

Bachelor and Harem Stallion Behavior and Endocrinology¹

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ABSTRACT

Horses naturally breed within a harem social unit that typically includes one mature breeding stallion with several mares and their immature offspring. Non-harem stallions comprise relatively stable social groups known as bachelor bands. When a harem position becomes vacant, a stallion emerges from a bachelor band to fill the vacancy. We studied harem and bachelor stallion phenomena using a model of pony stallions pastured together under semi-feral conditions. In this model, one stallion assumed the role of "harem stallion," vigilantly guarding an area within the stallion pasture along the fence line facing nearby mare pastures. The remaining stallions interacted as a bachelor band. If the harem stallion was removed from the pasture, a stallion from the bachelor group rapidly emerged to fill the position. If we replaced to the pasture a former harem stallion, the former harem stallion typically displaced the incumbent harem stallion back to the bachelor band. Order of emergence from the bachelor band to fill harem position vacancies, while highly repeatable, was not strongly associated with bachelor age, height, weight, testosterone concentrations, ranked level of aggressive behavior, or ranked leader-follower behavior. Emergence from bachelor to harem status consistently resulted in a sudden sharp rise in testosterone concentration, which remained high for the duration of harem status. Displacement from harem status back to the bachelor band was consistently associated with a sharp decrease in testosterone concentration. Testosterone concentrations with harem status were significantly higher than those with bachelor status for all months of the year. These changes in behavior and testosterone concentrations of sexually experienced mature stallions suggest social modulation of behavior and endocrinology, with enhancement of reproductive function as a harem stallion and/or suppression as a bachelor. Extremely wide variation in testosterone concentrations due to sociosexual conditions raises important questions about basic neuroendocrinology of stallions, including methodological concerns. Equally significant are questions raised regarding management of domestic breeding stallions.

INTRODUCTION

Most equids, including free-running domestic and feral horses, Przewalski horses, and common zebra, breed within a harem social unit [Berger, 1977; Feist & McCullough, 1975; Hoffmann, 1985; Klingel, 1975; Kownacki et al., 1978; McCort, 1984; Miller, 1981; Penzorn, 1984; Penzorn & Novellie, 1991; Salter & Hudson, 1982; Schilder & Boer, 1987; Tilson et al., 1988; Turner et al., 1981; Wells & von Gold-Schmidt-Rothschild, 1979]. Each harem typically includes one mature breeding stallion with 5-10 adult mares and their immature offspring. Male offspring are evicted from their natal band around the time of puberty. They then typically join with other young adult and mature males

(that do not have a harem) to form social groups of 5-20 animals, known as bachelor bands. The bachelor band is a relatively stable social unit. Although most of the bachelor males are post-pubertal, they remain heterosexually inactive until and unless they become a harem stallion. Bachelor bands generally travel near harem bands, but apparently do not continuously challenge harem stallions for access to females. When a harem becomes available due to death or incapacitation of the harem stallion, one of the bachelors emerges from the band to assume the position. Transition from a bachelor band to a harem is a relatively orderly event, with apparently little fighting among the bachelors at the time one takes a harem. Descriptions of behavior of free-running bachelor bands indicate day-to-day fighting, both play and serious, and elimination marking sequences among bachelors.

At our facility, for several years we have kept pony stallions pastured together under semi-feral conditions. In any one grouping, one stallion reliably assumes the role of "harem stallion," vigilantly guarding an area within the stallion pasture and the fence line facing nearby mare pastures. The remaining stallions interact as a

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group, with behavior similar to that described for bachelor bands among free-running equids. If we remove the harem stallion from the pasture, one of the bachelor stallions quickly emerges from the band to fill the vacated position. Casual observations have suggested to us that, within a bachelor band, there may be an established order in which bachelors take over the harem position when a vacancy arises. In instances when we have returned a former harem stallion to the pasture, he has invariably resumed his previous position within a few minutes to a few hours. The incumbent harem stallion has either immediately retreated with little aggressive interaction or has been aggressively displaced from harem status by the returning former harem stallion.

Considering that our pastured pony groups provide a suitable model, we have been studying behavior and endocrinology of harem and bachelor stallions. The work reported here includes description of behavior associated with harem and bachelor status, evaluation of stallion characteristics associated with achieving harem status, and evaluation of testosterone concentrations associated with bachelor and harem status. Specific objectives for these experiments included the following:

Experiment 1. General description of behavior and preliminary quantitative time budgets for bachelor and harem stallions during periods of stability as well as during periods when the harem position was contested.

Experiment 2. Evaluation of repeatability of the order of emergence of stallions from an established bachelor band into harem status.

Experiment 3. Evaluation of associations of age, physical size, tenure in the herd, leadership and aggression within the bachelor band, and testosterone concentrations with order of emergence to harem status.

Experiment 4. Comparison of testosterone concentrations of harem and bachelor stallions, including longitudinal evaluation of stallions as they emerged from bachelor to harem status.

Experiment 5. Evaluation of displacement from harem status in this model, and description of associated behavior and testosterone concentrations.

MATERIALS AND METHODS

Experiment 1

Study site. The study site consisted of one main pasture (2.1 hectares) and several nearby smaller (0.4-1.2 hectares) holding pastures.

The main pasture contained a natural stream with adjacent light forest running diagonally across the long axis of the pasture. Also used were two traditional horse stables with a combination of individual box or tie-stalls for housing stallions for short periods. These facilities were adjacent to an equine reproduction clinical and teaching facility where mares were pastured and stabled throughout the year. Approximately 20 horse and pony mares were kept in several small pastures within 15-300 m of the western fence line of the main pasture. The main bachelor and harem pasture shared no fence lines with mare pastures.

Subjects. A total of twenty-five Shetland-sized mixed-breed pony stallions (2-21 yr of age; 100-275 kg; all sexually experienced) were used. At pasture, these stallions were left undisturbed and were maintained on grass alone (March through November) or grass and supplemental hay dispersed throughout the pasture once daily (December through February). Throughout the year, stallions were removed or added to the main pasture, with the number of stallions at any one time ranging from 10 to 19.

Behavior observations and measures. Over a period of two years, the herd was observed 10-60 daylight hours (0600-2000 h) weekly, in 4-h sessions with equivalent weekly coverage of morning, afternoon, and evening periods. Observers were on foot when inside the pasture or in vehicles when outside the pasture. The method of observation was to continuously scan the herd to record ongoing maintenance activities (grazing, drinking, moving, elimination-marking, standing rest or recumbency, and rolling) of each stallion as well as each occurrence of self or mutual grooming, masturbation, and aggressive interaction, as previously defined by McDonnell & Haviland [1995]. Hand-held computer event-recorders and prepared checksheets enabled scanning of the entire herd approximately once every 5 min. For most scans, one to three stallions were out of sight, and were recorded as such. Observers moved about within the pasture as necessary to locate each stallion at least once every 10 min. In addition, the harem or bachelor status and location within the pasture of each stallion was recorded 1-3 times daily during 10-min drive-by observations with prepared pasture maps. Harem stallion status was defined as maintaining proximity to and control of the fence line closest to the mare pastures. Bachelor status was defined as affiliation with the

non-harem stallions and/or apparent avoidance of the area guarded by the harem stallion.

For each stallion, the percentages of time spent grazing, moving, resting (standing or recumbent), interacting aggressively with other bachelor/s (play, sparring, and serious), and performing elimination/markings were calculated, on the basis of total durations of each behavior and total time observed over all sessions. Frequencies (episodes per hour) of drinking, self-grooming, mutual grooming, and masturbation were similarly obtained for each stallion. Of the 25 stallions, 24 were observed as bachelors and 15 as harem stallions. For stallions observed as both, harem and bachelor values were calculated separately. Paired t-test procedures were used to compare harem and bachelor masturbation frequency, drinking frequency, and percentages of time spent performing elimination-marking.

Experiment 2

Sixteen pony stallions were pastured together as described in experiment 1. After a stallion had established his harem position for at least 1 wk (range 1-3 wk), he was removed from the pasture, allowing another stallion to emerge from the bachelor band to fill the vacancy. Removal of the established harem stallion was repeated, with the goal of allowing each of the 16 stallions the opportunity to establish harem status. After 13 harem stallions had been removed, none of the three remaining stallions established harem status within 4 wk. The series of removals was terminated, and then the 13 previously removed stallions were simultaneously returned to the pasture, and the removal procedure was repeated twice for 8 sequential harem stallions. Spearman rank order correlation procedures were used to evaluate repeatability of order of emergence.

Experiment 3

Twenty-five pony stallions (described in experiment 1) were ranked according to their order of emergence from bachelor to harem status in this system as described in experiment 2. For each stallion, the following measures were obtained at the time of assuming harem status:

Age: estimated on the basis of dentition.

Height: measured in inches to the top of the withers.

Weight: estimated from girth circumference.

Tenure within the herd: estimated as the

number of years the stallion had been kept at this study site.

Leader-follower rank: based on nine 4-h observation sessions representing morning, afternoon, and evening daylight hours over a 3-wk period beginning 1 wk after the group had been assembled. For each observed movement of a group or sub-group of bachelors to water, rest areas, or grazing areas, each stallion involved was recorded as having led or directed the group or as having been a follower. For each session, each stallion was ranked from 1 (least leadership) to 5 (most leadership). For each stallion, a mean rank over all observation sessions was calculated.

Aggressiveness rank: based on number of aggressive interactions initiated. Specific behaviors considered aggressive included arched neck threat, posturing, bite or bite threat, box chase, head and neck wrestling, head threat, kick or kick threat, stomp, and strike or strike threat [McDonnell & Haviland, 1995]. For each session, each stallion was ranked from 1 (least aggressive) to 5 (most aggressive). For each stallion, a mean rank over all observation sessions was calculated.

Testosterone concentrations: based on jugular plasma samples obtained 1-3 times weekly while in the bachelor band. All samples were obtained between 1400 and 1700 h (in preliminary studies of diurnal variation in testosterone of these pony stallions, concentrations were found to be relatively stable within this time window. Testosterone concentration was measured by RIA with use of a commercially available kit (Coat-A-Count Total Testosterone, Diagnostic Products Corporation, Los Angeles, CA) validated for equine plasma by a commercial clinical veterinary laboratory (BET Reproductive Laboratories, Inc., Lexington, KY). Sensitivity is 0.02 ng/ml. Cross-reactivity with dihydrotestosterone is < 5%. Inter-assay and intra-assay coefficients of variation were 8.1% and 4.1%, respectively. For each stallion, mean testosterone concentrations a) for the entire period in the bachelor band and b) for the week preceding transition to harem status were calculated.

Spearman rank order correlation procedures were used to evaluate associations of these variables with order of emergence from the bachelor band.

Experiment 4

Over a period of one year, testosterone concentrations were measured (as described in ex-



FIG. 1. Harem stallion fighting with intruder bachelor along harem fence line.

periment 3) 1-3 times weekly for all bachelor and harem stallions. Stallions and pasture arrangements were similar to those described in the earlier experiments. Monthly means for harem and bachelor status were calculated on the basis of monthly averages of individual stallion monthly means (varying number of bachelor and harem stallions for each month). Also, for comparison, testosterone concentrations were similarly obtained for 12 horse and pony stallions stabled in barns with other stallions at the adjacent breeding facility described in experiment 1.

Experiment 5

Fifteen stallions were sequentially removed from harem status as described in experiment 2, and were held in individual stalls or holding paddocks. The stallions were sequentially returned at approximately 1-wk intervals to the pasture in the reverse order of their emergence. Each time a stallion was returned to the pasture, the herd was observed continuously during daylight hours until the harem position appeared stable. Observations focused on the harem fence line area, with methods followed as described in experiment 1. Jugular plasma samples were obtained 1-3 times weekly from all stallions throughout for assay of testoster-

one as described in experiment 3. Sampling was continued for stallions when outside the pasture in barns or holding paddocks.

RESULTS

Experiment 1

General behavior patterns. Harem stallion behavior primarily included guarding of the harem fence line area, with most harem stallions pacing along a portion of the fence line most of the time with attention apparently focused on the mares in nearby pastures. Grazing and resting typically occurred in bouts lasting less than 5 min interspersed with longer bouts of pacing of the fence line. For most harem stallions, their interactions with other stallions were limited to serious fighting (Fig. 1) and aggressive chases of stallions from the harem fence line area and periodic unprovoked raids on the bachelor band, in which the bachelors were herded together to the area of the pasture furthest from the harem fence line area. Individual harem stallions varied with regard to their level of vigilance, tolerance, and aggressiveness in guarding the harem fence line area and keeping bachelors away. Unprovoked raids on bachelors occurred as frequently as every hour and lasted as long as 10

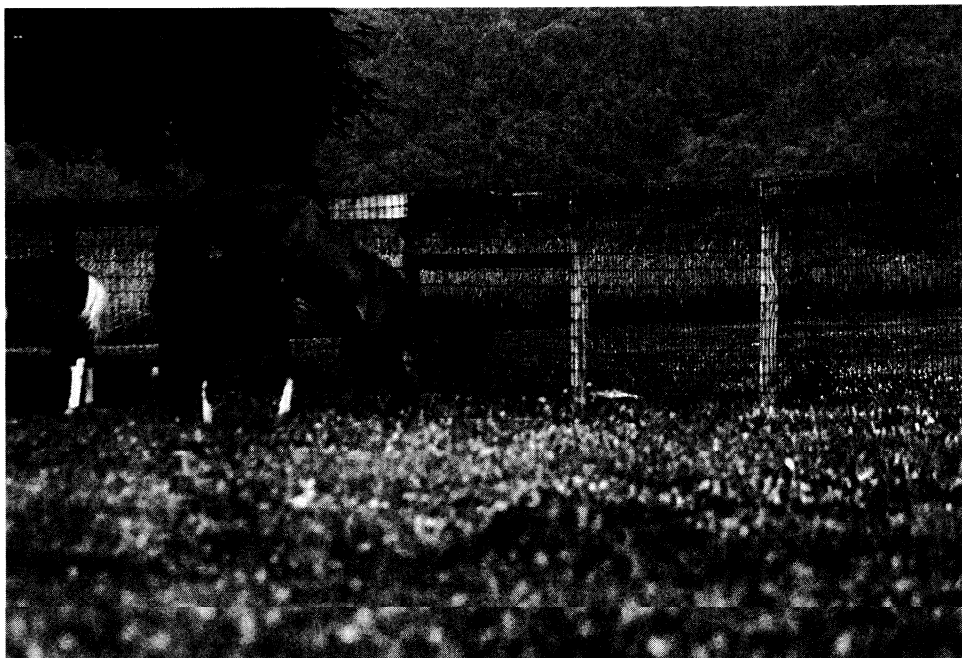


FIG. 2. Stallion with erection mounting another bachelor stallion.

min for some harem stallions. For others, raids were as infrequent as once every 5 h and were as brief as 2 min. Five harem stallions did not perform unprovoked raids at regular intervals.

Elimination-marking behavior occurred at least once per hour for most harem stallions. Once a stallion had established harem status, all elimination-marking behavior was solitary.

Bachelor stallions interacted almost continuously with other bachelor stallions, with most of their time spent in quiet side-by-side grazing and resting. These quiet interactions are similar to those of mares at pasture (McDonnell, unpublished observations). They included mutual grooming, usually as a pair, but sometimes involving three or four participants, at a rate of approximately one episode per 4-h observation session for a band of 12-18 bachelors. Interspersed with these quiet grazing and resting periods were episodes of aggressive interaction. Aggressive interaction among bachelors consisted mostly of sparring. Serious fighting and play-like aggressive interaction were seen much less frequently. Any one aggressive episode usually involved only 2 or 3 stallions, and typically did not disturb ongoing activities of the remaining bachelors.

Male-male mounting, sometimes with erection, was a relatively common occurrence among bachelors (see Fig. 2). Roughly half of

the time, the target stallion appeared to present his rump, soliciting and tolerating the mount. In two such instances, anal insertion occurred and ejaculation was apparent. In three additional instances, ejaculation occurred with thrusting of the penis against the flank or perineum of the target stallion. The remaining mounts appeared to be unsolicited and occurred during sparring and chasing episodes. During these encounters, the mount was often sideways or even head-on across the back or shoulder of the target stallion. In these seemingly unsolicited mounts, erection, thrusting insertion, and ejaculation were rare.

All bachelor stallions within the pasture interacted as a group. Most of these stallions were together in the same area of the pasture, engaging in the same activities together within a 50-m span (Fig. 3a). Within the group, there were obvious sub-associations of pairs and groups of three to five individuals that typically grazed, rested, moved about in close consort, and engaged in periodic sparring (Fig. 3, b-d). A common association was an older stallion and one or two 2-yr-old stallions, with the older stallion herding and guarding the younger as a harem stallion would herd and guard a mare. Also, usually one or two bachelors spent a large percentage of each day grazing and resting within the area of the other

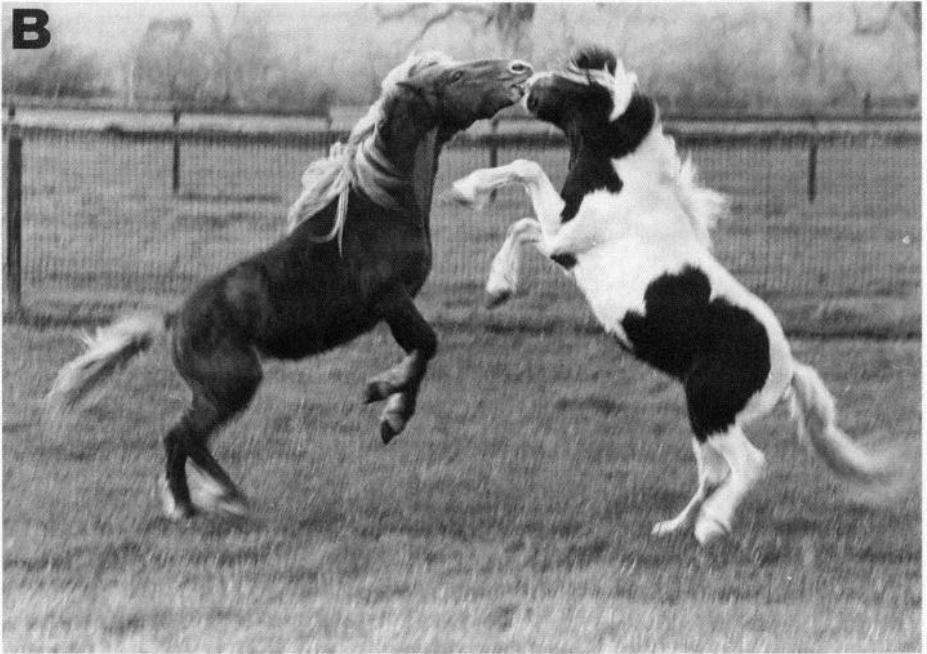


FIG. 3. a) Typical band of bachelor stallions grazing quietly together at pasture. A sub-association of two stallions (b) sparring, and moments later (c) grazing together, then (d) resting together with simultaneous masturbation.

bachelors, but with no close association to a sub-group. More rarely, a "loner" bachelor grazed and rested at a relatively great distance from the other bachelors, maintaining a seemingly independent activity pattern. When an

environmental event or disturbance occurred, the bachelors quickly came together and moved about within the pasture as a single tight band spanning less than 15 m. For example, during raids by the harem stallion, lon-



ers almost always joined the tightly banded bachelor group, or in some cases were chased and herded into the bachelor band by the harem stallion. Bachelor stallions in general appeared submissive to an established harem stallion. Most bachelors appeared to remain the location of the harem stallion and retreated when he approached.

the experiment, stallions to pair off or graze alone. They also maintained affiliations with particular individual ponies, even after periods of weeks or months of separation.

Time budgets. Bachelor and harem time budgets are summarized in Table 1. The most

TABLE 1. Behavioral time budgets of harem and bachelor stallions.

	Harem (n = 15)	Bachelor (n = 24)
Percentage of time		
Grazing	29	53
Moving	49	12
Resting	13	30
Aggression		
Play	0	<1
Sparring	0	4
Serious	5	<1
Elimination-marking	3	<1
Rolling	<1	<1
Frequency (episodes/h)	(n = 14)	
Drinks	0.06	0.12
Masturbation	0.68	0.62

salient difference was that for harem stallions, the percentage of time spent moving was approximately seven times that for bachelors, reflecting the pacing of the harem fence line and the raids on bachelors. Percentage of time spent resting and grazing was considerably less for harem than for bachelor stallions.

For the 14 stallions observed during both harem and bachelor status, masturbation frequency was similar with harem and bachelor status (dependent t-tests, 13 *df*, $p > 0.10$). Masturbation episodes occurred similarly during resting and grazing for both harem and bachelor stallions. For bachelor stallions, a mean of approximately 60% of masturbation episodes were simultaneous (Fig. 3d) that is, they occurred while another bachelor was also masturbating in close proximity. Quite curiously, on four occasions, two stallions were observed in what we have called simultaneous synchronous masturbation. This involved standing nose-to-nose, simultaneously achieving erection, commencing synchronous movements of the penis, and then simultaneously losing erection and retracting the penis. Drinking frequency was also similar for harem and bachelor status (dependent t-tests, 13 *df*, $p > 0.10$). Percentage of time spent engaging in elimination-marking behavior was greater with harem status than with bachelor status (dependent t-test, 13 *df*, $p < 0.05$).

Transition from bachelor to harem status.

Twelve transitions from bachelor to harem status were included in these observations. In all cases, we removed the harem stallion from the pasture, creating a vacancy. Within 1 min to 3 h of removal of the harem stallion, one or

more bachelors approached the harem fence line area and engaged in posturing, elimination-marking, and rolling sequences along the fence line. Usually within 1-5 min of such interaction, one bachelor appeared to assume the harem position, pacing the harem fence line and chasing other bachelors away from the area. In 8 of these 12 observed transitions, a second stallion commenced similar guarding of the harem fence line. The two then engaged in more intense aggressive sparring, chasing, and serious fighting for the position. Usually within less than 1 h, one of these two succeeded in forcing the other to retreat back to the bachelor band. For all 12 transitions, uncontested control of the harem line area was established by a single stallion within less than 5 min for 4 stallions, within 30 min for 1 stallion, 1 h for 5 stallions, 12 h for 1 stallion, and 24 h for 1 stallion.

Transition from bachelor-type behavior to harem-type behavior was remarkably rapid in all cases. Immediately, affiliative contact with former bachelor herd mates ceased for the duration of harem status. In several instances, within minutes of quietly grazing, mutually grooming, and resting together with a bachelor companion, an emerging harem stallion viciously attacked and chased his former herd mate away from his newly attained harem area.

Experiment 2

Order of emergence was identical for replicates one and two. In replicate three, the 3rd and 4th stallions emerged in reversed order. Therefore, the order of emergence was highly repeatable (Spearman rho = 0.96; $p < 0.05$).

Experiment 3

Results are summarized in Table 2. For all variables, Spearman rank order correlation coefficients for association with order of emergence to harem status were not significant (Spearman rho $< \pm 0.30$, NS). It is noteworthy that none of the three 2-yr-old stallions assumed harem status in this experiment, even when they were the only stallions remaining in the pasture. (We had collected semen from each of them and all three showed normal sexual response to an estrous mare and ejaculated normal numbers of viable sperm.)

Figure 4 summarizes mean monthly testosterone concentrations for bachelor and harem

stallions. Testosterone concentrations of harem stallions were significantly higher than those of bachelors for all months of the year.

Figure 5 illustrates mean testosterone concentrations associated with 30 transitions from bachelor to harem status of 18 different stallions. Testosterone concentrations were consistently higher with harem than with bachelor status. Mean testosterone concentrations for the last weekly sample before emergence to harem status (during Weeks 2-12 of bachelor status) and the first weekly sample during harem status were significantly different (dependent t-tests, 29 *df*, $p < 0.001$). The increase in testosterone concentration ranged from 29% to 1931% (mean of 281%). Testosterone concentrations remained high for the duration measured (1-15 wk). These effects occurred throughout all months of the year. The mean percentage increase in testosterone concentration tended to be greater (independent t-tests, $p < 0.10$) during nonbreeding season months (September-February, 537%) than during breeding season months (March-August, 152%), with 3 increases exceeding 1000% associated with winter low bachelor concentrations. Testosterone concentrations of horse and pony stallions stabled in barns with other stallions at the same facility closely followed those of bachelors in this model.

Experiment 5

Behavior associated with displacement. In all 15 cases, the returning stallion displaced the incumbent harem stallion back to the bachelor band, usually without serious or prolonged fighting. Latency from entry into the pasture until re-establishment of harem status ranged from 0 to 7 h, with a mean of 53.4 (SEM 28.08) min. In three instances, the incumbent harem stallion retreated back to the bachelor band when the returning former harem stallion simply vocalized as he was being brought toward the pasture, twice even before the former harem stallion was within sight of the incumbent harem stallion. For the remaining twelve instances, the returning and incumbent harem stallions engaged in varying degrees of aggressive interaction. This included mostly posturing, elimination-marking sequences, and serious fighting along the entire length of the harem fence line. Some prolonged aggressive chases occurred, extending well away from the harem fence line into the bachelor band areas of the pasture. In eight instances, the displaced

TABLE 2. Spearman rank order correlation with order of emergence from bachelor to harem status (25 pony stallions)

Age	-0.17
Height	-0.13
Weight	-0.13
Tenure	-0.27
Leader-follower rank	-0.30
Aggressiveness rank	-0.25
Testosterone concentration	
Week before harem status	-0.23
Entire bachelor period	-0.19

stallion exhibited submissive gestures toward the former harem stallion before retreating from the area of the harem fence line. These included female posture, rump presentation, solicitation, and tolerance of mounting, occasionally with anal insertion and ejaculation.

The aggressive encounters clearly evoked alert attention of the bachelors in the pasture. During 7 of the 12 displacements involving aggressive engagements along the harem fence line, several bachelors (4-9) approached the vicinity of the skirmish, standing alert in groups of 2-5, facing the combatants (see Fig. 6). These onlooking bachelors stood alert, but relatively relaxed and uninvolved even when intense chases passed close to their position. In 4 instances, one or more bachelors became involved in the agonistic interactions of the returning and incumbent harem stallions, either by approaching them near the harem fence line area, or during chases extending into the bachelor band area.

Most displaced harem stallions did not immediately rejoin the bachelor band. For 1-3 days after displacement from the harem position, they typically moved about alone in the area of the pasture furthest from the harem fence line, at a distance from the bachelors. Re-entry into the bachelor band was gradual and usually included interactions with the bachelors, during which the returning displaced harem stallion appeared extraordinarily submissive. This included tolerance of one or more bachelors sniffing his head, neck, genitals, and perineum. Remarkably, the displaced former harem stallions assumed mare-typical estrous postures during these teasing-like interactions, including, in several instances, presentation of the hindquarters and toleration of mounting. In some cases, several bachelors sequentially mounted the displaced harem stallion.

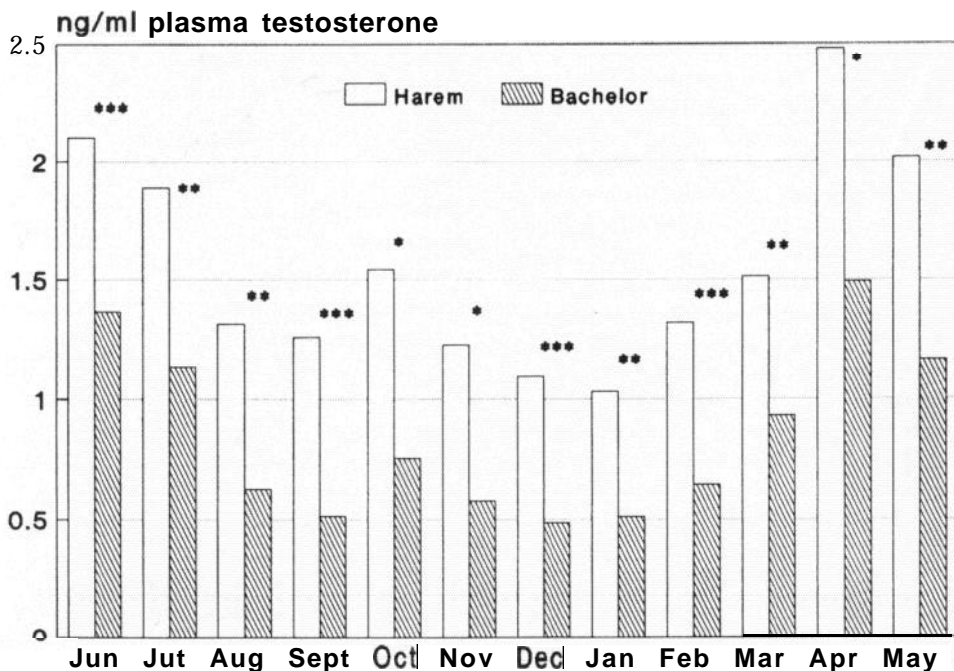


FIG. 4. Mean monthly testosterone concentrations of harem and bachelor stallions. Asterisks indicate significant differences between harem and bachelor groups: * denotes $p < 0.05$; ** denotes $p < 0.01$; *** denotes $p < 0.001$.

Testosterone concentrations. Testosterone concentrations of the 15 displaced stallions dropped 36-94% within the first week (Fig. 7; mean 62%; SEM 5.0%). Within the first week after displacement, testosterone concentrations were significantly lower than the last sample during harem status of 2-12-wk duration (dependent t-test, 14 df , $p < 0.001$).

Two "natural" displacements of the incumbent harem stallion by a challenging stallion

from the bachelor band within the pasture occurred over the 2-yr course of all the experiments reported here. In each case, displacement occurred after prolonged periods (8 days and 23 days) of intermittent aggressive interaction of the harem stallion and the challenger. In each case, the retreating harem stallion's testosterone dropped to an extremely low concentration (similar to those of mares or castrated males) during the first week after displacement and then increased to within the range of long-term bachelors by the second week after displacement. The two displaced stallions appeared extremely dejected for several days following defeat. Each displayed extreme submissiveness at the fringe of the bachelor band for prolonged periods before rejoining the group.

Testosterone concentrations of harem stallions removed from the main pasture to a barn or smaller holding pasture dropped in almost all cases, but variably with the diverse conditions under which they were held. Testosterone concentrations dropped precipitously for harem stallions taken to a barn in which other stallions were stabled. Testosterone concentrations dropped less for stallions taken to a barn

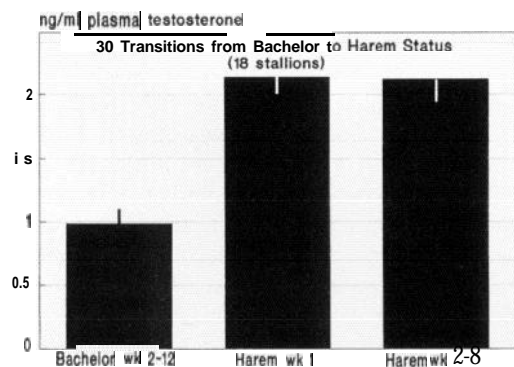


FIG. 5. Mean (\pm SEM) testosterone concentrations associated with emergence from bachelor to harem status.



FIG. 6. Four bachelor stallions that have approached vicinity of skirmish, and are calmly observing contest for harem line status.

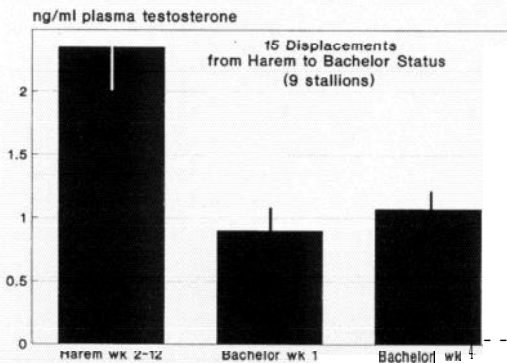


FIG. 7. Mean (\pm SEM) testosterone concentrations associated with displacement from harem status back to bachelor band.

with no other horses ($p < 0.05$) and even less when taken to a barn with breeding access to mares ($p < 0.05$). The drop in testosterone concentrations was not significant ($p > 0.10$) for stallions taken from harem status to individual holding paddocks adjacent to or facing pastures with mares,

DISCUSSION

Behavior and testosterone concentrations were markedly different with harem and bachelor status in this model, consistently and rapidly changing with change in status. Harem stallion behavior generally focused on guarding the harem fence line area, aggressively evicting intruders, and periodically harassing bachelor stallions. Time budgets of harem stallions included more moving, and less grazing and resting than for bachelors. Bachelor behavior included quiet affiliative grazing and resting with other bachelors, periodic sparring-type aggression among bachelors, and avoidance of the harem stallion. These general patterns of behavior in this model are similar to those described for free-running equid bachelor and harem stallions. Masturbation frequencies were similar for bachelor and harem stallions and were consistent with previously reported values for pastured and stabled stallions [McDonnell, 1989]. Behaviors not previously reported to occur among stallions but observed among stallions in this model included mutual grooming,

mounting with anal insertion, pairs or groups masturbating simultaneously, and mare-typical estrous posturing and presentation.

Testosterone concentrations were consistently higher with harem than with bachelor status. Remarkable, sudden changes in testosterone concentrations were observed among mature stallions. The changes clearly followed emergence from bachelor to harem status or displacement from harem status back to the bachelor band. Bachelor and harem status for stallions was easily manipulated with changes in the social groupings. These changes in testosterone concentration and behavior suggest a hypothesis of a mechanism for enhancement of reproductive function as a harem stallion and/or suppression as a bachelor. Both the increases in testosterone concentrations associated with emergence from bachelor to harem status and the decrease following displacement from harem status were observed in all seasons of the year, suggesting readiness to respond to social modulation throughout the year. In this experiment, there were numerous instances of wintertime harem testosterone concentrations reaching or exceeding published normal levels for domestic stallions during summer breeding season months [Douglas & Umphenour, 1992]. Further work is under way to evaluate the time course of these changes in testosterone concentrations, as well as to characterize GnRH, gonadotropin, and other neuroendocrine changes associated with bachelor and harem status in this model.

Such extremely wide variation in testosterone concentrations due to sociosexual conditions raises important questions about basic neuroendocrinology of stallions, including methodological concerns. For example, there is a broad range of testosterone concentrations considered normal for mature domestic stallions [Berndtson et al., 1974]. Sociosexual conditions of domestic existence, simulating more or less bachelor or harem conditions, may be a factor in this wide variation. Equally significant are questions of the relevance of these observations to management of domestic breeding stallions. Our findings suggest that group-housed domestic stallions may have testosterone concentrations similar to those of bachelor stallions in this model. For most months of the year, testosterone concentrations with harem status were higher than published norms for stabled breeding stallions (same assay [Douglas & Umphenour, 1992]). It is possible, therefore, that inter-male effects

may be involved in behavior-related subfertility seen in some domestic breeding stallions or in the generally lower behavioral vigor and apparent fertility of stabled stallions compared to pasture-bred stallions. Pasture-bred horses, for example, typically exhibit very high levels of fertility and greater sexual behavior endurance than stabled, hand-bred stallions [Bristol, 1982, 1987]. Increased testosterone concentrations with harem status and/or suppression due to stabling stallions together may play a role in this phenomenon.

Throughout this work, emergence of a stallion from an established bachelor band to the harem position was relatively orderly, with little fighting among bachelors. Harem status was clearly established within minutes to a few hours of a vacancy. Serious or prolonged fighting was limited mostly to initial placement of stallions in the pastures and to two occurrences of spontaneous displacement of an incumbent harem stallion by a bachelor. Within a given group of stallions, order of emergence to harem status was highly repeatable. However, no individual characteristic studied was predictive of order of emergence as harem stallion. Certainly, the 25 stallions studied so far limit us to a simple correlational approach to these few factors. Further work with larger numbers of stallions would enable a multivariate approach that might reveal a set of predictive factors. Among feral horses of the Pryor Mountains, Feist & McCullough [1975] observed three instances of a bachelor gaining a mare from a harem. In each instance, the bachelor obtaining the mare had been the dominant stallion within a bachelor band. In that work, it was found that most bachelor bands had one clearly dominant stallion that controlled the movement of the group, was vigilant with regard to intruders, and was the most likely to engage in aggressive interactions with other bachelors or harem stallions. In our model, we have not been able to identify clearly dominant stallions within bachelor bands. Bachelors that have led or directed movement of the bachelor band have not consistently had the higher aggressiveness ranks. These differences warrant further study.

None of the three 2-yr-old stallions assumed harem status or experienced a rise in testosterone concentrations, even when no other stallions remained in the pasture. After this series of experiments, two of these stallions were each pastured with a group of cycling pony mares. Although they readily bred mares, they

TABLE 3| Sociosexual components| differing| between bachelor and harem status|

Bachelor 	Close constant contact with other males strong affiliative interactions frequent group elimination-marking sequences frequent low-level aggressive interaction Periodic harassment by a vigilant harem stallion Thwarted access to females Displaced bachelors suffer defeat
Harem 	Dominance of a limited resource (females) Closer contact to females (limited in this model) Increased locomotor activity (extreme in this model) Harassment of other males

initially showed little concern with regard to herding and guarding the mares. In each case, testosterone concentrations rose dramatically within the first few days. Within two weeks, harem-like herding and guarding behavior reached levels typical of older stallions.

Several mechanisms may be involved in these extraordinary changes in behavior and circulating testosterone concentrations associated with bachelor and harem status. Other work, principally in rodents [Huffman et al., 1991; Miczek et al., 1991; van de Poll et al., 1982] and nonhuman primates [Eberhart et al., 1980], both in laboratory and field studies, indicates measurable effects of social status and physical or psychological defeat on male reproductive behavior and endocrinology. Some obviously different sociosexual components of bachelor and harem status are listed in Table 3. Further work should address the features of bachelor and harem status contributing to differences in associated testosterone concentrations. An important aspect of this model is that stallions do not actually contact the harem. Mares are in nearby pastures, with no common border. This precludes tactile contact, and provides only visual and auditory contact, and the possibility of distant olfactory contact, with mares. Studies are presently under way in which the harem stallion has varying levels of access to mares with and without the presence of a bachelor band. One intriguing aspect of bachelor social interaction that may contribute to lowered testosterone concentrations and subdued aggressive behavior among bachelors is the constant olfactory exposure to excrement of other males during elimination-marking behavior. Urine-mediated inter-male suppressive reproductive effects have been demonstrated in other species [Lawton & Whitsett, 1979].

It is interesting to consider the nature of the message among stallions as to their social po-

sition within the group and, for example, their order of access to harem status. Certainly, pheromonal signals, simple behavioral postures, or complex behavior including learning may be involved. In this model system, learning and memory for individual stallions appeared evident. Stallions appeared to remember their relative rank among herd mates, even after considerable separation. In experiment 5, for example, incumbent harem stallions apparently recognized individual former harem stallions from a distance by their voice or audible hoof steps. Incumbent stallions typically appeared anxious or alarmed and submissively retreated from the harem fence line area, sometimes even before the returning former harem stallion was within sight. In instances in which bachelor stallions were removed and returned to the pasture, the incumbent stallion apparently recognized them and remained aggressive toward them, rather than retreating from the harem position.

In summary, mature pony stallions in this model exhibited distinctly different harem and bachelor type behavior and correspondingly high testosterone concentrations with harem status and low testosterone concentrations with bachelor status. These socially mediated changes in behavior and testosterone concentrations occurred throughout the year.

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