Species Differences in the Vasopressin-Immunoreactive Pathways in the Bed Nucleus of the Stria Terminalis and Medial Amygdaloid Nucleus in Prairie Voles (*Microtus ochrogaster*) and Meadow Voles (*Microtus pennsylvanicus*)

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Vasopressin-immunoreactive (AVP-ir) cells in the bed nucleus of the stria terminalis (BST) and medial amygdaloid nucleus (MA) and their AVP-ir projections to the lateral septum were studied in monogamous prairie voles (*Microtus ochrogaster*) and promiscuous meadow voles (*M. pennsylvanicus*). A sexually dimorphic AVP-ir pathway was found in both species; males had more AVP-ir cells in the BST and MA, as well as denser AVP-ir fibers in the lateral septum, than did females. A significant species difference was also found. Overall, meadow voles had more AVP-ir cells in the BST and MA than did prairie voles. Male prairie voles, however, had a higher density of AVP-ir fibers in the lateral septum than male meadow voles. The species difference in the sexually dimorphic AVP-ir projections in the BST and MA is implicated in the rodents' different life strategy and behavior.

Rodents show remarkable diversity in social organization and parental behavior. At one end of the spectrum, animals such as meadow voles (*Microtus pennsylvanicus*) live in mother–young cohorts in which mothers are the unique providers of parental care. At the other end of the spectrum, animals such as prairie voles (*M. ochrogaster*) live in extended-family groups in which both parents share the responsibility for rearing of young (Gruder-Adams & Getz, 1985; Oliveras & Novak, 1986; Wang & Novak, 1992). To explain this variation in reproductive strategies, studies have been carried out to correlate ecological factors with behavior and to examine the selective pressures that are responsible for the evolution of behavior (Gruder-Adams & Getz, 1985; Wang & Novak, 1992; Wilson, 1982).

A recent approach, however, is to study central neural systems that may contribute to the aforementioned species differences in reproductive strategies. For example, oxytocin has been implicated in maternal behavior, and variations in the distribution of oxytocin receptors in the brain are associated with different social organization and behavior in voles (Insel & Shapiro, 1992). Sexually dimorphic vasopressin-immunoreactive (AVP-ir) projections in the lateral septum have been implicated in behavior and a number of functions that change during reproduction (Kasting, Veale, & Cooper, 1978; Koolhaas, Van den Brink, Roozendaal, & Boorsma, 1990; Landgraf, Neumann, & Pittman, 1991). Recently, it was found that

in monogamous prairie voles, the density of AVP-ir fibers in the lateral septum was lower in fathers than in sexually naive males. No such difference was seen in promiscuous meadow voles (Bamshad, Novak, & De Vries, 1993).

Studies of other rodent species indicate that the lateral septum receives AVP-ir projections from the bed nucleus of the stria terminalis (BST) and medial amygdaloid nucleus (MA; Caffe & Van Leeuwen, 1987; De Vries & Buijs, 1983; De Vries, Buijs, Van Leeuwen, Caffe, & Swaab, 1985). The AVP-ir cells in these areas have not been studied in voles. Therefore, in the present study, I examined AVP-ir cells in the BST and MA as well as their AVP-ir projections in the lateral septum in prairie and meadow voles. The purpose for the current study was twofold: (a) to examine whether sexually dimorphic patterns of AVP-ir cells are present in the BST and MA and (b) to determine whether there are species differences in these pathways that may be implicated in differences in social strategy and behavior in voles.

Method

The F$_3$ generation of the laboratory breeding colony of prairie voles (*M. ochrogaster*) and meadow voles (*M. pennsylvanicus*) was used in the study. The subjects of each species were housed in same-sex pairs in plastic cages (26 × 30 × 51 cm) that contained peat moss, wood chips, and a substantial amount of hay covering. Food and water were provided ad libitum. All cages were maintained on a 14:10-hr light–dark photoperiod, with lights on at 0600 hr. The temperature was kept at about 20 °C.

At 70–90 days of age, 17 prairie voles (8 females and 9 males) and 14 meadow voles (7 females and 7 males) were stereotaxically injected with colchicine (15 μg/50 g body weight) into the lateral ventricle under ketamine anesthesia (2.5 mg/50 g body weight). Two days later, all subjects were deeply anesthetized and perfused through the ascending aorta with 0.9% saline followed by 5% (vol/vol) acrolein in 0.1 M phosphate buffer (pH 7.6). The brains were removed, and 35-μm transverse sections were cut with a vibratome. The floating

sections were then processed for AVP immunocytochemistry (Bamshad et al., 1993).

To reduce variability in the background, all sections were processed in the same immunocytochemical staining. Sections were pretreated with 0.1% sodium borohydride for 15 min, rinsed three times for 15 min each in 0.05 M Tris-HCl (pH 7.6) containing 0.9% NaCl (Tris-NaCl), and then incubated with the following solutions: (a) Tris-NaCl with 0.3% Triton X-100 (Tris-Triton) and 20% goat serum, 15-min incubation; (b) anti-AVP serum (ICN, Immunobiologicals, Lisle, IL) 1:8,000 in Tris-Triton containing 2% goat serum (Tritrigo), 1.5 hr incubation at 37 °C; (c) Tritrigo, 3 × 15-min rinse at 37 °C; (d) biotinilated goat–anti-rabbit in Tritrigo, 45-min incubation at room temperature; (e) Tritrigo, two 15-min rinses, followed by one 15-min rinse in Tris-NaCl; (f) ABC complex in Tris-NaCl, 45-min incubation; (g) Tris-NaCl, with three 15-min rinses; (h) 0.05% 3-3'-diaminobenzidine in Tris-NaCl with 0.0015% H_2O_2, 25-min incubation. After three rinses in Tris-NaCl, sections were mounted on slides, air-dried, and coverslipped. Specific staining was not observed in control sections incubated with rabbit anti-AVP that was pretreated with 50 μM AVP. Furthermore, specific staining was observed in control sections incubated with rabbit anti-AVP that was pretreated with 50 μM oxytocin.

The number of AVP-ir cells in the BST and MA on each side of the brain was identified in bright-field microscopy and counted in four consecutive sections that spanned the area with the highest number of AVP-ir cells (corresponding to Plates 20–22 in the atlas of Paxinos & Watson [1986] for the BST and Plates 28–30 for the MA). The density of AVP-ir fibers in the lateral septum was measured bilaterally in the two consecutive sections that contained the highest fiber density (corresponding to Plate 19 in the atlas of Paxinos & Watson). The slides were studied with a Zeiss Axioscope. Images of fibers were obtained with the 20× objective and a CCD 72 camera (Dage, MTI, Michigan City, IN) connected to a QuickCapture frame grabber board (Data Translation Inc., Marlboro, MA) in a Macintosh IIfx computer and analyzed with the Image 1.44 program (Rasbaud, 1992). To standardize measurements, the light and camera settings were kept constant across the brain sections so that the density of the background remained the same for all sections. The AVP-ir fiber density was counted with the use of computerized gray-level thresholding (Shipley, Luna, & McLean, 1989) by displaying the image in two colors, one corresponding to pixels below a variable set point and one to pixels equal to or above that set point. The set point was established at the level at which fibers appeared in one color and background in another. The number of pixels representing images of the fibers were determined in a 200 × 250-μm sampling area immediately bordering the lateral ventricle and centered along the length of ventricular wall. This sampling area covered the densest part of the plexus of AVP-ir fibers in the lateral septum. Cell counts and analysis of fiber densities were done in coded sections so that the experimenter could not know the identity of the specimens.

For each subject and for each side of the brain, the peak number of AVP-ir cells in the BST or MA, as well as the density of AVP-ir fibers in the lateral septum, was chosen. The averages from both sides of the brain in each area were used for data analysis. The data were analyzed by a two-way analysis of variance (ANOVA) with species and sex as between-subjects variables. Significant interactions were further examined by a Newman–Keul's post hoc test.

Results

AVP-ir Cells in the BST and MA

AVP-ir cell bodies that were either multipolar or bipolar were found in the BST and MA. Overall, males had more AVP-ir cells in the BST, $F(1, 27) = 60.7$, $p < .0001$ (see Figures 1 and 2), and MA, $F(1, 27) = 64.4$, $p < .0001$ (see

Figure 3), compared with females. In addition, a species difference was found; prairie voles had fewer AVP-ir cells in the BST, $M = 57.3$, $SE = 8.9$, $F(1, 27) = 4.7$, $p < .05$, and MA, $M = 14.8$, $SE = 2.8$, $F(1, 27) = 9.3$, $p < .01$, than meadow voles had ($M = 72.3$, $SE = 10.5$, for the BST and $M = 22.8$, $SE = 4.2$, for the MA). No Sex × Species interactions were detected in the numbers of AVP-ir cells in both areas.

AVP-ir Fibers in the Lateral Septum

AVP-ir fibers were found in the lateral septum. These fibers were also sexually dimorphic, in that males had denser AVP-ir fibers than females had, $F(1, 27) = 87.1$, $p < .0001$ (see Figures 4 and 5). In contrast to the number of AVP-ir cells, prairie voles had denser AVP-ir fibers in the lateral septum than meadow voles had, $F(1, 27) = 9.5$, $p < .01$. A Sex × Species interaction was also found, $F(1, 27) = 7.0$, $p < .05$. The post hoc test indicated that male prairie voles had denser AVP-ir fibers than male meadow voles had, whereas no difference was found between females.

AVP Immunoreactivity in Other Areas of the Brain

AVP-ir cells were also found in dense clusters in the supraoptic, suprachiasmatic, and paraventricular nuclei. In addition, AVP-ir fibers were present in the paraventricular, dorsomedial, and lateral habenular nuclei, as well as in the medial preoptic area of the brain. However, none of these nuclei or fibers showed any notable sex or species differences except for AVP-ir fibers in the lateral habenular nucleus, in which males showed higher density of AVP-ir fibers than females.

Discussion

Male prairie and meadow voles have a higher density of AVP-ir projections in the lateral septum and lateral habenular nucleus than do females of either species (Bamshad et al., 1993, 1994). The present study confirmed that finding and extended the observation to the BST and MA—the brain areas from which AVP-producing cells project into the lateral septum and lateral habenular nucleus (Caffe & Van Leeuwen, 1987; De Vries & Buijs, 1983; De Vries et al., 1985). In the current study, males had more AVP-ir cells in the BST and MA and a higher density of AVP-ir projections in the lateral septum and lateral habenular nucleus compared with females. These data suggest that sexually dimorphic AVP pathways in the BST and MA in voles closely resemble those in other species of rodents, such as rats, mice, hamsters, and gerbils (Bittman, Bartness, Goldman, & De Vries, 1991; Crenshaw, De Vries, & Yahr, 1992; Hermes, Buijs, Masson-Pevet, & Pevet, 1990; Van Leeuwen, Caffe, & De Vries, 1985).

Although both prairie and meadow voles showed a similar sexual dimorphism in AVP-ir pathways from the BST and MA, a species difference was found. Meadow voles had more AVP-ir cells in the BST and MA than prairie voles had. Male prairie voles, on the other hand, had a higher density of AVP-ir fibers in the lateral septum than did male meadow voles. This species difference was also found in previous studies, in which
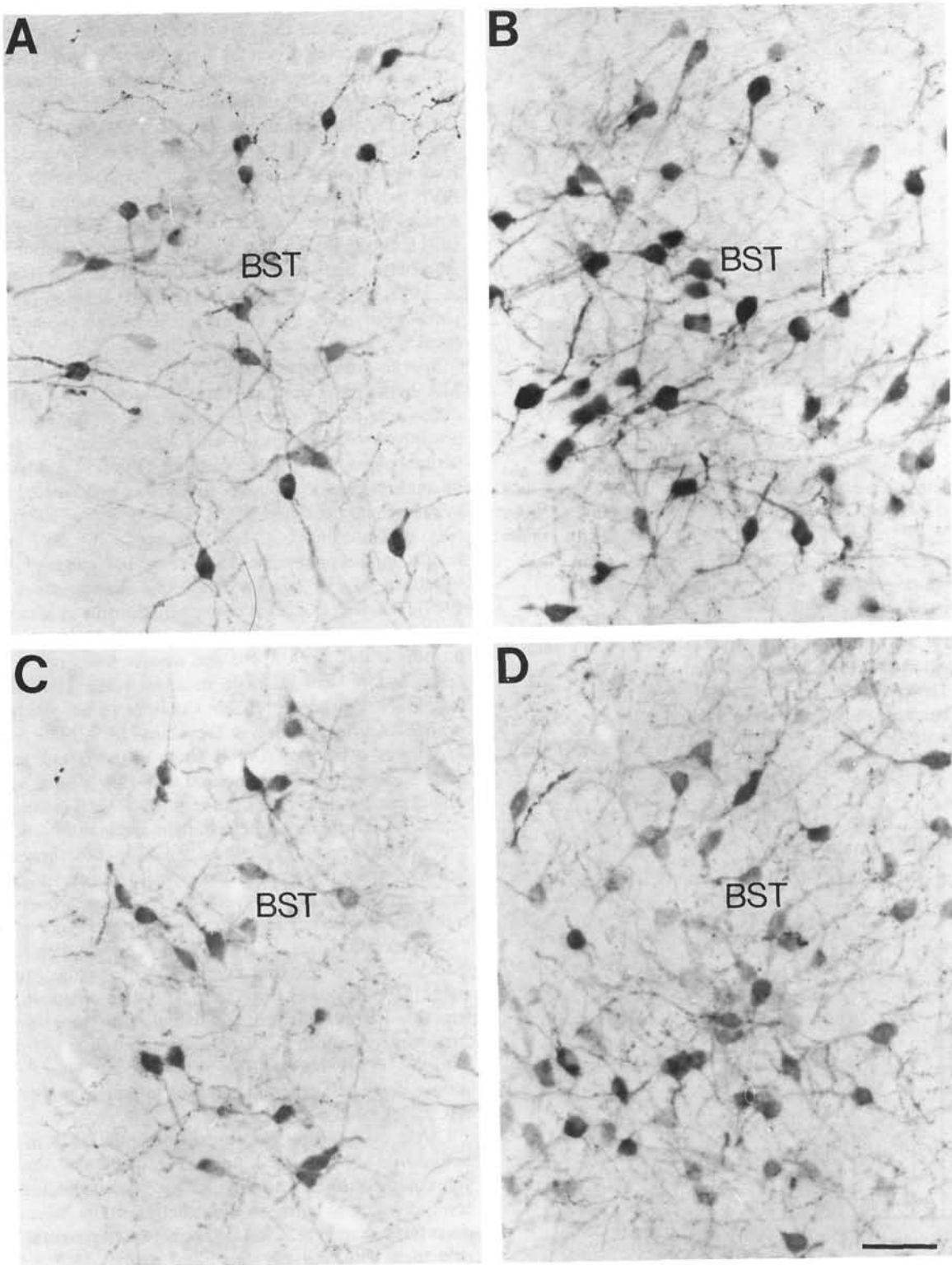
Figure 1. Photomicrographs displaying vasopressin-immunoreactive cells in the bed nucleus of the stria terminalis (BST) in a meadow vole female (A) and male (B) and a prairie vole female (C) and male (D). Scale bar = 50 μm.
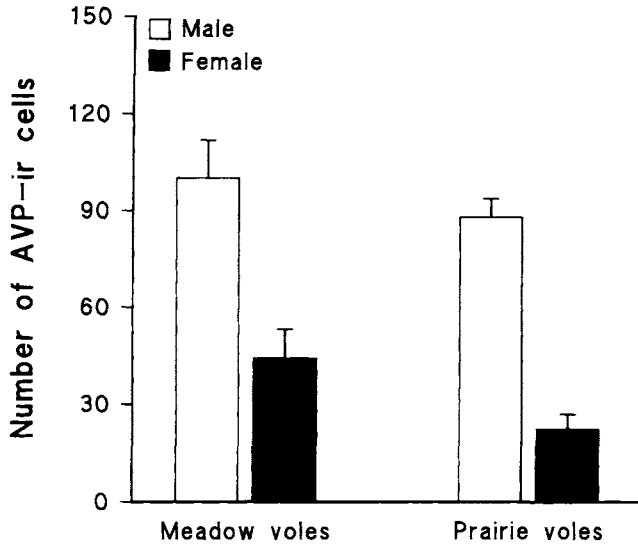
Figure 2. Mean number of vasopressin-immunoreactive (AVP-ir) cells in the bed nucleus of the stria terminalis of meadow voles and prairie voles. Males had more AVP-ir cells than females had ($p < .0001$). Overall, meadow voles had more AVP-ir cells than prairie voles had ($p < .05$). Error bars indicate standard errors of the means.

meadow voles seemed to have more BST cells labeled for AVP mRNA and a lower density of AVP-ir fibers in the lateral septum than prairie voles (Bamshad et al., 1993; Wang, Smith, Major, & De Vries, 1994).

In the current study, voles were treated with colchicine to visualize AVP-ir cells in the BST and MA. A previous study
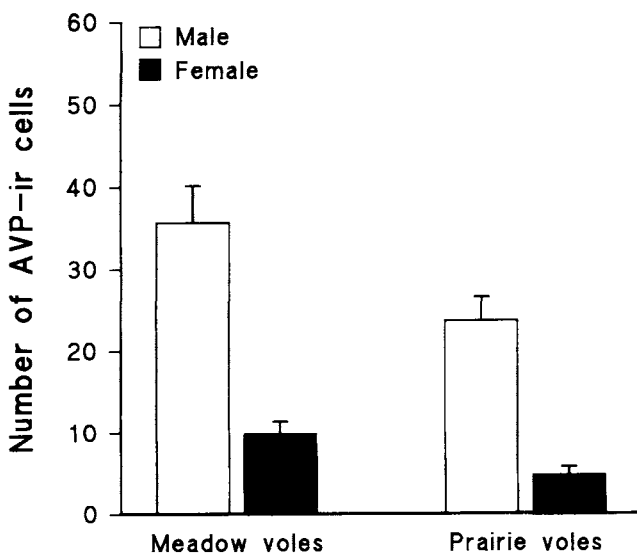

Figure 3. Mean number of vasopressin-immunoreactive (AVP-ir) cells in the medial amygdaloid nucleus of meadow voles and prairie voles. Males had more AVP-ir cells than females had ($p < .0001$). Overall, meadow voles had more AVP-ir cells than prairie voles had ($p < .01$). Error bars indicate standard errors of the means.

suggested that biosynthesis of several neurotransmitter systems is influenced by colchicine and that the direction of this effect depends on the particular transmitter and the site of synthesis (Cortes, Ceccatelli, Schalling, & Hokfelt, 1990). In studies of rats, however, colchicine treatment did not influence the number of AVP mRNA-labeled cells in the BST (Miller, De Vries, Al-Shamma, & Dorsa, 1992) or the density of AVP-ir fibers in the lateral septum (G. J. DeVries, personal communication, Oct. 1994). Although colchicine effects on AVP pathways in voles have not been studied, the sex and species differences in the AVP-ir fibers and AVP-producing cells found in this study are similar to those found in previous studies that did not include colchicine treatment (Bamshad et al., 1993; Wang et al., 1994), suggesting that such differences in the AVP-ir pathways are not attributed to colchicine treatment.

Species differences in the AVP-ir pathways in the BST and MA between prairie and meadow voles may reflect their differences in behavior. For example, the BST and MA, and possibly the AVP pathways within these areas, are involved in sexual behavior in rodents. Lesioning the BST or MA disrupts intromission and ejaculatory patterns of male sexual behavior in rats (Emery & Sachs, 1976; Harris & Sachs, 1975). Castration, which reduces AVP-ir staining in the BST and MA, results in disappearance of male sexual behavior, whereas injections of AVP agonist delays this disappearance (Bohus, 1977). Behavioral studies suggest differences in sexual behavior between prairie and meadow voles. Male prairie voles intromit with slower thrusts and require fewer ejaculations to reach satiety than do male meadow voles. However, male meadow voles show a reliable Coolidge effect, whereas male prairie voles do not (Gray & Dewsbury, 1973, 1975).

A lower density of AVP-ir fibers in the lateral septum of male meadow voles as compared with male prairie voles may reflect species differences in the physiological involvement of septal AVP in parental behavior. In seminatural and laboratory conditions, male meadow voles do not show parental behavior toward litters, whereas male prairie voles exhibit considerable parental care, such as grooming, crouching over, touching, and retrieving their pups (Gruder-Adams & Getz, 1985; Oliveras & Novak, 1986; Wang & Novak, 1992). There is evidence suggesting that central AVP may be involved in parental behavior. Long-Evans rats, for example, display superior parental behavior in comparison with Brattleboro rats, which have an AVP deficiency mutation (Wideman & Murphy, 1990). Injections of AVP into the lateral ventricle induce persistent parental behavior in female rats (Pedersen, Asche, Monroe, & Prange, 1982).

Direct evidence of involvement of septal AVP in parental behavior in voles can be found in recent studies. Male prairie voles that cohabited with a female for 3 days exhibited a higher level of parental behavior than their sexually naive counterparts (Bamshad et al., 1994). This increased parental behavior coincided with possibly increased septal AVP release, as indicated by reduced AVP-ir staining in the lateral septum, increased AVP mRNA expression in the BST, and increased level of plasma testosterone (Bamshad et al., 1994; Wang et al., 1994). Injections of AVP into the lateral septum enhanced parental behavior, whereas injections of the AVP antagonist
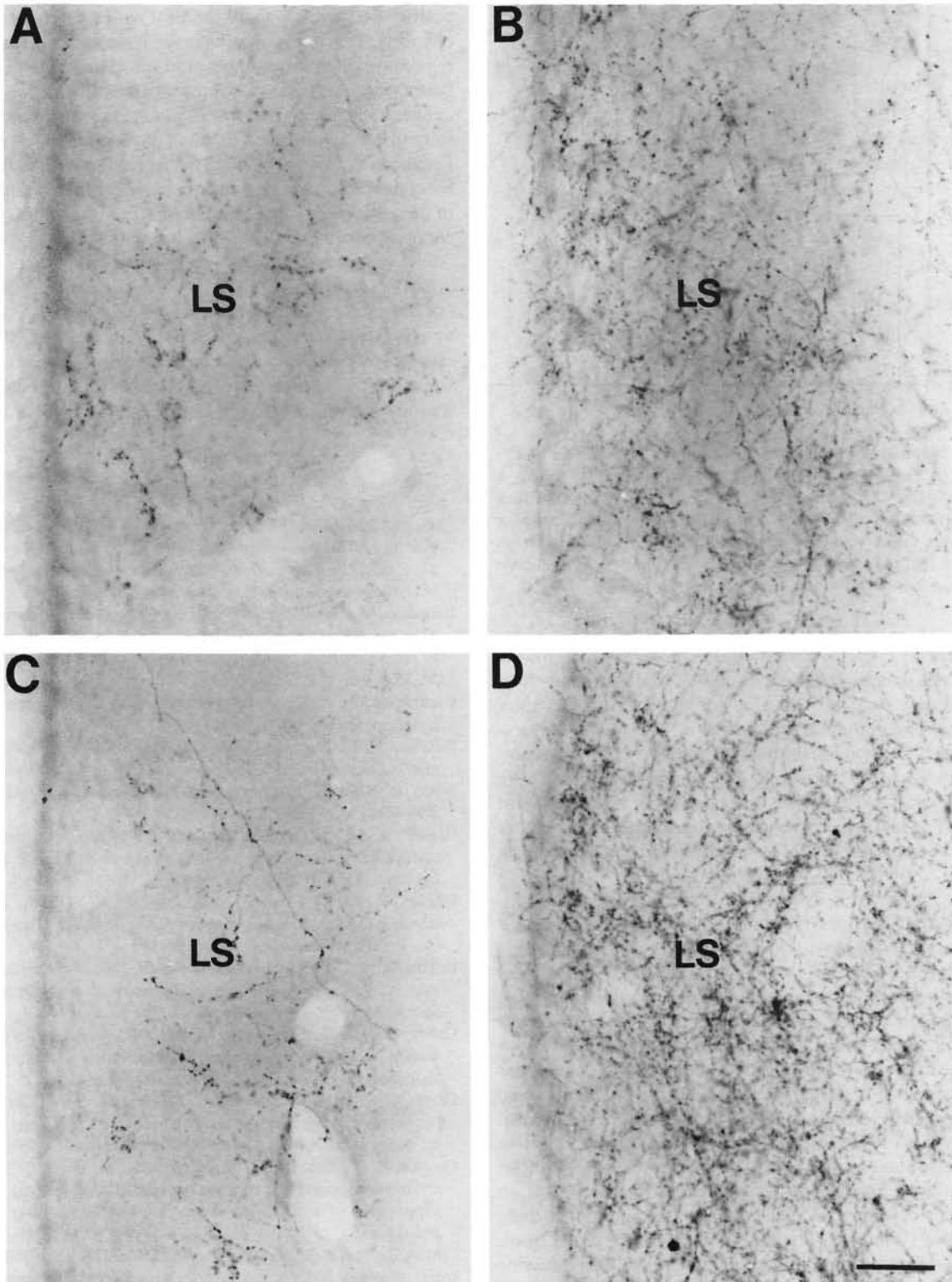
Figure 4. Photomicrographs displaying vasopressin-immunoreactive fibers in the lateral septum (LS) of a meadow vole female (A) and male (B) and a prairie vole female (C) and male (D). Scale bar = 50 μm.
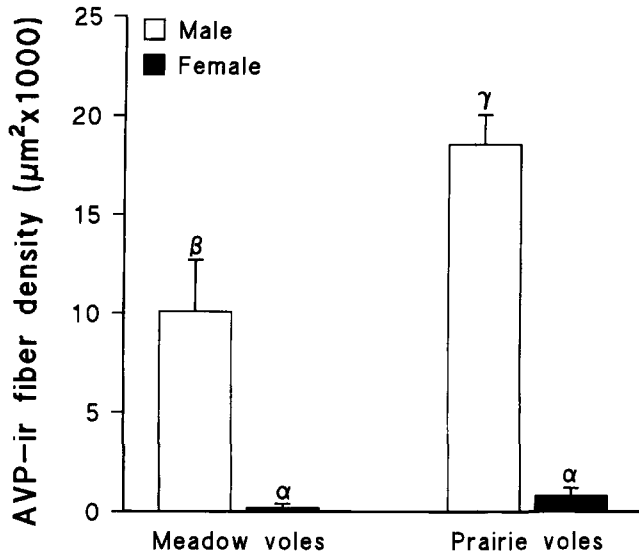
Figure 5. Mean area covered by vasopressin-immunoreactive (AVP-ir) fibers in the lateral septum of meadow and prairie voles. A significant Species × Sex interaction was found ($p < .05$). The Greek letters represent the post hoc test results: The AVP-ir fiber density for meadow vole males was lower than that of prairie vole males but higher than that of females. No difference was found between female groups. Error bars indicate standard errors of the means.

diminished AVP effects on parental behavior of male prairie voles (Wang, Ferris, & De Vries, 1994). Male meadow voles neither display parental behavior nor show changes in their AVP-ir staining in the lateral septum or AVP mRNA expression in the BST after cohabiting with females or after becoming fathers (Bamshad et al., 1993; Oliveras & Novak, 1986; Wang et al., 1994). These data suggest that the higher levels of septal AVP in male prairie voles may contribute to their higher levels of parental activity in comparison with male meadow voles.

AVP-ir innervations in the lateral septum are also implicated in other behaviors in rodents. For example, septal AVP release is involved in conspecific recognition and social memory in rats (Bluthe & Dantzer, 1990; Bluthe, Schoenen, & Dantzer, 1990). Prairie voles recognize and accept familiar partners versus strangers. Under multiple-mate situations, prairie voles show preferences for the familiar partner and aggression toward the unfamiliar conspecifics, whereas promiscuous voles do not show such behavior (Carter, Getz, & Cohen-Parsons, 1986; Dewsbury, 1987; Fuentes & Dewsbury, 1984). Central infusions of AVP induced partner preference and selective aggression, whereas infusions of the AVP antagonist reduced mating-induced changes in these behaviors, suggesting an involvement of central AVP in partner recognition in male prairie voles (Winslow, Hastings, Carter, Harbaugh, & Insel, 1993). The effects of central manipulation of AVP on behavior of promiscuous voles need to be further studied.

In addition to behavioral effects, septal AVP has also been implicated in physiological functions such as temperature regulation and osmoregulation (Cooper, Kasting, Lederis, & Veale, 1979; Demotes-Mainard, Chauveau, Rodriguez, Vin-

cent, & Poulain, 1986; Landgraf, Neumann, & Schwarzberg, 1988; Naylor, Ruwe, Kohut, & Veale, 1985). In nature, male prairie voles usually share the nest with the female and their offspring. This group-nesting may influence their temperature regulation differently than would individual nesting. In addition, these males exhibit extensive parental behavior, including anogenitally licking their pups, which may involve ingestion of salty urine, as observed in rats (Baverstodk & Green, 1975; Friedman & Bruno, 1976). Therefore, these males may need functional mechanisms to compensate for the presumable rise in the osmolarity of ingested fluids (Bamshad et al., 1993). In contrast, because male meadow voles neither live in extended-family groups nor anogenitally lick their pups, they may face different challenges regarding their thermoregulation and osmoregulation. Therefore, differences in septal AVP-ir projections may also reflect the different physiological involvement of central AVP in prairie and meadow voles. Nevertheless, the actual mechanisms underlying AVP effects on behavior and reproductive strategy in voles need to be further studied.

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