Paternal Behavior in Rodents

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SYNOPSIS. The literature on paternal behavior in rodents includes reports of many species; however, paternal behavior appears more prevalent among muroid and hystricomorph rodents than in the sciurids. Many reports of paternal behavior are based on small numbers of animals observed under special conditions. Where systematic studies have been conducted, the most salient feature of rodent paternal behavior is its lability. The occurrence varies with observer constraints, genotype, experience, social conditions during observation, and stimulus characteristics. This intraspecific variability renders application of the comparative method in understanding evolution difficult but may provide a key in the remarkable adaptation of rodents to diverse habitats. Although species differences exist the evolution of rodent paternal behavior appears to entail changes in the thresholds and conditions for the occurrence of a relatively few basic motor patterns of paternal care.

INTRODUCTION
Surveys of the evolution of paternal behavior in such taxa as fishes and birds have generally resulted in lists of species in which males are categorized as paternal or not paternal (e.g., Baylis, 1981; Ridley, 1978). The comparative study of some behaviors, such as copulatory behavior, in rodents also reveals a pattern of relatively discrete and stable species differences (e.g., Dewsbury, 1975). However, careful examination of the literature on paternal behavior in rodents reveals a picture in which the magnitude of reliable species differences appears less salient than the great variability and flexibility of paternal behavior within species under varying conditions. The literature is a difficult one with a nonrandom sample of species and many different methods used. Although species differences exist, they appear to represent not the evolution of divergent complex motor patterns but of varying thresholds and conditions for the occurrence of a few relatively basic motor patterns of parental care. Some of the proximate and ultimate factors affecting rodent paternal behavior will be considered.

WHAT MALE RODENTS DO
Parental care can be defined to include "all nongametic investments in offspring following fertilization" (Wittenberger, 1981). Parental investment may be either direct, in that it has "an immediate physical influence" on the young that increases survivorship, or indirect, which includes "acts a male may perform in the absence of the young which increase the latter's survivorship" (Kleiman and Malcolm, 1981).

Being there
The mere presence of a male can be important both pre- and post-natally. Female Microtus montanus and M. ochrogaster have been found to have a higher probability of conception if a male is left in the cage with her for 1–7 days after mating than if he is removed soon after mating (Berger and Negus, 1982; Richmond and Stehn, 1976). If it is true that females fail to conceive if left by males soon after mating the implications for the evolution of male mating strategies would be considerable. The possibility that by leaving, a male may render a completed mating infertile would have to be weighed against the possible benefits of potential additional matings with other females.

Direct investment
Male mammals do not lactate; the probable reasons have been discussed by Daly.

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(1979). However, male rodents can and do perform all other direct parental activities displayed by females. The following will be emphasized: huddling—sleeping with, crouching over, or adopting the nursing position with the young; grooming—cleaning, licking, or otherwise grooming the young; retrieving—carrying or transporting the young from place to place, generally returning to the nest; play—engaging in play behavior with the young; tutoring—behavioral patterns that facilitate learning by the young; providing food—bringing food to the young; greeting—engaging in species-typical greeting displays; manipulation in nest—manipulating the young while in the nest.

Huddling, grooming, and retrieving have obvious functions in such contexts as thermoregulation, care of pelage, and protection and have been described in numerous species. Although the function of play is controversial it is likely that play contributes to development. Parents function in learning situations, as with the acquisition of feeding patterns (e.g., Galef and Clark, 1971). Provision of food can sometimes represent indirect investment. However, where males feed young as do naked mole rats (Jarvis, 1978) the investment appears direct. The functions of greeting and manipulation in nest are less clear.

Indirect investment

Among the behavioral patterns that may generally be classified as indirect investment are nest building and maintenance, protection from predators, protection from conspecifics, and warning of predators. Each of these behavioral patterns can be performed in the absence of young. Thus, although they are of obvious functional significance, their inclusion as specific paternal behaviors is not always clear. On the other hand, these patterns can be so closely tied to the young that they may fall within the range of direct investment. The distinction between direct and indirect investment is not an absolute one.

Comparative Survey

The results of a literature search for descriptions of rodent paternal behavior, arranged by family (after Honacki et al., 1982), are presented in Table 1. Following such authors as Kleiman and Malcolm (1981) and Elwood (1983) I have included all reports of paternal behavior that were located. The spotty nature of this record requires emphasis. In only a few cases do researchers explicitly state that males play no role in care of the young (e.g., Holmes, 1983). More often, the matter is not addressed and interpretation is difficult. A list of species that do not display any paternal care would be more difficult to generate than the list of those that have been observed to do so.

The other major reason that surveys such as this are somewhat deceptive is that many reports are based on small numbers of animals or even on a small percentage of the animals observed. Although it is clear from such reports that males of the species can and do show paternal behavior, it would be a mistake to regard this as the modal pattern. The classical descriptions of paternal behavior in Peromyscus leucopus (Horner, 1947) and Reithrodontomys humulis (Layne, 1959) are based on one male each. Dieterlen (1959) reported paternal behavior in two male hamsters. Horner and Taylor (1969) maintained a breeding colony of Rattus fuscipes with litters sired by 54 males, 40 of which were permitted to remain with their mates. Their report is based on two males that displayed paternal behavior. Such reports are fascinating and worthwhile. However, one must be very careful in interpreting incidental observations on a few animals as species-typical adaptations.

As can be seen from the table, there are many reports of paternal behavior in muroid rodents and various reports in hysticomorphs. Paternal behavior appears rare in most sciurids.

Factors Affecting Paternal Behavior

Laboratory studies of the determinants of paternal behavior are probably more numerous for rodents than for most other taxa. Perhaps because of this and perhaps because of real differences between rodents and other species, a great lability of paternal behavior has been revealed. The care-
PATERNAL BEHAVIOR IN RODENTS

A further complication stems from the lack of standardization. Even where animals are observed in the laboratory the testing conditions and behavioral categories used vary so greatly from study to study that it is difficult to compare studies from different laboratories. One solution to this problem is more comparative studies of various species under identical conditions. For example, presented in Figure 1 are data from our laboratory on the time males and females of seven species spent on the nest during a one-half hour period when their mates were removed from their home cages.

Observer constraints

Some apparent species differences in paternal behavior stem from the conditions imposed by the observer. Under field conditions, for example, it may be impossible to observe many paternal behaviors even if they occur. This is particularly the case for small, nocturnal, secretive, burrow-dwelling rodents. The absence of reports does not necessarily indicate non-occurrence of the behavior. In the laboratory, on the other hand, the simplicity of the environment precludes certain observations. For example, it is rare for a male to have the opportunity to defend young against either a conspecific or a predator other than the observer. Because some species have been most often studied in the field (e.g., squirrels) and others in the laboratory (e.g., muroid rodents) these differences can have important effects on summaries such as that in Table 1.

Ful reader of this literature must be struck with the enormous range of factors affecting paternal behavior.

FIG. 1. Amount of time spent by the male and female parents in the nest with pups in one-half hour in the absence of the mate in seven species of muroid rodents. Data from Hartung and Dewsbury (1979) and Sawrey et al. (1984).
### TABLE 1. Comparative survey of literature on rodent paternal behavior.

<table>
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<tr>
<th>Species</th>
<th>LO (L occup., O offspring)</th>
<th>HA (Haching)</th>
<th>G (Grooming)</th>
<th>R (Retrieval)</th>
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### Table 1. Continued.

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<th>Species</th>
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<th>Nest build</th>
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<td>Wilson and Kleiman, 1974</td>
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**Abbreviations:** B, babysit; C, defend from conspecific; D, defend from predators; E, enurinate; F, feed; G, greet; M, manipulate pups in nest; N, no details; P, play; T, tutor; W, warn of predators.

### Genetic determinants

Presumably, many species differences in paternal behavior result, at least in part, from genetic differences. However, differences attributable to genotype can be found within species as well. Jakubowski and Terkel (1982) found that whereas naive wild house mice typically kill young, laboratory strains generally displayed paternal care. The differences were attributed to genotype and the effects of artificial selection. Henderson (1983) found male mice from wild genotypes to be exceptionally good retrievers of pups. There were also considerable differences among inbred strains. Long-Evans male rats are more likely to
kill pups than are Wistar or Sprague-Dawley males (Brown, 1981).

Experiential determinants

A variety of long- and short-term experiential variables affect the responses of males to pups and the occurrence of paternal behavior. A role of early experience was found by Jakubowski and Terkel (1982) who found that whereas naive wild house mice typically killed young, those that remained with their parents while the parents reared a subsequent litter displayed paternal behavior. Early handling affects paternal behavior in laboratory rats (Mayer et al., 1979). Although naive male laboratory rats often kill young, those that are exposed to young for several days begin to display paternal responses (LeBlond, 1938; Rosenblatt, 1967). A shorter-term sensitization was observed by Noirot (1964) who found that contact with a “strong” stimulus (a live pup) increased the responsivity of male house mice to “weaker” stimuli (dead pups). The effect appeared to persist for several days.

Perhaps the most salient experiential effect may result from cohabitation by a male with a female throughout her pregnancy. Many of the incidental observations of paternal behavior are on such stable breeding pairs. Brown (1982) found that whereas male laboratory rats bought directly from a breeder killed pups, those that cohabited with a female for 14–20 days were paternal. Elwood and Ostermeyer (1984) found that for male house mice it was cohabitation with a pregnant female, rather than copulation per se, that was important in inhibiting infanticide. Elwood (1977) found changes in the responsivity of male gerbils to pups occurring through their mate’s pregnancy. The effect did not appear persistent (Elwood, 1983). Hartung and Dewsbury (1979) found male deer mice of multiparous pairs to lick pups less than those in primiparous pairs but few other effects of parity.

The occurrence of paternal behavior in house mice is affected by such factors as the male’s intrauterine position, stress to the male’s mother, dominance status, and sexual experience (vom Saal, 1983; vom Saal and Howard, 1982).

Effects such as these are nontrivial and can have major effects on the behavior observed. One of the major controversies in the study of rodent paternal behavior resulted from the discrepancy between the results of Elwood (1975), who observed considerable paternal behavior in Mongolian gerbils, and Ahroon and Fidura (1976), who observed most litters left with males in the cage dead within a few days postpartum. The differences appear due to several factors including Ahroon and Fidura’s use of animals that had been already pregnant when purchased from a dealer, lighting conditions, age at mating, nutritional status, and developmental history (Elwood and Broom, 1978; Gerling and Yahr, 1979; Klippel, 1979).

Social conditions during observation

The occurrence of paternal behavior is greatly affected by the presence and behavior of conspecifics at the time of observation. Perhaps the single most important determinant is the response of the female. In species after species it is reported that the female actively excludes the male from the nest and pups for the first few days after birth. The male works his way back into the nest gradually over days. Representative species include oldfield mice (Smith, 1966), Mongolian gerbils (Elwood, 1977), southern grasshopper mice (Horner and Taylor, 1968), and agoutis (Smythe, 1978). The presence of a highly aggressive postpartum female can deter even a highly motivated new father. Marques and Valenstein (1977) found female golden hamsters to vary greatly in levels of aggression directed at their partner; only those males paired with minimally aggressive females displayed appreciable paternal behavior. The size and complexity of the testing environment appear to play a major role in altering patterns of paternal care. Meadow voles, for example, appear to display little paternal behavior in the field (Madison, 1980) or in a semi-natural enclosure (McGuire and Novak, 1983) but are paternal to some degree in smaller cages (Hartung and Dewsbury, 1979; Wilson,
1982). Male rats also are more likely to be paternal in small than in large cages (Brown, 1981).

Other social factors are also important. Csermely and Mainardi (1981) found differences in paternal behavior as a function of the dominance status of male house mice and the other animals present when they were tested. Gandelman \textit{et al.} (1970) found male mice to display little caretaking in a communal situation but a full range of behavior when housed individually with young.

In the field Barash (1975) found that male hoary marmots living in isolated colonies provided more paternal care than did those in more interactive social situations.

\textbf{Stimuli}

The characteristics of the pups used as stimulus objects in tests of paternal behavior affect its occurrence. Changes in the pattern of paternal behavior throughout the development of the young have been described in several species (e.g., McCarty and Southwick [1977a] for southern grasshopper mice and white-footed mice and Priestnall and Young [1978] for house mice). Such changes probably are due in part to changes in the characteristics of the pups but also may be affected by changes in the adults. Brown and Douglas (1983) presented male laboratory rats with pups of different ages and found males more responsive to the older of the two groups of pups. Such designs are necessary to dissociate effects of changes in the adults from those in the stimuli.

Other characteristics of the pup may also be important. The paternal behavior of gerbils is affected by litter size; males engage in more body contact and lick pups more in large litters than do more nest building with small litters (Elwood and Brown, 1978). Jakubowski and Terkel (1982) and Henderson (1983) found that mouse pups of domesticated lines were more effective stimuli for retrieval than wild-type pups.

The male, in turn, provides stimuli that affect other aspects of the dynamic family interaction patterns. A male deer mouse is attractive to and approached by the young and does not expel them (Savidge, 1974). Paternal urine elicits increased maternal care in grasshopper mice (Duvall \textit{et al.}, 1982). Although the presence of the father during development affects the response of gerbil pups to other males, pups are not attracted to the male's odor (Gerling and Yahr, 1982). In mice, a male's urine has the same effect on pup activity as does his presence (Csermely, 1981).

The stimuli effective in triggering paternal behavior are multi-sensory and may vary as a function of age, species, and other factors. Motion may be one important cue; one reason that \textit{Microtus} pups elicit more retrieval than \textit{Peromyscus} pups may be that they are out of the nest more (Hartung and Dewsbury, 1979). Adult \textit{Microtus} males of three species were found to orient to ultrasonic cries from pups in a maze apparatus (Colvin, 1973). Whereas lactating female rats leave the nest in response to recorded pup calls, males merely orient to the sound source (Allin and Banks, 1972). Olfactory cues appear to be important in the discrimination by paternal mice of their own from alien young (Ostermeyer and Elwood, 1983).

\textbf{Effects of Paternal Care}

Although effects of paternal care are discussed by Wuensch (1983), it is necessary to at least note the pervasive effects of male presence on pup development. Paternal care in California mice affects growth, development, and body temperature (Dudley, 1974). In southern grasshopper mice male presence generated increased female open-field activity, increased aggression toward \textit{Mus} opponents and a decreased prevalence of convulsive seizures (McCarty and Southwick, 1977b, c). In house mice paternal presence affects the locomotor activity of four-day old mice and the development of aggression, open-field behavior, and of various morphological characteristics (Csermely, 1980; Fullerton and Cowley, 1971; Mugford and Nowell, 1972). Even the strain of the male foster parent can affect the development of social behavior (Smith and Simmel, 1977). Male presence in gerbils affects not only offspring development but female behavior as well.
ULTIMATE CAUSATION

As a devotee of the comparative method wherein species differences in behavior are correlated with ecological and other variables I would like to be able to apply this method to rodent paternal behavior. It is clear that species differences exist. In some species males appear rarely, if ever, paternal whereas in others they appear paternal across a wide range of conditions. In those species that have been most widely studied, however, it is the variability of paternal behavior across conditions that is most salient.

Males of a number of species (e.g., Microtus pennsylvanicus) appear not to be paternal in the field but to aid in pup care in laboratory cages. There are at least two ways to treat such findings. One is to dismiss the occurrence of paternal care as a "laboratory artifact." The alternative is that if the males are paternal under laboratory conditions there may also be some conditions in the field, such as at low population densities, where they may sometimes be paternal. One may view the males as being very flexible in adapting to varying conditions rather than as acting "abnormally" under laboratory conditions. This approach merits at least exploration. It may be this very flexibility that requires explanation in evolutionary terms. That paternal care can have great influence on pup development has been demonstrated. Under what conditions in the field might such behavior be shown? How will it vary both among and within species?

The costs and benefits of paternal behavior must be assessed separately for each sex (e.g., Wittenberger and Tilson, 1980). A major determinant of paternal behavior is whether or not the female permits the male near the young. As many effects of paternal care on the young appear beneficial, the female may increase her fitness by permitting males to aid care for young. However, the incidence of infanticide is appreciable in many rodent species. Therefore, females might be expected to protect their young from males until males "prove" themselves as non-infanticidal. The energetic demands and costs of replacement of the young increase as they develop. The pattern wherein females exclude males from the nest soon after the birth of a litter but admit them later may be the product of the effects of such costs and benefits.

From the viewpoint of the male the benefits of remaining with the female and aiding the young must be weighed against the potential benefits and costs of seeking out additional mates (Dewsbury, 1982; Emlen and Oring, 1977; Wittenberger and Tilson, 1980). The relative benefits of the alternative strategies will vary with operational sex ratios, the economic defensibility of mates and resources, and a variety of other constraints. Where a male cannot monopolize a disproportionate share of mates it may be to his advantage to remain with one. If he remains with the female and litter it may generally, but not always (e.g., Holmes, 1983), be to his advantage to act paternally. Again this would depend on costs and benefits. The statement that "paternal care is not a cause of the male staying with the female and young but a result of his staying" (Elwood, 1983, p. 241) may be too strong; however, male presence certainly is a strong predisposing factor for paternal behavior.

Considerations such as these may help explain species differences. The fascinating questions concern intraspecific variation. Do animals of a given genotype in the field alter their parental strategies in conjunction with changed conditions and do these changes make sense in terms of a cost-benefit analysis? Carlisle (1982) developed a model that built in considerable intraspecific variability in paternal care and predicted that males could adjust their level of care to match prevailing conditions. It is this match that now requires study.

In the view most proposed that species varying with respect to paternal investment will vary with respect to their patterns of sperm competition as males will invest in care of young only where there is some certainty of paternity (e.g., Ridley, 1978). This may generally mean a last-male advantage in situations of sperm competition. Although this view has been challenged on theoretical grounds (e.g., Wittenberger, 1981), data on sperm competition in insects appear
consistent with it (Gwynne, 1984). What few data exist on rodents appear less consistent (see Dewsbury, 1984). There is a first-male advantage in house mice, a last-male advantage in prairie voles and no order effect in deer mice and laboratory rats. Although the last-male advantage in prairie voles is consistent with their generally high levels of paternal investment, the remaining differences are difficult to explain.

Conclusion

Rodents have been remarkably successful in their radiations and in occupying a wide range of habitats. Various authors have noted that their flexibility in adapting to varying environments has been one important component of this success. Getz (1978) stressed the variability of vole social organization and the degree to which changes in social interactions may generate population cycles. Whereas deer mice may sometimes form pair bonds (e.g., Bronson, 1983) there is appreciable evidence of multiple paternity of litters (Birdsall and Nash, 1973). Bronson (1983) contrasted the social organization of various feral and commensal populations of house mice and concluded that "the social system of the house mouse probably is best characterized as being markedly flexible" (p. 206). Similar observations have been made on other species. Thus, variability in paternal behavior may be just one part of a general social flexibility.

The within-species variability and sensitivity of rodent paternal patterns to experiential and environmental variables constitute major roadblocks for the student of comparative behavior. However, they may be the most salient feature of rodent paternal behavior and for rodents fundamental features facilitating diversity and success.

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