



ELSEVIER

Animal Reproduction Science 60–61 (2000) 211–219

www.elsevier.com/locate/anireprosci

ANIMAL
REPRODUCTION
SCIENCE

Reproductive behavior of stallions and mares: comparison of free-running and domestic in-hand breeding

Sue M. McDonnell

*Equine Behavior Laboratory, Section of Medicine and Reproduction, University of Pennsylvania School of
Veterinary Medicine, New Bolton Center, Kennett Square, PA 19348, USA*

Abstract

Based on observational studies comparing social organization and reproductive behavior of equids breeding under feral, semi-feral, and domestic conditions, a series of comparisons and findings on reproductive physiology and behavior are presented. Simple changes in management and handling of mares and stallions that can improve reproductive efficiency and fertility or that can overcome specific breeding problems are discussed. © 2000 Published by Elsevier Science B.V. All rights reserved.

Keywords: Horse; Domestic; Feral; Reproduction; Reproductive behavior; Fertility

1. Introduction

A long-standing curiosity in equine reproduction science and veterinary practice concerns what appears to be lower rates of sexual vigor and fertility and higher rates of sexual behavior dysfunction among hand-bred domestic horses compared to equids breeding at liberty. For example, stallions at pasture breed as often as every 1 to 2 h throughout the day and night with excellent sustained fertility (Bristol, 1982, 1987; Henry et al., 1991; McDonnell and Bristol, unpublished 1987–1988; McDonnell, unpublished observations with semi-feral ponies 1994 to present). For most hand-bred stallions, libido and fertility diminish with breeding schedules of more than once or twice per day.

This paper presents a series of examples of observed differences in reproductive social organization and behavior of feral, semi-feral, and pasture-bred domestic horses compared to hand-bred horses that may influence reproductive efficiency and fertility. Based on these differences, changes in management and handling of domestic hand-bred

horses are discussed as a strategy for improving their reproductive efficiency or for alleviating sexual behavior dysfunction in particular animals. These observations will be presented in the form of a series of concepts which I believe to be “important lessons” learned from observing free-running equids. For the most part, the concepts presented stem from the author’s collective observations and data from field studies of domestic pasture breeding horses and semi-feral herds of ponies and donkeys together with laboratory research and clinical experience at the Equine Reproductive Behavior Laboratory of the University of Pennsylvania School of Veterinary Medicine at New Bolton Center over the period of 1981 through 1999. This experience involved collaboration with other scientists, students, veterinary practitioners, and breeding farm managers.

2. A harem stallion and his mares interact almost continually

A strikingly consistent feature of reproductive behavior among equids breeding at liberty is that a harem stallion and his mares are together and are interacting continually on a moment-to-moment basis year round (Bristol, 1982; Feist, 1976; McDonnell and Bristol, unpublished observations 1987–1988; McDonnell, unpublished observations 1994 to present). The frequency and intensity of the sexual interactions vary throughout the year, but nonetheless continue at a steady rate. Ongoing year-round interactive behaviors of stallions with their mares (whether estrous, diestrous, anestrus, or pregnant) include quiet affiliation or “tending”, periodic approaching and retreating, and olfactory investigation of urine and feces. When a mare is in estrus, the frequency of interaction of the stallion and a mare increases to as many as hundreds of such encounters and communications per day and with precopulatory “teasing” sequences as often as every few minutes. The frequency and type of interaction also appears to vary among individual mares and stallions, but nonetheless is remarkably frequent and continuous.

In contrast, domestically hand-bred stallions and mares are typically allowed almost no contact other than brief and hand-directed precopulatory interaction immediately before copulation. In considering the marked difference in opportunities for interaction, it is quite remarkable that most domestic stallions can have what is considered a normal domestic breeding career with such minimal precopulatory contact of mares. Some successful domestic breeding stallions never actually touch a mare or contact urine, feces, or urovaginal secretions of mares before mounting for natural cover or for collection of semen. This is probably due to the ability of most stallions to respond to sub-optimal stimuli, either naturally or as a result of conditioning. There are breeding stallions, however, that simply require more interaction with mares or breed much more efficiently with more precopulatory contact with mares. While most breeding farm managers intuitively recognize and accommodate these apparent needs, some expect all stallions to do well with limited contact and perceive inadequate response in certain stallions as sexual behavior dysfunction. In our clinical practice, many stallions that have been referred with sexual behavior dysfunction, particularly slow starting novice breeding stallions, have improved and become successful breeders when simply provided greater access to mares. Increased access has been achieved by prolonged

hand-teasing, by placing the stallion in a box stall next to a mare or in a barn with many mares, along a safe fence line of an adjacent pasture with mares, in a “teasing box” within a pasture of mares, or in a pasture directly with mares.

A related observation among harem breeding equids is that harem stallions show different behavior toward mares of varying social relationship. Mature mares within a harem are guarded and actively courted and bred by the harem stallion. Young mares of a harem band are similarly guarded closely by the harem stallion, except when in estrus. When in estrus, young harem mares are no longer guarded by the harem stallion, but rather allowed to stray among neighboring harem and bachelor groups. They are not courted nor are they bred by the harem stallion. Young mares passing nearby or visiting from neighboring bands typically are not protected, courted or bred; they may be tolerated by the harem stallion as visitors for brief periods on the fringe of a harem or may be actively chased away by the harem stallion. Mature mares of another band typically are actively chased away by a harem stallion (as well as the harem mares). This indicates that stallions have the capacity to recognize and behave differently according to social categories of mares. In domestic hand-bred stallions, there are occasions when a stallion may not accept or may not perform as well with a particular mare or mares. Perhaps in such cases, natural mechanisms for accepting certain mares and rejecting others may be at play.

2.1. The mare plays an important role in the timing of copulation

Observations of breeding in equids at liberty indicates that the female is a far more important player in mate location, stimulation of the male, and actual timing of breeding than is typically assumed or allowed for hand-bred horses. At liberty, the estrous mare is most conspicuous by a general increased movement as well as particular repeated approaches to the stallion. In pasture breeding horses (McDonnell and Bristol, unpublished observations 1987–1988) and in a semi-feral pony herd (McDonnell, unpublished observations 1994 to present), for example, we have observed that during early estrus almost all sexual interactions begin with the mare approaching the stallion, as opposed to the stallion approaching the mare. As estrus progresses, the frequency of stallion approaches to the mare increase. Nonetheless, almost all (88%) of stallion and mare precopulatory interactions that lead to successful copulation are initiated by the mare approaching the stallion as opposed to the stallion approaching the mare. The mare’s stationary “sawhorse” receptive posture appears to eventually stimulate the stallion to mount, but the head-to-head approach of the mare to the stallion followed by movement forward, or swinging of the hips toward the head of the stallion, appears to be the most important stimulus for initial sexual interest of the stallion in a particular mare. During the ongoing interactions of a stallion with a mare over the many days of estrus, there is usually a pattern of apparently increasing attractively and receptivity of the mare. In the early days of estrus, most mares appear ambivalent in that they approach the stallion, initially appear solicitous during precopulatory interaction, and then resist and terminate the interaction just before or as the stallion initiates mounting. In many cases, continued persistent teasing over periods of minutes or hours by the stallion appears to lead to eventual tolerance of mounting. Even when the stallion’s persistence leads to eventual

tolerance of mounting, it clearly appears that the behavior of the mare more than the stallion initiates interactions and determines the time of actual mating. The mare's active role continues during copulation. Her movement and postures facilitate insertion and appear to accommodate the stallion during thrusting.

By contrast, in domestic breeding in North America and many other regions of the world, the active role of the mare in breeding is limited by management practices. For example, the emphasis in preparation of a mare for breeding is to apply restraint to ensure immobility before the breeding stallion is brought to the mare (Rossdale, 1992; Umphenour and Steiner, 2000). Typical methods of restraint, for example a lip or ear twitch, or a foreleg lifted, evoke head, ear, tail, leg, and whole body postures that are visibly different from the receptive estrous posture of the mare. Handlers of domestic stallions often direct the stallion to approach the mare directly to the hind-quarters, deliberately limiting the stallion's access to the head and fore body of the mare. The practice of restraining mares for natural cover by hand-bred stallions has a reasonable basis in safety for animals and personnel. Mares that are in the ambivalent early stages of estrus or that are mistakenly in diestrus pose a clear safety threat to stallions and personnel working in close confinement.

Most experienced domestic breeding stallions with vigorous libido respond adequately with restrained mares, much as they will with a dummy mount mare. However, when working with a slow starting novice, or a low libido stallion, it is often useful to allow for a more naturally active role of the stimulus mare. Simple management changes which allow greater mobility of the mare and less alteration of her normal estrous posture will often enhance the sexual response and behavioral efficiency of stallions. If it is not considered safe or feasible to allow full natural interaction, particular elements of mare estrous posture and behavior can be modeled. For example, walking the mare from a distance toward the stallion may be more stimulating for a stallion than bringing the stallion the mare. Allowing a head-to-head approach of the mare and stallion, as well as allowing the stallion to sniff, lick, and nuzzle the mare in the typical sequence from (head, to neck, shoulder, flank, tail, and perineum) are also typically more stimulating to both the stallion and mare than an immediate and focused approach of the stallion to the hindquarters of the mare. Simple movement by the mare, forward and back a step or two, or in a quick turn from head-to-head to hips-to-head can also be a strong positive stimulus for most stallions. Allowing or encouraging the mare to turn her head back toward her abdomen or to naturally flex her foreleg on the side near the stallion (the natural mounting invitation) will likely increase the stallion's sexual interest. Providing exposure to a mare that is mildly aggressive or ambivalent when first encountered, similar to that which occurs under natural conditions, can similarly stimulate sexual response in most stallions.

From the mare perspective, the limited precopulatory contact allowed in domestic hand-breedings may be a causative factor of the high frequency of mare resistance to mounting. The brief teasing before mounting allows little opportunity for the mare to make the natural transition from resistant to receptive behavior that is seen in mares at liberty. Also, restraints applied to the mare often appear to provoke fear and resistance in otherwise apparently receptive mares. The restraint also inhibits the mare's forward movement during thrusting, which may cause discomfort and intolerance. While safety

concerns are always important, we have on many occasions found that much better sexual arousal of the stallion and greater tolerance by the mare can be achieved by increasing the duration of precopulatory interaction and reducing the amount of physical restraint on the mare.

2.2. Mounting without erection is normal and frequent

Among free-running or pasture-bred equids, most copulations are preceded by one or more mounts without erection (Henry et al., 1991; McDonnell and Bristol, unpublished observations 1987–1988; McDonnell, unpublished observations 1994 to present). This is true both for novice and for experienced stallions. The ratio of two mounts without erection to each mount with erection remains quite constant between equid species (McDonnell unpublished personal observations of zebra, donkeys, Przewalski, horses, and ponies, 1982 to present). Mounting without erection, then, must be considered to be a normal element of the precopulatory interactive sequence, just as vocalization, sniffing, nuzzling, nipping, or flehmen response. It appears to be a test and/or inducer of the solid estrous stance of the mare.

In domestic hand-breeding throughout most of the world, stallions are typically not allowed to mount without an erection (example, Rossdale, 1992). If a stallion should mount without an erection, it is common for the handler to immediately force the stallion to dismount, usually in a rough manner with physical or verbal discipline. The basis for intolerance for a stallion mounting without erection is no doubt complex. There certainly are reasonable safety concerns for avoiding unnecessary repeated mounting. In confined indoor breeding areas, additional mounts may increase the risk for injury to animals and personnel. Also restrained mares often are less tolerant of repeated mounting and may explosively resist. Another concern expressed by stallion handlers is that allowing a stallion to mount without an erection prolongs the total breeding time. Data collected in our laboratory and clinical studies indicate this is not typically the case. In fact, for some slow starting novice stallions, stallions mounting without erection can actually speed the breeding process.

Most stallions, even from their initial hand-breeding experience can skip mounting without erection and go on to have a normal efficient breeding career. But for slower starting novice breeding stallions, it is often obviously more efficient to accommodate mounting without erection. This may require selection of a mare that will tolerate repeated mounting while restrained or one that can be trusted with minimal or no restraint.

2.3. “Dismounting” is unique to hand-breeding

In equids breeding at liberty, in the moments immediately following ejaculation the stallion need only relax on the back of the mare (McDonnell and Bristol, unpublished observations 1987–1988; McDonnell, unpublished observations 1994 to present). The stallion sometimes appears dazed and unsteady for a few seconds. The mare supports the stallion during this period. Then as the stallion appears to regain his alertness and stability, she steps forward easing the stallion's chest down over her hind quarters enabling a gentle landing on the front feet.

In contrast, the hand-bred stallion is usually required to actively dismount. This involves lifting the forebody while backing up from the mare or dummy mount, usually dropping to an abrupt landing on the front feet. This active dismounting appears to require considerable effort immediately after the extraordinary hind-limb work of supporting the weight and thrusting during copulation. Some stallion handlers tend to rush the stallion to dismount immediately after ejaculation to immediately leave the breeding area. The usual explanation is that they wish to separate the stallion and mare to safety as soon as possible. For some stallions, particularly older and/or lame stallions, dismounting appears to represent an aversive or difficult experience, particularly when rushed or when landing abruptly on a hard surface. Stallions may hyperextend a foreleg or lose their footing when rushed to dismount. After even only a few such experiences, some stallions appear to anticipate the negative experience and become reluctant to mount or to ejaculate. Some may also begin to dismount during ejaculation. Simple management changes can be made to reduce undue effort of dismounting. Examples include arranging for the mare to step forward after a few seconds easing the stallion down, as she would at liberty. Hard or slippery breeding surfaces, particularly around a dummy mount, can be modified to provide a softer more secure footing. Modifying handling to provide gentle respectful accommodation of the stallion's needs or limitations can resolve or avoid most problems.

2.4. Reproductive function of stallions is socially modulated

In equid breeding systems, some of the mature stallions gain access to a harem or breeding territory, and some remain non-breeding "bachelors" (Keiper, 1985; Klingel, 1975, 1982). Important behavioral and physiological differences resulting from harem or bachelor status are just recently being appreciated. It appears that the harem status imparts an upgrading of reproductive endocrinology and function including increases in androgen levels, sexual and aggressive behavior, accessory sex gland size and character, testicular size and character, and semen quality. Bachelor status imparts changes in the opposite direction (McDonnell and Haviland, 1995; McDonnell and Murray, 1995; McDonnell and Pozor, 1995; McDonnell, unpublished observations 1994 to present).

On multi-stallion breeding farms, it is common to house the stallions together in stallion barns away from mares. Data is accumulating which indicates that traditional group housing of stallions may impose bachelor status on breeding stallions. That is, stallions kept in barns with only other stallions appear to have suppressed reproductive function, compared to when they are housed in barns as the only stallion with mares. In domestically housed stallions, sociosexual conditions can be manipulated to effect physiological and behavioral changes corresponding to those of bachelor and harem status (McDonnell, 1995a). Both in research animals and in clinical cases, we have found that simply moving a stallion to a barn with mares can increase libido, testosterone levels, testicular volume, and sperm production efficiency.

2.5. Spontaneous erection and masturbation are frequent and normal equid behaviors

Free-running and pastured equid stallions regardless of age (newborn to aged), sociosexual environment, bachelor or harem status, or species, exhibit periodic sponta-

neous erections and penile movements known as masturbation (McDonnell, 1989, 1995b; McDonnell et al., 1991). These erections occur at the rate of about one 3-min episode every 90 min. Ejaculation is rare (less than 0.01% of episodes). The frequency of spontaneous erection and masturbation is the same for domestic horse stallions regardless of breed, type of housing, type and level of work, sociosexual environment, breeding status, androgen levels, libido, or fertility. Similar periodic erections are common to all mammals studied, including humans. This phenomenon appears to be normal behavior.

A considerable portion of the horse breeding and performing industries still views spontaneous erection and penile movements as inappropriate or abnormal behavior that should be eliminated. Anti-masturbatory devices for stallions are still widely used in many regions of the world. Unfortunately, stallion rings, cages, spike pads, and brushes can still be easily acquired from saddle shops and mail-order catalogs. In 1995, a shock collar device recommended for stopping masturbation in stallions was released from a Colorado manufacturer and widely marketed internationally. Our observations and systematic studies (McDonnell and Hinze, unpublished observations, 1996–1997) indicate that anti-masturbatory devices rarely reduce spontaneous erection and penile movements, but in most cases increase the frequency and duration of episodes. Nonetheless, horse managers continue to try to stop the behavior. In our clinic we see many cases each year involving penile injury associated with anti-masturbatory devices, presented for libido, erection, and/or ejaculation dysfunction.

2.6. Mares at liberty appear highly fertile on the first postpartum estrus

Available observations on horses bred at liberty suggest that the first postpartum estrus is likely highly fertile. For example, we have kept a herd of ponies breeding under semi-feral conditions for several years in which all breeding, pregnancy, and foaling events are recorded. In that herd, nearly all foaling mares have conceived at postpartum estrus (57 of 60). Nearly all those pregnancies have gone to term (55 of 57). Related factors in this particular herd include no known dystocia, retained fetal membranes, postpartum endometritis, or related peri-parturient complications. One striking difference in behavior of these semi-feral mares compared to that of domestically managed mares is an extraordinary increase in physical activity during the peri-parturient period compared to any other period. Immediately following parturition, mare activity increases markedly (2 to 10 times seasonal average rates of footsteps). This increase appears to be associated with (1) more intense vigilant herding by the stallion to maintain greater than usual distances away from other groups and (2) the mare's constant guarding and retrieval of the neonate during this period. Post-parturient activity typically reaches a maximum during the first postpartum estrus and then wanes to seasonal averages by about 3 weeks after parturition. In contrast, domestic mares typically experience a decrease in physical activity immediately before and for some time after parturition, in association with the practice of increased confinement in the periparturient period. These observations suggest further work to investigate possible positive effects of increased locomotor activity on involution and postpartum fertility.

2.7. Social organization and breeding behavior of donkeys is different from that of horses

There are at least two distinct types of equid social organization (Klingel, 1975, 1982). Domestic horses, Przewalski wild horses, and certain zebra breed in harem groups of one stallion to several mares. Domestic donkeys, most wild asses, and certain zebra are territorial breeders, a system in which each breeding male guards a territory and thereby has breeding access to the females passing through or residing within the territory. There are notable differences in mate location and precopulatory behavior between horses and donkeys reflecting harem and territorial type social organization (Henry et al., 1991). For example, jennes in estrus form a sexually active group which lingers a short distance from the jack. These jennes, like cows, tease and mount one another. This interfemale sexual behavior appears to stimulate the interest and sexual response of the jack. The jack does not herd and guard the jennes as a horse stallion does, but rather stands off in seemingly disinterested manner waiting for the sexually active group to approach. In contrast to stallions, jacks achieve erection at a distance from the jennes, often in association with a rolling and marking sequence and while gazing away from the jennes. Approach and mount immediately follows erection. Actual copulatory behavior including insertion latency, number of thrusts, and total time mounted is similar between horses and donkeys, as we have found among all equid species studied.

Traditionally (in North America at least), jacks have been considered slow and difficult in-hand breeders. Recognition and accommodation of territorial social organization and related differences in precopulatory behavior of horses and donkeys can markedly improve the efficiency of hand-breeding of donkeys. For example, jacks are notoriously slow to achieve erection and mount (hours to days) during in-hand breeding if the jack is taken close to the jennes to tease in the manner used for breeding horses. Approximating the natural condition by allowing the jack to remain at a distance from the female or to move freely in a large area with the female loosely tethered so that she can get his attention with her movements can reduce breeding time to within the normal range for free-running donkeys (minutes). Providing a sexually active group of jennes can further improve the response time of the jack.

References

- Bristol, F., 1982. Breeding behavior of a stallion at pasture with 20 mares in synchronized oestrus. *J. Reprod. Fertil., Suppl.* 32, 71–77.
- Bristol, F., 1987. Fertility of pasture bred mares in synchronized oestrus. *J. Reprod. Fertil., Suppl.* 35, 39–43.
- Feist, J., 1976. Behavior patterns and communication in feral horses. *Zeitschrift fur Tierpsychology* 41, 337–371.
- Henry, M., McDonnell, S.M., Lodi, L.D., Gastal, E.L., 1991. Pasture mating behavior of donkeys (*Equus asinus*) under natural and induced oestrus. *J. Reprod. Fertil., Suppl.* 44, 77–86.
- Keiper, R.R., 1985. *The Assateague Ponies*. Tidewater Publishers, Centreville, MD, USA.
- Klingel, H., 1975. Social organization and reproduction in equids. *J. Reprod. Fertil., Suppl.* 23, 7–11.
- Klingel, H., 1982. Social organization of feral horses. *J. Reprod. Fertil., Suppl.* 32, 89–95.

- McDonnell, S.M., 1989. Spontaneous erection and masturbation in equids. In: Proceedings 35th Annual Meeting of Association of Equine Practitioners, Bopston, MA. pp. 567–580.
- McDonnell, S.M., 1995a. Stallion behavior and endocrinology: what do we really know? In: Proceedings 41st Annual Meeting of Association of Equine Practitioners, Lexington, KY. pp. 18–19.
- McDonnell, S.M., 1995b. Spontaneous erection and masturbation in equids. In: Proceedings Second International Workshop on Erection and Ejaculation in Horse and Men, Mount Joy, Pennsylvania. pp. 29–30.
- McDonnell, S.M., Haviland, J.C.S., 1995. Agonistic ethogram of the equid bachelor band. *Appl. Anim. Behav. Sci.* 43, 147–148.
- McDonnell, S.M., Murray, S.C., 1995. Bachelor and harem stallion behavior and endocrinology. *Biol. Reprod. Monogr.* 1, 577–590.
- McDonnell, S.M., Pozor, M.A., 1995. Accessory sex gland size and character differ between harem and bachelor stallions. In: Proceedings Second International Workshop on Erection and Ejaculation in Horse and Men, Mount Joy, Pennsylvania. pp. 43–44.
- McDonnell, S.M., Henry, M., Bristol, F., 1991. Spontaneous erection and masturbation in equids. *J. Reprod. Fertil., Suppl.* 44, 664–665.
- Rossdale, P., 1992. *Horse Breeding*. David and Charles, Devon, Great Britain, revised.
- Umphenour, N.W., Steiner, J.V., 2000. Breeding management of the thoroughbred stallion. In: Samper, J.C. (Ed.), *Equine Breeding Management and Artificial Insemination*. Saunders, Philadelphia, pp. 63–80.