ELSEVIER

Animal Reproduction Science 89 (2005) 77–92

ANIMAL REPRODUCTION SCIENCE

www.elsevier.com/locate/anireprosci

# Aversive conditioning of periodic spontaneous erection adversely affects sexual behavior and semen in stallions☆

Sue M. McDonnell*, Amy L. Hinze

*Equine Behavior Laboratory, University of Pennsylvania School of Veterinary Medicine, New Bolton Center, 382 West Street Road, Kennett Square, PA 19348, USA*

**Abstract**

Periodic spontaneous erection and penile movements known as masturbation (SEAM) occur normally at approximately 90 min intervals in awake equids. SEAM in horses has traditionally been misunderstood by many horsemen as aberrant behavior that should be eliminated. Accordingly, it is not uncommon for trainers of performance stallions or managers of breeding stallions to punish SEAM in an attempt to eliminate the behavior. Previous clinical observations and preliminary unsystematic trials had suggested that attempts to stop stallion SEAM may lead to an increase rather than a decrease in SEAM, and at the same time may suppress sexual behavior (SB) in a breeding stallion. The present work evaluated the effects of aversive conditioning of SEAM on SEAM, SB, and semen. In Experiment 1, four mature pony stallions were subjected to aversive conditioning of SEAM in a within- and between-subjects half cross-over design. The SEAM erection interval tended to be less after aversive conditioning, suggesting an increase in SEAM frequency. Eleven other SEAM measures were each similar before and after aversive conditioning of SEAM. In standard sexual behavior trials with a stimulus mare and dummy mount, erection latency, ejaculation latency, mount readiness latency, and number of mounts to ejaculation increased after aversive conditioning of SEAM; erection rigidity score, number of ejaculatory pulses, and vocalization rate decreased. Number of thrusts to ejaculation was similar before and after aversive conditioning of SEAM. All affected SB measures indicated suppressed sexual arousal and breeding efficiency after SEAM. In Experiment 1, ejaculated semen was not evaluated. Because in Experiment 1, the number of ejaculatory urethral pulses was

☆ This paper is part of the special issue entitled "Proceedings of the 4th International Symposium on Stallion Reproduction", Guest Edited by Dr. Edward Squires.

* Corresponding author. Tel.: +1 610 444 5800x6221; fax: +1 610 925 8124.
*E-mail address:* suemcd@vet.upenn.edu (S.M. McDonnell).

0378-4320/$ – see front matter 
doi:10.1016/j.anireprosci.2005.06.016

less after aversive conditioning, Experiment 2 was similarly designed, but included evaluation of semen, both immediately and again 1 week after aversive conditioning was completed. Experiment 2 included 12 aversively conditioned stallions, and 4 yoked controls. In Experiment 2, masturbation episode duration tended to be less after aversive conditioning, while the remaining 11 SEAM measures were unaffected by aversive conditioning of SEAM. Of SB measures, erection latency, mount readiness latency, thrusts to ejaculation, and ejaculation latency were significantly greater after aversive conditioning. Erection rigidity score and number of ejaculatory pulses were less after aversive conditioning. These differences are consistent with suppressed sexual arousal and reduced breeding efficiency. Semen volume and total number of sperm per ejaculate were significantly less after aversive conditioning. These findings are consistent with clinical anecdotes and preliminary trials indicating that aversive conditioning of SEAM in stallions suppresses sexual arousal and breeding behavior. Of considerable interest both clinically and theoretically, is the finding that aversive conditioning target behavior of SEAM was not suppressed by aversive conditioning, while SB and semen during semen collection trials were both adversely affected.


*Keywords:* Horse; Masturbation; Erection; Aversive conditioning; Sexual behavior; Ejaculation; Semen

## 1. Introduction

Periodic spontaneous (non-sexual) erection and penile movements or manipulation have been described in a wide range of mammalian species, including bulls, stallions, rams (Jainudeen and Hafez, 1987), cats (Aronson, 1949; Hafez, 1962), dogs (Hafez, 1962), boars, bucks (Roberts, 1986), porpoises, porcupines, red deer, primates (Beach, 1976), shrews (Pearson, 1944), kangaroo (Crump, 1986), bats (Wimsatt, 1945), bears (Alt, personal communication, 1992), whales (Wilson, personal communication, 2004), elephants (Jainudeen et al., 1972), and rats (Schmidt et al., 1994). In domestic species, in which spontaneous erection and penile movements or manipulation occur in an awake state, the behavior is commonly known as masturbation. In men, similar periodic erections occur in association with rapid eye movement sleep, and are known as nocturnal penile tumescence (NPT) (Ohlmeyer et al., 1944; Karacan et al., 1976). In male infants, spontaneous erections occur during both sleep and wakeful states (Conn and Kanner, 1940; Karacan et al., 1976).

In equids, spontaneous erection involves extension of the penis from the prepuce with engorgement to the full length and rigidity typical of sexual erection as shown in Fig. 1. Penile movements include rhythmic dorsoflexion typically with bouncing, pressing, and/or sliding of the erect penis against the abdomen achieved by rhythmic contraction of the ischiocavernosus muscles and/or pelvic thrusting. The interval between bouts of SEAM is about 90 min occurring continuously throughout the day and night in undisturbed stallions. It can occur during standing rest or any "quiet" ongoing maintenance behavior. Each episode lasts approximately 2 min (McDonnell, 1989, 1995). Ejaculation during SEAM in stallions is rare, occurring in less than 1% of observed episodes (McDonnell, 1989). Episodes of SEAM do not occur during standing or recumbent sleep, however, greater than 85% of episodes of standing or recumbent sleep are followed by SEAM within 1–5 min of waking or transition to a more alert state (Wilcox et al., 1991; McDonnell, 1995). Startle of a

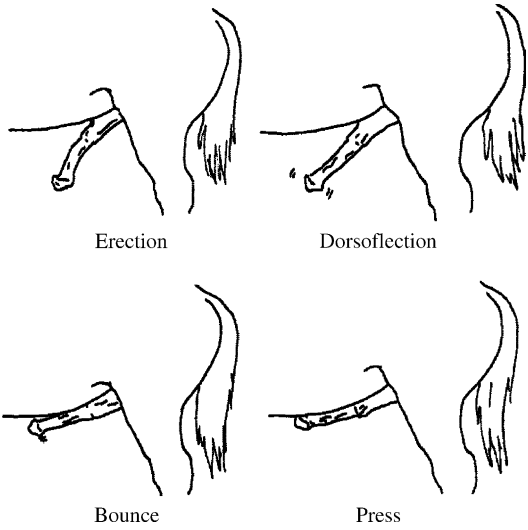


Fig. 1. Spontaneous erection and penile movements known as “masturbation” in stallions.

stallion during any ongoing activity will conspicuously result in SEAM within 5 min of return to calm in almost all instances (McDonnell and Pozor, unpublished observations). The frequency, duration, and intensity of SEAM in stallions are not associated with age, libido, fertility, socio-sexual conditions, or basal testosterone concentrations (McDonnell, 1989). Equids exhibit masturbation in feral and wild conditions, whether harem stallions with continuous access to mares or bachelor stallions generally without access to mares (Feist, 1971; Tyler, 1972; Penzhorn, 1984; Keiper, 1985; McDonnell, 1989; Boyd, 1991; Henry et al., 1991; McDonnell et al., 1991; McDonnell and Murray, 1995). The frequency and duration of SEAM of wild or feral equids are similar to those of captive or domestic stallions (McDonnell, 1989; Henry et al., 1991; McDonnell et al., 1991). The frequency and duration of SEAM are similar among the equid species, including zebra, horses, Przewalski horses, donkeys, and asses. As with sleep-related erections in humans (Karacan et al., 1976), periodic spontaneous erections in equids occur in males of all ages (McDonnell, 1989; Henry et al., 1991; McDonnell et al., 1991). In equids, the frequency and duration of SEAM are similar in males from birth to old age (McDonnell, 1989, 1995).

Occurrences of SEAM in stallions and other domestic livestock have been traditionally considered as aberrant behavior and a potential cause of infertility (Hafez, 1962; Pickett, 1974; Evans, 1981; Waring, 1983; Roberts, 1986; Beaver, 1994). It has been misunderstood as: (1) sexual erection, either normal or aberrant; (2) a stereotypy or vice behavior resulting from domestic conditions of boredom, inactivity, or inaccessibility to breeding; (3) an unnecessary waste of general energy that will reduce athletic or sexual energy and performance; (4) attributable to an individual stallion’s hyper- or homo-sexuality. Despite scientific and lay publications in the past two decades aimed at educating horsemen and veterinarians as to the normal nature of SEAM, traditional beliefs of its aberrant nature persist. Even in current academic publications (for example, Waring, 2003), SEAM is presented as

an aberrant behavior resulting from excess sexual energy. In stallions, SEAM is typically considered unaesthetic during show situations. For all these reasons, attempts to deter or eliminate SEAM remain in certain regions and equine disciplines of horse showing and breeding. Commercially available or custom-made equine anti-masturbatory devices that have been developed and used for decades include constricting bands (made of metal, plastic, or fabric) known as "stallion rings," abrasive devices such as a nail patch or stiff bristled brush applied to the ventral midline at the point of belly contact during masturbation, metal or fabric constricting "cages" or "baskets" applied to the prepuce or glans penis, and electronic shock collars, or girth straps similar to dog-training collars (Mountjoy, 1974). Simple physical punishment, for example, striking the belly, penis, or hind legs of the stallion with a riding crop or whip, is a fairly common technique employed to interrupt SEAM. More elaborate punishment schemes employed by horsemen to eliminate SEAM that have been reported anecdotally include abrading and lacerating the penis before applying caustic topical preparations, and severely beating the erect penis with blunt or sharp objects resulting in trauma.

A common clinical problem of stallions is sexual behavior dysfunction coincident with attempts to discourage SEAM. The typical complaint of owners is that attempts to stop their stallion's masturbation are ineffective, or actually lead to an apparent increase in SEAM, while coincidentally libido and sexual arousal for breeding diminish (McDonnell, unpublished clinical observations). In unsystematic preliminary trials with normal mature stallions, we have attempted to explore the effectiveness of the most common equine industry anti-masturbatory devices, including the stallion ring, the brush, the basket, and an electronic dog-training collar (McDonnell, unpublished preliminary trials, 1985–1987). Remarkably, none of these devices appeared to be effective in suppressing SEAM. With the anti-masturbatory devices in place, periodic erections and penile movements continued with greater than normal frequency and duration of episodes, even though in some cases the penis became deformed and the range of movement was constrained by the device. Frequency and duration of SEAM appeared to return to normal frequencies after the devices were removed. Coincident with participation in these preliminary trials, each stallion in which attempts were made to suppress SEAM exhibited a noticeable decrease in sexual arousal in response to a mare or exhibited an obvious decrement in erection and/or ejaculation performance in sexual behavior trials. This apparent suppression of sexual performance persisted for as long as several months following the use of anti-masturbatory devices.

The present experiments were designed to systematically evaluate the effects of aversive conditioning of SEAM on SEAM, SB, and semen.

## 2. Materials and methods

### *2.1. Experiment 1*

#### *2.1.1. General design*

Measures of SEAM and SB were evaluated before and after aversive conditioning of SEAM in a within-subjects half cross-over design. During a first replicate, half of the subjects received aversive conditioning and half served as sham-conditioned controls. A

second replicate followed in which the control subjects of the first replicate received aversive conditioning. Considering clinical anecdotes and results of preliminary trials described earlier, our hypothesis was that aversive conditioning of SEAM would not decrease and may increase SEAM and would decrease SB.

*2.1.2. Subjects*

Four mature pony stallions (150–200 kg body weight; ages 2–6 years) were obtained at local stock auction over the 30-day period preceding the present study. All were in excellent physical condition, had two scrotal testicles of normal size and consistency, normal concentrations of circulating testosterone for mature stallions, normal pre-copulatory and copulatory behavior, and normal semen. Subjects were stabled in tie-stalls in a barn with a total of 10 stallions and no other horses for the duration of the study, which included a 1-week housing and procedural acclimation period. Grass hay was provided twice daily and fresh water ad libitum to maintain good body condition. The study was conducted over a continuous 24-day period during the breeding season (June). The first 6 days included acclimation to the barn (Days 1–6). Days 4–6 also included once daily ejaculation in sexual behavior trials. This was followed by 3 days of sexual rest (Days 7–9). Replicate 1 consisted of 3 days of pre-conditioning baseline measures (Days 10–12) and then 3 days of aversive conditioning in which two subjects received aversive conditioning and two subjects served as controls (Days 13–15). This was followed by 3 days of post-conditioning measures (Days 16–18). At that time, the two subjects that received aversive conditioning in Replicate 1 were finished with the experiment. In Replicate 2, the two Replicate 1 control stallions were crossed over to receive 3 days of aversive conditioning (Days 19–21), followed by 3 days of post-conditioning measures (Days 22–24). During the 3 days of aversive conditioning, the stallions were at sexual rest. Sexual behavior trials were conducted at the same time each day. This schedule allowed a standard 3 days of sexual rest before both the baseline and the post-conditioning SB measures.

*2.1.3. Aversive conditioning*

Aversive conditioning consisted of 10 pairings of electrical shock (1–2 s pulse unipolar ac, 480 Hz, 25 mA) with visually estimated full shaft erection during SEAM. This was accomplished using a commercially available horse training device (Vicebreaker Inc., Whitewater, CO; stimulus level 5) applied to the ventral midline on a leather girth strap positioned approximately 3 cm caudal to the fore limbs in the traditional saddle girth position. This stimulus was judged to be sufficient to interrupt ongoing activity without causing panic. During each conditioning session, the subject was kept under continuous video surveillance by a technician in a remote laboratory. Upon full erection and at least one penile movement, a shock was delivered via radio transmitter activation from that remote location. The shock stimulus was continued at approximately 10 s intervals until detumescence commenced. Each conditioning session lasted from 3 to 9 h. Sessions continued daily over a 2-day period, ranging between subjects from 5.25 to 15 h total time to complete 10 pairings of shock and SEAM. Conditioning sessions were video taped for subsequent characterization of the conditioning process. During conditioning sessions, sham conditioning for the control animals consisted of wearing a similarly fitted dummy shock device and video taping. Stallions remained in their individual stalls within a stable for the conditioning.

*2.1.4. SEAM measures*

Once before and once after aversive conditioning, SEAM was evaluated using a standard 8 h continuous video taped sample of penile activity. To standardize interval from last ejaculation, these samples were obtained during the evenings of the 3-day series of sexual behavior trials described below. Video taping was conducted between 18:00 and 02:00 h, a time window during which conditions within the barn were most consistently undisturbed. Video tapes were reviewed to derive the following measures (McDonnell and Diehl, 1990).

*Erection frequency*: The number of spontaneous erections occurring during the 8 h sample. Erection was defined as extension and rigidity of the penile shaft.
*Erection total duration*: The total duration in seconds of erection during the 8 h sample.
*Erection episode mean duration*: The mean duration in seconds of erection episodes during the 8 h sample.
*Mean erection interval*: The mean interval in minutes between erection episodes during the 8 h sample.
*Masturbation episode frequency*: The number of masturbation episodes during the 8 h sample. Masturbation was defined as one or more of any of the specific movements of the penis illustrated in Fig. 1.
*Masturbation episode total duration*: The total duration in seconds of all masturbation episodes during the 8 h sample. Duration of each episode was measured from the first through the last distinct penis movement.
*Masturbation episode mean duration*: The mean duration in seconds of masturbation episodes during the 8 h sample.
*Total penis movements*: Total number of penis movements during the 8 h sample.
*Penis movements per masturbation episode*: The mean number of penis movements per episode during the 8 h sample.
*Mean masturbation episode intensity index*: An intensity score for each masturbation episode calculated as the sum of points assigned to each type of increasingly intense penis movements as shown in Fig. 1. (dorsoflexion without contacting abdomen= 1; bounce of glans against abdomen = 2; press against abdomen = 3; pelvic thrust during accompanying penis movement = 1 additional point). Mean masturbation episode intensity index was calculated as the mean of all episode intensities during the 8 h sample.
*Total masturbation episode intensity index*: The total of episode intensities during the 8 h sample.
*Ejaculation frequency*: The number of ejaculations observed during the 8 h sample.

During the aversive conditioning and sham control conditioning sessions, *erection interval* was measured in minutes as described above.

*2.1.5. SB measures*

Measures of SB were evaluated before and again after the aversive conditioning in a series of three standard daily sexual behavior trials. Each 3-day series of sexual behavior trials followed a standard 3-day period of sexual rest as described above. Each trial consisted of exposure to a stimulus mare until erection and readiness to mount, followed by mounting of a dummy mount for manual stimulation to ejaculation (McDonnell and Love, 1990). Briefly,

manual stimulation involves use of one hand supporting the distal penis the other hand supporting the proximal penis. When used for semen collection, a plastic bag is fitted over the erect penis to contain the ejaculate. Because our purpose in Experiment 1 was simply to induce ejaculation for SB measures and not to collect the semen for evaluation, no semen collection bag was applied. The SB trials were video taped for subsequent recording of the following measures (McDonnell and Diehl, 1990).

*Number of vocalizations*: The number of sexual vocalizations per minute while in the breeding area.
*Erection latency*: The interval in seconds from entering the breeding area to first full shaft erection.
*Erection rigidity score*: The subjective rating of rigidity of the penile shaft at readiness to mount and during the manual stimulation procedure, 1 (least) to 3 (greatest).
*Mount readiness latency*: The interval in seconds from entering the breeding area to resting of chin on rump of stimulus mare, with full erection, with one or more front feet lifted from the floor.
*Ejaculation latency*: The interval in seconds from entering the breeding area to ejaculation.
*Mounts to ejaculation*: The number of mounts to achieve ejaculation.
*Thrusts to ejaculation*: The number of rhythmic full-sweep pelvic thrusts on the ejaculatory mount to ejaculation.
*Ejaculatory pulses*: The number of palpable ejaculatory urethral pulses.

For each measure, a mean for each pre- and post-aversive conditioning three-trial series was used for analysis.

#### 2.1.6. Data analysis

For each measure, within-subjects differences before and after aversive conditioning were evaluated using dependent *t*-tests. A probability level of $p < 0.05$ was considered significant. A probability level between 0.05 and 0.10 was considered a tendency for significance. Independent *t*-test comparisons of aversively conditioned and control subjects were done for each measure for the baseline and post-aversive conditioning period of Replicate 1.

### 2.2. Experiment 2

#### 2.2.1. General design

A second experiment was conducted to include a greater number of stallions and to include semen measures. The general design was a repeated measures half cross-over design as described for Experiment 1 with the exception that: (1) 12 stallions were used; (2) 4 additional stallions were used as yoked controls; (3) the aversive conditioning was done for a fixed period as opposed to a fixed number of shocks (to more precisely approximate horse industry aversive conditioning practices); (4) semen was evaluated. In addition to evaluation of SEAM, SB, and semen measures on the 3 days before the start and on Days 1–3 following completion of aversive conditioning of SEAM, SB and semen were evaluated again on Days 8–10 after the completion of aversive conditioning. Considering that in Experiment 1, ejaculatory urethral pulses appeared suppressed following aversive conditioning of SEAM,

and that in other work in our laboratory sperm number per ejaculate is highly associated with pulse strength and number, our additional hypothesis for Experiment 2 was that aversive conditioning of SEAM would suppress the number of sperm per ejaculate. A second additional question concerned whether non-SEAM-contingent aversive experience (yoked control) would affect SEAM, SB, or semen.

*2.2.2. Subjects*

Sixteen mature pony stallions (120–240 kg; ages 4–20 years), belonging to the University of Pennsylvania research herd were used. Twelve served as subjects for the aversive conditioning of SEAM. The remaining four served as yoked controls. All were in excellent physical condition, with normal concentrations of circulating testosterone for mature stallions, normal pre-copulatory and copulatory behavior, and semen measures within the range of normal for pony stallions. Ten of the subjects had two scrotal testicles of normal size and consistency. The remaining two stallions had only one scrotal testicle. One of these presumed cryptorchid stallions was assigned to Replicate 1 control and the other to Replicate 1 aversive conditioning groups. Subjects were housed in box-stalls (3 m × 3 m) together in a barn with no other animals ($n = 4$) or at pasture ($n = 8$) where they had been acclimated for at least 1 week before the start of the experiment. Stabled stallions were fed grass hay twice daily and fresh water ad libitum to maintain good body condition.

The study was conducted over a period of 39 days during the breeding season (May–June). The first 7 days included acclimation to housing (Days 1–7) and to once daily semen collection procedures (Days 5–7). This was followed by 4 days of sexual rest (Days 8–11). Replicate 1 consisted of 3 days of pre-conditioning baseline measures (Days 12–14) and 4 days of aversive conditioning in which six subjects received aversive conditioning and six subjects served as controls (Days 15–18). After the aversive conditioning, there were 3 days of post-conditioning measures (Days 19–21). At this point the stallions receiving aversive conditioning in Replicate I were sexually rested for 4 days (Days 22–25) and then received 3 days of additional post-conditioning SB and semen measures (Days 26–28). Beginning after the Days 19–21 post-conditioning measures, the six Replicate 1 control stallions received 4 days sexual rest (Days 22–25) followed by 4 days of aversive conditioning (Days 26–29), followed by 3 days of post-conditioning measures (Days 30–32), 4 days of sexual rest (Days 33–36) and then 3 days of post-conditioning measures (Days 37–39). This schedule allowed a standard 4 days of sexual rest before both the baseline and the two sets of post-conditioning SB and semen measures. For each replicate two additional stallions served as yoked controls, receiving shock in tandem with a paired stallion, independently of their own SEAM.

*2.2.3. Aversive conditioning*

The aversive conditioning stimulus was as described in Experiment 1. The conditioning was done during two successive daily sessions, Day 1 lasting 14 h and Day 2 lasting 10 h, for a total of 24 h, with no set maximum of shocks. This resulted in 9–60 (mean of 28.9) pairings of shock and SEAM. Except for one subject, the number of shock-SEAM pairings exceeded the fixed number of 10 pairings used in Experiment 1. Sham conditioning as in Experiment 1 was not done in Experiment 2. Two yoked control subjects were included in

each replicate. Each yoked control stallion was paired with one of the aversively conditioned subjects and received shock stimuli at the same time as the paired subject, independent of the yoked stallion's own SEAM behavior.

#### 2.2.4. SEAM and SB measures

SEAM and SB measures were as described in Experiment 1, with the exception that sexual behavior trials included the additional procedures to enable semen collection as described below. The time required for these procedures (typically less than 1.5 min) was subtracted from mount readiness and ejaculation latency measures. In addition, vocalizations were not included as a measure of SB.

#### 2.2.5. Semen collection and measures

Semen was collected in the standard sexual behavior trials (conducted once daily during each 3-day period of baseline and post-aversive conditioning measures). Procedures were as described in Experiment 1, with the addition of washing the penis and applying a plastic bag for collection of semen. After erection was achieved, the penis was washed with warm water and the semen collection bag positioned (McDonnell and Love, 1990). Semen was evaluated using methods described by Kenney et al. (1983). Measures of raw semen immediately after collection included: percentage total motile spermatozoa (visually estimated at 40×), percentage progressively motile spermatozoa (visually estimated at 40×), gel-free semen volume, gel volume, pH, and concentration of spermatozoa ("A" Model Densimeter, Animal Reproduction Systems, Chino, CA, USA). Total number of spermatozoa was calculated. For each measure, a mean of the second and third day of each of the pre- and post-aversive conditioning 3-day series of trials was used for analysis.

#### 2.2.6. Data analysis

For each measure, repeated measures ANOVA procedures were used to evaluate within-subjects differences before and at 1–3 days and again at 8–10 days after aversive conditioning was completed. A probability level of $p < 0.05$ was considered significant. Follow-up pair wise comparisons were done using dependent *t*-test procedures. A probability level of $p < 0.05$ was considered significant. A probability level between 0.05 and 0.10 was considered a tendency for significance.

## 3. Results

### 3.1. Experiment 1

Sexual behavior and SEAM measures were similar during baseline for subjects assigned to aversive conditioning and sham control for Replicate 1. Data for SB and SEAM before and after aversive conditioning of SEAM are summarized in Table 1. For SEAM, mean erection interval tended to be less after aversive conditioning ($p < 0.10$). For all other measures of SEAM, mean values before and after aversive conditioning were similar ($p > 0.10$). As is typical for SEAM in stallions, no ejaculations occurred.

Table 1
The spontaneous erection and penile movements (SEAM) and sexual behavior (SB) measures before and after aversive conditioning of SEAM in Experiment 1 (means ± S.E.M., $n = 4$)

| | Before aversive conditioning of SEAM | Days 1–3 after aversive conditioning of SEAM |
|---|---|---|
| SEAM measures[a] (8 h sample) | | |
| Erection episodes | | |
| Frequency | 8.2 (1.7) | 8.2 (1.1) |
| Total duration (s) | 879.0 (152.0) | 984.8 (138.1) |
| Mean duration (s) | 110.0 (10.4) | 119.3 (5.5) |
| Mean interval (min) | 89.0 (14.1)[a] | 59.6 (4.5)[b] ($p < 0.10$) |
| Masturbation episodes | | |
| Frequency | 7.2 (1.1) | 7.7 (1.1) |
| Total duration (s) | 329.3 (68.5) | 355.8 (83.4) |
| Mean duration (s) | 44.3 (5.9) | 44.8 (5.0) |
| Penis movements | | |
| Total | 53.0 (12.3) | 69.5 (28.0) |
| Mean (per episode) | 7.3 (1.1) | 8.2 (2.3) |
| Mean intensity index | 13.6 (2.7) | 13.0 (4.6) |
| Total intensity index | 98.2 (25.5) | 112.3 (53.6) |
| Ejaculation frequency | 0 | 0 |
| SB measures | | |
| Vocalization rate (per min) | 8.2 (2.5)[a] | 5.6 (2.2)[b] |
| Erection latency (s) | 46.2 (44.5)[a] | 115.9 (86.0)[b] ($p < 0.10$) |
| Erection rigidity score (1–3) | 2.6 (0.1)[a] | 2.0 (0.3)[b] |
| Mount readiness latency (s) | 73.1 (61.5)[a] | 183.5 (122.8)[b] ($p < 0.10$) |
| Ejaculation latency (s) | 122.3 (90.0)[a] | 300.6 (156.9)[b] |
| Mounts to ejaculation | 1.1 (0.1)[a] | 2.0 (0.4)[b] |
| Thrusts to ejaculation | 8.8 (0.5)[a] | 9.8 (1.7)[a] |
| Ejaculatory pulses | 11.7 (0.5)[a] | 9.1 (0.4)[b] |

[a,b] Within rows, different superscripts indicate differences at $p < 0.05$, except where indicated.

With the exception of thrusts to ejaculation, all pre- and post-aversive conditioning SB measures were different ($p < 0.05$) or tended to be different ($p < 0.10$). Erection latency, mount readiness latency, ejaculation latency, and mounts to ejaculation were each greater after aversive conditioning of SEAM; number of vocalizations, erection rigidity score, and ejaculatory pulses were each less after aversive conditioning of SEAM. These differences are consistently in the direction of suppressed libido, erection response, and overall ejaculation efficiency.

During the conditioning sessions, the mean spontaneous erection interval (from shock-interrupted erection to subsequent erection) was 29.3 min ($n = 4$, S.E.M. = 6.3 min). During the sham control conditioning sessions, mean erection interval was 76.7 min ($n = 4$, S.E.M. = 6.6 min). This difference is significant (dependent $t = 3.82$, 3 d.f., $p < 0.05$). For most applications of the aversive stimulus, erection was immediately lost with startle. In 17 of 34 observed intervals following delivery of the aversive stimulus, erection resumed within 5 min, coincident with the stallion's apparent return to a visually assessed calm state.

Table 2
The spontaneous erection and penile movements (SEAM), sexual behavior (SB) and semen measures before and after aversive conditioning of SEAM in Experiment 2 (means ± S.E.M., $n = 12$)

| | Before aversive conditioning | Days 1–3 after aversive conditioning | Days 8–10 after aversive conditioning |
|---|---|---|---|
| SEAM measures[a] (8 h sample) | | | |
| Erection episodes | | | |
| Frequency | 9.4 (1.3) | 10.8 (2.0) | |
| Total duration (s) | 1528.9 (200.0) | 1690.4 (348.8) | |
| Mean duration (s) | 163.7 (12.8) | 153.5 (8.8) | |
| Mean interval (min) | 59.0 (7.0) | 61.6 (12.7) | |
| Masturbation episodes | | | |
| Frequency | 7.1 (1.2) | 8.4 (1.4) | |
| Total duration (s) | 598.2 (108.2) | 558.4 (98.0) | |
| Mean duration (s) | 83.1 (8.1)[a] | 71.7 (7.4)[b] ($p = 0.09$) | |
| Penis movements | | | |
| Total | 77.0 (12.1) | 76.5 (12.5) | |
| Mean (per episode) | 10.9 (0.8) | 10.6 (1.3) | |
| Mean intensity index | 165.3 (24.1) | 154.2 (24.1) | |
| Total intensity index | 23.7 (2.2) | 21.6 (2.8) | |
| Ejaculation frequency | 0 | 0 | |
| SB measures | | | |
| Erection latency (s) | 11.7 (4.5)[a] | 20.6 (6.4)[b] | 66.3 (37.3)[b] |
| Erection rigidity score (1–3) | 2.2 (0.1)[a] | 1.3 (0.1)[b] | 1.4 (0.1)[b] |
| Mount readiness latency (s) | 20.9 (11.5)[a] | 38.2 (17.9)[b] | 87.3 (45.2)[b] ($p = 0.09$) |
| Ejaculation latency (s) | 43.7 (14.7)[a] | 76.9 (24.4)[b] | 119.1 (43.2)[b] |
| Mounts to ejaculation | 1.0 (0.02)[a] | 1.2 (0.12)[b] | 1.7 (0.38)[a] |
| Thrusts to ejaculation | 8.7 (0.5)[a] | 10.6 (0.5)[b] | 11.0 (1.1)[b] |
| Ejaculatory pulses | 9.2 (0.4)[a] | 7.3 (0.5)[b] | 8.04 (0.4)[b] ($p = 0.09$) |
| Semen measures | | | |
| Gel volume (cc) | 11.1 (6.4)[a] | 6.9 (2.6)[a] | 10.4 (5.4)[a] |
| Gel-free semen volume (cc) | 29.3 (4.4)[a] | 22.2 (3.5)[b] | 23.5 (3.2)[ab] |
| Percentage of total motile | 72.2 (4.6)[a] | 71.0 (5.4)[a] | 72.0 (4.9)[a] |
| Percentage of progressively motile | 63.2 (5.0)[a] | 62.1 (5.5)[a] | 62.7 (5.0)[a] |
| Concentration ($10^6$/cc) | 286.0 (84.3)[a] | 255.8 (60.2)[a] | 239.8 (50.3)[a] |
| Total number sperm ($10^9$) | 6.2 (1.0)[a] | 4.5 (0.7)[b] | 4.9 (0.9)[a] ($p = 0.07$) |
| pH | 7.1 (0.03)[a] | 7.1 (0.13)[a] | 7.1 (0.17)[a] |

[a,b] Within rows, different superscripts indicate differences at $p < 0.05$, except where indicated.

### 3.2. Experiment 2

The SB, SEAM, and semen measures were similar during baseline for subjects assigned to aversive conditioning and sham control for Replicate 1. Data for the SB, SEAM, and semen measures before and after aversive conditioning of SEAM for the 12 stallions that received aversive conditioning of SEAM are summarized in Table 2. For SEAM, mean masturbation duration tended to be less after aversive conditioning ($p < 0.10$). For all other

measures of SEAM, mean values before and after aversive conditioning were similar ($p > 0.10$). As is typical for SEAM in stallions, no ejaculations occurred.

With the exception of mounts to ejaculation, all pre-aversive conditioning SB measures were different ($p < 0.05$) or tended to be different ($p < 0.10$) from post-aversive conditioning measures, both for the trials conducted the 3 days immediately following aversive conditioning and for trials conducted 1 week after aversive conditioning ended. Erection latency, mount readiness latency, ejaculation latency, and thrusts to ejaculation were each greater after aversive conditioning of SEAM; erection rigidity score and ejaculatory pulses were each less after aversive conditioning of SEAM. Of note, 8 of the 12 stallions had considerable increases in ejaculation latency, requiring from 39 to 538% greater time to achieve ejaculation. These differences are consistently in the direction of suppressed libido, erection, and overall breeding efficiency at a level of practical significance.

Gel-free semen volume and total sperm number were less for both post-aversive as compared with pre-aversive conditioning period ($p < 0.05$). For 9 of the 12 stallions, the total number of sperm per ejaculate was less than in pre-aversive conditioning ejaculates, the decline ranging from 11 to 67%. Gel volume, percent total and progressively motile, sperm concentration, and pH were similar for pre- and post-aversive conditioning periods.

For the 4 yoked control stallions, all SEAM, SB, and semen measures before and after non-SEAM-contingent shock experience were similar ($p > 0.10$).

Eight of the 12 stallions receiving SEAM-contingent aversive conditioning exhibited abnormal behaviors during the aversive conditioning. These included colic-like gazing back toward abdomen, anxious facial grimace, ear pinning, repeated partial dropping and then retracting the penis, posturing to urinate without dropping the penis, pawing, kicking toward the caudal abdomen, stomping with a hind leg, quivering, and rapid respiration associated with penis dropping. These behaviors had not been seen previously in these stallions and were observed beginning as early as 5 h into the aversive conditioning. None of the four yoked controls showed these behaviors.

## 4. Discussion

In the present work, aversive conditioning of SEAM did not suppress SEAM. Aversive conditioning of SEAM clearly suppressed sexual arousal, breeding efficiency, and semen. Total number of sperm per ejaculate was markedly depressed in 9 of 12 stallions receiving SEAM-contingent aversive conditioning. At 10 days after completion of aversive conditioning, sexual behavior and total sperm number per ejaculate continued to be depressed. For the 4 yoked control subjects, pre- and post-aversive conditioning SEAM, SB, and semen measures were similar, indicating that the SEAM-independent shock experience did not adversely affect SB or semen. These findings are consistent with clinical anecdotes and preliminary trials suggesting that direct punishment of periodic spontaneous erections or use of anti-masturbatory devices do not effectively reduce or eliminate SEAM, while at the same time suppress libido and sexual behavior in stallions.

In Experiment 1, there was a tendency for the mean masturbation episode interval to be reduced after aversive conditioning. This is the only one of several measures of SEAM that may have been affected by aversive conditioning. In Experiment 1, which included sham-

conditioned matched control subjects during the conditioning sessions themselves, erection interval of aversively conditioned subjects was about one-third of that for sham conditioning. Explanation for this may lie in the observations of horses (Wilcox et al., 1991; McDonnell, 1995), hibernating bats (Wimsatt, 1945), cats (Aronson, 1949), and primates (Linnankoski et al., 1981) that erection often occurs within minutes of returning to the calm state following a startle or disturbance, or similarly within minutes of an increased arousal from sleep or transition from the drowsy to alert state. Erection upon arousal from sleep is also common in humans. At least two alternative hypotheses for "morning erection" in men (interrupted REM-related nocturnal penile tumescence and full bladder-induced reflexogenic erection) have apparently not been systematically evaluated (Sachs, 1995, 2000). Episodes of SEAM can be elicited in awake stallions simply by disturbing the animal (e.g. with a loud noise, an un-signaled pinch, moving an animal within the stable) and then allowing calming to resume (McDonnell, unpublished). As in the present experiment, the startle of the aversive stimulus initially interrupts SEAM, but then SEAM begins again when the calm state returns. In fact, if the aversive stimulus used in the present experiments is presented to a stallion during a period when there is no SEAM, SEAM commences within 5 min in more than 70% of trials (McDonnell, unpublished trials; Fisher's exact, $p < 0.001$). It is possible that involuntary erection is evoked as sympathetic dominance subsides. This phenomenon of startle-related SEAM might explain increased SEAM during the conditioning sessions themselves, and may explain the horseman's perception that punishing SEAM tends to increase the behavior.

The intensity and duration of aversive conditioning were relatively mild and brief in the present experiments. In the horse industry, aversive conditioning is typically more severe and persistent. The most commonly used equine anti-masturbatory devices are applied continuously, as opposed to a specific conditioning period as was done in the present study, and the goal of fitting the apparatus is often to inflict severe pain upon erection and/or movement of the erect penis. In our preliminary research (1985–1987), there were instances in which aversive conditioning continued considerably longer and the aversive stimuli were more severe than in the present work. With increasing duration of conditioning and more severe aversive stimulation, total frequency and duration of SEAM were markedly increased. Similarly, the adverse effect on sexual behavior was more profound and long lasting than in the present experiment, and seemed related to the intensity and duration of aversive conditioning.

These findings taken together are difficult to understand in light of learning theory. Firstly, it would be expected that aversive conditioning would suppress the target behavior, SEAM (Solomon, 1964; Schwartz, 1978). Apparently, there are no other examples of a behavior which when punished increases rather than decreases. It is not clear to what extent SEAM in stallions or other animals is under voluntary and/or involuntary control. Both autonomic and voluntary responses in general (Miller, 1969), and penile erection response in particular (Beach et al., 1956; McConaghy, 1970; Linnankoski et al., 1981; McDonnell et al., 1985; Sachs, 1995) are, however, known to be suppressed by response contingent aversive conditioning.

The mechanism by which aversive conditioning of SEAM adversely affects sexual response is perhaps less puzzling. Simple association of a negative stimulus with the sensation of commencing erection might subdue sexual arousal, erection, and overall sexual performance. There is ample evidence in several species including horses, that male sex-

ual behavior is particularly sensitive to conditioned suppression (Beach et al., 1956; Laws and Rubin, 1969; McDonnell et al., 1985; Jainudeen and Hafez, 1987). Also, the aversive conditioning experiences may render the animal more wary in general of his environment and handlers, effectively delaying and subduing sexual response. Simply evaluating sexual response before and after similar aversive stimulation that is not contingent on spontaneous erection might clarify this possible explanation.

The practical significance of the present research is that attempts to stop SEAM in stallions is not likely to be effective and is likely to adversely affect sexual arousal, breeding behavior and semen. For performance stallions with no future in breeding, reduced sexual arousal and erection may actually be a desirable result of punishing SEAM. In clinical cases of stallion sexual behavior dysfunction associated with anti-masturbatory devices, we have had some success using anxiolytic drugs (at doses similar to those which have proven useful for reversal of directly aversively suppressed sexual behavior) as an aid to overcoming suppressed sexual behavior (McDonnell et al., 1985, 1987). Clinical cases often appear quite complex in that sexual arousal and erection response to mares and SEAM both have been punished during years of the stallion's performance career before being taken to stud. In addition to employing anti-masturbatory devices, handlers and trainers typically have verbally and physically reprimanded the stallion for sexual arousal or SEAM. Particular handlers and sometimes people in general appear to have become conditioned negative stimuli for erection or sexual arousal. Apparently, no critical data are available on effects of aversive conditioning of non-sexual erections in other animal species or in humans.

Development of abnormal behavior suggesting anxiety or anticipation of pain related to dropping of the penis for urination or for SEAM in aversively conditioned stallions suggests that use of this device or of this type of aversive conditioning of SEAM in horses is likely inhumane.

## Acknowledgments

This is a Dorothy Russell Havemeyer Foundation Project conducted at the Georgia and Philip Hofmann Center for Animal Reproduction, with partial support from NIH #K04-NS01537. Emily Graves and Georgina Russell assisted with animal procedures.

## References

Aronson, L.R., 1949. Behavior resembling spontaneous emissions in the domestic cat. J. Comp. Physiol. Psychol. 42, 226–227.

Beach, F.A., 1976. Cross-species comparisons and the human heritage. Arch. Sex. Behav. 5, 469–485.

Beach, F.A., Conovitz, M.W., Steinberg, F., Goldstein, A.C., 1956. Experimental inhibition and restoration of mating behavior in male rats. J. Genet. Psychol. 89, 165–181.

Beaver, B.V., 1994. The Veterinarian's Encyclopedia of Animal Behavior, vol. 22. Iowa State University Press, Ames, IA, p. 70.

Boyd, L.E., 1991. The behavior of Przewalski's horses and its importance to their management. Appl. Anim. Behav. Sci. 29, 301–318.

Conn, J., Kanner, L., 1940. Spontaneous erections in early childhood. J. Pediatr. 16, 337–340.

Evans, J.W., 1981. Horses: A Guide to Selection, Care and Enjoyment, second ed. W.H. Freeman and Company, NY, p. 484.
Feist, J.D., 1971. Behavior of feral horse in the Pryor Mountain wild horse range. Thesis. University of Michigan, Ann Arbor, MI, pp. 112–114.
Hafez, E.S.E., 1962. The Behavior of Domestic Animals. The Williams and Williams Co., Baltimore, pp. 269, 382, 435, 472–473.
Henry, M., McDonnell, S.M., Lodi, L.D., Gastal, E.L., 1991. Pasture mating behaviour of donkeys (*Equus asinus*) at natural and induced estrus. J. Reprod. Fertil. Suppl. 44, 77–86.
Jainudeen, M.R., Katongole, C.B., Short, R.V., 1972. Plasma testosterone levels in relation to musth and sexual activity in the male Asiatic elephant, *Elephas maximus*. Reprod. Fertil. 29, 99–103.
Jainudeen, M.R., Hafez, E.S.E., 1987. Reproductive behavior. In: Hafez, E.S.E. (Ed.), Reproduction in Farm Animals, fifth ed. Lea and Febiger, Philadelphia, pp. 260–294.
Karacan, I., Salis, P.J., Thornby, J.I., Williams, R.L., 1976. The ontogeny of nocturnal penile tumescence. Wak. Sleep. 1, 27–44.
Keiper, R.R., 1985. The Assateague Ponies. Tidewater Publishers, Centreville, MD, p. 58.
Kenney, R.M., Hurtgen, J., Pierson, R., Witherspoon, D., Simons, J., 1983. Society for Theriogenology Manual for Clinical Evaluation of the Stallion. Society for Theriogenology, Hastings, NE.
Laws, D.R., Rubin, H.B., 1969. Instructional control of an autonomic sexual response. J. Appl. Behav. Anal. 2, 93–99.
Linnankoski, I., Hytonen, Y., Leinonen, L., Hyvarinen, J., 1981. Determinants of sexual behavior of *Macaca arctoides* in a laboratory colony. Arch. Sex. Behav. 10, 207–222.
McConaghy, N., 1970. Penile response conditioning and its relationship to aversion therapy in homosexuals. Behav. Ther. 1, 213–221.
McDonnell, S.M., 1989. Spontaneous erection and masturbation in equids. In: Proceedings of the 35th Annual Convention American Association of Equine Practitioners, Boston, MA, pp. 567–580.
McDonnell, S.M., 1995. Spontaneous erection and "masturbation" in equids. In: Proceedings of the Second International Workshop on Erection and Ejaculation in Horses and Men, Mount Joy, PA, pp. 29–30.
McDonnell, S.M., Diehl, N.K., 1990. Computer-assisted recording of live and videotaped horse behavior: reliability studies. Appl. Anim. Behav. Sci. 27, 1–7.
McDonnell, S.M., Love, C.C., 1990. Manual stimulation collection of semen from stallions: training time, sexual behavior, and semen. Theriogenology 33, 1201–1210.
McDonnell, S.M., Murray, S.C., 1995. Bachelor and harem stallion behavior and endocrinology. Biol. Reprod. Mono. 1, 577–590.
McDonnell, S.M., Garcia, M.C., Kenney, R., 1987. Pharmacologic manipulation of sexual behavior in stallions. J. Reprod. Fertil. Suppl. 35, 45–49.
McDonnell, S.M., Henry, M., Bristol, F., 1991. Spontaneous erection and masturbation in equids. J. Reprod. Fertil. Suppl. 44, 664–665.
McDonnell, S.M., Kenney, R.M., Meckley, P.E., Garcia, M.C., 1985. Conditioned suppression of sexual behavior in stallions and reversal with diazepam. Physiol. Behav. 34, 951–956.
Miller, N.E., 1969. Learning of visceral and glandular responses. Science 163, 434–445.
Mountjoy, P.T., 1974. Some early attempts to modify penile erection in horse and human: an historical analysis. Psychol. Rec. 24, 291–308.
Ohlmeyer, P., Brilmayer, H., Hullstrung, H., 1944. Periodische vorgange im schlaf. Pflugers Arch. 248, 559–560.
Pearson, O.P., 1944. Reproduction in the shrew (*Blarina brevicauda* Say). Am. Anat. 75, 39–93.
Penzhorn, B.L., 1984. A long-term study of social organization and behavior of Cape Mountain zebras (*Equus zebra zebra*). Z. Tierpsychol. 64, 97–146.
Pickett, B.W., 1974. Evaluation of stallion semen. In: Adams, O.R. (Ed.), Lameness in Horses, third ed. Lea and Febiger, Philadelphia, pp. 60–90.
Roberts, S.J., 1986.Veterinary Obstetrics and Genital Diseases, Woodstock, Vermont.
Sachs, B.D., 1995. Placing erection in context: the reflexogenic–psychogenic dichotomy reconsidered. Neurosci. Biobehav. Rev. 19, 211–224.
Sachs, B.D., 2000. Contextual approaches to the physiology and classification of erectile function, erectile dysfunction, and sexual arousal. Neurosci. Biobehav. Rev. 24, 541–560.

Schmidt, M.H., Valatx, J.-L., Schmidt, H.S., Wauquier, A., Jouvet, M., 1994. Experimental evidence for penile erections during paradoxical sleep in the rat. Neuroreport 5, 561–564.
Schwartz, B., 1978. Aversive control: punishment and avoidance. In: Schwartz, B. (Ed.), Psychology of Learning and Behavior. W.W. Norton, NY, pp. 222–265.
Solomon, R.L., 1964. Punishment. Am. Psychol. 19, 239–253.
Tyler, S.J., 1972. The behaviour and social organization of the New Forest ponies. Anim. Behav. Mono. 5, 85–196.
Waring, G.H., 1983. Horse Behavior. Noyes Publications, Park Ridge, NJ, p. 106.
Waring, G.H., 2003. Horse Behavior, second ed. Noyes Publications, Park Ridge, NJ, p. 384.
Wilcox, S., Dusza, K., Houpt, K., 1991. The relationship between recumbent rest and masturbation in stallions. Equine Vet. Sci. 11, 23–26.
Wilson, S., 2004. http://www3.vet.upenn.edu/labs/equinebehavior/Havemeyer%20Day/hvday04jw.htm (personal communication).
Wimsatt, W.A., 1945. Notes on breeding, pregnancy, and parturition in some vespertilionid bats on the eastern United States. Mammal 26, 23–33.