

Sexual behavior of mares

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Received 27 March 2007; revised 27 March 2007; accepted 28 March 2007

Available online 1 April 2007

Abstract

The mare is seasonally polyestrous, having an anovulatory period during the short light days of late fall and early winter, and beginning to ovulate as the days become longer during the winter. The complete estrus cycle is typically about 3 weeks, with 5 to 7 days of estrus and approximately 2 weeks of diestrus. When a mare lives within the natural social structure of the horse, i.e. a family band with several adult mares and one or more stallions, estrus is characterized by repeatedly approaching the stallion, frequent urination, deviating the tail away from the perineum, and standing still with the hind limbs spread apart. Diestrus is characterized by avoidance of an approaching stallion, and aggression toward the stallion, such as squealing, striking, and kicking, if he persists in attempting to court the diestrus mare. However, mares and stallions with long-term social relationships will often rest together, graze together and groom each other, all without sexual interactions. Hormonally, estrous behavior in the mare is initiated by estradiol that is secreted by the follicle, while estrous behavior is suppressed by progesterone, secreted by the corpus luteum. Mares are unusual among the ungulates in that they periodically exhibit estrous behavior during the anovulatory period. This is probably due to the release of estrogenic steroids secreted by the adrenal cortex. The display of sexual behavior by the mare throughout the year is thought to facilitate maintenance of the horse's social structure, in which the male remains with a group of females year round, in contrast with most ungulates in which the females and males only come together during the mating season.

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Keywords: Horse; Mare; Reproduction; Behavior; Sexual; Estrus; Diestrus

Introduction

The sexual behavior of the mare has evolved in the social context of family groups that typically consist of multiple adult mares and their young offspring, plus one or more adult stallions. This long-term cohesive family structure is probably an important factor in the evolution of the unusually long period of estrus in the mare, i.e. 5–7 days versus 1–2 days for other female ungulates. The long period of estrus in all the mares of the herd would facilitate maintenance of proximity to the mares by the herd's stallion. While strong social bonds develop between the mares and the stallion(s), the social core of the group is formed by the mares, and it is not necessary for the stallion to be present for the mares to remain as a cohesive group. Nevertheless, the stability of a mare's consort relationship with a given stallion significantly correlates with her lifetime reproductive success (Kaseda et al., 1995). In the

context of sexual interactions with the stallion, however, the mares may become very competitive, and if more than one mare is in estrus at one time, the higher ranking mare will actively disrupt interactions between the subordinate mare and the stallion and drive the subordinate away from proximity to the stallion (Asa et al., 1979).

Normal estrus cycle

The mare is seasonally polyestrous, with estrus cycles beginning in mid to late winter and continuing through the early fall. Increasing daylight length plays a major role in the initiation of cycling, and the use of artificial light can induce a resumption of cycling earlier than would happen under natural conditions (Allen, 1977; Colquhoun et al., 1987; Hughes et al., 1972; Kooistra and Ginther, 1975; Palmer et al., 1982; Sharp, 1980). With an 11-month gestation period, this timing maximizes the likelihood that foals will be born and spend their first few months of life at a time when the weather is warm and food is plentiful. The exact months that a mare will ex-

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perience estrous cycles depend on the latitude at which she lives. On Assateague Island National Seashore, which lies off the east coast of the United States, most foals born to the feral ponies that live on this island are conceived in May, June, and July and born the following April, May, and June (Keiper and Houpt, 1984). A period of follicular growth and ovulation, accompanied by behavioral estrus, generally lasts 5–7 days. Insemination by a fertile stallion 48 to 72 h before ovulation will generally result in conception (Brinsko and Varner, 1993). While insemination 4–5 days before ovulation can potentially result in conception, rates are much lower. If the mare does not conceive during this period, a period of diestrus, with the development of corpora lutea and an absence of sexual activity, lasting approximately 2 weeks, will occur (Back et al., 1974; Fig. 1). Post-partum mares experience estrus, commonly called “foal heat”, during the first week after birth and may conceive at this time. Mares become anovulatory sometime in the fall and remain so until increasing day length triggers a resumption of estrous cycles.

Behavior that identifies mares as being estrous or non-estrous status is arbitrarily grouped into three categories: attractivity, proceptivity, and receptivity (Beach, 1976). As applied to the mare, attractivity refers to the stimulus value of the mare that elicits appetitive sexual responses from the stallion. Thus, attractivity is actually measured by the behavior of the stallion, but is a consequence of various behavioral and non-behavioral attributes of the mare, such as posture and olfactory cues, respectively. Proceptivity refers to appetitive behaviors shown by the mare in response to stimuli received from the stallion. These would include such behaviors as approaching the stallion and rotating the body so that the hindquarters are in front of the stallion. The mare’s proceptive behavior occurs as a response to the sexual attractivity of the stallion. Certain attributes of the stallion are more or less likely to elicit proceptive behavior from the mare. For example,

stallions that have a high frequency of vocalizations are more attractive to mares than stallions with a low frequency of vocalizations (Pickarel et al., 1993). Finally, receptivity refers to behavior by the mare that facilitates copulation with the stallion, the most important of which is simply standing still so that the stallion can mount and intromit. These three categories are clearly not mutually exclusive. Nevertheless, they can be useful constructs when discussing various aspects of sexual behavior.

The estrous mare will approach the stallion more frequently than the diestrous mare and will turn her hindquarters toward him. The estrus mare will also frequently adopt a posture in which she lowers her pelvis, spreads her hind limbs, and deviates her tail either to the side or straight back from the body, exposing the perineal region (Fig. 2). This posture is accompanied by a rhythmic eversion of the clitoris, called clitoral winking (Asa et al., 1983; Back et al., 1974; Clayton et al., 1981). Estrous mares will also void small quantities of urine very frequently, while diestrous mares void larger quantities of urine less frequently. In a test situation, stallions show no difference in olfactory response, including flehmen, to the urine of estrous and non-estrous mares. Therefore, the stallion appears to be unable to distinguish the two. However, in the field situation, the frequent urination of estrous mares causes an increased frequency of showing flehmen in the stallion. Therefore, the frequent urination of estrous mares may function in chemosensory priming of the stallion for reproduction (Marinier et al., 1988; Stahlbaum and Houpt, 1989).

The estrous mare also has a unique facial expression, with relaxed facial muscles, slightly lowered head and ears turned to the side (Fig. 3). One case has been reported of a mare that exhibited an atypical facial expression when she was in estrus that was similar to snapping behavior, also referred to as champing or tooth-clapping, of immature horses. She exhibited the facial expression when she first noticed the stallion or heard him neighing. When the stallion approached, she would flex her

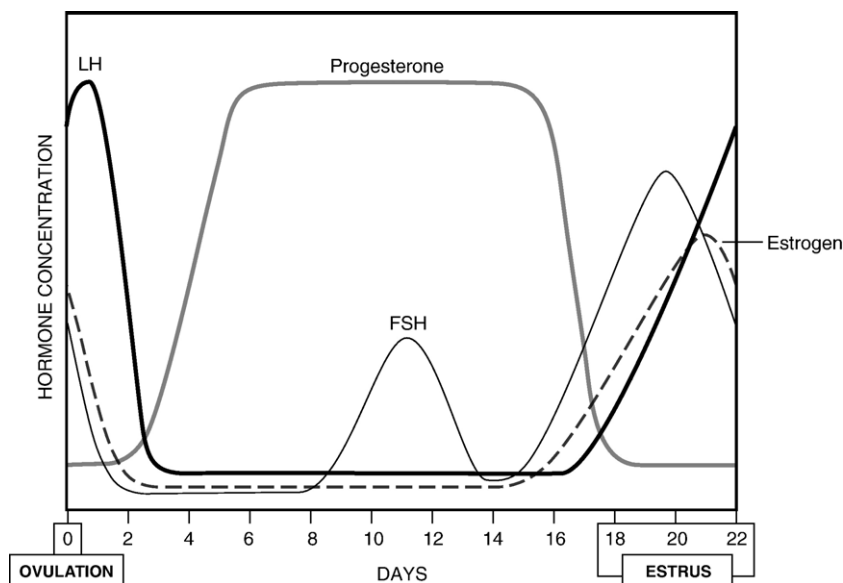


Fig. 1. Changes in the concentration of LH, FSH, estrogen and progesterone over the course of a typical estrous cycle. Behavior of estrus declines rapidly following ovulation and in conjunction with the rapidly rising levels of progesterone, so that the mare will actively reject the stallion 12–48 h after ovulation.

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