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A Comparison of Maternal Behavior in Three Species of Voles (*Microtus pennsylvania, M. pinetorum,* and *M. ochrogaster*) Using a Laboratory System

B. A. McGuire
University of Massachusetts, Amherst, Massachusetts

M. A. Novak
University of Massachusetts, Amherst, Massachusetts

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B.A. McGuire. Department of Zoology, University of Massachusetts, Amherst, 01003

M.A. Novak. Department of Psychology, University of Massachusetts, Amherst, 01003.

Abstract

A system has been developed to describe and compare the maternal behavior of three species of microtine rodents within a naturalistic environment. The apparatus consists of two interconnected Plexiglas-based tables with a peat substrate and hay cover. A pregnant female and her mate are placed within the tables, once the female has shown a thirty percent weight gain and pups can be felt by palpating her abdomen. Maternal behavior, as well as male-female interactions and information on pup physical and behavioral development, are recorded daily for twenty-five days immediately following parturition. Unrestricted observation of female behavior during neonatal, preweaning and post-weaning phases of pup development is possible from below the tables. Preliminary observations indicate that pup behavioral development rate, and male-female social interactions and spatial relationships during the breeding period, differ between the three species. This system provides for ease and clarity of observation of individual microtines, thus combining the best attributes of both field and laboratory studies.

Introduction

Formulation of an effective program to control microtines requires knowledge of the social behavior of these rodents. Parameters of social biology such as spacing pattern, social structure, and specific behavioral interactions, are expressions of both the reproductive biology and the ecology of a species. In particular, interspecific differences in mating system and parental care often reflect differences in reproductive strategies and/or habitat.

Microtus pennsylvanicus, M. (= Pitymys) pinetorum, and M. ochrogaster reportedly differ in certain aspects of habitat preference (De Coursey, 1957; Getz, 1978; Miller, 1969; Paul, 1970), and reproductive characteristics such as age at sexual maturity, gestation period, and average litter size (Hasler, 1975). Closely associated with these differences are the postulated dissimilarities in mating system and social organization. M. pennsylvanicus appears to display a social system based on territoriality by reproductively active females during the breeding season (Madison, 1980). Males overlap these territories and compete for estrous females in what seems to be a promiscuous mating situation. In contrast, the existence of monogamy and stable family units has been proposed for M. ochrogaster (Getz, 1978; Getz and Carter, 1980; Thomas and Birney, 1979). Although little information exists on the mating system of M. pinetorum, individuals of this species reportedly occur in loose colonial associations (Paul, 1970).

Parental care, a component necessary to complete the comparison of these three species, has received little attention. Recent radiotelemetric studies provide information on the movement patterns of free-ranging female meadow voles (M. pennsylvanicus) at the time of parturition (Madison, 1978), as well as the frequency and duration of nest visitation by lactating females (Madison, 1981). Laboratory investigations by Thomas and Birney (1979) describe parental behavior in M. ochrogaster and present data in the form of an ethogram. Getz and Carter (1980) also describe care of offspring by M. ochrogaster and provide information on time spent in the nest with the young by both parents and older litters. However, comparative studies involving detailed observation and quantification of parent-young interactions among different species of microtines has not been undertaken.

The present study represents an attempt to quantify and compare maternal behavior in M. pennsylvanicus, M. pinetorum and M. ochrogaster. Male-female interactions and early physical/behavioral aspects of pup development were noted, as well as post-weaning interactions between the female and her offspring. All observations were made in a laboratory environment which was designed to capture the conditions under which voles are found in the wild, and therefore minimize the various difficulties associated with both field and laboratory studies.

Materials and Methods

Experimental animals were selected from a laboratory colony which contained the following three species; 1) M. pennsylvanicus - trapped locally in Amherst, MA in 1980, 2) M. pinetorum - trapped from two orchards in Fairfield County, Connecticut in 1980, and 3) M. ochrogaster - received from the Animal Science department at University of Massachusetts in 1977. Voles were housed as male-female pairs or as single sex groups in aquaria (26 cm by 51 cm) or wire cages (25 cm by 52 cm) with a peat-wood shaving substrate and hay cover. Sunflower seeds, rye seeds, lab chow, and water were provided ad libitum. Greens, in the form of sprouted rye and sunflower, were supplied once a week. All animals were maintained on a 15L: 9D photoperiod.

Experiments were conducted in two 4' x 4' x ¼" Plexiglas tables which were joined by two Plexiglas tunnels. Each table contained a 1" peat substrate and extensive hay cover. Initial runways were constructed by the observer prior to the start of a run, to ensure immediate visibility from below the tables. Food, water, and photoperiod in the experimental rooms were similar to colony conditions.

To accurately assess pregnancy and to obtain individual breeding histories, all females were weighed weekly on a triple beam balance. The following information was recorded: 1) date, 2) weight, 3) birth of a litter, 4) number of pups born/present. The determination of pregnancy was based on two parameters; 1) significant weight gain and 2) palpation of the abdomen. Females used in this study had been paired with males with whom they had produced at least one previous litter and successfully reared to weaning.

Prior to placement of a pair into the tables, the female was weighed again and the ventral surface of the male was dyed with Nyanzol-D for identification purposes. Trial runs indicated no difference in behaviors between dyed males and those males without dye.

Data collection began with the birth of a litter and continued for twenty-five days thereafter. Females were observed from below the

tables for fifteen minutes each day between the hours of 9:00-11:00 A.M. Animals were removed from the tables and data collection stopped for the following reasons; 1) death of a litter, 2) unusually small litter size. Suitable litter sizes for each species were determined from values in the literature (Hasler, 1975) with slight adjustments made in accordance with the litter sizes observed in our laboratory (see Table 1). Determined litter sizes served only as guidelines to eliminate from the study those runs which involved unusually small litters. Larger litters were not culled in order to minimize disruption at the nest. In most instances, however, large litters were naturally reduced to an appropriate size within a few days of parturition.

Table 1. Determination of suitable litter sizes for each species.

Species	Average litter size (literature)	Average litter size (colony)	Litter sizes used
M. pennsylvanicus	5.5	4.2	4,5
M. pinetorum	1.8	2.5	2,3
M. ochrogaster	3.9	2.2	3,4

During each observation period, the frequency and duration of seventeen behaviors (see Table 2) were recorded using a More data acquisition system. Developmental information concerning the pups was also recorded. Physical parameters such as appearance of hair and eye opening were noted, in addition to the onset of the following behavioral characteristics; 1) eat solid food, 2) out of nest, 3) last observed nipple attachment. Paternal care, and nest number and location were noted in daily records.

Table 2. Behaviors.

1	grooming self	10	passive
2	grooming pup	11	approach male
3	contact	12	approach pup
4	retrieve	13	withdraw from male
5	nest building and maintenance	14	withdraw from pup
6	tunnel building and maintenance	15	female in/out of nest
7	food caching	16	male in/out of nest
8	eat or drink	17	nursing
9	locomote		

Results

Determination of species differences with respect to the frequency and duration of particular behaviors awaits the completion of future runs and final data analysis. Preliminary observations refer to eleven completed runs and four trial runs.

Male-female social interactions, spatial relationships, and degree of paternal care constitute the most obvious and consistent difference between the three species. M. pennsylvanicus males and females maintained separate nests and six out of seven females reacted aggressively toward males in the vicinity of the natal nest. Paternal care in this species was nonexistent. In contrast, M. pinetorum mates nested together and males participated in some parental activities such as grooming pups and nest building. Nest cohabitation was also observed in M. ochrogaster. In two of the three runs of this species a second, temporary nest was constructed in which the male occasionally brooded part of the litter while the female remained at the primary nest site with the remaining pups. Male prairie voles exhibited extensive paternal care in the form of brooding, retrieving, grooming, and nest building. Females were frequently observed to leave the nest upon the male's arrival and his immediate assumption of parental responsibilities. As a result, pups were rarely left unattended.

Length of period of maternal care and post-weaning spatial relationships differed somewhat between species. M. pennsylvanicus females stopped nursing and abandoned the nest when the pups were approximately two weeks old. Construction of a second nest by the female further ensured separate nesting by the male, female, and litter. Nursing and all other aspects of maternal care continued for close to three weeks in M. pinetorum and family members continued to share a nest for the length of a run. Cessation of nursing in M. ochrogaster occurred when the pups were two and a half to three weeks of age and communal nesting also persisted after weaning.

Physical parameters of pup development were similar in all three species. Fur appeared on approximately day three and eye opening occurred at the age of ten to twelve days. Pups were usually observed out of the nest within one day of eye opening. Last observed nipple attachment for M. pennsylvanicus pups varied from twelve to fourteen days and consumption of solid food was first noted on days thirteen and fourteen. Relative to M. pennsylvanicus, M. pinetorum pups showed slightly delayed development in these two behavioral parameters as nursing continued for twenty to twenty-one days and solid food was first consumed at the age of fifteen to eighteen days. Intermediate values of eighteen to twenty-one days for last observed nipple attachment and twelve to sixteen days for solid food consumption were obtained for M. ochrogaster pups.

Females of all three species frequently gave birth to a second litter during the twenty-five day run, thus permitting observation of female reactions to older offspring in the presence of a new litter. Six out of seven M. pennsylvanicus females reacted aggressively toward older offspring in the vicinity of the new nest. However, aggression was not continuously displayed and seemed to increase prior to and just following parturition. Females of the remaining two species, M. pinetorum and M. ochrogaster, were never observed to react aggressively toward older offspring and all family members continued to share a single nest.

Discussion

Observed species differences such as nesting pattern, male-female interactions, degree of paternal care, and reaction to older offspring, provide further evidence to support the proposed dissimilarities in mating system and social organization between the three species.

Radiotelemetric studies (Madison, 1980) indicate that during the breeding season, reproductively active female meadow voles are territorial, self-sufficient rearing units. M. pennsylvanicus females in the present study defended the nest against males and frequently were intolerant of older offspring in the vicinity of the new nest and litter. This pattern appears to support the self-sufficient maternal-young unit described by Madison (1980). Getz (1978) cites trapping data and laboratory results to suggest a promiscuous mating system in M. pennsylvanicus. Lack of a single case of sustained nest cohabitation in the field led Madison (1980) to the same conclusion. Intense intrasexual competition among males for access to receptive females exists in the meadow vole (Madison, 1980). Webster (1979) cites a field situation in which at least five males were observed in the vicinity of an estrous female, and four attempted mounting. Females in our study were extremely aggressive to males in the area of the natal nest. Nonselective aggression (displayed toward male and presumably toward other males) by female M. pennsylvanicus may be related to the occurrence of repeated copulations with different males and the resultant uncertainty of paternity. Aggression displayed by the female around the nest may represent an attempt to prevent infanticide by males. Finally, lack of paternal care and separate nesting seem to further imply a promiscuous mating system.

Based on trapping data, Paul (1970) proposed a loose, colonial social organization for the pine vole, in agreement with earlier anecdotal reports of scattered aggregations (Benton, 1955; Hamilton, 1938). In the present study, M. pinetorum individuals displayed a high degree of social tolerance. This was demonstrated most strongly by the communal nesting of the original breeding pair, older offspring, and new litter. Results suggest that the extended family may be the unit of colonial social organization.

Getz (1978) and Getz and Carter (1980) claim that at normal population densities, M. ochrogaster individuals exist in relatively stable family units in which only the founding pair contribute to population recruitment. The sustained nest cohabitation by all family members in the three completed M. ochrogaster runs in indicative of the proposed stable family group. In addition to reports of paternal care (Getz and Carter, 1980; Thomas and Birney, 1979), experimental studies which involve the behavioral and physiological factors controlling reproduction (Getz and Carter, 1980) strongly point to a monogamous mating system. Our documentation of extensive paternal care is therefore consistent with earlier reports. Male participation in care of the offspring may decrease the amount of time that the female must spend in the nest, thus allowing her increased time for foraging and other activities. Analysis of the frequency and duration of specific behaviors such as female in/out of nest, male in/out of nest, and eat or drink, may serve to reveal this trend.

M. pinetorum pups exhibited the longest nursing period. First consumption of solid food and last observed nipple attachment occurred at a later age in this species than in M. pennsylvanicus and M.

ochrogaster. Schadler and Butterstein (1979) note that the reproductive potential of M. pinetorum is lower than that of most other vole species. Litter sizes are small and puberty occurs at a relatively late age in both males and females. Delayed pup development seems to be consistent with this trend.

In conclusion, this system provides information which supports the different mating systems and social organizations which have been postulated for these three species in the field, and therefore appears to represent a viable method for observing microtines under laboratory conditions. It is anticipated that final results will provide information on the activities of female voles during the breeding period. Any observed differences in maternal behavior will further complete the comparison of the social biologies of M. pennsylvanicus, M. pinetorum, and M. ochrogaster.

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