Post-castration retention of reproductive behavior and olfactory preferences in male Siberian hamsters: Role of prior experience

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Abstract

Reproductive behavior of virtually all adult male rodents is dependent on concurrent availability of gonadal steroids. The ejaculatory reflex is incompatible with long-term absence of testicular steroids and typically disappears within 3 weeks after castration. Male Siberian hamsters are an exception to this rule; mating culminating in the ejaculatory reflex occurs as many as 6 months after castration (persistent copulation). The emergence of persistent copulation many weeks after gonadectomy is here shown not to require repeated post-castration sexual experience. Preoperative sexual experience, on the other hand, significantly increases the percent of males that copulate after gonadectomy, but is not required for the emergence of this trait in 25% of males. Castration prior to puberty prevents persistent copulation in all individuals in adulthood. Persistent copulators, unlike males that cease mating activity after castration, prefer the odors of estrous over non-estrous females when tested 4 months after castration and 7 weeks after the last mating test. Neural circuits of persistent copulators retain the ability to mediate male sex behavior and preferences for female odors in the complete absence of gonadal steroids; they are influenced by preoperative sexual experience and organizational effects of gonadal hormones at the time of puberty.
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Keywords: Siberian hamster; Male copulatory behavior; Olfactory preferences; Sexual experience

Introduction

Copulatory behavior of most adult male mammals is dependent on concurrent availability of gonadal hormones. In the most well studied animal models, castration of adults leads to a rapid decline in male sexual behavior that is reversible with testosterone treatment (Young, 1961; Sachs and Meisel, 1988). Testicular hormones affect both appetitive and consummatory components of male copulation (Beach, 1956; Davidson, 1972). Beginning a few weeks after castration male rodents paired with estrous females no longer display the distinct intromission and ejaculatory behaviors characteristic of intact animals (rats, Davidson, 1966; guinea pigs, Grunt and Young, 1952; Syrian hamsters, Beach and Pauker, 1949; mice, McGill and Tucker,

1964). Only rarely do males of these species sustain ejaculatory behavior for more than a few weeks after castration (e.g., Davidson, 1966). B6D2F-1 hybrid mice, 30–80% of which retain the ejaculatory reflex 5–6 months after orchidectomy (Manning and Thompson, 1976; Clemens et al., 1988; Wee and Clemens, 1989), and Siberian hamsters, approximately one third of which maintain the complete copulation pattern for 4–6 months after castration (Park et al., 2004), are exceptions to this rule. Furthermore, 50% of Siberian hamsters that undergo testicular regression in short winter photoperiods also continue to display the ejaculation reflex despite low to undetectable blood testosterone concentrations (Park et al., 2004). The long-term persistence of copulation in inbred mice does not require the presence of adrenal hormones (Thompson et al., 1976).

Preoperative sexual experience facilitates retention of male sex behavior in mice (Manning and Thompson, 1976), cats (Rosenblatt and Aronson, 1958) and Syrian hamsters (Bunnell and Kimmel, 1965; Lisk and Heimann, 1980) castrated in

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adulthood as well as Syrian hamsters subjected to ablation of the vomeronasal organ (Meredith, 1986). In contrast, prior sexual experience does not promote retention of sex behavior in orchidectomized rats (Rabedeau and Whalen, 1959; Bloch and Davidson, 1968) and dogs (Hart, 1968; Beach, 1970).

In a previous study, male Siberian hamsters that continued to copulate many weeks after castration (persistent copulators) were sexually experienced at the time of orchidectomy, and were tested bi-weekly beginning 1 week after castration (Park et al., 2004). The present study, which assesses the role of pre- and postoperative sexual experiences in the retention of mating behavior after castration, parallels earlier investigations of B6D2F-1 mice (Manning and Thompson, 1976; Wee and Clemens, 1989). Because pubertal testicular hormones organize sex behavior in hamsters (reviewed in Schulz and Sisk, 2006), we also determined whether prepubertal castration was compatible with persistent copulation in adulthood.

Copulation in rodents is conceived as completely dependent on a combination of chemosensory cues and hormones (Wood, 1997; Wood and Newman, 1995). Sexually experienced male rats (Stern, 1970; Paredes et al., 1998) and Syrian hamsters (Fiber and Swann, 1996; Swann, 1997) prefer the odors of estrous females over those of non-estrous females or males. This preference disappears a few weeks after castration, and is restored by testosterone treatment (e.g., Stern, 1970 for rats; Gregory et al., 1975 for Syrian hamsters). The loss of this olfactory preference may contribute to the males' reduced mating activity after castration.

The present investigation further characterizes the post-castration persistent copulator phenotype of Siberian hamsters by extending observations to another behavior: the male's preference for estrous female odors. Males that displayed the ejaculation reflex 7 or more weeks after castration were designated persistent copulators. To test the hypothesis that persistent copulators would remain attracted to odors of estrous females, we assessed olfactory preferences of castrated male Siberian hamsters that either had stopped copulating or continued to mate for several months after castration. Testing was conducted 4 months after castration and approximately 7 weeks after the most recent mating test.

Materials and methods

Animals

Siberian hamsters (*Phodopus sungorus sungorus*) were from our local breeding colony, descended from stock originally supplied by Bruce Goldman (University of Connecticut, Storrs, CT) and later outbred to hamsters supplied by Katherine Wynne-Edwards (Queen's University, Kingston, ON). All procedures were approved by the Animal Care and Use Committee of the University of California at Berkeley.

To facilitate behavioral testing during the daytime, hamsters entrained to an LD 14:10 photocycle (14 h light/day with onset of darkness at 1300 h PST) were mated. Males weaned at 18 days of age were housed individually in polypropylene cages ($25 \times 14 \times 12$ cm). Food (Purina rodent chow 5015) and water were provided *ad libitum*, and the ambient temperature was $22 \pm 2°C$.

Female hamsters used in behavioral testing were ovariectomized at approximately 60 days of age and were treated with 4 mm Silastic capsules implanted subcutaneously (Dow Corning, Midland, MI, USA; ID 1.98 mm, OD 3.18 mm). Capsules filled with crystalline estradiol benzoate (EB; Sigma Che-

mical, St. Louis, MO, USA) were soaked in sterile saline solution for 24 h prior to implantation. To induce behavioral estrus each female was injected with progesterone (0.6 mg/0.1 ml peanut oil, sc; Sigma) 6 h prior to testing. Stimulus females were maintained in the same 14 L photoperiod as the males.

Mating test

Testing, conducted under dim red light between 1400 and 1700 h in the male's home cage, began with the introduction of a hormonally-treated stimulus female. If the female failed to display receptive behavior in response to male approaches within 10 min, she was replaced with another female. Otherwise the male's behavior was recorded for 30 min, or until 2 ejaculation reflexes were observed, whichever occurred first. Observation was terminated after 20 min if the male failed to mount the second female.

Data were collected as described by Park et al. (2004). The information recorded included: the number of mounts not accompanied by an intromission that preceded an ejaculation, the number of intromissions that preceded each ejaculation, latencies to the first mount, first intromission, and first ejaculation, and the duration of the post-ejaculatory interval, which is the time between an ejaculation and the next intromission. Males that failed to mount, intromit, or ejaculate were assigned the maximum copulation latency of 1800 s. Males were considered persistent copulators when mating culminating in the ejaculation reflex was recorded on one or more post-castration tests at least 7 weeks after gonadectomy.

Olfactory preference testing

Feces were collected from hormonally primed, sexually receptive females and from untreated ovariectomized females. Females were housed without bedding for 4–6 h during fecal collection. Feces were removed just before the onset of the dark phase (1300 h), 4–6 h after hormonally-treated females had been injected with progesterone. Five feces of each type, placed into separate Petri dishes (5 cm in diameter), were inserted to opposite ends of the male's home cage, and his behavior recorded for 10 min. The positions of the two dishes (A and B) were randomized. The amount of time the males spent investigating each dish in which the male was in direct physical contact with the feces was recorded. Groups were considered to prefer odors from dish A if the mean of investigatory time spent in contact with feces from dish A was significantly higher than that spent investigating feces from dish B.

Morphological parameters

Hamsters were anesthetized with isoflurane vapors, and the testes were weighed (± 0.1 mg) within 10 min of extraction. Body weights were obtained at the time of surgery (± 0.1 g).

Statistical analysis

The Statview program (Statview 5; SAS Institute, Cary, NC, USA) was used for all analyses. Differences in copulatory behavior between groups at certain weeks were assessed with the Chi square measure. Repeated measures ANOVAs were used to analyze changes in the number of mounts and intromissions, and mount, intromission and ejaculation latencies over time. When an effect of time was present, paired *t*-tests were used to analyze differences between two time points within groups. Post-hoc comparisons were conducted using the Fisher Protected Least Significant Difference test where appropriate. Observed differences were considered significant if $p < 0.05$.

Experiment 1: Effects of post-castration experience on persistent copulation

After successfully completing three of four mating tests ending in ejaculation, 20 hamsters were castrated as described in Park et al. (2003); 9 of these males were tested for copulatory behavior every other week for 7 weeks, beginning 1 week after castration. The remaining 11 animals were first re-tested 7 weeks after castration.

Experiment 2: Effects of preoperative sexual experience and puberty on copulation in adulthood

Twelve sexually naive male hamsters were castrated at 18 days of age, approximately 2–3 weeks before puberty (Hoffmann, 1978). Twenty-four hamsters were castrated postpubertally at ∼70 days of age. Twelve of the latter animals had been given sexual experience culminating in ejaculation once a week for 3 weeks prior to castration, and 12 were sexually naive at the time of castration. All castrated males were tested with sexually receptive females once a week for 3 weeks, beginning at approximately 4 months of age. The interval between castration and the first mating test was approximately 13, 7, and 7 weeks for the prepubertal, sexually naive and sexually experienced males, respectively. Seven weeks after completion of the mating behavior tests and 4 months after the hamsters were orchidectomized, male attraction to female odors was assessed.

Results

Experiment 1: Effects of post-castration experience on persistent copulation

Males first re-tested with estrous females 7 weeks after castration were at least as likely to be persistent copulators as were males tested with females every 2 weeks post-castration (91% vs. 67%, respectively; $p > 0.05$; Fig. 1A). Repeated post-

operative sexual experience at bi-weekly intervals is not a prerequisite for the emergence of persistent copulation.

There were no significant differences between the two groups of persistent copulators with respect to mount, intromission, or ejaculation latencies or the duration of the post-ejaculatory interval during the postoperative test 7 weeks after castration ($p > 0.05$), although a trend toward shorter latencies was apparent in the males given their first postoperative test 7 weeks after castration (Figs. 1B–E; only males that ejaculated on postoperative test 7 were included in this analysis).

During preoperative testing, mount latency (ML), intromission latency (IL), ejaculation latency (EL), and the post-ejaculatory interval (PEI) were progressively shorter on successive mating tests for both groups of hamsters (Figs. 1B–E). The difference was significant for 3 of the 4 measures for each group ($p < 0.05$ for week −4 versus week −1 values; Figs. 1B–E).

The EL and the PEI were significantly longer during the first two postoperative tests of males tested bi-weekly beginning 1 week after castration ($p < 0.05$ in each case), but by the fourth test 7 weeks after castration, both measures returned to values that did not differ significantly from preoperative baseline values 1 week prior to castration. ML, IL, and EL values of males first
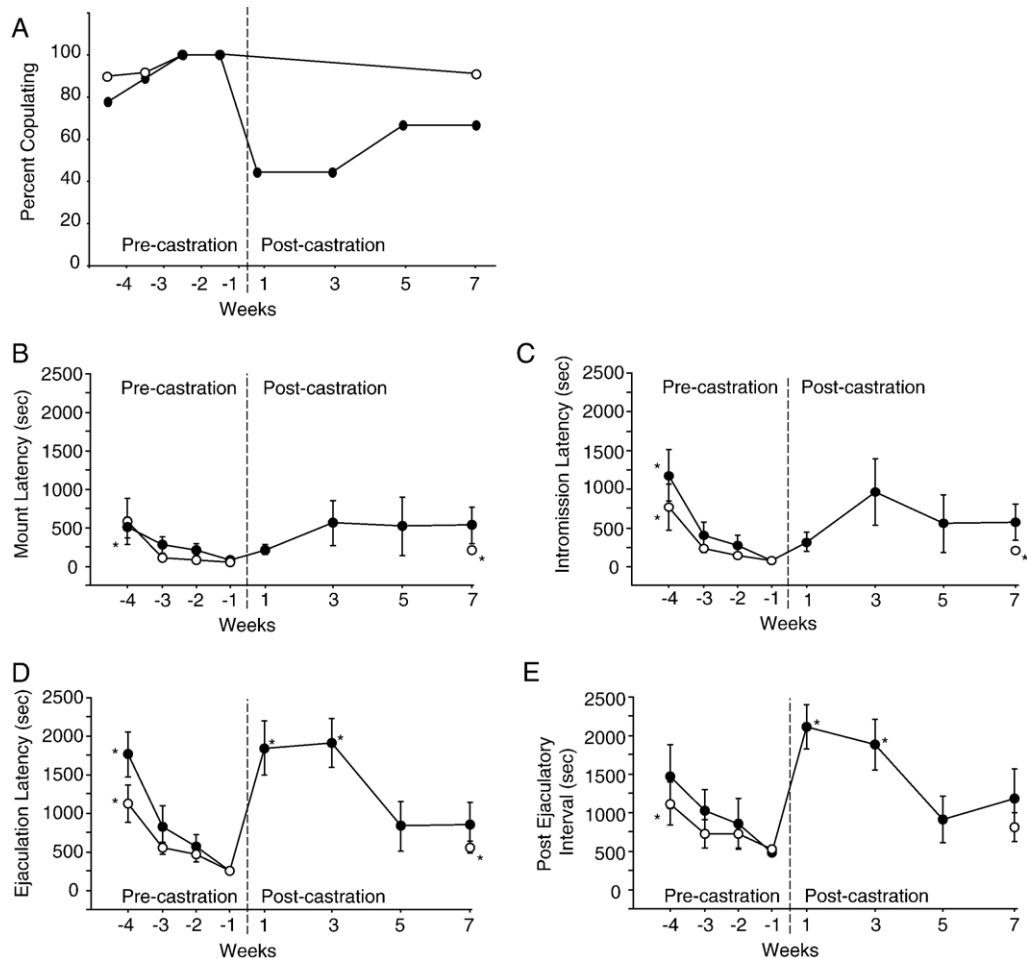

Fig. 1. (A) Percent of males copulating each week to a criterion of behavioral ejaculation. One group of males was tested bi-weekly beginning 1 week after castration (filled circles; N = 9) and the other was first tested 7 weeks after castration (open circles; N = 11). Mean ± SEM (B) mount, (C) intromission, and (D) ejaculation latencies and (E) post ejaculatory interval of persistent copulators (those that that ejaculated 7 weeks after castration) tested bi-weekly beginning 1 week after castration (filled circles; N = 6) and first tested 7 weeks after castration (open circles; N = 10). *Significantly different from respective pre-castration values at week −1 ($p < 0.05$).

retested 7 weeks after castration were significantly higher than preoperative week − 1 baseline values (Fig. 1B–D), whereas their PEI values were not (Fig. 1E). Although the latency measures at week 7 of the animals tested bi-weekly were also higher than their week − 1 baseline values, these comparisons failed to reach significance (p values ranged from 0.08 to 0.13).

Experiment 2: Effects of preoperative sexual experience and puberty on copulation in adulthood

Copulatory behavior

As in experiment 1, a majority (58%) of the adult sexually experienced males copulated to a criterion of behavioral ejaculation 7 or more weeks post-castration, compared to 25% of sexually naive males ($p < 0.05$, Fig. 2A). None of the males
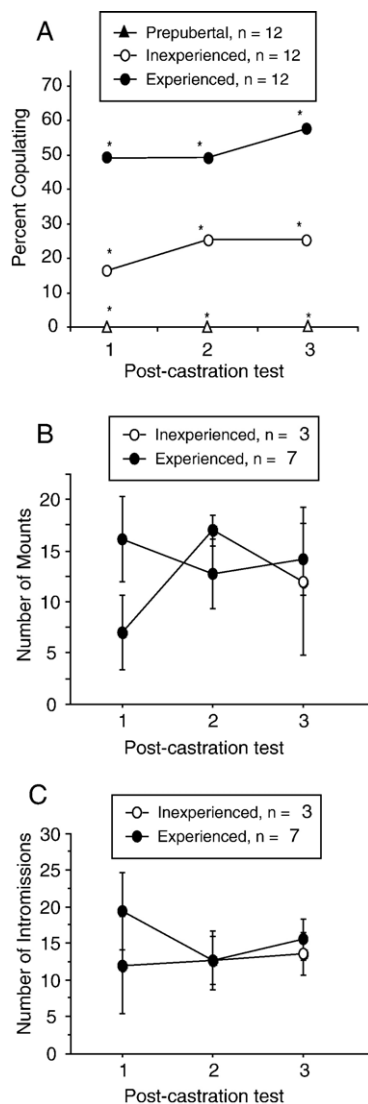

Fig. 2. (A) Percent of males copulating to a criterion of behavioral ejaculation after castration. The interval between castration and the subsequent mating test was ~13, 7, and 7 weeks for the prepubertal, adult sexually naive, and adult sexually experienced males, respectively. *The three groups were significantly different from each other ($p < 0.05$). Mean±SEM number of (B) mounts and (C) intromissions by persistent copulators preceding the first behavioral ejaculation in each of the postoperative tests.
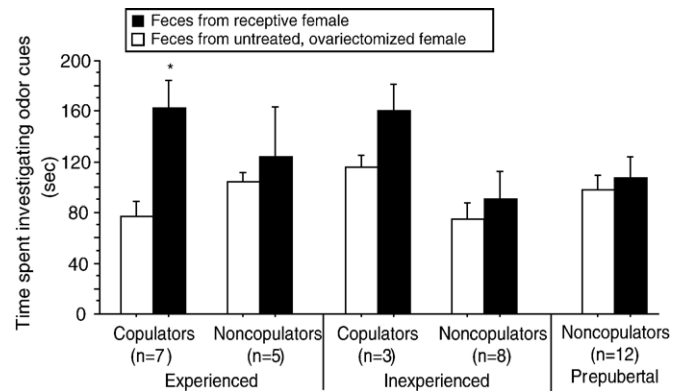

Fig. 3. Mean±SEM investigatory time directed toward feces from sexually receptive females or untreated ovariectomized females. Only sexually experienced persistent copulators ($n = 7$) spent significantly more time investigating feces from estrous than non-estrous females (*$p < 0.05$).

castrated prior to puberty mounted the females, and thus never successfully intromitted or ejaculated.

There were no differences in either the number of mounts or intromissions ($p > 0.05$; Figs. 2B, C) or latencies to mount or intromission ($p > 0.05$; data not shown) between the sexually experienced and sexually naive males once they displayed these behaviors.

Morphology

Body weights were significantly different between all three treatment groups at the time of castration; sexually naive males were heaviest and prepubertal males lightest ($p < 0.05$, not illustrated). The experienced and inexperienced males were castrated at approximately the same age, but the prepubertal males were about 7 weeks younger at the time of gonadectomy.

Testes mass

At the time of castration sexually-experienced adult males had heavier testes than inexperienced males of the same age, 660±17 mg and 514±50 mg, respectively, as previously reported for male rats (Taylor et al., 1983). The testes removed from prepubertal hamsters were undeveloped (106±6 mg).

Olfactory preference tests

Sexually experienced persistent copulators that were castrated after puberty spent a significantly greater portion of time investigating feces from sexually receptive than non-receptive females ($p < 0.05$; Fig. 3). Although inexperienced persistent copulators also spent more time investigating feces from estrous females, this comparison was not statistically significant ($p > 0.05$), likely because of small sample size. None of the non-copulator groups showed a preference for either type of feces ($p > 0.05$).

Discussion

Sexually experienced males successfully bridged a long gap without sexual activity and manifested the complete sex behavior repertoire when first re-tested 7 weeks after castration. The

persistence of copulatory behavior in long-term castrated Siberian hamsters was not dependent on intermittent post-operative sexual experience or priming provided by such tests. Weekly testing after castration also was not necessary for the emergence of persistent copulation in B6D2F1 mice (Wee and Clemens, 1989). Pre-operative sexual experience did, however, increase the incidence of post-castration sex behavior, perhaps in part by inducing long-term changes in penile morphology (Taylor et al., 1983); in the present study 58% of sexually-experienced hamsters, compared to 25% of sexually-naive hamsters, continued to copulate postoperatively.

The decreased incidence of gonad-independent sex behavior in naive hamsters was not unexpected. Prior sexual experience renders neural substrates less dependent on androgens (Hart, 1974). The benefits of sexual experience for retention of mating behavior after castration have been documented in cats and Syrian hamsters (Rosenblatt and Aronson, 1958; Bunnell and Kimmel, 1965; Bunnell and Flesher, 1965; Lisk and Heimann, 1980). Remarkably, 25% of sexually naive males copulated to a criterion of behavioral ejaculation when first tested 7 weeks after castration. Concurrent availability of gonadal hormones is required by most sexually naive adult Siberian hamsters for activation of copulatory behavior in adulthood, but a minority of naive males is not so constrained. The neural substrate of the latter hamsters was able to support sex behavior many weeks after the withdrawal of gonadal steroids. The extent to which activation of neural mating circuits is similar in castrated persistent copulators and gonadally-intact males, is unknown.

Persistent copulation was absent in males castrated prepubertally and tested in adulthood. None of these males even attempted to mount females. The combined absence of pre-castration sexual experience and pubertal hormone secretion was incompatible with persistent copulation in adulthood; the absence of mounting behavior reflects a lack of sexual arousal and motivation (Sachs and Meisel, 1988). The significantly lighter penises of prepubertal castrates (Park et al., 2003) may also prevent normal copulation. The experimental design we employed controlled for age at the time of testing, but the interval between castration and the first postoperative mating test was 13 weeks for the prepubertal and 7 weeks for the postpubertal males and may have contributed to the mating deficit in the former animals. The extended interval after castration is unlikely to explain the complete absence of copulatory behaviors in this group, as 40% of adult Siberian hamsters continue to display the complete repertoire of mating behaviors 13 weeks after castration (Park et al., 2004). Differences in methodologies between the two studies, however, prevent definitive conclusions. Pubertal testicular hormone secretion is required for normal adult mating behavior of Syrian hamster (reviewed in Schulz and Sisk, 2006) and here is implicated in the emergence of gonad-independent persistent copulation of Siberian hamsters.

Emancipation from strict hormonal control of mating activity in male mammals was formerly thought to be restricted to carnivores and primates. Some dogs continue to copulate for years after gonadectomy (Hart, 1968) and some untreated men reportedly engage in sexual intercourse a decade after bilateral

orchidectomy (Heim and Hursch, 1979; Weinberger et al., 2005). Increased cerebral cortical influences were the proposed mediators of long-term maintenance of mating behavior in gonadectomized males (Ford and Beach, 1951) but subsequent analyses failed to document a correspondence between degree of brain development and corticalization on the one hand, and post-castration retention of male sex behavior, on the other (Aronson, 1959; Hart, 1974; Manning and Thompson, 1976; McGill and Manning, 1976; Clemens et al., 1988; Park et al., 2004, present study).

Persistence of olfactory preferences in castrated males has not to our knowledge been reported previously for any rodent (see Paredes et al., 1998 for a review of the older literature). We demonstrated that sexually experienced persistent copulators prefer the odors of estrous females, but such preferences were absent in experienced and inexperienced non-persistent copulators, as well as males castrated prior to puberty. Male rat preferences for odors of estrous females disappear 3 weeks after castration and are restored by testosterone treatment (Stern, 1970). The robust preference of sexually-experienced persistent copulators for the odors of sexually receptive females is therefore remarkable, considering that tests were conducted 7 weeks after the last mating test and 4 months after castration. Responsiveness to sexually salient odors may be causally related to post-castration emergence of persistence copulation.

Our results suggest but do not definitively establish that the amount of prior sexual experience may influence post-castration preference for estrous odors. It is unknown whether gonadal steroids are required for initial establishment of the male's preference for estrous odors or if this preference subsequently becomes steroid-independent. Alternatively, a subset of sexually naive castrated male hamsters may have strong preferences for the odors of estrous females prior to the first mating test; perhaps only those males subsequently develop persistent copulation.

During odor tests, fos-like immunoreactivity is detected in more brain areas throughout the vomeronasal pathway and the nucleus accumbens of sexually experienced than sexually naive male rats. Sexual experience may be necessary for full activation of this pathway (Hosokawa and Chiba, 2005). It remains to be specified whether the olfactory mating circuit of persistent copulators responds differently than that of non-persistent copulators to salient female odors (cf. Kollack-Walker and Newman, 1997; Wood and Newman, 1995), although we consider this likely. Retention of mating and olfactory behaviors in persistent copulators may be dependent on neurosteroids (Frye, 2001), or constitutively activated steroid receptors (Blaustein, 2004), but is unlikely to depend on adrenal estrogens or androgens, as evidenced by the persistence of male sexual behavior in castrated hybrid B6D2F1 hybrid mice after adrenalectomy (Thompson et al., 1976).

It is also unknown whether all gonadally-mediated traits are retained to a greater extent in persistent copulators than in males that cease mating activity after castration. Persistent copulators may fail to manifest the increased aggressive behavior that follows castration in Siberian hamsters (Jasnow et al., 2000). Castration does not affect all androgen-dependent traits or all

genotypes equally; e.g., all Long–Evans rats failed to copulate several weeks after castration but ultrasonic vocalizations decreased markedly in half the animals and increased above preoperative values in the remaining rats (Matochik and Barfield, 1994). Similarly diverse responses were observed in meadow voles subject to castration; heavier voles decreased and lighter voles increased their body mass postoperatively (Dark et al., 1987).

Future studies of persistent copulators stand to increase our understanding of the mechanisms by which environmental factors, sensory systems, and neurotransmitters sustain male sex behavior in the absence of gonadal steroids.

Acknowledgments

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