evidence to suggest that grasshopper mice are monogamous under natural conditions (Horner & Taylor, 1968, Dewbsury & Janzen, 1972). Duvall, Scudder, Southwick and Schultz (1982) found that if the male (*Onychomys torridus*) was removed from his mate and the litter, then maternal pup licking significantly declined. However, if isolated dams with pups were exposed to the father's urine, then maternal pup licking increased to previous levels. Male *P. m. nubiterrae* (deer mice) exhibit more paternal behavior than male *P. leucopus*. *P.m. nubiterrae* retrieved pups, nested with the female and the pups and formed longer associations with females than *P.leucopus* males (Wolff & Cicirello, 1991).

Male *Mus musculus* were never observed retrieving pups and rarely groomed them when they were housed with virgin females and mothers. They were also observed to attack, chase and mount mothers and virgin females, which resulted in pups being scattered and left unattended. However, if males were housed individually with one pup, they retrieved the pup within 5 minutes, and 24 hours later built nests and assumed the nursing position over the pup (Gandelman et al., 1970).

The composition of the litter influences maternal and paternal behavior and offspring growth in wild *Mus musculus* (Mendl & Paul, 1990). Mothers that had litters composed of three female and one male pup (MF group) spent more time engaged in maternal care (nursing, nestbuilding, grooming and carrying pups) up to weaning, while mothers of all male litters (MM group) spent more time lying with their pups without nursing them after weaning (indicating earlier independence from the mother than in the MF group). Despite increased levels of maternal care and delayed weaning in the MF group, pups in these litters were lighter at weaning that litters of all males (MM group). MM fathers were observed to engage in more paternal behavior (nest building, grooming pups and carrying pups) than MF fathers (Mendl & Paul, 1990).

Male California mice (*Peromyscus californicus*) displayed as much parental behavior as females (except for nursing) and spent comparable amounts of time in the nest (Ribble & Salvioni, 1990, Dudley, 1974, Gubernick & Alberts, 1987). Both male and female parents licked the anogenital area of pups to stimulate reflexive urination. Both parents consumed the urine to conserve water and salt (Gubernick & Alberts, 1987). Fathers were rarely excluded from the nest and new fathers sniffed and licked pups at birth. Mothers nurse for at least 4 weeks and fathers and mothers both carry young and build nests (Gubernick & Alberts, 1987). Males and females also defended a common territory (Ribble & Salvioni, 1990).

Domestic *Mus musculus* males have been observed to provide the same amount and type of parental care as females, except for nursing. The most common paternal behaviors are licking pups, huddling over pups, retrieving pups and nest building (Priestnall & Young, 1978, Jakubowski & Terkel, 1982, Wuensch & Cooper, 1981, Ostermeyer & Elwood, 1983, Barnett & Dickson, 1985, Dewsbury, 1985). Males also defended a territory against other intruding males (Hurst, 1990).

Male captive collared lemmings (*Dicrostonyx richardsoni*) diplayed as much parental behavior toward their pups as females in the lab but not under natural conditions. Shilton and Brooks (1989) concluded that the paternal care shown in collarded lemmings was either an artifact of the lab setting or that it had its effects through factors that were not studied such as the protection of offspring from infanticide. Male arctic ground squirrels (*Spermophilus parryii*) may invest indirectly in their offspring as male territorial behavior protects the offspring when they are vulnerable to attacks from conspecifics (McLean, 1983). Males acted as lookouts when females were feeding and if the resident male was removed, immigrant males killed the pups.

1.2 D. Inhibition of infanticide

In order for parental behavior to occur, infanticide must be inhibited. Infanticide is a reproductive strategy that increases male and female reproductive success by ensuring that they do not invest in offspring that are not their own. This assumes that males and females have some mechanism to determine if pups are their own, so they will not kill their own offspring (vom Saal & Howard, 1982). In white-footed mice (*Peromyscus leucopus*), house mice and gerbils, both males and females kill strange pups (Cicirello & Wolff, 1990, Elwood, 1979, Jakubowski & Terkel, 1982, Perrigo et al., 1993). Some of the possible cues to indicate whether the male sired the current litter are copulation with the female, cohabitation with the female, cues from the pups (phenotype or odor), parental experience or neural timing (Perrigo et al., 1993). Perrigo et al. (1993) suggested that male mice were sensitive to the amount of time that elapsed between mating with the female and the arrival of the pups.

Male gerbils (*Meriones unguiculatus*) housed in monogamous pairs displayed more parental than infanticidal behavior toward both gerbil and mouse pups when their mates were in the final 6 days of pregnancy. However, after the male gerbils had experience with their own litter, they attacked more mouse pups than unfamiliar gerbil pups (Elwood & Ostermeyer, 1986) which suggested that copulation and cohabitation with their mate inhibited infanticide. Male mice (*Mus musculus*) were more paternal (measured by amount of time males spent, sniffing, licking, and retrieving pups or nest building) toward strange mouse pups than toward gerbil pups when tested prior to the birth and after the birth of their first litter. Experience with their own litter did not change how male mice responded to strange mouse and gerbil pups (Elwood & Ostermeyer, 1986). Copulation and cohabitation with a female inhibited infanticide in *Mus musculus* males regardless of whether the pup is a gerbil or a mouse although their response is more paternal when presented with a mouse pup (Elwood & Ostermeyer, 1986).

Sororker and Terkel (1988) documented the change from infanticidal to parental behavior in wild *Mus musculus* . They noted that similar numbers of males and females showed parental behavior toward alien pups. Toward the end of the gestation period, breeding females killed alien pups while the majority of their male partners were either parental or ignored alien pups. During lactation, both males and females behaved parentally toward their own and unrelated pups. A month after weaning, all females were infanticidal toward alien pups while only half of the males were infanticdal toward alien pups (Sororker & Terkel, 1988). Both copulation and cohabitation with their pregnant mate were necessary to inhibit infanticide in male mice.

Cicirello and Wolff (1990) found that cohabitation with the female did not inhibit infanticide in male white-footed mice, but both cohabitation and copulation did inhibit infanticide. Males and females were not capable of distinguishing between familiar and unfamiliar pups. Wolff and Cicirello (1989) found that neither males nor females used familiar nest odor cues to distinguish between related and unrelated pups. McCarthy and vom Saal (1986) found that cohabitation without successful mating did not inhibit infanticide in wild male house mice. When males were placed with lactating females, infanticidal males produced their own litter faster (by killing the female's current litter) than noninfanticidal males. The results of McCarthy and vom Saal's (1986) experiment suggest that infanticide is a strategy to increase the male's reproductive success and can be an adaptive trait.

Labov (1980) found that both cohabitation and copulation were not necessary to reduce infanticidal behavior in wild male house mice (*Mus musculus*). Male house mice that copulated with females before cohabitation, reduced their infanticidal behavior. There also was no difference in the number of pups killed between males that copulated and cohabitated with their mates and males that only cohabitated with their mates. So either factor alone reduced infanticidal behavior. He also found that pup phenotype (wild vs. albino) had no effect on infanticidal behavior.

Copulation and cohabitation were necessary for the inhibition of infanticide in male *Mus musculus* since being housed with a female for just one day after mating significantly reduced infanticidal behavior (Elwood, 1985). Brooks and Schwarzkopf (1983) and Huck et al. (1982) confirmed that copulation and cohabitation were necessary for the inhibition of infanticide in male *Mus musculus*. Huck et al. (1982) found that males killed their own pups if they were placed in the nest of a strange female while most males did not kill unrelated pups if they were in the nest of a familiar female. Familiarity with the female and not individual pup recognition seemed to be the important factor for the inhibition of infanticide in male *Mus musculus*. Therefore, male mice inhibit infanticidal behavior after copulation with the female, while female mice remain infanticidal up to the time of the birth of their own litter (Elwood, 1977, Sororker & Terkel, 1988, Elwood & Kennedy, 1991).

Sex, reproductive maturity and parental experience influence the behavior of Siberian hamsters toward strange pups. For inexperienced animals, mature males attacked pups more often than immature males, immature females or mature females. Parental experience significantly decreased attacks on pups by males and females. Parental experience increased the amount of time females spent carrying and nesting with pups (Gibber et al., 1984). Virgin male and female wood mice (*Apodemus sylvaticus*) also were infanticidal. In wood mice, copulation with the female may inhibit male infanticidal behavior as males housed with perforate females are less infanticidal (Wilson et al., 1993).

Perrigo et al. (1990, 1991) have determined that the change in male behavior in CF-1 house mice from infanticidal to parental behavior was influenced by the number of light:dark cycles experienced by the male following copulation. Pup killing did not stop until many days after mating but nearly always before his own pups were born (about 3 weeks). Males became parental around the same time that infanticidal behavior disappeared, and infanticide spontaneously reemerged after the offspring had been weaned. (vom Saal, 1984). These timed behavioral changes that were initiated by ejaculation occurred in different house mouse strains (Kennedy &

Elwood, 1988, McCarthy & vom Saal, 1986). In virgin CF-1 male mice, approximately 50% of the males were infanticidal when they encountered a pup while 50% were parental (retrieved the pup or licked the pup). Mating, particularly ejaculation, provides the stimulus that causes most males to become infanticidal. Yet 3 weeks later, when the male's offspring are born, the male becomes parental (Perrigo et al., 1989).

Perrigo et al. (1990, 1992) investigated what the neural timing mechanism is that gauges the passage of time, between ejaculation and birth of the pups. In one experiment, male CF-1 mice were entrained to a 22 h (L:D 11:11) or 27 h (L:D 13.5:13.5) daylength. Twenty days after mating, males in the 22 hour day groups ceased killing pups while most of the males in the 27 hour day groups killed pups. Males in the 22 h day group experienced 4 more light:dark cycles after mating than those in the 27 h day group. Since the transition from infanticidal to parental behavior coincided with the number of light:dark cycles experienced, instead of real time, it was suggested that a photoperiodic timing mechanism was coupled with ejaculation (Perrigo et al., 1990).

The behavior of males toward pups also was examined when males were housed under constant light or constant dark conditions. In males that displayed parental behavior or ignored pups when pretested as virgins, a light:dark cycle of 12:12 and constant light accelerated inhibition of infanticide and the emergence of parental behavior. The transition to parental behavior was prolonged under conditions of constant dark. In males that were infanticidal when pretested as virgins, parental behavior was not accelerated in any of the lighting conditions. However, these males were parental when their own litter was born. So while light accelerated parental behavior in virgin males that were originally parental or noninfanticidal, all males became parental by the time their pups arrived, even under conditions of total darkness (Perrigo et al., 1991).

Female mice also were infanticidal just after being mated and up until the time parturition (Jakubowski & Terkel, 1982, McCarthy & vomSaal, 1985). However, female mice rely on cues from the developing fetuses and do not use photoperiodic cues to determine the length of gestation (Lanman & Seidman, 1977). Females that had been entrained to light:dark cycles that mimiced a 20 or 28 hour day, still gave birth the same absolute number of days after insemination (Davis & Menaker, 1981). Male mice seem to have evolved a time keeping mechanism to gauge when infanticidal behavior should cease and parental behavior should begin (Perrigo, 1990).

The onset of parental behavior and inhibition of infanticide varies among male California mice (*Peromyscus californicus*) that have similar social and sexual experience. The majority of males became parental only after their own young had been born, and contact with their mate was necessary to maintain paternal behavior. However, a minority of males became parental before the birth of their own young, after only 24 hours of postcopulatory cohabitation with the female and did not require contact with the female to maintain paternal behavior (Gubernick, Schneider & Jeannotte, 1994). In this experiment, disruption of the pair bond influenced paternal behavior only if the onset of paternal behavior had not been induced by copulation and cohabitation with the female. Otherwise, the mothers presence was necessary to prevent male infanticidal behavior.

In species which exhibit male parental behavior, the type and amount of parental care varies greatly. These differences raise several questions as to what evolutionary and environmental factors influence paternal care. Some of the possible factors are the social and mating systems that have evolved in different species (section 1.4). Male parental behavior may also vary as a result of housing conditions, whether the species is housed in a laboratory cage, large pen or under natural conditions (chapter 3). This thesis will explore these questions as well as theories on how paternal behavior evolved in fish, birds and mammals (section 1.3) and how male parental care benefits the young (section 1.5).

1.3 The evolution of paternal investment

There are three general theories used to study the evolution of parental invesment. These include theories: a) based on general principles of evolutionary theory, b) those that examine sex differences in parental investment and c) those that rely on correlational analyses and taxonomy.

1.3 A. Theories based on general evolutionary principles

Trivers's (1972) and Maynard Smith's (1977, 1982) theories of parental investment are based on general evolutionary principles. Trivers (1972) argues that females should be the main care givers as ova require more investment to produce than sperm. Anisogamous sexual reproduction involves the parasitism of large eggs by small sperm. Females produce a few large gametes (eggs) and males produce many small ones (sperm). Males can potentially fertilize eggs at a faster rate than females can produce them, so females become a scarce resource for which males compete. Males increase their reproductive success by finding and fertilizing many different females, while females increase their reproductive success by converting food to eggs or offspring at a faster rate (Daly & Wilson, 1983).

Both males and females are selected for producing the number of offspring that results in maximal reproductive success, which is measured by determining the difference between the number of offspring produced (benefit) and the decrease in future reproductive potential due to present offspring (cost, Trivers, 1972). In mammals, the female invests more in each offspring than the male due to her investment during gestation and lactation. Therefore, the cost of parental investment increases more rapidly for females for each additional offspring than for males. Since male cost per offspring increases less rapidly than female cost per offspring, males are selected to produce more offspring than females. Due to lower costs to males, they seek additional matings. If the costs of additional offspring are lower for females than males, then females would seek additional matings and compete for access to males. Trivers (1972) argues that the high initial investment in offspring by females predisposes females to care for offspring. The result is greater variance in reproductive success among males than among females. Some males will be successful in inseminating many females and some males wil be unsuccessful, while almost all females will be mated. There also is greater competition among males than among females for access to mates resulting in more elaborate courtship displays and risky behavior among the sex that invests less in the offspring (Barash, 1980).

Trivers's theory of parental investment and the calculation of the costs and benefits of parental investment for each parent has stimulated considerable discussion. Dawkins and Carlisle (1976) pointed out that the failure of infants to survive and reach breeding age due to the lack of parental investment selected against both sexes. According to these authors, the deserted female would continue to raise offspring not because her larger past investment commited her to providing care, but because providing investment in partially developed offspring resulted in a greater benefit in terms of reproductive fitness than deserting the young, finding a new mate and investing in new offspring.

Maynard Smith (1977, 1982) used game theory to specify the conditions under which uniparental male care, uniparental female care, biparental care or no parental care were likely to be maintained within a population once parental care (or no parental care) had been established. Whether a male or female will care for the offspring or desert the offspring depends on the strategy that the majority of other individuals of the same sex in the population adopt. The first assumption of his model is that reproduction is confined to discrete breeding seasons. The second assumption is that reproductive success depends on the female's large initial investment in the production of eggs and on investment by males and females after fertilization. Finally, the third assumption is that, a female that invests substantially in her eggs does not have enough energy left to invest heavily in guarding her eggs.

Three probabilities for egg survival are defined by this model: the number of eggs that would survive if left unguarded, the number of eggs that would survive if guarded by one parent, and the number of eggs that would survive if guarded by two parents. The model specifies that the number of eggs that survives if guarded by two parents is greater than or equal to the number of eggs that survive if guarded by one parent, which is greater or equal to the number of eggs that survive if left unguarded. For females, the main variable that determines reproductive success or failure is the number of eggs laid that survive under different levels of parental care and the ability to lay more eggs in the future. For males, the main variable that determines reproductive success or failure is their ability to inseminate other females. However, males must take into account the ability of the eggs of the first female to survive under different levels of parental care.

There are four possible evolutionary stable strategies (ESSs) that arise from the model; no parental care, female only parental care, male only parental care, and biparental care. All ESS's have separate consequences for males and females. An ESS is defined as "one of a specified set of behavioral (or other phenotypic) options that, if adopted by a sufficient number of individuals in the population, cannot be superseded by any other available strategy. Evolutionarily stable strategies become relevant to behavior when the fitness return from an act depends on what others in the population are doing" (Barash, 1980, p. 391). If biparental care increases the survival of offspring over uniparental care and mate desertion does not result in increased matings, then both parents would be expected to care for the offspring. If the absence of parental care does not result in fewer offspring than uniparental care then both males and females would desert the young and no parental care would be provided. If uniparental care results in more young surviving than the absence of parental care but survival of the young is the same as biparental care, then one parent would remain with the eggs. The male will desert the female and young, if he can easily remate whereas the male will stay, if opportunities to remate are remote. The female will stay to care for the young if it does not use valuable resources that can be allocated to additional eggs, otherwise she will desert the young (Maynard Smith, 1980).

A mate desertion model developed by Grafen and Sibly (1978), based on Maynard Smith's model, also assumes that the species have a uniform breeding season, a stable population and an equal adult population sex ratio. They make the additional assumption that the benefit of parental investment (defined as the number of offspring that survive to breed) depends on the amount of time that each parent stays with the offspring before deserting. The expected benefit, depends on the current state of development of the brood and on whether the male or female has already deserted. For example, if two single females raised broods alone and both broods had reached the same stage of development, then both females were equally capable of providing care. According to the model, this assumption is valid, even if for one female, the male deserted after egg laying and it took longer for the offspring to reach this stage of development while for the other female her mate deserted later and her offspring reached this stage of development sooner. Other variables that would determine the probability of mate desertion are the population sex ratio (which affects the opportunity to remate) and the ability of each parent to contribute to the survival of the offspring (if a male parent could contribute little to offspring survival then he would be selected to desert the offspring). One of Grafen and Sibly's predictions is that if both sexes provide parental care that benefits the offspring and two parents raise more offspring to maturity, then only when sex ratios are extremely biased (i.e. there are more females than males in the population available to breed), will the male parent desert the young. Their model indicates that these variables could influence which parent remains to care for the young or deserts the young after parental behavior had evolved.

One variable which can influence whether males show parental care or desert is paternity certainty. Paternity certainty refers to the probability that the male sires the offspring that he will potentially care for. Males that display parental care should ensure that they sired the offspring as energy placed in a current litter is not available for courting and remating with other females (Barash, 1980). Whenever an individual increases its reproductive success through parental behavior, the energy available to increase reproductive success through mating effort (competing with other males for access to more females) decreases (Kurland & Gaul, 1984). Therefore, a male should be reluctant to invest in offspring if he is unsure if he is the father (Trivers, 1985).

Maynard Smith (1977) asserted that paternity certainty was not a factor that determined whether a male exhibited parental care because he would be as uncertain of his paternity with a current brood as a later brood. Maynard Smith argued that certainty of paternity may have an indirect effect on the distribution of paternal care among species. Those species where the opportunity for males to remate was high would be selected to desert the offspring and would have a lower certainty of paternity, whereas in those species where there was little opportunity for males to remate, males would remain to care for young and have a higher certainty of paternity.

Zeh and Smith (1985) revised Maynard Smith's model to include certainty of parentage for both males and females. Certainty of parentage did not have a direct effect on the model's predictions as to which species should be selected for caring or for deserting the young because certainty of parentage was the same for individuals that cared for offspring and for those that deserted offspring. However, Zeh and Smith (1985) suggested that certainty of parentage could have an indirect effect on the selection for caring or deserting offspring, if caring for offspring increased a male's certainty of paternity. They provided evidence from arthropods to suggest how paternity certainty increased as paternal care increased. Xia (1992) indicated in his model (using the perspective of fitness costs to a paternal gene versus a deserting gene) that uncertainty of paternity could select against paternal care, although this factor may have a minor influence in large populations.

The above models indicate that males, females or both parents may be selected to show parental care. Which parent acts parentally is determined by the amount they have invested in the offspring, the probability of gaining future matings and the likelihood of the young surviving to breed in the absence of any parental care. Whether or not a male shows paternal care may depend on the number of potential mates in the population and his certainty of paternity. The more uncertain a male is about his paternity, the more likely he will desert and attempt to remate. However, male parental care can increase paternity certainty, as males are in close association with females, and prevent intruding males from contacting females and offspring on his territory. This not only prevents females on his territory from remating but also indirectly protects offspring from intruding males (Zeh & Smith, 1985).

Differences in the mode of reproduction, ecology and mating systems are variables used in models of parental investment. This has resulted in separate models of parental investment for arthropods, fish, birds and mammals. In most of these models, however, maximal reproductive success in females is limited by the number of eggs they can produce and maximal reproductive success in males is limited by the number of additional matings they can obtain. As male parental care increases, opportunities to obtain additional mates decreases. Thus the main cost to males of parental investment is the reduction in the number of new offspring he can sire.

1.3 B. The evolution of sex differences in parental investment

Maynard Smith's model (1977) explains how parental investment is maintained after it has evolved, but it does not explain how parental investment originally became established in a population. Zeh and Smith (1985) suggest that male parental care may have evolved in arthropods as a result of increased paternity certainty. A male may have originally maintained a territory and nest site and excluded other males from his territory. Patrolling a territory would decrease the number of females that the male had access to, but he would copulate with all females that used his territory. By preventing other males from entering his territory and blocking the entrance of larval parasites into the nest, the male inadvertently invested in his offspring. A male that adopted a "patrolling" strategy, by mating with females outside his territory, theoretically would be less successful and would be one of several males that would contribute to fertilizing a female's eggs. Therefore, male parental care could evolve from a strategy that originally increased paternity certainty (Zeh & Smith, 1985).

Van Rhijn (1984) used Maynard Smith's ESS theory to argue that the most likely pathway for the evolution of parental investment in birds is from no parental care to male only care. He then supports this theoretical argument with evidence from shorebirds (Van Rhijn, 1990) and computer models (Van Rhijn, 1991). He suggests that the evolution of male parental care in vertebrates with internal fertilization is preceded by a stage in which the male benefits by remaining with the female after copulation.

Van Rhijn (1990) argues that the origin of parental care in birds is related to body temperature and the necessity of regulating egg temperature. Assuming a stage without prolonged parental care after egg laying as in reptiles, Van Rhijn (1991) suggests that parental care would become established if those individuals that incubate their eggs rear more offspring than those that abandon their eggs.

Parental care could have originated in three ways from an ancestor that provided no parental care. First, both parents could have simultaneously evolved the ability to care for offspring. Van Rhijn (1991) argues that this is unlikely as females must be present at egg laying but males need not be present (Maynard Smith, 1977). It also is difficult to envision how the aid of a second parent would further increase the number of surviving young over one parent, especially if the young are adapted to survive with no parental care. There also is evidence in fish that care by one parent preceded biparental care (Gittleman, 1981, see section 1.3C).

The second possibility is that females evolved the ability to care for offspring before males. This is plausible since females must be present when the eggs are laid. Care by the female alone would evolve if the time she spent on parental investment resulted in the survival of more offspring than the same time invested in extra egg laying or increased egg size (increased yolk). However, female birds allocate a great deal of reproductive effort to the production of eggs and ancestral birds may have put more energy into eggs than do present species. It is possible that the extra investment in egg care after the eggs are laid would lead to a decreased investment in egg size and lead to fewer surviving offspring.

The third option is that males evolved the ability to care for offspring. This could occur if there was a reason for the male to stay near the female after copulation and remain with her until after she laid her eggs. If females copulated with several males before laying a single clutch of eggs, then there would be an advantage for the male to stay and guard his eggs as he would be protecting his investment in future offspring. Van Rhijn (1991) used computer simulations to study the costs and benefits of post-copulatory mate guarding by males. Guarding was promoted by asynchrony in fertility of females, high copulation frequencies of females, preference of females for males using the guarding strategy and mate fidelity of guarded females. The simulations suggest that mate guarding is an intermediate step between no parental care and male only parental care in birds. Van Rhijn (1991) also proposes that male only parental care is the primitive state in birds, since it can evolve easily toward all known mating systems in birds.

Wesolowski (1994) used a comparative approach to discuss the evolution of parental behavior in birds. Since birds are descendants of reptiles and most reptiles display no parental care, it is assumed that avian parental care is derived from an ancestral state of no parental care. This model assumed that birds also went through an initial stage of no parental care and females spent their energy on larger eggs. If females remained to guard and incubate the eggs, they would do so at a great cost to their future fecundity, whereas if males remained to guard and incubate eggs, they would do so at a after the eggs are laid would lead to a decreased investment in egg size and lead to fewer surviving offspring.

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1.3 C. Theories based on correlational analyses and taxonomy

The third type of model of parental investment examines the evolution of parental care by determining which species are evolutionarily the most primitive and which are the most recent, determining how often different types of parental care have evolved in various species, and establishing how widespread each parental care pattern is. These models have been developed using fish and bird species to test their predictions.

Gittleman (1981), for example, assumed that when one species within a genus or family exhibited a different pattern of parental care from others, then common ancestors must have existed which were characterized by transitional states. A transitional state is defined as the existence of at least two types of parental care in a genus or family. His review suggested that in fish, these transitions followed a pattern from no parental care to male parental care, male parental care to biparental care, biparental care to female care and female care to no parental care.

After reviewing the literature on mating systems in birds, Emlen and Oring (1977) concluded that the evolution of biparental care was the first transition from no parental care. The phylogenetic analysis of 60 taxa using parental care data in combination with anatomical data indicated that biparental care was primitive for birds. They also concluded that biparental incubation arose from an ancestral condition in which neither parent incubated the eggs.

Silver et al. (1985) used canonical correlation analysis to determine the influence of ecological and life history correlates on male involvement in five parental behaviors in birds. The five male parental behaviors examined were: feeding the female during courtship and feeding the female on the nest, nest building, incubating the eggs, feeding the young and escorting the young. From their analysis, four significant dimensions were found that accounted for 38% of the variability in the five paternal behaviors. Although this left 62% of the variance unaccounted for, Silver et al. noted that this was twice as much of the total variance accounted for as other analyses conducted on simulated rather than actual data. Silver et al. suggested that the unaccounted variance could be due to such factors as one or more important predictor variables not being identified and subsequently not being included in the analysis or an error component based on collecting material from many researchers that may have used different criteria for such things as the absence or presence of behaviors or in classifying mating systems.

The first dimension identified by Silver et al. (1985) as influencing whether or not males would show parental behavior is the developmental mode of the young. In species with precocial young, the male incubates the eggs and escorts the young. In those with altricial young, the male feeds his mate and young but does not incubate or escort the young. As the energy needs of the young increase, the male's nonshareable parental investment increases. As the number of young increase, his ability to provide adequately for all of them decreases (Wittenberger, 1981). A monogamous mating system is also correlated with the male feeding both the young and his mate. The male's parental sharable activities such as incubation and escorting mobile young are also associated with a monogamous mating system.

The second dimension arising from Silver et al.'s analysis indicates that there is a positive correlation between having precocial young and feeding on easily obtainable food such as seeds, vegetation and insect larvae. For example, seabirds which are specialized to feed on fish (difficult to obtain) have altricial or semi-precocial young (Ricklefs, 1983).

The third dimension of male parental behavior indicates that species with polygynous or lek polygynous mating systems, do not build nests, incubate the eggs or feed the young. The fourth dimension indicates that species in which females lay large clutches or clutches that are large in relation to the female's body weight, have mates that feed the female prior to egg laying and during incubation but the male does not feed the young. This correlational analysis reveals that biparental care is prevalent in bird species believed to be primitive. If the idea that a character which is taxonomically more widespread is likely to have evolved first is accepted, then biparental care may have evolved first in Aves and allowed for the altricial mode of development.

McKitrick (1992) takes the historical approach in an attempt to determine what type of parental care is most primitive in birds. Instead of examining how many genera or families displayed the trait, she examined several species from the same taxonomic family and determined the number of times a particular type of parental behavior arose. Thus she determined whether the trait arose once or many times and the pattern of origin and loss. She used hindlimb musculature (69 characters) to determine ancestry and correlated parental behavior (15 characters) with hindlimb musculature to determine patterns of parental care exhibited by ancestral birds. These two factors were analysed using a PAUP (Phylogenetic Analysis Using Parsimony) program which generated phylogenetic trees. From these phylogenetic trees it was possible to determine how many times a trait arose, in which lineages it arose and the pattern of origin and loss of these traits. For example, it was possible to determine the pattern of origin and loss of male-only care of the young. The results of the analysis of morphology and behavior were very similar to the analysis of morphology alone which suggested that neither data set was biasing the results. It was hypothesized from the trees generated that some form of biparental care (defense of young) was the primitive state for birds.

The theories discussed in this section were based on correlational analyses and taxonomy. They attempted to determine which type of parental behavior was anscestral for fish and birds or determine what developmental and social factors influenced male parental care in birds. These models attempted to explain the evolution of parental care, determined that male parental care arose from no care in fish and biparental care arose from no care in birds. Theories that refer to the evolution of parental behavior, highlight the difficulty of hypothesizing about which pattern of parental care was anscestral. In addition, theories based on the evolution of sex differences in parental investment (section 1.3 B) indicated that male parental care arose from no parental care which conflicts with the predictions derived from theories based on taxonomy and correlational analyses.

1.4 Correlation of male parental behavior with species social organization and mating system

Male parental investment is correlated with certain patterns of social behavior, such as territoriality, paternity certainty and mating systems, and these factors interact with each other and environmental contraints such as food abundance and availability of other mates to determine the amount of parental care shown by males to their offspring.

1.4 A. Parental care and territoriality

The association between male parental care and territoriality has been most extensively studied in fish (Gross & Sargent, 1985), but has also been examined in birds and mammals (Van Rhijn, 1990, Wesolowski, 1994, 1991, Klein, 1977). In fish, good spawning sites in fresh and inshore waters heavily influence egg survival (Baylis, 1981, Johannes, 1978, Perrone & Zaret, 1979). Good spawning sites are limited leading to an aggregation of males defending optimal spawning sites to attract females. Since males begin their courtship by defending a territory, it would not be energetically expensive to continue guarding a territory after the eggs are deposited on it (Gross & Sargent, 1985).

The cost of paternal care to a male fish is measured in terms of the decreased number of spawnings that he can achieve during a breeding season. This cost can be reduced by displaying territorial behavior rather than engaging in a promiscuous mating system in which males follow females to obtain matings. Therefore, several males may fertilize the eggs of one female and in such a promiscuous mating system, parental care is not advantageous to the male since the gain in terms of benefit to his own offspring would be small and the mating cost would be high. In a strictly territorial system, however, all the male's spawning would occur on his own territory. Territoriality thus reduces the male's mating cost since females are attracted to a good territory and males need not follow females.

Barlow (1962) first suggested that male parental care evolved from no care because males exhibited territorial behavior and maintained a territory after spawning, which would result in overlapping broods. Another prerequisite is that demersal eggs did not disperse out of the territory (Baylis, 1981). Baylis (1978, 1981) suggests the following sequence of events would lead to male parental behavior. Beginning with a fish that scatters demersal eggs, some eggs may have survived better than others in certain areas on the ocean floor and this differential survival would lead fish to prefer certain spawning sites. If these preferred sites are more rare than potential mates, then there would be selection for defending the site. Defense of the nest site from conspecifics would be necesary to monopolize the site and the site could be made more attractive to females through modification of the site. This modification could become the basis for nest building and the need for a good site to spawn would favor territoriality.

The peacock wrasse (*Symphodus tinca*) is an example of a territorial fish which can show several intermediate stages between no parental care and parental care, but defending one nesting site does not seem to be necessary for males to engage in parental behavior (van den Berghe, 1990). A small percentage of males went through transitional stages from no parental care to full care as the season progressed. These stages consisted of 1) out of nest spawning (no parental care), 2) following females over large areas, 3) focusing on an area and chasing other fish from the area, 4) focusing spawns into a small area that has been modified by collecting algae, and 5) remaining at the site until eggs hatch and young disperse. In this species, suitable spawning sites were not limited, which did not support the suggestion that a shortage of spawning sites was a prerequisite for spawning on a territory.

An association between territoriality and male parental care also exists for some birds and mammals. Male red-winged blackbirds (*Agelaius phoeniceus*) defend a territory and the males feed nestlings of their primary and secondary females who have nested on this territory. The reproductive success of females is enhanced by the male assisting in feeding offspring (Muldal, Moffat & Roberston, 1986, Beletsky & Orians, 1990). In the spotted sandpiper (*Arctitis macularia*), the female lays one clutch which the male incubates and then a second or third clutch which another male or the female herself incubates (Oring & Knudsen 1972). The females which probably are territorial, cooperate only with the last male in rearing the brood. Jacana (*Jacana spinosa*) males defend small territories from each other within the female's territory. The male builds the nest, incubates the eggs and rears the young (Jenni, 1974).

In primates, both male gibbons (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) display parental investment through maintaining a territory and protectiing infants. These two species are monogamous. Male gibbons chased male intruders from their territory and females chased female intruders. Adult males were the principle protectors against humans and other predators and were the more active aggressors in intergroup encounters (Leighton, 1987, Chivers, 1974).

Male territorial behavior in arctic ground squirrels (*Spermophilus parryii*) may be an investment in their offspring as it protects the offspring when they are vulnerable (McLean, 1983). Males act as lookouts when females are feeding and if the resident male is removed, immigrant males kill the pups. White-footed mice (*Peromyscus leucopus novevoracensis*) and deermice (*P. maniculatus nubiterrae*) exhibit paternal behavior and maintain territories (Wolff & Cicirello, 1991). Field studies also indicate that male and female prairie voles and California mice share a nest, defend a common territory and display paternal behavior (Getz et al., 1981, Getz et al., 1987, Gubernick & Alberts, 1987, Ribble & Salvioni, 1990).

1.4 B. Relationship between external fertilization, paternity certainty and patterns of parental care in fish

In 89% of fish families, fertilization is external while in 11% fertilization is internal. Male parental care is correlated with external fertilization while female parental care is correlated with internal fertilization. Approximately 76% of parental care is provided by the male in external fertilizing species, while 86% of parental care is provided by the female in internal fertilizing species. Male parental care is found in only 3 families with internal fertilization (Gross & Shine, 1981).

If sex differences in parental care evolved due to differences in opportunities to be near offspring following fertilization, then several predictions can be made. For example, if oviposition in a male's territory is a preadaptation for the evolution of male parental care, then male parental care should be more common among territorial males than nonterritorial males. This prediction is upheld within teleosts (bony fish) but does not explain why some territorial males are not parental. For species with internal fertilization whose eggs are deposited immediately after fertilization, there is a potential association between the male and his offspring. Therefore, male parental care should occur just as often in oviparous internal fertilizers and oviparous external fertilizers but there is a correlation between internal fertilization and female parental care. Once internal fertilization has developed in a species, little restructuring is needed to increase the length of embryo retention in females, a common pattern in internal fertilizing teleosts and amphibians. This creates a long association between the female and her offspring, increasing the likelihood of female parental care. The prediction that internal fertilization followed by immediate egg release, should result in the same amount of female parental care as external fertilization, has received some support (Gross & Shine, 1981). This last prediction is based on the fact that the female is in association with the embryos about the same amount of time.

Another hypothesis which attempts to explain the relationship between external fertilization and male parental care is referred to as the "Gamete Order" hypothesis. The "Gamete Order" hypothesis is based on the assumption that the sex that spawns first has a better opportunity to desert the eggs (Gross & Shine, 1981). This hypothesis assumes that in external fertilizers, females are the first to release gametes and could thus easily desert the eggs. If females deserts their eggs, this leaves the males to make the choice of caring for the offspring or deserting them (Dawkins & Carlisle, 1976). Based on this argument, female parental care evolved in internally fertilizing species since the female could not abandon the offspring before the male. One problem with this hypothesis, is that gamete release is usually synchronous in fish and female-first is the second most common pattern of gamete release. The gamete order hypothesis predicts that when gametes are released synchronously, the occurrence of male and female parental care should be of equal probability. But there is a predominance of male parental care in species with synchronous gamete release (Gross & Shine, 1981, Gross & Sargent, 1985). The second prediction from the gamete order hypothesis is that male parental care could not evolve if it is impossible for the female to desert, as when sperm are released before the ova. However, in two families of fish (*Callichthyidae* and *Belontidae*) the male builds a foam nest, releases sperm first into the nest and remains to guard the eggs. In other species, females provide parental care when they have the opportunity to desert first (Ridley, 1978). Female mouth brooding cichlids, for example, spawn in a nest, remove the eggs from the nest and swim to a brooding ground while the male remains at the nest (Ridley, 1978, Perrone & Zaret, 1979, Gross & Shine, 1981). Thus, the gamete order hypothesis does not account for the sex differences seen in parental investment in fish.

Trivers (1972) hypothesized that male parental care was associated with external fertilization in fish since external fertilization increased certainty of paternity. Gross and Shine (1981) tested two predictions that were generated from this certainty of paternity hypothesis. They found support for the prediction that paternal care should be higher in families with external fertilization than in families with internal fertilization. However, they found no support for the prediction that female parental care should be equal among external and internal fertilizers. This prediction arises from the fact that females are always related to their offspring (certain of their parentage) in both external and internal fertilizers so the mode of fertilization should not affect female parental care. Female parental care is greater among internal fertilizers. In addition, greater paternity certainty with external versus internal fertilization has never been demonstrated (Gross & Shine, 1981). Finally, alternative mating tactics, like "sneaking" and "female mimicry" are common in fish, so it is not clear if Trivers basic assumption, that external fertilization increases paternity certainty, is correct (Baylis, 1981, Gross, 1984).

Another problem with the proposed association between paternity certainty, external fertilization and paternal care is that in three families of internal fertilizers, males guard the eggs. In a few species of sculpins, the male posesses an intromittent organ and fertilization is internal (Breder & Rosen, 1966). The male mates with several females, and the females which only breed once, deposit their eggs on the territory of a single male. The eggs, and sometimes the fry, are guarded by the male for about six weeks. There is not a good explanation for the relationship between male care and internal fertilization, but internal fertilization may be a secondary development after uniparental male care is established. If internal fertilization increases the amount of sperm transfer to the female, then it is plausible it would develop in species where the male cared for the eggs (Breder & Rosen, 1966).

The studies reviewed in this section suggest that, territoriality may be the male fishes method of ensuring certainty of paternity in external fertilizers. In fish, birds and mammals with internal fertilization, the monogamous mating system may be the method the male uses to increase paternity certainty.

1.4 C. Parental care and mating system

Birds and mammals may be solitary, polygamous or monogamous (Elwood, 1983) and more male parental care is associated with monogamy and to a lesser degree polyandry in birds and mammals (Kleiman, 1977, Kleiman & Malcolm, 1981, Wittenberger & Tilson, 1980, Dewsbury, 1981) due to differing degrees of paternity certainty. Monogamy (and polyandry) should have the highest degrees of paternity certainty while promiscuity should have the lowest (Kleiman, 1977).

A monogamous mating system usually refers to the situation where "neither sex has the opportunity of monopolizing additional members of the opposite sex" (Emlen & Oring, 1977, p. 217) and polyandry refers to a mating system where "individual females frequently control or gain access to multiple males" (Emlen & Oring, 1977, p. 217). Facultative monogamy, where monogamy exists because males and females are greatly scattered and do not have the opportunity to mate with other individuals, and obligate monogamy, where a female can not rear her offspring without male parental investment, should have the highest degrees of paternity certainty while promiscuity should have the lowest (Kleiman, 1977). Although monogamy and polyandry are often associated with male parental care, there are exceptions. Tarsiers (*Aotus trivirgatus*) form monogamous pairs, yet no paternal care has been observed in this species (Wright, 1990).

There has been confusion as to which criteria are relevant for determining monogamy (Gubernick, 1990). Monogamy is used to refer to mating exclusivity, (a male and female only mate with each other), the establishment of pair bonds (where there is a prolonged and exclusive association between a particular male and female) and to biparental care (Gubernick, 1990). However, mating exclusivity and pair bonds do not always lead to biparental care (Gubernick, 1990). In the following discusion monogamy refers to mating exclusivity.

In birds, uniparental male care is associated with monogamy and polyandry (Clutton-Brock, 1991). Most of the subfamilies of birds where the male provides no care, have a polygynous mating system and the cost to the male's reproductive success is high if he uses energy for parental care (Van Rhijn, 1984, Silver et al., 1985).

The majority of these species also have precocial young that are fed little or not at all by the parents (Clutton-Brock, 1991).

Biparental care is associated with three different types of mating systems in birds. The first is where both sexes are monogamous as in passerines and many colonial birds (Wittenberger & Tilson, 1980, Clutton-Brock, 1991). The second is where males are polygynous and females are monogamous as in the red-winged blackbird, where the reproductive success of females is enhanced by the male assisting in feeding offspring (Muldal, Moffat & Roberston, 1986, Beletsky & Orians, 1990). The third is where females are polyandrous and several males cooperate with the breeding female to raise the young. For example, in the Tasmanian native hen (*Tribonyx mortierii*) where adults form either pairs or trios of two males (often brothers) and one female, the percentage of eggs reared is greater in the trios than in the pairs (Maynard Smith & Ridpath, 1972).

Uniparental male care is associated with four different mating systems (Clutton-Brock, 1991). The first is monogamy combined with the production of one or two broods as in kiwis, some cassowaries, some tinamous and some shorebirds. The second is where females double clutch combined with monogamy or sequential polyandry (Clutton-Brock, 1991). In the spotted sandpiper, (*Arctitis macularia*), the female lays one clutch, which the male incubates and then a second or third clutch which another male incubates or she incubates the clutch herself (Oring & Knudsen, 1972). The third mating system associated with uniparental male care is sequential and simultaneous polyandry, combined with uniparental care and monogamous breeding in males. This mating system is confined mostly to shorebirds from five families, jacanas, painted snipes, plovers, sandpipers and phalaropes (Clutton-Brock, 1991). Jacanas (*Jacanidae*) show complete role-reversal where the female defends a harem of males. The sexes have identical plumage and the female is larger. Jacana males defend small territories from each other within the female's territory. The male builds the nest, incubates the eggs and rears the young (Jenni, 1974). In some polyandrous species such as the red-necked phalarope (*Phalaropus lobatus*), dotterel (*Eudomias morinellus*) and some cassowaries, some females pair with more than one male in succession in the course of a single breeding season but the male mates with only one female. Females may lay two clutches and remain with the eggs until the young hatch afterwhich they leave and the male completes the rearing of the young (Hohn, 1968, 1971).

In some cursorial birds, males compete for harems of females who lay eggs in a single nest, which the male incubates (Handford & Mares, 1985). This type of breeding resembles that found in many fish. Greater rheas (*Rhea americana*) are an example, as they are gregarious during the non-breeding season and then break up into small groups of 6 to 8 individuals. After obtaining a harem, the male leads them to a nesting site, where they lay a combined clutch of 10-50 eggs. The male starts to incubate the eggs after the first few females have laid eggs and becomes increasingly aggressive to females returning to lay eggs. After they lay their eggs in one male's nest the females leave and join another male and lay more eggs. The male is left to incubate the eggs and rear the young (Bruning, 1974).

In some species of ostriches (*Struthio camelus*), only the male incubates and cares for the brood (Clutton-Brock, 1991).

Some species of birds such as tree swallows (*Tachycineta bicolor*) and savannah sparrows (*Passerculus sandwichensis*) exhibit both monogamous and polygynous mating systems within the same population. DNA fingerprinting indicated that polygynous and monogamous tree swallow females copulated with neighboring males in addition to their own mate. All polygynous male nests had at least one offspring sired by another male, while only 50% of the monogamous male nests had at least one unrelated nestling. Both polygynous and monogamous males fed their offspring at the same rate as females and did not reduce provisioning based on how many illegitimate offspring were in the nest (Lifjeld et al., 1993).

Paternity certainty has been directly manipulated in tree swallows by removing the female's mate and allowing him to watch (from a cage with one way glass) the female engage in extra-pair copulations. Male's were removed from their mates for either 1 or 3 days and upon being returned to their nest did not respond to the manipulation. Even though their confidence of paternity had been reduced, males did not show any reduction in how often they fed offspring or defended the nest. This study indicated that males did not reduce the amount of parental care they provided to offspring until their certainty of paternity was very low (Whittingham et al., 1993).

In savannah sparrows, polygynous females laid as many eggs per clutch and as many clutches per season as monogamous females. In addition, polygynous and monogamous males fledged young of equal size. Males fed the offspring of primary females more than those of secondary females. Secondary females without assistance, made the same number of food deliveries per hour as both the male and primary female working together. Even though unassisted females foraged longer than assisted females, unassisted females produced the same number and size of offspring as assisted females (Wheelwright et al., 1992). Thus, being the second female on a good territory where food was abundant may be more important than assistance from the male.

The dunnock (*Prunella modularis*) also displays a variety of mating systems which include monogamy (territory is defended by one male), polyandry (territory is defended by two unrelated males) and polygynandry (two unrelated males defend territories of two or more adjacent females). Polyandrous males that are removed temporarily during the mating cycle (lowered confidence of paternity) do not feed chicks unless they have mated with the female during the egg laying period whereas this manipulation has no effect on chick feeding by monogamous males. Davies et al. (1992) concluded that paternal effort is modified by cues based on access to the female during mating and possibly paternity certainty.

In most mammals, the female invests more in offspring than the male because internal fertilization forces her to invest in gestation and only females lactate. Therefore, the cost of parental investment increases more rapidly for females with each additional offspring than for males (Barash, 1980). Male mammals are, therefore, more likely to desert their offspring and have a polygynous mating system, yet some mammals, (mainly carnivores, primates and rodents) are monogamous and have biparental care (Kleiman, 1977, Kleiman & Malcolm, 1981, Wittenberger & Tilson, 1980).

Marmosets and tamarins display communal care of offspring, where the mother, father and other group members care for offspring (Tardif et al., 1990). In cotton-top and saddleback tamarins (*Saguinus fuscicollis, Saguinus oedipus*), groups commonly contain multiple adult males and females. There is a high degree of variability in the mating system both between groups and within groups over time. In four out of five, two male groups in which copulations were observed, both males mated the same female. This system was one of cooperative polyandry where two or more males mated with the same female but neither monopolized the female around ovulation (Tardif et al., 1985, Goldizen, 1987).

Captive studies (Epple, 1975, Kleiman, 1978), have found that marmosets (*Callithrix jaccus*) and tamarins (*Saguinus fuscicollis, Saguinus oedipus*), display extensive paternal care but monogamy is not the [illegible] mating system. These species usually have a communal breeding [illegible], with several adult males and females (Garber et al., 1984, Terborgh & Goldizen, 1985). Saddle-backed tamarins have 2 to 4 males that are not related to the female in the breeding groups, each of which copulates with her with similar frequency (Goldizen, 1990, 1987a). All the males in the group carry, share and play with the infants. This cooperative breeding system is important to the survival of the offspring.

Larger monogamous primates show less extensive paternal care. Siamang (*Hylobates symphalanges*) fathers carry two year olds across tree gaps but mothers are the primary care givers during the first year. In gibbons (*Hylobates ssp.*) and indiri (*Indiri indiri*), paternal care extends only to the protection of offspring from predators (Leighton, 1987). Where primate mating systems consist of multimale/multifemale groups, interactions between males and infants seem to be based on reciprocity, that is, a mating strategy instead of parental care (see section 1.4 D).

Paternity is difficult to establish in primates but there does appear to be an association between polyandry and monogamy and the amount of time and energy a male invests in parental care. The common marmoset (*Callithrix jaccus*), titi monkey (*Callicebus moloch*), saddleback tamarin (*Saguinus fuscicollis*), cotton-top tamarin (*Saguinus oedipus*) and owl monkey (*Aotus triviergatus*) are species where males invest much time and energy in carrying and babysitting offspring and live in groups of several adult males and females with one breeding female (Goldizen, 1987a & b, Epple, 1977, Ingram, 1977, Tardif et al., 1990). Often the dominant male in the group monopolizes the breeding female.

Male white sifakas (*Propithecus verreauxi*) carry infants (in captivity) more than male diademed sifakas (*Propithecus diamema*) and this could be due to a difference in paternity certainty. The white sifakas in this experiment were housed in monogamous pairs while diademed sifakas were housed in groups of several males and females. Female diademed sifakas often mated with nonresident males when housed in groups, which would decrease certainty of paternity (Grieser, 1992).

Although monogamy and polyandry increase the likelihood of paternity certainty, there is evidence that other mating systems are associated with infants interacting with their fathers. Paternity certainty is higher in one male troops than in multimale/multifemale troops. Hamadryas baboon (*Papio hamadryas*) troops consist of one single mature male, several females and their young. Additional males that are close to maturity are excluded from the primary group. Both males and females transfer between groups, so paternity certainty is not as high as that in monogamous species (Redican & Taub, 1984).

Several lines of evidence suggest that male rhesus macaques (*Macaca mulata*) interact with infants that they have sired, and that males of greatest seniority in the groups are most often close to the infants (Smith, 1980, Berenstein et al., 1981). Capitanio and Taub (1992) reported that a male rhesus macaque carried one of a pair of twins and there was the possibility (although unconfirmed) that the male was the father.

Vervet monkeys (*Cercopithecus aethiops*) live in multimale groups from which males emigrate to neighbouring groups, while females stay within their natal group (Cheney & Seyfarth, 1983). A linear dominance hierarchy exists within captive vervet monkey groups (Hector, Seyfarth & Raleigh, 1989). Males respond more frequently to distress calls of infants that they have a high probability of fathering and alpha males are more friendly to infants that are most likely their own (Hauser, 1986, Hector et al., 1989). Females may choose familiar males to mate with based on how they interact with their infants. Subordinate males are more friendly to infants if the mother is watching them and females are less aggressive to subordinate males if subordinate males are more affiliative toward infants (Hector et al., 1989).

Although the evidence for the influence of paternity certainty on paternal care is inconsistent, there is still some evidence that it has an effect. But increased paternity certainty is not invariably associated with male parental care. Paternity certainty is high among monogamous gibbons and one-male groups of gorrillas, yet little male parental behavior has been observed in these primates (Taub & Redican, 1984).

Monogamy is the main mating system in canids and this seems to be strongly correlated with the inability of females to rear a litter, without male parental investment (Moehlman, 1987). Kleiman and Malcolm (1981) report that male care is found in 17 of 35 species of Canidae. In most canids, pairs or groups defend multipurpose territories and all adults help raise offspring (Kleiman & Eisenberg, 1973). Male parental investment is extensive in canids and usually takes the form of feeding offspring (Moehlman, 1987).

Moehlman (1989) suggests that a relationship exists between body weight and mating systems in canids. Small species are often monogamous and occasionally polygamous. Some monogamous species may have helpers. This association between small size and polygyny could occur because small canids tend to have fewer and heavier pups which require less investment than the more altricial pups of the larger canids. Within smaller canids, females have fewer and heavier newborns (compared to the mothers' weight) and invest more in the offspring than males. Thus, there would be the potential for males of these species to invest in more than one female and polygyny would result with males being more likely to disperse (Trivers, 1972). This has been observed to be the case in red foxes (*Vulpes vulpes*, MacDonald, 1981, 1983). If this correlation exists, then Blanford's fox, which is a small canid, should be polygynous but is actually monogamous (Geffen & Macdonald, 1992). Geffen and Macdonald (1992) suggest the reason Blanford's fox may not be polygynous is that their altricial young require more paternal care than predicted for a canid of this size.

There also appears to be an association between monogamy, paternity certainty and biparental care in rodents. The reproductive success of solitary or paired females (with a mate or sister) was examined for the monogamous Djungarian hamster (*Phodopus campbelli*). Mated pairs were the most successful, rearing 95% of their pups to weaning, while solitary females were the least successful, only rearing 47% of their pups to weaning. The reproductive success of mothers paired with a sister was not significantly better than a solitary female (Wynne-Edwards, 1987).

Wild Mongolian gerbils (*Meriones unguiculatus*) appear to be monogamous. Adolescents help care for younger offspring and males show extensive paternal behavior (Elwood, 1983). Both pine and prairie voles (*Microctus ochrogaster*) are monogamous while meadow voles (*Microtus pennsylvanicus*) are promiscuous. Male pine and meadow voles display extensive paternal behavior while meadow voles do not (Oliveras & Novak, 1986). California mice (*Peromyscus californicus*) are monogamous and show extensive paternal behavior, thus paternal behavior is associated with paternity certainty and monogamy (Gubernick, 1987). These examples indicate that the development of pair bonds, mating exclusivity and biparental care are often associated with each other in rodents (Gubernick, 1990). The proximate mechanisms of social bonding (behavioral and physiological) and their relevance to biparental care is being investigated in prairie voles (Carter et al., 1986), and California mice (Gubernick, 1990).

Prairie voles are monogamous and there is a prolonged and exclusive assocation between male/female pairs (Getz, et al. 1981). Males participate in parental care (Hartung & Dewsbury, 1979) and spend about the same amount of time huddling with pups as the female (Gruder-Adams & Getz, 1985). Field studies indicate that male and female prairie voles share a nest and defend a common territory (Getz et al., 1981, Getz et al., 1987). In the the lab, males and females showed high levels of aggression toward strangers, whereas aggression is rare among established pairs (Carter et al., 1986). When prairie voles are placed in two male/one female breeding groups or in one male/one female breeding units, more pups survive in the monogamous situation (Gavish et al., 1981). Reproduction is under social control in the prairie vole instead of photoperiodic control. Estrus and ovulation in the female prairie vole are governed by male stimuli: if no males are present females do not cycle (Carter et al., 1986). Therefore, prairie voles meet most of the criteria for monogamy and are a good model for investigating the proximate mechanisms of social bonding (Carter et al., 1992).

Pair bonding, as measured by the amount of physical contact between males and females, is influenced by copulatory interactions.

Females that cohabitated and copulated with a male spent more time in contact with the male than females that were tested with an unfamiliar male partner (Carter et al., 1988). Mating facilitated the onset of partner preference but was not essential for its development (Williams et al., 1992). If females cohabitated with the male for a short period (6 hours) they displayed a preference for their partner only if they mated with the partner during cohabitation or received oxytocin injections. Oxytocin, thus, facilitated the development of preferences for a partner (Williams et al., 1992, Carter et al., 1992). Injections of oxytocin reduced male-directed aggression and increased affiliative behavior in the prairie vole (Witt et al., 1990). Pair bonding (monogamy) is influenced by social factors (cohabitation, copulation) and hormonal factors, which may prepare this species for male parental care. However, a link between pair bonding and male parental behavior has not been established in the prairie vole.

The California mouse is another monogamous rodent, which is found in pairs in the wild, forms long term associations or pair bonds, exhibits mating exclusivity and exhibits extensive male parental care (Gubernick & Alberts, 1987, Ribble & Salvioni, 1990, Ribble, 1991). In a series of experiments, Gubernick established that a link existed between pair bonding and male parental care by removing the male (disrupting the pair bond) and deterimining its affect on parental care. Spontaneous parental behavior did not usually occur in adult virgin *P. californicus* males living alone or housed with another male (Gubernick & Alberts, 1989). Pup stimulation was needed for postpartum maintenance of maternal behavior in *P. californicus.* as the removal of pups reduced the number of mothers acting parentally, when tested with a single pup. The father's presence did not influence maternal behavior. Parental behavior in the male was maintained by the mother and not the offspring (Gubernick & Alberts, 1989) as fathers continued to be parental in the absence of pup stimulation. Direct contact with the mother was not important in maintaining paternal behavior as fathers exposed to only their mate's excreta remained parental (Gubernick & Alberts, 1989). Therefore, removal of the mother and disruption of the pair bond reduced paternal behavior.

Other affects of the mother on maintenance of paternal behavior also were investigated. Maintenance of paternal behavior was specific to the male's mate as males exposed to the excreta from virgin or lactating females were less likely to parental than if exposed to their mate's excreta. In addition, mere familiarity with a female was not sufficient to maintain paternal behavior (Gubernick & Alberts, 1990). These data therefore, indicated that disruption of the pair bond altered paternal behavior in California mice.

Disruption of pair bonds by removing the father, influenced maternal behavior in the grasshopper mouse as well (*Onychomys torridus*). If the father was removed, maternal licking decreased (Duvall et al., 1982). Pair bonds and paternal behavior, therefore, have physiological correlates in prairie voles and California mice, and disruption of pair bonds leads to disruptions in male parental behavior but not female parental behavior.

Brown (1993) suggests that the current investigation of male parental behavior in rodents is flawed because researchers have modeled male parental behavior on female parental behavior. For example, the stimuli from mating and cohabitation with a pregnant mate have been shown to be important for the initiation and maintenance of male parental behavior but not female parental behavior. The mating system of the species is important as monogamous males are more likely to show paternal behavior than polygynous males. Laboratory studies where food, water and nesting material are abundant may be inappropriate for examining the contribution the male makes to offspring survival. The importance of the male's parental care may only be apparent in situations where the female has to leave the nest to forage for food or collect nesting material. The male's social status and experience with previous litters may also influence the quality of parental care.

Among rodent species, prairie voles and California mice may be the best models for a monogamous mating system as prairie voles exhibit pair bonds and biparental care while California mice also exhibit these characteristics and mating exclusivity (Carter et al., 1988 , Getz, Carter & Gavish, 1981, Gubernick 1987, 1990). *Mus musculus* may be a good model for a polygynous mating system as territorial males mate with several females on their territory and exclude subdominant and subordinate males from mating (Hurst 1987, DeFries & McLearn, 1972). This is discussed further in Chapter 3.

1.4 D. Paternal behavior as a mating strategy: agonistic buffering and reciprocal altruism

Should all male-infant interactions be classified as parental investment? In primates, adult males often carry and interact with infants that are not their own. Although it may appear that this is a form of parental investment, it may be a mating strategy to gain access to females (Smuts, 1987).

Reciprocity occurs when one animal (the altruist) incurs a small cost performing a behavior which benefits another, but the altruist then reaps a larger benefit for him/herself in terms of inclusive fitness when the favour is returned (Barash, 1980). There would have to be a high probability that the favour would be returned so the original altruist could reap his/her payback from a low risk behavior of the recipient. Finally, there must be recognition of the individuals to whom the low cost aid has been given and received. If this is not the case, then altruism would go unrewarded and the original behavior would have a selective disadvantage in terms of promoting one's own inclusive fitness (Trivers, 1985).

Smuts (1987) proposes that paternal behavior in nonhuman primates could be explained in terms of reciprocity. Male primates would care for and protect infants (and their mothers) in order to derive reciprocal benefits from mothers and their infants. The possible benefits of reciprocal altruism, are acceptance into a new social group, female support during competition with other males and greater mating opportunities. Females would have the opportunity to compare the parental behavior of different males and on the basis of this comparison distribute benefit to some males at the expense of others. Since females must have the opportunity to compare the behavior of different males it seems most likely that reciprocity would evolve in groups of primates with several males.

Several lines of evidence indicate that within multimale/multifemale troops, males gain acceptance into the group and access to females by displaying parental behavior toward infants. Gouzoules (1977) found a positive correlation, in stumptail and Japanese macaques (*Macaca arctoides* and *Macaca fuscata*), between maternal rank and the amount of huddling, touching, ventral clinging, dorsal clinging, and grooming that the infant received from adult males. Attention that males displayed toward nonrelated infants allowed the male to maintain proximity to and contact the mother. The amount of harassment received by infants (slapping, chasing, dragging) from troop members was negatively associated with the mother's rank (Gouzoules, 1977). Dominant males retrieved infants from low ranking mothers even though mothers showed resistance to such approaches (Estrada & Sandoval, 1977).

Several studies have reported that the increase in male attention to infants is due to agonistic buffering in Japanese macaques (Gouzoules, 1984, Mitchell, 1969, Alexander, 1970) and savannah baboons (Redican & Taub, 1981). Agonistic buffering refers to a strategy of low ranking males to avoid attack by high ranking males. Low ranking males hold infants that are unrelated to them and possibly related to a high ranking male when they are threatened by a high ranking male. This behavior reduces the likelihood that the high ranking male will attack (Ransom & Ransom, 1971). However infant Japanese monkeys benefited from male parental care as 1-2 year old infants were cared for almost exclusively by males.

Itani's (1959) classic study of wild Japanese macaques found that most paternal care is exhibited in the delivery season and by adults of high rank. The male is observed to hug, walk with, groom and protect infants from predators and other adults. Subleaders that attempted to move into the troop did so by hugging infants and succeeded in increasing their rank and toleration by females and leaders.

Some evidence suggests that female olive, yellow and chacma baboons (*Papio anubis, P. cynocephalus* and *P. ursinus*) choose to mate with males that interact frequently with infants. Females may be maximizing the probability that the male she mates with will remain in the troop and provide infant care (Bercovitch,1991).

Barbary macaques (*Macaca sylvanus*) live in highly promiscuous multimale societies where sexual associations among males and females are brief. Male Barbary macaques carry and protect infants but the infants are often not their own as revealed by DNA fingerprinting (Paul et al., 1992). Thus, parental behavior may be a strategy to gain acceptance into the group or gain access to females.

Male parental care in cotton top tamarins (*Saguinus oedipus*) is also associated with the male's attempts to gain access to the breeding female (Price, 1990, 1992). Groups of these prosimians commonly contain multiple adult males and females. The mating system is one of cooperative polyandry where two or more males mate with the same female but neither monopolizes the female around ovulation (Tardif et al., 1985, Goldizen, 1987). Price (1990, 1992) noted that males pick up an infant prior to mounting the breeding female. Breeding male tamarins may use infants as part of a courtship strategy, to demonstrate their willingness and capacity to carry infants and increase the likelihood of their acceptance by the breeding female.

Following this argument, Mesitripieri and Alleva (1991) suggested that the parental behavior shown by male house mice could be a strategy to reduce maternal aggression. They found that when males exhibited parental care, maternal aggression was significantly reduced and therefore, this behavioral interaction was an example of reciprocity in rodents.

As the above examples indicate, the reciprocity hypothesis treats male parental behavior as a mating strategy instead of parental strategy (Smuts, 1987) as caring for young has the benefit of increasing the male's access to females in the group. If parental behavior costs the male little and benefits him by providing mating opportunities then such behavior should be observed irrespective of its effects on the infants. These behaviors should not however be equated with parental investment since they concern mating effort. The female would have to be available for the male to reciprocate, and she would also have to be able to recognize the male she does the favor for.

Territoriality, external fertilization and monogamy are all influential factors in the evolution of male parental behavior as they reduce the cost of male parental behavior and increase paternity certainty. Male defense of a territory probably originated as a mating strategy and defense of eggs, females and young on the territory is probably a secondary development. Male defense of a territory would increase paternity certainty, as other males would be chased from the territory before they contacted females or young on the territory (also benefitting the young by protecting them from predators and intruding males). External fertilization is associated with increased paternity certainty in some fish species whereas internal fertilization is associated with decreased paternity certainty. Internally fertilizing species, of fish, birds and mammals can increase paternity certainty through the social organization and mating system of the species as monogamy is associated with increased paternity certainty. All male adult-infant interactions are not examples of male parental investment since in several species, these interactions are strategies whereby the male increases his access to females.

1.5 The benefits of paternal care to offspring

Wittenberger and Tilson (1980) suggest that "monogamy should evolve when male parental care is both nonshareable and indispensable to female reproductive success" (p. 199). Monogamy should evolve, when the female needs the male's assistance to rear their offspring. The presence of the male and his parental behavior should, therefore, have some beneficial effect on the offsprings' survival and development. However, there is some controversy as to how beneficial the male's presence is and, at least in some bird species, there does not appear to be any consistent tendency for species with biparental care to show higher fledging success than species with uniparental care (Clutton-Brock, 1991).

1.5 A Effects of paternal care on offspring survival and development

The following are some examples of how male parental behavior affects the survival and development of offspring in fish, birds and mammals. The main benefits of egg guarding, the most common behavior in fish, is to reduce the number of offspring consumed by egg predators and hence increase offspring survival (Baylis, 1981).

By contrast, in groups of northern sandpipers (*Calidridanae*) and plovers (*Charadriidae*), there is no difference in fledging success whether one or both parents feed and protect the young (Erkmann, 1983). In studies of the monogamous killdeer (*Charadrius vociferus*), Lenington (1980) found that the young are more closely guarded when both parents shared parental care, but if only one parent was present, similar numbers of offspring were fledged. One parent can rear a brood in many shorebirds, as parents do not feed the young and the young are protected through crypsis and predator distraction displays (Erkmann, 1983). Since parents of larger shorebirds actively and more effectively defend young, a second parent may help in protecting the young. This could be an explanation for polygamy evolving in smaller species and why in larger monogamous species, males and females rarely abandon their broods before they fledge (Erkmann, 1983).

A more direct method of determining the role of the male parent in chick survival is to experimentally remove the male during incubation or just after hatching. Bart and Torne (1989) reviewed 15 male removal studies in several bird species such as waterfowl, shorebirds, raptors, pigeons, ptarmigans and passerines and determined that, in general, survival of the young was higher when the male was present. In three species (pigeon, kestrel, sandpiper), the removal of the male during incubation resulted in a decline of 85% to 100% in nestling success (Bart & Torne, 1979).

However, Bart and Torne (1979) also found that in species where males show some degree of parental care, there is great variation in fledging success. Several examples were found in which the removal of the male resulted in only a small decrease in the survival of the young. To try to understand this variablity, males were classified as being of much value or little value depending on whether they incubated eggs, fed the incubating female, brooded the young or defended the female or offspring. The male parental behavior that contributed the most to increased fledging success was assisting during incubation (incubating the eggs and feeding the incubating female).

The removal of males from their territories had little effect on the female's reproductive success in monogamous tree swallows (*Tachycineta bicolor*, Dunn & Hannon, 1992) and in white-throated sparrows (*Zonotrichia albicollis*, Whillans & Falls, 1990). Female white-throated sparrows whose mate had been removed, increased the number of trips made to the nest to feed the young and decreased their brooding time but fledged as many young as females that had their mate present.

In the red-winged blackbird (*Agelaius phoeniceus*), which is polygynous, males commonly assist females in feeding nestlings. The addition of male parental care resulted in increased numbers of surviving offspring (Muldal et al., 1986). However, females not receiving male assistance on territories where males fed the offspring of other females, did not suffer a greater decrement in reproductive success compared to females on territories where the male fed the offspring of the female (Muldal et al., 1986). So in this case, the male's provisioning of a good territory was as important as male parental care in facilitating offspring survival.

Wolf et al. (1988) grouped male removal experiments into studies where male removal influenced offspring survival and studies where male removal had no influence on offspring survival. Where the male greatly influenced offspring survival, birds were either cavity nesters or bred at higher latitudes. Cavity nesters laid larger clutches than open nesters (controlling for body size). If males can protect offspring from predators, then clutch size can increase and species with larger brood sizes will benefit from male parental care. Open nesters have small clutches and are pressured to have small clutches because they often lose eggs to predation and renest frequently. Birds that nest at higher latitudes face more severe temperature stress, especially when the young first hatch. The prolonged absence of the female from the nest in a cold climate could result in the loss of offspring. If the male provisions the female with food, this gives the female more time to incubate the eggs and brood the young.

In the dark-eyed junco (*Junco hyemalis*), male removal studies indicated that the presence of the male tended to increase offspring survival during the first half of the nestling period. Broods without male help survived only half as well as those with help. So in this example, male parental care benefits the young by increasing their survival and benefits males by increasing their reproductive success (Wolf et al., 1988).

If male willow ptarmigan (*Lagopus lagopus*) are removed during incubation or when eggs hatched, lone hens fledge the same number of offspring, suggesting that male parental care is not essential (Martin & Cooke, 1987). Hanon (1984) compared the reproductive success of willow ptarmigan hens that are monogamous, or experimentally made polygynous. Hanon found that both groups fledged similar numbers of chicks but that the percentage of polygynous hens found with broods was lower in 1 of the 3 years in which they were studied and they returned at lower rates in the following years than monogamous hens. It was not determined why the polygynous hens had a reduced reproductive success as measured by their rate of return to the breeding grounds. Males may have provided parental care, because if their mates were removed after hatching they could rear the brood on their own. Males also guarded their mates and offspring from other males and males which stayed with their mates gained paternity for any replacement clutches (Hanon, 1984).

The benefit of male parental care to offspring is varied in bird species. In male removal studies, offspring in some species suffer a cost of reduced survival while others do not. Since male parental investment is expensive in mammals in terms of limited opportunities to remate, we would expect that when males do provide substantial parental investment, it should increase the survival of offspring or the weaning weight of offspring.

Medium sized canids such as jackals, appear to be monogamous, with both male and female adults helping to rear pups. Silverbacked and golden jackals are monogamous and have relatively large litters with a long period of infant dependency (Moehlman, 1987). Silverbacked jackals depend on grass rats and fruit for food, which are energetically costly to obtain thus, paternal care is critical to pup survival. If a male split his investment among several litters, the reproductive success of both the male and female would decline (Moehlman, 1987). Golden jackals also have large litters of dependent young, but because they make use of larger food (young of Thompsons's gazelle), paternal care may not be as important as it is in the silverbacked jackal. Since pup survival is not limited by food provisioning and greater food availability might enable a female to provision a litter with little help, the male could possibly provision two litters successfully. The pair bonds between golden jackals are not as strong as those between silverbacked jackals (Moehlman, 1987). Both species of jackals have helpers (male and female offspring from previous litters), which stay with the parents and help protect, provision and socialize the next litter. Helpers increase the likelihood of survival of the litter (Moehlman, 1979).

Larger species such as the African hunting dog (*Lycaon pictus*) and the timber wolf (*Canus lupus*) are usually monogamous but tend toward polyandry with male helpers since their pups require a large investment. A pair of African wild hunting dogs can not successfully raise a litter without helpers (Malcolm & Marten, 1982). African huntings dogs hunt cooperatively and larger packs are more successful in hunting and defending carcasses (Frame, Malcolm, Frame & van Lawick, 1979). African wild dogs form stable patrilineal social groups that rear large litters cooperatively. Timber wolves and dholes have similar mating and breeding strategies as the African hunting dog (Harrington, Mech & Fritts, 1983, Johnsingh, 1982). Recently a small group of wild wolves, consisting of two females and one male, were observed sucessfully rearing a litter. This unusual pattern may have been due to the low density of wolves and high density of available prey (Boyd & Jimenez, 1994).

Male gerbils with experience rearing a litter of siblings, had offspring which gained more weight than those of inexperienced males and this could be due to male gerbils building better nests and subsequently improving heat retention in the litter (Salo & French, 1989). Gerbil pups reared in the presence of the father were more advanced in their behavior and eye opening than those reared by only the female. When the male is present, he provides additional tactile stimulation and this may accelerate behavioral development in gerbils (Elwood & Broom, 1978).

Storey and Snow (1987) found that male meadow voles (*Microtus pennsylvanicus*) displayed parental behavior toward their own pups and pups that had both parents present gained more weight than pups housed with only their mothers. However, Wang and Novak (1992) found that meadow vole pups reared by only their mother developed faster than pups housed with both parents. In prairies voles, fathers assisted in rearing pups and litters developed faster with the father present (Wang & Novak, 1992).

Simmel and Smith (1977) determined that *Mus musculus* pups that were fostered to a male of the same strain were more likely to survive than pups that were fostered to a male of another strain. Female grasshopper mouse pups (*Onychomys torridus*) that were exposed to odours from their fathers, were heavier at weaning and matured sexually at an earlier age (Duvall et al., 1982). Dudley (1974) found that *Peromyscus californicus* pups reared with both their mother and father were heavier than pups reared with only their mother, especially if the mother was removed for 12 hours each day.

Whether male parental behavior in house mice increases offspring survival is the matter of some debate. Barnett and Dickson (1985) examined the survival of pups when two different stocks of wild-type house mice (*Mus musculus*) were used. These two stocks were maintained at either 3°C or 23°C. Females mated to males that had been raised in the cold environment, weaned more pups than females mated to males raised in the warm environment, when they were challenged to breed under cold conditions. The male's and not the female's contribution was considered to be the most important.

1.5 B. Effect paternal behavior on offspring behavior

As well as increasing pup survival and physical development, the father's presence could influence parenting, agonistic and sexual behaviors. The presence of the father influences the behavior of juvenile prairie voles. Juveniles housed with both parents displayed more parental behavior toward their younger siblings (sitting in the natal nest) when the father was present than when he was absent (Wang & Novak, 1994).

Two studies have indicated that the presence of the father enhances aggression in house mice offspring (Wuensch & Cooper, 1981, Mugford & Nowell, 1973), while one failed to demonstrate that the father had any impact on aggressive behavior in offspring (Smith & Simmel, 1977). The presence of the father may reduce the amount of parental behavior displayed by weaned juveniles (Lyons, 1993). In several experiments, exposure to a male parent reduced the number of pups that weaned juveniles retrieved and increased the latency to retrieve the first pup, whereas exposure to a second litter of pups had the opposite effect on weaned juveniles (Lyons, 1993).

The presence of the father or his pheromones can accelerate sexual maturation in young female rodents (Bronson & Maruniak, 1975) and retard sexual maturation in young males (Lawton & Whitsett, 1979). Sexual preferences can be influenced by the fathers' presence as house mice reared with both parents preferred to mate with a male of a different strain but not a different subspecies. It was suggested that the fathers' presence promoted optimal outbreeding in their offspring (Mainardi, 1964, Wuench, 1985).

1.5 C. Parent-offspring conflict

Parents and offspring do not always agree on the amount of parental behavior that should be displayed toward each offspring. This conflict arises because parents are equally related (50% genetic representation in all offspring is due to each parent, assuming the male has not been cuckolded) to all of their offspring and therefore benefit most if parental care is evenly distributed amongst all current offspring. This allocation of resources would ensure that parents rear the mamimum number of offspring to independence. Offspring, however, are more related to themselves, (100% genetic representation) than to their parents or their siblings (50% genetic representation) and therefore demand as much parental assistance for growth and survival as possible for themselves. More formally, for any parental behavior, parents are selected to maximize the difference between the benefits derived (increased offspring survival) and the costs (incubation, gestation, feeding etc.) and when the costs exceed the benefits then parental behavior would be expected to withdraw parental behavior. Specifically, the time at which the costs exceed the benefits occurs sooner for parents than for offspring, so one of the results is weaning conflict. Weaning conflict consists of the offspring resisting the parents attempts at weaning. The offspring is selected to get as much food as possible from the parent, whereas the parent would do better in terms of reproductive success by allocating that energy to new offspring once the young are old enough to fend for themselves (Trivers, 1974).

The influence of male parental behavior on offspring survival and development is varied in bird species. The removal of the male reduces offspring survival in some species, while the female is able to compensate for reduced male assistance in other species. In the majority of studies on mammals, the father's parental behavior increases offspring survival and results in offspring that mature earlier and are heavier at weaning. The father's presence also has a beneficial influence on offspring behavior, as offspring raised with both parents, exhibit appropriate parenting, aggressive and sexual behaviors when they mature. Parents and offspring do not always agree on the amount of investment offspring should receive, as offspring are selected to receive more investment than parents are selected to give.

Parental investment as defined by Trivers (1972) is an evolutionary concept and is measured in terms of cost to the parent and benefit to the offspring (Trivers, 1972, Maynard Smith, 1977). Since Trivers (1972) definition is an evolutionary concept, a method for determining costs and benefits must be developed which has lead to the concepts of direct shareable, direct nonshareable, indirect shareable and indirect nonshareable parental care and parental input. In fish, birds and mammals, males exhibit parental behavior and help increase their own reproductive success by enhancing offspring survival. Fathers increase offspring survival by engaging in such behaviors as aerating and guarding eggs, incubating eggs, feeding offspring, carrying, babysitting, and protecting offspring.

The evolution of male parental behavior is in need of explanation, as it is not obvious what environmental circumstances would influence males to sacrifice their opportunities to mate with several females. Three types of theories try to explain the evolution of male parental care. These theories are based on general evolutionary principles, the evolution of sex differences in parental investment and correlational analyses and taxonomy. Theories based on general evolutionary principles use game theory to investigate the question of how male parental behavior could be maintained within a population once it had been established and discuss whether paternity certainty can influence the evolution of male parental behavior. Theories based on differences between males and females in parental investment seek to explain how male parental behavior originally became established and focus on how male parental behavior could have evolved from a state of no parental behavior. Theories based on correlational analysis and taxonomy attempt to establish how male parental behavior evolved by determining which species are evolutionarily the most primitive and which are the most recent. These theories then determine how often different types of parental care have evolved in different species and try to establish how widespread each parental care patterns is.

The social organization of a species can influence whether male parental behavior is exhibited. Territoriality, external fertilization and monogamy appear to influence the occurrence of male parental behavior by reducing the cost of parental behavior (territoriality) and by increasing paternity certainty (territoriality, external fertilization and monogamy). Not all male adult-infant interactions are examples of parental behavior, as males occasionally interact with infants to increase the likelihood they will be accepted into a social group or to gain access to females. Males parental care usually, but not always, increases offspring survival and development and results in offspring acquiring appropriate parenting, aggressive and sexual behaviors. Finally, parents and offspring do not always agree on the amount of parental care that should be received.

Studies in rodents revealed that male parental behavior is variable depending on the type of housing they were exposed to. In laboratory studies where all food and water is provided, males may behave parentally, since there is nothing better for them to do. If placed in large enclosures or observed under natural conditions, male parental behaviors may not be observed as the male spends his time defending his territory or foraging for food. The next chapter deals with how reproductive development and parental behavior is altered in rodents by the environment and photoperiod.

Chapter 2

The effects of food restriction, wheel running and the light:dark cycle on adult reproduction, parental behavior and pup development and behavior.

The highest priority for energy demands in mammals are cellular maintenance, thermoregulation and the locomotor costs of foraging (McNab, 1963). Once these primary demands are satisfied, energy can be allocated to reproduction, growth and nonforaging activities (Bronson, 1984). Due to the small size and high metabolic rate of rodents, they must consume relatively large amounts of food daily, so a major part of their day is spent foraging. When food is scarce, mice travel several kilometers a day to forage (Justice, 1961). Traditionally, laboratory studies on the effects of food restriction on reproduction in mice have used food rationing. But food restriction may not be a good model for studying the extra foraging required by animals in poor environmental conditions because foraging and food intake are inseparable in the real environment (Perrigo, 1983, Perrigo & Bronson, 1983).

For this thesis, I decided to use wheel running for food to simulate foraging, as it should be less artificial than food restriction. Since the biological value of behavior may depend on when it occurs during the day (Rusak, 1981), I was also interested in how foraging and parental behavior were organized during the light and dark phases of the light:dark cycle (LD cycle). The first section of this chapter, therefore, compares the effects of food restriction and wheel running for food on the reproductive and parental behavior of rodents and on pup survival and development. The second section reviews the effects of the LD cycle on rodent wheel running (foraging) and parental behavior.

2.1 The effects of food restriction and wheel running for food on adult reproductive and parental behavior and pup survival and development

Hamilton and Bronson (1985) examined the effect of food restriction on sexual maturation in wild male and female house mice during a 7 week experimental period. They fed female mice 50% less than *ad libitum* food intake, a diet level which allowed for no body growth after 24 days of age. Females on the restricted diet showed the same reproductive development as *ad lib* females at 10 weeks of age, but the *ad lib* females had significantly heavier uteri than food restricted females at 10 weeks of age. Males responded differently to food restriction than females. There was no difference in reproductive development between the food restricted and *ad lib* males at 10 weeks of age, but food restricted males weighed less than *ad lib* males.

There also were sex differences in the response to food restriction in adult mice, especially in extreme environmental conditions. Pryor and Bronson (1981) fed five groups of male and female pairs of *Mus domesticus* four diets that might be encountered in the wild and a balanced lab chow diet. At an ambient temperature of 23^{0}C, female mice on the natural diets (except for wheat seeds) produced fewer litters than those on standard lab chow. In the cold environment (3^{0}C), female mice on all of the four natural diets produced fewer litters than those on lab chow. Males fed the lab chow gained weight at both 23^{0}C and 3^{0}C whereas those fed the natural diets lost 1 to 2% of their body weight at 3^{0}C but maintained their weight at 23^{0}C.

In female rodents, food restriction alters the estrous cycle, rate of pregnancy and number of surviving embryos. When female white-footed mice (*Peromyscus leucopus*) were food restricted they showed a reduced incidence of estrus and at the severest restriction levels (70% of *ad lib* food consumption which was 3.4 g per day), females did not become pregnant (Merson & Kirkpatrick, 1981).

Food deprivation may have different effects depending on the time during the reproductive cycle in which it occurs. When 48 hour food deprivation was initiated during diestrus in female CF-1 mice, ovulation was delayed but when food deprivation was initiated during estrus, ovulation was not delayed (Bronson & Marsteller, 1985) Short periods of total starvation in female mice (*Mus musculus*) around the time of mating, may cause infertility (McClure 1958, 1966).

Zamiri (1978) restricted the food available to albino mice (Quakenbush strain) for 16 to 21 days after copulation. The *ad lib* food level was defined as 8 g per mouse per day and different groups were restricted to 85% of *ad lib*, 70% of *ad lib* and 55% of *ad lib*. Some females from each group were sacrificed on day 16 and the number of live embryos were counted while the remaining females delivered their litters. They found that embryonic survival to day 16 of pregnancy decreased at all levels of food restriction. The two lowest levels of food availability (70% and 55% of *ad lib*) resulted in a decreased proportion of females giving birth and increased foetal resorptions. At the lowest level of food availability (55% of *ad lib*), there was an increase in the length of the oestrous cycle and a decrease in the implantation rate.

Durst-Zivkovic (1977) and Berg (1965) found that when rats (Wistar and Sprague-Dawley respectively) were food deprived during pregnancy, dams lost weight and fetal weights were subsequently reduced. If female CF-1 mice were food deprived on the second day after birth they consumed their young whereas females that were food deprived beginning 12 days after the birth of their pups did not consume their offspring (Bronson & Marsteller, 1985).

Underfeeding also influences parental behavior in rodents. Female *Mus domesticus* were food restricted (20% less than *ad libitum*) during lactation (22 days) and the effects on maternal behavior were observed. The composition of the litter was also manipulated by limiting litter size to eight pups and cross-fostering four unrelated pups on day 1 of lactation onto each dam. Each litter then consisted of 4 pups that were the mother's and 4 pups that were unrelated. Underfeeding and cross-fostering did not influence how much time mothers spent nursing or licking their young, however, they could not wean the entire litter. Mothers cannibalized both related and unrelated young, thereby reducing their litter sizes to an average of 2.7 pups (Konig, 1989).

Food restricted female Norway rats spent more time in contact with their offspring (lying near pups or nursing pups) during the light phase of the LD cycle than females fed an *ad lib* diet whereas there was no difference between the two groups during the dark phase of the LD cycle (Leon et al., 1983). Massaro et al. (1974) found that Sprague-Dawley (*Rattus norvegicus*) rat dams eating a low protein diet increased the amount of time they spent in the nest area in close proximity to their pups (either in a lying or upright position) compared to dams on a control diet but not until 7 days postpartum. Weiner et al. (1977) found that protein restricted Sprague-Dawley rat dams retrieved fewer pups in a 10 minute test than dams fed a control diet, however the difference in the number of pups retrieved did not occur until 9 days postpartum. Dams fed a low protein diet had deficits in the rate of nest building. Low protein mothers built fewer nests than control mothers one hour after being presented with new nesting material but this difference disappeared when tested 5 hours after being presented with new nesting material. Dams fed the low protein diet also spent more time in contact with their offspring between days 3 and 12 postpartum, while control dams decreased the amount of time spent in contact with their pups as pups aged (Weiner et al., 1977).

Female hooded rats that were mildly food restricted or were pregnant again with a second litter while nursing a current litter, weaned litters earlier than control mothers fed *ad lib* (Smith, 1991). Smart and Preece (1973) found that hooded Lister rat dams fed 50% less than control dams throughout pregnancy and lactation spent more time in their nests during the dark phase while rat dams fed *ad lib* spent more time in their nests during the light phase of the LD cycle. Contrary to expectation, rat dams fed *ad lib* cannibalized more pups than underfed dams. However underfed dams retrieved fewer offspring in a 10 minute test even though some measures of retrieving (such as number of young retrieved) favoured the control dams due to reduced litter sizes. Underfed mothers also took longer to leave the nest to retrieve the first pup than did control mothers (Smart & Preece, 1973). Syrian hamster mothers on restricted diets cannibalized more pups and maintained fewer pups than mothers on unrestricted diets (Schneider & Wade, 1989).

Maternal underfeeding also influences pup development and behavior. Chow and Lee (1964) found that restricting dietary intake in female rats during gestation and lactation by as little as 25% of that consumed by unrestricted rats resulted in offspring with stunted growth (lower weights in offspring were observed one year later as well), anaemia and decreased resistance to hypothermia. Similar effects occurred when the dietary restrictions were imposed only during gestation.

Weiner et al. (1977) found that mother rats fed a low protein diet had pups that were lighter in weight than pups of mothers fed *ad lib* on lab chow. Jen et al. (1977) investigated the effects of food restriction (75% of *ad lib* initiated during the 3rd trimester of pregnancy) and litter size on pup weight and development. Rat dams were randomly assigned to four groups: food restricted/small litter size (4 pups), food restricted/large litter size (12 pups), *ad lib* food/small litter size and *ad lib* food/large litter size. Pups gained weight fastest in the *ad lib* food/small litter size group, followed in descending order, by the food restricted/small litter size group, *ad lib* food/large litter size group and food restricted/large litter size group. Pups fed by food restricted dams or dams with large litters gained weight less rapidly and showed ear opening at a later age.

These two variables interacted as pups raised by food restricted dams with a large litter had the longest delay for ear opening. The same pattern occurred for eye opening, as pups fed by a food restricted dam with a large litter had eye opening significantly delayed (Jen et al., 1977). In rat pups, the frequency of climbing and rearing (locomotor behavior) and the mean time spent drinking or feeding from a food cup was reduced in those fed by protein restricted mothers (Massaro et al., 1974).

Rat pups (*Rattus norvegicus*) engaged in significantly more social play when their mothers were food restricted (25% less than *ad lib*) during lactation but did not weigh less at weaning than control pups. Mothers that were food restricted, weaned pups (refused to suckle pups) at an earlier age than *ad lib* controls and these early weaned pups showed increased social play (Smith, 1991).

Underfeeding thus influences weight gain, sexual development, reproductive and parental behavior and also influences pup survival, development and behavior. Wheel running may be a better model of foraging than food restriction (Perrigo & Bronson, 1983). Wheel running in rats has been used to investigate patterns of activity and feeding over the LD cycle and the results indicated that the daily patterns of wheel running and food intake influenced each other. Stewart et al. (1985) for example, found that small, frequent meals and more rapid wheel running occurred early in the dark phase in rats, and larger, less frequent meals occurred later in the dark phase when wheel running had declined.

Wheel running is influenced by the LD cycle. Tokuyama et al. (1982) and Eikelboom and Mills (1988) found that female Sprague-

Dawley rats ran more than males, mostly during the dark phase. Running peaked at the beginning of the dark phase and dropped to low levels by the beginning of the light phase. Tokuyama et al. (1982) also found that the food intake of males and females that were running increased when compared to sedentary rats and that the rate of food intake was greater for females than for males. For both sexes, those that exercised gained less weight than those that were sedentary.

Access to a running wheel is rewarding as rats will perform operant tasks to gain access to a running wheel, and then will run thousands of revolutions per night (Eikelboom & Mills, 1988). Rats given access to a running wheel will also initially lose weight (Looy & Eikelboom, 1988). When CF-1 female mice that were fed *ad libitum* were given access to a running wheel, they increased their spontaneous wheel running by sevenfold over a 24 day period (Perrigo & Bronson, 1983). When wheel running was prevented by locking the wheel, female mice altered their pattern of food consumption. Mice with access to free running wheels increased the amount of food they consumed over the 24 day period, while mice with access to locked wheels, increased their food intake for the first 4 days, then food consumption plateaued. Females that were housed with a locked wheel had a lower body weight, higher fat content and delayed sexual maturation when compared to females with the free running wheels. Thus, when the behavioral and physiological changes that occur when wheel running is used to mimic foraging are considered, it is apparent that providing access to a running wheel is not a trivial manipulation. Access to a running wheel can be used as a model for foraging and has great value in studying the reproductive ecology of mice.

The effects of wheel running for food on adult reproduction vary depending on the age, sex and species of the subjects. Perrigo and Bronson (1983) determined the effects of foraging effort and food intake on the reproduction of CF-1 mice (*Mus musculus*). They designed their experiment so that animals must run a programmable number of revolutions on a running wheel to obtain a pellet of food. Food scarcity was simulated by requiring a large number of revolutions per food pellet. In female peripubertal mice, an increase in the revolutions required per pellet had the greatest effect on sexual maturation and body weight. The number of ovulatory cycles that occurred in females during the 24 day experiment was dramatically reduced as the number of revolutions per pellet increased and this occurred before a significant decrease in body weight was observed.

Perrigo and Bronson (1985) investigated behavioral and physiological responses of female house mice (*Mus domesticus*) to cool (9^0C) or warm (23^0C) ambient temperatures and to different foraging requirements. Mice were housed with running wheels and either fed *ad libitum* or were required to run different numbers of revolutions per food pellet over a six week period. Female house mice maintained at 9^0C, required about 50% more food to maintain normal body growth than mice maintained at 23^0C. At 9^0C, females also engaged in less wheel running and despite having *ad lib* food, their reproductive development was retarded. Females housed at 9^0C and required to run 200 revolutions per food pellet ceased running extra revolutions, could not maintain normal body growth and their reproductive development was retarded. Perrigo and Bronson (1985) concluded that female mice first channelled energy to maintain their own body weight, then to stimulate growth, then to support reproduction and finally to support nonforaging activity.

Sex differences in energy allocation were investigated in intact or gonadectomized *Mus musculus* which were required to run 200 or 300+ revolutions per food pellet. The 200 revolutions per pellet regime allowed normal body growth and reproductive development whereas requiring 300+ revolutions per food pellet allowed survival but not normal body growth. Reproductive growth was totally inhibited in intact females at 300+ revolutions whereas intact males developed normal reproductive function regardless of their stunted growth. At both feeding levels, females showed more locomotor activity and consumed more food than males in both the intact and gonadectomized groups (Perrigo & Bronson, 1985). The number of extra revolutions (generating food that was not consumed) run by intact males increased as they became sexually mature but were reduced to zero in gonadectomized males (Perrigo & Bronson, 1985, Perrigo, 1990).

Sex differences in the rate of food consumption, growth, fertility onset, fat deposition and spontaneous locomotor activity were examined in wild and domestic CF-1 male and female mice (*Mus musculus*) housed in a running wheel during peripubertal development. CF-1 females had puberty onset earlier than wild females whereas there was no difference in the time of puberty onset in males. Male and female CF-1 mice consumed more food, had a higher body weight, a higher growth rate and lower locomotor activity than wild mice (Bronson 1984).

There are species and strain differences in response to increasing the work (wheel running) required per food pellet. *Mus musculus* and *Peromyscus maniculatus* were exposed to one of six feeding requirements for 7 to 10 weeks. One group was given access to a running wheel and fed *ad libitum* while the other four groups were required to run 75, 125, 175 or 275 revolutions per 45 mg pellet of food. Wheel running behavior, body weight and food consumption were measured when females were pre-reproductive (first 3 weeks), pregnant and lactating. *Mus* did not alter the number of revolutions they ran or the time spent wheel running as the work requirements increased, while *Peromyscus maniculatus* increased the number of revolutions they ran as work levels increased, especially during lactation. Most *Peromyscus* at the highest work levels did not become pregnant. But if they became pregnant, the size of their litters (5 to 6 pups) did not differ from that of dams in the other groups at birth and weaning. *Peromyscus* pups decreased in weight as the dams' work load increased. *Mus* attempted reproduction regardless of the feeding conditions but cannibalized young up to 12 days of age at the highest work levels. As the litter size decreased in *Mus*, most surviving pups had similar body weights at weaning (Perrigo, 1987, 1990).

As mentioned at the beginning of this chapter, small rodentss require relatively large amounts of food, so a major part of their day is spent foraging. Foraging uses energy and requiring rodents to run on a wheel for food takes into account that the energy expended in foraging is an important component of a rodents' reproductive ecology. Foraging imposes limitations on what other activities rodents can engage in. When a running wheel is used as a model of foraging, several of the same effects found with food restriction are observed. These include delayed sexual maturity and reduced weight gain in adults. However, wheel running also allows investigators to determine how animals partition their time and energy between foraging for food (wheel running) and meeting the demands of adult growth, sexual development, pregnancy, lactation and parental behavior. When food is scarce, a female could increase the amount of time spent foraging in order to maintain her reproductive behavior or redirect the use of her energy to meet survival and maintenance demands first and then reproductive demands (Perrigo & Bronson, 1983, 1985). Therefore, food restriction as a method for studying the effects of reduced food availability may limit and obscure some of the behaviors that rodents would engage in to solve the problem of food scarcity. Using a running wheel system such as that described by Perrigo and Bronson (1983) would be advantageous when trying to answer questions about how animals adapt to changing food availability in their environment.

Virtually all of the studies that have examined the effects of male parental care on offspring survival and development have provided animals with all the food, bedding and water they need. Under these "standard" laboratory conditions, the male's contribution may have been obscured because the mother need not forage for food and can adequately care for offspring herself. The influence of paternal care may only be revealed when the mother must forage for food or cope with adverse environmental conditions (see Brown, 1993). Food restriction may not be an appropriate model for foraging as it eliminates the locomotor requirements of foraging and this behavior must be alternated with maternal and paternal behavior when animals live in their natural environment. Male parental care may only be useful in terms of enhancing the survival and development of pups, when the energy demands of foraging compete directly with parental behavior and hence a second parent would be needed.

2.2 Effects of the LD cycle on wheel running, parental behavior and reproductive activity

Biological rhythms with periods of approximately 24 hours (circadian rhythms) are thought to be endogenous to the organism but synchronized by environmental stimuli, especially light (Ader and Grota, 1970). Seasonal rhythms are found in the wheel running and maternal behavior of the rat (Perrigo, 1990, Dewsbury, 1980, Ader & Grota, 1970, 1974), but appear to be absent in the reproductive activity of *Mus* (Pryor & Bronson, 1981)

Perrigo (1987, 1990) compared the activity of *Mus musculus* and *Peromyscus maniculatus* in running wheels. *Peromyscus maniculatus* showed an activity rhythm which was rigidly entrained to the LD cycle and were active only during the dark phase. *Mus* activity was loosely organized around the LD cycle with day to day variation. Most of the activity was displayed during the dark phase but considerable activity also was displayed during the light phase.

When lactating *Mus* and *Peromyscus* females were fed *ad libitum* they both responded by reducing wheel running during the dark phase, below what was observed before lactation. Most of the light phase was spent nursing their litters. When *Mus* were required to work for food, females shifted their wheel running behavior to the light hours with the mother feeding herself in sporadic bouts of 1-5 hours. The length of the feeding bouts increased as the work required increased. *Peromyscus* females did most of their wheel running during the dark phase with a few bouts of 1-2 hours during the light phase.

Dewsbury (1980) described the number of revolutions and periodicity of wheel running over the LD cycle in a twelve species of male rodents, including *Peromyscus maniculatus*, *Microtus pennsylvanicus* and *Mus musculus*. *Peromyscus* species ran more revolutions than *Microtus* and there was no signficiant difference between *P. maniculatus* and *Mus musculus*. All species ran the majority of revolutions during the dark phase. Thus, we would expect our mice to run more in the dark phase than during the light phase of the LD cycle.

Males of many rodent species restrict breeding to the spring and summer but some males reproduce all year. Moffatt et al. (1993) were interested in the differences between male prairie voles and deer mice and what factors enabled some males to remain reproductive all year. They measured circadian locomotor activity, basal metabolic rate, capacity for nonshivering thermogenesis, nest building, body mass and daily food intake in males that were maintained under long daylengths (LD 16:8) or short daylengths (LD

8:16). These males were classified as being reproductively regressed or nonregressed (as measured by testes size). Males that maintained reproductive function during short daylengths resembled long daylength animals on some measures and short day-length animals on others. Long-day male voles ran more revolutions in a running wheel than short day males in both species (regressed and nonregressed). Male deer mice maintained under conditions of long or short-days showed differences in entrainment of locomotor activity. Short-day mice, regardless if they were reproductively regressed or nonregressed, began wheel running about 1 hour after lights off while long-day deer mice began wheel running much earlier (0.15 hr after lights off). Food intake was regulated by daylength and long-day males consumed more food than short-day males.

Photoperiod seems to have little influence on reproductive activity in male and female *Mus musculus* maintained under 16L:8D or 8L:16D cycles. Diet and temperature were important for the production of litters but photoperiod did not influence production of litters or interact with diet and temperature (Pryor & Bronson, 1981). Other studies have shown no relationship between daylength and reproduction and *Mus* have bred successfully when maintained for long periods in constant darkness in the lab (Bronson, 1979). *Peromyscus maniculatus* are restricted to seasonal breeding and require long days to be reproductively active (Dejardins & Lopez, 1983).

Wild California mice (*Peromyscus californicus*) are crepuscular, having the highest levels of activity within a few hours of nightfall and predawn (Marten, 1978). Breeding occurs throughout the year in both the field and in the laboratory (Drickamer & Vestal, 1973) but litter production is most successful under a 16:8 LD cycle (Gubernick & Alberts, 1987). Therefore, reproductive activity may be more entrained to the photoperiod in *Peromyscus* than in *Mus*.

Ader and Grota (1970) continuously recorded the amount of time that lactating female rats spent with their litters from birth until weaning and found that a 24 hour rhythm existed for maternal behavior. Under a 12:12 LD cycle, the female rat spent the most time in contact with her litter in the middle of the light phase and the least time with her litter during the dark phase. Females that were maintained under a 6:6 alternating LD cycle also displayed a 24h rhythm of maternal behavior. The greatest amount of time spent with the litter was equally divided between the two 6h periods of light. When females raised litters under continuous light, they displayed a free-running rhythm with an average period of 24 hours (Ader & Grota, 1970, Leon, 1975). Mothers that raised pups under conditions of constant light had pups that gained weight at a slower rate than mothers raising litters under 12:12 LD cycle (Leon, 1985). The amount of time spent with the litter decreased as the litter aged (Ader & Grota, 1974) and the principle behavior when the female and pups were together was nursing. Activity, feeding and drinking behavior were more frequent during the dark phase.

One possible reason for maternal contact being elevated in the light phase and suppressed in the dark phase is that there are fluctations in the mother's body temperature (Ader & Grota, 1970, Grota & Ader, 1969, 1974, 1975, Lee & Williams, 1977). The body temperature of the Norway rat (*Rattus norvegicus*) fluctuates over the 24 hour day and peaks in the dark phase of the LD cycle. Leon et al. (1984) found that this nocturnal peak in maternal temperature corresponded with the termination of nursing bouts in the dark phase.

Food availability can influence the periodicity of maternal behavior in rats. When food iss supplied *ad libitum* all day or only during the dark phase, maternal behavior was diurnal whereas when food was available only during the light phase, maternal behavior was nocturnal (Stern & Levin, 1976).

Gubernick and Alberts (1987) found diurnal and nocturnal variations in some parental behavior patterns of *P. californicus*. Nest attendance was the highest during daylight hours and pups were left alone less in the day than during the night. During the night, fathers stayed with the pups while the mother was out of the nest and fathers did more pup licking during the day. The mother displayed no differences in the amount of pup licking during the light or dark phases of the LD cycle.

This chapter shows that wheel running is a better measure of the effort required to forage for food than food restriction and that female reproductive effort is more sensitive to food availability than male reproduction. The patterning of locomotor (foraging) activity and parental behavior depends of the LD cycle and the LD cycle organizes the timing of locomotion, feeding, reproduction and parental behavior in rodents. Thus, an important question in my experiment is how the LD cycle influences the pattern of wheel running and parental behavior under different environmental demands. I am interested in the interaction of the male and female in parental behavior and wheel running (foraging) in the light and dark phases of the LD cycle and in determining whether male parental behavior shows a circadian rhythm. Finally, I want to determine whether the male's parental behavior benefits the pups more during light phase or the dark phase of the LD cycle. For example, male parental care may be of less benefit during the light phase, when the female is usually on the nest, but may be of great benefit during the dark phase when she leaves the nest to forage. Thus in pairs which must forage for food, male parental care may show a different circadian pattern than in pairs who received *ad lib* food.

Chapter 3

Ecology and reproductive behavior of *Mus musculus* and *Peromyscus californicus*

Male parental care may be more likely to occur in species that evolved in an environment where food resources and the local population are stable (K-strategists) as opposed to species that evolved in a more variable environment (r-strategists). A K-selected species is concerned with maintaining the current population since it is at the carrying capacity of the environment. The emphasis is on efficiently utilizing limited resources to produce a few viable offspring. In an r-selected species, the environment encountered, occasionally allows swift increases in population numbers and these species have adapted to take advantage of these unpredictable environmental conditions. When the environment is favorable, breeding is prolific and the quickest breeders will have the greatest share of the gene pool (Daly & Wilson, 1983). Characteristics of K-strategists include few offspring, high parental investment in offspring, low infant mortality, slow development, large body size, stable population size and the occupation of one suitable habitat. Characteristics of r-strategists include, many offspring, low parental investment in each offspring, high infant mortality, rapid development, small body size, variability in population size and the colonization of several habitats (Daly & Wilson, 1983).

As discussed in Chapter 1, male parental behavior occurs more often in species with monogamous mating systems than those with polygynous mating systems. This thesis compares the effects of male parental care in two species of mice (*Mus musculus* and *Peromyscus californicus*) which differ in their reproductive strategies and mating systems. This chapter examines the evidence from the ecology and mating systems of these two species which suggests that *M. musculus* is an r-strategist and polygynous while *P. californicus* is a K-strategist and monogamous. Based on the evidence from Chapter 1, male parental behavior should be more likely in *P. californicus* than *M. musculus.*

3.1 Ecology of house mice (*Mus musculus*) and California mice (*Peromyscus californicus*)

House mice are extremely adaptable and are found worldwide in diverse habitats ranging from residential buildings, farms and storage warehouses to corn ricks and open fields (Reimer & Petras, 1968, Smith, 1954, Laurie, 1946, Brown, 1953, Southern & Laurie, 1946). They live as commensals of man or in feral habitats (Bronson, 1979, Berry 1981). Commensal populations have high stable densities and are characterized by the division of space into territories that are dominated by one male. Feral populations are characterized by temporal, spatial and social instability since territories are impossible to maintain over the large home ranges necessary in feral habitats (Bronson, 1979). *Mus* feed on diets ranging from an omnivorous mixture of plant and animal materials (insect larvae or crustacea) to white flour (Bronson, 1979). This small mammal's success at colonizing such diverse habitats is partially due to the fact that house mice do not use predictive seasonal cues such as hours of light per day and temperature changes to regulate reproduction. They are capable of breeding in total darkness year round, even at subfreezing temperatures, if provided with enough food (Pryor & Bronson, 1981). Therefore, dietary requirements seem to be the main factor in determining where and when *Mus* are capable of breeding (Bronson, 1979). House mice become reproductively mature at 42 to 56 days of age but have a low life expectancy of 100 to 150 days after birth (Konig & Markl, 1987, Pennycuick et al., 1986). Juvenile mortality is usually high (from 50-85%) in open enclosures (Pennycuick et al., 1986). Adult *Mus* weigh 20 to 30 g, have a gestation period of 21 days, produce an average of 8 offspring per litter and pups are weaned after 21 days of age (Priestnall & Young, 1978).

California mice are found predominantly in chaparral and sage scrub regions of coastal California as far south as the Baja Peninsula. The California mouse often inhabits large surface dens of wood rats (*Neotoma fuscipes*) and on occasion both species are found in the same den (Merritt, 1978, Cranford, 1982). One of the factors limiting the distribution of *P. californicus* is the availability of these dens for hiding places (Merritt, 1974).

These mice are diet specialists, living mostly on the seeds of the California laurel, but also will eat scrub fruits and flowers (Merrit, 1978). These animals are fairly sedentary and have low but stable population sizes and a low reproductive potential (Gubernick, 1987). Breeding occurs throughout the year in the lab (Gubernick, 1987) but seasonally, from November to April, in the wild. (Ribble, 1990). The average age of first reproduction is 250 days (Ribble, 1992b). Adults weigh 30 to 50 g and the gestation period is 31 to 33 days, after which, 1 to 4 young are produced and pups are weaned after 32 days of age (Gubernick 1988, Rood, 1966). Females produce an average of 2.5 litters and 1.7 offspring per 8 month breeding season (Ribble, 1992b). Ribble (1992a) found adult *P. californicus* females were resident on a home range for an average of 280.9 days (s.d.=248.0) and adult males were resident on a home range for an average of 342.2 days (s.d.=217.4). Juvenile mortality in the nest was low as 94% of births produced at least one weaned offspring.

3.2. Social organization and mating system of *Mus musculus* and *Peromyscus californicus*

Mus musculus have been found in monogamous pairs (Lidicker, 1976) but usually the social organization of the house mouse involves the division of space into territories and the dispersal of mice over these territories depends on their sex and social class (Hurst, 1987). Based on their movements within an enclosure, their access to resources (nesting boxes, water and food), breeding status and tolerance of other individuals, Hurst (1987) defined five social classes for male *Mus* and five social classes for females. Some males were exclusively territorial, would not tolerate other males on their territory and also excluded some females. These males mated with females that were on their territory and rarely invaded other territories in the enclosure (Hurst, 1987, Crowcroft & Rowe, 1963, Poole & Morgan, 1976, Bronson, 1979). Using genetic markers to determine paternity, it was found that the dominant male in the breeding group produced over 90% of the offspring (DeFries & McLearn, 1972). There is evidence to suggest that larger males are more successful at gaining a territory with a resource situated on it and reproducing while such a relationship between body weight and access to males for reproduction is not important among females (Krackow, 1993). Females prefer to mate with males that have territories with a resource (Wolff, 1985).

Males who defended an area against other males were described as dominant territorial. Some subdominant and subordinate males were tolerated on these territories although subdominant and subordinant males were frequently attacked and chased by the dominant male on the territory (Reimer & Petras, 1967, Mackintosh 1970, Poole & Morgan 1976, Hurst, 1987). Subdominant males lived within territories controlled by the dominant male and sometimes contributed to defense and frequently crossed territorial boundaries into neighboring territories. They were attacked by females in home and neighboring territories but were generally in good physical condition and were never seen mating. Subordinate males lived within territories of dominant males and their movements were more restricted than subdominant males. They were in medium to poor condition, were largely nonaggressive and were never seen mating. Young subordinate males spent most of their active time near resources even though they were chased by the dominant male and females. They were in excellent condition and were never observed mating. Dominant males retained their status for several months and spent much of their time patrolling territory boundaries (Reimer & Petras, 1967, Crowcroft, 1955).

Breeding females can have unrestricted, restricted or partial access to resources (Hurst, 1987). Dominant breeding females with unrestricted access to resources moved freely between nest boxes and food sources and some moved around the entire enclosure (through several males' territories). They defended resources in the territory against invading males and females and were the only females observed to attack the resident territorial male. They often mated with more than one territorial male (Hurst, 1987). Breeding females with restricted access to resources, lived in and helped defend territories that were not situated around a resource (nest box or food source). These females mated only with the territorial male and never reared their offspring to independence. Females with partial access to resources spent much of their time around the nest boxes even though they were attacked by the resident male. These females mated with neighboring territorial males, but not the resident male that had the nest box on his territory. Females with partial access to resources also did not have offspring that survived to weaning. They were chased from all resource areas by males and females (Hurst, 1987).

Nonbreeding females could have either unrestricted or restricted access to resources. Those females that had unrestricted access to resources had a similar distribution as the breeding females that had partial access to resources but were never seen mating, pregnant or lactating (Hurst, 1987). Nonbreeding females that had restricted access to resources were chased from the resource areas by resident males and females and were never seen, mating, pregnant or lactating. Therefore, *Mus musculus* is a polygynous species in which the dominant males mate with many females and the dominant females mate with many males.

The survival of offspring in house mouse populations is influenced by population density, season, aggressive behavior, access to undisturbed nesting sites and the number of adult males within the nest (DeLong, 1978, Southwick, 1955, Lloyd, 1975, Pennycuik, Johnston, Westwood & Reisner, 1986, Hurst, 1987). Pup survival is reduced at high population densities (fewer adult females were pregnant at higher densities as well) and more pups survived during the late summer-early autumn (Pennycuik et al, 1986, DeLong, 1978, Lloyd & Christian, 1969, Crowcroft & Rowe, 1957). Seasonal fluctuations in population density are due to the number of dispersing juveniles that enter the population and not due to availability of food and shelter (Pennycuik et al., 1986). Increased aggression associated with maintenance of territories contributes to high mortality of neonates as does the trampling of nest sites or lack of protected nest boxes with two entrances (only one entrance does not allow a fleeing mouse to escape through another entrance before the nest area iss disturbed, DeLong, 1978, Lloyd 1975, Hurst, 1987, Crowcroft & Rowe, 1963).

If more than one female is pregnant at the same time in a population, females will combine their offspring into one nest. When pups are raised communally, they have faster growth rates because several females share nursing and pups receive more milk Werboff, et al., 1970, Sayler & Salmon, 1969, Southwick, 1955). In addition, Wilkinson and Baker (1988) found that female house mice prefer to communally nest with closely related females rather than unrelated females.

Young male and female *Mus* both, disperse from their natal area after weaning. Young females may be successful in entering an established territory while young males have great difficulty entering an established territory or establishing their own territory (Bronson, 1979). There is high mortality among young dispersing males as intense fights occur for territories and dominance and the losers may be killed (Reimer & Petras, 1967, Crowcroft, 1955, Lidicker, 1976, Singleton & Hay 1982).

As reviewed in chapter 1, domestic male *Mus* have been observed to provide the same amount and type of parental care as females, except for nursing. The most common paternal behaviors are licking pups, huddling over pups, retrieving pups and nest building (Jakubowski & Terkel, 1982, Weunsch & Cooper, 1981, Ostermeyer & Elwood, 1983, Barnett & Dickson, 1985, Dewsbury, 1985).

The home ranges of male and female *P. californicus* overlap extensively and overlap relatively little with other pairs' home ranges. Female home ranges are smaller than male home ranges. The fact that adjacent adults have exclusive home ranges provides evidence that mated pairs defend territories. Pairs remain together permanently unless one of the pair dies. A paired male and female may associate together for several months before reproducing (Ribble, 1992). Gubernick and Nordby (1994) suggest that a female's preferred social partner is not necessarily their preferred mating partner in the lab. This anomally in female preference for social and mating partners, could be the result of certain environmental factors being absent in laboratory. In their laboratory experiments, the social organization of these animals was different than that found in the wild since males usually defended their own territory against other intruding males and the female normally would not have the opportunity to associate with another male (Gubernick & Nordby, 1994).

P. californicus in the wild are monogamous across their range and in different habitats (Merritt, 1978). Monogamy occurs at various population densities suggesting that a low number of dispersing females is not a factor influencing this mating system (Ribble, 1992b). DNA fingerprinting has shown that the offspring from 28 families were due to the exclusive matings between single males and females over a 2 year period. No cases of multiple paternity were discovered (Ribble, 1992b). The number of offspring produced by males and females in their lifetime was similar as would be expected in a monogamous species (Ribble, 1992b). Females prefer to mate with their own partner rather than a strange male, but 15-20% of females will mate with an unfamiliar male if given the opportunity whether their mate is present or not (Gubernick & Nordby, 1993). Males preferred to associate with their mate and did not copulate with an unfamiliar estrous female regardless of whether their mate was present or not. Monogamy in *P. californicus* seems to be due to a preference for their own pairmate and self restraint in mating with others (Gubernick & Nordby, 1993).

Juvenile female *P. californicus* disperse further than juvenile males. Ribble (1992a) gives evidence that intrasexual mate competition drives female dispersal and resource competition drives male dispersal. The male usually settles first on a home range and is then joined by a female. Puberty is delayed if juvenile females have direct contact with their mother. Gubernick and Nordby (1992) determined that physical contact with the mother is necessary for the delay and not a urinary chemosignal.

Mates of lactating females spent similar amounts of time in the nest as their female partner. Although there was no direct evidence of the male caring for the young, the male was in the nest at the same time as the female (Ribble & Salvioni, 1990). Males displayed as much parental behavior as females except for nursing and spent comparable amounts of time in the nest (Ribble & Salvioni, 1990, Dudley, 1974, Gubernick & Alberts, 1987). Mated pairs spend more time in the nest when they are in the lab than when they are in the wild (Ribble & Salvioni, 1990).

In summary, *Mus musculus* are r-strategists in that they are opportunistic colonizers, utilize various food sources, breed when food is abundant regardless of season, have a short gestation and lactation period and produce many offspring. *P. californicus* are K-strategists in that they occupy a more stable environment, are diet specialists, are seasonal breeders, have longer gestation and lactation periods and produce fewer offspring. *Mus musculus* have a social organization that reflects their polygynous mating system, and *P. californicus* have a social organization that reflects their monogamous mating system.

These two species were chosen for the research in this thesis because I was interested in the difference in male parental care displayed by a monogamous, K-strategist versus a polygynous r-strategist when they were placed in the same semi-natural environment. In addition, I was interested in the value of male parental care to the offspring, for although male parental care has been observed in *Mus musculus*, its value has been debated (Barnett & Dickson, 1985, Priestnall & Young, 1977, Wuensch & Cooper, 1981, Mugford & Nowell, 1973, Smith & Simmel, 1977). Male parental care should increase offspring survival in *P. californicus*, whereas this may not be the case for *M. musculus* as Southwick (1955) has noted that the presence of one or more adult male *Mus* in a nest box reduced litter survival.

Chapter 4

Research objectives, experimental design and pilot studies

4.1 Research objectives.

The objectives of this thesis were to examine six research questions. The first objective was to determine if the housing environment of mice influenced the number of pups surviving to weaning and the weight of pups at weaning. In particular, we wanted to know if requiring adult mice to run for food would alter their pups survival and development. The second objective was to determine if the presence of the father influenced the number of pups surviving to weaning and the weight of the pups at weaning. The third objective was to determine if the father displayed the same parental behaviours as the mother and if the father spent the same amount of time in these behaviours as the mother. The fourth objective was to determine whether mothers and fathers differed in (a) time spent running on the wheel (foraging) and (b) consumption of food pellets earned. The fifth objective was to determine how mice partition their wheel running and parental care during the light and dark phases of the LD cycle and to determine if there were differences in how their time (parental behavior, wheel running and eating) was partitioned due to the fathers' absence or presence and type of foraging schedule. The sixth objective was to determine whether there were differences between a polygynous species (*Mus musculus*) and a monogamous species (*Peromyscus californicus*) in these behaviors. We were particularly interested in whether these two species differed in terms of the father's effect on pup survival and growth and whether the two species engaged in different types of parental behaviours and different amounts of parental behaviour.

4.2 Pilot study 1.

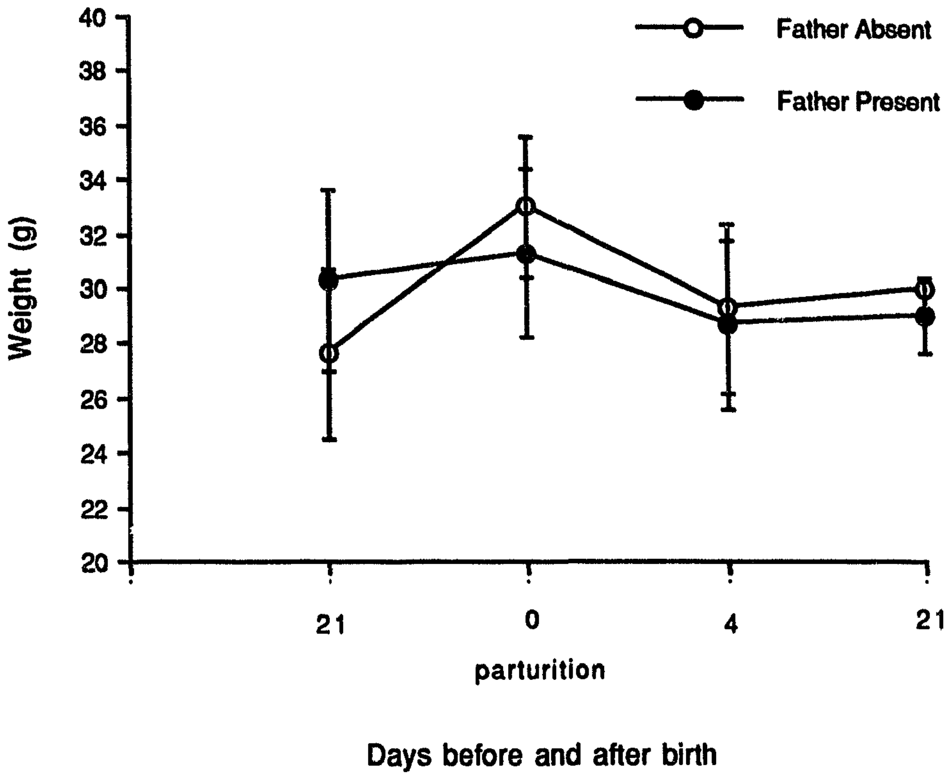
This pilot study was conducted to determine a) the number of revolutions mice would be required to run for each food pellet and b) the method chosen to observe behavior would provide the information to answer the research questions summarized in section 4.1. In order to estimate the number of revolutions we would require mice to run per pellet, we placed 4 paired females (with their mate) and 4 single females, in cages with running wheels connected to counters (counters displayed the number of revolutions digitally). The number of revolutions was read from the counter and recorded manually once a day, for 30 days. As there were only 4 running wheel cages available at one time, mice were run in two squads which consisted of two paired females and two single females (paired females were pregnant). The number of pellets of food was recorded for the second squad by placing 50-80, 190 mg Noyes pellets in each cage and recording the food left unconsumed the next day. The results showed that paired mice ran an average of 24711 revolutions (s.d.=1174) and consumed an average 70 pellets (s.d.=10) and single females ran an average of 14786 revolutions (s.d.=1469) and consumed an average of 33 pellets (s.d.=9). I therefore, decided to use 400 revolutions per pellet, as paired mice would receive an average of 62 pellets per day and single mice would receive 37 pellets per day.

Eight female *Mus musculus* were paired with males and placed in running wheels. After one week, the males were removed from half of the cages to create Father Absent and Father Present groups. Mice were required to run 400 revolutions for a 190 mg Noyes pellet for 18 days, after which the number of revolutions to earn a pellet was reduced to 300 revolutions. The reduction in revolutions was necessary as the mice were not gaining weight. Mice then ran 300 revolutions per pellet up to 19 days prior to parturition and during lactation. All 4 females in the Father Present group had pups and 3 of 4 females in the Father Absent group had pups.

Pup survival and growth. Of the 3 litters born in the Father Absent group, 2 litters died and one litter was reduced from 5 to 3 pups. Of the 4 litters born in the Father Present group, 2 litters died, one pair reduced their litter from 7 to 3 pups and one pair reduced their litter from 9 to 5 pups. Only 43% of the litters survived (3 of 7 litters) and 21% of the pups survived (12 of 58 pups). At birth, pups in the Father Present group, weighed an average of 1.7 grams (s.d.= 0.2) and pups in the Father Absent group weighed an average1.4 g (s.d.=0.3). At weaning (21 days), pups in the Father Present group weighed an average of 5.8 g (s.d.= 0.3) and pups in the Father Absent group weighed an average of 6 g (s.d.=0, based on one litter).

Mothers weights (Figure 4.1). Mothers in the Father Present group (n=4) weighed an average of 30.3 g (s.d.=3.3) at the beginning of the experiment, 31.3 g (s.d=3.1) after parturition (day 0, n=4), 28.7 g (s.d.=3.1) on day 4 after parturition (death of 2 litters, n=2) and 29 g (s.d.=1.4, n=2) at weaning (day 20). There was no

Figure 4.1. Mean body weight (± S.D.) of Mus musculus mothers in the Father Absent and Father Present groups in pilot study 1



large weight gain by day 20 to indicate that mothers were pregnant again.

Mothers in the Father Absent group (n=3) weighed an average of 27.6 g (s.d.=3.1) at the beginning of the experiment, 33.0 g (s.d.=2.6) at parturition (Day 0, n=3), 29.3 g (s.d.=3.1) on day 4 after parturition (death of 2 litters, n=1), and 30 g (s.d.=0, n=1), by weaning (days 20). These mothers did not have enough energy for growth. Since mothers severely reduced or killed their entire litters, it was concluded that the 400 revolutions per pellet schedule was too high for mice to maintain a litter. The schedule was reduced to 300 revolutions per pellet for the second pilot study.

Number of revolutions and food earned (Figures 4.2 and 4.3). The number of revolutions run was recorded daily from 20 days before parturition to 20 days after parturition. The days were condensed into blocks of 5 days resulting in four, 5 day blocks of time before birth and four, 5 day blocks after birth. However, as so few females retained their pups in this study, there was only enough wheel running data for four, 5 day blocks before birth. The number of revolutions was totaled during the light and dark phases of the LD cycle each day and then each 5 day block of data was averaged, resulting in a 2 (Father Absent or Present) x 2 (light or dark phase) x 5 (days) ANOVA.

Mus in the Father Present group (n=4) ran significantly more revolutions overall than *Mus* in the Father Absent group ($F_{(1,5)}$=55.2, p<.001, n=3). *Mus* ran significantly more revolutions during the dark phase ($F_{(1,5)}$=331.1, p<.001) than during the light phase of the LD

Figure 4.2. Mean revolutions during the a) light phase and b) dark phase for Mus musculus in pilot study 1.

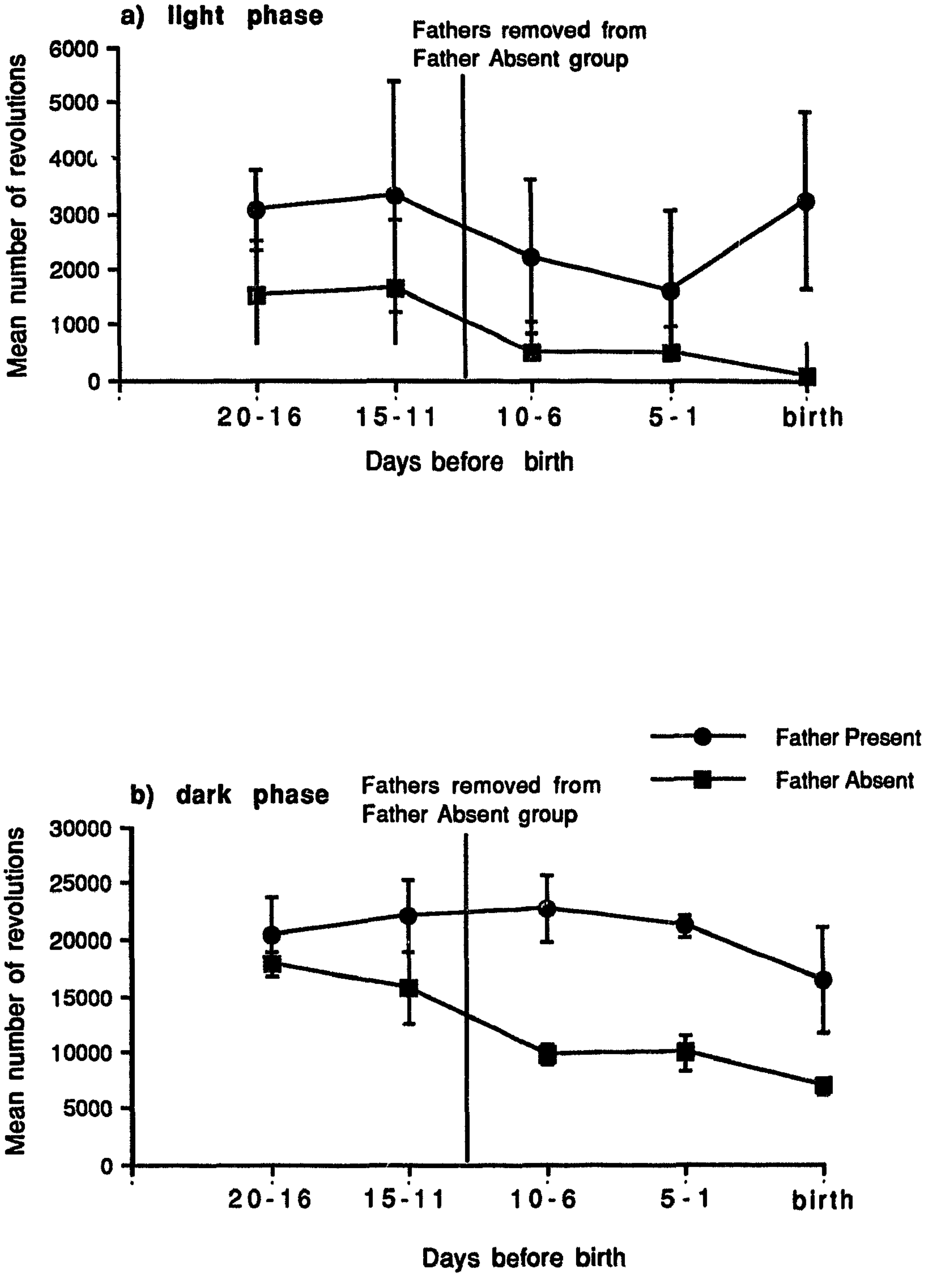
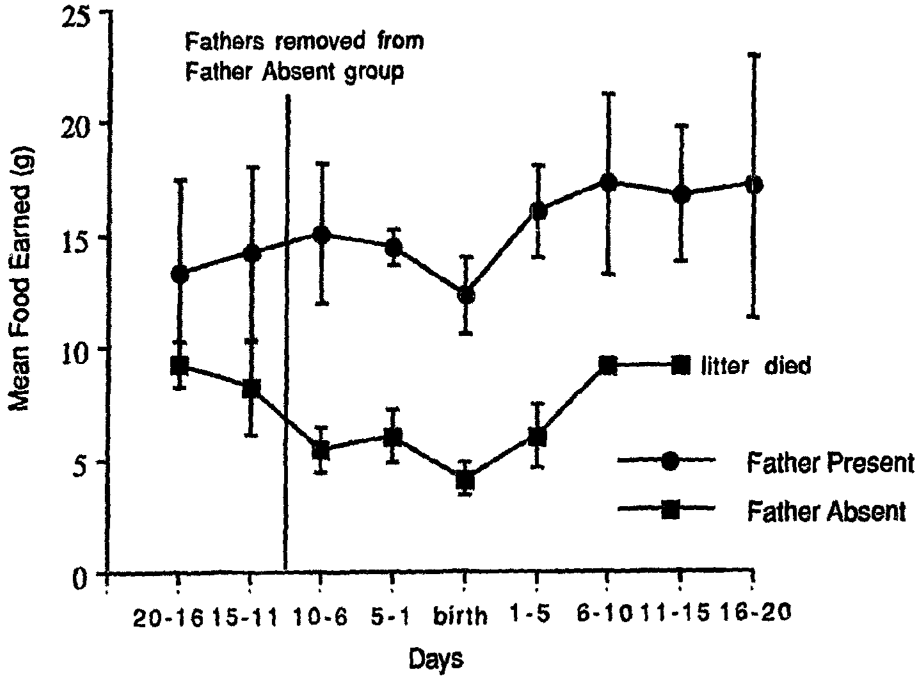


Figure 4.3. Amount of food earned by Mus musculus in pilot study 1.



cycle. There was a significant interaction between the LD cycle and parenting groups ($F_{(1,5)}=17.7$, $p<.01$) as *Mus* in the Father Absent group ran fewer revolutions during the light phase than did those in the Father Present group (due to the removal of the father). There was a significant effect of days ($F_{(4,20)}=16.3$, $p<.001$), as mice reduced the number of revolutions they ran on the day of parturition, and a significant interaction between days and parenting ($F_{(4,20)}=6.3$, $p<.01$) as those in the Father Absent group reduced the number of revolutions they ran over days more than those in the Father Present group. There was a significant effect of days as *Mus* ran fewer revolutions as females approached parturition ($F_{(4,20)}=19.7$, $p<.001$). There was a significant interaction between the LD cycle and days ($F_{(4,20)}=5.9$, $p<.01$) as *Mus* reduced the number of revolutions more during the light phase than during the dark phase over days. There was a significant interaction between the LD cycle, days and parenting ($F_{(4,20)}=3.4$, $p<.05$). *Mus* in the Father Absent group reduced the number of revolutions over days more during the light phase than those in the the Father Present group. *Mus* in the Father Present group maintained the same number of revolutions throughout during the dark phase while those in the Father Absent group reduced the number of revolutions they ran after block 2.

Mice in the Father Present group generated more food each day (an average of 13.9 g) than mice in the Father Absent group (an average of 6.6 g, $F_{(1,5)}=65.9.9$, $p<.001$). There was no significant effect of days before parturition ($F_{(4,20)}=1.8$) and there was no significant interaction between the parenting groups and days ($F_{(4,20)}=1.4$) for the amount of food generated. Mice did not always consume all of the food they generated, especially during the first two weeks. For Pilot study 2, any food not consumed was counted and removed from the cage 24 hours later.

Behavioral observations. Observations were conducted for 15 minutes per cage during the dark phase of the LD cycle. Time sampling was used to record the most frequent behavior in each 15 second interval, resulting in a total of 60 observation periods per day. The parental behaviors recorded were sniff pup, touch pup, lick pup, carry pup, crouch over pups in nursing position, rest and touch pups and nest building. The nonparental behaviors recorded were wheel running, eating, drinking, gnawing, resting, self groom, explore cage, bite mate, lunge at mate, chase mate, flee from mate, sniff body, anogential sniffing of mate, mount, and lordosis. Parental and nonparental behaviors were observed within the same observation session as were the mother and father. Since several litters died between day 0 and day 4, substantive data on parental behavior were not collected.

The frequency of parental behavior was averaged over 16 days of observations during the dark phase of the LD cycle. Only parental behavior frequency is reported, as the frequency of nonparental behaviors can be calculated by subtracting the frequency of parental behavior from 60. Mothers in the Father Present group showed an average of 9.9 (s.d.=13.9, n=2) periods of parental behavior and fathers showed an average of 3.0 (s.d.=9.0, n=2) periods of parental behavior per 15 minute observation period. Mothers in the Father Absent group showed an average of 16.0 (s.d.=25.6, n=1) periods of parental behavior. It was apparent that mothers and fathers in all groups spent more time in nonparental behavior than parental behavior during the dark phase of the LD cycle.

Several behaviors were rarely observed, therefore, the number of behaviors scored was reduced for Pilot study 2. Furthermore, this method of sampling behavior appeared inaccurate as two or more behaviors often occurred within a 15 second interval. Time sampling was used in Pilot study 2, however, an event recorder replaced time sampling after Pilot study 2 was completed. Observations revealed that behavior was qualitatively different in the light phase than in the dark phase of the LD cycle (females spent more time in the light phase nursing pups and spent more time in the dark phase wheel running), so the second pilot study recorded behavior in both the light and dark phases of the LD cycle.

4.3 Pilot study 2.

This experiment was conducted to determine (a) if 300 revolutions per food pellet was an adequate wheel running regime for maintaining pup survival, and (b) to determine if the recording of behavioral data could be improved by observing *Mus* during both the light and dark phase of the LD cycle. A second housing condition was added in Pilot study 2. One group of mice had to run on the wheel to earn food (as in Pilot study 1, Wheel Contingent) while a second group had the running wheel present but were fed *ad libitum* (Wheel Noncontingent). This allowed us to determine if 300 revolutions per food pellet was too difficult for mice to maintain a litter of pups. Of the eight pairs of mice bred (two per group), only five had litters: two in the Father Present Wheel Contingent group;

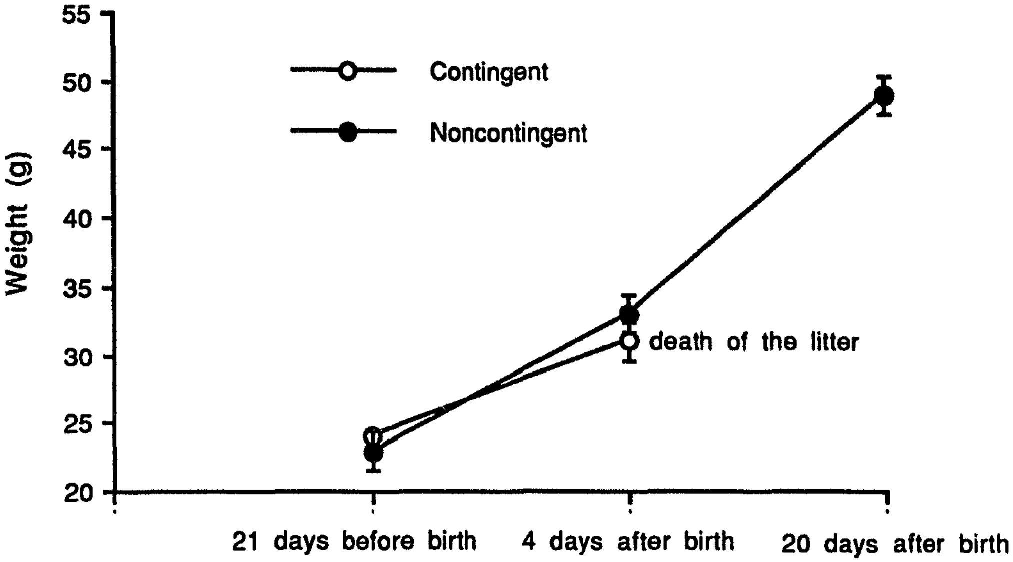
two in the Father Present Wheel Noncontingent group and only one of two in the Father Absent Wheel Contingent group. Neither mother in the Father Absent Wheel Noncontingent group had a litter.

Pup survival and growth. The one litter born to the female in the Father Absent Wheel Contingent group survived although the litter was reduced from 5 to 4 pups. Both of the two litters born in the Father Present Wheel Contingent group died and both of the two litters born in the Father Present Wheel Noncontingent group survived. One litter in the Father Present Wheel Noncontingent group was reduced from 6 to 5 pups and the other litter was maintained at 7 pups. Of the 5 litters born, 3 litters survived (60%) and of 37 pups born 10 pups survived (27%).

In the Father Present Wheel Contingent group, pups weighed an average of 1.5 grams (s.d=0.3) at birth and none survived to weaning. In the Father Present Wheel Noncontingent group, pups weighed an average of 1.8 grams (s.d.=0.07) at birth and 10.5 grams (s.d.=0.4) at weaning. In the Father Absent Wheel Contingent, pups weighed an average of 2 grams (s.d.=0.0, based on one litter) at birth and 8 grams at weaning.

Mothers weights (Figure 4.4). In the Father Present Wheel Contingent group, mothers weighed an average of 24 grams (s.d.=0.0) at the beginning of the experiment and 31 grams (s.d.=1.4) by day 4 after parturition (death of the litters). In the Father Present Wheel Noncontingent group, mothers weighed an average of 23 grams (s.d.=1.4) at the beginning of the experiment and 33 grams (s.d.=1.4) by day 4 after parturition and 49 grams (s.d.=1.4) by weaning.

Figure 4.4. Mean body weight (± S.D.) of Mus musculus mothers in the Father Present group in pilot study 2.



The mothers weight gain at weaning (day 20) was due to a second pregnancy.

Number of revolutions and food earned (Figures 4.5, 4.6 and 4.7). As only one mother in the Father Absent groups had a litter, an ANOVA was only conducted on the data for the Father Present groups from 20 days before parturition to parturition. The number of revolutions after parturition was not analysed as data collection ceased when litters died. There was no significant difference in the number of revolutions between the Father Present Wheel Contingent and Father Present Wheel Noncontingent groups ($F_{(1,2)}<1.0$). Both groups of mice ran more in the dark phase than in the light phase ($F_{(1,2)}=84.3$, $p=.01$) of the LD cycle. The two groups did not differ in their pattern of running over days. When the number of revolutions was graphed over all days available, the mother in the Father Absent Wheel Contingent group ran fewer revolutions than did the Father Present groups in both the light and dark phase of the LD cycle. The number of revolutions declined as parturition approached in the Father Absent group in both the light and dark phase and increased again after parturition, especially in the light phase.

The Father Present groups were generating similar amounts of food from block 1 to block 5 (Wheel Contingent, an average of 14 g, s.d.=.06, Wheel Noncontingent, an average of 13.1 g per day, s.d.=1, $F_{(1,2)}=3.8$, Figure 4.7.). The mother in the Father Absent group was generating much less food until parturition (an average of 7.1 g per day, s.d.=3.5, not shown in Figure 4.7).

Figure 4.5. Mean number of revolutions in the Father Present group during a) the light phase and b) the dark phase in pilot study 2.

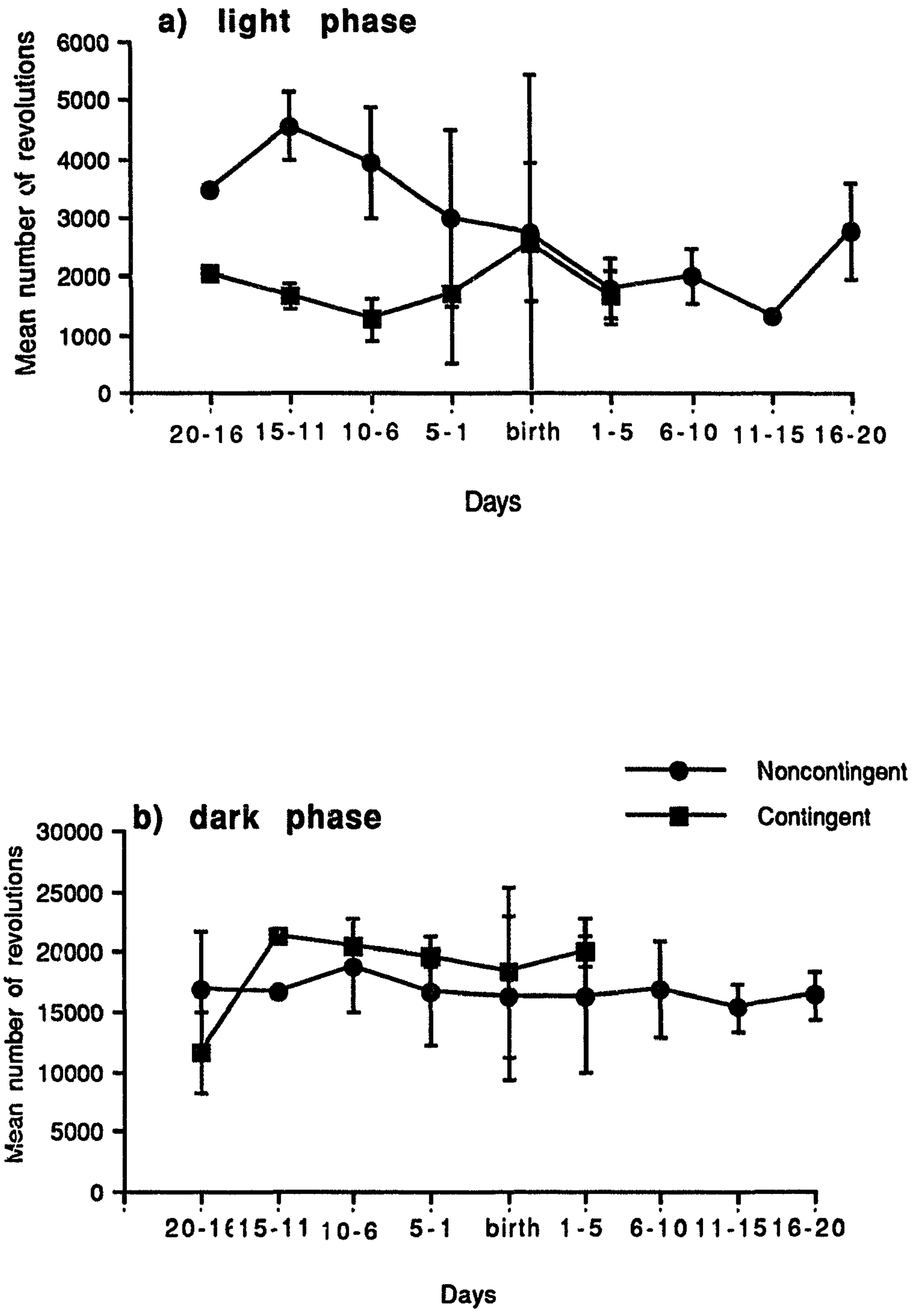
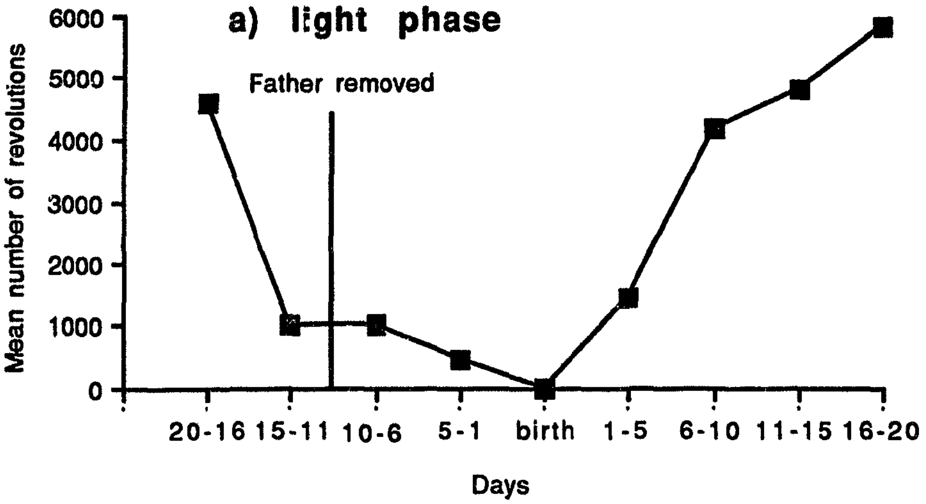


Figure 4.6. Mean number of revolutions for Father Absent Wheel Contingent group for the a) light phase and b) dark phase in pilot study 2.



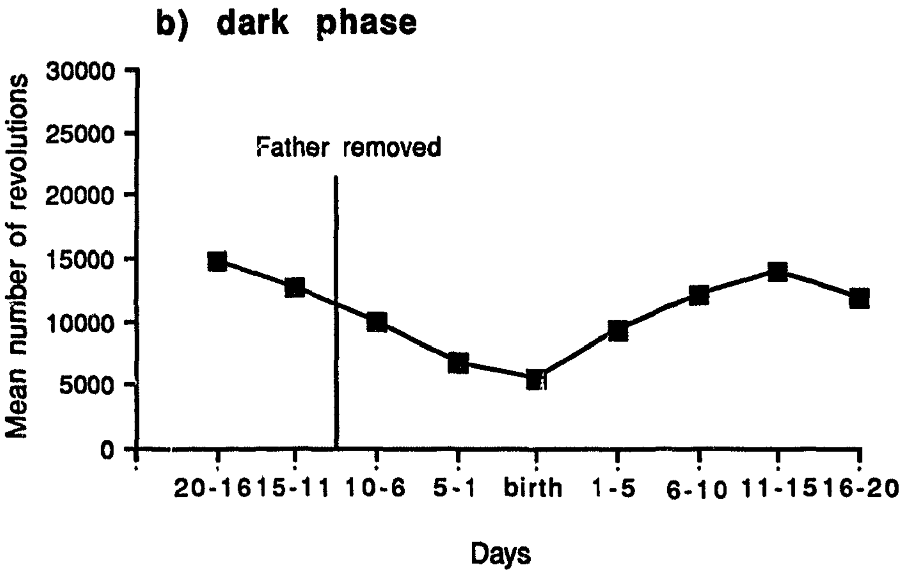
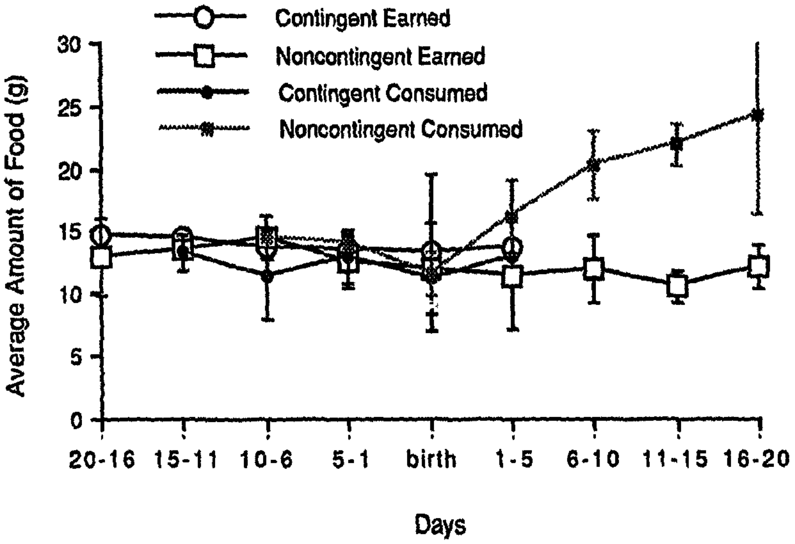


Figure 4.7. Food earned and consumed for Father Present groups in pilot study 2.



After parturition, mice in the Father Present Wheel Noncontingent group were consuming more food than they would have generated by running, beginning day 5-1 before parturition. Prior to this time they were potentially generating extra food through running on the wheel. Both Father Absent Wheel Contingent and Father Present Wheel Contingent groups were working for more food than they consumed before parturition, but by parturition the mother in Father Absent group consumed all food she worked for and maintained herself and her pups for 20 days. One pair of adults in the Father Present Wheel Contingent group began to consume all the food produced by parturition while the other pair did not (both of their litters died).

Behavioral observations. Behavioral observations were alternated between observing mice in the dark on days 0, 2, 4, 6, etc. to observing mice in the light on day 1, 3, 5, 7, etc. since it was noted that different behaviors occurred in the dark phase than in the light phase in Pilot study 1. The nonparental behaviours scored were wheel running, eating, gnawing, resting, self groom, and explore cage. The parental behaviors scored were sniff pup, lick pup, carry pup, crouch over pups in nursing position, rest and touch pups, and nest building. Observations were recorded by using time sampling as in Pilot study 1.

The parental behavior data were described in the same way as in Pilot study 1, as several litters died before substantive data could be collected. Only the frequency of parental behavior is reported, as the frequency of nonparental behavior can be calculated by subtracting the frequency of parental behavior from 60. During the light phase of the LD cycle, mothers in the Father Present Wheel Contingent group were observed engaged in parental behavior for an average of 55 observation periods (s.d.=7.1, n=2, for 2 days only) and during the dark phase, these mothers were engaged in parental behavior for an average of 3.3 observation periods (s.d.=4.6, n=2, for 2 days only). During the light phase, fathers in the Father Present Wheel Contingent group had an average of 33.3 observational periods (s.d.=3.9, n=2 for 2 days only) for parental behavior and during the dark phase, these fathers were engaged in parental behavior for an average of 45.0 observational periods (s.d.=21.2, n=2 for 2 days only).

During the light phase, mothers in the Father Present Wheel Noncontingent group were observed in parental behavior for an average of 54 observation periods (s.d.=10.6, n=2, for 8 days) and during the dark phase, mothers showed parental behavior for an average of 19.2 observation periods (s.d.=19.9, n=2, for 8 days). During the light phase, fathers showed parental behavior for an average of 46.3 observation periods (s.d.=14.5, n=2, for 8 days) and during the dark phase, these fathers engaged in parental behavior for an average of 7.2 observation periods (s.d.=12.9). Mothers and fathers were both contributing to offspring care in both running wheel conditions, but during the light phase, mothers engaged in more parental care. Nonparental behavior was more confined to the dark phase for both mothers and fathers in both the Wheel Noncontingent and Wheel Contingent groups.

The mother in the Father Absent Wheel Contingent group had an average of 31.7 observation periods (s.d.=29.2, n=1, for 8 days) for parental behavior during the light phase and an average of 28.9 observation periods (s.d.=29.8, n=1 for 8 days) for parental behavior in the dark phase. The mother in this group was performing both parental and nonparental behavior in the light and dark phases of the LD cycle. Parental care was not more frequent during the light phase than during the dark phase when the mother was alone.

4.4. Decisions for experimental design.

The data from the two pilot studies indicated that 300 revolutions per pellet would not allow pups to survive in the Father Present Wheel Contingent group. Since one of the main objectives was to determine how the father influenced pup survival, parents had to generate enough food for pup survival, so it was possible to determine if parenting, not just lack of energy, influenced pup development. To ensure that pups would survive in the Wheel Contingent group, I decided that the number of revolutions would be 300 per pellet until parturition and then the number of revolutions would be reduced to 250 during lactation. It also was decided to add a third foraging condition, (a No Wheel group) to the experiment. In this group, mice were maintained in rat cages without a wheel in order to determine the effect of wheel running on behavior independent of the requirement to run for food.

In order to collect frequency and duration data on behaviors exhibited it was decided to record behavioral observations using a computer event recorder. All of the parental behaviors (sniff pup, lick pup, carry pup, crouch over in lactation position, rest and touch pups, nest build) were recorded as well as six most frequent nonparental behaviors (wheel running, eating, gnawing on bars or shavings, resting, grooming, exploring). Behavior observations were alternated between the light and dark phases on a daily basis to collect data on the difference in parental behavior and wheel running in the light and dark phase of the LD cycle.

Chapter 5

Methods

Based on the research objectives and the results of the two pilot studies described in Chapter 4, the experimental methods described in this chapter were used. The experimental design involved two parental groups: single mothers (Father Absent) and paired mothers (Father Present) housed under three conditions: No Wheel, Wheel Noncontingent and Wheel Contingent. Mothers in the Father Absent group were left with the father until two to four days before parturition. The female alone then cared for the pups for the period of lactation (20-30 days). Mothers in the Father Present group remained with the father for the duration of the experiment. Mice in the No Wheel condition were fed 190 mg Noyes pellets *ad libitum* while those in the Wheel Noncontingent condition had a running wheel present but were fed 190 mg Noyes pellets *ad libitum*. Mice in the Wheel Contingent condition were required to run in the wheel to obtain 190 mg Noyes pellets as determined by the pilot studies.

5.1 Subjects:

Mus musculus. Fifty-three female and fifty-three male CD-1 Swiss Webster albino *Mus musculus* were purchased from Charles River Canada (LaSalle, Quebec) when they were 60 days of age with an average weight of 22 g. They were initially housed in same sex pairs in 48.5 x 21.5 x 30.5 cm clear polypropylene cages with wire lids, with Purina lab chow and water available*ad libitum.* When they were 67 to 74 days of age they were randomly divided into three groups and put in mated pairs into the different housing conditions. Of the 53 pairs, 51 had litters. Fathers were marked with nontoxic black felt pen on their flanks for identification beginning one week before parturition whereas mothers were not marked. Animals were housed in a windowless room with a 12:12 L:D cycle with lights off at 10 am. The light level was determined by using a light meter (Sekonic L-28c2), taking 5 measures each during the light and dark phases from different areas in the room and averaging these measures. The room had a light level of 50±2 lux during the light phase and 2±0.5 lux during the dark phase. The temperature was maintained at 21° C.

Peromyscus californicus. Fifty-one female and fifty-one male *Peromyscus californicus* (California mice) were obtained from Dr. David Gubernick at the University of Wisconsin (Madison). They were 120 days of age and weighed an average of 40 g when they entered the lab. They were initially housed in same sex pairs in 48.5 x 21.5 x 30.5 cm clear polypropylene cages with wire lids, fed Purina lab chow *ad libitum* and had free access to water. They were 127 to 134 days of age then they were divided into three groups and put into mated pairs in different housing conditions. Of the 51 pairs, 49 had litters. Fathers were marked by shaving patches of fur on their flanks beginning one week before parturition whereas mothers were not marked. Animals were housed in a windowless room with an 16:8 L:D cycle with lights off at 10 am. This was instituted because *P. californicus* breed during long days (D. Gubernick, personal communication). The room had a light level of 50 lux during the light phase and 2 lux during the dark phase. The temperature was maintained at 21°C.

5.2 Apparatus:

Housing system. Mice in the Wheel Contingent and Wheel Noncontingent groups were housed in 48.5 x 21.5 x 30.5 cm cages which had three sides made of stainless steel, one side of plexiglas and a removable stainless steel tray on the bottom of the cage. A wire mesh lid was fitted to the top of the cage. Food (190 mg Noyes Precision Pellets, Formula "A" Improved) was delivered through a spout on the back wall of the cage and water was delivered through a spout on the side wall of the cage. Each cage had a running wheel which was 8 cm wide and 17 cm in diameter (Figure 5.1). The food spout was connected to an automatic food dispenser as depicted in Figure 5.2. In order to record wheel running and determine food delivery, the center rod of the running wheel was attached to a plastic disk containing a magnetic switch which was connected to an interface and an Apple IIe computer. A computer program, written by Raven Software (1987), controlled the number of revolutions required to obtain a food pellet and recorded and printed the number of revolutions run and the number of food pellets dispensed every hour. Mice in the No Wheel group were housed in 43.5 x 23.0 x 15.5 cm clear polypropylene cages with wire lids and fed the same 190 mg Noyes pellets as the other two groups. All three housing groups had water available *ad libitum*.

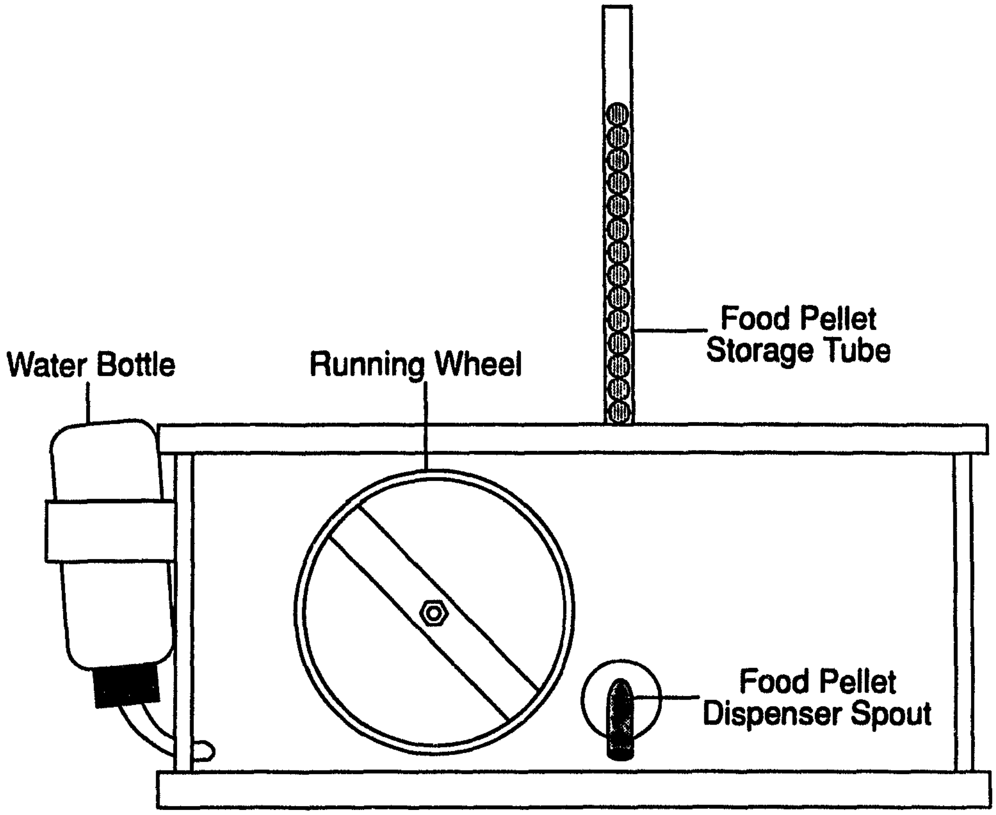


Figure 5.1. Design of the wheel running cages for the Wheel Noncontingent and Wheel Contingent groups

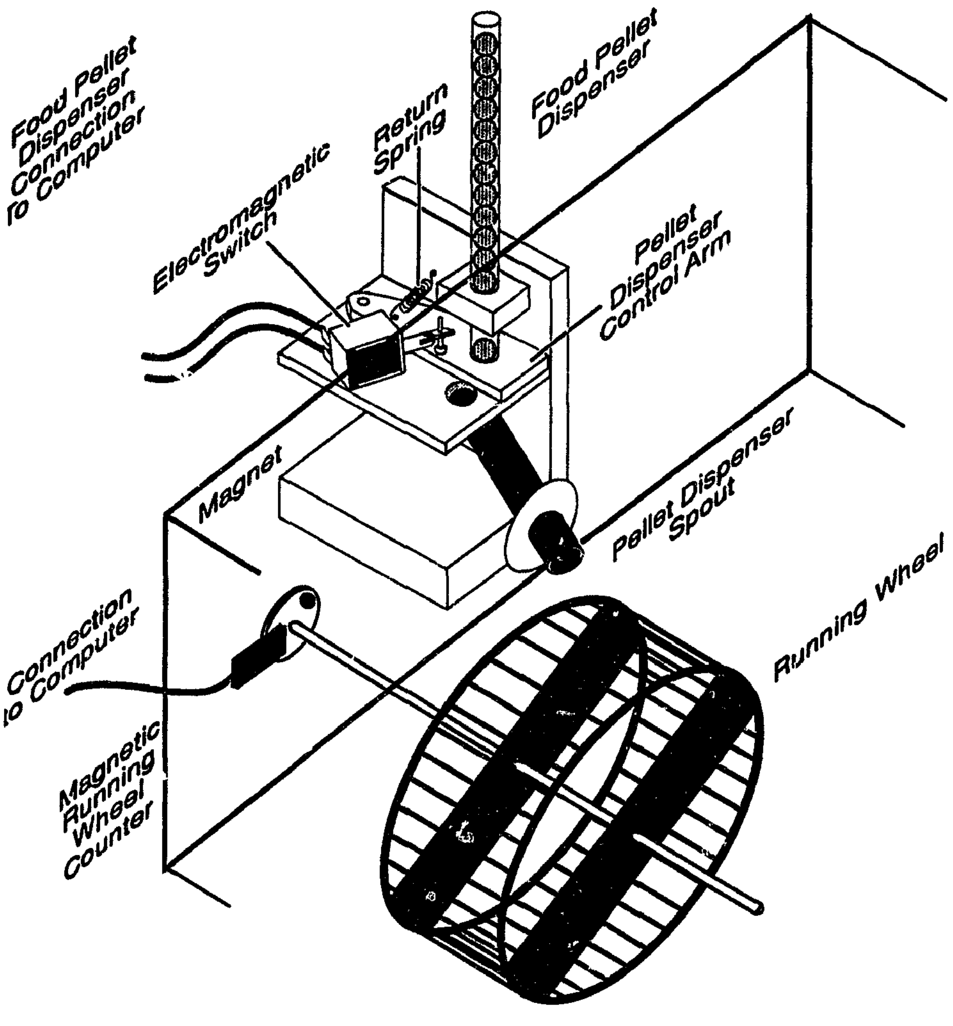


Figure 5.2. Side view of the wheel running cages and the design of the food pellet dispenser

5.3 Behavioral observation system

Behaviours were recorded using an Apple IIe computer and an event recorder program, written by Raven Software, which recorded the frequency and duration of each behaviour. The behaviors recorded were **wheel running** (mouse turns the running wheel), **explore** (moving around the cage but not on the running wheel), **eat** (holding food near mouth and consuming food), **gnaw** (gnawing on wood shavings or on bars of cage), **groom** (licking own fur or the fur of mate), **rest** (lying down without contacting another mouse), **crouch** (adopting the nursing position where the mouse curves its body over a litter of pups), **rest/touch pups** (lying on top of pups or beside them but not in the nursing position), **nest build** (carrying strips of paper from various locations within the cage and placing them around the pups and adults), **lick pup** (the adult mouse licks any part of the body of a pup), **sniff pup** (the adult mouse brings its nose in contact with any part of the pup's body), and **carry pup** (an adult mouse picks up a mouse pup, usually by the back of the neck and transports them from location to another), for both the male and female parents.

5.4 Video camera system

Mice were videotaped during the dark phase of the LD cycle using GE 100 W red flood lights mounted on light stands. The camera used was a Panasonic CCTV camera (model WVBL200) with a Panasonic TV zoom lens which was mounted on a camera stand that had two mounting platforms, one of which was 875 cm from the floor and the other was 1550 cm from the floor. A Panasonic time lapse video recorder (model AG-6050) was connected to the camera. A Beaumark black and white, 12 inch TV (model HB 1400) was used as a monitor.

5.5 Procedure

There were four components to the experiment: (a) preliminary wheel training after which mice were mated and put into the three housing groups; (b) wheel running and food consumption were recorded; (c) mice were counted and weighed at regular intervals and (d) behavioral observations were made daily. The same four components occurred for both *Mus musculus* and *Peromyscus californicus.*

a) Preliminary wheel training. *Mus musculus* were kept in standard mouse cages for two weeks before being placed in the running wheel cages. Male and female mice were each placed in the running wheel cages alone for one week, to habituate them to the new environment, to condition them to run on the wheel for food and to determine the number of revolutions they ran alone. If there was not enough time to run both males and females alone, then males were run only. Males and females were then randomly assigned to one of the six groups and placed in mixed sex pairs into one of the three housing conditions (No Wheel, Wheel Contingent, Wheel Noncontingent). *Peromyscus californicus* were treated in the same way.

b) Recording wheel running and food consumption. *Mus* and *Peromyscus* were treated in the same way, with some exceptions which are noted. The number of revolutions run by *Mus* was recorded and printed every hour, 24 hours a day for the Wheel Contingent and Wheel Noncontingent groups. In the Wheel Contingent group, from Day 0 to parturition (3-4 weeks in *Mus*; 4-6 weeks in *Peromyscus*) mice ran 300 revolutions (160.2 metres) per pellet and after parturition, mice were required to run 250 revolutions (135.8 metres) per pellet (21 days in *Mus*; 24 days in *Peromyscus*). Mice in the Wheel Noncontingent group had the wheel present but were provided with ad lib food. Mice in the No Wheel group had no wheel in their home cages and were fed ad libitum by placing 50-140 (*Mus musculus*) or 60-160 Noyes pellets (*Peromyscus californicus*) in their cages every morning. Any pellets not consumed during the day were removed the next morning and the number removed was recorded. Pellets were removed to determine how much food was consumed each day and to prevent food hoarding.

c) Counting and weighing mice. Adult mice were weighed once a week until females appeared pregnant and were then weighed 2 or 3 more times until their weight gain confirmed that they were pregnant. Weighing of pups and adult mice began on the 4th day after birth and then every four days after (up to day 20 for *Mus* and day 24 after parturition for *Peromyscus*). In the Father Absent groups, the male was removed 2 to 4 days prior to parturition. Pups were counted on the day of birth (handling them as little as possible with surgical gloves) and weighed 4 days after parturition. This ensured that pup survival was minimally influenced by handling for the first few days after birth. The number of pups was counted daily. *Mus* pups were sexed and weighed at 20 days of age whereas *Peromyscus* pups were sexed and weighed at 24 days of age.

d) Behavioral observations. Behavioral observations began when the pups were born. Each cage was observed for 10 minutes every day. Half of the cages were observed during the light phase and half of the cages were observed during the dark phase of the L:D cycle on any one day. Therefore, every two days one cage was observed in both the light and dark phase. Observations in the dark phase began 1 to 3 hours after the lights went off and ended at least one hour before the lights came on. Observations in the light phase began 1 to 3 hours after the lights came on and ended at least one hour before the lights went off. The order in which cages were observed was randomized. The twelve behaviors described in section 5.3 were recorded for both male and female adults.

Videotaped observations were conducted during the dark phase of the LD cycle. One to four cages were videotaped at one time. The animals were videotaped for between 15 minutes and 6 hours using time lapse recording (2 to 24 hours on one tape), every 2 to 5 days depending on the number of cages videotaped. The animals that could be recorded were initially limited to two cages (one Father Present Wheel Contingent and one Father Present Wheel Noncontingent) since the other two cages contained only mothers from the Father Absent groups. This allowed mice from different groups to be evenly distributed around the room but severely limited what could be videotaped (especially if one of the Father Present pairs did not have pups or cannibalized their litter). The camera stand could be moved every 15 minutes to videotape the next cage, but this system was not feasible since the camera could not be adjusted to stop in a position that allowed for clear videotaping. In addition, lighting was inadequate for two thirds of the taping. In order to increase the number of cages available for taping, on three occasions, cages from the top shelf were moved to the bottom shelf. During the last replicate of animals, the camera stand was adjusted to allow videotaping of the top shelf, the camera remained stationary in front of one cage for 2 to 6 hours and pairs were distributed in the room so that they were all available for videotaping.

Research schedule. As only 12 wheel running cages were available, the experiment was run in nine squads as indicated in Table 5.1. An effort was made to collect data from animals in all groups in each squad. However, due to the number of *P. californicus* subjects available, this was not always possible.

Table 5.1. Testing schedule, indicating the number of *Mus musculus* and *Peromyscus californicus* litters tested in each parenting group and housing condition and the date that each squad was started

		Number of Subjects					
Housing Conition:		No Wheel		Wheel Noncontingent		Wheel Contingent	
Squad	Father	Absent	Present	Absent	Present	Absent	Present
M. musculus							
1	Feb 89	3	3	3	3	3	3
2	Aug 89	3	3	3	3	3	3
3	April 91	3	3	3	3	3	2
	Total	9	9	9	9	9	8
P. californicus							
4	Oct 89	1	1	3	3	3	3
5	April 90	5	5	3	3	3	3
6	Nov 90	0	0	2	3	3	3
7	Jan 91	4	4	0	3	0	3
8	Aug 92	1	1	2	3	2	2
9	Dec 92	2	2	3	0	2	1
	Total	13	13	13	15	13	15

Chapter 6

Results for *Mus musculus*

The dependent variables examined in this chapter are parental weights, maternal fertility and fecundity (Part One, sections 6.1 to 6.3); the survival and growth of pups (Part Two, sections 6.4 and 6.5); the parental and nonparental behavior shown by each parent (Part Three, sections 6.6 and 6.7) and the wheel running behavior required to obtain food (Part Four, sections 6.8 and 6.9). A comparison of wheel running and parental behavior during the dark phase of the LD cycle is given in (sections 6.10 and 6.11) and the amount of food consumed by each parent is discussed in Part 6 (sections 6.12 to 6.14).

Part One: Parental weight, maternal fertility and fecundity

6.1 Parental weights

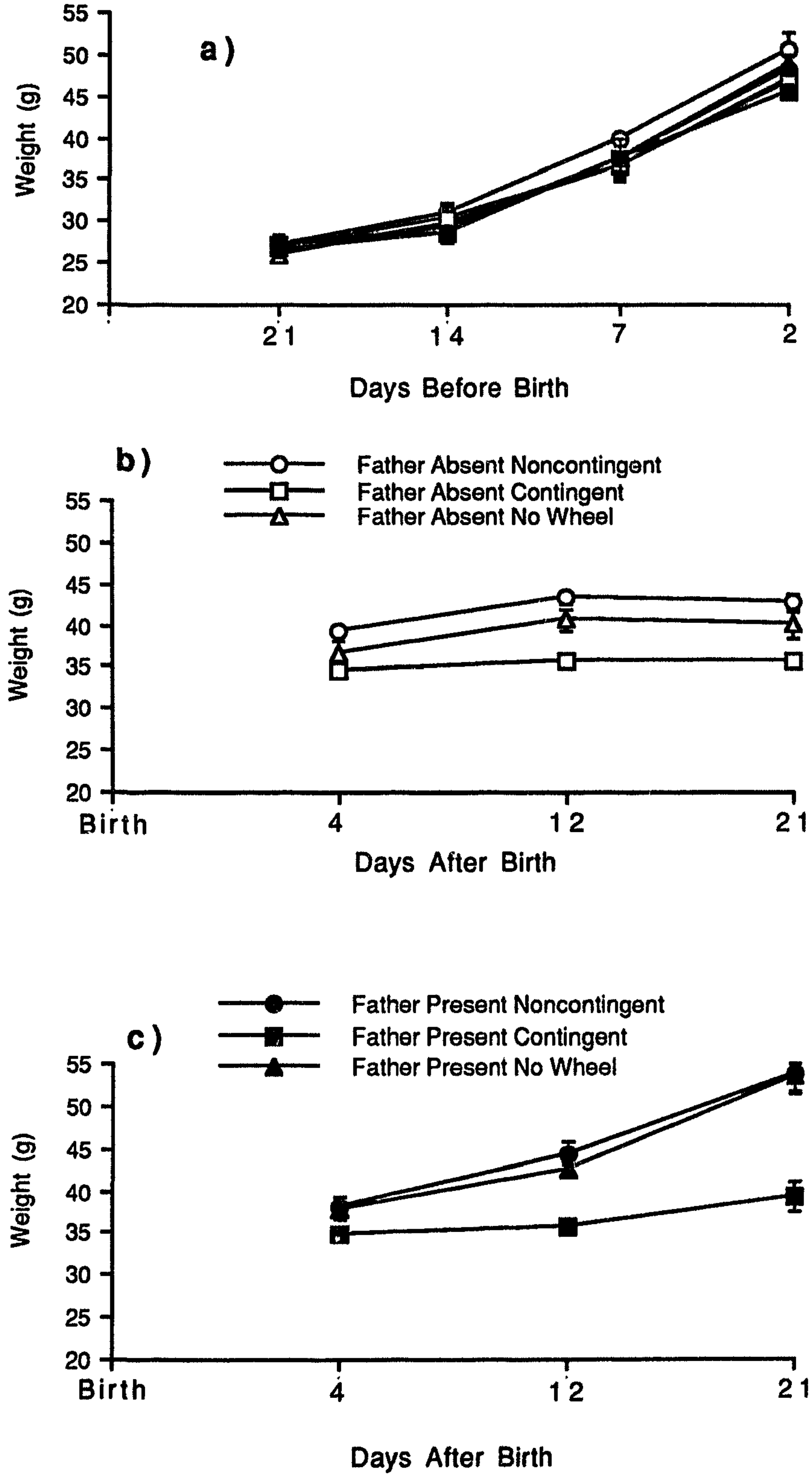
The mothers' weight in the Father Present groups was compared to the mothers' weight in Father Absent groups on days 21, 14, 7 and 2 before parturition and 4, 12, and 21 days after parturition. The fathers' weights for all six groups were compared on days 21, 14, 7 and 2 before parturition and fathers' weights in the Father Present group were compared on days 4, 12 and 21 after parturition.

a. Mothers' weights before and after parturition (Figure 6.1)

Mothers' weights before birth were analyzed by a 2 (parenting: Father Present or Absent) x 3 (housing: Wheel Contingent, Wheel Noncontingent, No Wheel) x 4 (days) ANOVA. Mothers in the Father Present and Father Absent groups did not differ in weight before parturition ($F_{(1,45)}<1.0$) nor were there significant effects of housing on maternal weight ($F_{(2,45)}<1.0$). There was no significant interaction between parenting and housing ($F_{(2,45)}<1.0$) on maternal weight, but there was a significant effect of days as mothers increased in weight as they approached parturition ($F_{(3,135)}=691.5$, $p<.0001$). There were no significant interactions between days and parenting ($F_{(3,135)}=1.4$), days and housing ($F_{(6,135)}=1.5$) nor between days, parenting and housing on maternal weight ($F_{(6,135)}<1.0$, Figure 6.1a).

Mothers' weights after birth were analyzed by a 2 (parenting) x 3 (housing) x 3 (days) ANOVA. There was a significant effect of parenting on mothers' weight after birth ($F_{(1,43)}=17.0$, $p<.001$) as mothers in the Father Present group became pregnant again during postpartum estrus and thus gained more weight than those in the Father Absent group. There also was a significant effect of housing ($F_{(2,43)}=28.7$, $P<.001$) as mothers in the Wheel Noncontingent and No Wheel conditions were similar in weight while mothers in the Wheel Contingent conditions weighed less. There was no significant interaction between parenting and housing on maternal weight ($F_{(2,43)}=1.9$).

Figure 6.1 Mus musculus: Mothers' weights in all six groups before the birth of their pups (a) and in the father absent (b) and father present (c) group after the birth of the pups. The legends in b and c also apply to a.



Since the mothers in the Father Present group were pregnant, separate analyses of days effects after birth were conducted for each parenting group. In the Father Absent group (Figure 6.1b) there was a significant effect of days ($F_{(2,42)}=18.6$, $p<.001$) as these mothers gained weight throughout the lactation period. There was no significant interaction between days and housing ($F_{(4,42)}=1.7$) as mothers made small gains in weight in all housing groups as weaning approached. In the Father Present group (Figure 6.1c) there also was a significant effect of days ($F_{(2,44)}=80.7$, $p<.001$) as mothers gained weight throughout the lactation period. There was a significant interaction between days and housing ($F_{(4,44)}=7.7$, $p<.001$) as mothers in the Wheel Contingent condition gained less weight throughout the period of lactation than did mothers in the other two housing conditions. The weights of the mothers in the Wheel Noncontingent and No Wheel conditions suggested that these mothers were pregnant again. Although the birth of second litters was not recorded, the only reason mothers would gain 15 to 20 grams was due to pregnancy. The smaller weight gain of mothers in the Wheel Contingent condition may indicate that they were not pregnant, had a delayed pregnancy or had a smaller litter size, which made small weight gains difficult to interpret.

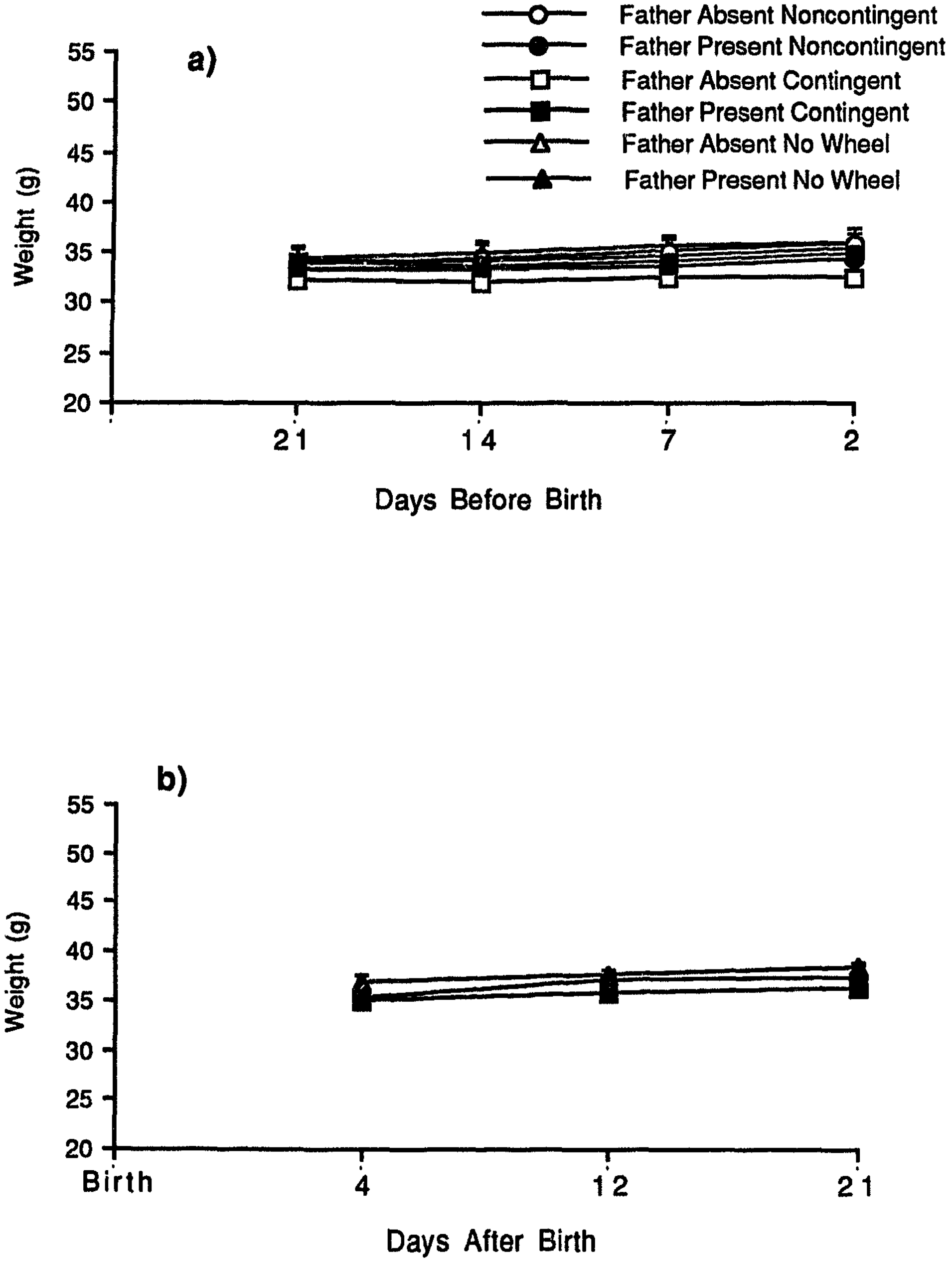
b. Fathers' weights before parturition (Figure 6.2a) and after parturition (Figure 6.2b)

Fathers were present in both parenting groups until 1 to 2 days before birth, thus before the birth of the pups, there were six groups of males. The fathers' weights in the six groups on days 21, 14, 7 and 2 before parturition were analyzed by a 2 (parenting) x 3 (housing) x 4 (days) ANOVA.

Before parturition, fathers did not differ in weight due to parenting conditions ($F_{(1,45)}<1.0$) nor to housing conditions ($F_{(2,45)}=1.5$). There was no significant interaction between parenting and housing on fathers' weights ($F_{(2,45)}=1.3$) but there was a significant effect of days as fathers increased in weight as the day of birth approached ($F_{(3,135)}=13.2$, $p<.0001$). There were no significant interactions between days and parenting ($F_{(3,135)}<1.0$), days and housing ($F_{(6,135)}<1.0$) or days, parenting and housing on fathers' weight before birth ($F_{(6,135)}<1.0$, Figure 6.2a).

After birth, there were only the three groups of males in the Father Present group and fathers' weights on days 4, 12, and 21 after parturition were analyzed by a 3 (housing) x 3 (days) ANOVA. There was no significant effect of housing ($F_{(2,22)}=1.5$), thus fathers in the Wheel Noncontingent, Wheel Contingent and No Wheel conditions weighed the same after the birth of the pups. There was however, a significant effect of days ($F_{(2,44)}=22.9$, $p<.001$), as fathers in all groups increased in weight during the period of lactation. There was no significant interaction between days and housing ($F_{(4,44)}<1.0$, Figure 6.2b).

Figure 6.2. Mus musculus: Fathers' weights (a) before the birth of the pups for six groups and (b) after the birth of pups for the three Father Present groups



6.2 Mothers' fertility (Table 6.1)

There were no differences in the number of females giving birth in the Father Present or Father Absent groups ($\chi^2_{(1)}$= 0.5 n.s.) and no differences in the number of females giving birth between the No Wheel, Wheel Noncontingent and Wheel Contingent housing conditions ($\chi^2_{(2)}$=1.1, n.s.). Thus neither parenting nor housing conditions influenced the fertility of the mothers.

6.3 Mothers' fecundity (Table 6.2)

Because litter size may be influenced by maternal weight (Konig, 1993, Myers & Master, 1983), litter size was analyzed by a 2 (parenting) x 3 (housing) ANCOVA with mother's weight (21 days before birth) as the covariate. The results of this ANCOVA demonstrated that there were no significant differences in litter size at birth between the parenting groups ($F_{(1,44)}<1.0$), or housing conditions ($F_{(2,44)}<1.0$) and no significant interaction between parenting and housing ($F_{(2,44)}<1.0$). Over all groups, mothers produced an average of 11 pups. Since the results of the ANCOVA indicated that there were no significant effects of parenting groups or housing conditions, future analyses of litter size were not corrected for mother's weight.

Summary of Part One. From conception to parturition mothers gained the same amount of weight in all six groups. After parturition, mothers in the Wheel Contingent condition in both the Father Absent and Father Present groups gained less weight than mothers in the No Wheel and Wheel Noncontingent conditions.

Table 6.1. Fertility of mothers. The number of *Mus musculus* mothers in each housing condition giving birth (pups) and failing to give birth (no pups) in the father absent or present groups.

	Father Absent		Father Present		
Housing	pups	no pups	pups	no pups	Total
No Wheel	9	0	9	0	18
Wheel Noncontingent	8	1	8	1	16
Wheel Contingent	9	0	8	0	17
Total	26	1	25	1	

Table 6.2. Fecundity of mothers. The mean litter size at birth and 20 days of age (±SEM) for *Mus musculus* in each housing condition when fathers were absent or present

Housing	Father Absent	Father Present
No Wheel	10.9 ± 1.1	10.9 ± 0.7
Wheel Noncontingent	12.3 ± 0.8	11.5 ± 0.8
Wheel Contingent	11.6 ± 0.7	10.8 ± 0.9

This result suggests that the mothers in the Wheel Contingent condition were expending more energy than mothers in the other two housing conditions. Mothers did not differ in fertility or fecundity due to parenting conditions and the mothers' weight at pregnancy had no significant effect on her litter size at birth. Before parturition, fathers did not differ in weight between groups and gained weight up to the birth of their pups. Fathers in the Father Present groups all gained the same amount of weight after parturition. This is in contrast to the mothers' in the Wheel Contingent condition who gained significantly less weight during lactation than mothers in the the other two conditions.

Part Two: Survival, growth and gender of pups

6.4 Litter and pup survival rate

a. Survival of whole litters (Tables 6.3 and 6.4)

A Chi-square analysis was used to determine if there was a significant difference in the number of litters surviving to 20 days of age between the groups. In the Father Present group 25 of 25 litters (100%) survived to 20 days of age while 92.3% of the litters in the Father Absent group (24 of 26) survived to 20 days of age, a difference that was not significant ($\chi^2_{(1)}=2.0$, Table 6.3). In both the No Wheel and Wheel Noncontingent housing conditions, 100% of litters survived (18 of 18 and 16 of 16) while 88% of the litters survived in the Wheel Contingent condition, a difference that was not significant ($\chi^2_{(2)}=4.1$). Only two entire litters died and they were both in the Father Absent Wheel Contingent condition (Table 6.4).

Table 6.3. Total number of litters surviving to 20 days of age in the father absent or present groups collapsed across housing conditions for *Mus musculus*

Pups	Lived	Died	Total
Father Absent	24 (92.3%)	2	26
Father Present	25 (100.0%)	0	25
Total	49	2	51

$X^2_{(1)}$=2.0, n.s.

Table 6.4 Total number of litters surviving to 20 days of age in the three housing conditions collapsed across parenting groups for *Mus musculus.*

Pups	Lived	Died	Total
No Wheel	18 (100%)	0	18
Wheel Noncontingent	16 (100%)	0	16
Wheel Contingent	15 (88.0%)	2	17
Total	49	2	51

$X^2_{(2)}$=4.1, n.s.

b. Litter size at 20 days of age (Table 6.5)

The difference in mean litter size between birth and 20 days of age (Table 6.8) was determined, then a 2 (parenting) x 3 (housing) ANOVA was conducted to determine if there was a differential rate of pup survival across the different groups. There was a significant effect of housing conditions on pup survival ($F_{(2,45)}=4.0$, $p<.05$) as fewer pups survived in the Wheel Contingent condition than in the other two housing conditions. Litter size was, therefore, smaller in the Wheel Contingent condition than in the other two conditions by day 20. There were no significant effects of parenting ($F_{(1,45)}=1.2$) and no significant interaction between parenting and housing ($F_{(2,45)}=1.0$) on the mean litter size by day 20.

c. Pup survival to 20 days of age (Table 6.6)

Pup survival was assessed by a Chi-square analysis to determine if there was a significant difference in the proportion of pups that survived to 20 days of age between the groups. Significantly more pups survived in the Father Present groups (248 of 276, 89.9%), than in the Father Absent groups (250 of 300, 83.3%, $\chi^2(1)=4.7$, $p<0.05$). There also was a significant difference in pup survival due to housing. In the No Wheel condition, 90.3% of the pups survived (177 of 196), while 94.7% survived in the Wheel Noncontingent condition (180 of 190) and only 74.2% (141 of 190) survived in the Wheel Contingent condition ($\chi^2_{(2)}=35.9$, $p<0.001$). There was no difference in pup survival between the No Wheel and Wheel Noncontingent conditions ($\chi^2_{(1)}=2.1$) so these two groups were combined and compared to the Wheel Contingent condition.

Table 6.5. Mean (±SEM) litter size at birth and 20 days of age for *Mus musculus* in each housing condition in the father absent and father present groups

Age	birth		20 days	
Father	Absent	Present	Absent	Present
Housing Condition				
No Wheel	10.9 ± 1.1	10.9 ± 0.7	9.4 ± 1.0	10.2 ± 0.8
Wheel Noncontingent	12.3± 0.8	11.5 ± 0.8	11.9 ± 0.8	10.6 ± 1.1
Wheel Contingent	11.6 ± 0.7	10.8 ± 0.9	7.8 ± 1.6	8.9 ± 2.0

Table 6.6a. Pup survival in the No Wheel group for *Mus musculus* with the father absent or present

	Lived	Died	Total
Father Absent	85 (86.7 %)	13	98
Father Present	92 (93.9 %)	6	98
Total	177	19	196

$X^2_{(1)}=2.1$, n.s.

Table 6.6b. Pup Survival in the Wheel Noncontingent group for *Mus musculus* with the father absent or present.

	Lived	Died	Total
Father Absent	95 (96.9%)	3	98
Father Present	85 (92.4%)	7	92
Total	180	10	190

$X^2_{(1)}=1.2$, n.s.

Table 6.6c. Pup survival in the Wheel Contingent group for *Mus musculus* with the father absent or present.

Pups	Lived	Died	Total
Father Absent	70 (67.3%)	34	104
Father Present	71 (82.6%)	15	86
Total	141	49	190

$X^2_{(1)}=4.9$, $p<.05$

Significantly more pups survived in the No Wheel/Wheel Noncontingent condition (92.5% survived) than in the Wheel Contingent condition (74.2% survived, $\chi^2_{(1)}=34.7$, $p<.001$).

Differences in pup survival between the Father Absent and Father Present groups were analyzed for each housing condition separately (Table 6.6). There was no difference in pup survival between parenting conditions in the No Wheel ($\chi^2_{(1)}=2.1$) or Wheel Noncontingent ($\chi^2_{(1)}=1.2$) conditions but in the Wheel Contingent condition, the Father Present group had significantly greater pup survival than the Father Absent group ($\chi^2_{(1)}=4.9$, $p<.05$), which suggested that the fathers' presence increased pup survival in this group. Thus, pup survival was lower in the Wheel Contingent condition than in the No Wheel and Wheel Noncontingent conditions and within the Wheel Contingent condition more pups survived when the father was present than when the father was absent. These results may be due to the fact that two whole litters died in the Wheel Contingent Father Absent condition, and in no other conditions did whole litters die (Table 6.3).

6.5 Pup growth: Mean total litter weight and mean pup weight within each litter (Tables 6.7 and 6.8)

Pup growth was assessed by determining the total litter weight and mean pup weight per litter at 4 and 20 days of age. Since I was interested in the effects of the father's presence and the housing conditions on development and since heavier females have heavier pups (Myers & Master, 1983), I wanted to be certain that any differences between groups in pup development were not due to differences in mothers' weight. An analysis of covariance was, therefore, conducted to examine whether the mother's weight 21 days before parturition (nonpregnant weight) influenced the mean total litter weight or mean pup weight on day 4 and day 20 after birth.

a. Mean total litter weight (Table 6.7)

The results of the ANCOVA demonstrated that there was a significant effect of housing on total litter weight at 4 days of age as litters in the Wheel Contingent condition weighed the least ($F_{(2,44)}=6.9$, $p<.01$). There were no significant effects of parenting on litter weight ($F_{(1,44)}<1.0$) and no significant interaction between parenting and housing ($F_{(2,44)}<1.0$). When litters were 20 days old the effect of housing became more significant ($F_{(2,42)}=25.6$, $p<.001$) and there was still no effect of parenting on mean total litter weight ($F_{(2,42)}<1.0$) and no interaction ($F_{(2,42)}<1.0$). Litters in the Wheel Contingent condition weighed just over half as much as litters in the No Wheel condition at 20 days of age.

b. Mean pup weight per litter (Table 6.8)

The results of the ANCOVA demonstrated that there was a significant difference in mean pup weight at 4 days of age between the housing conditions ($F_{(2,44)}=3.9$, $p<.05$) as pups in the Wheel Contingent condition weighed less than pups in the other two housing conditions but there was no significant difference in pup weight between the Father Present and Father Absent groups ($F_{(1,44)}<1.0$), and no significant interaction between parenting and housing ($F_{(2,44)}<1.0$).

Table 6.7 Mean (±SEM) total litter weights at 4 and 20 days of age for *Mus musculus* in each housing condition when fathers were present or absent

Age	4 days		20 days	
Father	Absent	Present	Absent	Present
No Wheel	24.8 ± 10.9	33.5 ± 14.7	94.7 ± 36.4	93.9 ± 17.7
Wheel Noncontingent	30.6 ± 6.1	29.3 ± 6.2	88.3 ± 13.5	85.5 ± 15.0
Wheel Contingent	20.0 ± 5.1	21.1 ± 5.4	48.5 ± 8.6	48.7 ± 11.5

Table 6.8. Mean (±SEM) pup weights per litter at 4 and 20 days of age for *Mus musculus* in each housing condition when fathers are absent and present

	4 days		20 days	
Father	Absent	Present	Absent	Present
No Wheel	2.4 ± 0.6	2.6 ± 0.7	9.5 ± 1.3	9.4 ± 1.4
Wheel Noncontingent	2.5 ± 0.4	2.6 ± 0.3	7.7 ± 1.8	8.4 ± 1.8
Wheel Contingent	1.8 ± 0.4	2.1 ± 0.4	4.9 ± 1.1	5.8 ± 1.2

At 20 days of age, the mean pup weight per litter did not differ between Father Absent and Father Present groups ($F_{(1,42)}=1.2$) but did differ significantly between housing conditions ($F_{(2,42)}=30.7$, $p<.001$) as pups in the Wheel Contingent condition weighed significantly less than pups in the other two conditions. There was no significant interaction between parenting and housing ($F_{(2,42)}<1.0$) on mean pup weight.

6.6 Gender of pups (Table 6.9)

A Chi-square analysis was used to determine if there was a significant difference in the total number of males and females that survived to 20 days of age between the groups. There was no significant difference between the six groups ($\chi^2_{(5)}=7.2$) in the number of male and female pups that survived to 20 days of age nor was there a difference in the number of male and female pups within each of the three housing conditions (Table 6.9). There was no significant difference ($\chi^2_{(1)}=2.5$) in the number of male and female pups that survived to 20 days of age between the Father Absent and Father Present groups, nor between the housing conditions ($\chi^2_{(2)}=4.4$).

Summary of Part Two. Pup survival was influenced by the fathers' presence and the housing conditions as pup survival was lower in the Wheel Contingent condition than in the No Wheel and Wheel Noncontingent conditions and within the Wheel Contingent condition more pups survived when the father was present. This result may be due to the death of two whole litters in the Father Absent Wheel Contingent condition. There were no differences

Table 6.9a. Pup gender in the No Wheel group for *Mus musculus* with the father absent or present

	Male	Female	Total
Father Absent	46 (54.1 %)	39	85
Father Present	45 (48.9 %)	47	92
Total	91	86	177

$X^2_{(1)}<1.0$, n.s.

Table 6.9b. Pup gender in the Wheel Noncontingent group for *Mus musculus* with the father absent or present.

	Male	Female	Total
Father Absent	47 (49.5%)	48	95
Father Present	36 (42.4%)	49	85
Total	83	97	180

$X^2_{(1)}<1.0$, n.s.

Table 6.9c. Pup gender in the Wheel Contingent group for *Mus musculus* with the father absent or present.

Pups	Male	Female	Total
Father Absent	44 (62.9%)	26	70
Father Present	36 (52.9%)	32	68
Total	80	58	138

$X^2_{(1)}<1.0$, n.s.

among the six groups in litter size at birth but by 20 days of age, litter size in the Wheel Contingent condition was significantly lower than in the other two housing conditions.

The analysis of mean litter and pup weights indicated that the pups in the Wheel Contingent condition were smaller than those in the other two housing conditions and that the fathers' presence had no effect on pup weights in any housing condition. There was no effect of either housing or parenting conditions on the number of male and female pups surviving to 20 days of age.

In order to analyze the contribution of the fathers' presence on pup survival, we analyzed time spent in parental behavior by mothers and fathers in each group. In order to understand how mice in the Wheel Contingent group partitioned their time, we analyzed the wheel running behavior and the eating behavior of males and females in the Wheel Contingent housing condition.

Part Three: Direct behavioral observations

As discussed in chapter 4, two general categories of behavior were recorded using the event recorder: parental behavior (section 6.6) and nonparental behavior (section 6.7). Beginning at parturition, data were collected for each mouse for a total of 20 days, 10 days in the light phase and 10 days in the dark phase (light and dark observations were alternated each day). For the analysis, the total durations of all parental behaviors and all nonparental behaviors were combined for each 10 minute observation period, producing two duration measurements per session.

Mothers in both Father Absent and Father Present groups were observed for a total of 100 minutes during the light phase over 10 days and 100 minutes during the dark phase over 10 days. Both the mother and father were observed in the father present group while only the mother was observed in the father absent group.

6.6 Direct observations of parental behavior

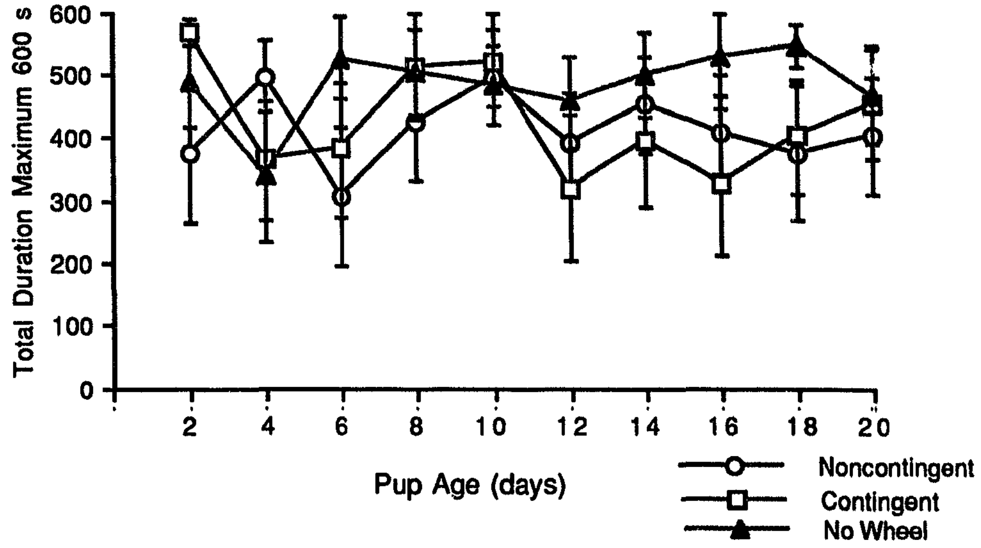
Parental behaviors included crouching over pups in the nursing position, resting and touching pups, nestbuilding, sniffing pups, grooming pups, and carrying pups. Because mothers and fathers spent significantly more time engaged in parental behavior during the light phase than in the dark phase of the LD cycle, light cycle was a variable in many analyses, and to reduce repetition, significant results are cited only once in each analysis. Likewise, while all interactions were examined in the analyses, only those that were significant are reported.

6.6.1 Parental behavior of mothers in the Father Absent group (Figure 6.3)

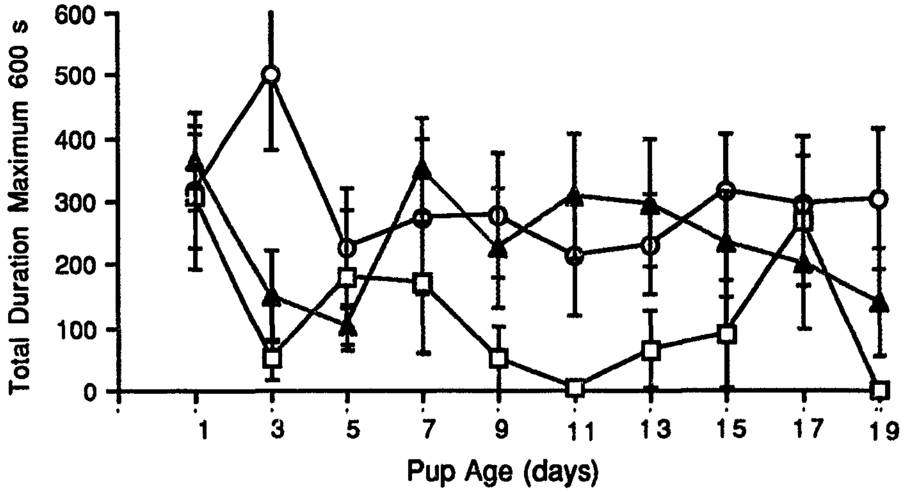
Differences in the amount of time spent engaged in parental behavior analyzed using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. Mothers spent significantly more time engaged in parental behavior in the light phase of the LD cycle than the dark phase ($F_{(1,21)}$=43.4, $p<.001$). Mothers in the No Wheel and Wheel Noncontingent housing conditions spent marginally more time engaged in parental behavior than mothers in the Wheel Contingent

Figure 6.3. Mus musculus: Parental behavior of mothers in the Father Absent groups

a. Light phase



b. Dark phase



conditions ($F_{(2,21)}=3.0$, $p=.07$). There was no main effect of days on the amount of parental behavior mothers displayed ($F_{(9,189)}=1.2$).

6.6.2 Parental behavior of mothers in the Father Present group (Figure 6.4)

Differences in the amount of time spent engaged in parental behavior were compared between housing groups using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. Significantly more time was spent in parental behavior in the light phase of the LD cycle than in the dark phase ($F_{(1,22)}=88.9$, $p<.001$). There was a significant main effect of housing as mothers in the Wheel Noncontingent housing condition spent the most time engaged in parental behaviour and mothers in the Wheel Contingent condition spent the least amount of time engaged in parental behavior ($F_{(2,22)}=9.1$, $p<.01$). Mothers in the No Wheel condition were intermediate between the Wheel Noncontingent and Wheel Contingent conditions in how much time was spent engaged in parental behavior. There was a significant effect of days ($F_{(9,198)}=2.9$, $p<.01$) as mothers decreased the amount of time they spent engaged in parental behavior as pups aged.

6.6.3 A comparison of parental behavior of mothers in the Father Absent and Father Present groups (Figure 6.5)

Data were collapsed over the LD cycle and days and mothers were compared for parental behavior, using a 2 (parenting) by 3 (housing) ANOVA. There was no significant difference between mothers in the Father Absent and Father Present groups in the amount of time they spent in parental activities ($F_{(1,45)}<1.0$) but, there was a significant difference between housing conditions

Figure 6.4. Mus musculus: Parental behavior of mothers in the Father Present groups

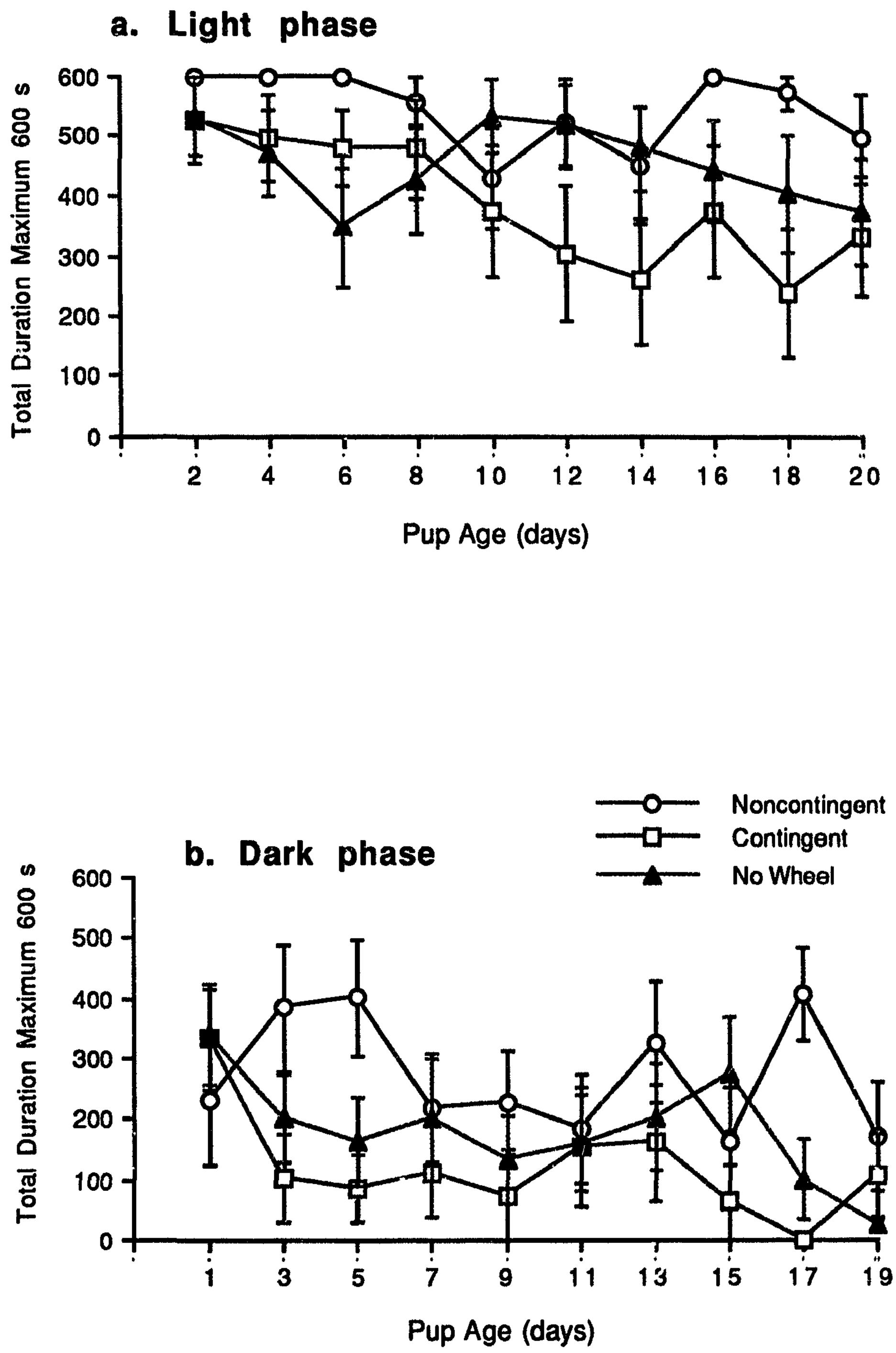
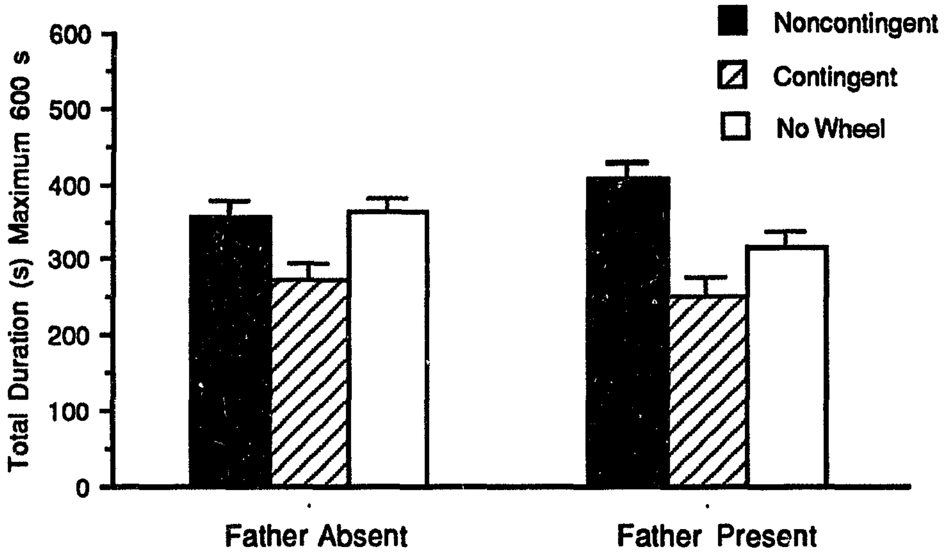


Figure 6.5. Mus musculus: Duration of parental behavior of mothers in the Father Absent and Father Present groups for all housing conditions collapsed over the LD cycle and days



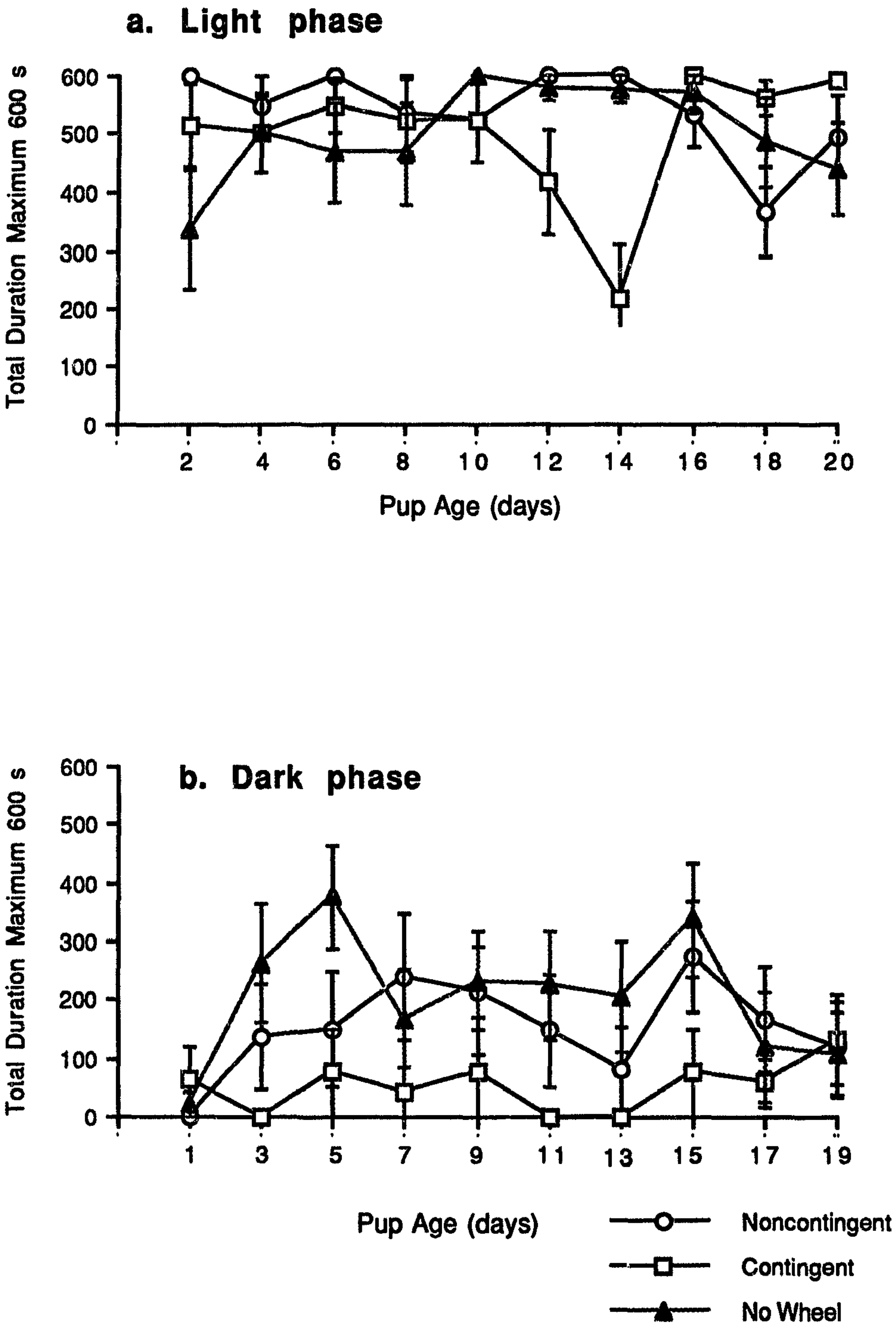
($F_{(2,45)}=6.5$, $p<.01$). Post Hoc comparisons (Tukey's HSD) indicated that mothers in the Wheel Contingent condition spent significantly less time in parental behavior than mothers in the Wheel Noncontingent condition ($p<.01$) and mothers in the No Wheel condition ($p<.05$).

6.6.4 Parental behavior of fathers in the Father Present groups (Figure 6.6)

Differences in the amount of time engaged in parental behavior by fathers were analyzed using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. Like mothers, fathers spent significantly more time engaged in parental behavior during the light phase of the LD cycle than during the dark phase ($F_{(1,22)}=230$, $p<.001$). There was no significant main effect of housing on the amount of parental behavior displayed by fathers ($F(2,22)=2.4$) but there was a significant interaction between the LD cycle and housing ($F_{(2,22)}=3.5$) as fathers in the Wheel Contingent condition engaged in less parental behavior than fathers in the other two housing conditions during the dark phase.

There was a significant effect of days ($F_{(9,198)}=2.8$, $p<.01$) as fathers exhibited the least amount of parental behavior the day after birth (day 1). There was a significant interaction between days and housing conditions ($F_{(18,198)}=2.3$, $p<.01$) as fathers in the Wheel Contingent condition decreased the amount of time spent engaged in parental behavior from day 1 to day 14, and then increased the amount of time spent in parental behavior up to day 20. Fathers in the Wheel Noncontingent and No Wheel conditions maintained a

Figure 6.6. Mus musculus: Parental behavior of fathers in the Father Present groups



similar amount of time engaged in parental behavior from day 1 to day 20 after birth.

6.6.5 A comparison of parental behavior of mothers and fathers in the Father Present groups (Figures 6.7 and 6.8)

In order to compare the amount of parental behavior shown by mothers and fathers in the father present groups, the duration of parental behavior exhibited by mothers and fathers was compared using an ANOVA with two between factors (housing and gender) and two within factors (LD cycle and days).

Mothers and fathers did not differ in the amount of time they engaged in parental behavior ($F_{(1,44)}<1.0$) but there was a significant interaction between the LD cycle and gender ($F_{(1,44)}=7.4$, $p<.01$, Figure 6.7). Fathers and mothers engaged in the same amount of parental behavior during the light phase of the LD cycle while mothers engaged in more parental behavior than fathers during the dark phase of the LD cycle.

There was a significant effect of housing on parental behavior ($F_{(2,44)}=8.6$, $p<.001$, Figure 6.8). Post Hoc comparisons (Tukey's HSD) indicated that both parents in the Wheel Contingent condition spent significantly less time in parental behavior than parents in the Wheel Noncontingent condition ($p<.01$) and the No Wheel condition ($p<.05$).

As shown in Figures 6.4 and 6.6, the time that mothers and fathers spent in parental behavior declined significantly from birth to weaning ($F_{(9,396)}=2.0$, $p<.05$). There was a significant interaction between days and gender ($F_{(9,396)}=3.7$, $p<.001$). Fathers engaged in significantly less parental behavior than mothers at parturition and

Figure 6.7. Mus musculus: Parental behavior of mothers and fathers in the Father Present groups in the light and dark phase of the LD cycle collapsed over housing and days

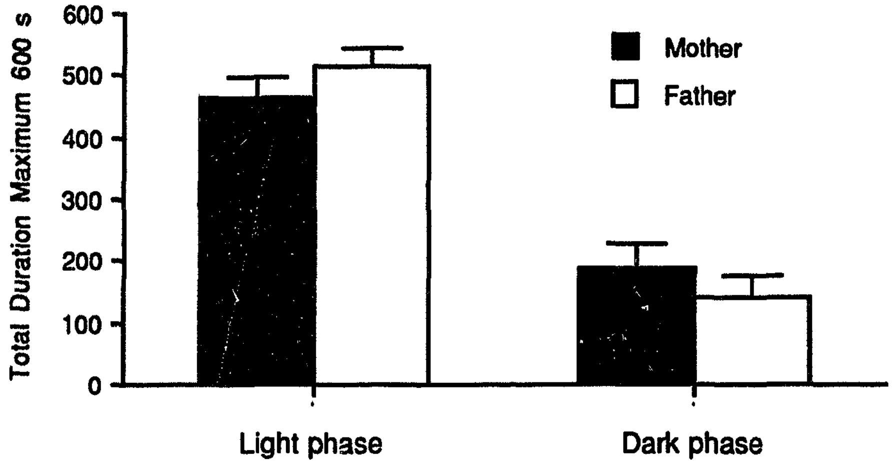
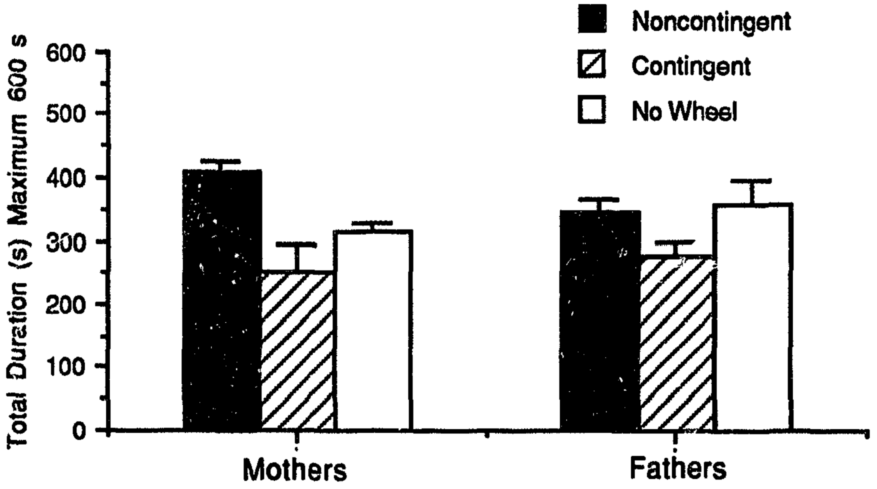


Figure 6.8. Mus musculus: Duration of parental behavior of mothers and fathers in the Father Present group for all housing conditions collapsed over the LD cycle



for the first day after parturition, after which, mothers and fathers displayed similar amounts of parental behavior up to weaning. There was a significant interaction between days and housing ($F_{(18,396)}=2.0$, $p<.01$). Mothers and fathers in the Wheel Noncontingent and No Wheel conditions increased the amount of parental behavior displayed for 4 days after parturition, then showed a decrease in parental behavior the day before weaning. *Mus* in the Wheel Contingent condition, showed a gradual decrease in parental behavior after parturition.

A comparison of Figures 6.4 and 6.6 indicates that there was a significant interaction between days, gender and housing ($F_{(18,396)}=1.8$, $p<.05$). Fathers in the Wheel Contingent condition decreased the amount of time spent in parental behavior the day after parturition, then increased the amount of time spent engaged in parental behavior from day 16 to day 20 after parturition. Mothers in the Wheel Contingent condition decreased the amount of time they spent engaged in parental behavior as weaning approached. Fathers in the Wheel Noncontingent and No Wheel conditions increased the amount of time spent engaged in parental activities the day after parturition and sustained that amount of parental behavior to weaning. Mothers in the Wheel Noncontingent and No Wheel conditions gradually decreased the amount of time spent in parental activities during the lactation period.

6.7 Direct observations of nonparental behavior

Nonparental behaviors included, wheel running, exploring, eating, grooming, resting without touching pups and gnawing wood shavings or bars on cage. Over all analyses, mothers and fathers spent significantly more time engaged in nonparental behavior during the dark phase of the LD cycle. Interactions that were not significant were not reported below.

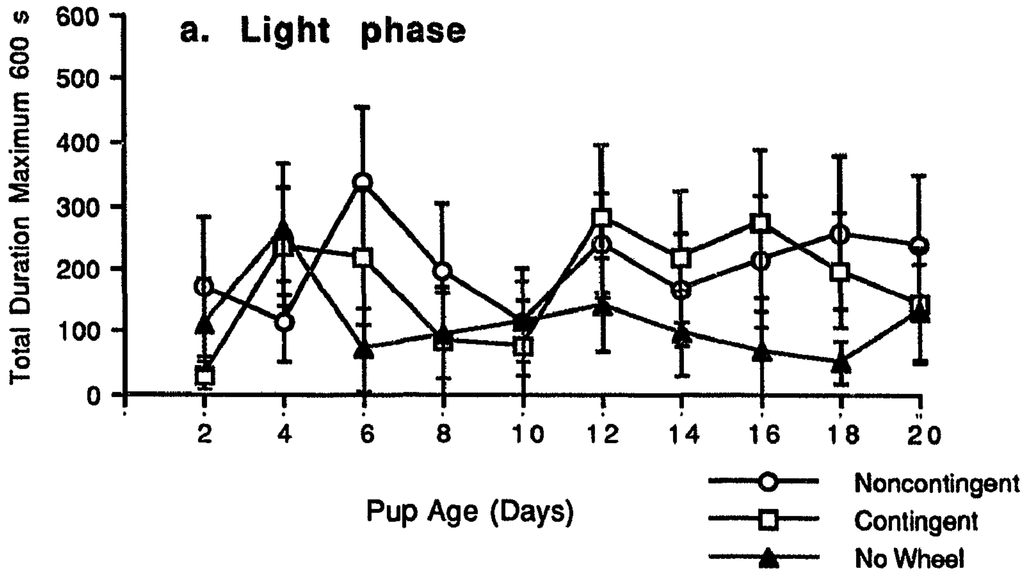
6.7.1 Nonparental behavior of mothers in the Father Absent groups (Figure 6.9)

Nonparental behaviors were analyzed using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. Mothers spent more time in the dark phase than in the light phase of the LD cycle engaged in nonparental activities ($F_{(1,21)}=48.2$, $p<.001$). There was no significant effect of housing on nonparental behavior ($F_{(2,21)}=2.8$, $p=.09$). However, mothers in the Wheel Contingent condition spent more time engaged (327.9 s) in nonparental behaviors than mothers in the Wheel Noncontingent (253.7 s) and No Wheel conditions (238.7 s). There was no significant effect of days on the amount of nonparental behavior displayed by mothers ($F_{(9,189)}=1.5$)

6.7.2 Nonparental behavior of mothers in the Father Present groups (Figure 6.10)

There was a significant effect of the LD cycle on the amount of time mothers engaged in nonparental activities ($F_{(1,22)}=83.4$, $p<.001$). Mothers in the Wheel Contingent condition (350.6 s) spent significantly more time engaged in nonparental behaviors than mothers in the Wheel Noncontingent (194.0 s) and No Wheel conditions (282.5 s, $F_{(2,22)}=10.1$, $p<.001$). There was a significant effect of days on nonparental behavior as paired mothers engaged in

Figure 6.9. Mus musculus: Nonparental behavior of mothers in the Father Absent groups



b. Dark phase

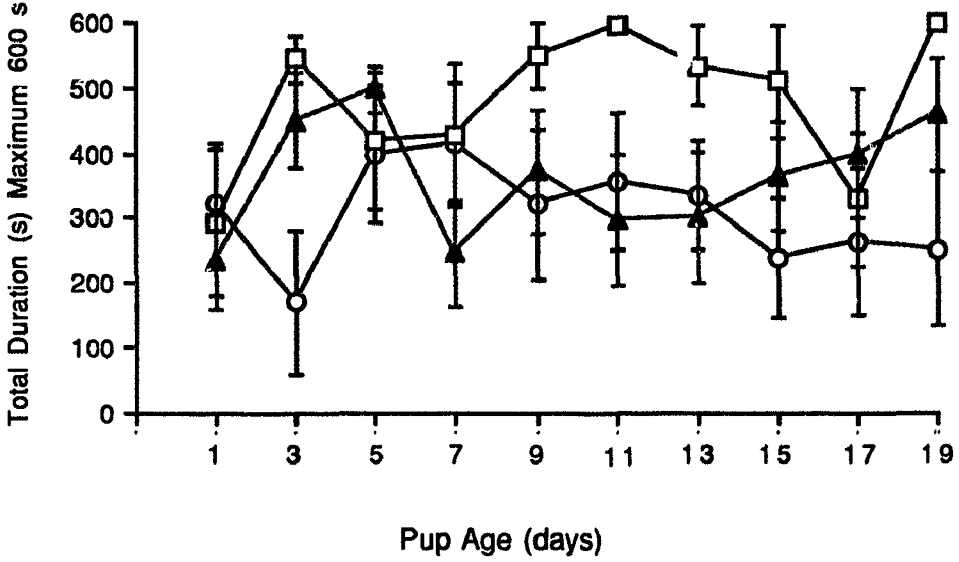
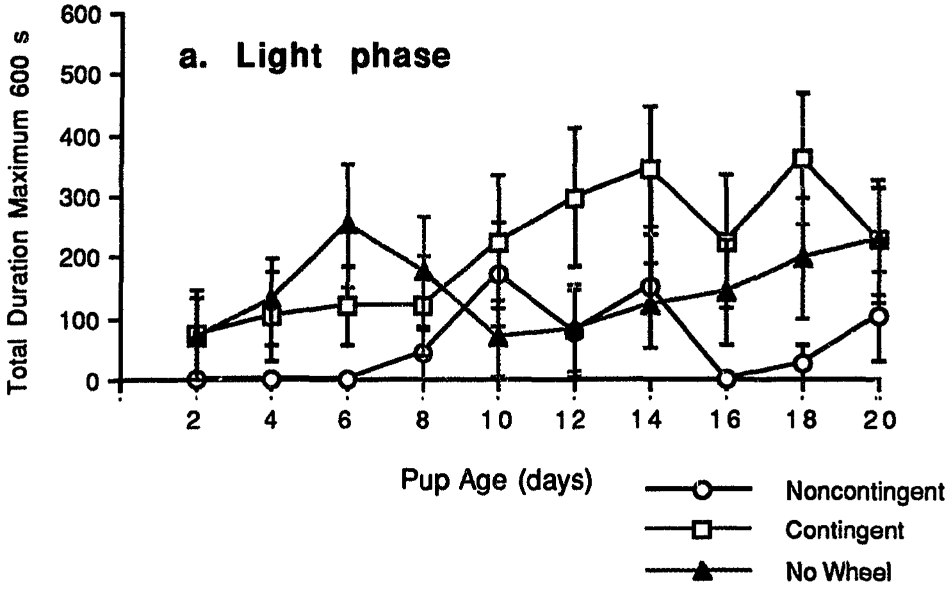
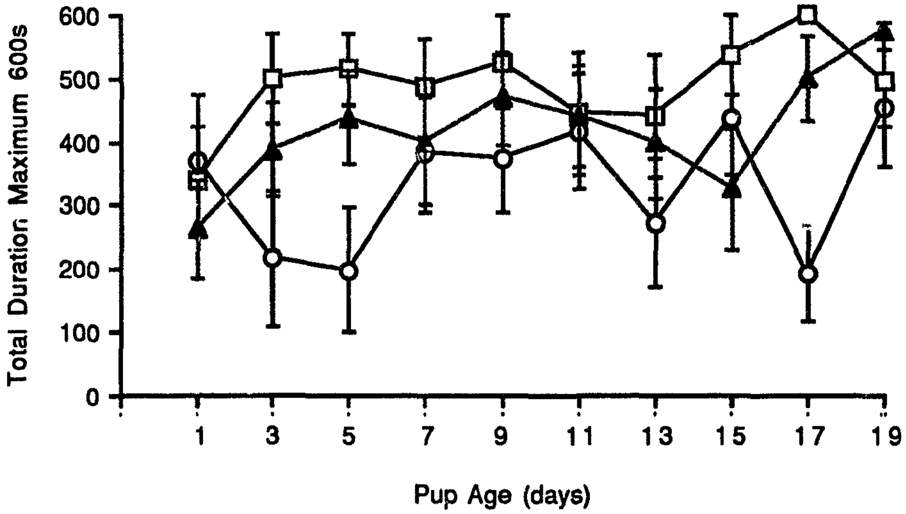


Figure 6.10. Mus musculus: Nonparental behavior of mothers in the Father Present groups



b. Dark phase



progressively more nonparental behavior as pups aged ($F_{(9,198)}=2.6$, $p<.001$).

6.7.3 A comparison of nonparental behavior of mothers in the Father Absent and Father Present groups (Figure 6.11)

Data were collapsed over the LD cycle and days and mothers were compared between different groups for nonparental behavior, using a 2 (parenting) by 3 (housing) ANOVA. There was a significant effect of housing on the amount of time spent in nonparental behavior ($F_{(2,45)}=6.3$, $p<.01$). Mothers in the Wheel Noncontingent condition spent the least amount of time in nonparental activities, while mothers in the Wheel Contingent condition spent the most time in nonparental acttivies. Post Hoc comparisons (Tukey's HSD) indicated significant differences between the Wheel Contingent condition and the Wheel Noncontingent condition ($p<.01$) and between the Wheel Contingent condition and the No Wheel condition ($p<.05$). There was no significant effect of parenting on the amount of time spent in nonparental behavior ($F_{(1,45)}<1.0$).

6.7.4 Nonparental behavior of fathers in the Father Present groups (Figure 6.12)

Fathers spent more time engaged in nonparental behavior during the dark phase than the light phase of the LD cycle ($F_{(1,22)}=228.3$, $p<.001$). There was no significant effect of housing on the amount of nonparental behavior performed by fathers ($F_{(2,22)}=2.3$) but there was a significant interaction between the LD cycle and housing ($F_{(2,22)}=3.5$), $p<.05$) as fathers in the Wheel

Figure 6.11. Mus musculus: Duration of nonparental behavior of mothers in the Father Absent and Father Present groups for all housing conditions collapsed over the LD cycle and days

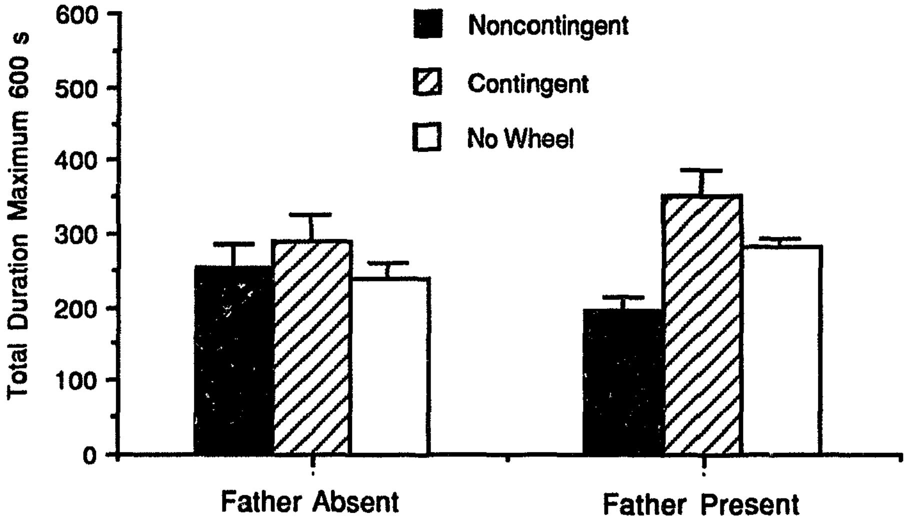
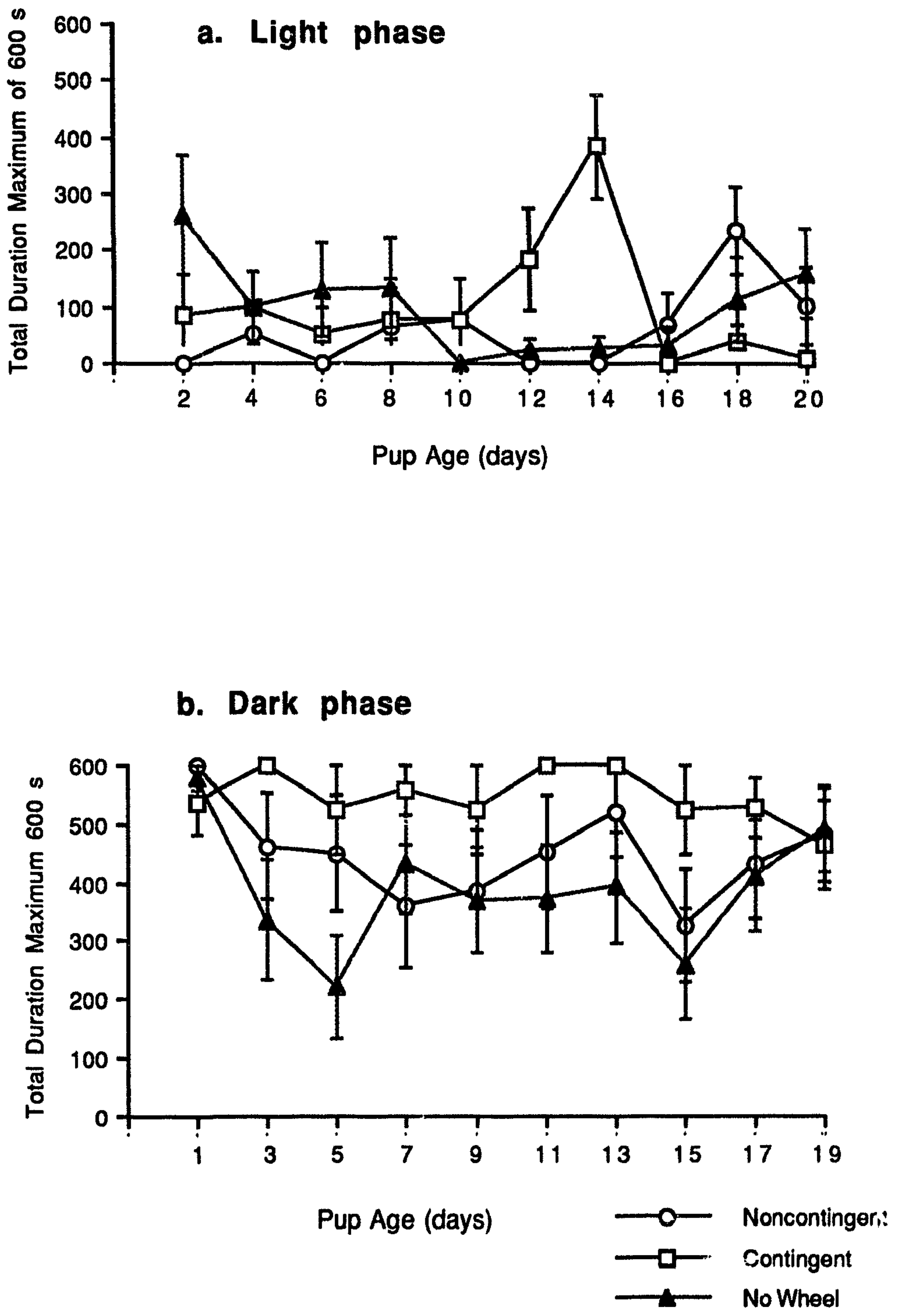


Figure 6.12. Mus musculus: Nonparental behavior of fathers in the Father Present groups



Contingent condition spent the most time during the dark phase engaged in nonparental behaviors.

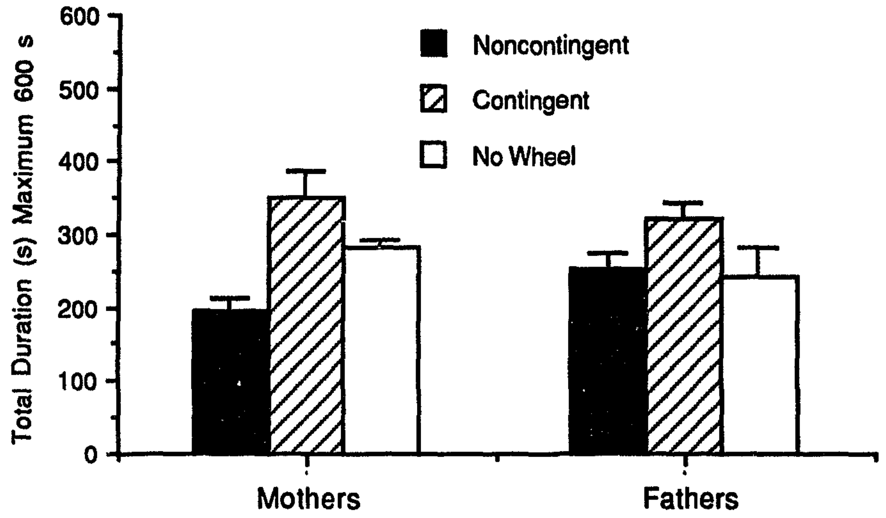
There was a significant effect of days on the amount of nonparental behavior performed by fathers ($F_{(9,198)}=2.9$, $p<.01$) as fathers exhibited the most nonparental behavior the day after birth (day 1). There was a significant interaction between days and housing ($F_{(18,198)}=2.4$, $p<.01$) as fathers in the Wheel Contingent condition increased the amount of time spent in nonparental behavior for the first 14 days after birth of the pups then decreased the amount of time up to 20 days after birth. Fathers in the Wheel Noncontingent and No Wheel conditions maintained a steady amount of time engaged in nonparental behavior.

6.7.5 A comparison of nonparental behavior of mothers and fathers in the Father Present groups (Figure 6.13)

The amount of nonparental behavior mothers and fathers exhibited was compared using an ANOVA with two between factors (housing and gender) and two within factors (LD cycle and days). Comparison of Figures 6.10 and 6.12 shows that there was significantly more nonparental behavior in the dark phase of the LD cycle than in the light phase ($F_{(1,44)}=277.5$, $p<.001$). There was a significant interaction between the LD cycle and gender ($F_{(1,44)}=6.6$, $p<.05$). Mothers and fathers engaged in similar amounts of nonparental behavior during the light phase but fathers engaged in more nonparental behavior than mothers during the dark phase of the LD cycle.

As shown in Figure 6.13, mothers and fathers did not differ in the amount of time engaged in nonparental behavior ($F_{(1,44)}<1.0$) but

Figure 6.13. Mus musculus: Duration of nonparental behavior of mothers and fathers in the Father Present Group for all housing conditions collapsed over the LD cycle



there was a significant effect of housing on nonparental behavior ($F_{(2,44)}=9.0$, $p<.001$). *Mus* in the Wheel Contingent condition spent more time engaged in nonparental behavior than *Mus* in the Wheel Noncontingent ($p<.01$) and No Wheel condition ($P<.01$).

There was a significant effect of days as *Mus* gradually increased the amount of time spent engaged in nonparental activities throughout the period of lactation ($F_{(9,396)}=2.0$, $p<.05$). There was also a significant interaction between days and gender ($F_{(9,396)}=3.3$, $p<.001$). Fathers engaged in significantly more nonparental behavior than mothers at parturition and for the first day after parturition, after which, mothers and fathers displayed similar amounts of nonparental behavior up to weaning. There was a significant interaction between days and housing ($F_{(18,396)}=1.9$, $p<.05$). *Mus* in the Wheel Noncontingent and No Wheel conditions decreased the amount of nonparental behavior displayed for 4 days after parturition, then showed an increase in nonparental behavior the day before weaning. *Mus* in the Wheel Contingent condition, showed a gradual increase in nonparental behavior after parturition.

There was a significant interaction between days, gender and housing ($F_{(18,396)}=1.8$, $p<.05$). Fathers in the Wheel Contingent condition increased the amount of time spent engaged in nonparental behavior the day after parturition, then decreased the amount of time spent engaged in nonparental behavior by day 16 of lactation to weaning. Mothers in the Wheel Contingent condition increased the amount of time they spent engaged in nonparental behavior as weaning approached. Fathers in the Wheel Noncontingent and No Wheel conditions decreased the amount of time spent engaged in nonparental activities the day after parturition and sustained that amount of nonparental behavior to weaning. Mothers in the Wheel Noncontingent and No Wheel conditions gradually increased the amount of time spent in nonparental activities during the lactation period.

Summary of Part Three. More time was spent in parental behavior during the light phase and more time was spent in nonparental behavior during the dark phase of the LD cycle. Mothers spent the same amount of time in parental and nonparental behavior whether the father was absent or present. Fathers spent the same amount of time as mothers engaged in parental behavior during the light phase but more time engaged in nonparental behavior during the dark phase of the LD cycle. Mothers and fathers spent less time in parental behavior and more time in nonparental behavior in the Wheel Contingent condition. More details about the time spent wheel running and eating are given in sections 6.9 and 6.14.

Part Four: Wheel Running

6.8 Number of revolutions run by *Mus musculus* after pairing in the Wheel Noncontingent and Wheel Contingent conditions (Figures 6.14 and 6.15)

The number of revolutions run in the wheel was recorded hourly from the time *Mus* were placed together in pairs, to the weaning of pups. This time period consisted of 42 days (21 days prior to birth and 21 days from birth to weaning). For analysis, the data were pooled into blocks of 5 days. This resulted in four 5 day blocks before birth and four, 5 day blocks after birth, with one day for parturition. The number of revolutions was calculated during the light phase and dark phase of the LD cycle for each 5 day period. Data were analysed using a 2 (parenting) x 2 (housing) x 2 (LD cycle) x 9 (blocks of time) analysis of variance with two between factors (parenting and housing) and two within factors (LD cycle and blocks of time). Days 20 to 6 before parturition (Blocks 1 to 3) were analyzed independently of the remaining data (Blocks 4 to 9) as males were removed from the Father Absent groups on days 2 to 4 before parturition. Therefore, during the first 15 days the only difference between the groups was housing. Over all conditions *Mus* ran more revolutions during the dark phase than during the light phase of the LD cycle. Interactions that were not significant were not reported.

a. Blocks 1 to 3 (fathers present in all groups)

Mus ran significantly more during the dark phase of the LD cycle than the light phase ($F_{(1,29)}=235.4$, $p<0.001$, Figures 6.14 and 6.15). There was no significant difference between Father Absent and Father Present groups in the number of revolutions they ran in the first 3 blocks of days ($F_{(1,29)}<1.0$), but there was a near significant difference in the number of revolutions *Mus* ran between the Wheel Noncontingent and Wheel Contingent conditions ($F_{(1,29)}=4.0$, $p=.06$).

Mus gradually ran more revolutions from block 1 to 3 ($F_{(2,58)}=7.8$, $p<.01$) but this interacted with the light cycle. The number of revolutions declined over these 3 blocks of days during the light phase while the number of revolutions increased during the dark phase ($F_{(2,58)}$=14.3, p<.001).

b. Blocks 4 to 9 (father removed from Father Absent groups)

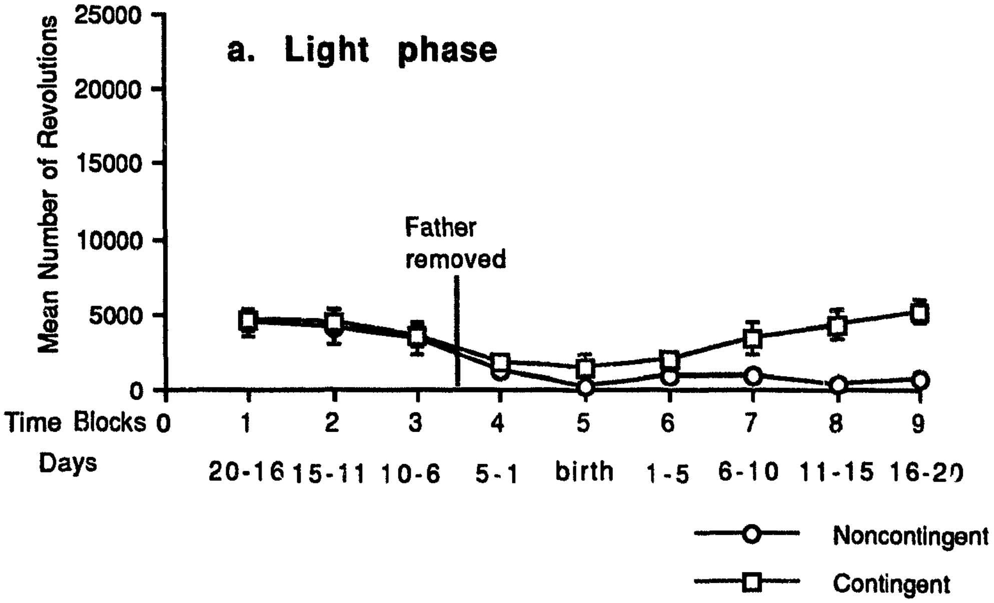
Since a mother and a father were running in the Father Present groups and only a mother was running in the Father Absent groups, these groups were analyzed separately. Therefore, for both Father Absent groups and Father Present groups, a 3 (housing) by 2 (LD cycle) by 6 (blocks of days) ANOVA was used.

Father Absent groups (Figure 6.14)

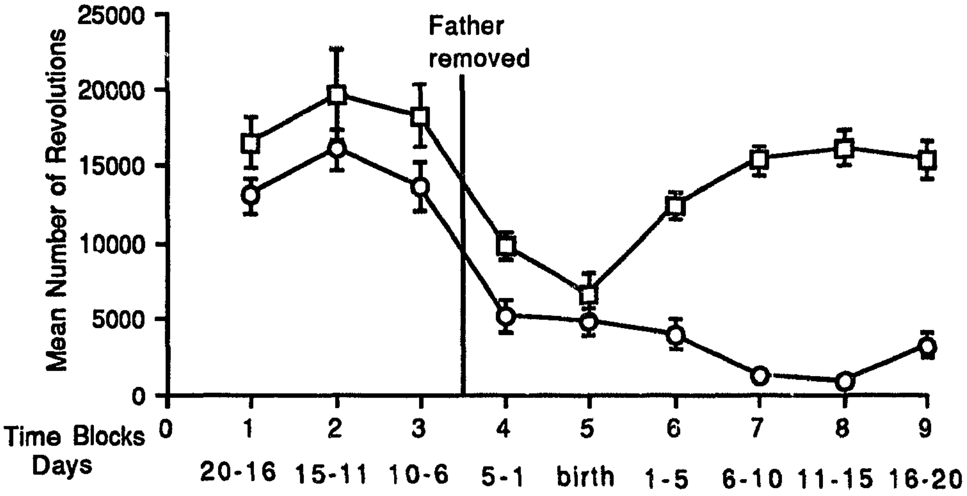
Mothers in the Wheel Contingent condition ran on average, four times as many revolutions as those in the Wheel Noncontingent condition (7808 vs. 1933), a difference which was highly significant ($F_{(1,13)}$=265.1, p<.0001). Mothers ran four times as many revolutions during the dark phase as during the light phase of the LD cycle ($F_{(1,13)}$=145.7, p<.0001) and there was a significant interaction between the LD cycle and housing ($F_{(1,13)}$=50.2, p<.001). While mothers in the Wheel Noncontingent condition ran 681 revolutions in the light phase and increased this to 3186 revolutions in the dark phase, those in Wheel Contingent condition ran 2996 revolutions in the light phase and increased this to 12621 revolutions in the dark phase.

The number of revolutions mothers ran decreased from block 4 to 5, and then steadily increased up to block 9 ($F_{(5,65)}$=8.7, p<.001). There was a significant interaction between days and housing

Figure 6.14. Mean number of revolutions for Mus musculus in the Father Absent groups



b. Dark phase



($F_{(5,65)}$=25.7, p<.001) as mothers in the Wheel Noncontingent condition decreased the number of revolutions they ran from block 5 to 8 and then increased the number of revolutions they ran from block 8 to 9. Mothers in the Wheel Contingent condition ran a similar number of revolutions as mothers in the Wheel Noncontingent condition during Block 4, and at parturition but then almost doubled the number of revolutions they ran during Block 6 and continued to increase the number of revolutions they ran up to block 9.

There was a significant interaction between the LD cycle, days and housing ($F_{(5,65)}$=9.1, p<.001). During the light phase of LD cycle, mothers in the Wheel Noncontingent condition decreased the number of revolutions they ran from block 6 to block 8, then increased the number of revolutions in block 9, while mothers in the Wheel Contingent condition steadily increased the number of revolutions they ran from blocks 5 to 8. During the dark phase of the LD cycle, mothers in the Wheel Noncontingent condition decreased the number of revolutions they ran from block 5 to 8, then increased the number of revolutions for the last block of days, while mothers in the Wheel Contingent condition reached a peak number of revolutions by block 7 and maintained this rate of running up to block 9.

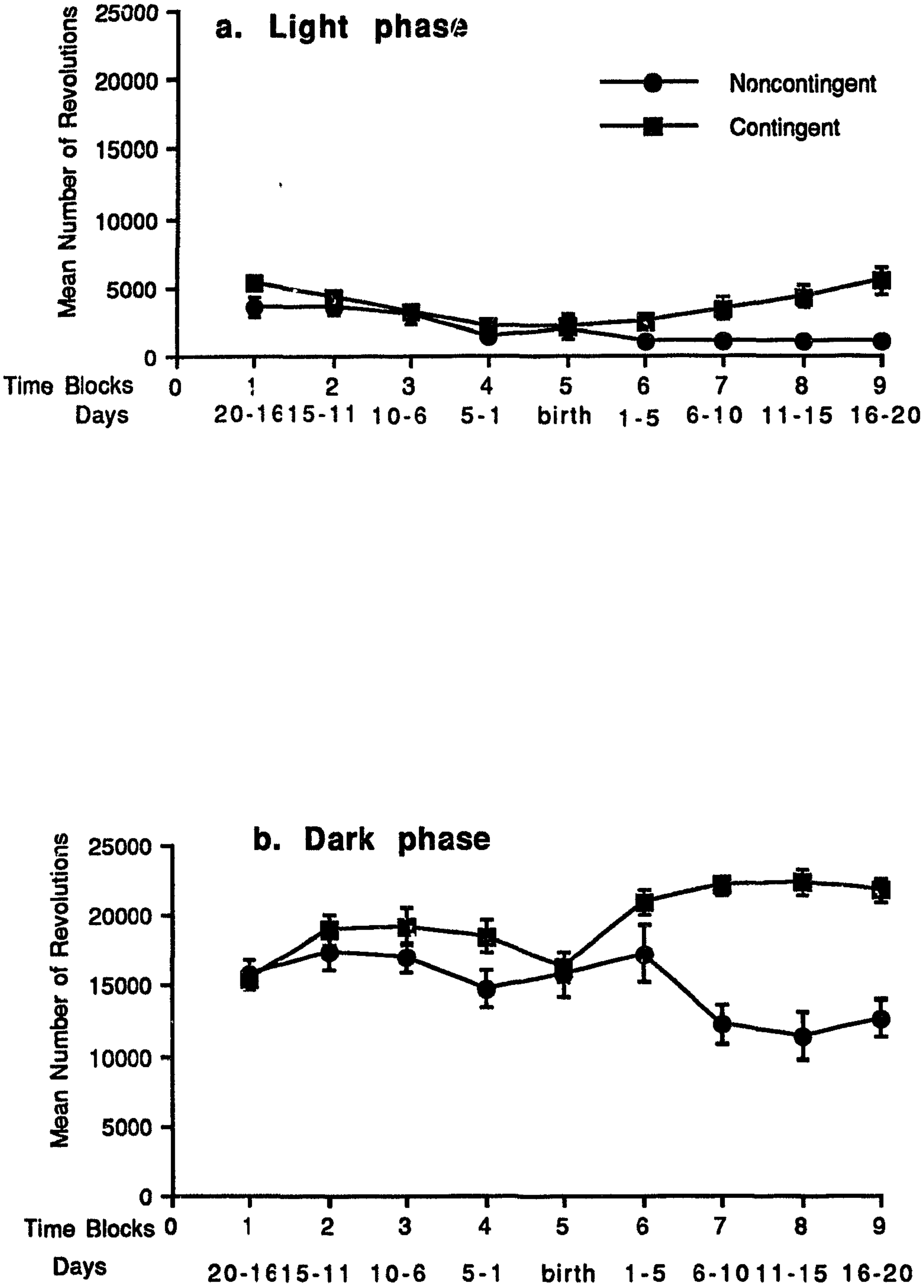
Father Present group (Figure 6.15)

There was a significant effect of housing conditions on the number of revolutions run ($F_{(1,14)}$=451.2, p<.001). Mothers and fathers in the Wheel Contingent condition ran about one and a half times more revolutions (11826) than those in the Wheel Noncontingent condition (7670). Mothers and fathers ran over seven times more revolutions during the dark phase (17167) than during the light phase (2328.0) of the LD cycle ($F_{(1,14)}=382.0$, $p<.001$). There was a significant LD cycle by housing interaction ($F_{(1,14)}=7.9$, $p<.05$), as *Mus* in the Wheel Contingent condition ran only about 1.4 times more revolutions during the dark phase than *Mus* in the Wheel Noncontingent condition (20309 vs. 14026) but during the light phase *Mus* in the Wheel Contingent condition ran 2.5 times as many revolutions as *Mus* in the Wheel Noncontingent condition (3343 vs. 1313).

There was a significant effect of days on the number of revolutions run ($F_{(5,70)}=3.3$, $p=0.01$). Mothers and fathers decreased the number of revolutions they ran on the day of parturition (block 5), then increased and maintained the number of revolutions they ran until weaning (block 9). There was a significant days by housing interaction ($F_{(5,70)}=21.8$, $p<0.001$) as mothers and fathers in the Wheel Noncontingent condition increased the number of revolutions they ran up to block 7, and then decreased the number of revolutions they ran, while those in the Wheel Contingent condition decreased the number of revolutions they ran at birth then steadily increased and maintained a high number of revolutions by block 8.

There was a significant LD cycle by days interaction ($F_{(5,70)}=4.5$, $p=0.01$). Mothers and fathers increased the number of revolutions they ran during the light phase beginning in block 8 and continuing up to block 9 while they increased the number of revolutions they ran during the dark phase starting in block 7 and maintained the number of revolutions until weaning. There was a significant interaction between the LD cycle, days and housing

Figure 6.15. Mean number of revolutions for Mus musculus in the Father Present groups



($F_{(5,70)}=6.2$, $p<.001$). Mothers and fathers in the Wheel Noncontingent condition increased the number of revolutions they ran during the light phase at parturition and then decreased the number they ran after parturition up to weaning while *Mus* in the Wheel Contingent condition did not decrease the number of revolutions they ran at parturition and gradually increased the number of revolutions up to weaning. *Mus* in the Wheel Noncontingent condition decreased the number of revolutions they ran during the dark phase beginning in block 7 while mice in the Wheel Contingent condition increased the number of revolutions they ran beginning one day after birth and continuing to weaning.

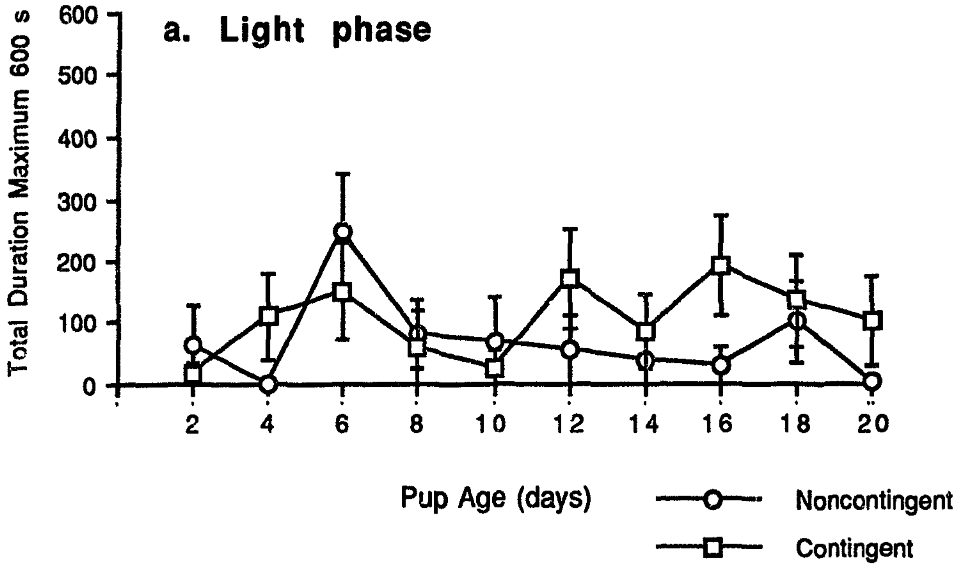
6.9 Observations of wheel running behavior

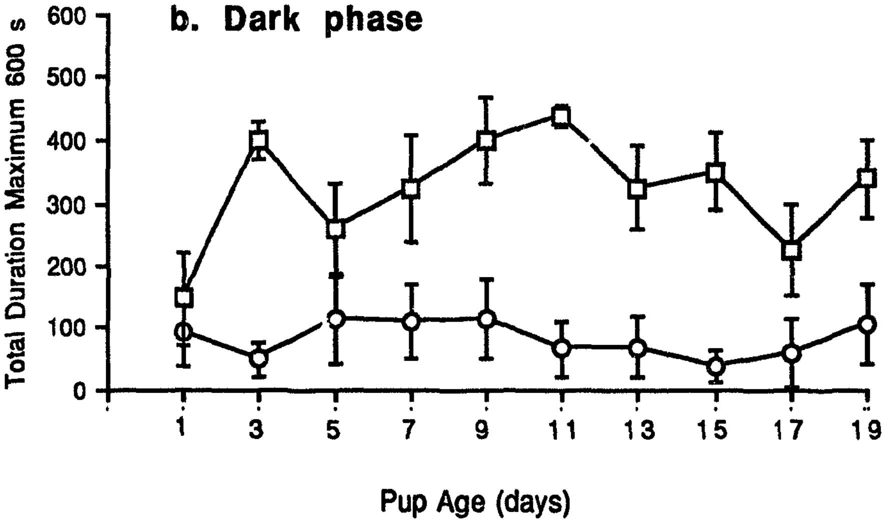
In order to determine which animal was running on the wheel, we analyzed the wheel running behavior observations separately from the other nonparental behaviors. Differences in the amount of time spent in wheel running behavior were compared between housing groups using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. Nonsignificant interactions were not reported.

6.9.1 Wheel running behavior of mothers in the Father Absent groups (Figure 6.16)

Mothers in the Wheel Contingent condition ran significantly more during the observation period than did mothers in the Wheel Noncontingent condition ($F_{(1,13)}=55.6$, $p<.001$). There was a significant interaction between the LD cycle and housing ($F_{(1,13)}=16.7$, $p<.01$). Mothers in both groups ran for similar amounts

Figure 6.16. Mus musculus: Duration of wheel running behavior of mothers in the Father Absent group





of time during the light phase but mothers in the Wheel Contingent condition ran three times as much as mothers in the Wheel Noncontingent condition during the dark phase.

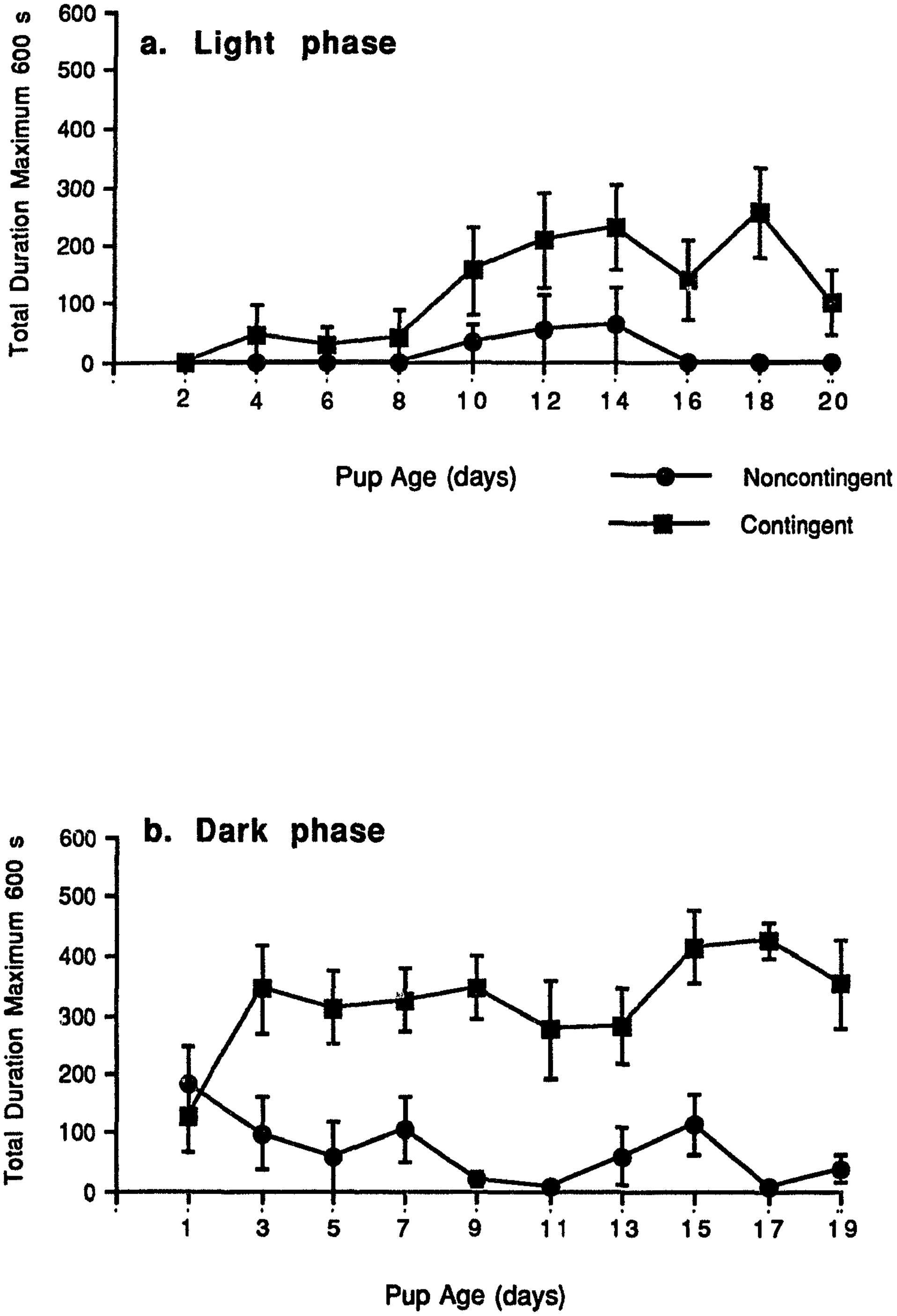
There was no significant effect of days on the amount of time spent wheel running ($F_{(9,117)}=1.5$) as mothers spent similar amounts of time engaged in wheel running behavior over the period of lactation. There was a significant interaction between days and housing ($F_{(9,117)}=2.8$, $p<.01$). Mothers in both groups spent only a small amount of time wheel running at parturition. After parturition, the amount of time mothers in the Wheel Contingent condition spent wheel running increased dramatically while the amount of time mothers spent wheel running in the Wheel Noncontingent condition increased only slightly.

6.9.2 Wheel running behavior of mothers in the Father Present groups (Figure 6.17)

Mothers in the Wheel Contingent condition spent significantly more time wheel running than mothers in the Noncontingent condition ($F_{(1,14)}=32.8$, $p<.0001$). There was a significant interaction between the LD cycle and housing ($F_{(1,14)}=18.0$, $p<.001$). Mothers in the Wheel Contingent condition spent 7.9 times longer wheel running during the light phase and only 4.6 times longer wheel running during the dark phase than mothers in the Wheel Noncontingent condition.

There was no significant effect of days on the amount of time mothers spent wheel running ($F_{(9,126)}=1.2$) but there was a significant interaction between days and housing ($F_{(9,126)}=3.0$, $p<.01$).

Figure 6.17. Mus musculus: Duration of wheel running behavior of mothers in the Father Present group



Mothers in both groups spent only a small amount of time wheel running at parturition. After parturition, the amount of time mothers in the Wheel Contingent condition spent running increased dramatically while the amount of time mothers spent running in the Wheel Noncontingent condition increased only slightly.

There was a significant interaction between the LD cycle and days ($F_{(9,126)}=3.2$, $p<.01$). During the light phase, mothers did not spend any time wheel running on the day of parturition, then slowly increased the amount of time spent wheel running up to 14 days after parturition. During the dark phase, mothers spent more time wheel running but there was no change in the amount of time mothers spent wheel running over the 20 day period of lactation.

6.9.3 A comparison of wheel running behavior of mothers in the Father Absent and Father Present groups

In order to reduce the redundancy of the analyses, results that were already reported have been omitted. For example, results pertaining to housing conditions were reported in section 6.9.1 and 6.9.2 and therefore were not reported again.

Comparison of Figures 6.16 and 6.17 indicates that there was no significant effect of parenting group on the amount of time mothers were observed to run on the wheel ($F_{(1,27)}<1.0$). There was a significant effect of housing as mothers in the Wheel Contingent condition spent more time wheel running than mothers in the Wheel Noncontingent condition ($F_{(1,27)}=41.0$, $p<.001$).

There was a significant interaction between the LD cycle, days and parenting ($F_{(9,243)}=2.6$, $p<.01$). During the light phase, mothers in the Father Absent group spent more time wheel running for the first 8 days after parturition than mothers in the Father Present group. During the dark phase, mothers in both groups were observed to spend similar amounts of time wheel running for the period of lactation.

6.9.4 Wheel running behavior of fathers (Figure 6.18)

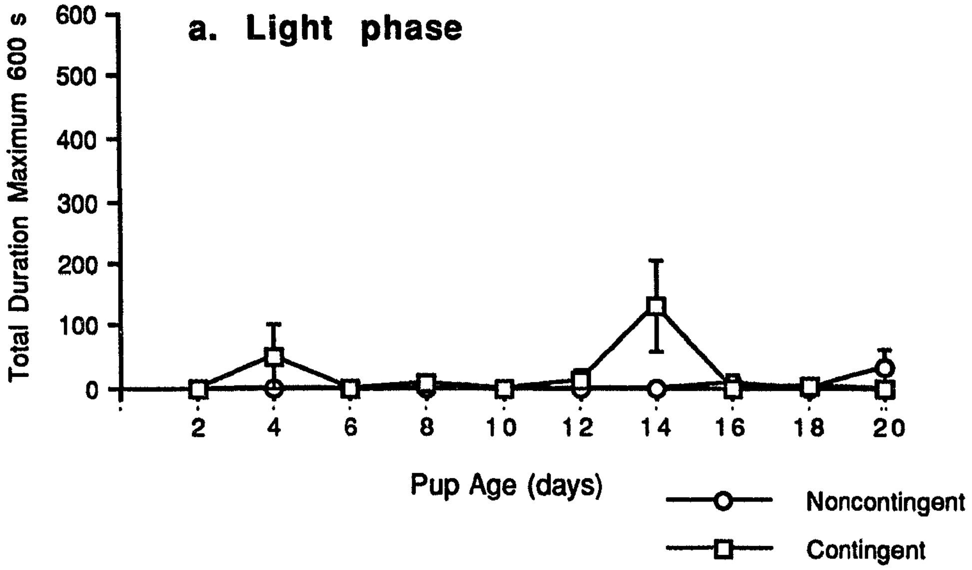
There was a significant effect of housing on wheel running behavior ($F_{(1,14)}=5.7$, $p<.05$) as fathers in the Wheel Contingent condition ran more than fathers in the Wheel Noncontingent condition. Fathers in both housing conditions ran more in the dark phase of the LD cycle than the light phase ($F_{(1,14)}=234.3$, $p<.001$). There was no significant effect of days on wheel running behavior of fathers ($F_{(9,126)}=1.7$).

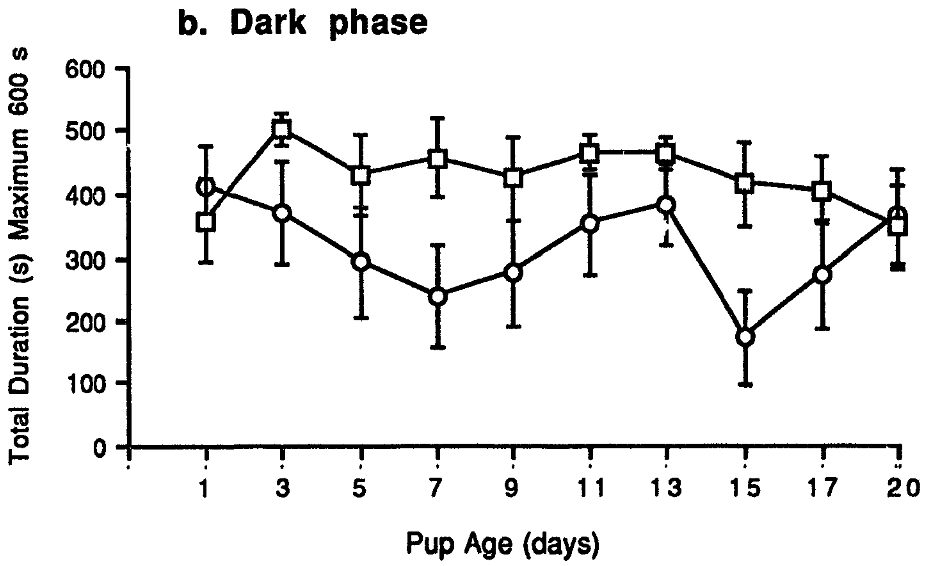
6.9.5 A comparison of wheel running behavior of mothers and fathers in the Father Present groups (Figures 6.17 and 6.18)

This analysis is a 2 (gender) x 2 (housing) x 2 (LD cycle) x 10 (days) ANOVA. There was a significant interaction between the LD cycle and gender on the amount of time *Mus* were observed wheel running ($F_{(1,28)}=64.1$, $p<.001$). Mothers ran more than fathers during the light phase while fathers ran more than mothers during the dark phase.

There was a significant effect of gender on the amount of time *Mus* were observed wheel running ($F_{(1,28)}=8.4$, $p<.01$) as fathers were observed running on the wheel for longer periods of time than mothers. There was a significant interaction between gender and

Figure 6.18. Mus musculus: Duration of wheel running behavior of fathers in the Father Present groups


a. Light phase


b. Dark phase

housing ($F_{(1,28)}=7.3$, $p<.05$). Mothers in the Wheel Noncontingent condition were observed wheel running for the least amount of time, while mothers in the Wheel Contingent condition were observed wheel running for longer amounts of time (about 4 times longer). Fathers in the Wheel Contingent condition spent the same amount of time wheel running as mothers in the Wheel Contingent condition, while fathers in the Wheel Noncontingent condition spent less time running than mothers and fathers in the Wheel Contingent condition but more than mothers in the Wheel Noncontingent condition. There was a significant interaction between the LD cycle, days and gender ($F_{(9,252)}=1.9$, $p<.05$).

Summary of Part Four. When wheel running was measured by the number of revolutions, mothers and fathers ran slightly more in the Wheel Contingent condition than in the Wheel Noncontingent condition up to 5 days before birth of the pups. After the birth of the pups, mothers in the Father Absent group and mothers and fathers in the Father Present group ran more revolutions in the Wheel Contingent condition than in the Wheel Noncontingent condition. *Mus* ran more revolutions during the dark phase than during the light phase of the LD cycle.

The wheel running behavior observations showed that mothers spent similar amounts of time running in both the Father Absent and Father Present groups and mothers and fathers spent more time wheel running in the Wheel Contingent condition. Overall, fathers spent more time running than mothers in the Father Present groups. Specifically, mothers and fathers in the Wheel Contingent condition ran for the same duration of time and were observed spending more time wheel running than mothers and fathers in the Wheel Noncontingent condition. Fathers in the Wheel Noncontingent condition ran for longer durations than mothers in the Wheel Noncontingent condition.

Part Five: Wheel running versus parental behavior in the dark phase in the Wheel Contingent and Wheel Noncontingent conditions

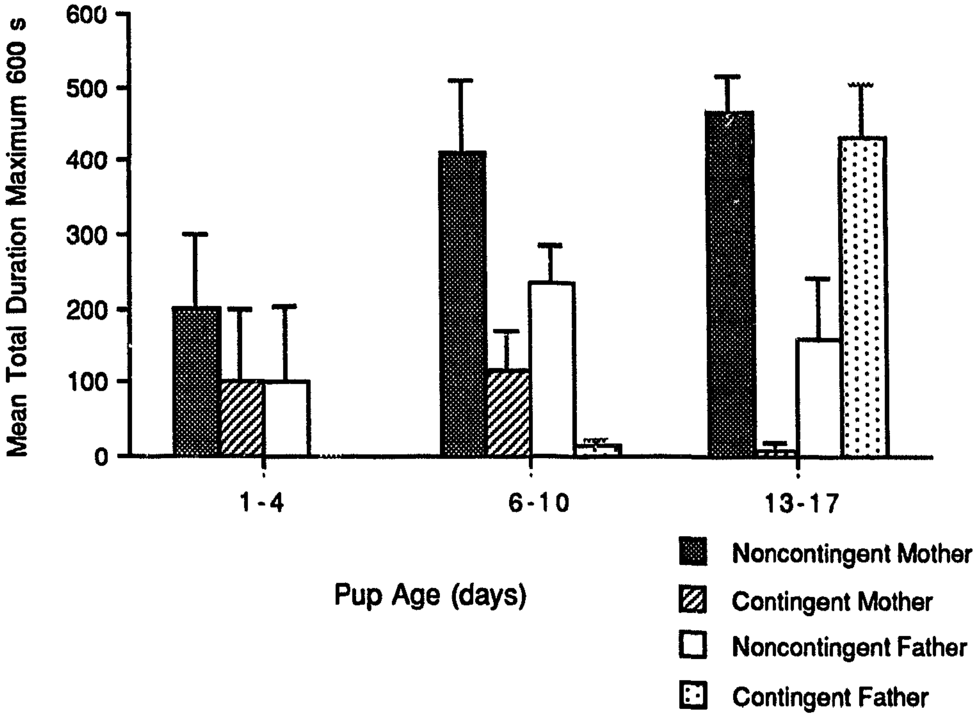
Mus were videotaped during the dark phase of the LD cycle in the Father Present, Wheel Contingent and Wheel Noncontingent conditions to determine if the mother or father was in the nest (section 6.10) or wheel running (section 6.11). Videotaping was conducted during the dark phase only as *Mus* stayed in the nest for most of the light phase and only ran on the wheel for short durations. It was, therefore, decided that more information could be collected during the dark phase on the differences between mothers' and fathers' contribution to their own and their pups survival. Four pairs of *Mus* were observed in each condition on days 1 to 4 while only 3 pairs of mice from each condition were observed for the other days as two litters were cannibalized (one each from the Wheel Contingent condition, by day 6 and Wheel Noncontingent condition, by day 13). The same pairs of *Mus* were videotaped for 3 to 6 hours between postpartum days 1 to 4, 6 to 10 and 13 to 17. Two different 10 minute time samples were scored from the videotapes for each pair of *Mus* observed on these days. The two time samples were randomly selected from the first half of the dark phase and the second half of the dark phase. Therefore the videotape was divided into two segments, representing the early half (first 1.5 to 3 hours) and the late half of dark phase (last 1.5 to 3 hours). The duration of wheel running and time in the nest for both the father and mother were recorded using the event recorder. The data were pooled over the two 10 minute observation periods and an ANOVA was conducted separately for each set of postpartum days and for both measures (duration in nest and duration of wheel running). In addition, it was decided to use only pairs of *Mus* that had pups that survived to weaning so a 2 (housing) by 2 (gender) by 2 (days) ANOVA could be conducted.

6.10 Videoanalysis of duration in the nest (Figure 6.19)

There was a significant effect of housing ($F_{(1,8)}=16.7$, $p<.01$) as *Mus* in the Wheel Contingent condition spent less time in the nest than those in the Wheel Noncontingent condition. Overall, mothers and fathers spent similar amounts of time in the nest ($F_{(1,8)}=2.5$) but there was a significant interaction between housing and gender ($F_{(1,8)}=13.2$, $p<.01$). Mothers in the Wheel Noncontingent condition spent more time on the nest than did fathers while in the Wheel Contingent condition fathers spent more time in the nest than did mothers but this was confounded by the days effect.

There was a significant effect of days ($F_{(2,16)}=5.2$, $p<.05$) as Mus increased the amount of time spent in the nest over the period of lactation. There also was a significant interaction between days, housing and gender ($F_{(2,16)}=7.6$, $p<.01$). Mothers in the Wheel Noncontingent condition increased the amount of time in the nest and fathers in this housing condition decreased the amount of time in

Figure 6.19. Mus musculus: Duration spent in the nest from videoanalysis during the dark phase



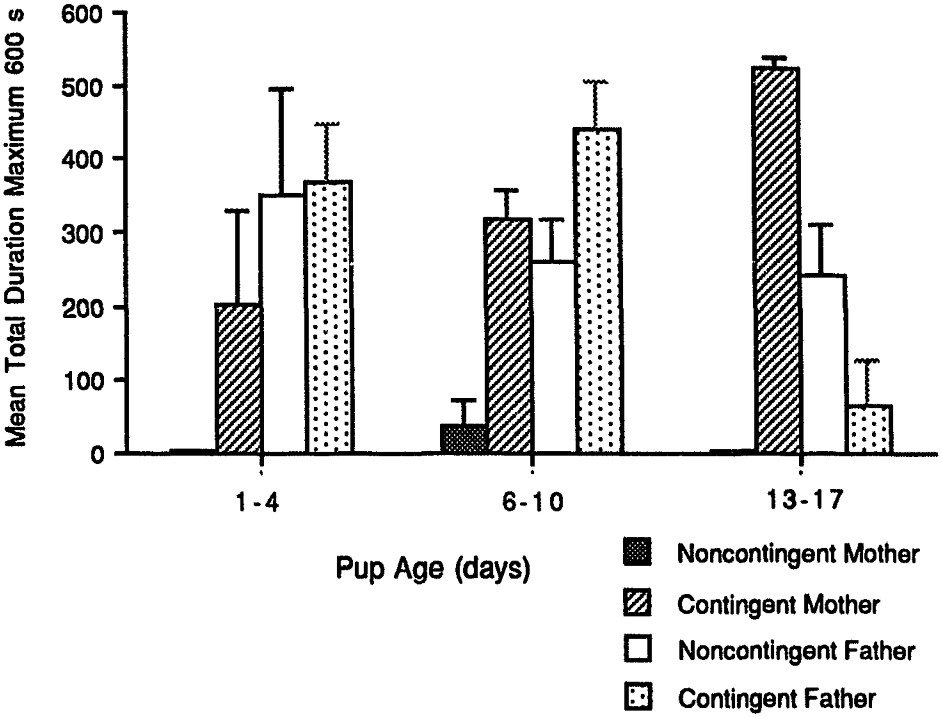
the nest over days. Mothers in the Wheel Contingent condition decreased the amount of time in the nest and fathers increased the amount of time in the nest over days. There were no significant interactions between days and housing ($F_{(2,16)}=1.7$) nor between days and gender ($F_{(2,16)}=2.1$).

6.11 Videoanalysis of duration of wheel running (Figure 6.20)

There was a significant effect of housing ($F_{(1,8)}=19.9$, $p<.01$) as *Mus* in the Wheel Contingent condition spent more time running than those in the Wheel Noncontingent condition. There was a significant effect of gender ($F_{(1,8)}=7.8$, $p<.05$) as fathers spent more time running than mothers. There was also a significant interaction between housing and gender ($F_{(1,8)}=18.3$, $p<.01$). Mothers in the Wheel Noncontingent condition ran less than fathers whereas mothers and fathers in the Wheel Contingent condition ran for similar amounts of time.

There was no significant effect of days ($F_{(2,16)}<1.0$) nor a significant interaction between days and housing ($F_{(2,16)}<1.0$). There was a significant interaction between days and gender ($F_{(2,16)}=6.7$, $p<.01$) as mothers increased the amount of time spent running over days while fathers decreased the amount of time spent running over days. There was also a significant interaction between days, housing and gender ($F_{(2,16)}=4.8$, $p<.05$). Mothers in the Wheel Noncontingent condition ran for short durations over all days whereas fathers decreased the amount of time spent running over the period of lactation. Mothers in the Wheel Contingent condition increased the

Figure 6.20. Mus musculus: Duration spent wheel running from videoanalysis during the dark phase



amount of time spent running while fathers decreased the amount of time spent running over the period of lactation.

Summary of Part Five. Mothers and fathers spent the same amount of time in the nest, but how mothers and fathers alternated parental duties was affected by the housing conditions. Mothers in the Wheel Noncontingent condition spent more time in the nest than fathers while in the Wheel Contingent condition fathers spent more time in the nest than mothers. *Mus* in the Wheel Contingent condition spent more time wheel running than those in the Wheel Noncontingent condition and fathers spent more time running than mothers. The housing conditions influenced how long mothers and fathers spent wheel running as mothers in the Wheel Noncontingent condition ran less than did fathers whereas mothers and fathers in the Wheel Contingent condition ran for similar amounts of time.

Part Six: Amount of food consumed versus food earned and behavioral observations of eating behavior

Pilot studies indicated that *Mus* often consumed more food if they had to work for food and often ran for more food than they consumed. This section addresses whether *Mus* continued to generate more food than they consumed when mothers were pregnant or lactating or if they eventually consumed all the food they generated. In addition, I was interested in whether mothers in the Wheel Noncontingent condition would earn less food than they consumed when they were pregnant or lactating.

6.12 Amount of food consumed (Figure 6.21)

The amount of food consumed in each group was determined by subtracting the number of grams of uneaten food left in the cage after each 24 hour period from the number of grams of food earned or placed *ad lib* in the cage. The amount of food eaten was averaged every 5 days, from 20 days before birth to 20 days after birth resulting in the same 9 blocks of time used for the number of revolutions run in the wheel.

The data were partitioned into two sets, blocks 1 to 3 (days 1 to 15 before parturition) and blocks 4 to 9 (days 16 before parturition to weaning). This was done because the only difference between groups for the first 15 days was housing. Both Father Absent and Father Present groups had two mice per cage (i.e. mother and father). The data were analyzed by a 2 (parenting) x 3 (housing group) x 3 (blocks of time) ANOVA for the first 15 days before parturition. After day 15 before parturition (block 4) the data were analyzed by a 3 (housing) x 6 (blocks of time) ANOVA separately for Father Absent and Father Present groups.

a. Blocks 1 to 3 (father present in all groups)

There was no significant effect of parenting on the amount of food consumed by *Mus* ($F_{(1,45)}<1.0$); both groups consumed similar amounts of food. There was a significant effect of housing on the amount of food consumed ($F_{(2,45)}=16.8$, $p<.001$). *Mus* in the Wheel Contingent and Wheel Noncontingent conditions consumed more food than *Mus* in the No Wheel condition. Post Hoc comparisons (Tukey's HSD) indicated significant differences between the Wheel Contingent condition and the No Wheel condition ($p<.01$) and between the Wheel Noncontingent and No Wheel condition ($p<.01$). There was no significant interaction between parenting and housing ($F_{(2,45)}<1.0$).

The amount of food consumed changed significantly over days ($F_{(2,90)}=21.9$, $p<.001$). *Mus* in all groups consumed more food in blocks 2 and 3 than they did in block 1. There was a significant interaction between days and parenting ($F(2,90)=4.6$, $p<.01$). *Mus* in the Father Absent group increased the amount of food consumed between blocks 1 and 2 and consumed a similar amount in blocks 2 and 3. *Mus* in the Father Present group gradually increased the amount of food consumed from block 1 to block 3. There was a significant interaction between days and housing ($F_{(4,90)}=3.5$, $p<.01$). *Mus* gradually increased the amount of food consumed in the Wheel Contingent and Wheel Noncontingent conditions while *Mus* in the No Wheel conditions consumed the same amount of food over days.

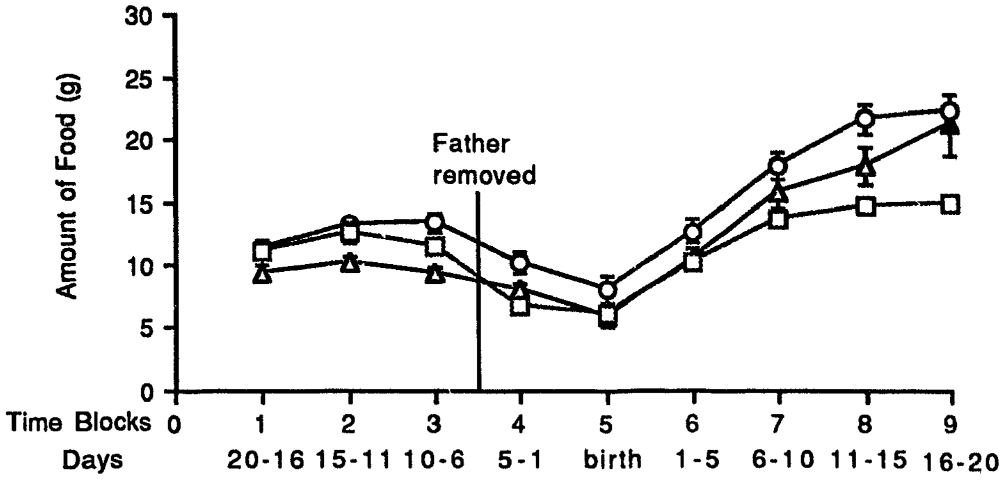
b. Blocks 4 to 9: Father Absent group (Figure 6.21a)

There was a significant effect of housing on food consumption ($F_{(2,21)}=6.1$, $p<.01$). Mothers in the Wheel Noncontingent condition consumed the most food while mothers in the Wheel Contingent condition consumed the least amount of food. Mothers in the No Wheel condition consumed an intermediate amount of food. Post Hoc comparisons (Tukey's HSD) indicated that there was a significant difference between the Wheel Contingent condition and the Wheel Noncontingent condition ($p<.05$).

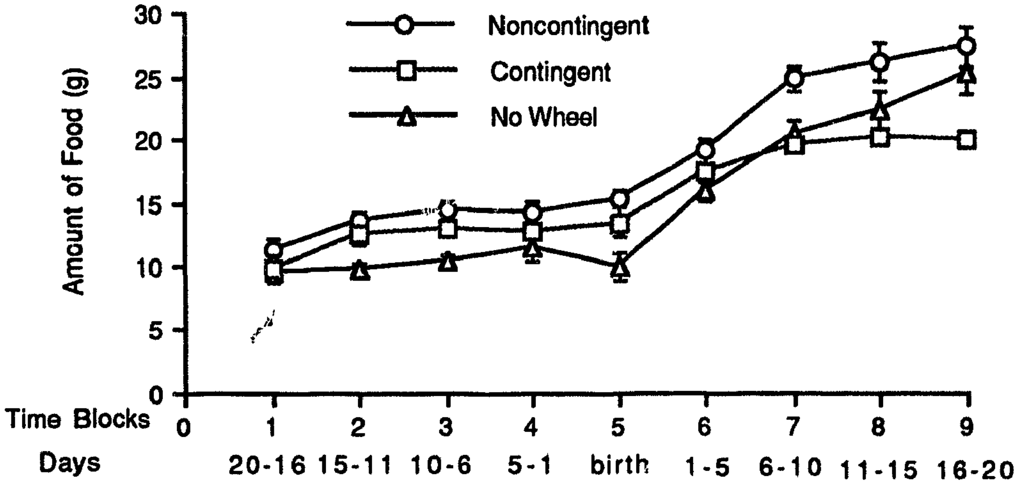
Mothers decreased the amount of food they consumed at parturition, then steadily increased the amount of food consumed up

Figure 6.21. Amount of food consumed by Mus musculus

a. Father Absent



b. Father Present



to weaning ($F_{(5,105)}=116.1$, $p<0.001$). There was a significant interaction between days and housing ($F_{(10,105)}=2.6$, $p<.01$) on the amount of food consumed. Mothers in the Wheel Noncontingent condition decreased the amount of food they consumed on the day of parturition (Block 5) while mothers in the Wheel Contingent condition consumed the same amount of food on the day of parturition as during Block 4. Both the Wheel Contingent and Wheel Noncontingent conditions increased the amount of food consumed after block 5.

c. Blocks 4 to 9: Father Present group (Figure 6.21b)

Mothers and fathers consumed the most food in the Wheel Noncontingent condition while they consumed less food in both the Wheel Contingent and No Wheel conditions ($F_{(2,22)}=6.0$, $p<.001$). Post Hoc comparisons (Tukey's HSD) indicated there was a significant difference between the Wheel Noncontingent condition and the Wheel Contingent condition ($p<.05$).

There was a significant effect of days on food consumption ($F_{(5,110)}=158.1$, $p<0.001$). Mothers and fathers steadily increased the amount of food they consumed from Block 4 to Block 9 (5 days before parturition to weaning). *Mus* consumed twice as much food by Block 9 as they had during Block 4. There was a significant days by housing interaction ($F_{(10,110)}=6.4$, $p<.001$). Mothers and fathers in the No Wheel and Wheel Noncontingent conditions steadily increased the amount of food consumed as the pups approached weaning while those in the Wheel Contingent condition increased their food consumption until block 7 then maintained that level of consumption to weaning.

6.13 Amount of food earned versus amount of food consumed in the Wheel Contingent and Wheel Noncontingent groups (Figure 6.22)

The amount of food that *Mus* earned versus the amount they consumed was compared for the Wheel Contingent and Wheel Noncontingent conditions over the 9 blocks of days. The amount consumed was measured as described in section 6.12, while the amount earned was calculated by dividing the number of revolutions run each day by the number of revolutions required per pellet (300 before parturition, 250 after parturition) and multiplying by 0.19 g per pellet. Thus a mouse which ran 20,000 revolutions per day before birth would earn 20,000/300 x 0.19 g= 12.7 g of food. A mouse which ran 20,000 revolutions per day after parturition would earn 20,000/250 x 0.19 g = 15.2 g of food. It could consume all or some of this food within a 24 hour period.

The analysis was the same as described in section 6.12 except that the No Wheel condition was not included. Both the Father Absent and Father Present groups were analyzed together in the ANOVA for the first 15 days after mating (blocks 1 to 3), and separate ANOVAs were done for Father Absent and Father Present groups from day 16 of pregnancy to weaning (blocks 4 to 9).

a. Blocks 1 to 3 (father present in all groups)

a.1 Amount of food earned (Figure 6.22)

There were no significant differences between Father Absent and Father Present groups ($F_{(1,29)}<1.0$) nor between Wheel Contingent and Wheel Noncontingent conditions ($F_{(1,29)}=3.3$, $p=.08$) for the amount of food earned nor was there a significant interaction between parenting and housing ($F_{(1,29)}<1.0$).

Mus increased the amount of food they earned over days ($F_{(2,58)}=6.8$, $p<.01$). There were no significant interactions between days and parenting ($F_{(2,58)}=2.6$, $p=.08$), days and housing ($F_{(2,58)}<1.0$) or days, parenting and housing ($F_{(2,58)}<1.0$).

a.2 Amount of food consumed

There was no significant difference between Father Absent and Father Present groups ($F_{(1,29)}<1.0$) nor between Wheel Contingent and Wheel Noncontingent conditions ($F_{(1,29)}=3.3$, $p=.08$) in the amount of food consumed. There also was no significant interaction between parenting and housing ($F_{(1,29)}<1.0$).

Mus increased the amount of food they consumed over days ($F_{(2,58)}=19.0$, $p<.001$). There were no significant interactions between days and parenting ($F_{(2,58)}=2.6$, $p=.08$), days and housing ($F_{(2,58)}<1.0$) or days, parenting and housing ($F_{(2,58)}<1.0$).

a.3 Comparison of food earned and consumed (Table 6.10)

A direct comparison of the amount of food earned and consumed in blocks 1 to 3, was achieved by subtracting the amount of food consumed from the amount of food earned. These difference scores were analyzed by a 2 (parenting) x 2 (housing) x 3 (block of time) ANOVA. Negative scores in the Wheel Noncontingent condition indicated that mice consumed more than they would have earned by running.

There was no significant effect of parenting on the difference between the amount of food earned and consumed ($F_{(1,29)}<1.0$). There was, however, a significant effect of housing ($F_{(1,29)}=8.1$, $p<.01$). *Mus* in the Wheel Noncontingent condition consumed more food than they earned while those in the Wheel Contingent condition earned more food than they consumed. There was no significant interaction between parenting and housing ($F_{(1,29)}<1.0$).

There was a significant effect of days on the difference between the amount of food earned and consumed ($F_{(2,58)}=11.1$, $p<.001$). For blocks 1 and 2, *Mus* earned more food than they consumed while during block 3 *Mus* consumed more food than they earned. There were no significant interactions between days and parenting ($F_{(2,58)}=1.3$), days and housing ($F_{(2,58)}=2.4$) nor between days, parenting and housing ($F_{(2,58)}<1.0$). Even though there were no significant interactions, the pattern of the means indicated that mothers and fathers in the Wheel Noncontingent condition earned more food than they consumed during block 1, then consumed more food than they earned during blocks 2 and 3 while those in the Wheel Contingent condition earned more food than they consumed for all 3 blocks.

b. Blocks 4 to 9: Father Absent group (Figure 6.22a)

b.1 Amount of food earned

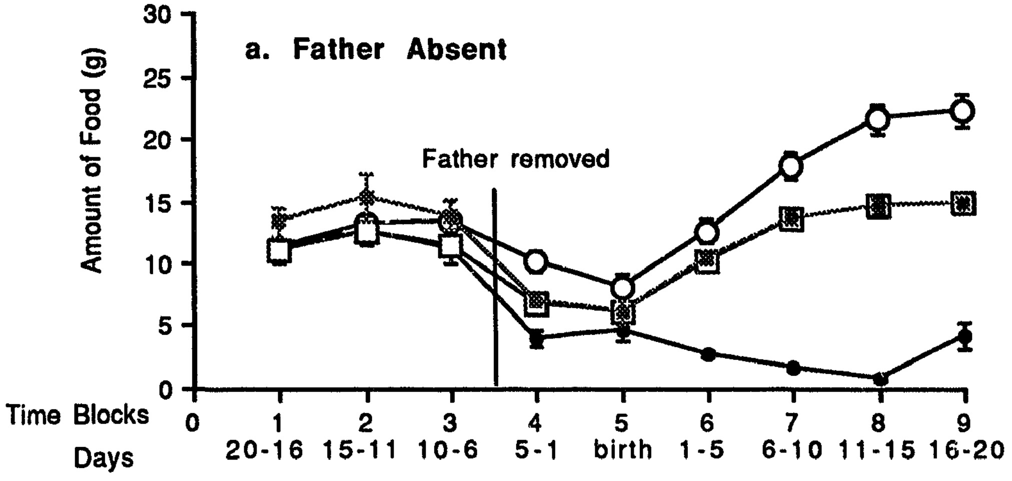
There was a significant difference between Wheel Contingent and Wheel Noncontingent conditions ($F_{(1,13)}=156.4$, $p<.001$). Mothers in the Wheel Contingent condition earned three and a half times as much food as mothers in the Wheel Noncontingent condition.

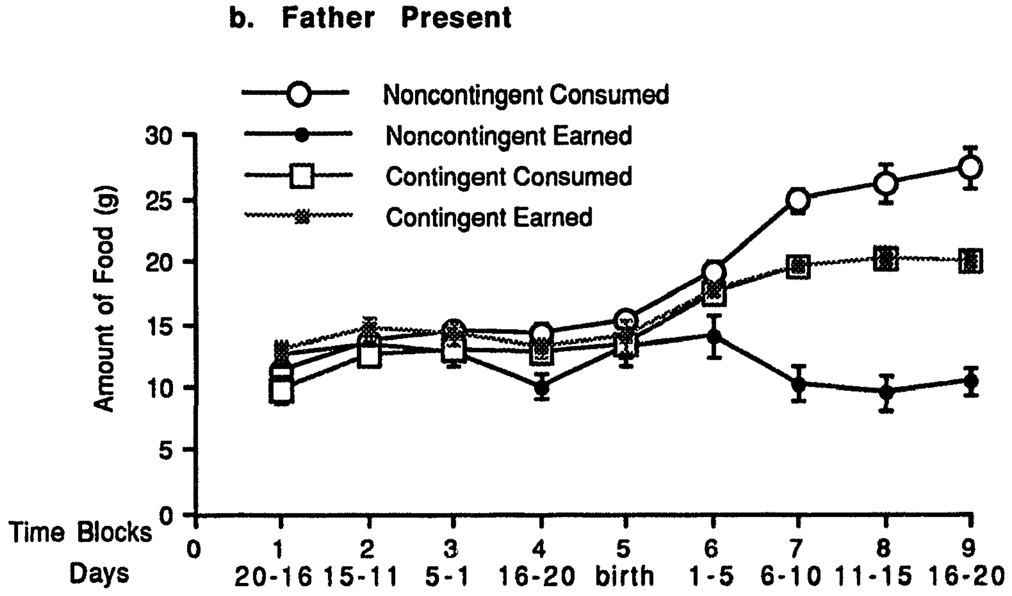
Mus increased the amount of food they earned over days ($F_{(5,65)}=12.9$. $p<.001$). There was a significant interaction between days and housing ($F_{(5,65)}=32.3$, $p<.001$). Mothers in the Wheel Noncontingent condition increased the amount of food they earned up to and including parturition then decreased the amount they earned while those in the Wheel Contingent condition continued to increase the amount of food they earned up to weaning.

b.2 Amount of food consumed

There was a significant effect of housing on the amount of food consumed ($F_{(1,13)}=20.1$, $p<.001$), as mothers in the Wheel Noncontingent condition consumed more food than mothers in the Wheel Contingent condition. There was a significant effect of days on the amount of food mothers consumed ($F_{(5,65)}=96.6$, $p<.001$) as mothers decreased the amount of food they consumed at parturition, then gradually increased the amount of food they consumed up to weaning. There was a significant days by housing interaction ($F_{(5,65)}=5.2$, $p<.001$) as mothers in the Wheel Noncontingent decreased the amount of food they consumed at parturition while those in the Wheel Contingent condition did not.

Figure 6.22. Amount of food consumed and earned by Mus musculus in Wheel Noncontingent and Contingent groups when a) the father was absent and b) the father was present





b.3 Direct comparison of food earned and consumed (Table 6.10a)

A direct comparison of the amount of food earned and consumed on blocks 4 to 9 was achieved by subtracting the amount of food consumed from the amount of food earned. These difference scores were analyzed separately for Father Absent and Father Present groups resulting in two 2 (housing) by 6 (days) ANOVAs.

There was a significant effect of housing on the amount of food consumed versus earned ($F_{(1,13)}=156.4$, $p<.001$) as mothers in the Wheel Noncontingent condition consumed more food than they earned while those in the Wheel Contingent condition consumed almost all of the food they earned.

There was a significant effect of days on the amount of food consumed versus earned ($F_{(5,65)}=61.6$, $p<.001$) as mothers overall increased the amount of food they consumed and decreased the amount of food they earned up to weaning. There was a significant days by housing interaction ($F_{(5,65)}=59.5$, $p<.001$) as mothers in the Wheel Noncontingent condition increased the amount of food they consumed and decreased the amount of food they earned up to weaning while those in the Wheel Contingent condition consumed all the food they earned by 6 days after parturition.

c. Blocks 4 to 9: Father Present group (Figure 6.22b)

c.1 Amount of food earned

There was a significant effect of housing as mothers and fathers in the Wheel Contingent condition earned one and a half times as much food as those in the Wheel Noncontingent condition ($F_{(1,14)}=23.1$, $p<.001$). There was a significant effect of days

Table 6.10 Mean difference scores (± SEM) for the amount of food consumed vs. earned for *Mus musculus*.

a) Father Absent

	Blocks 1-3	Blocks 4-9
Wheel Noncontingent	-0.8 ± 1.2	-12.5 ± 1.2
Wheel Contingent	2.4 ± 2.1	0.1 ± 0.05

b) Father Present

	Blocks 1-3	Blocks 4-9
Wheel Noncontingent	-0.3 ± 1.1	-9.9 ± 2.2
Wheel Contingent	2.2 ± 1.0	0.2 ± 0.1

($F_{(5,70)}=12.4$, $p<.001$) as mothers and fathers increased the amount of food they earned up to weaning. There was a significant days by housing interaction ($F_{(5,70)}=22.8$, $p<.001$) as mothers and fathers in the Wheel Noncontingent condition increased the amount of food they earned up to block 6, then decreased the amount of food they earned while those in the Wheel Contingent condition steadily increased the amount of food they earned up to weaning.

c.2 Amount of food consumed

Mothers and fathers consumed significantly more food in the Wheel Noncontingent than in the Wheel Contingent condition ($F_{(1,14)}=14.1$, $p<.01$). There was a significant effect of days on the amount of food consumed ($F_{(5,70)}=88.4$, $p<.001$). Mothers and fathers increased the amount of food they consumed up to weaning. There was a significant days by housing interaction ($F_{(5,70)}=7.6$, $p<.001$) as mothers and fathers in the Wheel Noncontingent condition steadily increased the amount of food they consumed while those in the Wheel Contingent condition increased the amount of food they consumed up to block 7, then consumed the same amount of food up to weaning.

c.3 Direct comparison of food earned and consumed (Table 6.10b)

There was a significant effect of housing on the amount of food consumed versus earned ($F_{(1,14)}=22.6$, $p<.001$). Mothers and fathers consumed more food than they earned in the Wheel Noncontingent condition while they consumed as much food as they earned in the Wheel Contingent condition.

There was a significant effect of days on the amount of food consumed versus earned ($F_{(5,70)}$=86.1, p<.001). When both housing groups were pooled over days, mothers and fathers increased the amount of food they consumed and decreased the amount of food they earned throughout the period of lactation. There was a significant interaction between days and housing ($F_{(5,70)}$=77.9, p<.001). Mothers and fathers in the Wheel Noncontingent condition increased the amount of food they consumed and decreased the amount of food they earned up to weaning while those in the Wheel Contingent condition earned more food than they consumed until block 5, after which they consumed all the food they earned.

6.14 Observations of eating behavior

In order to determine who was eating the food generated, I analyzed the behavioral observations of eating separately from other nonparental behaviors. Whereas the analysis of wheel running behavior included only two housing conditions (Wheel Contingent and Wheel Noncontingent), this analysis included all three housing conditions (No Wheel). Mothers and fathers spent more time eating during the dark phase of the LD cycle. All interactions that were not significant were not reported.

6.14.1 Eating behavior of mothers in the Father Absent groups (Figure 6.23)

There was a significant effect of the LD cycle on eating behavior as more eating was done in the dark phase ($F_{(1,21)}=26.2$, $p<.001$). There was no significant effect of housing on the amount of time mothers were observed eating ($F_{(2,21)}=1.7$). Mothers spent significantly less time eating on the day of parturition ($F_{(9,189)}=2.2$, $p<.05$), then gradually increased the amount of time spent eating up to 16 days after parturition. There was a significant interaction between the LD cycle, days and housing ($F_{(18,189)}=1.9$, $p<.05$).

6.14.2 Eating behavior of mothers in the Father Present groups (Figure 6.24)

There was a significant main effect of the LD cycle ($F_{(1,22)}=50.9$, $p<.001$) on the amount of time mothers spent eating as more eating was done in the dark phase. There was no significant effect of housing on the amount of time mothers were observed to spend eating ($F_{(2,22)}<1.0$) nor was there a significant effect of days on the amount of time mothers were observed to spend eating ($F_{(9,198)}=1.8$, $p=.08$).

6.14.3 Comparison of eating behavior of mothers in the Father Absent and Father Present groups (Figure 6.25)

There was no significant effect of parenting ($F_{(1,43)}<1.0$) or housing ($F_{(2,43)}<1.0$) on the amount of time mothers were observed eating and no significant interaction between parenting and housing ($F_{(2,43)}=1.2$). Mothers in all groups were observed to spend similar amounts of time engaged in eating.

Figure 6.23. Mus musculus: Duration of eating behavior of mothers in the Father Absent groups

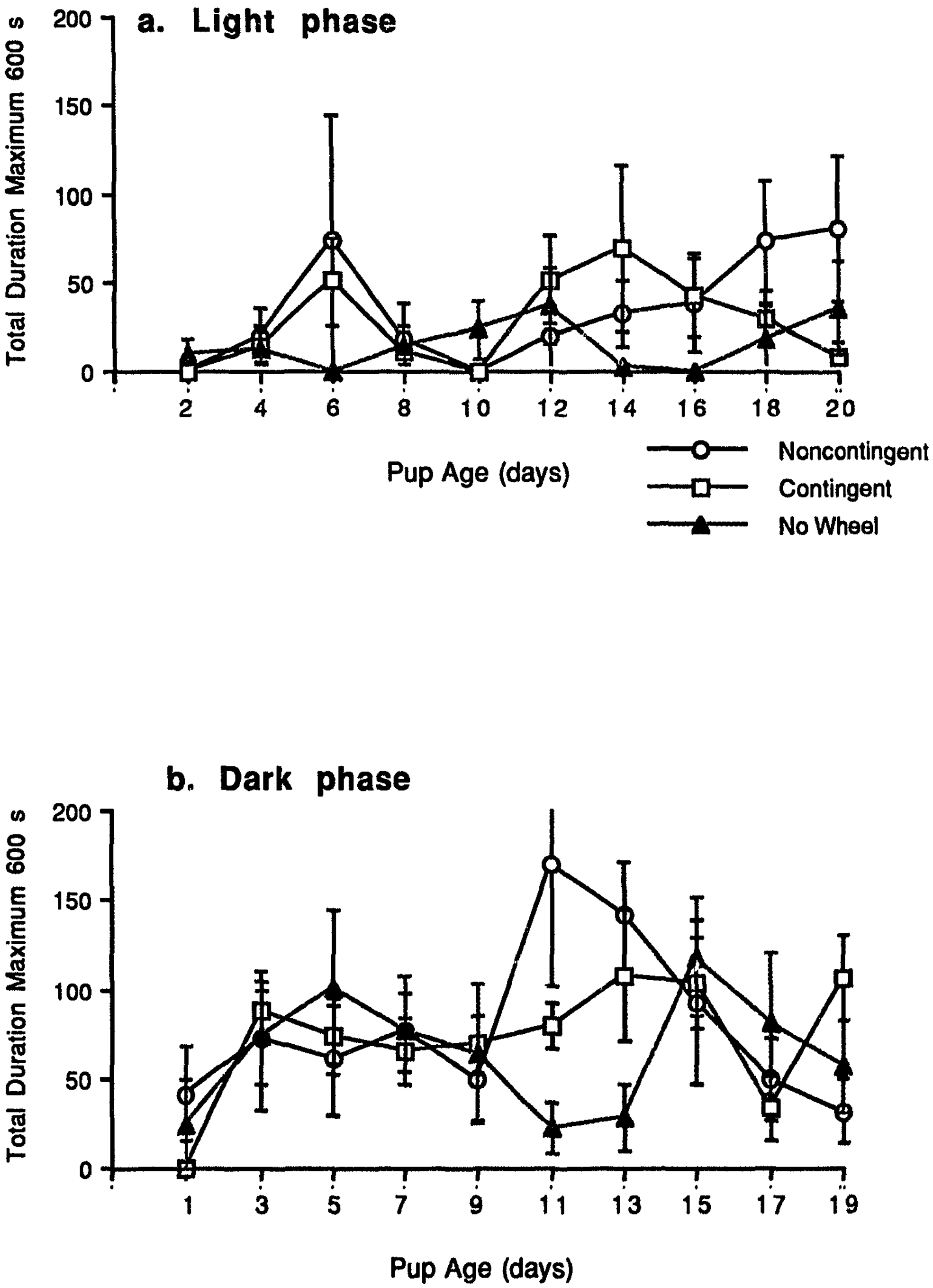


Figure 6.24. Mus musculus: Duration of eating behavior of mothers in the Father Present groups

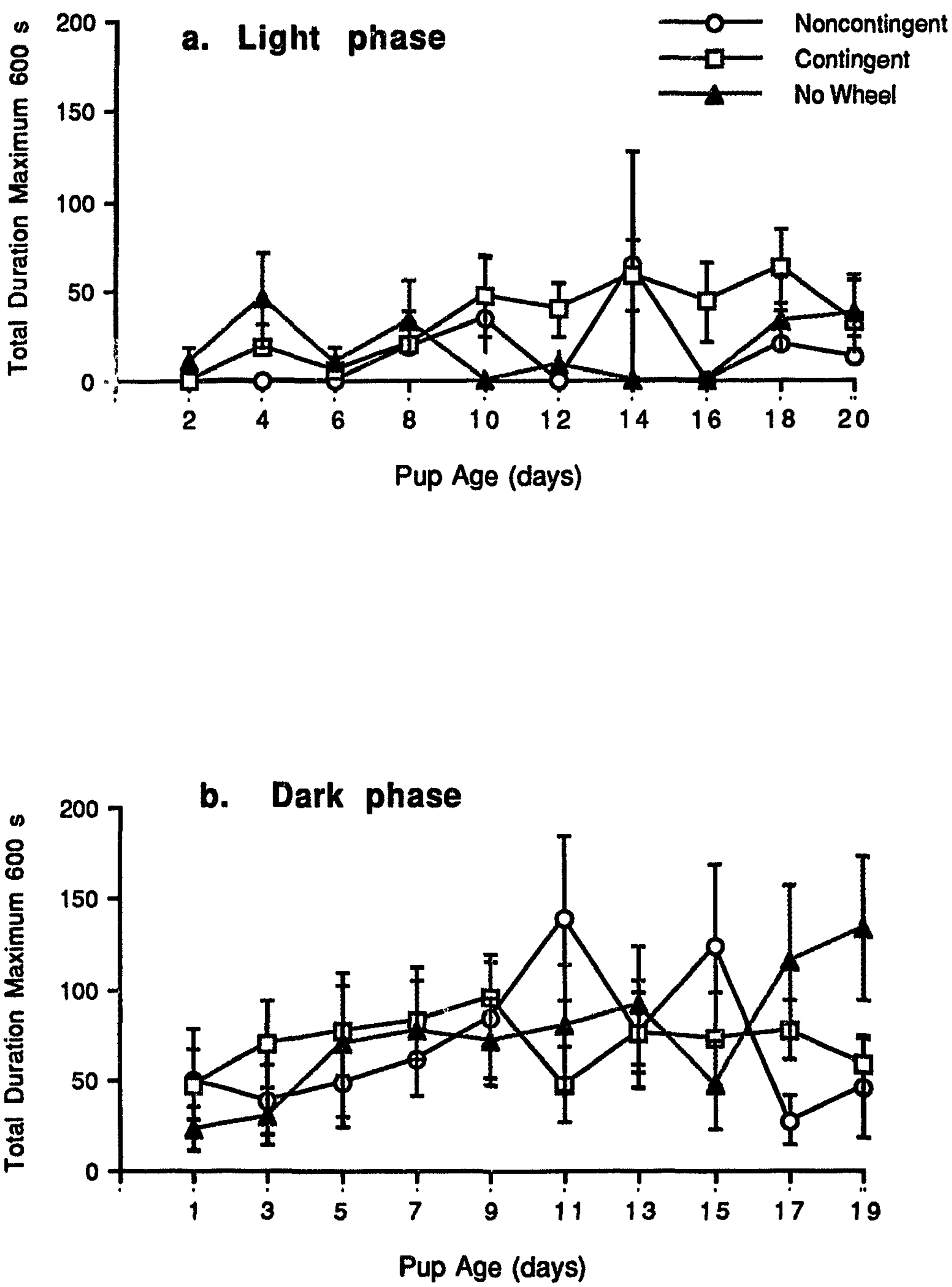
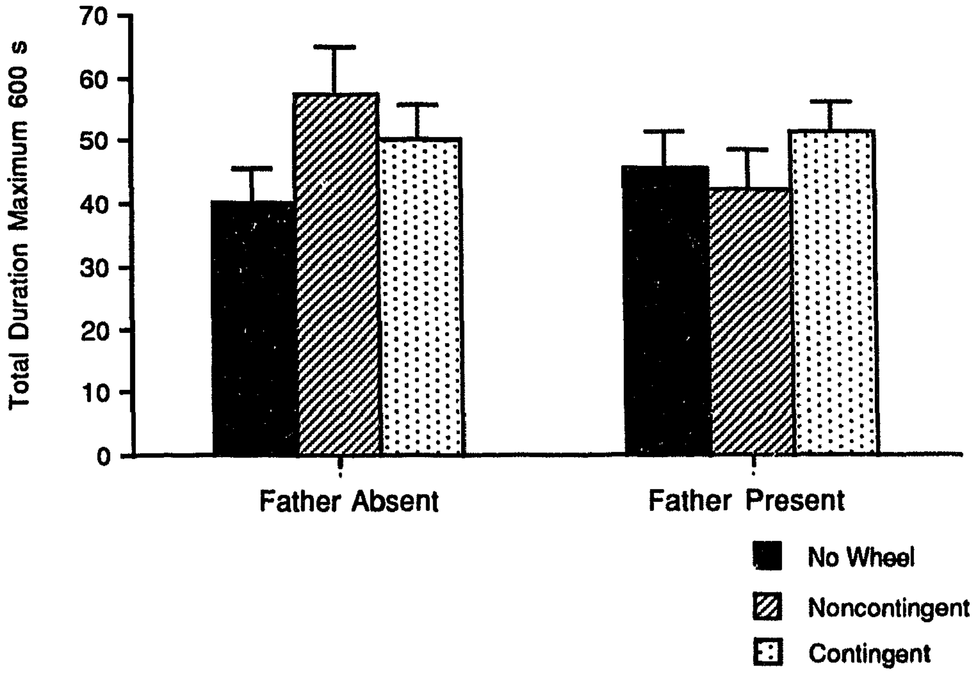


Figure 6.25. Mus musculus: Duration of eating behavior of mothers in the Father Absent and Father Present group for all housing conditions collapsed over the LD cycle



6.14.4 Eating behavior of fathers in the Father Present groups (Figure 6.26)

There was no significant effect of housing ($F_{(2,22)}<1.0$) on the amount of time fathers spent eating. There also was no significant effect of days on the amount of time fathers spent eating ($F_{(9,198)}<1.0$).

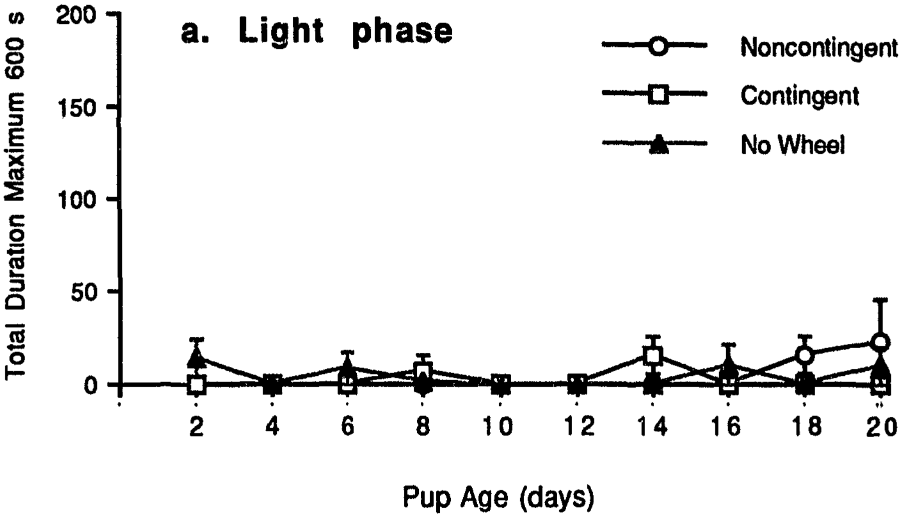
6.14.5 Comparison of eating behavior of mothers and fathers in the Father Present groups (Figure 6.27)

There was a significant effect of gender ($F_{(1,28)}=28.3$, $p<.001$) on the amount of time spent eating as mothers spent more time eating than fathers during the observation period. There was no significant effect of housing ($F_{(1,28)}<1.0$).

Summary of Part Six. Mothers and fathers in the Wheel Contingent and Wheel Noncontingent conditions consumed more food that those in the No Wheel condition from day 20 to day 5 before parturition. Mothers in the Father Absent group and mothers and fathers in the Father present group, from day 5 before parturtion to weaning, consumed the most food in the Wheel Noncontingent condition and less food in the Wheel Contingent and No Wheel conditions.

Mothers and fathers in the Father Absent and Father Present groups, between day 20 to day 5 before parturition, consumed more food than they earned in the Wheel Noncontingent condition and earned more food than they consumed in the Wheel Contingent condition. Mothers in the Father Absent group and mothers and

Figure 6.26. Mus musculus: Duration of eating behavior of fathers in the Father Present groups



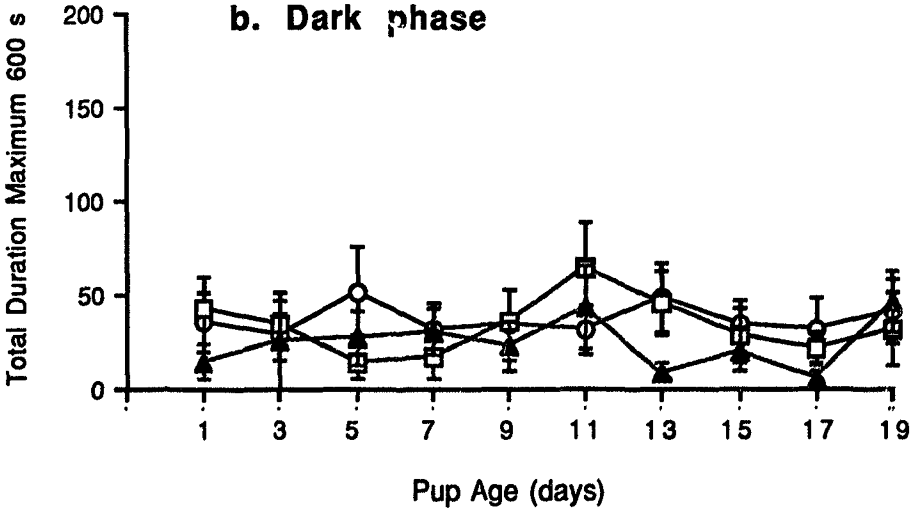
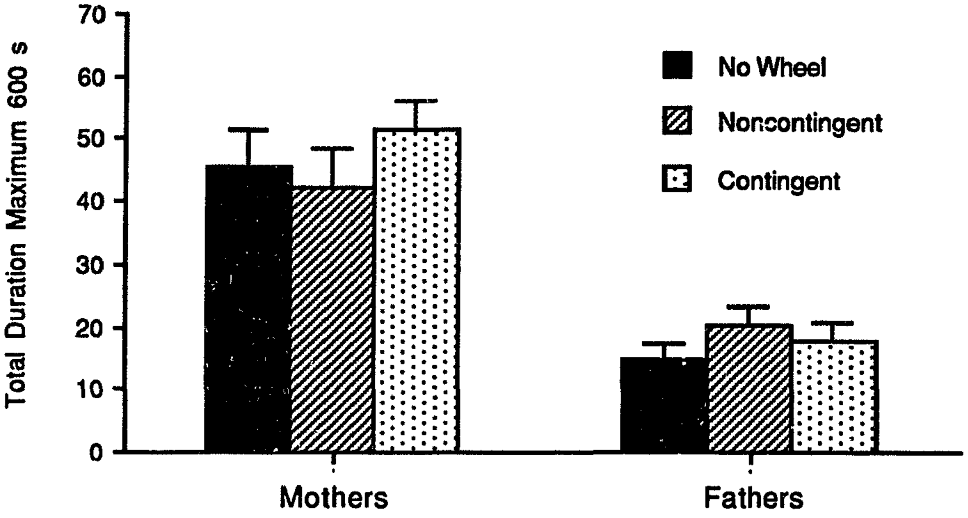


Figure 6.27. Mus musculus: Duration of eating behavior of mothers and fathers in the Father Present group for all housing conditions collapsed over the LD cycle



fathers in the Father Present group, between day 5 to weaning, consumed more food than they earned in the Wheel Noncontingent condition while those in the Wheel Contingent condition consumed all the food that they earned. Mothers in the Father Absent group and Father Present group were observed eating for the same amount of time, while fathers spent less time eating than mothers in the Father Present group.

Chapter 7

Results for *Peromyscus californicus*

This chapter presents the results of the effects of the fathers' presence and housing conditions on parental weight, fertility and fecundity (Part One, sections 7.1 to 7.3); the survival, growth and gender of pups (Part Two, sections 7.4 and 7.5); parental and nonparental behavior shown by each parent (Part Three, sections 7.6 and 7.7) and wheel running behavior required to obtain food (Part Four, sections 7.8 and 7.9). A comparison of wheel running and parental behavior during the dark phase of the LD cycle is given in Part Five (sections 7.10 and 7.11) and the amount of food consumed by each parent is discussed in Part Six (sections 7.12 to 7.14).

Part One: Parental weight, maternal fertility and fecundity

7.1 Parental weights

The weights of mothers and fathers were analyzed to determine if there were differences in parental weights due to housing conditions. Lower weight gains by adults in the Wheel Contingent conditions would indicate that foraging for food was more strenuous than being fed ad libitum in a running wheel cage or standard laboratory housing. The mothers' weights in the Father Present groups were compared to the mothers' weights in the Father Absent groups on days 30, 21, 14, 7 and 2 before parturition and on days 4, 12, and 24 after parturition. Fathers' weights for all six groups were compared before parturition and fathers' weights in the

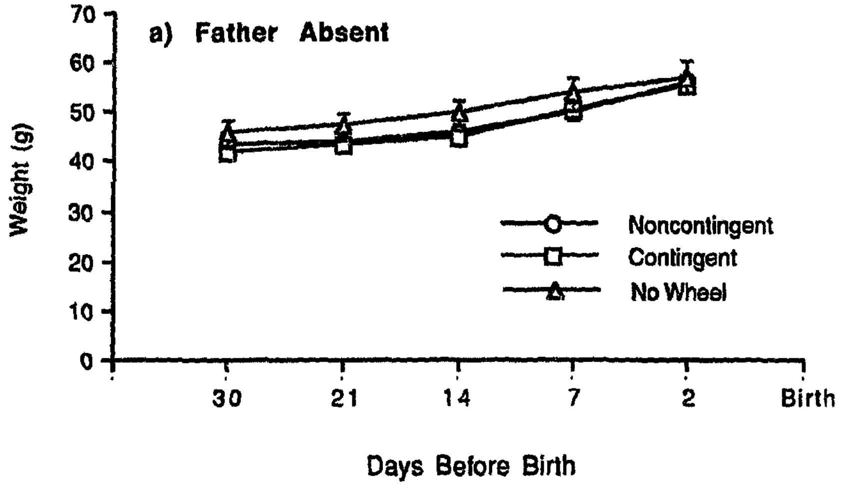
Father Present groups were compared on days 4, 12 and 24 after parturition.

a. Mothers' weights before and after parturition (Figures 7.1 and 7.2)

The mothers' weights in the Father Absent groups were compared to the mothers' weights in Father Present groups and were analyzed by a 2 (parenting: Father Absent or Present) x 3 (housing: Wheel Contingent, Wheel Noncontingent, No Wheel) x 5 (days) ANOVA (Figure 7.1). Mothers in the Father Absent and Present groups did not differ in weight before parturition ($F_{(1,67)}=1.5$) nor were there significant effects of housing on maternal weight ($F_{(2,67)}=2.9$, $p=.06$). However, the mothers in the No Wheel condition were heavier than mothers in the other two conditions. There was no significant interaction between parenting and housing on maternal weight ($F_{(2,67)}<1.0$) but there was a significant effect of days as mothers increased in weight as they approached parturition ($F_{(4,268)}=316.6$, $p<.0001$). There were no significant interactions between days and parenting ($F_{(4,268)}<1.0$), days and housing ($F_{(8,268)}=2.5$) nor between days, parenting and housing ($F_{(8,268)}=1.1$).

Mothers' weights after parturition were analyzed by a 2 (parenting) x 3 (housing) x 3 (days) ANOVA (Figure 7.2). There was no significant effect of parenting on maternal weights after birth ($F_{(1,41)}=2.6$) as mothers weighed approximately the same in the Father Absent and Father Present groups. There also was no significant effect of housing ($F_{(2,41)}=1.2$) as mothers weighed approximately the same in the Wheel Noncontingent, Wheel

Figure 7.1. Peromyscus californicus: Mothers' weights before parturition in the a) Father Absent and b) Father Present groups. The legend in a. also applies to b.



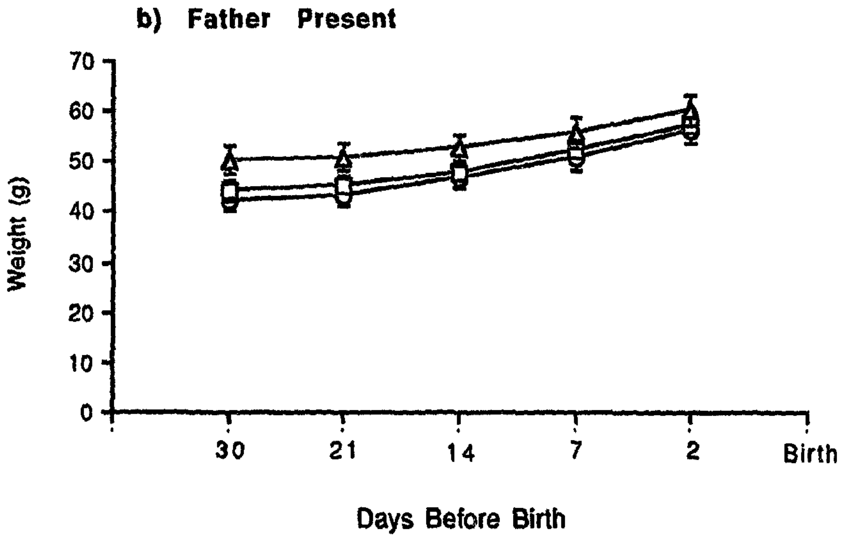
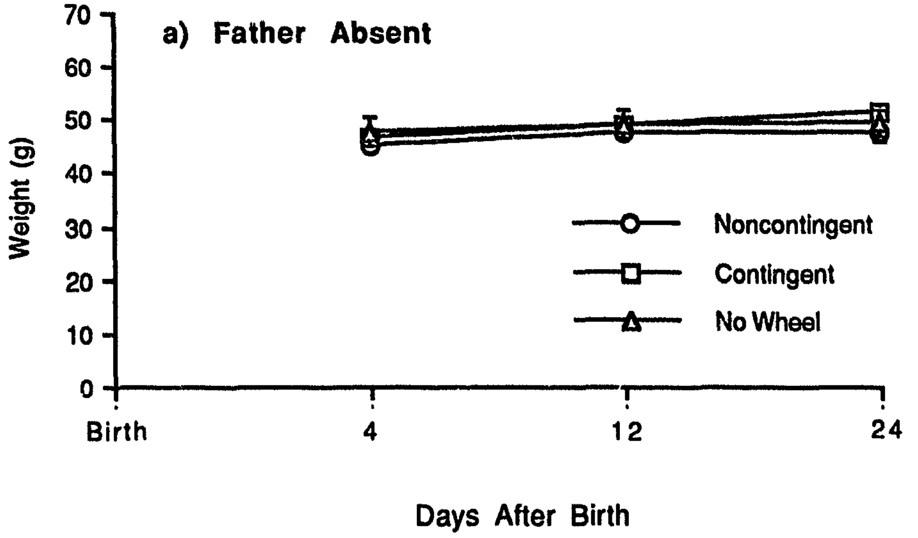
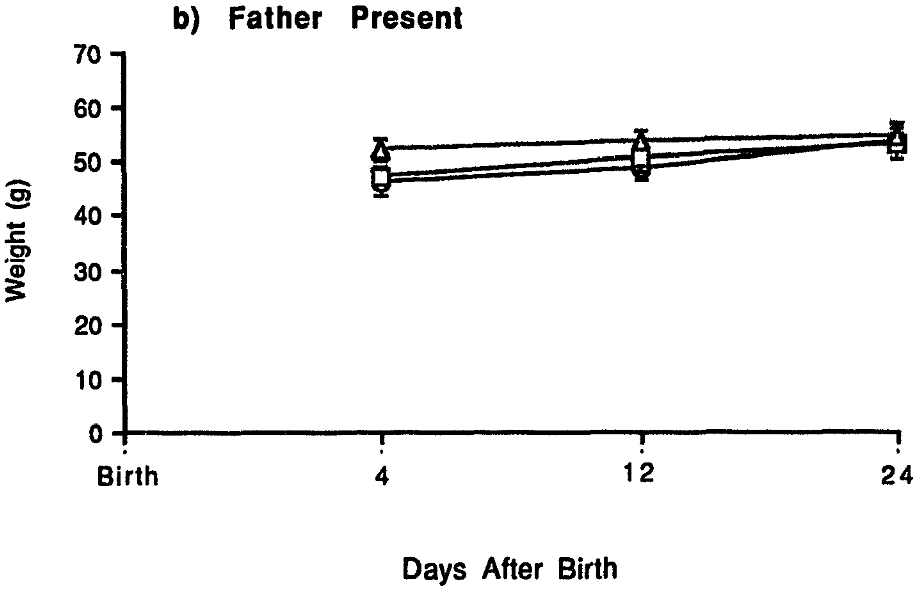


Figure 7.2. Peromyscus californicus: Mothers' weights after birth in the a) Father Absent and b) Father Present groups





Contingent and No Wheel conditions and no significant interaction between parenting and housing ($F_{(2,41)}<1.0$).

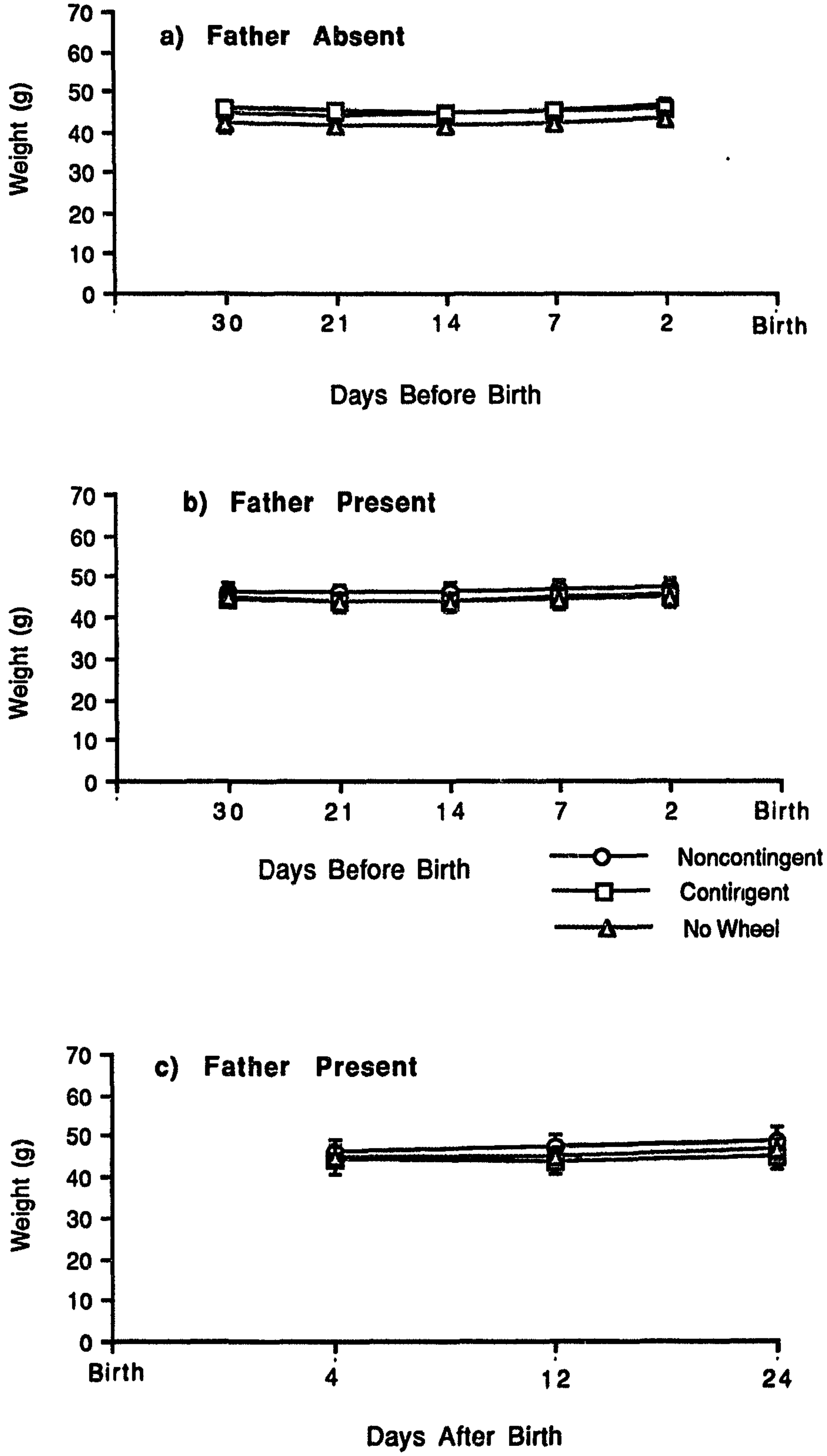
Since the mothers in the Father Present group were probably pregnant, separate analyses of days effects were conducted for each parenting group. There was a significant effect of days on mothers in the Father Absent groups (Figure 7.2a) as they gained weight steadily up to 24 days after birth ($F_{(2,38)}=11.0$, $p<.001$). There was, however, no significant interaction between days and housing ($F_{(4,38)}<1.0$) in the Father Absent group. There was a significant effect of days on maternal weight in the Father Present groups (Figure 7.2b) since all mothers gained weight steadily up to 24 days after birth ($F_{(2,44)}=35.9$, $p<.001$). Mothers in the No Wheel condition were significantly heavier than mothers in the Wheel Contingent and Wheel Noncontingent conditions up to twelve days after parturition and then weighed the same as mothers in the No Wheel condition by 24 days after parturition ($F_{(4,44)}=3.4$, $p<.05$).

b. Fathers' weights before and after parturition (Figure 7.3)

Fathers were present in both the Father Present and Father Absent groups until 2 to 4 days before the birth of the pups, thus before the birth of the pups, there are six groups of males. The fathers' weights in all six groups were compared on days, 30, 21, 14, 7 and 2 before parturition and were analyzed by a 2 (parenting: Father Present or Absent) x 3 (housing: Wheel Contingent, Wheel Noncontingent, No Wheel) x 5 (days) ANOVA.

Before parturition (Figures 7.3a and 7.3b), fathers did not differ in weight due to parenting conditions ($F_{(1,67)}<1.0$) nor due to

Figure 7.3. Peromyscus californicus: Fathers' weight before birth in the a) Father Absent and b) Father Present groups and after parturition in the c) Father Present group



housing conditions ($F_{(2,67)}<1.0$). There was no significant interaction between parenting and housing ($F_{(2,67)}<1.0$) but there was a significant effect of days as fathers steadily gained weight as the day of birth approached ($F_{(4,268)}=9.0$, $p<.001$). There were no significant interactions between days and parenting ($F_{(4,268)}<1.0$), days and housing ($F_{(8,268)}<1.0$) nor between days, parenting and housing ($F_{(8,268)}<1.0$) on paternal weight before birth.

Fathers' weights within the Father Present groups were compared on days 4, 12, and 24 after parturition and were analyzed by a 3 (housing) x 3 (days) ANOVA (Figure 7.3c). There was no significant effect of housing on the weights of fathers in the Father Present groups ($F_{(2,22)}<1.0$) but there was a significant effect of days as fathers in all groups steadily gained weight after the birth of their pups ($F_{(2,44)}=10.7$, $p<.001$). There was no significant interaction between days and housing ($F_{(4,44)}=1.1$).

7.2 Mothers' fertility (Table 7.1)

There were no differences in the number of females that gave birth to pups between the Father Absent and Father Present groups ($\chi^2_{(1)}=0.05$, n.s.) and no differences in the number of females that had pups between the No Wheel, Wheel Noncontingent and Wheel Contingent conditions ($\chi^2_{(2)}=0.86$, n.s.).

7.3 Mothers' fecundity (Table 7.2)

Mothers in all groups produced an average of 2.2 pups per litter. A 2 (parenting) by 3 (housing) ANCOVA was conducted with mothers' weights (30 days before birth) as the covariate and litter

Table 7.1. Fertility of mothers. The number of *P. californicus* mothers in each housing group giving birth (pups) and failing to give birth (no pups) when fathers were absent of present

	Father Absent		Father Present	
	pups	no pups	pups	no pups
No Wheel	12	1	12	1
Wheel Noncontingent	13	2	12	3
Wheel Contingent	12	2	12	4
	37		36	

Table 7.2. Mean litter size (±SEM) at birth and 24 days of age for *P. californicus* in each housing condition in the father absent and father present groups

Age	birth		24 days	
Father	Absent	Present	Absent	Present
Housing Condition				
No Wheel	2.3 ± 0.2	2.1 ± 0.2	1.6 ± 0.3	1.8 ± 0.3
Wheel Noncontingent	2.2 ± 0.2	2.0 ± 0.2	1.5 ± 0.4	1.4 ± 0.4
Wheel Contingent	2.6 ± 0.2	2.6 ± 0.2	1.2 ± 0.4	1.9 ± 0.4

size, as the dependent variable. This was conducted to ensure that differences in litter size were not significantly influenced by the mothers' weights. The results of this ANCOVA indicated that there was a significant difference in litter size due to the housing conditions at birth ($F_{(2,66)}=3.4$, $p=.04$) as litter size was slightly larger in the Wheel Contingent condition (2.6) than in the No Wheel (2.2) and Wheel Noncontingent (2.1) group. There was no significant difference in litter size due to parenting ($F_{(1,66)}=1.5$) nor was there a significant interaction between parenting and housing ($F_{(2,66)}<1.0$). Since the results from the ANCOVA indicated that there was an effect of housing on litter size, future analyses of litter size were corrected for mothers' weights.

Summary of Part One. The results indicated that mothers in all groups gained weight up to parturition and did not differ in weight after parturition due to the parenting or housing conditions. However, mothers in the Father Absent and Father Present groups had a different pattern of weight gain after parturition. Mothers in the Father Absent groups steadily gained weight during the period of lactation in all housing conditions. However, in the Father Present group, mothers in the No Wheel condition gained significantly more weight up to twelve days after birth than mothers in the Wheel Noncontingent and Wheel Contingent conditions, but this difference disappeared by twenty-four days after birth. Before parturition there were no differences in fathers' weights between groups and fathers gained weight up to the birth of their pups. After parturition, different housing conditions had no effect on fathers' weights and fathers ir all groups gained weight throughout the period of lactation.

There were no differences in fertility, as the same number of females in all groups had litters. The mothers' fecundity, however, was influenced by housing conditions, as mothers in the Wheel Contingent condition had slightly larger litter sizes at birth.

Part Two: Survival, growth and gender of pups

7.4 Litter and pup survival rate

a. Survival of whole litters (Tables 7.3 and 7.4)

Litter survival was assessed by the proportion of litters born that survived to 24 days of age. A Chi-square analysis (Table 7.3), indicated there were no significant differences between the six groups in the proportion of whole litters which survived to 24 days of age ($\chi^2_{(6)}$=4.6, n.s.). When analyzed by parenting condition, 22 of 37 litters (69.4%) survived to 24 days of age in the Father Present group while 22 of 37 litters (59.5%) in the Father Absent group survived to 24 days of age, a difference that was not significant ($\chi^2_{(1)}<1.0$). When analyzed by housing conditions, 13 or 24 litters (54%) in the Wheel Contingent condition and 15 of 25 (60%) of the litters in the Wheel Noncontingent condition survived whereas 19 of 24 (79%) in the No Wheel condition survived to 24 days of age, a difference which was not significant ($\chi^2_{(2)}$=3.6, n.s.). When the Wheel Contingent and No Wheel conditions were compared there was a marginally significant difference between them ($\chi^2_{(1)}$=3.4, p=0.06) as more litters died in the Wheel Contingent condition than in the No Wheel condition (Table 7.4).

Table 7.3. Survival of whole litters to 24 days of age for *P. californicus* in each parenting group collapsed across housing conditions

Pups	Lived	Died	Total
Father Absent	22(59.5%)	15	37
Father Present	25 (69.4%)	11	36
Total	47	26	73

$X^2_{(1)}<1.0$, n.s.

Table 7.4. Survival of whole litters to 24 days of age for *P. californicus* for the No Wheel and Wheel Contingent groups collapsed across parenting conditions

Pups	Lived	Died	Total
No Wheel	19(79.0%)	5	24
Wheel Contingent	13 (54.2%)	11	24
Total	32	16	48

$X^2_{(1)}=3.4$, $p=.06$

b. Litter size at 24 days of age (Table 7.2)

The difference in litter size between birth and 24 days of age was determined and a 2 (parenting) by 3 (housing) ANCOVA was conducted with mothers' weights (30 days before birth) as the covariate and the difference score as the dependent variable. There was no significant effect of parenting ($F_{(1,66)}=3.0$, $p=.09$) on the number of pups that survived, however, mothers in the Father Present group kept more pups alive than mothers in the Father Absent group. There were no significant differences in pup survival due to housing ($F_{(2,66)}=1.6$) nor was there a significant interaction between parenting and housing ($F_{(2,66)}<1.0$).

c. Pup survival (Tables 7.5 to 7.7)

Pup survival was assessed by the proportion of pups born that survived to 24 days of age. A Chi-square analysis indicated that there were no significant differences between the six groups in the proportion of pups at 24 days of age ($\chi^2_{(5)}=6.3$, n.s.). When analyzed by parenting condition, 62 of 80 pups (77.5%) survived to 24 days of age in the Father Present group while in the Father Absent group 52 of 85 pups (61%) survived to 24 days of age, a difference that was statistically significant ($\chi^2_{(1)}=5.1$, $p=.02$).

Differences in pup survival between the Father Absent and Father Present groups were then analyzed for each housing condition separately (Table 7.5). There were no significant differences in pup survival between the Father Absent and Father Present groups in the No Wheel condition ($\chi^2_{(1)}=2.4$) nor in the Wheel Noncontingent condition ($\chi^2_{(1)}<1.0$). In the Wheel Contingent condition, however,

Table 7.5a. Pup survival in the No Wheel group for *P. californicus* with the father absent or present

	Lived	Died	Total
Father Absent	19 (70.4%)	8	27
Father Present	22 (88.0%)	3	25
Total	41	11	52

$X^2_{(1)}=2.4$, n.s.

Table 7.5b. Pup survival in the Wheel Noncontingent group for *P. californicus* with the father absent or present

	Lived	Died	Total
Father Absent	19 (65.5%)	10	29
Father Present	17 (63.0%)	7	24
Total	36	17	53

$X^2_{(1)}<1.0$, n.s.

Table 7.5c. Pup survival in the Wheel Contingent group for *P. californicus* with the father absent or present

Pups	Lived	Died	Total
Father Absent	14 (48.3%)	15	29
Father Present	23 (71.9%)	8	31
Total	37	23	60

$X^2_{(1)}=4.3$, $p<.05$

Table 7.6. Pup survival to 24 days of age for *P. californicus* in each housing group collapsed across parenting groups

Pups	Lived	Died	Total
No Wheel	41 (78.8%)	11	52
Wheel NonContingent	36 (67.9%)	17	53
Wheel Contingent	37 (60.6%)	23	60
Total	114	52	165

$X^2_{(2)}=3.9$, n.s.

Table 7.7a. Pup survival in the No Wheel and Wheel Noncontingent groups for *P. californicus* collapsed over parenting groups

Pups	Lived	Died	Total
No Wheel	41 (78.8%)	11	52
Wheel Noncontingent	36 (67.9%)	17	53
Total	77	28	105

$X^2_{(1)}=1.6$, n.s.

Table 7.7b. Pup survival in the No Wheel and Wheel Contingent groups for *P. californicus* collapsed over parenting groups

Pups	Lived	Died	Total
No Wheel	41 (78.8%)	11	52
Wheel Contingent	37 (61.6%)	23	60
Total	78	34	112

$X^2_{(1)}=3.9$, $p=.05$

significantly more pups survived in the Father Present group than in the Father Absent group (Table 7.5c, $\chi^2_{(1)}$=4.3, p=0.04).

There was no significant difference in the percentage of pups that survived in the different housing conditions (Table 7.6, $\chi^2_{(2)}$=3.9, n.s.). Pup survival in the No Wheel condition was then compared with the Wheel Noncontingent and Wheel Contingent conditions separately. There was no significant difference in pup survival between the No Wheel and Wheel Noncontingent conditions (Table 7.7a, $\chi^2_{(1)}$=1.6, n.s.). When the No Wheel and Wheel Contingent conditions were compared, however, there was a significant difference (Table 7.7b, $\chi^2_{(1)}$=3.9, p=.05) as more pups survived in the No Wheel condition (78.8%) than in the Wheel Contingent condition (61.6%). Thus pup survival was lower in the Wheel Contingent condition than in the No Wheel and Wheel Noncontingent conditions and within the Wheel Contingent condition more pups survived when the father was present than when the father was absent.

7.5 Pup Growth: Mean total litter weight (Table 7.8) and mean pup weight within each litter (Table 7.9)

Pup growth was assessed by determining the mean total litter weight and mean pup weight per litter at 4 and 24 days of age. An analysis of covariance was conducted to control for differences in the mothers' weights 30 days before parturition (nonpregnant weight) which could influence litter weight or pup weight on day 4 after birth.

a. Mean total litter weight (Table 7.8)

The results of the ANCOVA for litter weight demonstrated that there was no significant effect of parenting ($F_{(1,56)}<1.0$) or housing ($F_{(2,56)}<1.0$) on litter weight at 4 days of age nor was there a significant interaction between parenting and housing ($F_{(2,56)}<1.0$). When the pups that survived were 24 days of age, there were no significant effects of parenting ($F_{(1,40)}<1.0$) or housing ($F_{(2,40)}<1.0$) on litter weight nor was there a significant interaction between parenting and housing ($F_{(2,40)}<1.0$).

b. Mean pup weight per litter (Table 7.9)

The results of the ANCOVA for pup weight indicated that pups at 4 days of age weighed significantly more in the No Wheel condition than in the either the Wheel Contingent or Wheel Noncontingent conditions ($F_{(2,56)}=3.1$, $p=.05$). There were no significant differences in mean pup weight at 4 days of age due to parenting ($F_{(1,56)}<1.0$) nor was there a significant interaction between parenting and housing ($F_{(2,56)}=1.1$). When the pups that survived were 24 days of age (n=5, 7, 8, 9, or 10 litters per group), the results of the ANCOVA for mean pup weight per litter indicated that there was a significant difference in mean pup weight due to housing conditions ($F_{(2,40)}=5.3$, $p<.01$) as pups weighed more in the No Wheel condition than in the other two conditions. There was no significant effect of parenting ($F_{(1,40)}<1.0$), nor was there a significant interaction between parenting and housing ($F_{(2,40)}<1.0$) on pup weight at 24 days of age.

Table 7.8. Total mean litter weights (±SEM) at 4 and 24 days of age for *P. californicus* in each housing condition when fathers were present or absent

	4 days		24 days	
Father	Absent	Present	Absent	Present
No Wheel	11.9 ± 1.3	10.8 ± 1.3	34.7 ± 3.5	33.1 ± 4.3
Wheel Noncontingent	9.9 ± 1.1	10.8 ± 1.8	33.7 ± 1.7	35.2 ± 4.8
Wheel Contingent	10.6 ± 1.6	12.9 ±1.6	35.2 ± 3.0	35.7 ± 2.9

Table 7.9. Mean pup weights per litter (±SEM) at 4 and 24 days of age for *P. californicus* in each housing condition when fathers are absent and present

	4 days		24 days	
Father	Absent	Present	Absent	Present
No Wheel	5.6 ± 0.4	5.2 ± 0.3	16.0 ± 0.8	15.1 ± 1.0
Wheel Noncontingent	4.4 ± 0.5	4.7 ± 0.5	14.7 ± 1.1	14.3 ± 1.1
Wheel Contingent	4.1 ± 0.4	4.9 ± 0.2	13.0 ± 1.1	12.5 ± 0.6

7.6 Gender of pups (Table 7.10)

The gender of the pups surviving to 24 days of age was assessed by a Chi-square analysis. There was no significant difference between the six groups ($\chi^2_{(5)}$=4.5, n.s.) in the proportion of male and female pups that survived to 24 days of age. When analyzed by parenting groups, there was no significant difference ($\chi^2_{(1)}$<1.0) in the proportion of male and female pups that survived to 24 days of age nor was there a significant difference when analyzed by housing conditions ($\chi^2_{(2)}$<1.0).

Summary of Part Two. The fathers' presence significantly increased pup survival but only in the Wheel Contingent housing condition. This indicated that when parents were required to forage for food, the presence of the father increased pup survival. The analysis of mean litter and pup weights indicated that pups in the Wheel Contingent conditions were smaller than those in the other two groups and the fathers' presence had no effect in any housing condition. There also were no effects of parenting or housing on the proportion of male and female pups that survived to 24 days of age.

Part Three: Direct behavioral observations

As discussed in Chapter 4, two general categories of behaviors were recorded using an event recorder: parental behavior (section 7.6) and nonparental behavior (section 7.7). Beginning at parturition, behavioral observations were collected for a total of 20 days, 10 days in the light phase and 10 days in the dark phase (light and dark

Table 7.10a. Pup gender in the No Wheel group for *Peromyscus californicus* with the father absent or present

Gender	Male	Female	Total
Father Absent	11 (57.9%)	8	19
Father Present	8 (36.4%)	14	22
Total	20	22	42

$X^2_{(1)}=1.9$, n.s.

Table 7.10b. Pup gender in the Wheel Noncontingent group for *Peromyscus californicus* with the father absent or present.

Gender	Male	Female	Total
Father Absent	9 (47.4%)	10	19
Father Present	6 (54.5%)	11	17
Total	15	21	36

$X^2_{(1)}<1.0$, n.s.

Table 7.10c. Pup gender in the Wheel Contingent group for*Peromyscus californicus* with the father absent or present.

Gender	Male	Female	Total
Father Absent	4 (28.6%)	10	14
Father Present	10 (43.5%)	13	23
Total	14	23	37

$X^2_{(1)}<1.0$, n.s.

observations were alternated each day). For the analysis, all parental behaviors and all nonparental behaviors were combined for each 10 minute observation, producing two duration measurements per session. Mothers in both Father Absent and Father Present groups were observed for a total of 100 minutes during the light phase and 100 minutes during the dark phase over 10 days. Both the mother and father were observed in the Father Present group simultaneously while only the mother was observed in the Father Absent group as he had been removed 2 to 4 days prior to parturition.

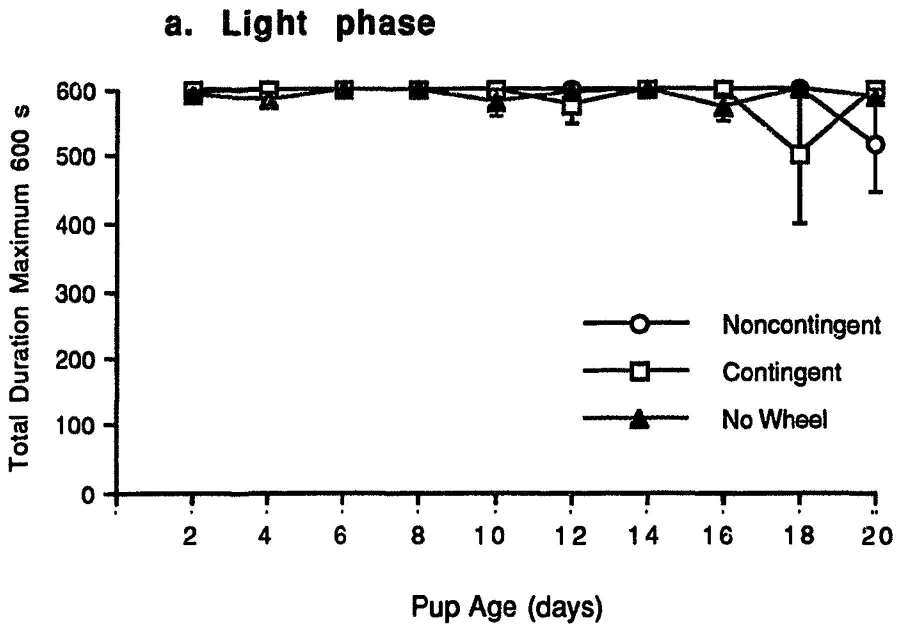
7.6 Direct observations of parental behavior

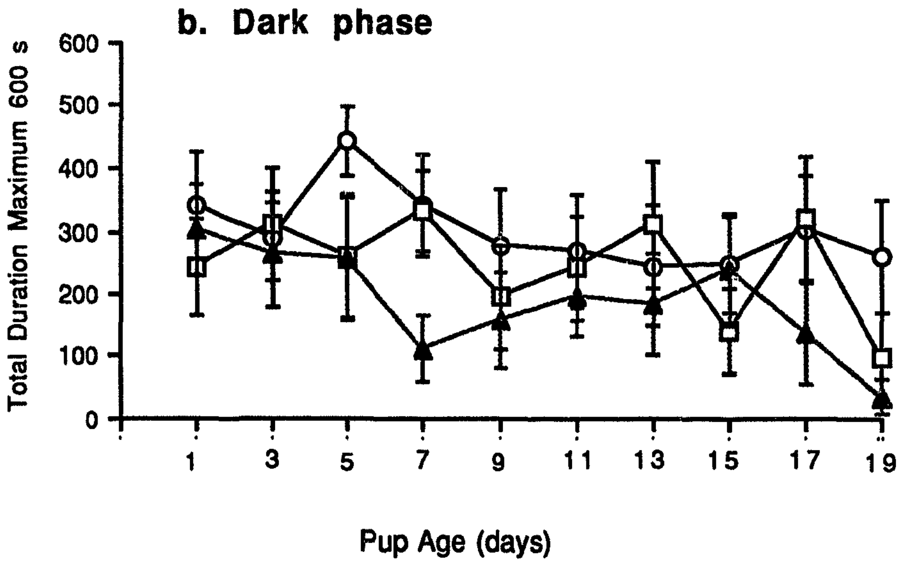
The parental behaviors recorded included crouching over pups in the nursing position, resting and touching pups, nest building, sniffing pups, grooming pups, and carrying pups. Since mothers and fathers spent significantly more time engaged in parental behavior during the light phase than during the dark phase, the LD cycle was a variable in many analyses and to reduce repetition, significant results were cited only once in each analysis. Likewise, while all interactions were examined in the analyses, only those that were significant were reported.

7.6.1 Parental behavior of mothers in the Father Absent group (Figure 7.4)

The amount of time spent engaged in parental behavior by mothers in the three Father Absent groups was analyzed using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. Significantly more

Figure 7.4. Peromyscus californicus: Parental behavior of mothers in the Father Absent groups





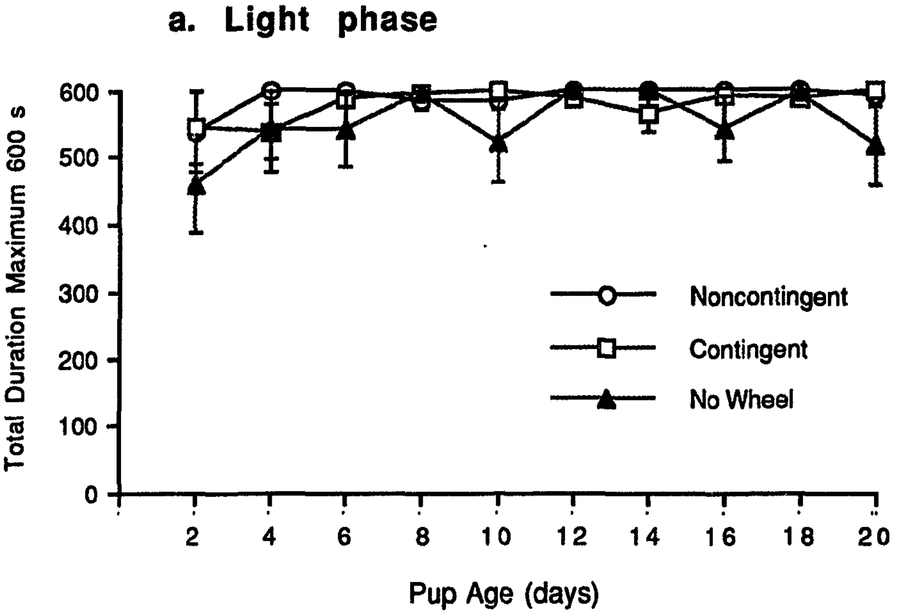
parental behavior was displayed during the light phase than during the dark phase of the LD cycle ($F_{(1,20)}=169.6$, $p<.001$). Mothers in all three housing conditions spent similar amounts of time engaged in parental activities ($F_{(2,20)}=1.9$). There was a significant effect of days ($F_{(9,180)}=2.1$, $p<.05$) as mothers decreased the amount of time they spent engaged in parental behavior as pups aged.

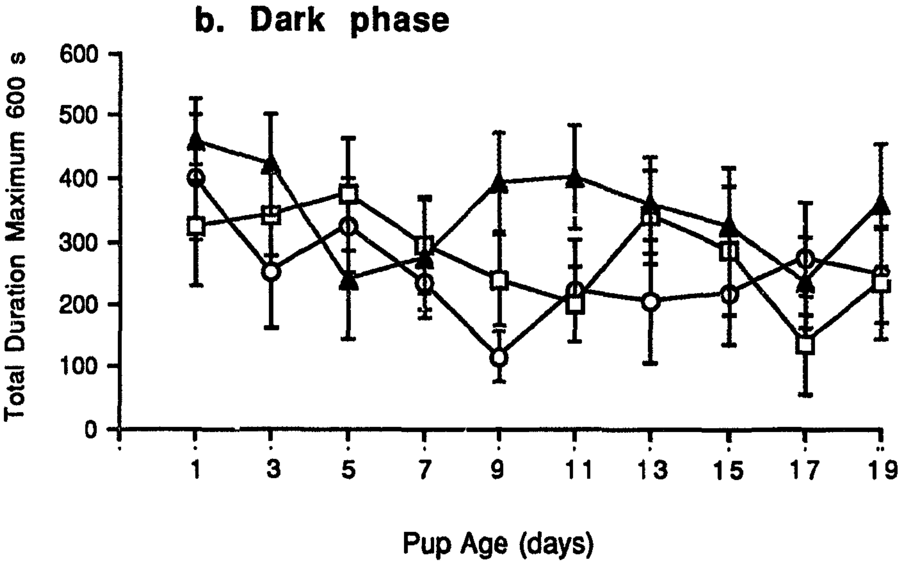
7.6.2 Parental behavior of mothers in the Father Present group (Figure 7.5)

Differences in the amount of time mothers housed with fathers spent engaged in parental behavior were compared between housing conditions using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. There was a significant effect of the LD cycle as more parental behavior occurred during the light than during the dark phase ($F_{(1,22)}=76.4$, $p<.001$). Mothers in all three housing conditions spent a similar amount of time engaged in parental behavior ($F_{(2,22)}<1.0$).

There was no significant effect of days on the amount of time mothers spent engaged in parental behavior ($F_{(9,198)}<1.0$) but there was a significant interaction between the LD cycle and days ($F_{(9,198)}=2.5$, $p<.01$). The amount of time mothers spent engaged in parental behavior during the light phase did not change over days but the amount of parental behavior during the dark phase decreased as pups aged.

Figure 7.5. Peromyscus californicus: Parental behavior of mothers in the Father Present groups



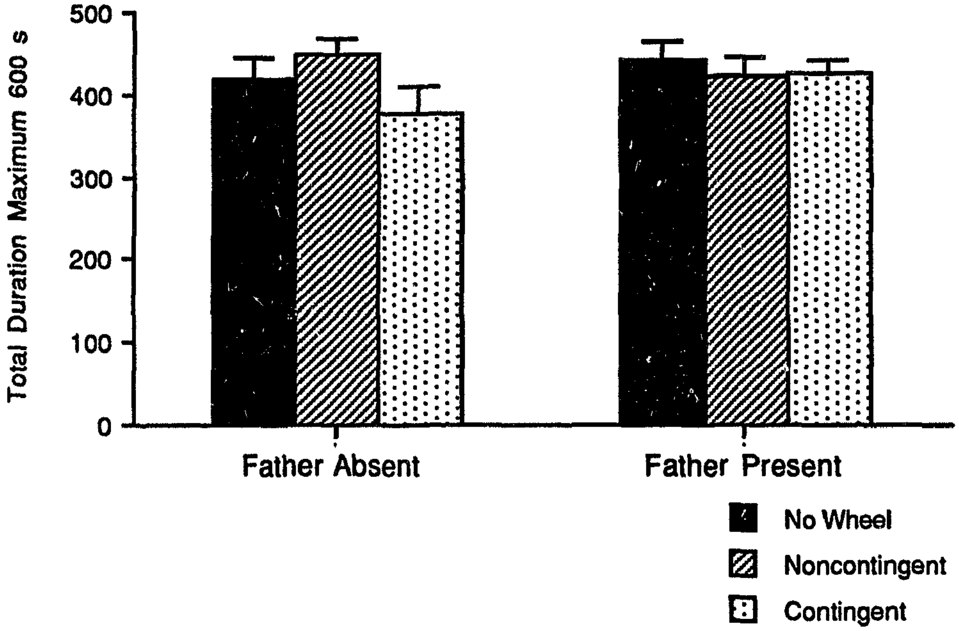


7.6.3 A comparison of parental behavior of mothers in the Father Absent and Father Present groups (Figures 7.4 to 7.6)

The amount of time spent by mothers engaged in parental behavior in the Father Absent and Father Present conditions was analyzed by using a 2 (parenting) by 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. There were no significant main effects of parenting ($F_{(1,41)}<1.0$, Figure 7.6) or housing ($F_{(2,41)}<1.0$) on the duration of parental behavior of mothers nor was there a significant interaction between parenting and housing ($F_{(2,41)}=2.1$). Mothers spent similar amounts of time engaged in parental behavior in all groups. There was, however, a significant effect of the LD cycle ($F_{(1,41)}=222.5$, $p<.001$) and a significant interaction between the LD cycle, parenting and housing ($F_{(2,41)}=3.4$, $p<.05$). During the light phase, mothers in the Father Present, No Wheel condition spent the least amount of time engaged in parental behavior whereas mothers in the other groups spent similar amounts of time engaged in parental behavior. During the dark phase, mothers in the Father Absent, No Wheel condition spent the least amount of time engaged in parental behavior while mothers in the Father Present No Wheel condition spent the most time engaged in parental behavior during the dark phase.

There was a marginally significant effect of days ($F_{(9,369)}=1.8$, $p=.06$) as mothers gradually decreased the amount of time spent engaged in parental behavior as pups approached weaning. There was a significant interaction between the LD cycle and days ($F_{(9,369)}=2.4$, $p<.01$) since during the light phase, mothers spent

Figure 7.6. Peromyscus californicus: Duration of parental behavior of mothers in the Father Absent and Father Present groups for all housing conditions collapsed over the LD cycle and days



similar amounts of time engaged in parental behavior but during the dark phase they decreased the amount of time spent engaged in parental behavior as pups aged.

7.6.4 Parental behavior of fathers in the Father Present groups (Figure 7.7)

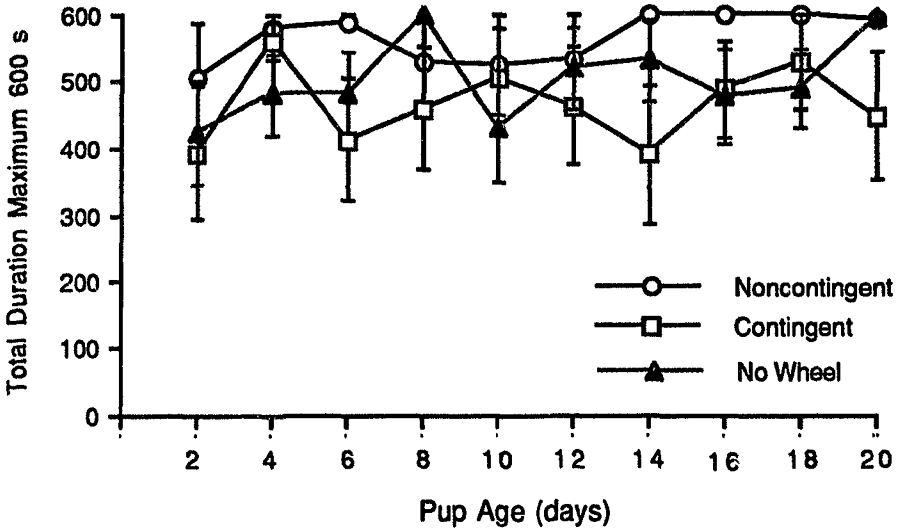
Differences in the amount of time fathers spent engaged in parental behavior in each housing condition were analyzed by using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. There was no significant effect of housing on the time spent in parental behavior by fathers ($F_{(2,22)}<1.0$). Like mothers, fathers spent significantly more time engaged in parental behavior during the light phase than during the dark phase of the LD cycle ($F_{(1,22)}=114.8$, $p<.001$). There was no significant effect of days ($F_{(9,198)}=1.0$) but there was a significant interaction between the LD cycle and days ($F_{(9,198)}=2.2$, $p<.05$). Fathers slightly increased the amount of time per day engaged in parental behavior during the light phase but decreased the amount of time per day engaged in parental behavior during the dark phase as pups aged.

7.6.5 A comparison of parental behavior of mothers and fathers in the Father Present groups (Figures 7.5, 7.7 and 7.8)

In order to compare the amount of parental behavior shown by mothers and fathers in the Father Present group, the duration of parental behavior exhibited by mothers and fathers was analyzed by using an ANOVA with two between factors (housing and gender) and two within factors (LD cycle and days). Fathers spent significantly

Figure 7.7. Peromyscus californicus: Parental behavior of fathers in the Father Present groups

a. Light phase



b. Dark phase

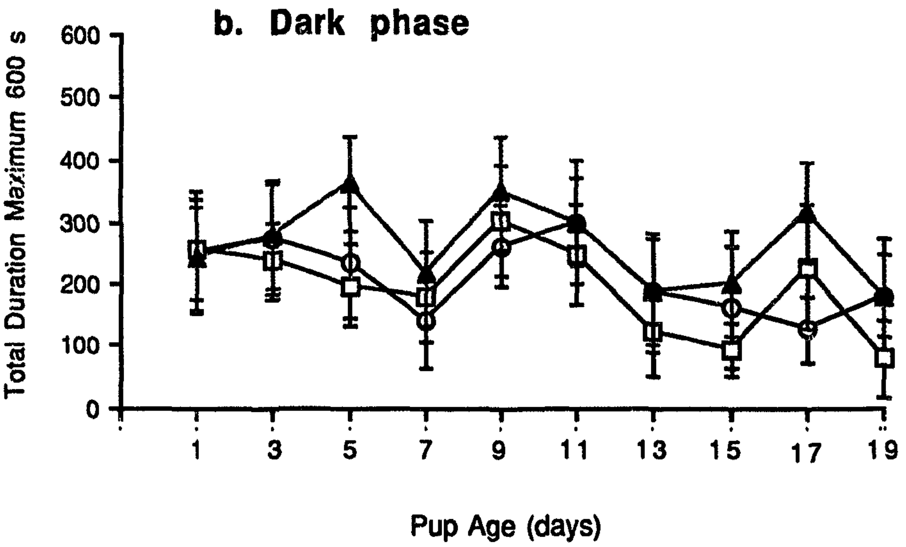
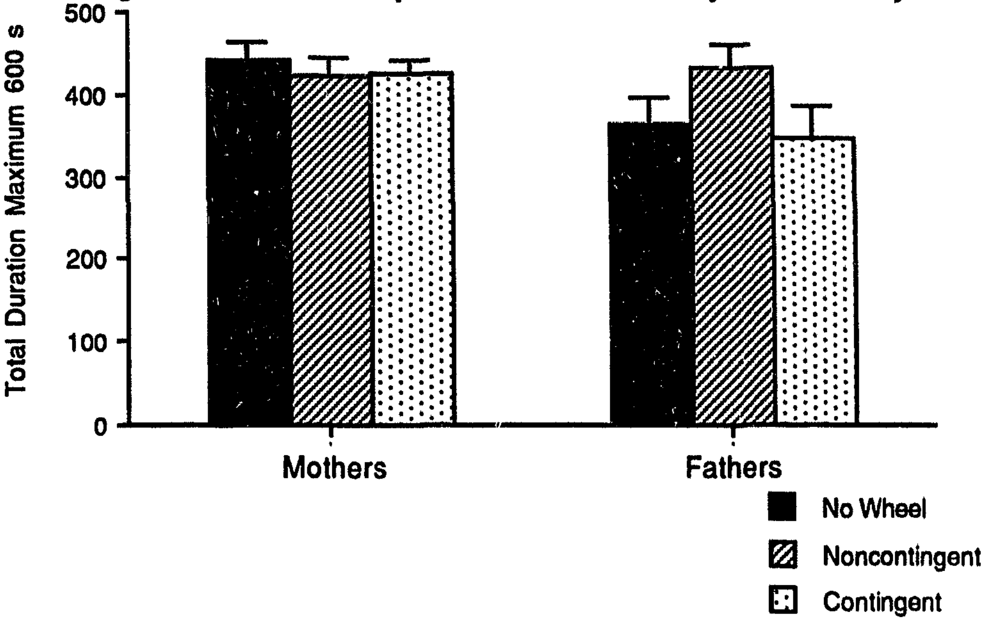


Figure 7.8. Peromyscus californicus: Duration of parental behavior of mothers and fathers in the Father Present groups for all housing conditions collapsed over the LD cycle and days



less time engaged in parental behavior than mothers ($F_{(1,44)}=6.0$, $p<.05$, Figure 7.8). Mothers and fathers spent a similar amount of time engaged in parental behavior in all three housing groups ($F_{(2,44)}<1.0$). There was a significant effect of the LD cycle ($F_{(1,44)}=184.1$, $p<.001$) as mothers and fathers both spent more time engaged in parental behavior during the light phase than during the dark phase. When mothers and fathers were compared, there was no significant effect of days ($F_{(9,396)}<1.0$) on the amount of time mothers and fathers spent engaged in parental behavior.

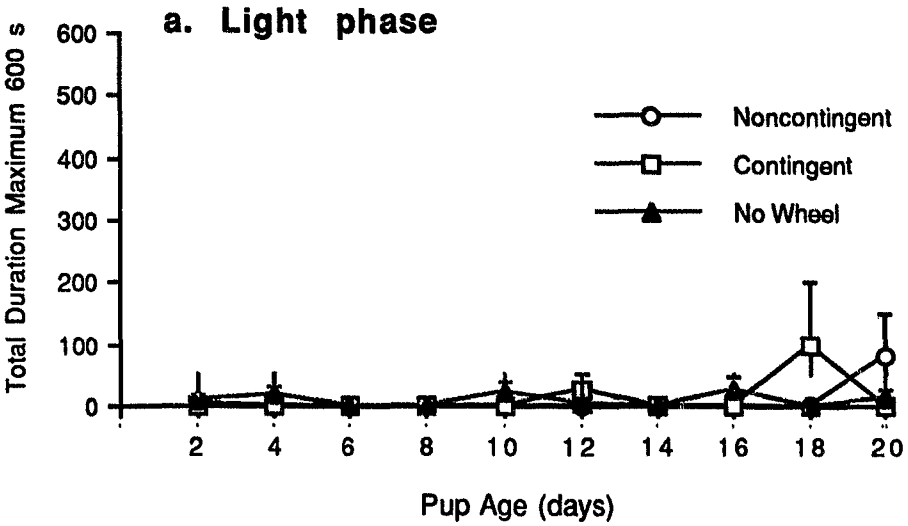
7.7 Direct observations of nonparental behavior

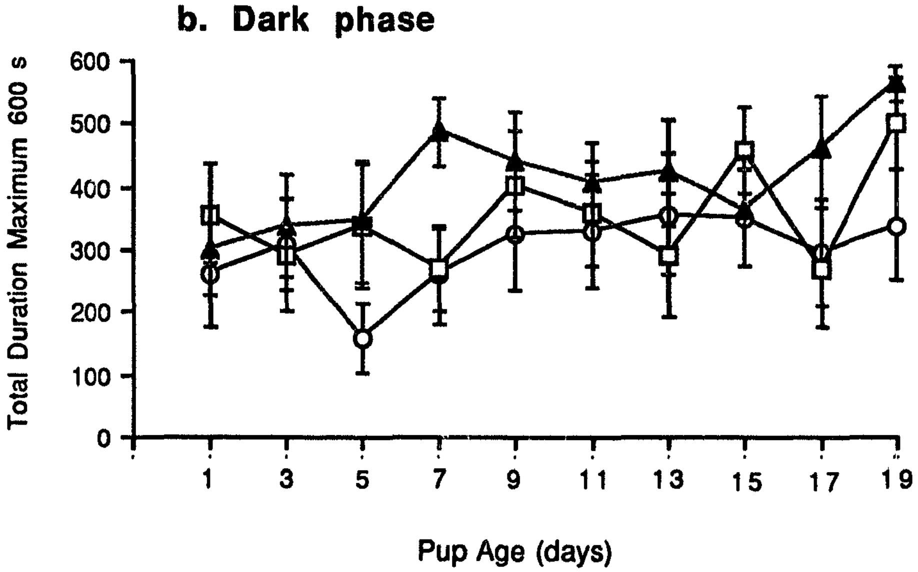
Nonparental behaviors included, wheel running, exploring the cage, eating, grooming, resting without touching the pups and gnawing wood shavings or the bars on cage. Interactions that were not significant were not reported.

7.7.1 Nonparental behavior of mothers in the Father Absent groups (Figure 7.9)

Nonparental behaviors were analyzed using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. Mothers spent a similar amount of time engaged in nonparental behavior in all three housing groups ($F_{(2,20)}=1.9$). Mothers spent significantly more time engaged in nonparental behavior during the dark phase than during the light phase of the LD cycle ($F_{(1,20)}=168.7$, $p<.001$) and mothers significantly increased the amount of time spent engaged in nonparental behavior as pups aged ($F_{(9,180)}=2.1$, $p<.05$).

Figure 7.9. Peromyscus californicus: Nonparental behavior of mothers in the Father Absent groups


a. Light phase


b. Dark phase

7.7.2 Nonparental behavior of mothers in the Father Present groups (Figure 7.10)

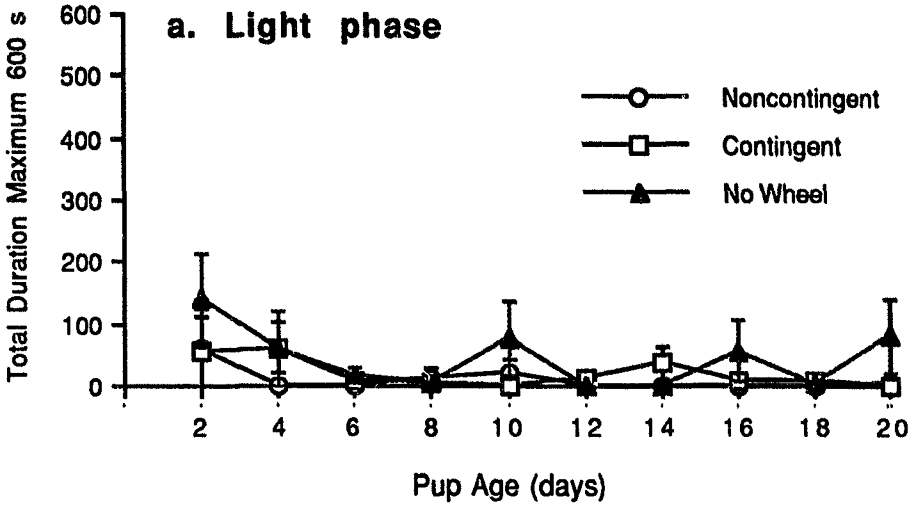
There was no significant effect of housing ($F_{(2,22)}<1.0$) on the amount of time mothers spent engaged in nonparental behavior, but mothers spent significantly more time engaged in nonparental behavior during the dark phase than during the light phase of the LD cycle ($F_{(1,22)}=78.1$, $p<.001$).

There was no significant effect of days ($F_{(9,198)}<1.0$) on the amount of time mothers spent engaged in nonparental behavior but there was a significant interaction between the LD cycle and days ($F_{(9,198)}=2.9$, $p<.05$). Mothers decreased the amount of time spent engaged in nonparental behavior during the light phase but increased the amount of time spent engaged in nonparental behavior during the dark phase as pups aged.

7.7.3 A comparison of nonparental behavior of mothers in the Father Absent and Father Present groups (Figure 7.11)

There were no differences in the duration of nonparental behavior between mothers in the Father Absent and Father Present groups ($F_{(1,42)}<1.0$). Mothers spent significantly more time ($F_{(1,42)}=223.9$, $p<.001$) engaged in nonparental behavior during the dark phase than during the light phase of the LD cycle and mothers significantly increased the amount of time spent engaged in nonparental activities as pups aged ($F_{(9,378)}=1.9$, $p<.05$). Mothers spent a similar amount of time engaged in nonparental behavior in all three housing conditions ($F_{(2,42)}<1.0$).

Figure 7.10. Peromyscus californicus: Nonparental behavior of mothers in the Father Present groups


a. Light phase

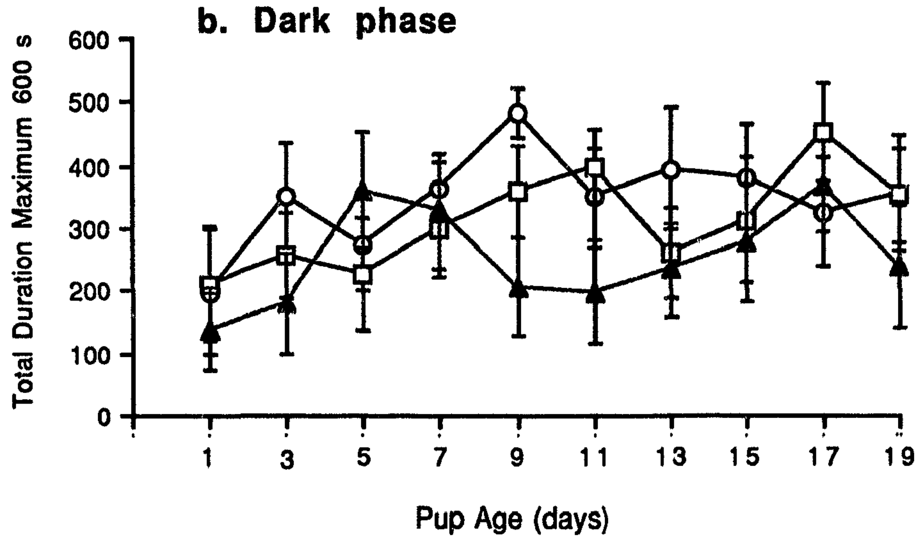
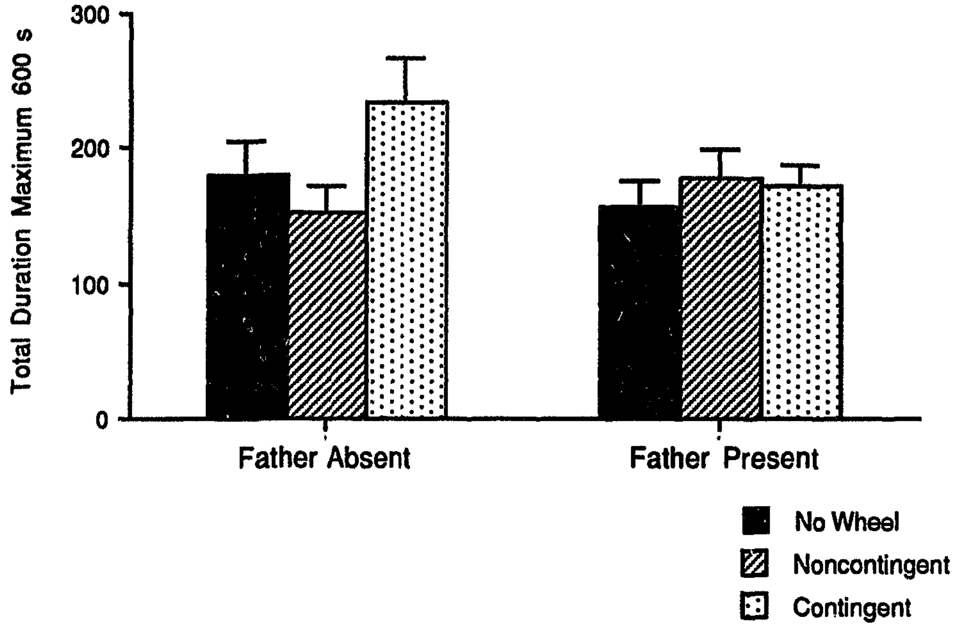

b. Dark phase

Figure 7.11. Peromyscus californicus: Duration of nonparental behavior of mothers in the Father Absent and Father Present groups for all housing conditions collapsed over the LD cycle and days



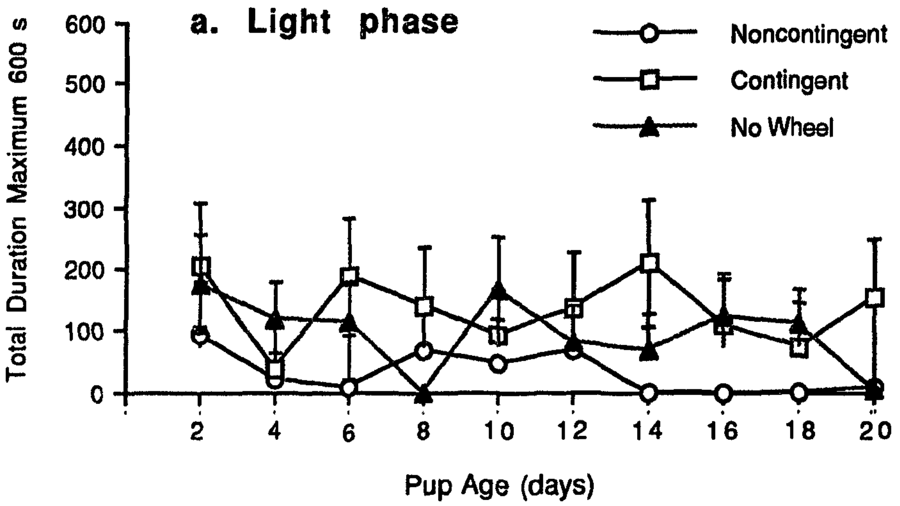
7.7.4 Nonparental behavior of fathers in the Father Present groups (Figure 7.12)

Fathers spent significantly more time during the dark phase engaged in nonparental behavior ($F_{(1,22)}=108.3$) than during the light phase. There was no significant difference in the amount of time spent by fathers in nonparental behavior in the three housing conditions ($F_{(2,22)}<1.0$) and there was no significant effect of days ($F_{(9,198)}=1.0$). There was a significant interaction between the LD cycle and days ($F_{(9,198)}=2.3$, $p<.05$) as fathers decreased the amount of time spent in nonparental behavior during the light phase and increased the amount of time engaged in nonparental behavior during the dark phase as pups aged.

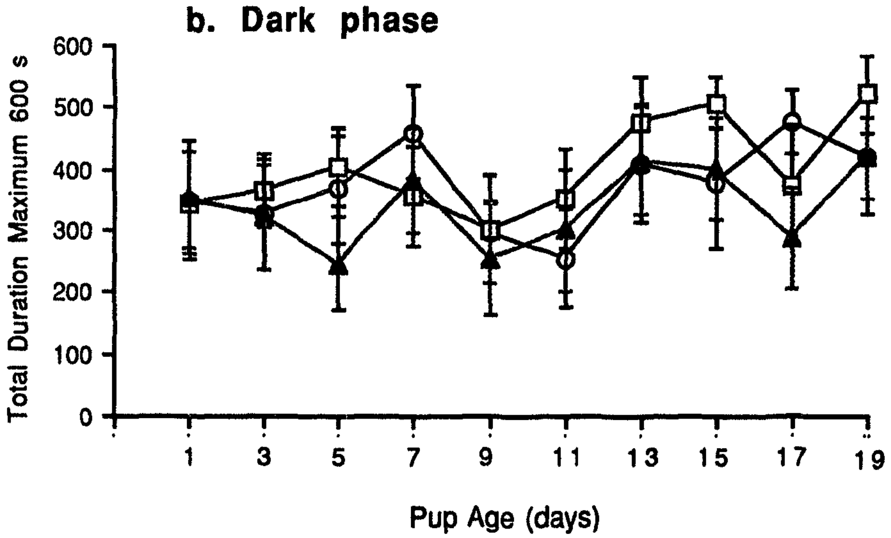
7.7.5 A comparison of nonparental behavior of mothers and fathers in the Father Present groups (Figure 7.13)

Data were analyzed by using an ANOVA with two between factors (housing and gender) and two within factors (LD cycle and days). Fathers spent significantly more time engaged in nonparental behavior than mothers ($F_{(1,44)}=5.7$, $p<.05$). Mothers and fathers both engaged in more nonparental behavior during the dark phase than during the light phase of the LD cycle ($F_{(1,44)}=181.7$, $p<.001$). Mothers and fathers spent similar amounts of time engaged in parental behavior in all three housing conditions ($F_{(2,44)}<1.0$). There was no significant effect of days on the amount of time mothers and fathers spent engaged in nonparental behavior ($F_{(9,396)}<1.0$) but there was a significant interaction between the LD cycle and days ($F_{(9,396)}=3.4$, $p<.001$). Mothers and fathers engaged in nonparental

Figure 7.12. Peromyscus californicus: Nonparental behavior of fathers in the Father Present groups

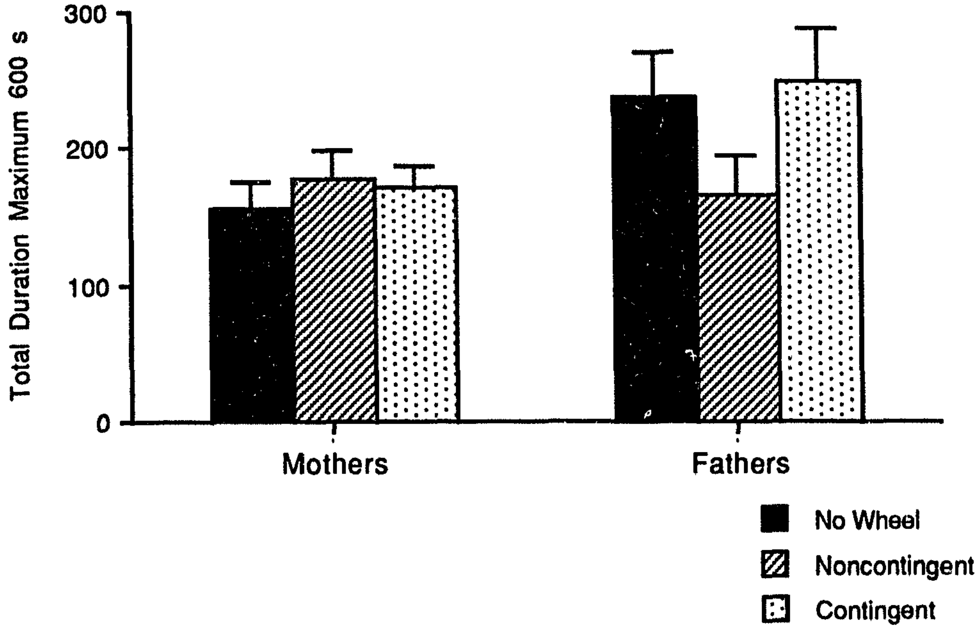


a. Light phase



b. Dark phase

Figure 7.13. Peromyscus californicus: Duration of nonparental behavior of mothers and fathers in the Father Present group for all housing conditions collapsed over the LD cycle and days



behavior for a similar amount of time during the light phase but increased the amount of time engaged in nonparental behavior during the dark phase as pups aged.

Summary of Part Three. The housing conditions did not influence the amount of time mothers and fathers spent in parental and nonparental behavior. Mothers spent the same amount of time in parental and nonparental behavior when the father was present and absent. Fathers spent less time engaged in parental behavior and more time engaged in nonparental behavior than mothers. Both mothers and fathers spent more time in parental behavior during the light phase and more time in nonparental behavior during the dark phase of the LD cycle. Therefore, pups in the Father Present group were receiving more parental care than pups in the Father Absent group because of the fathers' contribution.

Part Four: Wheel running

7.8 Number of revolutions by *Peromyscus californicus* after pairing in the Wheel Noncontingent and Wheel Contingent conditions (Figures 7.14 and 7.15)

The number of revolutions run in the wheel was recorded hourly from the time *Peromyscus californicus* were placed together in pairs, to the weaning of pups. This time period consisted of 56 days (32 days prior to birth and 24 days from birth to weaning), however, only the data from 21 days prior to birth and 21 days after birth were analysed. This was done so that the data analyses were consistent with the *Mus musculus* results. For analysis, the data were pooled into blocks of 5 days. This resulted in four, 5 day blocks before birth and four, 5 day blocks after birth, with one day for parturition. The number of revolutions was calculated during the light phase and dark phase of the LD cycle for each day and then each 5 days of data were averaged. Data were analysed using a 2 (parenting) x 2 (housing) x 2 (LD cycle) x 9 (blocks of time) analysis of variance with two between factors (parenting and housing) and two within factors (LD cycle and blocks of time). Days 20 to 6 before parturition (Blocks 1 to 3) were analyzed independently of the remaining data (Blocks 4 to 9), as males were removed from the Father Absent groups 2 to 4 days before parturition. Therefore, during the first 3 blocks the only difference between the groups was housing. Although *Peromyscus* pups were not usually weaned until the pups were 30 days of age, the number of revolutions *Peromyscus* ran in the wheels was terminated at 24 days since pups interfered with wheel running. In all analyses, mothers and fathers ran more revolutions during the dark phase of the LD cycle. Interactions that were not significant were not reported below.

a. Blocks 1 to 3: (fathers present in all groups)

There was no significant difference between Father Absent and Father Present groups in the number of revolutions *Peromyscus* ran over the first 3 blocks ($F_{(1,45)}=2.8$), but *Peromyscus* in the Wheel Contingent conditions ran significantly more revolutions than those in the Wheel Noncontingent conditions ($F_{(1,45)}=6.4$, $p<.05$). Significantly more revolutions were run in the dark than in the light phase of the LD cycle ($F_{(1,45)}=305.2$, $p<.001$).

Peromyscus decreased the number of revolutions they ran over the first 3 blocks ($F_{(2,90)}$=18.8, p<.001). There was a significant interaction between days and parenting ($F_{(2,90)}$=8.11, p<.001). Mice in both the Father Absent and Father Present groups maintained a steady number of revolutions for blocks 1 and 2 but mice in the Father Absent groups reduced the number of revolutions they ran during block 3. There was a significant interaction between the LD cycle and days ($F_{(2,90)}$=5.0, p<.01) since during the light phase, *Peromyscus* decreased the number of revolutions they ran, while during the dark phase, they ran the same number of revolutions over the first 3 blocks. There was also a significant interaction between the LD cycle, days and parenting ($F_{(2,90)}$=9.5, p<.001). During the light phase, *Peromyscus* in both parenting groups decreased the number of revolutions they ran over days. During the dark phase, *Peromyscus* in the Father Absent group decreased the number of revolutions they ran while those in the Father Present group maintained the number of revolutions they ran over days.

b. Blocks 4 to 9: (father removed from the Father Absent groups)

Since a mother and father were running in the Father Present groups and only a mother was running in the Father Absent groups, these groups were analyzed separately using 3 (housing) by 2 (LD cycle) by 6 (blocks of days) ANOVAs. Due to the loss of litters, the number of animals in the analysis was reduced from 12 or 13 litters in blocks 1 to 3, to 6 to 8 litters in blocks 4 to 9. As this was a repeated measures analysis, when missing data occurred in any of the blocks, the entire case was deleted from the analysis.

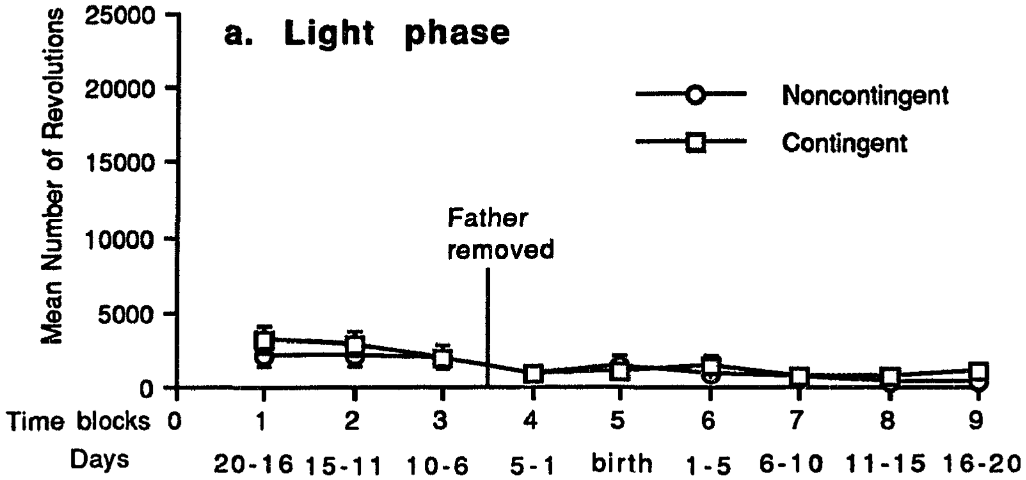
Father Absent groups (Figure 7.14)

Mothers in the Wheel Contingent condition ran on average, twice as many revolutions over blocks 4 to 9 as mothers in the Wheel Noncontingent condition (6707 vs. 3480), a difference which was significant ($F_{(1,12)}=5.3$, $p<.05$). Mothers ran ten times as many revolutions during the dark phase as during the light phase ($F_{(1,12)}=35.6$, $p<.001$) and there was a significant interaction between the LD cycle and housing ($F_{(1,12)}=4.6$, $p=.05$). Mothers in the Wheel Noncontingent condition ran eight times as many revolutions in the dark phase as during the light phase (776 vs. 6184) while those in the Wheel Contingent condition ran thirteen times as many revolutions in the dark phase as during the light phase (973 vs. 12441). Mothers did not differ in the number of revolutions they ran over days ($F_{(5,60)}=1.0$).

Father Present groups (Figure 7.15)

Mothers and fathers ran a similar number of revolutions in the Wheel Noncontingent and Wheel Contingent conditions ($F_{(1,13)}<1.0$). They also ran over ten times more revolutions during the dark phase (16098) than during the light phase (1533) of the LD cycle ($F_{(1,13)}=228.0$, $p<.001$). There was no significant difference in running over days ($F_{(5,65)}=1.9$) but there was a significant interaction between the LD cycle and days ($F_{(5,65)}=3.2$, $p<.05$). During the light phase, mothers and fathers increased the number of revolutions they

Figure 7.14. Peromyscus californicus: Mean number of revolutions for in the Father Absent groups


a. Light phase

b. Dark phase

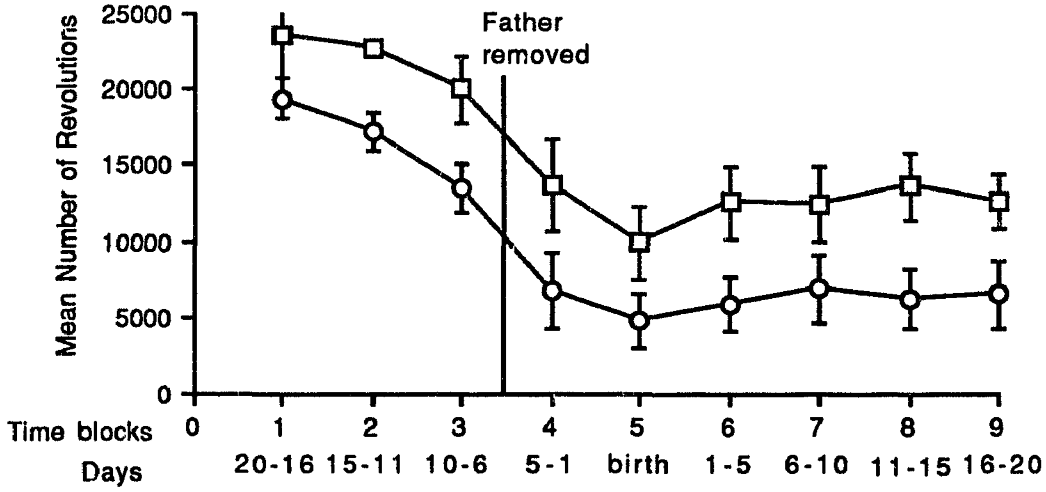
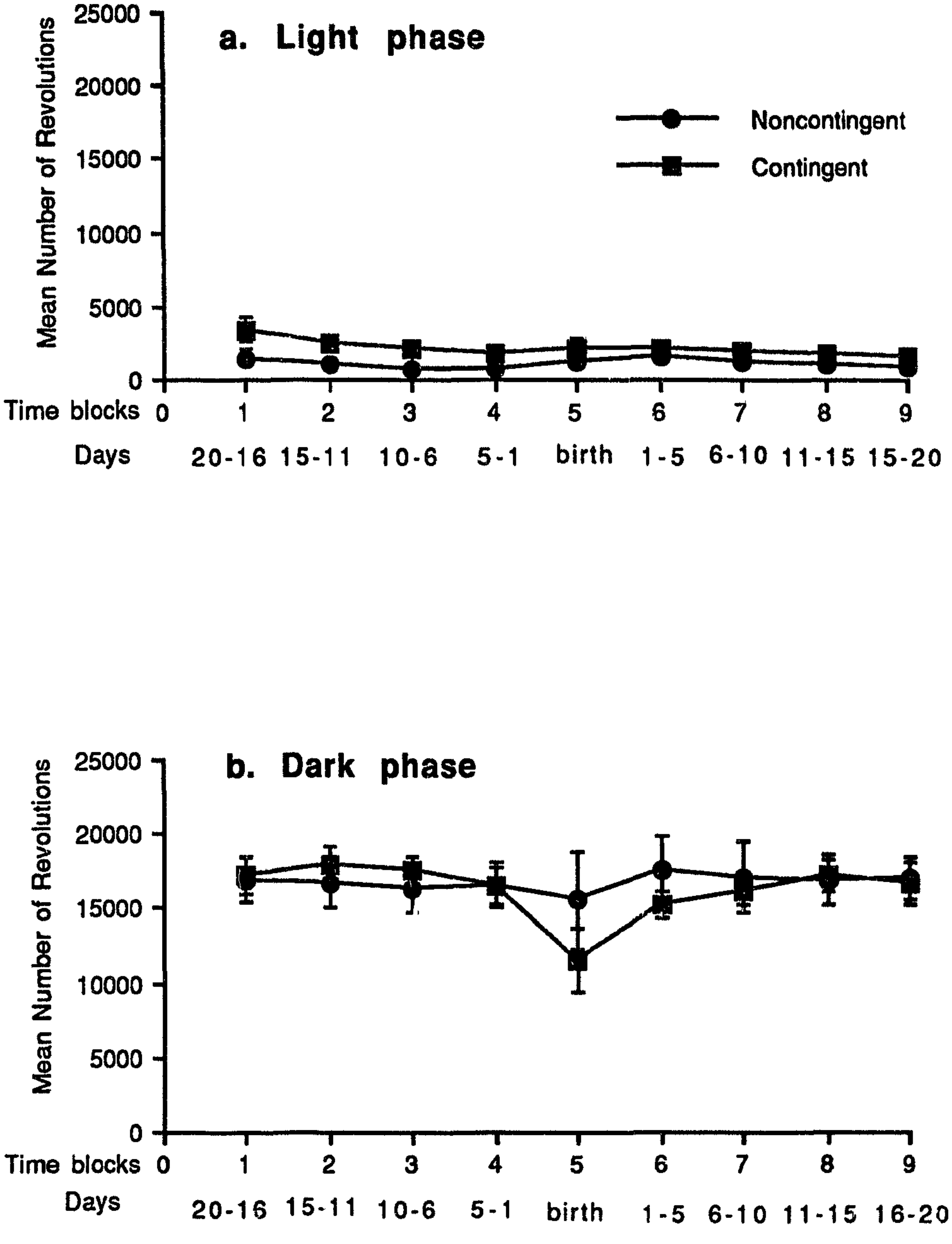


Figure 7.15. Peromyscus californicus: Mean number of revolutions in the Father Present groups



ran between block 4 and 6 and then decreased the number of revolutions they ran. During the dark phase, mothers and fathers decreased the number of revolutions they ran on block 5 (the day of birth) and then increased and maintained a steady number of revolutions up to weaning (block 9).

7.9. Observations of wheel running behavior

In order to determine who was running on the wheel, we analyzed the behavioral observations for wheel running separately from other nonparental behaviors. Differences in the amount of time spent engaged in wheel running behavior were compared between housing conditions using a 3 (housing) by 2 (LD cycle) by 10 (days) ANOVA. Interactions that were not significant were not reported.

7.9.1 Wheel running behavior of mothers in the Father Absent groups (Figure 7.16)

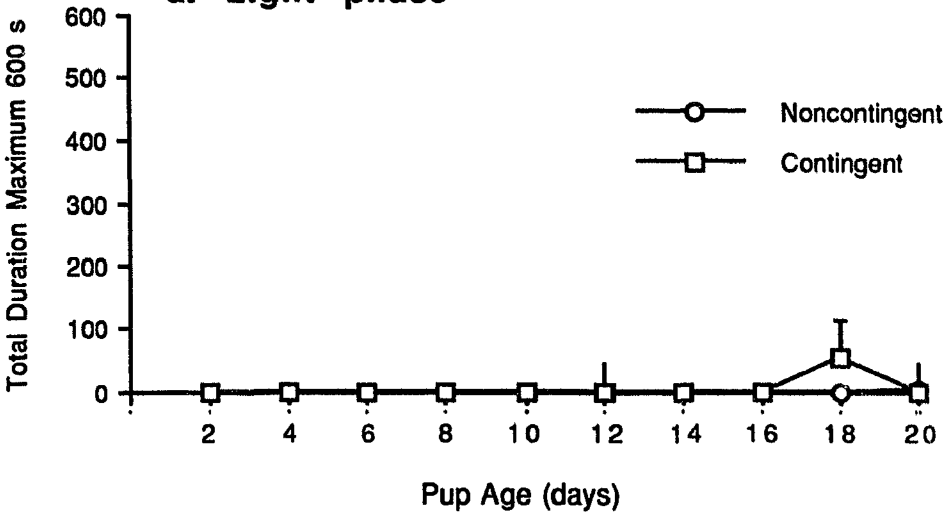
Although mothers in the Father Absent group spent a similar amount of time wheel running in all three housing conditions ($F_{(1,12)}<1.0$), they spent significantly more time wheel running during the dark phase than during the light phase of the LD cycle ($F_{(1,12)}=54.8$, $p<.001$). There was no significant effect of days ($F_{(9,108)}<1.0$) on the amount of time single mothers spent wheel running.

7.9.2 Wheel running behavior of mothers in the Father Present groups (Figure 7.17)

Mothers in the Wheel Contingent and Wheel Noncontingent conditions did not differ in the amount of time they spent wheel

Figure 7.16. Peromyscus californicus: Duration of wheel running behavior of mothers in the Father Absent groups

a. Light phase



b. Dark phase

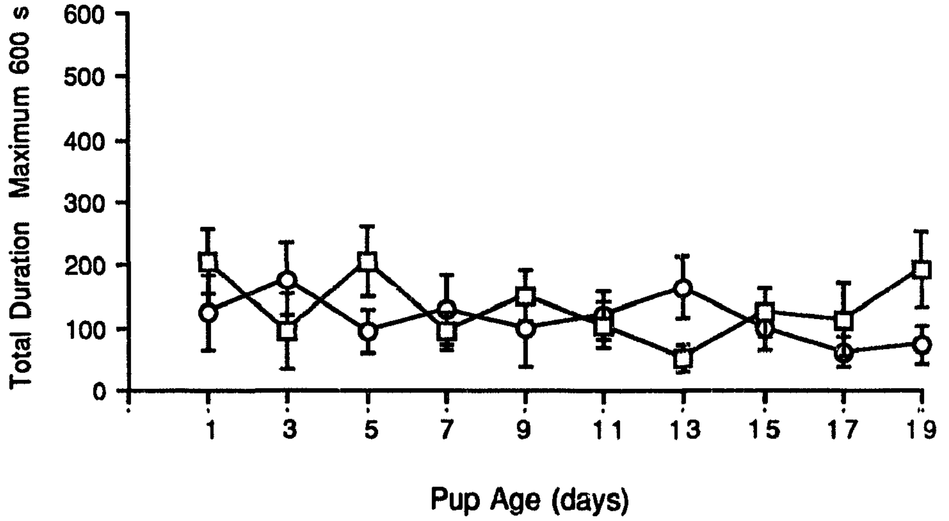
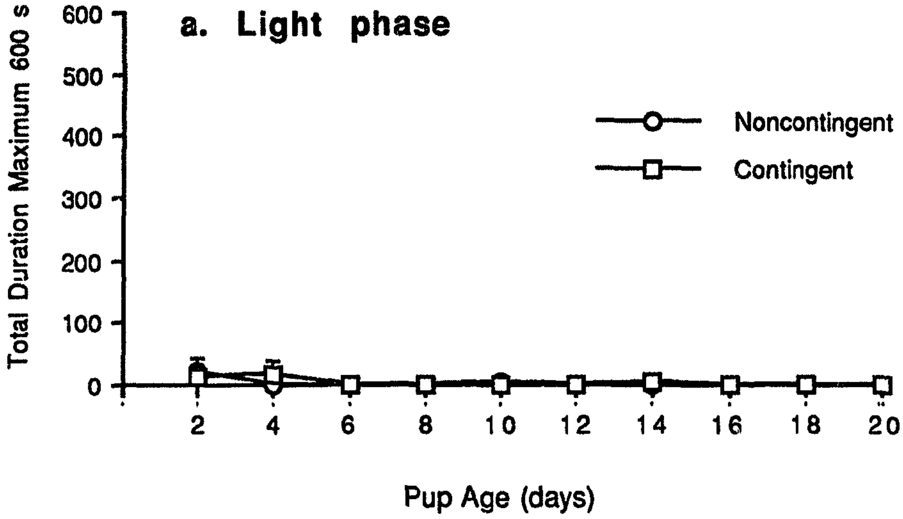
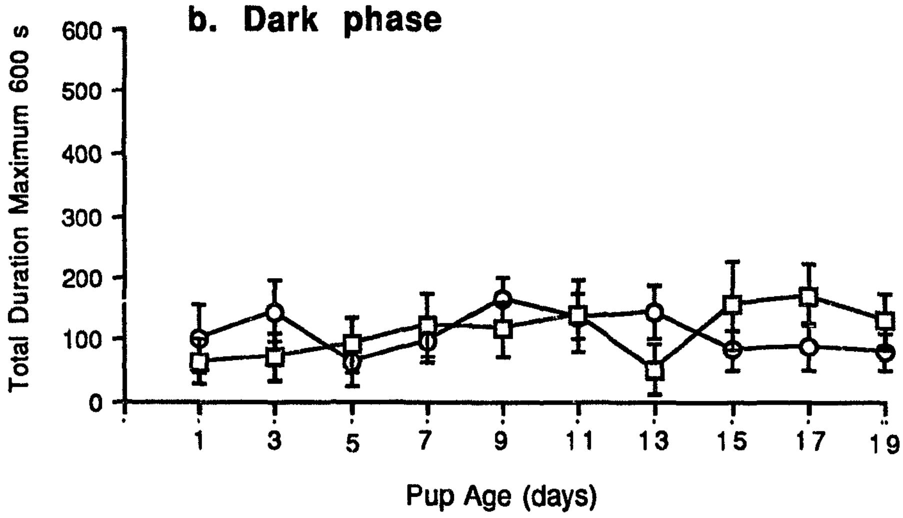


Figure 7.17. Peromyscus californicus: Duration of wheel running behavior of mothers in the Father Present groups


a. Light phase


b. Dark phase

running ($F_{(1,13)}<1.0$). There was, however, a significant effect of the LD cycle ($F_{(1,13)}=24.2$, $p<.001$) as mothers spent more time running during the dark phase of the LD cycle. There was no significant effect of days ($F_{(9,117)}<1.0$) on the amount of time mothers spent wheel running.

7.9.3 A comparison of wheel running behavior of mothers in the Father Absent and Father Present groups

A comparison of Figures 7.16 and 7.17 indicated that there was no significant effect of parenting ($F_{(1,25)}<1.0$) or housing ($F_{(1,25)}<1.0$) on the amount of time mothers spent wheel running. There was, however, a significant interaction between days and housing ($F_{(9,225)}=2.5$, $P<.01$) as mothers in the Wheel Noncontingent condition increased the amount of time spent wheel running during block 6 while mothers in the Wheel Contingent condition decreased the amount of wheel running during block 6. Mothers in the Wheel Noncontingent condition, also decreased the amount of time they spent wheel running while mothers in the Wheel Contingent condition increased the amount of they spent wheel running during block 8.

There was a significant interaction between the LD cycle, days and housing ($F_{(9,225)}=2.4$, $p<.05$) but like the interaction between days and housing there does not appear to be a systematic difference in behavior related to this interaction. During the light phase of the LD cycle mothers in the Wheel Noncontingent condition decreased the amount of time they spent running while those in the Wheel Contingent condition increased the amount of time they spent running during block 6. During the dark phase, mothers in the Wheel Noncontingent condition increased the amount of time spent wheel running while mothers in the Wheel Contingent condition decreased the amount of wheel running during block 6. Mothers in the Wheel Noncontingent condition, also decreased the amount of time they spent wheel running while mothers in the Wheel Contingent condition increased the amount of time they spent wheel running during block 8.

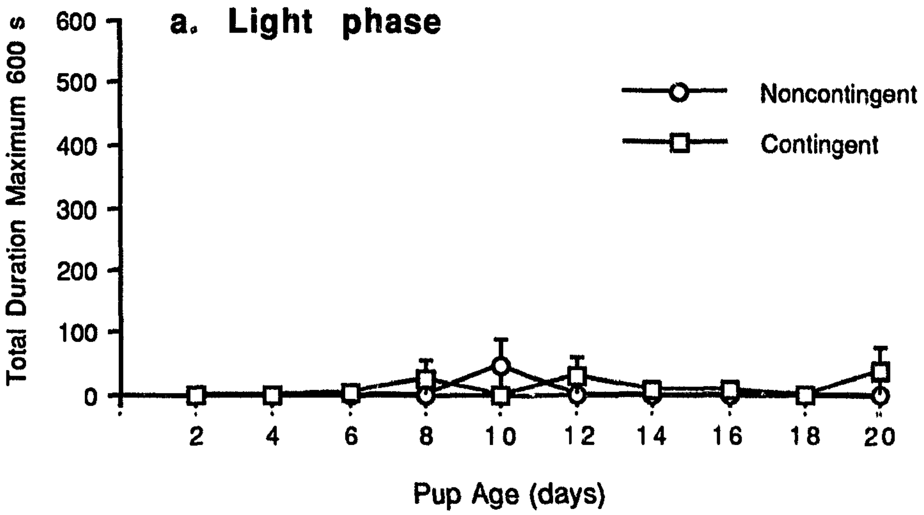
7.9.4 Wheel running behavior of fathers (Figure 7.18)

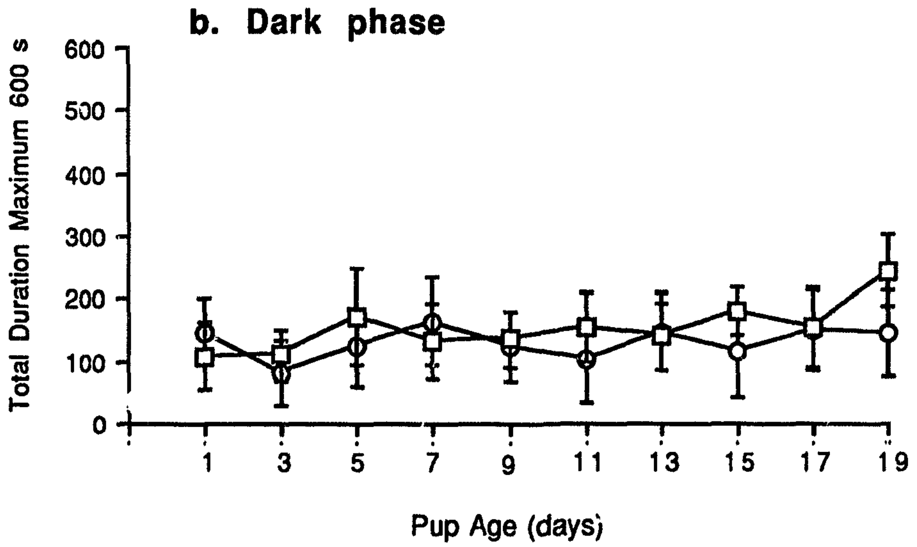
Fathers spent similar amount of time engaged in wheel running in all three housing conditions ($F_{(1,13)}<1.0$) but they spent significantly more time wheel running during the dark phase than during the light phase ($F_{(1,13)}=17.1$, $p<.01$). There also was no significant effect of days ($F_{(9,117)}=1.1$) on the amount of time fathers spent wheel running.

7.9.5 A comparison of wheel running behavior of mothers and fathers in the Father Present groups

A 2 (gender) by 2 (housing) by 2 (LD cycle) by 10 (days) ANOVA was conducted to analyze the results. There was no significant difference in the amount of time mothers and fathers spent wheel running ($F_{(1,26)}<1.0$) and they spent a similar amount of time wheel running in all three housing conditions ($F_{(1,26)}<1.0$). Mothers and fathers spent significantly more time engaged in wheel running during the dark phase of the LD cycle ($F_{(1,26)}=38.3$, $p<.001$) but there was no significant effect of days ($F_{(9,234)}=1.1$)

Figure 7.18. Peromyscus californicus: Duration of wheel running behavior of fathers in the Father Present groups





Summary of Part Four. Father Absent mothers in the Wheel Contingent condition ran more revolutions than Father Absent mothers in the Wheel Noncontingent condition however, mothers and fathers in the Father Present groups did not differ in the number of revolutions they ran in the Wheel Contingent and Wheel Noncontingent conditions. A Father Absent mother which ran an average of 13,000 revolutions per day, travelled 7.06 km per day for 40 days or about 282 km during the experiment. Both the number of revolutions run and direct behavioral observations of wheel running indicated that *Peromyscus* ran more during the dark phase than during the light phase of the LD cycle.

Direct behavioral observations of wheel running showed that mothers in the Wheel Noncontingent condition spent the same amount of time wheel running as mothers in the Wheel Contingent condition when the father was absent or present. However, the pattern of time spent wheel running over days differed between mothers in the Wheel Noncontingent and Wheel Contingent conditions. Mothers in the Wheel Noncontingent condition gradually decreased the amount of time spent wheel running as pups aged while mothers in the Wheel Contingent condition gradually increased the amount of time spent wheel running as pups aged. Mothers and fathers spent the same amount of time wheel running in the Father Present groups.

Part Five: Wheel running versus parental behavior in the dark phase in the Wheel Contingent and Wheel Noncontingent conditions

Peromyscus californicus were videotaped during the dark phase of the LD cycle in the Father Present Wheel Contingent and Father Present Wheel Noncontingent conditions to determine if the mother or father was in the nest (Section 7.10) or wheel running (section 7.11). Videotaping was conducted during the dark phase only as *Peromyscus* stayed in the nest for most of the light phase and only ran on the wheel for short durations. It was therefore, decided that more information could be collected during the dark phase on the differences between the mothers' and fathers' contribution to their own pups survival. Six pairs of *Peromyscus* in the Wheel Contingent condition and seven pairs in the Wheel Noncontingent condition were observed on days 1 to 4 while only five pairs in the Wheel Contingent condition and four pairs in the Wheel Noncontingent condition were observed for the other days as some litters did not survive. The same pairs of *Peromyscus* were videotaped for 3 to 6 hours between postpartum days 1 to 4, 6 to 10 and 13 to 17. Two different 10 minute time samples were analyzed from the videotapes for each pair of *Peromyscus* observed on these days. The two time samples were randomly selected from the first half of the dark phase and the second half of the dark phase. These two time periods were averaged for the analysis. The time spent in the nest and wheel running by each parent was recorded using the event recorder. Separate ANOVAs were conducted for each set of postpartum data and for both measures (duration in the nest and duration of wheel running). In addition, it was decided to use only pairs of *Peromyscus* that had pups that survived to weaning so a 2 (housing) by 2 (gender) by 3 (days) ANOVA could be conducted.

7.10 Videoanalysis of duration in the nest (Figure 7.19)

Peromyscus in the Wheel Noncontingent condition spent more time in the nest than *Peromyscus* in the Wheel Contingent condition ($F_{(1,12)}=13.3$, $p<.01$). Mothers and fathers spent similar amounts of time in the nest ($F_{(1,12)}=1.6$) and there was no significant interaction between housing and gender ($F_{(1,12)}=2.9$). There was no significant effect of days ($F_{(2,24)}<1.0$) on the amount of time *Peromyscus* spent in the nest nor were there significant interactions between days and gender ($F_{(2,24)}=1.9$), days and housing ($F_{(2,24)}<1.0$) or days, gender and housing ($F_{(2,24)}<1.0$).

7.11 Videoanalysis of the duration of wheel running (Figure 7.20)

Fathers spent significantly more time wheel running than mothers ($F_{(1,12)}=5.5$, $p<.05$) and *Peromyscus* in the Wheel Contingent condition spent significantly more time wheel running than *Peromyscus* in the Wheel Noncontingent condition ($F_{(1,12)}=20.5$, $p<.001$). There also was a significant interaction between housing and gender ($F_{(1,12)}=14.3$, $p<.01$). Fathers in the Wheel Contingent condition spent more time running than mothers whereas in the Wheel Noncontingent condition mothers and fathers spent similar amounts of time wheel running. There was no significant effect of

Figure 7.19. Peromyscus californicus: Duration in the nest from videoanalysis during the dark phase

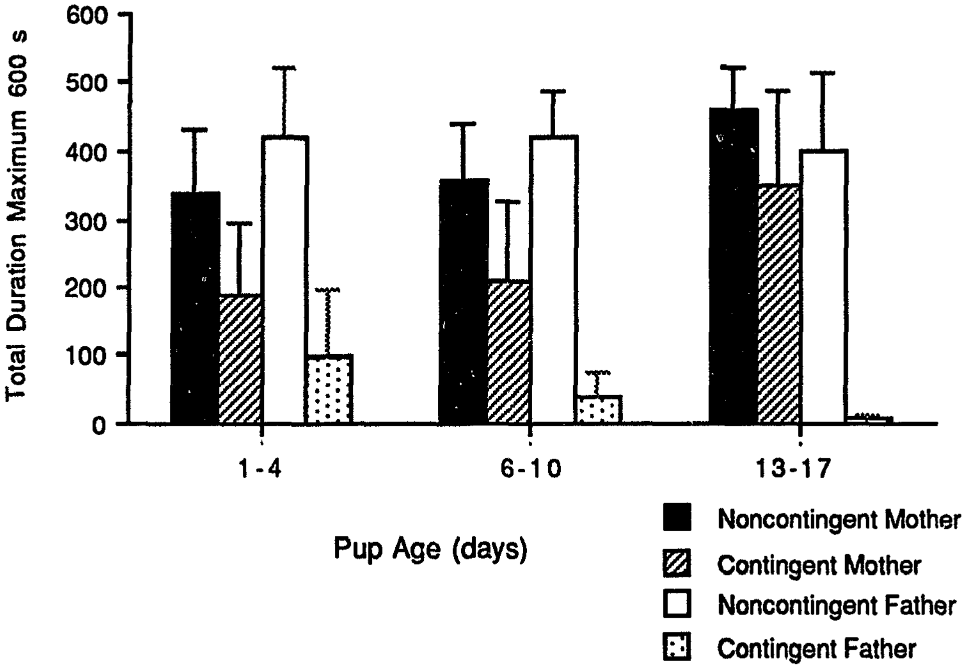
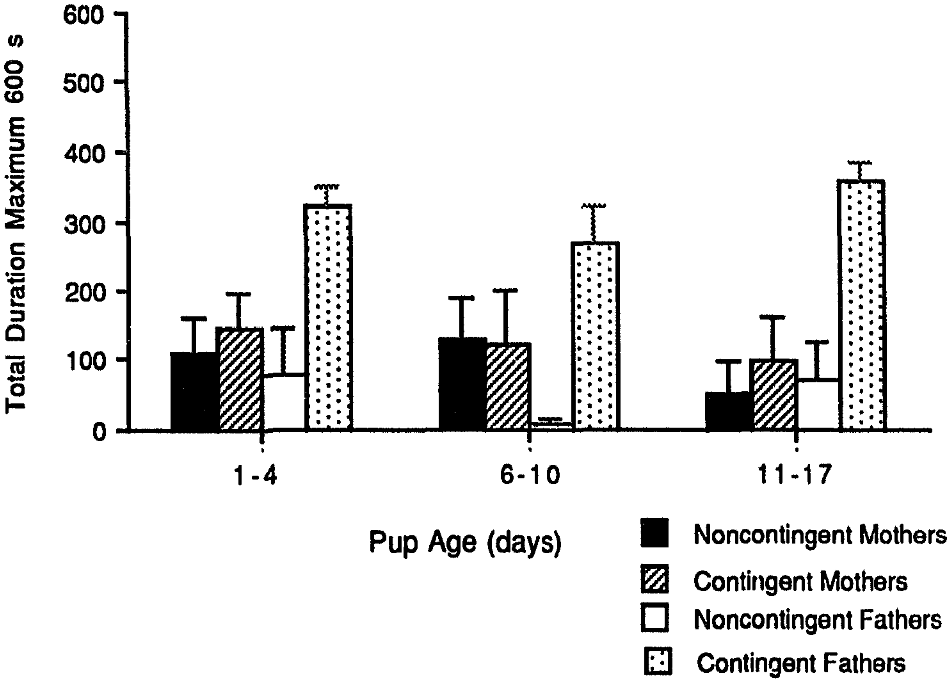


Figure 7.20. Peromyscus californicus: duration of wheel running from videoanalysis during the dark phase



days ($F_{(2,24)}<1.0$) on the amount of time mothers and fathers spent wheel running and there were no significant interactions between days and gender ($F_{(2,24)}=1.5$), days and housing ($F_{(2,24)}<1.0$) nor between days, gender and housing ($F_{(2,24)}<1.0$).

Summary of Part Five. Mothers and fathers did not differ in the amount of time they spent in the nest, however, mothers and fathers in the Wheel Noncontingent condition spent more time in the nest than those in the Wheel Contingent condition. Fathers spent more time wheel running than mothers and those in the Wheel Contingent condition spent more time running than those in the Wheel Noncontingent condition. In addition, fathers in the Wheel Contingent condition spent more time wheel running than mothers, while in the Wheel Noncontingent condition, there was no difference between mothers and fathers in the amount of time spent wheel running.

Part Six: Amount of food consumed versus food earned and behavioral observations of eating behavior

7.12 Amount of food consumed (Figure 7.21)

The amount of food consumed in each group was determined by subtracting the number of grams of uneaten food left in the cage after each 24 hour period from the number of grams of food earned or placed *ad lib* in the cage. The amount of food eaten was averaged every 5 days, from 20 days before birth to 20 days after birth resulting in the same 9 blocks of time used for the number of revolutions run in the wheel.

The data were partitioned into two sets, blocks 1 to 3 (days 1 to 15 before parturition) and blocks 4 to 9 (day 6 before parturition to weaning). This was done because the only difference between groups for the first 15 days was housing. Both Father Absent and Father Present groups had two *Peromyscus* per cage (a mother and a father). Males were removed from the Father Absent groups one to three days before parturition (block 4). The data were analyzed by a 2 (parenting) by 3 (housing condition) by 3 (blocks of time) ANOVA for the first 15 days before parturition. After 5 days before parturition (block 4) the data were analyzed by a 3 (housing) by 6 (blocks of time) ANOVA separately for Father Absent and Father Present groups.

a. Blocks 1 to 3 (father present in all groups, Figure 7.21)

There was no significant effect of parenting on the amount of food consumed by *P. californicus* ($F_{(1,67)}<1.0$) as both groups consumed similar amounts of food. *P. californicus* in the No Wheel condition consumed significantly less food than those in the Wheel Contingent condition ($F_{(2,67)}=4.4$, $p<.05$). Post hoc comparisons (Tukey's HSD) indicated a significant difference between the Wheel Contingent and the No Wheel conditions ($p<.01$). There were no significant differences in the amount of food consumed between the No Wheel and Wheel Noncontingent condition nor between the Wheel Noncontingent and Wheel Contingent condition. There also was no significant interaction between parenting and housing ($F_{(2,67)}=1.2$) on the amount of food consumed.

The amount of food consumed remained constant over days ($F_{(2,134)}=1.1$) but there was a significant interaction between days and housing ($F_{(4,134)}=2.6$, $p<.05$). *Peromyscus* in the No Wheel condition consumed a similar amount of food for blocks 1 and 2 and then increased the amount of food they consumed; *Peromyscus* in the Wheel Noncontingent condition increased the amount of food they consumed between blocks 1 and 2 and those in the Wheel Contingent condition decreased the amount of food they consumed over the first 3 blocks. There also was a significant interaction between days and parenting as *Peromyscus* in the Father Absent group decreased the amount of food they consumed in block 3 whereas those in the Father Present group increased the amount of food consumed over the first 3 blocks ($F_{(2,134)}=4.9$, $p<.01$). Finally, there was a significant interaction between days, housing and parenting ($F_{(4,134)}=2.6$, $p<.05$) and like the other interactions there does not appear to be a systematic pattern to the differences in the amount of food consumed. *Peromyscus* in the Father Absent No Wheel condition increased the amount of food they consumed over the first 3 blocks while those in the Father Present No Wheel condition decreased the amount of food consumed after the first block then increased the amount of food consumed (block 3). *Peromyscus* in the Father Absent Wheel Noncontingent condition increased the amount of food consumed in block 2 then decreased the amount of food consumed in block 3 while those in the Father Present Wheel Noncontingent condition increased the amount of food consumed over the first 3 blocks of days. *Peromyscus* in the Father Absent Contingent group decreased the amount of food they consumed over the first 3 blocks while those in the the Father Present Wheel Contingent condition consumed the same amount of food over the first 3 blocks.

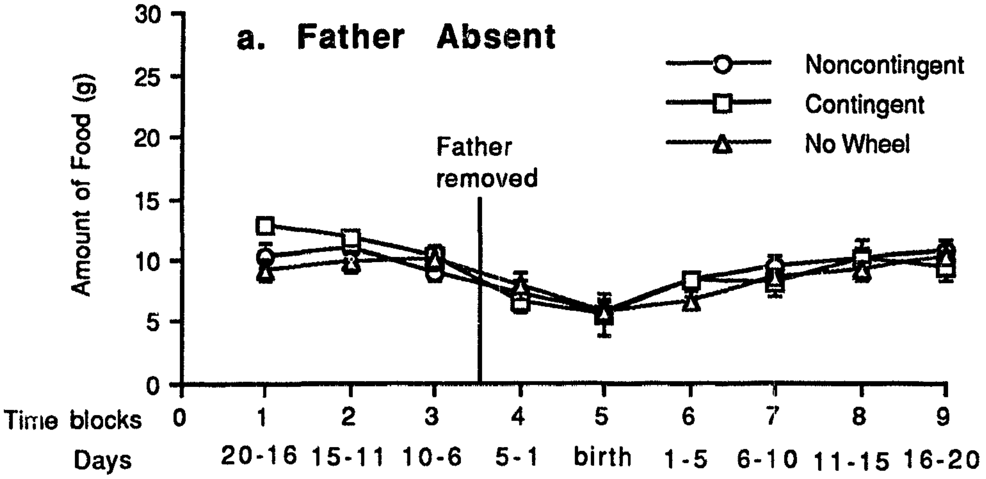
b. Blocks 4 to 9: Father Absent group (Figure 7.21a)

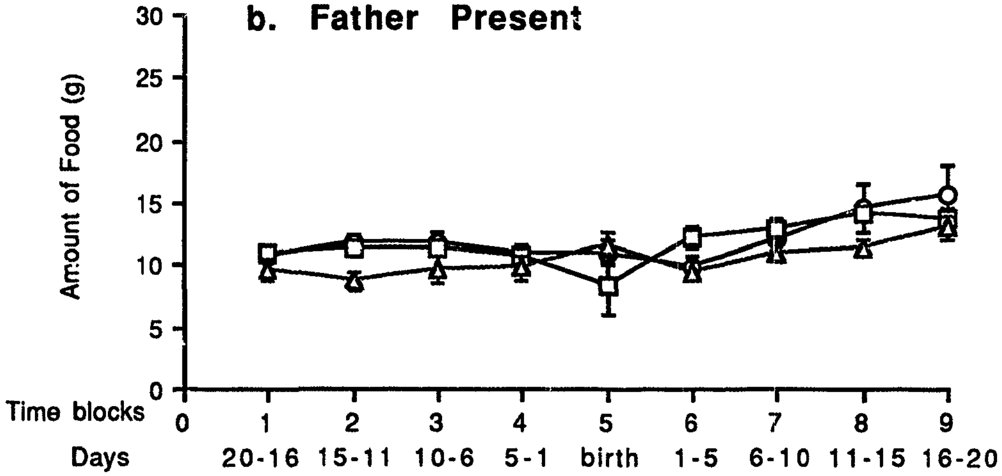
There was no significant effect of housing conditions on the amount of food consumed ($F_{(2,20)}<1.0$) but there was a significant effect of days on the amount of food consumed ($F_{(5,100)}=17.6$, $p<.001$). *Peromyscus* decreased the amount of food consumed on the day of parturition (block 5) and then gradually increased the amount of food consumed. There was no significant interaction between days and housing ($F_{(10,100)}<1.0$).

c. Blocks 4 to 9: Father Present group (Figure 7.21b)

Mothers and fathers consumed the same amount of food in all three housing conditions ($F_{(2,22)}<1.0$) but they significantly increased the amount of food they consumed over days ($F_{(5,110)}=11.2$, $p<.001$). There was also a significant interaction between days and housing ($F_{(10,110)}=2.4$, $p<.05$). *Peromyscus* in the No Wheel condition increased the amount of food consumed on block 5, decreased the amount of food consumed for block 6, then gradually increased the amount of food consumed (blocks 7 to 9). *Peromyscus* in the Wheel Noncontingent condition decreased the amount of food consumed for block 6, then gradually increased the amount of food for the remaining days (block 7 to 9). *Peromyscus* in the Wheel Contingent condition decreased the amount of food consumed for block 5, then gradually increased the amount of food consumed (blocks 6 to 9).

Figure 7.21. Peromyscus californicus: Amount of food consumed





7.13 Amount of food earned versus amount of food consumed in the Wheel Noncontingent and Contingent groups (Figure 7.22)

The amount of food that *Peromyscus* earned versus the amount they consumed was compared for the Wheel Contingent and Wheel Noncontingent conditions over the 9 blocks of days. The amount of food consumed was measured as described in section 7.12, while the amount of food earned was calculated by recording the number of revolutions run each day and dividing by the number of revolutions per pellet (300 before parturition, 250 after parturition) and multiplying by 0.19 g per pellet. Thus a mouse which ran 20,000 revolutions per day before birth would earn 20,000/300 x 0.19 g= 12.7 g of food. A mouse which ran 20,000 per day after birth of the pups would earn 20,000/250 x 0.19 g = 15.2 g of food. The mouse could consume all or some of this food within a 24 hour period.

The analysis is the same as described in section 7.12 except that the No Wheel condition was not included. Both the Father Absent and Father Present groups were analyzed together by one ANOVA for the first 15 days after mating (blocks 1 to 3), and separate ANOVAs were conducted for the Father Absent and Father Present groups from day 5 before birth to weaning (blocks 4 to 9).

a. Blocks 1 to 3 (father present in all groups)

a.1 Amount of food earned (Figure 7.22)

Mothers and fathers in the Wheel Contingent condition earned significantly more food than mothers and fathers in the Wheel Noncontingent condition ($F_{(1,45)}=5.8$, $p<.05$). There was no significant difference between the Father Absent and Father Present groups

($F_{(1,45)}=2.7$,) as *Peromyscus* in both groups earned similar amounts of food for the first 3 blocks. There also was no significant interaction between parenting and housing ($F_{(1,45)}<1.0$). There was, however, a significant effect of days as *Peromyscus* in all groups decreased the amount of food they earned over the first 3 blocks ($F_{(2,90)}=20.6$, $p<.01$). There was a significant interaction between days and parenting ($F_{(2,90)}=8.1$, $p<.001$) as mothers and fathers in the Father Absent group decreased the amount of food they earned over days while those in the Father Present group earned a similar amount of food over days. There were no other significant interactions.

a.2 Amount of food consumed (Figure 7.22)

There was no significant difference between the Father Absent and Father Present groups ($F_{(1,45)}=1.1$) nor between the Wheel Noncontingent and Wheel Contingent conditions ($F_{(1,45)}=1.2$) in the amount of food consumed. There was also no significant interaction between housing and parenting ($F_{(1,45)}=2.2$). There was, however, a significant effect of days as mothers and fathers decreased the amount of food they consumed over the first 3 blocks ($F_{(2,90)}=3.5$, $p<.05$). There was also a significant interaction between days and parenting as those in the Father Absent group decreased the amount of food they consumed after block 2 whereas those in the Father Present group increased the amount of food they consumed after the first block ($F_{(2,90)}=7.9$, $p<.001$). There were no other significant interactions.

a.3 Comparison of food earned and consumed (Table 7.11)

A direct comparison of the amount of food earned and consumed was achieved by subtracting the amount of food consumed from the amount of food earned (Table 7.11). Negative scores in the Wheel Noncontingent condition indicated that mice consumed more than they would have earned by running. These difference scores were analyzed by a 2 (parenting) by 2 (housing) by 3 (blocks of time) ANOVA.

Mothers and fathers in both the Father Present and Father Absent groups earned more food than they consumed. Mice in the Father Absent group, however, earned significantly more food than they consumed compared to those in the Father Present group ($F_{(1,45)}=4.1$, $p<.05$). There was no significant effect of housing conditions on the amount of food earned and consumed ($F_{(1,45)}=3.0$) nor was there a significant interaction between parenting and housing ($F_{(1,45)}<1.0$).

Mothers and fathers significantly decreased the amount of food earned and increased the amount of food consumed over the first 3 blocks ($F_{(2,90)}=11.6$, $p<.001$). There was also a significant interaction between days and housing ($F_{(2,90)}=3.0$, $p=.05$). After block 2, *Peromyscus* in the Wheel Noncontingent condition consumed more food than they earned, while those in the Wheel Contingent condition continued to earn more food than they consumed for the first 3 blocks. There was no significant interaction between days and parenting ($F_{(2,90)}<1.0$) nor between days, parenting and housing ($F_{(2,90)}<1.0$).

b. Blocks 4 to 9: Father Absent group (Figure 7.22)

b.1 Amount of food earned

There was a marginally significant difference between the Wheel Noncontingent and Wheel Contingent conditions ($F_{(1,12)}=4.5$, $p=.06$) as mothers in the Wheel Contingent condition earned more food than mothers in the Wheel Noncontingent condition. There was no significant effect of days on the amount of food mothers earned ($F_{(5,60)}=1.6$) nor a significant interaction between days and housing ($F_{(5,60)}<1.0$).

b.2. Amount of food consumed

Mothers in both the Wheel Contingent and Wheel Noncontingent conditions consumed similar amounts of food ($F_{(1,12)}<1.0$). There was a significant effect of days on the amount of food consumed ($F_{(5,60)}=10.7$, $p<.01$) as mothers gradually increased the amount of food they consumed. There was no significant interaction between days and housing ($F_{(5,60)}<1.0$).

b.3 Direct comparison of food earned and consumed (Table 7.11)

A direct comparison of the amount of food earned and consumed was achieved by subtracting the amount of food consumed from the amount of food earned (Table 7.11). Negative scores in the Wheel Noncontingent condition indicated that mice consumed more than they would have earned by running. These difference scores were analyzed by a 2 (parenting) by 2 (housing) by 3 (blocks of time) ANOVA.

Figure 7.22. Peromyscus californicus: Amount of food consumed and earned in Wheel Noncontingent and Wheel Contingent conditions when a) father is absent and b) father is present

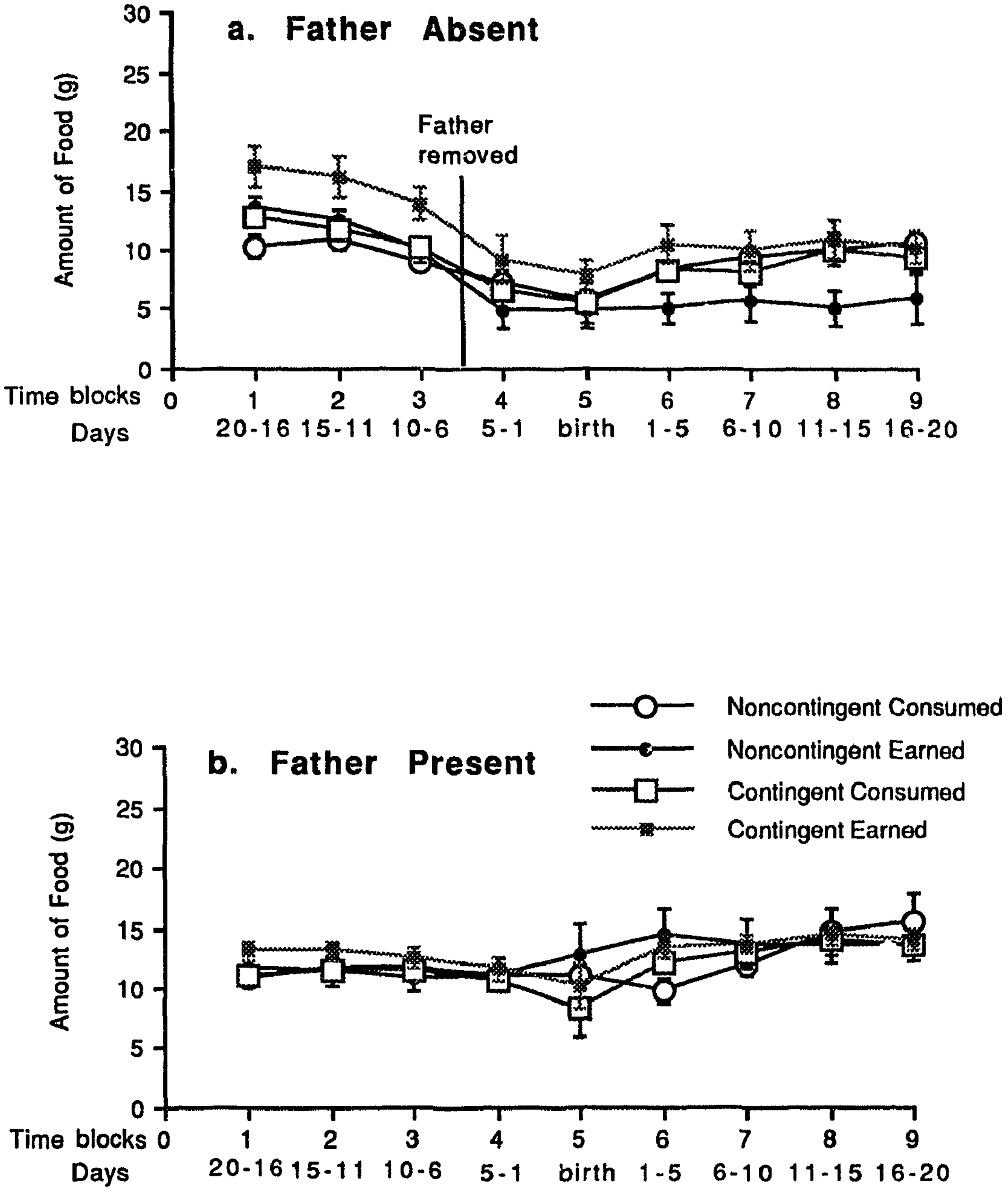


Table 7.11. Mean difference scores (±SEM) for the amount of food consumed vs. earned for *P. californicus*.

a) Father Absent

	Blocks 1-3	Blocks 4-9
Wheel Noncontingent	2.0 ± 1.3	-3.3 ± 1.9
Wheel Contingent	4.2 ± 1.5	1.8 ± 1.4

b) Father Present

	Blocks 1-3	Blocks 4-9
Wheel Noncontingent	-0.2 ± 1.3	0.6 ± 2.6
Wheel Contingent	1.6 ± 0.5	0.4 ± 0.9

There was a marginally significant difference between the Wheel Noncontingent and Contingent groups ($F_{(1,12)}=4.2$, $p=.06$) as mothers in the Wheel Noncontingent condition consumed more food than they earned and mothers in the Wheel Contingent condition earned more food than they consumed. There was a significant effect of days as *Peromyscus* increased the amount of food they consumed and decreased the amount of food they earned as weaning approached ($F_{(5,60)}=6.3$, $p<.001$). There was no significant interaction between days and housing ($F_{(5,60)}=1.1$).

c. Blocks 4 to 9: Father Present group (Figure 7.22b)

c.1 Amount of food earned:

There was no significant difference between the Wheel Noncontingent and Wheel Contingent conditions in the amount of food mothers and fathers earned ($F_{(1,13)}<1.0$). Mothers and fathers significantly increased the amount of food they earned up to block 9 ($F_{(5,65)}=3.9$, $p<.01$). There was no significant interaction between days and housing ($F_{(5,65)}<1.0$).

c.2 Amount of food consumed

There was no significant difference between the Wheel Noncontingent and Wheel Contingent condition in the amount of food that was consumed by mothers and fathers ($F_{(1,13)}<1.0$). There was, however, a significant effect of days on the amount of food consumed ($F_{(5,65)}=8.3$, $p<.01$) as mothers and fathers decreased the amount of food they consumed on the day of parturition (block 5) then gradually increased the amount of food they consumed up to block 9. There was no significant interaction between days and housing ($F_{(5,65)}=1.7$).

c.3 Direct comparison of food earned and consumed (Table 7.11)

There was no significant difference between the Wheel Noncontingent and Wheel Contingent conditions in the amount of food they earned and consumed ($F_{(1,13)}<1.0$) but there was a significant effect of days ($F_{(5,65)}=3.3$, $p<.05$) on the amount of food earned and consumed. Mothers and fathers earned more food than they consumed for blocks 5 to 7, then earned less food than they consumed for the remaining days (blocks 8 and 9). There was no significant interaction between days and housing ($F_{(5,65)}=1.7$).

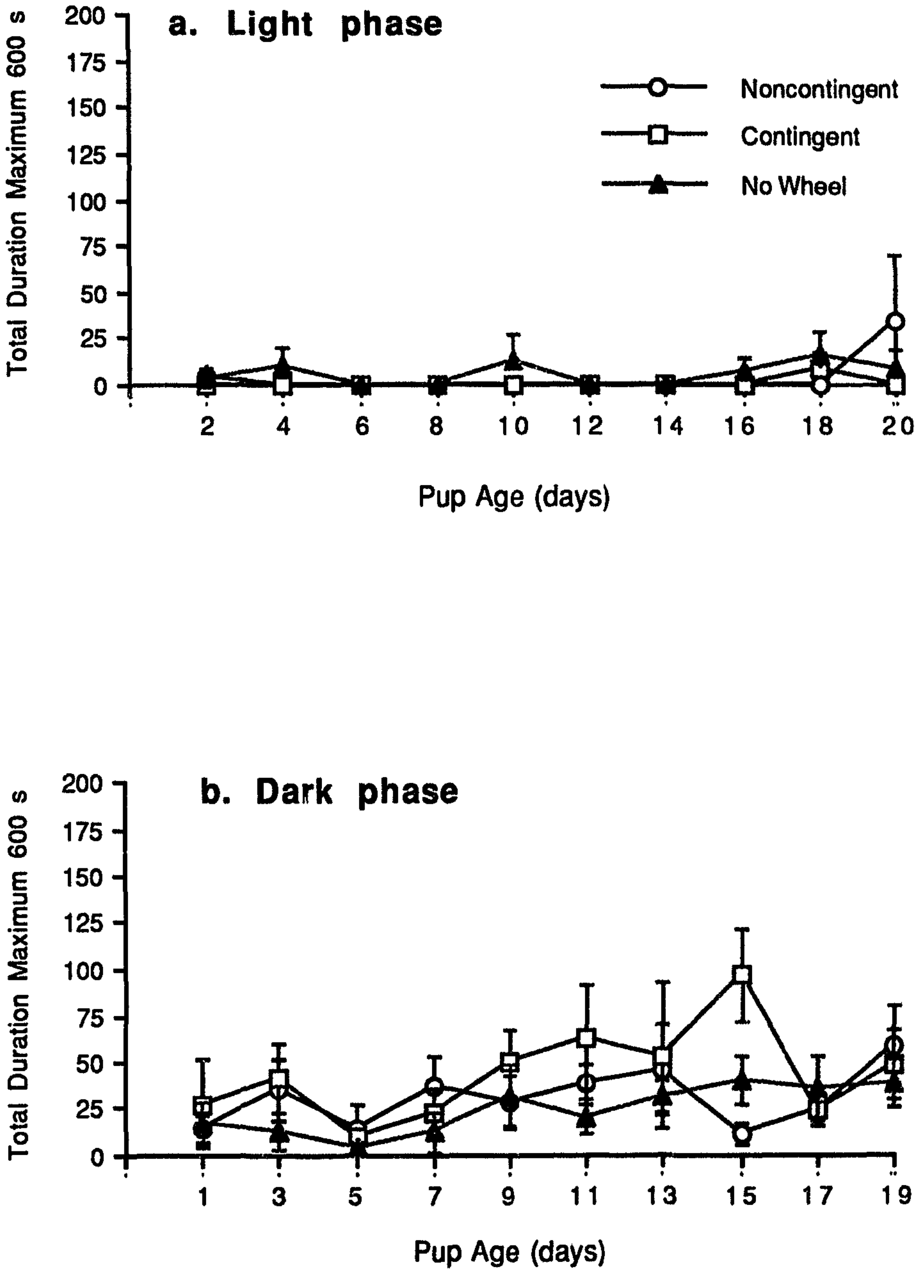
7.14 Observations of eating behavior

In order to determine who was eating the food generated, we analyzed the behavioral observations separately from other nonparental behaviors. Unless otherwise indicated, eating behavior was analyzed by 3 (housing) by 2 (LD cycle) by 10 (days) ANOVAs. Interactions that were not significant were not reported.

7.14.1 Eating behavior of mothers in the Father Absent groups (Figure 7.23)

Mothers spent the same amount of time eating in all housing conditions ($F_{(2,20)}<1.0$). There was a significant effect of the LD cycle on eating behavior ($F_{(1,20)}=44.1$, $p<.001$) as mothers spent more time eating during the dark phase than during the light phase. Mothers

Figure 7.23. Peromyscus californicus: Duration of eating behavior of mothers in the Father Absent groups



spent less time eating ($F_{(9,180)}$=2.8, p<.01) from blocks 5 to 6, then gradually increased the amount of time spent eating as pups aged.

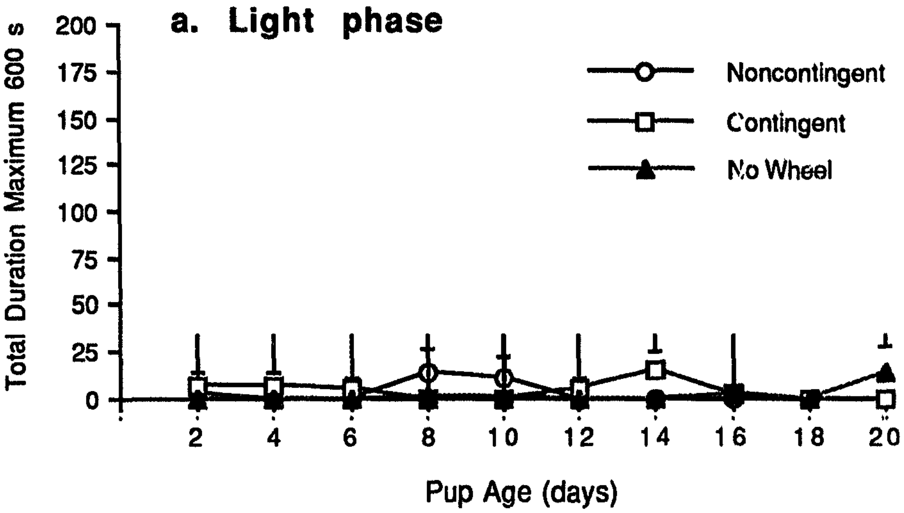
7.14.2 Eating behavior of mothers in the Father Present groups (Figure 7.24)

Mothers in the Wheel Contingent and Wheel Noncontingent condition were observed to spend significantly more time eating than mothers in the No Wheel condition ($F_{(2,22)}$=10.4, p<.001). Mothers spent significantly more time eating during the dark phase of the LD cycle ($F_{(1,22)}$=84, p<.001). There also was a significant interaction between the LD cycle and housing ($F_{(2,22)}$=9.9, p<.01) as mothers in the Wheel Noncontingent condition spent less time eating during the light phase than mothers in the Wheel Contingent condition. However, during the dark phase mothers in the Wheel Noncontingent condition spent more time eating than mothers in the Wheel Contingent condition. There was no significant effect of days on the amount of time mothers were observed to spend eating ($F_{(9,198)}$=1.4).

7.14.3 A comparison of eating behavior of mothers in the Father Absent and Father Present groups (Figure 7.25)

There was a significant effect of housing ($F_{(2,42)}$=5.3, p<.01) on the amount of time mothers spent eating as mothers in the No Wheel condition spent the least amount of time eating. Mothers in both the Father Absent and Father Present groups spent similar amounts of time eating ($F_{(1,42)}$<1.0). There was a significant effect of the LD cycle on the amount of time mothers spent eating ($F_{(1,42)}$=117.5), p<.001) and a significant interaction between the LD cycle and housing ($F_{(2,42)}$=8.0, p<.01). Mothers in the

Figure 7.24. Peromyscus californicus: Duration of eating behavior of mothers in the Father Present group



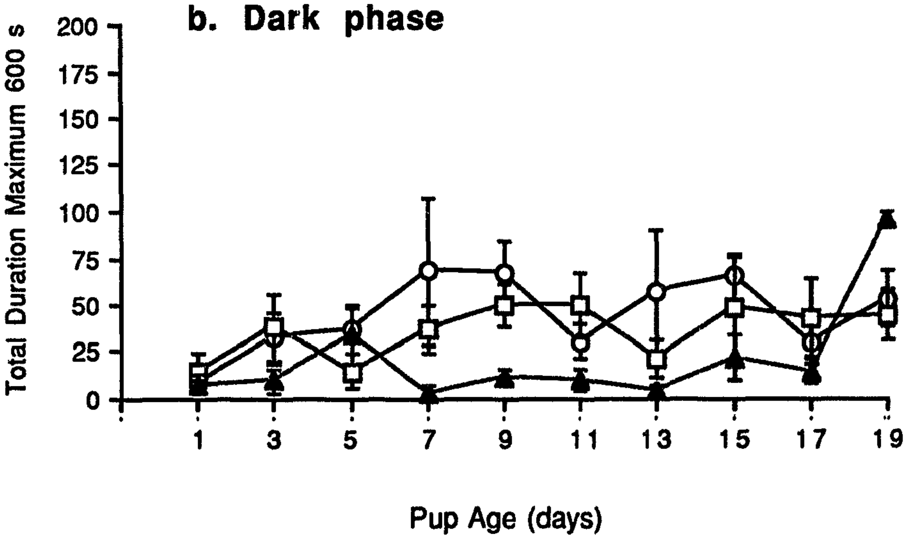
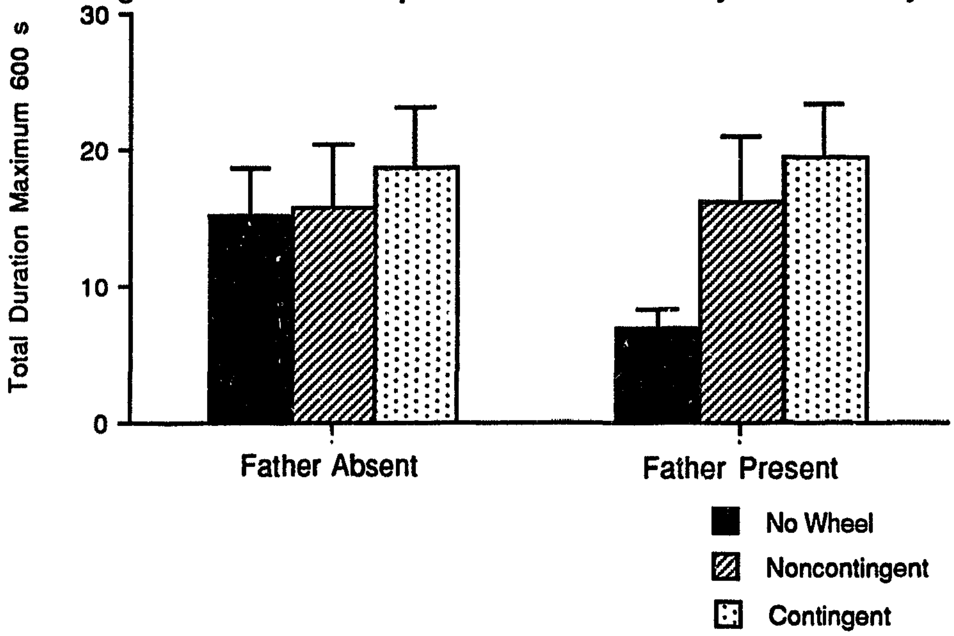


Figure 7.25. Peromyscus californicus: Duration of eating behavior of mothers in the Father Absent and Father Present groups for all housing conditions collapsed over the LD cycle and days



Wheel Contingent and Noncontingent conditions spent more time eating during the dark phase and less time eating during the light phase than mothers in the No Wheel condition.

Mothers spent the least amount of time eating the day after the birth of the pups and gradually increased the amount of time they were observed eating as pups aged ($F_{(9,378)}=3.2$, $p<.01$). There was a significant interaction between the LD cycle and days ($F_{(9,378)}=2.1$, $p<.05$) since during the light phase, mothers spent the most time eating during block 6 and block 9, whereas during the dark phase, mothers gradually increased the amount of time they spent eating as pups aged.

7.14.4 Eating behavior of fathers in the Father Present groups (Figure 7.26)

Fathers spent the same amount of time eating in all housing conditions ($F_{(2,22)}<1.0$). There was a significant effect of the LD cycle ($F_{(1,22)}=21.4$, $p<.001$) on the amount of time fathers spent eating but no significant effect of days ($F_{(9,198)}=1.1$).

7.14.5 A comparison of eating behavior of mothers and fathers in the Father Present groups (Figure 7.27)

There was a significant effect of housing ($F_{(2,44)}=5.0$, $p<.01$) as mothers and fathers in the No Wheel condition were observed eating for the least amount of time. There was also a significant interaction between gender and housing ($F_{(2,44)}=3.6$, $p<.05$) as fathers in the Wheel Noncontingent and Contingent conditions spent less time eating than mothers whereas mothers and fathers spent the same amount of time eating in the No Wheel condition.

Figure 7.26. Peromyscus californicus: Duration of eating behavior of fathers in the Father Present groups

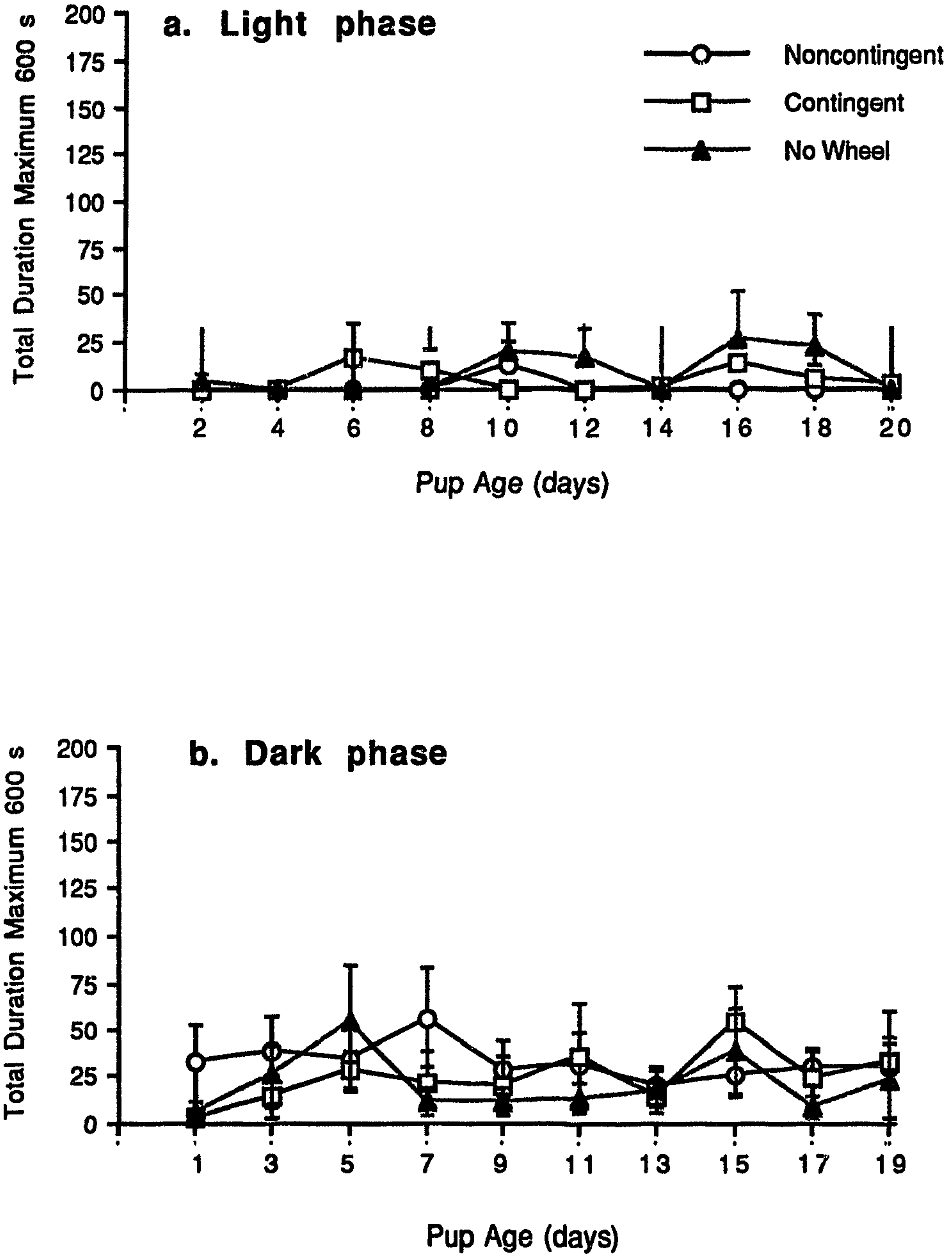
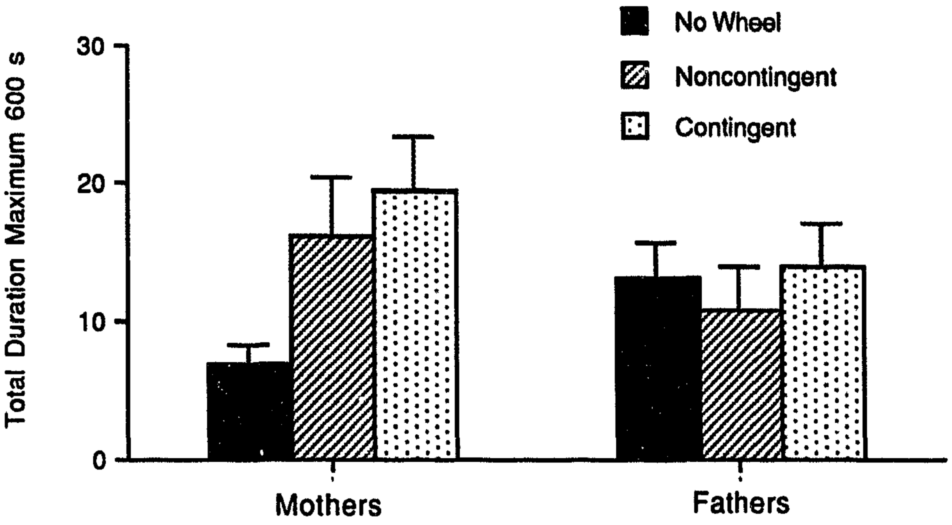


Figure 7.27. Peromyscus californicus: Duration of eating behavior of mothers and fathers in the Father Present group for all housing conditions collapsed over the LD cycle and days



Mothers and fathers were both observed eating for similar amounts of time ($F_{(1,44)}<1.0$).

There was a significant effect of the LD cycle ($F_{(1,44)}=80.4$, $p<.001$) on the amount of time mothers and fathers spent eating and a significant interaction between the LD cycle and housing ($F_{(2,44)}=7.7$, $p<.01$). During the light phase, mothers and fathers in the No Wheel condition spent more time eating than those in the Wheel Contingent and Noncontingent conditions while during the dark phase, those in the Wheel Noncontingent and Contingent conditions spent more time eating than than mothers and fathers in the No Wheel condition. There was a significant effect of days ($F_{(9,396)}=2.0$, $p<.05$) as *Peromyscus* increased the amount of time spent eating up to block 3, then decreased the amount of time spent eating.

Summary of Part Six. From days 1 to 15 before birth (blocks 1 to 3), mothers and fathers in the No Wheel condition consumed the least amount of food and those in the Wheel Contingent condition consumed the most. From blocks 4 to 9, mothers in the Father Absent group consumed the same amount of food in all housing conditions and mothers and fathers in the Father Present group consumed the same amount of food in all housing conditions. Mothers in Father Absent group consumed more food than they earned in the Wheel Noncontingent condition and earned more food than they consumed in the Wheel Contingent condition. Fathers and mothers in the Father Present group earned and consumed similar amounts of food in both the Wheel Contingent and Wheel Noncontingent conditions.

Mothers in the Father Absent and Father Present group were directly observed to spend the least amount of time eating in the No Wheel condition. Fathers in the Noncontingent and Contingent groups were directly observed to spend less time eating than mothers whereas mothers and fathers spent the same amount of time eating in the No Wheel condition.

Chapter 8

Discussion

This thesis examined the following six questions: 1) Do housing conditions influence the number of pups surviving to weaning and the weight of pups at weaning?, 2) Does the presence of the father influence the number of pups surviving to weaning and the weight of the pups at weaning?, 3) Does the father display the same type and amount of parental behavior as the mother?, 4) Do mothers and fathers differ in the time spent running on the wheel and eating the food pellets earned?, 5) Is there a difference in how the time spent in parental, wheel running and eating behavior was partitioned during the light and dark phases of the LD cycle depending on the housing conditions and presence or absence of the father? and 6) Are there species differences between *Mus musculus*, a polygynous species and *Peromyscus californicus*, a monogamous species in these behaviors. The results pertaining to the first five questions are presented for *Mus musculus* in section 8.1, *Peromyscus californicus* in section 8.2, and a comparison of the two species (question 6) in section 8.3. A general discussion of the issues raised (section 8.4), completes the chapter.

8.1 *Mus musculus* results

8.1.1 Do housing conditions influence pup survival and pup weight?

Fewer pups survived when mothers and fathers were required to run on a running wheel for food (Wheel Contingent condition) than when mothers and fathers were fed *ad libitum* (No Wheel and Wheel Noncontingent conditions). The survival of whole litters was not influenced by foraging conditions as *Mus* usually culled litters and rarely cannibalized whole litters. Perrigo (1987) also found that single *Mus* mothers challenged to run 175 to 275 revolutions per food pellet reduced their litter sizes by cannibalizing litters.

Pups were weaned at a significantly lighter weight when *Mus* were required to forage for food in my experiment. Perrigo (1987) however, did not find that *Mus* weaned lighter pups when challenged to run 175 to 275 revolutions per pellet. Once *Mus* reduced their litter size, pups were weaned around the same weight regardless of the work requirement. The discrepancy between my results and those of Perrigo (1987) could be due to *Mus* in my experiment weaning more pups. At higher work requirements (175 or 275 revolutions per food pellet), single female *Mus musculus* (CF-1) in Perrigo's (1987) experiment reduced pup numbers to 2-3 pups whereas in my experiment single female *Mus musculus* (CD-1) maintained litters of an average of 7 pups (range 0 to 12) and mothers and fathers maintained litters of an average of 9 pups (range 3-12). Konig (1989) found that wild *Mus* (*Mus musculus domesticus*) pups were weaned at a minimum weight of 9-10 g when

Mus mothers were underfed (20% less food than *ad lib* for the 22 days of lactation), but mothers also reduced the number of pups to an average of 2.7 per litter. Konig and Markl (1987) suggested that *Mus* mothers ensured that their pups were weaned at a minimum of 9 g by delaying or advancing the date of weaning. It was possible that *Mus* mothers in my study would have weaned pups at 9 g instead of 5 g if the experiment had not been terminated when pups were 21 days old (the experiment was terminated as pups interfered with wheel running). When mothers were returned to an *ad lib* diet after 21 days postpartum, informal observations revealed that they were still nursing some of their young. Pups were in the nest and the mother was in the nursing position. Some of the pups, however, also were observed eating solid food.

These results might indicate that *Mus* make a trade-off between offspring mass and litter size when their energy supplies are limited. In the greater white-toothed shrew, *Crocidura russula*, for example, larger mothers produced larger litters that resulted in smaller offspring at weaning (Genoud & Perrin, 1994). *Mus musculus* may have reduced litters to a size where as many pups as possible survived, but in doing so, weaning weight was sacrificed. If the **quality** of the pups was an important factor, why did mothers that were challenged to work for food not reduce their litter sizes more extensively? Konig et al. (1988) found that small size litters (6 pups) were weaned at heavier weights than intermediate size litters (8 pups) or large size litters (10 pups). In my experiment, mothers usually reduced large litters (11 to 12 pups) to intermediate size litters (8 pups)

The weaning weight of offspring has consequences for the reproductive success of those offspring. Larger males (*Mus*) are more likely to become dominant than smaller males and dominant males sire more offspring (Krackow, 1993, DeFries & McClearn, 1970, Singleton & Hay, 1983). In the laboratory, larger size in *Mus* females is associated with earlier maturity and larger first litters (Fuchs, 1981). In producing larger pups, however, the mother incurs the costs of longer lactation and longer delays between producing successive litters (Fuchs, 1981). If small pups are independent of the mother when they are 21 days of age, pups may be capable of finding food for themselves and increasing their own weight. The father could be instrumental in increasing pup weight gain by keeping them warm, allowing offspring to remain on his territory and use its resources, and defending the territory from intruders that could harm small offspring. Then offspring could delay sexual maturity and would have the potential to reproduce later. This would allow the mother and father to have some reproductive success with the current litter, and allow the mother to invest in subsequent litters. Thus in a harsh environment where the necessary resources for successful reproduction are scarce, mothers must develop a strategy of investing in more, but smaller pups or fewer larger pups. The presence of the father may allow for more larger pups to survive.

8.1.2 Does the presence of the father influence pup survival and pup weight?

The fathers' presence increased pup survival but only when *Mus* were required to run on the running wheel for food (Wheel Contingent groups). This is the first time that it has been shown that male *Mus* increase pup survival when they must forage for food. Most other studies have been conducted under standard laboratory conditions but have investigated the father's contribution to pup survival in a cold environment (Barnett & Dickson, 1985). Pup survival has been shown to be inversely related to the number of adult males in a population. Aggression due to the establishment and maintenance of territories among male *Mus* has been associated with high mortality among neonates (DeLong, 1978, Lloyd, 1975, Hurst, 1987, Crowcroft & Rowe, 1963, Southwick, 1955). Neonate survival is positively correlated with male social dominance; the higher a male is in the social hierarchy, the more likely his pups will survive (DeLong, 1978). My results may have been an artifact of two litters not surviving to weaning in the Father Absent Wheel Contingent group.

Like wild *Mus musculus*, Siberian hamsters have a social organization that suggests polygyny as males form dominance hierarchies (Wynne-Edwards & Lisk, 1989). Litter survival was not influenced in the Siberian hamster when the father was removed or when the ambient temperature was lowered. Since my experiment housed one female and one male together, aggression among males and females due to territory maintenance and establishing dominance relationships was absent. In a group housing system with many male and female mice, male-male aggression may be a factor.

Priestnall and Young (1977) also found that the fathers' presence had no effect on weight gain in *Mus* pups, even though fathers displayed parental behavior when housed with a lactating female and provided additional tactile and thermal stimulation. The fathers' presence also had no influence on pup weight in the polygynous Siberian hamster (Wynne-Edwards, 1989). However, Barnett and Dickson (1985) found that females mated to males that had been raised in a cold environment, weaned more pups than females mated to males raised in a warm environment, when they were challenged to breed under cold conditions. Thus, if males had prior experience with the running wheel environment, such as being born in a running wheel cage or having had several litters within a running wheel cage, they may have facilitated pup development more.

It is surprising that the fathers' presence did not influence pup weight. Larger pups would indirectly increase his fitness, since larger male pups have a competitive advantage when obtaining mates and heavier females reach sexual maturity earlier and have larger first litters (Krackow, 1993). The father may be incapable of directly influencing offspring growth as pups are dependent on the mother's ability to convert food into milk. Thus, males could have only an indirect effect on pup growth by providing the mothers with extra food.

Communal nesting may have more of an impact on pup weight as pups are likely to be fed more often by several females (Sayler &

Salmon, 1969). However, the fathers' presence could indirectly influence pup weaning weight if pups that had their fathers present were weaned sooner at the suggested minimum weight of 9 g than pups with the father absent (Konig, 1993). Early weaning might allow offspring to be accepted into neighboring territories or establish their own territory before the population density increased and subsequently increased competition for territories. There is some evidence that litters weaned earlier have more opportunities to disperse than litters weaned later when a colony of mice is being established (Lidicker, 1976). In addition, the father might be capable of influencing the weight of pups that were weaned below the suggested minimum weight by providing a protected area, free of competitors and aggressive encounters with conspecifics' offspring. In several bird species, males defend their brood more than females defend their brood (Regelmann & Curio, 1986). My experiment did not investigate these possiblities as the experiment was terminated before some mice had weaned their pups.

Another possible strategy to increase a parent's lifetime reproductive success would be to bias the sex ratio of surviving pups toward males or females in the Wheel Contingent condition (Trivers, 1971). Male reproductive development proceeds normally when mice are required to run a high number of revolutions per pellet whereas female reproductive development is delayed (Pryor & Bronson, 1981). Therefore, one might expect to have significantly more males than females in the Wheel Contingent groups. Alternatively, in a polygynous species, males must compete for access to females and larger males win dominance battles so smaller males might have little opportunity to breed. Even though females would experience a delay in reproductive maturity, most females would eventually mate and breed (Trivers & Willard, 1973). Therefore, one might expect a significant bias in the sex ratio at weaning, but this was not observed in my experiment.

8.1.3 Do mothers and fathers exhibit the same type and amount of parental behavior?

Mus musculus fathers engaged in the same parental behaviors as mothers (except lactation) and spent the same amount of time engaged in parental behavior as mothers. Pups that were housed with both parents, therefore, received more parental care than pups with only a mother. The extra parental care corresponded with increased pup survival but only if mice had to run on a wheel to obtain food. Several studies where mice were housed in mated pairs in standard laboratory cages indicated that domestic *Mus musculus* males provide the same amount and type of parental care as females (Priestnall & Young, 1978, Jakubowski & Terkel, 1982, Wuensch & Cooper, 1981, Elwood & Ostermeyer, 1983, Barnett & Dickson, 1985). Others studies indicate that although *Mus musculus* fathers engage in parental behavior when housed in pairs, they are not parental when housed in larger groups of male and female adult mice (Priestnall & Young, 1978, DeLong, 1978, Lloyd, 1975, Hurst, 1987, Crowcroft & Rowe, 1963, Southwick, 1955).

The amount of time mothers spent in parental behavior was not influenced by the father as mothers spent the same amount of time in parental behavior whether the father was absent or present.

The amount of time mothers and fathers spent in parental behavior was influenced by the housing conditions. When mothers had to run on a wheel to obtain food (Wheel Contingent condition), they spent significantly less time in parental behavior than mothers fed *ad libitum* (with or without a running wheel). Fathers in the Wheel Contingent condition spent less time in parental behaviour during the dark phase than fathers from the other two conditions. Videoanalysis also confirmed that mothers and fathers spent the same amount of time in the nest and parents in the Wheel Contingent condition spent less time in the nest than parents in the Wheel Noncontingent condition between days 6 to 10 postpartum. Thus, wheel running to obtain food, interfered with caring for pups in both the Father Absent and Father Present groups.

8.1.4 Do mothers and fathers differ in the time spent running on the wheel and eating the food pellets earned?

Fathers spent more time spent running on the wheel and less time eating than mothers. Fathers may help mothers indirectly by running more on the wheel for food (foraging longer) and/or allowing mothers to spend more time eating the food obtained. Single mothers (Father Absent) and paired mothers (Father Present) ran on the wheel for the same amount of time, so the father did not influence the amount of time mothers spent wheel running. Housing conditions influenced the amount of time mothers spent wheel running as those in the Wheel Contingent condition ran for longer periods of time than those in the Wheel Noncontingent condition. Mothers and fathers in the Wheel Contingent condition spent the same amount of time wheel running, which was more than mothers and fathers in the Wheel Noncontingent conditions. Fathers in the Wheel Noncontingent group spent less time running on the wheel than mothers and fathers in the Wheel Contingent group but spent more time running than mothers (their mates) in the Wheel Noncontingent group. Videoanalysis indicated that fathers in both the Wheel Noncontingent and Wheel Contingent groups spent more time running on the wheel than mothers between days 1 to 4 and days 6 to 10 postpartum when pups were most vulnerable to cannibalism. Between days 13 to 17 postpartum, the fathers' contribution to wheel running decreased and the mothers' increased.

Single and paired mothers were observed eating for the same amounts of time, so the fathers' presence did not influence the amount of time mothers spent eating nor did housing conditions influence the amount of time mothers were observed eating. When fathers and mothers were housed together, fathers were observed eating for less time than mothers. Mothers also increased the amount of time spent eating up to 12 days postpartum, which coincides with the fathers' increased amount of time spent wheel running and generating food and the mothers' decreased contribution to obtaining food. Therefore, when male *Mus* are housed in monogamous pairs in the lab, fathers could indirectly contribute to pup survival by running on the wheel longer to obtain food and allowing mothers to eat the food for longer periods of time.

8.1.5 Do *Mus musculus* differ in how they partition their wheel running time and parental care time during the light and dark phases of the LD cycle and as pups age?

The LD cycle influenced how mice partitioned their time and there was a sex difference in the pattern of time spent in parental behavior. Mothers and fathers spend equal amounts of time engaged in parental behavior during the light phase, but mothers engaged in more parental behavior than fathers during the dark phase. This difference in the distribution of parental behavior probably did not indicate that mothers and fathers were taking turns keeping pups warm since mothers in the Father Absent and Father Present groups did not differ in the amount of time they spent caring for pups. All mothers spent significantly more time in parental behavior during the light phase of the LD cycle, but spent a smaller amount of time in parental behavior during the dark phase. The benefit of the fathers' presence could be a reduced metabolic rate and reduced energy consumption as mice that were paired together have lower metabolic rates than single mice (Herried & Schlenker, 1980). Myrcha (1975) also found that the energy budget of mice living in groups was more economical than mice living alone. Mice living in groups expend less energy in metabolic processes and then can afford to consume less food (Myrcha, 1975).

Mus musculus in the three housing conditions differ in how they partitioned their wheel running time during the LD cycle. Mothers in the Father Absent Wheel Contingent group met the increased demands of lactation by increasing the time spent wheel running during the dark phase while mothers in the Father Present Wheel Contingent group met the increased demands by increasing the time spent wheel running during the light phase. Fathers contributed by spending more time running during the dark phase. Thus, mice increased the number of revolutions they run and the amount of food generated as mothers spent more time after parturtion wheel running during the light phase and fathers spent more time wheel running during the dark phase. Perrigo (1987) also found that single *Mus* females moved some of their activity to the light phase. Although mothers in the Father Present group must share food with the father, mothers probably saved energy as behavioral observations indicated that fathers ran for longer periods of time.

Mothers in the Wheel Contingent group gradually increased the amount of time spent wheel running and mothers in the Wheel Noncontingent group reduced the amount of time spent wheel running during the light phase as pups aged. This response was adaptive, since *Mus* should reduce their wheel running and spend more time caring for pups when food is readily available. They also should increase their wheel running, to the point of foraging in the light phase and spend less time caring for pups when food is scarce. Mothers' food requirements were increasing and they spent more time eating as pups aged and consumed more food. Fathers did not vary the number of revolutions they ran over days, as fathers in the Wheel Noncontingent group ran fewer revolutions than fathers in the Wheel Contingent group throughout.

Another response to increased foraging demands as pups aged was a decrease in recreational wheel running. From day 20 to day 5 before parturition, mothers and fathers in the Wheel Noncontingent condition consumed more food than they could potentially earn, and those in the Wheel Contingent condition earned more food than they consumed. Perrigo and Bronson (1985) found that females were responsible for running extra revolutions beyond what was needed for food when the foraging requirement was modest and these extra "recreational" revolutions disappeared as foraging requirements increased. After parturition, mothers in the Father Absent group, and mothers and fathers in the Father Present group increased the amount of food they consumed and decreased the amount of food they could potentialy earn in the Wheel Noncontingent condition, while those in the Wheel Contingent group consumed all the food they earned. Therefore, mice responded to the different foraging conditions, by foraging less and eating more if food was abundant and foraging more and eating less if food was scarce.

Father Absent mothers (in all housing conditions) did not decrease the amount of time spent engaged in parental behavior as pups aged. However, the pattern of the mothers' parental behavior in the Father Present groups did change as pups aged and this was influenced by the fathers' presence and housing conditions. Mothers in the Wheel Contingent condition reduced the time spent in parental behavior as pups aged, while fathers in the Wheel Contingent condition increased the amount of time spent in parental behavior as pups aged.

The fathers' increased contribution to pup rearing as pups aged would allow the mother more time to work for food or consume food already generated by the father. The energy needed for lactation increased as pups age and mothers consumed more food as pups approached weaning (Myrcha, 1975). From 5 days before parturition to weaning, *Mus* in both the Father Absent and Father Present groups consumed the most food when they were in the Wheel Noncontingent condition and less food if they were in the No Wheel or Wheel Contingent group. Mothers and fathers in the Wheel Contingent condition may have been running an energy deficit as they would need the same amount of food as those in the Wheel Noncontingent condition. This energy deficit also was evident in that mothers in the Wheel Contingent group gained less weight than mothers in the other housing groups. Mothers in the Wheel Noncontingent and No Wheel conditions responded the same as mothers in the Wheel Contingent condition in that the amount of parental behavior they displayed declined as pups aged. Fathers in the Wheel Noncontingent and No Wheel conditions did not respond to this decrease in parental care provided by the mother by increasing the amount of time they spent in parental behavior as pups aged while fathers in the Wheel Contingent condition did respond by increasing the amount of time they spent in parental behavior as pups aged. The father may have been instrumental in maintaining a minimum amount of parental care as pups aged which may have increased the pups' chances of survival.

Mothers in the Father Absent and Father Present groups were observed wheel running the least at parturition. After parturition, the time spent wheel running by mothers in the Wheel Contingent group increased dramatically while the amount of time spent wheel running by mothers in the Wheel Noncontingent group increased only slightly. Fathers did not alter the amount of time they spent wheel running as pups aged. If mice did not have to work for food, they reduced the amount of time spent wheel running and increased the amount of time spent in parental behavior. Mice that had to work for food made compromises as they reduced the amount of time spent with pups and increased the amount of time spent foraging. Some of the lost time spent foraging was compensated for by the presence of the father as he increased the amount of time he spent in parental behavior as pups aged but only when he and his mate had to forage for food.

8.2 *Peromyscus californicus* results

8.2.1 Do housing conditions influence pup survival and pup weight?

Housing conditions influenced pup survival as fewer pups survived when mothers and fathers were required to run revolutions on a running wheel for food (Wheel Contingent condition) than when mothers and fathers were fed *ad libitum* (No Wheel and Wheel Noncontingent conditions). The survival of whole litters also was influenced by foraging conditions as fewer litters survived in the Wheel Contingent condition than in the No Wheel condition. *Peromyscus californicus* did not cull litters, they cannibalized whole litters. In California mice, mothers and fathers reared more pups to weaning in cool temperatures than mothers that were alone. However this difference in survival was not evident when temperatures were warm (Gubernick et al., 1993). In the monogamous Djungarian hamster (*Phodopus campelli*), mothers and fathers reared more litters to weaning in warm temperatures than mothers that were alone and this difference was even more pronounced in cool temperatures (Wynne-Ewards & Lisk, 1989).

Housing conditions influenced pups' weights as pups in the Wheel Contingent group weighed the least at weaning. ***Peromyscus maniculatus*** mothers, weaned as many pups as possible but at lower weights when they were challenged to work for food (Perrigo, 1987). In Djungarian hamsters, pups raised in cool ambient temperatures weighed less at weaning than pups raised in warm ambient temperatures (Wynne-Edwards & Lisk, 1989). Therefore, harsh environmental conditions influenced pup survival.

8.2.2 Does the presence of the father influence pup survival and pup weight?

The father's presence increased pup survival when mice must forage for food (Wheel Contingent) but not when food was available *ad libitum* (Wheel Noncontingent and No Wheel). Studies mentioned in section 8.2.1 above, (Wynne-Edwards & Lisk, 1989, Gubernick et al, 1993) indicated that the presence of the father increased pup survival under cool ambient temperatures.

The fathers' presence did not influence pup weight at weaning. Dudley (1974), however, found that *Peromyscus californicus* pups raised with both parents were heavier at weaning. The father could directly influence pup weight by helping pups thermoregulate for the first 15 days and allowing pups to allot more energy to growth. Other studies did not support this finding. Gubernick et al. (1993) did not find that male California mice influenced pup weaning weight when they were reared under cold conditions and single mothers reared heavier pups to weaning than mothers and fathers in warm ambient temperatures. Djungarian hamster pups raised by both parents were just as heavy as pups raised by mothers alone under warm ambient temperatures (Wynne-Edwards & Lisk, 1989). The lack of the fathers' influence on pup weaning weight under adverse conditions suggests that male *P. californicus* contribute to pup survival rather than the quality of the pups that survive. My results also indicate that the influence of the father may only be noticeable when environmental conditions are less than optimal (cool temperatures or food shortages).

8.2.3 Do mothers and fathers exhibit the same type and amount of parental behavior?

P. californicus fathers engaged in the same parental behaviors as mothers but spent less time in parental behavior than mothers. The fathers' presence and housing conditions did not alter the amount of time mothers spent in parental behavior. Housing conditions also had no influence on the amount of time fathers' engaged in parental behavior. Running for food did not interfere with the amount of parental behavior observed and this was due to mothers and fathers being capable of alternating between parental behavior and wheel running. For example, mothers and fathers would carry pups that had crawled out of the nest, but before returning them to the nest they would run on the wheel (often dropping and retrieving pups several times), or they would briefly visit the nest and then return to wheel running. So although the amount of parental behavior recorded was not compromised by wheel running, the quality may have been.

Videoanalysis indicated that mothers and fathers did not differ in the amount of time they spent in the nest but indicated that parents in the Wheel Contingent condition spent less time in the nest than parents in the other housing conditions. The difference in time estimates between the direct observations and videoanalysis was due to the type of behavior observed. Direct observations focussed on parental behaviors that could occur in or out of the nest, while the videoanalysis focussed on the amount of time spent in the nest only. It was therefore, possible that mothers in the Father Absent group spent less time in the nest in the Wheel Contingent condition as well, since mothers engage in the same type and amount of parental behavior when the father is absent or present. Thus, wheel running interfered with the quality of the parental care that pups received. When mothers and fathers are in the nest, the mother nurses the offspring and both parents help the pups thermoregulate. This could explain why pups in the Wheel Contingent condition were significantly lighter at weaning. Gubernick and Alberts (1987) and Dudley (1972) also found that mothers and fathers (*Peromyscus californicus*) displayed the same parental behaviors and that mothers and fathers spent the same amount of time in the nest.

8.2.4 Do mothers and fathers differ in the time spent running on the wheel and eating the food pellets earned?

Mothers and fathers differed in the amount of time spent running on the wheel and in the amount of time spent eating food pellets. Fathers' could indirectly increase the survival of their offspring by running longer on the wheel and eating for shorter periods of time than mothers. Videoanalysis indicated that within the Wheel Contingent group fathers spent more time running than mothers whereas mothers and fathers spent the same amount of time wheel running in the Wheel Noncontingent group after pups were born. Direct behavioral observations, however, showed that mothers spent the same amount of time wheel running in both the Father Present and Father Absent groups and mothers and fathers did not differ in how much time they spent wheel running.

When the number of revolutions mice ran was examined, single mothers in the Wheel Noncontingent conditions (*ad lib* food) reduced the number of revolutions they ran during lactation, while mothers and fathers in the Wheel Noncontingent condition did not. Single mothers and mothers and fathers in the Wheel Contingent group either maintained or increased the number of revolutions they ran during lactation. It appears that if females do not have to work for food, they reduce their wheel running. The failure of mothers and fathers to reduce their wheel running in the Wheel Noncontingent group is probably due to the father running on the wheel. It is therefore possible, that fathers run more than mothers in the Wheel Contingent group. The pattern of wheel running differed between mothers in the Wheel Noncontingent and Wheel Contingent groups as mothers in the Wheel Noncontingent group decreased the amount of time spent wheel running as pups aged while mothers in the Wheel Contingent group increased the amount of time spent wheel running as pups aged.

Direct observations of eating behavior indicated that mothers in the Wheel Noncontingent and Wheel Contingent groups spent more time eating than mothers in the No Wheel group. This result would be consistent with the fact that mothers with the running wheel present were expending more energy. Fathers spent less time eating than mothers in the Wheel Noncontingent and Wheel Contingent groups, while mothers and fathers spent the same amount of time eating in the No Wheel group. Observation data and videoanalysis suggest that fathers help mothers by running on the wheel longer and allowing mothers to eat the food that is generated for a longer period of time.

8.2.5 Do *Peromyscus californicus* differ in how they partition their wheel running and parental care during the light and dark phases of the LD cycle and as pups age?

Peromyscus in the Father Absent group and in the Father Present group spent more time engaged in parental behavior during the light phase and ran more during the dark phase of the LD cycle. Single mothers in the Wheel Noncontingent and Wheel Contingent groups ran the same number of revolutions during the light phase, but Wheel Contingent mothers ran more revolutions during the dark phase. Mothers and fathers in the Wheel Noncontingent and Wheel Contingent groups did not vary the number of revolutions they ran during the light and dark phase of the LD cycle. The pattern of wheel running was influenced by housing conditions in single mothers but not in mothers with fathers.

Father Absent and Father Present mothers reduced the amount of time spent in parental behavior. However, the manner in which mothers in the Father Present group reduced parental behavior was different from that of mothers in Father Absent. Mothers in the Father Present group reduced the amount of time in parental behaviour as pups aged during the dark phase but not during the light phase of the LD cycle. Fathers responded in a similar manner as they increased the amount of time in parental behavior during the light phase and decreased the amount of time in parental behavior during the dark phase as pups aged. Mothers in the Father Absent group reduced their parental behavior in both the light and dark phases of the LD cycle as pups aged. This pattern of behavior would ensure that pups would receive more parental care in the Father Present group than in the Father Absent group. Gubernick and Alberts (1987) also found that parental behavior decreased as pups approached weaning.

8.3 Are there species differences in the amount of parental behavior and wheel running observed?

I wanted to know if there was a difference between species in the amount of time mothers and fathers spent in parental behavior. Since the LD cycles were different between the species, no direct attempt was made to compare the number of revolutions run during the light phase and dark phase and data were pooled over the LD cycle. This resulted in one score for every two days as light and dark observations were alternated each day. Data were analyzed using a 2 (species) x 2 (housing) x 10 (days) analysis of variance.

P. californicus mothers spent more time in parental behavior than *Mus musculus*, while the amount of parental behavior displayed by fathers did not differ between the two species. *P. californicus* mothers with the father absent spent significantly more time in parental behavior than *Mus musculus* mothers with the father absent ($F_{(1,41)}=17.9$, $p<.001$). *P. californicus* mothers with the father present also spent significantly more time in parental behavior than *Mus musculus* mothers with the father present ($F_{(1,44)}=29.5$, $p<.001$). In the monogamous species (*P. californicus*), mothers spent more time in parental behavior than in a polygynous species (*M. musculus*). *P. californicus* pups must have required more parental care to raise them to weaning if time spent in parental behavior can be used as an index. Fathers of the two species spent the same amount of time in parental behavior, which was not a result I anticipated.

I wanted to determine if the overall running wheel activity levels were different between these two species as well as the pattern of activity between the Wheel Contingent and Wheel Noncontingent conditions.

Overall, *Mus musculus* and *P. californicus* exhibited the same amount of wheel running. In the Father Absent group, mice in the Wheel Contingent group ran 2.7 times more revolutions (14600 vs. 5413) than those in the Wheel Noncontingent group ($F_{(1,25)}=42.2$, $p<.001$), but there was no significant difference in the amount wheel running between species ($F_{(1,25)}<1.0$). In the Father Present group, mice in the Wheel Contingent group ran 1.2 times more revolutions (20540 vs. 16516) than mice in the Wheel Noncontingent group ($F_{(1,27)}=7.3$, $p<.05$). Once again, *Mus musculus* and *Peromyscus californicus* had similar levels of running wheel activity ($F_{(1,27)}=1.6$). There was however, a significant interaction between housing and species ($F_{(1,27)}=9.0$, $p<.01$). *Mus* in the Wheel Contingent group ran 1.5 times as many revolutions as *Mus* in the Wheel Noncontingent group while *Peromyscus* in the Wheel Contingent group ran the same number of revolutions as those in the Wheel Noncontingent group.

From this analysis we could not determine if *Mus musculus* or *Peromyscus californicus* was more strictly nocturnal. However both species generated the same amount of food and ran a similar number of revolutions. Perrigo (1987) found that *Peromyscus maniculatus* increased their speed of running during the dark phase and generated more food while *Mus domesticus* ran at a slower speed but for a longer period of time (into the light phase).

Some other differences were also apparent between the behavior of *M. musculus* and *P. californicus*. When *Mus* did not have earn food in the Wheel Noncontingent condition, both Father Absent and Father Present mothers reduced their wheel running. However, in *Peromyscus* , only Father Absent mothers in the Wheel Noncontingent condition reduced their wheel running. *Mus* are faster to respond to the increased costs of lactation in that those in the Wheel Contingent condition did not delay in consuming all the food they earned whereas there was a delay in *Peromyscus*. *Mus's* quick response to increased energy demands may be one of the factors that allowed them to retain most of their litter, while the slower response of *Peromyscus* may be a factor responsible for the loss of entire litters.

8.4 General Discussion

In both a polygynous species, *Mus musculus* and a monogamous species, *Peromyscus californicus*, the fathers' presence enhances the survival of pups when adults are required to forage to food. The increased survival of pups in *Mus* due to the fathers' presence was not predicted as *Mus* are polygynous and spend most of their time defending a territory, on which females raise their litters. It was predicted that a polygynous male would enhance his reproductive success by allocating his time and energy into acquiring mates instead of helping to rear offspring that the mother can provide for (Daly & Wilson, 1983, Perrigo, 1987). However, other studies have shown that *Mus musculu*s males exhibit parental behavior when housed with one female (as we housed them) but not when housed with several females. When *Mus* males have access to several females, and density is high, males spend more time defending their territory and mates from other males. Communally nesting females may enhance the father's reproductive success more than if the male participates in parental care. When the population density is low, males may only have access to one female and intruders are likely to be scarce. Under these conditions, males have nothing to lose (and reproductive fitness to gain) by spending the time not used for territorial defense on increasing the survival of their pups. In addition, the male could compensate for some of the lost parental care that pups would receive under communal rearing conditions. Therefore, the males' influence on pup survival would only be noticeable the population density was low and food was widely spaced.

It is possible that male *Mus musculus* may help their mates in the wild as do other polygynous species such as red-winged blackbirds and house wrens. When male red-winged blackbirds mate monogamously they help feed nestlings of primary and secondary nests but not tertiary and later nests (Muldal, Moffatt & Robertson, 1986). Male red-winged blackbirds varied in the quality of brood care given with some males not feeding nestlings at all. Females (primary) that had broods fed by the male had enhanced nestling success. However, females not receiving assistance from males that actually fed offspring (secondary or tertiary) were just as successful rearing a clutch to independence when compared to females that nested on territories where males did not feed offspring at all. So being on a territory where the male would potentially feed offspring was better than being on a territory where males did not feed offspring (Muldal, Moffatt & Robertson, 1986).

In house wrens (*Troglodytes aedon*) when males mate monogamously they aid their mate by delivering food to the nestlings. Females can then remain on the nest for longer periods of time brooding their offspring. Sometimes males attract a second mate as well, but do not assist her as much as his first mate. The second female subsequently stays on the nest for shorter periods of time and spends longer foraging for food for herself and her offspring (Johnson & Kermott, 1993). Male *Mus musculus* may divide their time between caring for as many young as possible and maintaining a territory. If dominant females nested first on a territory they could possibly benefit from some male assistance.

P. californicus fathers increased pup survival, but only when mice must forage for food. This result was expected as these animals are monogamous. Monogamy usually does not occur in mammals unless fathers can increase their reproductive success more through monogamy than polygyny. Ribble (1992) suggested that monogamous *P. californicus* males enhanced their lifetime reproductive success by remaining with one female, since males that changed partners had to wait longer for the arrival of subsequent litters than males that remained with their original mate. He also noted that the survival of offspring was higher in *P. californicus* than in polygynous *P. maniculatus.* As males are found in the nest in the wild just as often as females, my data suggest that monogamy may prevail as fathers may need to spend substantial time caring for offspring to ensure pup survival. My data suggest that a male that abandoned his offspring would risk weaning no offspring, since *P. californicus* mothers tend to kill entire litters when they must forage for food and care for pups alone.

Pup weight did not decrease by the same magnitude in *P. californicus* as in *M. musculus.* For *M. musculus,* by 20 days of age, pups that survived in the Wheel Contingent group were 46% lighter in weight than pups in the No Wheel group, while pups in the Wheel Noncontingent were 15% lighter than pups in the No Wheel group. *P. californicus* did not tolerate such a large decrease in pup weight as pups in the Wheel Contingent group were 18% lighter than pups in the No Wheel group and pups in the Wheel Noncontingent group were only 7% lighter than those in the No Wheel group. *P. californicus* also cannibalized more entire litters (26 litters) than *M. musculus* (2 litters), however, *M. musculus* often culled large litters. *P. californicus* may decide within the first 4 days (when most litters are cannibalized) whether they are capable of maintaining pups at a minimum weight throughout lactation and if they are not, cannibalize entire litters and wait for better environmental conditions (including the presence of a mate). *Mus* may cull litters to a size that guarantees that some offspring from the litter will survive and may not be as sensitive to weight at weaning.

P. californicus mothers do not tolerate personal weight loss and may use their own body condition ito determine if they can maintain pups. *Peromyscus californicus* also showed a reduction in weight in response to the increased demands of foraging in both the Wheel Contingent and Wheel Noncontingent groups between parturition and day 12 after parturition. Mothers in the Wheel Noncontingent and Contingent condtions caught up to the No Wheel group after day 12 postpartum and by day 24 postpartum, mothers in all groups weighed the same. Mothers that maintained a minimum individual weight successfully reared a litter.

Mus musculus mothers in the Wheel Contingent group were more tolerant of weight loss. *Mus musculus* mothers showed a reduction in weight in response to the increased demands of foraging (Father Absent and Father Present Wheel Contingent groups) while caring for a litter. Results from Perrigo's (1987) experiment also found that single *Mus* mothers reduced their body weight while single *Peromyscus maniculatus* mothers did not lose weight at higher foraging requirements. For both species, mothers in the No Wheel and Wheel Noncontingent conditions did not diplay weight reductions after parturition and neither did the fathers in any of the groups. Perrigo (1987) also noted that *Mus* selectively culled their litters up to 12 days postpartum while *Peromyscus maniculatus* cannibalized their entire litter up to 4 days postpartum when foraging requirements increased. In my experiment *Mus* culled litters mostly up to 5 days after parturition and then the incidence of cannibalism decreased (range day 3 to day 14) while *Peromyscus californicus* canibalized entire litters most up to 3 days after parturition (range day 0 to day 9).

These results indicate that mothers in the Wheel Contingent group were challenged to obtain food to maintain their own weight while feeding pups, while the foraging conditions had no effect on the fathers' ability to maintain their weight. Mothers may therefore, be capable of using their own physical condition as an index as to their ability to successfully raise a litter to weaning.

Certainty of paternity may be a factor in the males' decision to help raise offspring. With both *Mus* and *Peromyscus*, monogamy was enforced in this experiment, and high levels of paternal care were observed. *Mus* are usually polygynous, and do not exhibit parental behavior when housed with several adult males and females. Wild *Peromyscus californicus* have a high certainty of paternity as indicated by DNA studies (Ribble, 1991) and also high levels of paternal care are observed in the lab (Gubernick, 1987).

Certainty of paternity influences how much male swallows (*Hirundo rustica*) feed their mates and offspring and how much they defend their mate and brood. The more extra-pair copulations their mate engaged in, the less the male fed and protected his mate and offspring (Moller, 1991, 1988). Even when male eastern bluebirds adopt offspring after the female's original mate is removed, paternity certainty may be a factor in how much food the new male brings to the female and her offspring (Meek & Robertson, 1991). Paternity certainty is one of the main explanations for male-infant interactions in primates. Males defend, babysit and interact with offspring that they most likely sired (Trivers, 1972, Smith, 1980, Berenstein et al., 1981).

So as Brown (1993) suggests several environmental and behavioral factors may influence a male rodents's decision whether to be parental, infanticidal or to ignore the female and her pups. Adult male *Mus* may be willing to help care for offspring if copulation patterns, time of arrival of the litter, and lack of other male competitors indicate that the offspring are most likely his and if there are no other reproductive opportunities with other females on his territory. In an open field situation, a subdominant male also could increase the likelihood that a female would mate with him, if females choose mates based on fathers' displaying parental behavior (reciprocity theory).

Mus musculus live in a wide variety of habitats, have a short lifespan and high juvenile mortality among dispersing young. *Mus musculus* are sensitive to food availability since when they are challenged to run for food they quickly consume all the food they earn within 4 days postpartum. They are also sensitive to work requirements to obtain food since *Mus* in the Wheel Noncontingent group drastically reduce the number of revolutions they run when females have pups and consume more food than they earn. *Mus musculus* females seem less sensitive to maternal body weight as an index of her capability of investing in offspring and less sensitive to pup weaning weight. At the same time, they retain as many pups as possible. Their quick response to energy input and output and ability to absorb some of the energy cost with their own fat reserves, may allow mothers in the Wheel Contingent group to wean relatively large litters even though pups' weights are low. *Mus musculus* live in unstable environments where population density and food availablity are constantly in flux. It would be adapative for a pregnant female to use some of her body fat reserves, wean a few pups and possibly those pups would find a better food source for themselves. When food is limited (feral habitat), the population density would be low and males would have little opportunity to be polygynous. Communal nesting by several females which benefits pup development would not be an option for a pregnant female. In a monogamous situation, the male exhibits parental care and the result is more pups survive to weaning.

When food is plentiful (as in barns and corn ricks), the population density would be high and polygyny would be an option for male mice. Polygyny allows the possibility of communal nesting for females which could be more beneficial to pup development (the pups would be fed more often) than the male contributing by keeping the pups warm. In this situation, the male is more likely to spend his time patrolling his territory and keeping intruding males away from his mates and offspring. The father would increase his reproductive success by having access to several females which communally nest and raise offspring. Therefore, expending energy in parental care may not raise his fitness in this situation.

Peromyscus californicus live in environments where food sources are not as variable. *Peromyscus californicus* are less sensitive to food availability than *Mus*. After parturition, *Peromyscus californicus* mothers and fathers in the Wheel Noncontingent and Wheel Contingent conditions did not differ in the amount of food they earned and consumed. *Peromyscus* in the Wheel Contingent condition take up to 12 days after parturition to consume all the food they earn. Females that retained their litter, initially lost weight in the Wheel Contingent but regained the lost weight by the time their pups were weaned. It is possible that mothers make a decision within the first ten days whether their own resources are adequate to maintain a litter of pups, and if they are not, cannibalize the entire litter. *Peromyscus californicus* are also more sensitive to changing seasons (as they are long day breeders) than *Mus* and do not attempt reproduction in the winter months when food would be scarce (Gubernick, 1988). If females bred during the winter months they would waste valuable energy during pregnancy and end up cannibalizing their litters when they were born. *Mus* breed all year round (Bronson, 1979), so they should be sensitive to changing food levels and be efficient at utilizing and saving energy.

Peromyscus are also less sensitive to increasing energy demands in that they do not reduce the number of revolutions they run when they are not required to run for food. Single female *Peromyscus* in the Wheel Noncontingent group did reduce their wheel running however males and females in the Wheel Noncontingent group ran as many revolutions as mice in the Wheel Contingent group. Even if the extra activity is due to the father running on the wheel, this species is not as sensitive as *Mus* to changing energy demands. Being less sensitive to energy demands could result in a reproductive strategy where females use their own body weight instead of environmental cues (like food availability) to determine if a reproductive attempt will be successful. *Peromyscus californicus* are more sensitive to pup weight than *Mus musculus* as they only tolerate modest weight reductions in their offspring. *Peromsyscus californicus,* therefore, seem more sensitive to pup quality than pup quantity.

The fathers' presence in *P. californicus* also may be necessary as mothers invest more time in their offspring than *Mus* mothers. *Mus* mothers spend less time in parental care and wean more pups while *P. californicus* mothers spend more time in parental care and wean fewer pups. *P. calfornicus* pups also have a longer period of dependency on the mother than *M. musculus.* This increased investment by *P. californicus* females may be another reason that the fathers' parental behavior is important for pup survival. Mothers are raising heavier pups for a longer period of time and without the fathers' assistance the likelihood they will be successful is limited. Heavier female pups would be beneficial, as heavier females have larger first litters (Ribble, 1992). In addition, *P. californicus* may not be willing to risk the viability of a possible second litter by delaying weaning of the current litter, whereas *M. musculus* may be willing to delay weaning of the current litter. Since I did not follow mothers and offspring after weaning, it is unknown how each species would respond to a small first litter with a second litter on the way. Mothers in both species did not respond to foraging requirements by not reproducing. There was no difference in the number of litters born to the different foraging groups. Considering that *Peromyscus californicus* mothers lose their entire litter, it would have been of benefit to determine during pregnancy whether the foraging requirements were too stringent to maintain a litter. Perhaps neither species had enough time to decide before the pups were born and if mothers had been foraging for food for a period of time prior to mating and pregnancy, they may have responded by delaying implantation, or resorbing or aborting the litter.

These experiments have raised several issues that should be investigated. *Mus musculus* males do not exhibit parental behavior when housed in open enclosures with several adults. It would be of interest to determine, if male *Mus* were housed polgynously in the Wheel Contingent group, whether the same amount of parental behavior would be observed. Another consideration is that the extra care provided by communally nesting females could be just as beneficial for reproductive success as male parental care. *Peromyscus californicus* housed in a polygynous group (two females and one male) in the Wheel Contingent condition would be expected to raise fewer offspring than a monogamous pair. This would likely be the case since females are intolerant of each other in the wild (Ribble, 1991) and males and females become aggressive when housed with same sex siblings (personal observation).

Weight gain in adult females was often difficult to interpret in this experiment as mothers in the Father Absent group were not pregnant again whereas mothers in the Father Present group were. In the Father Absent groups, fathers should remain with the mother until one day after birth of the pups. This would reduce the amount of time mothers are without fathers, but ensures that all mothers could potentially be pregnant again.

The interbirth interval and the number of days for pups to be weaned could be two useful measures in determining the role of the father. Monogamous pairs in both species may have shorter interbirth intervals than polygynous groups which would increase lifetime reproductive success. Future experiments should determine if underweight pups in the Wheel Contingent group are weaned later but at a similar weight as pups in the Wheel Noncontingent group. A further manipulation would be to determine if pairs of females housed without males, raised as many offspring as monogamous pairs in both species.

The type of housing can influence whether male parental behavior is observed. Hartung and Dewsbury (1979) observed promiscuous meadow vole fathers contacting pups. However, Oliveras and Novak suggested (1986) that fathers engaged in parental behavior due to the type of housing and lack of cover. When meadow voles were housed in large enclosures, fathers did not contact pups (Oliveras & Novak, 1986). Perhaps a future consideration should be to compare parental behavior and pup survival when animals are housed in open enclosures with several adults maintaining territories with parental behavior and pup survival observed when animals are housed in running wheel cages.

Finally, we could also allow mice to hoard food, to see if this is a strategy to maintain pups when foraging becomes difficult.
If we allowed the surplus food generated by the Wheel Contingent condition before parturition to be hoarded, it might have had a significant impact on adult weight, pup weight and pup survival after parturition.

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