

## Social and Environmental Factors Influence the Suppression of Pup-Directed Aggression and Development of Paternal Behavior in Captive Meadow Voles (*Microtus pennsylvanicus*)

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During summer, female meadow voles (*Microtus pennsylvanicus*) maintain territories and males do not engage in paternal care. As day length shortens, territories dissolve and males nest with females and young. Because paternal behavior has never been studied in free-living meadow voles during colder months or in the laboratory under short photoperiods, the authors examined whether males housed in short day (SD) lengths exhibited more frequent or better quality paternal behavior than males housed in long day (LD) lengths. Sexually and parentally inexperienced (naive) SD males exhibited proportionally more and qualitatively better paternal care than naive LD males. SD males were more responsive than LD males to classic social cues associated with prepartum aggression inhibition and paternal onset. SD sires also displayed qualitatively better paternal behavior than LD sires. These data suggest that meadow vole paternal state is regulated by specific social and environmental cues that may contain reliable information about ecological conditions that favor paternal care.

The majority of meadow vole breeding occurs during warmer months when males typically maintain overlapping and diffuse ranges that encompass the mutually exclusive territories of several adult females (Madison, 1980b). During this time, females provide sole parental care of preweaning young, and juveniles disperse immediately at weaning (Madison, 1980a). However, in early autumn, meadow voles are often found living in extended maternal family groups (Madison, FitzGerald, & McShea, 1984). In later fall, social nesting and breeding overlap in time, and reproductive males have been observed nesting and sleeping with females and preweaning young (Madison et al., 1984; Webster, 1979). As in other vole species, reproduction may occur year round; in autumn and winter in some years, up to 50% of meadow vole females are found with litters in the field (Christian, 1980; Tamarin, 1977), and in unusually warm winters, 100% of females may continue breeding (Webster & Brooks, 1981).

Although the presence of paternal care is often tied to social living and harsh breeding conditions (Trivers, 1972; Emlen & Oring, 1977; Kleiman & Malcolm, 1981; Clutton-Brock, 1991),

the possibility that free-living meadow voles initiate paternal attendance under the marginal breeding conditions that characterize autumn and winter months has not been investigated. However, other typically nonpaternal rodents engage in paternal care under similar circumstances (Kleiman & Malcolm, 1981; Lott, 1984). For example, free-living deer mice (Mihok, 1979), hoary marmots (Barash, 1975), and white-footed mice (Schug, Vessey, & Underwood, 1992) exhibit facultative paternal care during the colder months of the year. Limited observations of paternal attendance have been reported for nonpaternal Siberian dwarf hamsters (*Phodopus sungorus*) both in the field and in the laboratory (Wynne-Edwards, 1995), and in large, seminatural enclosures, typically nonpaternal collared lemmings (*Dicrostonyx richardsoni*; Gajda & Brooks, 1993) exhibit appreciable paternal behavior under a variety of circumstances. In all of these aforementioned cases, it has been suggested that the ability to provide paternal care evolved as a means to increase offspring survivorship during winter breeding.

In the laboratory, meadow voles show dramatic seasonal changes in development (Lee, Smale, Zucker, & Dark, 1987), reproductive behavior (Meek & Lee, 1993a, 1993b), maternal behavior (Reeves, 1994), and intraspecific social interactions and aggression (Ferkin, 1988a, 1988b; Ferkin & Gorman, 1992; Ferkin & Seaman, 1987) that are consistent with field studies and can be driven entirely by changes in photoperiod. Although meadow vole paternal behavior has been examined in the laboratory (Gruder-Adams & Getz, 1985; Hartung & Dewsbury, 1979; Oliveras & Novak, 1986; Storey, Bradbury, & Joyce, 1994; Storey & Joyce, 1995; Storey & Snow, 1987; Storey & Walsh, 1994; Wang & Novak, 1992; Wilson, 1982), no studies have investigated meadow vole paternal behavior under short photoperiods, when males would be most likely to exhibit paternal care in the field.

Thus, the goal of this series of experiments was to determine whether males housed under fall, short day lengths (SD), when males live socially with females and preweaning young in the

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field, would exhibit more frequent or better quality paternal behavior than males housed under summer, long day lengths (LD), when male and female meadow voles live separately in the field.

### Experiment 1

The goal of Experiment 1 was to determine whether SD-housed sires engaged in proportionally more or qualitatively better paternal behavior than sires housed under LD conditions. In some laboratory populations, LD males exhibit appreciable paternal care following delivery of the litter (Storey et al., 1994; Storey & Joyce, 1995; Storey & Snow, 1987). Because males may be more likely to exhibit paternal behavior under SD conditions, we predicted that when SD and LD males cohoused with females throughout pregnancy and parturition (which typically occurs under SD but not LD field conditions), SD sires would respond faster and more readily to pups when compared with LD sires.

### Method

**Subjects and housing conditions.** Subjects, derived from interbred wild-caught voles indigenous to northwestern Pennsylvania and southwestern New York, were born to breeding pairs in an established colony at the University of Michigan. Weanling meadow vole (*Microtus pennsylvanicus*) pups were removed from the dam and sire at 19 days of age and typically housed in same-sex sibling dyads in either LD (14 hr light–day) or SD (10 hr light–day) conditions. Voles were housed in 26.67 × 21.59 × 13.97-cm polypropylene cages on pine-shaving bedding with food (Purina Mouse Chow #5015; St. Louis, MO) and water available ad libitum. Animal rooms were maintained at 21 ± 2 °C with low ambient noise conditions. Voles remained so housed until the beginning of the experimental procedure.

**Experimental design.** A total of 30 sexually and parentally inexperienced (hereafter *naive*) adult male meadow voles ( $n = 18$  LD males;  $n = 12$  SD males) and 30 naive adult LD female meadow voles served as subjects. Because SD females rarely mate within 48 hr of pairing whereas nearly 100% of LD females do (Meek & Lee, 1993a, 1993b), we paired SD males with LD females to reduce variability in mating latency both within (i.e., SD) and between (SD vs. LD) groups. Test males were approximately 11 weeks of age, and females were roughly age matched for each experimental condition and ranged from 11 to 20 weeks of age.

Each male was paired with a female in a 10-gallon aquarium for videotaping (with ad lib access to food and water) to determine whether mating occurred. Pairs were housed in the male's photoperiod. During the dark phase of the light cycle, voles were continuously videotaped with a Panasonic camera and wide-angle lens on a time-lapse videocassette recorder using low-illumination red light. Each day, videotapes were watched to determine when mating occurred. Males that mated were transferred with their mates to a 48.26 × 26.67 × 20.32-cm cage, were placed in the proper photoperiod, and continuously cohoused with the female throughout her pregnancy (which lasts 21 days). Pairs were checked daily for litters, and males were tested for paternal behavior approximately 24 hr after delivery of the litter. Males paired with females that failed to give birth and females that did not give birth within 25 days after mating were excluded.

**Paternal behavior testing.** Each male was placed in a novel polypropylene 48.26 × 26.67 × 20.32-cm cage with fresh bedding. Males were allowed to become familiar with the new environment for 5 min, and then a 1-day-old pup from the sire's litter was introduced to the opposite end of the cage from the male. Male behavior was videotaped for 10 min. An experimenter was always present during the test. If any male was overtly aggressive to a pup (causing pup vocalization or injury), the pup was immediately removed from the cage and the test terminated. Attacked pups

were rarely injured, and consequently, they were returned to the home cage and reared normally by the parents.

**Data analysis.** On the basis of videotaped tests, male behavior was scored as pup aggressive (rough handling or charging pup, resulting in pup vocalization or injury), pup unresponsive (brief investigatory sniffing or no contacting or interacting with pup), or paternal (retrieval or grooming and huddling). Chi-square analysis was used to determine whether photoperiod affected the proportion of males that showed paternal behavior. The number and duration of specific types of interactions (sniffing and contacting the pup, grooming the pup, huddling over the pup, time spent near the pup, time spent alone far from the pup, number of approaches, and number of retrievals) were compared between LD and SD males using two-sample *t* tests (with Bonferroni corrections to protect against multiple comparisons). The latency to engage in any aggressive behavior and the latency to behave in any paternal behavior (see above) were compared between photoperiods using survival analysis, a statistical test that accounts for the probability of a behavioral event occurring during a fixed elapsed time period (Systat 7.0, Inc.).

### Results

Overall, 83% of sires displayed paternal behavior, 17% displayed pup-unresponsive behavior, and no voles displayed pup-aggressive behavior. Although photoperiod affected neither the proportion of males exhibiting these behaviors, Pearson  $\chi^2(1, N = 30) = 0.192$ , the frequency of specific pup-directed behaviors (e.g., approaching, retrieving, contacting, and grooming and huddling), nor the latency to initiate paternal activity,  $t(24) = 0.202$ , photoperiod did influence the quality of paternal attendance following delivery of the litter. Specifically, analyses conducted on only paternal voles ( $N = 26$ ) revealed that paternal SD sires engaged in longer grooming and huddling bouts,  $t(24) = 2.624$ ,  $p = .015$ , than LD sires. In contrast, LD sires displayed more investigatory behavior such as sniff counts,  $t(24) = 3.045$ ,  $p = .006$ , and sniff durations,  $t(24) = 3.335$ ,  $p = .003$ , and spent more time alone,  $t(24) = 2.065$ ,  $p = .050$ , than SD sires (see Figure 1).

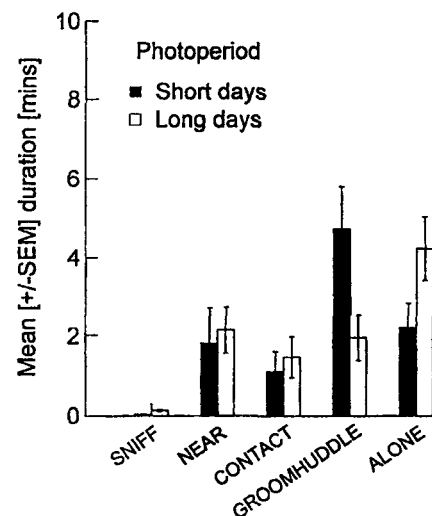


Figure 1. Mean ( $\pm$  SEM) long day (LD) and short day (SD) sire paternal behavior durations during 10-min paternal behavior tests with their own young 24-hr postpartum (frequencies not shown). \* Indicates a significant difference ( $p < .05$ ) between LD and SD males within behavior type.

## Experiment 2

Data from Experiment 1 indicated that although LD and SD males do not differ categorically in pup-directed behavior (i.e., the proportion of males that were pup aggressive, pup unresponsive, and paternal was not different between photoperiods), SD and LD sires do differ in paternal attendance quality. This finding supports the prediction that SD sires may more readily exhibit paternal care under field conditions, when they nest with pups. Voles, like other rodents (Howard, 1950), nest together for thermoregulatory reasons during colder months. Because pup exposure is a powerful regulator of paternal behavior in male rodents (rats; Rosenblatt, 1967), including meadow voles (Storey et al., 1994), we predicted that naive SD males (which are likely to be exposed to pups during overwinter nesting in the field) would exhibit more paternal care compared with naive LD males (which live alone under field conditions). Thus, the purpose of Experiment 2 was to examine whether SD males, compared with LD males, were more "prepared" to be paternal as naive animals.

### Method

SD ( $n = 64$ ) and LD ( $n = 61$ ) males were assessed for paternal behavior as naive animals between 11 and 13 weeks of age. Housing conditions, paternal behavior testing (except the use of alien, rather than own, pups), scoring, and data analysis were as delineated in Experiment 1.

### Results

A higher percentage of naive SD males exhibited paternal behavior compared with LD males, Pearson  $\chi^2(1, N = 125) = 5.724$ ;  $p = .017$ , and SD males exhibited paternal behavior faster than LD males,  $t(123) = 2.318$ ,  $p = .020$ . However, the proportion of SD and LD males exhibiting pup-unresponsive behavior,  $\chi^2(1, N = 125) = 2.826$ ;  $p = .093$ , and pup-aggressive behavior,  $\chi^2(1, N = 125) = 0.673$ ,  $p = .412$ , did not differ, nor did these males differ on latency to become aggressive,  $t(123) = 0.749$  (see Figure 2).

SD males engaged in retrieval, contacting, and grooming and huddling of pups significantly more often and for longer durations than LD males, whereas LD males spent more time far from the pup than SD males. However, LD and SD males did not differ on investigatory behaviors such as the number of pup approaches and amount of time spent near the pup, nor did they differ on sniffing counts or durations (see Table 1).

## Experiment 3

Previous research with LD meadow voles has shown that the onset of paternal behavior, in baseline pup-aggressive and pup-unresponsive naive males, occurs only after a 24-hr postpartum exposure to pups (following copulation and cohabitation with a female throughout her pregnancy and delivery; Storey et al., 1994). However, in fall, the ability to provide immediate postpartum paternal care might dramatically improve litter survivorship and confer increased fitness to SD males. In other rodent species, the suppression of pup-directed aggression or onset of paternal behavior may be regulated by prepartum social cues: copulation only (mice, Huck, Soltis, & Coppersmith, 1982; vom Saal & Howard, 1982; vom Saal, 1985), cohabitation with a pregnant mate (Mon-

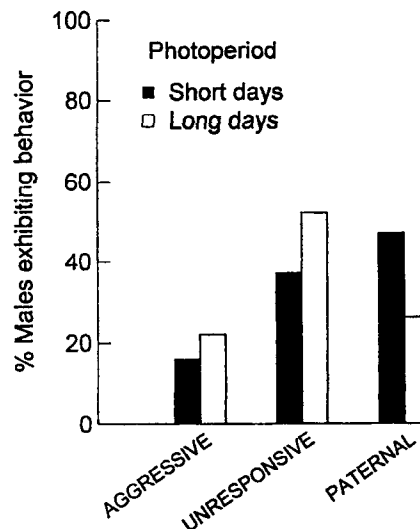


Figure 2. Proportion of males in each photoperiod that exhibited pup-aggressive, pup-unresponsive, or paternal behavior toward alien neonates during 10-min naive paternal behavior tests. \* Indicates a significant difference ( $p < .05$ ) between long day and short day males within behavior type.

golian gerbils, Elwood & Ostermeyer, 1984), and both copulation and cohabitation with a pregnant mate (mice, Elwood, 1985; rats, Brown, 1986).

Thus, the purpose of Experiment 3 was to examine whether SD and LD meadow voles differed in their ability to respond to prepartum social cues associated with the suppression of pup-directed aggression and onset of paternal behavior in other male rodents. Specifically, we hypothesized that SD males would respond faster and more readily to pups following brief cohabitation with a female without mating (Experiment 3A) and brief cohabitation with a female with mating (Experiment 3B) compared with LD males.

### Method

A total of 29 prescreened males ( $n = 15$  LD males: 7 pup-aggressive and 8 pup-unresponsive when naive;  $n = 14$  SD males: 7 pup-aggressive and 7 pup-unresponsive when naive) and 29 LD females served as subjects in Experiment 3A. It should be noted that 1 LD male and 1 SD male were not videotaped because of equipment failure. Thus, for these 2 males, although categorical assessment of behavior with pups was possible, quantitative measurement of behavior was not. A total of 43 males ( $n = 28$  LD males: 7 pup-aggressive and 21 pup-unresponsive;  $n = 15$  SD males: 6 pup-aggressive and 9 pup-unresponsive) and 43 LD females served as subjects in Experiment 3B. For both Experiments 3A and 3B, all test subjects were between 11 and 13 weeks of age. Only pup-aggressive and pup-unresponsive males were used in this experiment. Because prior research has shown that different mechanisms can be involved in the suppression of pup-directed aggression and in the onset of paternal behavior, particularly when male baseline behavioral states vary (Gubernick, Schneider, & Jeannotte, 1994), we chose to examine whether individual differences in baseline behavior influence the male's ability to respond to certain social cues associated with pup-directed aggression suppression and paternal behavior onset.

Approximately 1 day after assessing baseline paternal behavior (as in Experiment 2), each male was paired with an LD female, housed in the

Table 1  
*Mean and Standard Error of the Mean Frequency and Duration of Naive Male Behavioral Interactions With Pups*

Behavior	Measure	Naive long day males ( <i>n</i> = 61)		Naive short day males ( <i>n</i> = 64)		<i>t</i> (123)	<i>p</i> <sup>a</sup>
		<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>		
Sniffing	Frequency <sup>b</sup>	2.08	0.48	3.61	0.70	1.79	.379
	Duration <sup>c</sup>	0.11	0.03	0.11	0.02	0.21	1.000
Retrieving	Frequency	0.02	0.01	0.45	0.14	3.00	.016
Contacting	Frequency	1.74	0.48	6.16	1.13	3.54	.003
	Duration	0.34	0.13	1.06	0.23	2.70	.040
Grooming and huddling	Frequency	1.00	0.29	3.78	0.65	3.84	.001
	Duration	0.19	0.07	1.20	0.23	4.08	.001
Approaching	Frequency	2.46	0.72	5.25	0.89	2.42	.084
	Duration	0.58	0.18	0.59	0.16	0.03	1.000
Alone	Duration	8.81	0.30	7.03	0.43	3.35	.005

<sup>a</sup> Significance was set at  $p < .05$ ; all  $p$  values represent Bonferroni-corrected probabilities. <sup>b</sup> Frequency =  $M (\pm SEM)$  frequency of occurrence per 10-min test. <sup>c</sup> Duration =  $M (\pm SEM)$  duration of occurrence per 10-min test.

male's photoperiod, and assessed for mating as in Experiment 1. Males that did not mate were designated as Experiment 3A subjects and were tested for paternal behavior after 24–36 hr of brief cohabitation without mating (hereafter, *unmated cohabitation*), whereas males that did mate were designated as Experiment 3B subjects and were tested for paternal behavior after 24–36 hr of brief cohabitation with mating (hereafter, *mated cohabitation*). Mated cohabitation was defined as more than two observed copulatory episodes. Statistical analyses were performed within experimental condition (i.e., 3A and 3B subjects were not compared) and within baseline behavior type (i.e., baseline pup-aggressive and pup-unresponsive males were not compared), but were otherwise the same as delineated in Experiment 1.

## Results

**Experiment 3A.** Unmated cohabitation with a female did not affect SD or LD behavior in pup-aggressive males. However, in pup-unresponsive males, SD males exposed to a female for brief, unmated cohabitation were significantly more paternal, Pearson  $\chi^2(1, N = 15) = 11.484, p = .001$  (see Figure 3), engaged in paternal behavior faster,  $t(11) = 2.503, p = .012$ , and exhibited more grooming and huddling,  $t(11) = 2.807, p = .017$ , and investigatory,  $t(11) = 2.162, p = .054$ , behaviors than LD males. In summary, 24–36 hr of unmated cohabitation with a female did not change baseline pup-aggressive behaviors in either photoperiod. However, in baseline pup-unresponsive males, brief, unmated cohabitation induced the onset of paternal behavior in 100% of SD males but exposure to a female did not improve LD male behavior on any measure.

**Experiment 3B.** For naive aggressive males, exposure to a female for 24 hr of mated cohabitation suppressed aggression to pups (but did not induce paternal behavior) in SD but not LD males,  $\chi^2(1, N = 13) = 9.551, p = .002$  (see Figure 4). Mated cohabitation did not significantly alter behavior of either LD or SD baseline pup-unresponsive males.

## Discussion

This series of experiments determined that photoperiod is a predictor of the timing and quality of paternal behavior in meadow

voles. In summary, naive SD males exhibit proportionally more and better paternal care than naive LD males (Experiment 2). Short photoperiods also permit meadow voles to respond to social cues associated with suppression of pup-directed aggression and onset of paternal behavior reported for other rodent species (Brown, 1986; Elwood & Ostermeyer, 1984; Huck et al., 1982). Specifically, 24 hr of unmated cohabitation with a female induces paternal behavior in previously pup-unresponsive males, and 24 hr of mated cohabitation suppresses pup-directed aggression in previously pup-aggressive males (Experiment 3). Short photoperiods also enhance a male's ability to respond to social cues (e.g., presence of pups) after the delivery of a litter. In both LD and SD males, mated cohabitation and exposure to pups are powerful regulators of the expression of paternal behavior (Storey et al., 1994; Experiment 1). However, these cues appear to be more

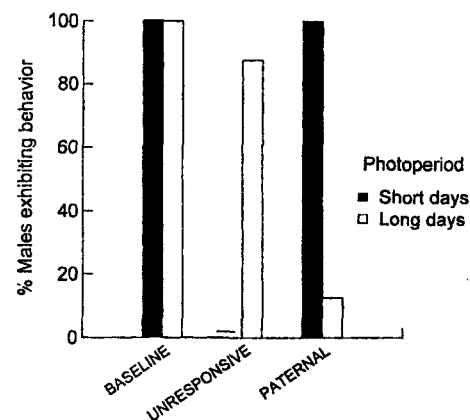


Figure 3. Proportion of baseline pup-unresponsive males in each photoperiod that exhibited pup-unresponsive or paternal behavior after 24 hr of unmated cohabitation with a female during 10-min paternal behavior tests. Line indicates there were zero values for this group. \* Indicates a significant difference ( $p < .05$ ) between long day and short day males within behavior type.

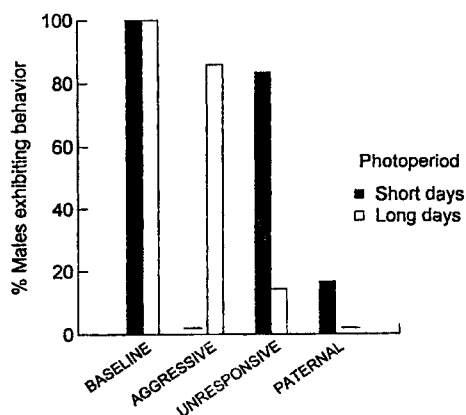


Figure 4. Proportion of baseline pup-aggressive males in each photoperiod that exhibited either pup-aggressive, pup-unresponsive, or paternal behavior following 24 hr of mated cohabitation with a female during 10-min paternal behavior tests. Lines indicate there were zero values for these groups. \* Indicates a significant difference ( $p < .05$ ) between long day and short day males within behavior type.

salient when presented in short photoperiods, as SD sires display qualitatively better paternal behavior following 24 hr of pup exposure when compared with LD sires.

Under summer photoperiods, neither living with a female (with or without mating) nor extended cohabitation with a pregnant female mate had an effect on LD male behavioral interactions with neonates. Similar to rats (Rosenblatt, 1967), exposure to pups was the most potent regulator of pup-directed aggression suppression and paternal behavior onset. This is consistent with the published literature (Storey & Joyce, 1995) and suggests that the mechanisms that regulate pup-directed aggression suppression and paternal behavior onset in LD males cannot be decoupled in time prior to parturition.

In contrast to LD meadow voles, males housed under winter photoperiods are more likely to be paternal prior to pup exposure (50% of SD males vs. 25% of LD males) and are also capable of suppressing pup-directed aggression or displaying paternal behavior after only brief mated or unmated cohabitation (respectively) with a female (Experiment 2). Like California mice (Gubernick et al., 1994), the mechanisms that regulate the inhibition of pup-directed aggression and the development of paternal behavior in SD males can be decoupled in time prior to the delivery of the litter and are sensitive to different social and environmental inputs. Although it is clear that short photoperiods enhance the male meadow vole's ability to respond to these prepartum social cues (when compared with LD males), individual variation in baseline paternal behavior (e.g., aggressive, nonpaternal, paternal) is also an important factor in determining whether SD males suppress pup-directed aggression or display paternal behavior after exposure to social cues. However, exactly why this occurs is unclear and merits investigation.

In light of the finding that LD and SD males respond to different social cues in the laboratory, it seems likely that LD and SD males develop paternal behavior in response to different socioecological circumstances under free-living conditions. During the summer breeding season, paternal behavior is not necessary for pup sur-

vival but may represent a facultative male strategy to offset fitness costs associated with reduced mating opportunities under low-density populations (Clutton-Brock, 1991; Kleiman & Malcolm, 1981; Lott, 1984; Trivers, 1972). Thus, for LD males, paternal behavior most likely occurs when extensive time is spent at the natal nest postpartum, and this may account for why LD males fully develop paternal care only after postpartum sensitization to pups (Storey & Walsh, 1994). For SD males, paternal behavior most likely occurs for two reasons: breeding conditions are such that they necessitate biparental care for offspring survival (e.g., intense thermoregulatory demands of the litter) combined with restricted access to mates (e.g., low-density breeding conditions), both of which characterize overwintering groups (reviewed by Tait & Krebs, 1985). For these reasons, prepartum exposure to a pregnant female would be a valuable cue to ensure that males are capable of providing paternal care immediately postpartum to improve litter survivorship over those requiring a 24-hr sensitization period (as previously reported for LD male meadow voles; Storey & Walsh, 1994). Such prepartum onset of paternal behavior has been documented for several rodent species in which males aid in immediate postpartum care of young (Mongolian gerbils, Elwood & Ostermeyer, 1984; California mice, Gubernick & Nelson, 1989; prairie voles, Bamshad, Novak, & DeVries, 1994; Djungarian dwarf hamsters, Jones & Wynne-Edwards, 2000).

In conclusion, this series of experiments provides the first evidence that day length is a strong environmental regulator of paternal care in meadow voles. Moreover, photoperiod, in combination with specific social variables associated with fall and winter breeding conditions (i.e., social living), may convey reliable information to free-living meadow voles about conditions that favor paternal care. Our laboratory data also suggest that it would be valuable to examine whether free-living meadow voles exhibit paternal behavior in response to seasonal changes in ecology (e.g., photoperiod, population density, temperature).

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