Special Issue:
The Feral Horse

Reviewed

HORMONES AND REPRODUCTION IN FERAL HORSES

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ABSTRACT

This report addresses the basic reproductive biology of the North American feral horse. With a basis of population records to establish a framework, experimental studies on specific and seasonal aspects of sexual behavior and social behavior are discussed with special attention to elimination marking (scent marking) behavior in stallions and estrus behavior in mares. In addition, the physiological basis for the hormonal control of reproduction in male and female feral horses is presented, with discussion of specific experiments. Definite and correlated seasonal patterns of plasma testosterone and elimination marking behavior in stallions are examined, and hormonal patterns and events of the estrus cycle of the mare are presented. These aspects of feral horse reproduction are then interpreted with attention to integration of processes, and comparisons between the feral and domestic horse are made.

The free-roaming feral horse is a magnificent animal. It is a proud animal which has demonstrated its capability to survive in harsh environs with cold, stark winters and hot, dry summers. Almost as a testimonial to its survival ability, the feral horse has reproduced effectively in these conditions, and growing populations have been the rule. It is the purpose of this paper to examine important aspects of feral horse reproduction, giving a composite picture based on our own studies and those of others. Our studies have focused in the Pryor Mountain Horse Range in south central Montana and in the Challis Horse Range of central Idaho, with some data also derived from ranges in California, Nevada and Oregon.

The most useful parameters for studying reproduction in wildlife populations are found in population records, behavior and physiology. In our feral horse research, we chose to examine population records, sexual behavior, elimination marking (scent marking) behavior and the levels of hormones in the blood.

Of course it is necessary to consider these parameters in the context of existing environmental factors, such as seasonality in temperature, photoperiod and precipitation, food availability and quality and predation. No reproductive pattern study can be complete without recording environmental conditions and correlating these conditions with changes in reproductive function across time to establish possible interactions.

Population Records

In some herds, reasonably consistent and accurate population data have been collected.[1,2,4,9] A striking and important aspect of feral horse biology is the distinct seasonality in foaling as shown in Figure 1. This seasonality appears to occur in all ranges studied and the similarity of pattern between the Pryor Mountain and Winemucca range are exemplary. A composite of some other useful measures of feral horse reproduction based on data from 7 ranges is presented in Table 1. Perhaps the most significant fact derivable from this table is the wide range of values for most measures. This reflects the range-specific and often non-generalizable characteristics of individual populations of feral horses. An important consequence of this, as will become apparent in the considerations of feral horse population control presented later in these proceedings, is that optimal management methodologies may be different for each range.

The average annual rate of population increase is near 14%, with a range of 11% to 20%. This rate of increase will produce population doubling about every 7 years. Pregnancy rates are highly variable both across years and among ranges, with a range of 35 to 85%, i.e. 35-85 pregnancies per 100 mature mares per year. There is also considerable difference in the pregnancy rates among different age groups as reported elsewhere in these proceedings and in

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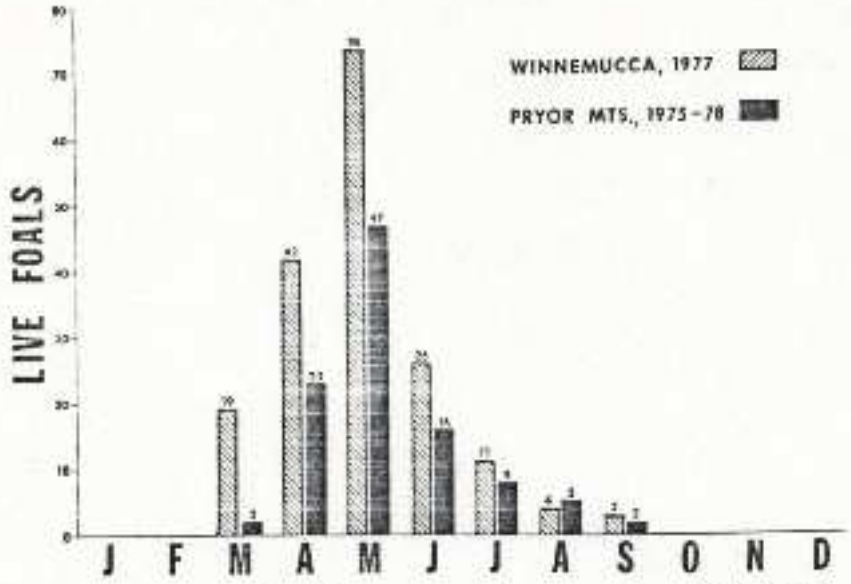

Figure 1. Seasonality in foal production in two feral horse ranges, Winnemucca, Nevada and Pryor Mountains, Montana

other studies.[10] Mares aged 4 to 15 years generally show the highest pregnancy rates. The length of gestation is approximately 340 days and, unlike other characteristics of reproduction, is quite uniform across herds and individuals. Reported foaling rates, again variable, across years and ranges, tend to be lower than reported pregnancy rates, suggesting significant fetal loss.

The sex ratio (M:F) appears to be less variable than other measures, averaging 0.985±0.075. Reports of feral horse lifespan in the early 1970's frequently gave 15-18 years as a maximum. However, as the number of horses studied has increased dramatically in the past 10 years and age assessment technique has improved, the lifespan has been found to be 18-25 years, with only a small number of horses, usually lone males, reaching 25.

Behavior

An understanding of feral horse reproductive patterns requires a knowledge of the behavioral framework in which the reproductive process occurs. This knowledge becomes extremely important when the impact of external forces associated with management practices must be assessed. The social unit of the feral horse is the band. There are harem bands and bachelor bands. The former usually consist of a harem stallion, several mares and their immature offspring. Occasionally, a second or third mature, but non-dominant male will reside in a harem band. The frequency of this latter condition is herd-specific and appears in the paper by Kirkpatrick and Turner in this proceedings.

The choice of useful behavioral endpoints in studies of feral horse reproduction is based on the frequency of occurrence and the importance of the behavior to the integrity of the social structure, especially to the maintenance of the harem. An example of the frequency of occurrence of various behavioral endpoints is presented in Table 2. Notice that sexual behavior (mounting and copulation) is

TABLE 1

What We Found In Population Records*

SUBJECT	RANGE
Annual Population Increase	11-20%
Pregnancy Rate	35-85%
Foaling Rate	30-52%
Sex Ratio M/F	0.91-1.06
Lifespan (years)	18-25
Reproductive Lifespan (years)	2-21
Band Size	3-24

*Data base is selected annual records from 1970-1983 in 7 different ranges in Montana, Idaho, Oregon, Nevada and Wyoming

TABLE 2

Frequency of Various Behaviors Exhibited by Feral Stallions

Behavior	Frequency of Display
Mounting	4
Copulation	2
Threat	8
Fight	4
Herding	10
Mutual grooming	8
Submission	6
Elimination marking	44

*Based on 68 h of observation of 23 stallions in April, May and June

very important for assessment of reproductive state, but the frequency of occurrence is so low that it is not a statistically reliable endpoint.

A brief description of the social life history of a harem band will make important harem behavioral endpoints readily identifiable. When males reach sexual maturity, they are routinely ejected from their band by the resident harem stud, who will usually not tolerate the presence of another sexually mature male. These ejected males usually join a bachelor group of other males. In a subsequent breeding season, the young stallion, sometimes through a cooperative effort with his bachelor cohorts, will attempt to gather a harem of several mares by methods ranging from aggression to outright thievery. During the breeding season, when mares periodically enter estrus and ovulate, he will keep these mares in close proximity by herding them, and he will mate with them. Also during the breeding season, he will demonstrate his claim to them by marking their eliminations with his own elimination (scent marking) and will aggressively defend the harem if necessary. Clearly, on the basis of this description, individual behavioral measures can be divided into two groups: 1) sexual behavior, including female estrus, male mounting and copulation and 2) non-sexual behavior which is primarily harem maintenance behavior and includes herding, harem defense, aggression and elimination marking (scent marking).

On the basis of frequency of occurrence and importance of the above parameters, we chose to examine seasonal patterns of the following behavioral endpoints: mounting, estrus, copulation and elimination marking behavior (scent marking). Details of protocol and results of these studies are reported elswhere.[13,14] The data are based on more than 500 hours of direct observation, often using 8X or 10X binoculars or a 20-40X zoom spotting scope. The method consisted of locating one to several bands of horses in the early morning and observing them throughout the day to establish sexual and marking behavior patterns in the context of other daily activities. Periodic observation periods of 24 hours revealed no major differences between daytime and nighttime behavior. Only data collected when horses were unaware of observers was used.

Figure 2. Feral stallion exhibiting flehmen, which is an olfactory behavior included in scent marking activity.

Mounting consisted of the stallion approaching the mare from behind, with or without perineal sniffing, rising up over her hind quarters and clasping her sides with his forelegs, with or without pelvic thrusting. Attempted mounts ending prematurely by female resistance were recorded as mounts. Intromission with or without ejaculation was recorded as copulation.

Stallion elimination marking behavior (EMB) was defined as the immediate behavioral response of a stallion to a urination and/or defecation made by another horse within 25 m of the stallion. EMB was rarely exhibited by band members other than the harem stallion, and was primarily directed toward eliminations made by mares.[13] An EMB response was recorded only when (1) the observer witnessed the elimination serving as a stimulus and (2) the marking response was initiated within 1 min of the elimination. The minimum criterion for an EMB response was (a) deliberate movement to the elimination site, (b) smelling of the feces or urine with or without flehmen (a scent-sampling behavior involving head extension and lip curling [Figure 2]) and (c) urination or defecation on the site. The behavior was quantified by dividing the number of responses by the number of eliminations which occurred (the elimination marking behavior quotient or EMBQ).

The results of the seasonal behavior pattern study are presented in Figure 3. Notice that male sexual behavior measures and EMBQ show a distinct and similar seasonal pattern, with highest frequencies during the breeding season. Thus, greatest male behavior frequencies occur during the period when mares show estrus cycles (bottom of Figure 3). However, it appears that the stimulation for EMB is not dependent upon estrus cycling, since significant EMB occurs in March, prior to the onset of estrus cycling and in response to pregnant mares. A more detailed representation

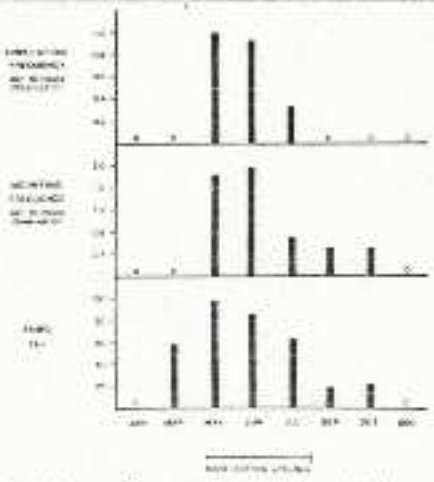

Figure 3. Incidence of mounting and copulation correlated with elimination marking behavior quotient (EMBQ) for feral stallions in various months during the year. Data base is more than 400 hours of direct observation of 27 harem stallions and their bands.

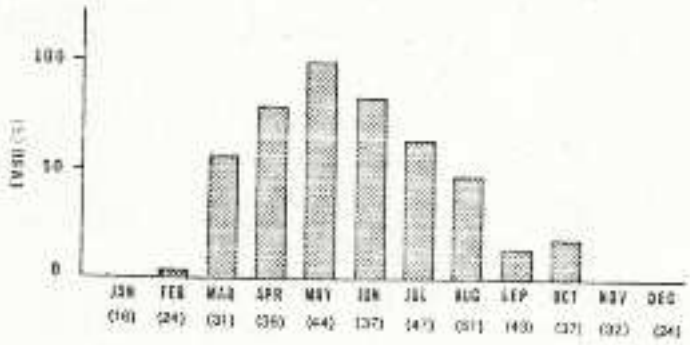

Figure 4. Frequency of elimination marking behavior by feral harem stallions in response to elimination by harem mares. Elimination marking behavior quotient (EMBQ) = number of stallion responses divided by number of mare eliminations within 25 meters of stallion. No responses occurred in November, December or January. Values in parentheses are numbers of observations.

of the seasonal pattern of EMB is presented in Figure 4. Notice that the EMB is highest in May and June, the peak breeding period and is almost non-existent from November through February.

PHYSIOLOGY

One of the most valuable yet difficult areas of study in wildlife reproduction is physiology. A feral horse can be extremely dangerous and difficult to capture, making collection of blood samples from these animals quite challenging. Nonetheless, we were fortunate to have access to horses periodically captured by the Bureau of Land Management and were able to take blood samples on these occasions. By measuring the levels of several hormones in blood taken at various times of the year, it was possible to roughly assess the seasonal reproductive state of stallions and mares.

Before describing these studies, however, it is necessary to review some very basic horse reproductive physiology. The gonads have two primary functions. One is the production of gametes (sperm or egg) and the other is production of steroid sex hormones (testosterone in male, estrogens and progesterone in female). In simplified fashion, we can state that these steroid sex hormones are involved in: 1) control of release from the pituitary gland of the reproductive hormones FSH (follicle stimulating hormone) and LH (luteinizing hormone), which are needed for making gametes and steroid sex hormones in the gonads, 2) control of sexual behavior and other reproduction-related behavior and 3) maintenance of the reproductive tissues and secondary sex characterisics.

In our studies, we were interested primarily in 1) and 2) above. This relationship is diagrammed in Figure 5. A classical feedback loop depicts the regulation of blood levels of pituitary and gonadal hormones. For the purposes of this discussion, the loops in the male and female are quite similar and they operate in the same fashion as the thermostat loop in a furnace (i.e., when the blood level of a hormone gets high, the hormone producing gland shuts down, when the hormone level then drops, the hormone-producing gland turns on).

Since hormones affect both gamete production and behavior, it was of interest to examine seasonal hormone patterns in the male and female and their relationship to behavior.

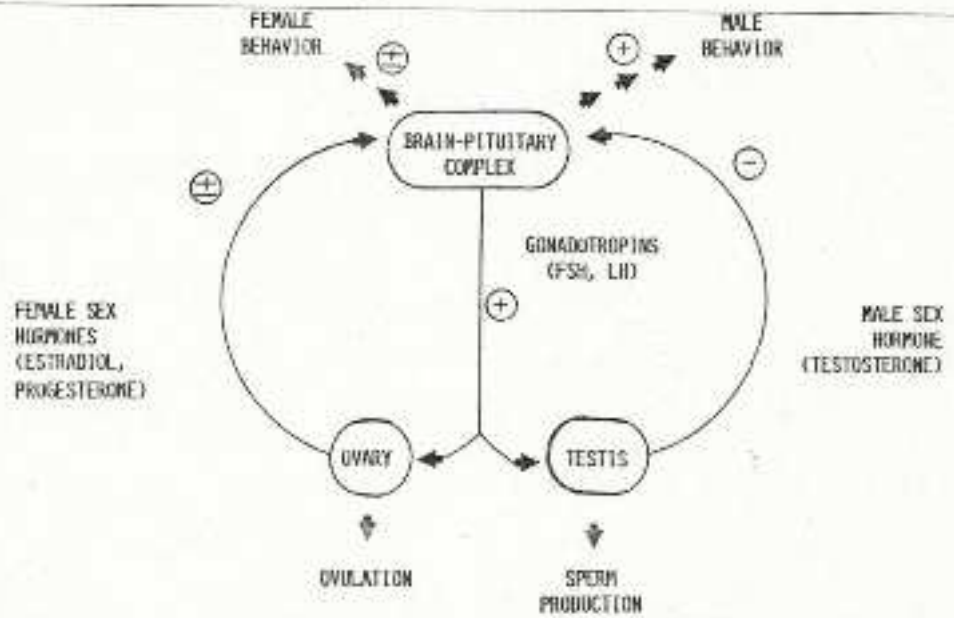

Figure 5. Simplified diagrammatic representation of hormonal control

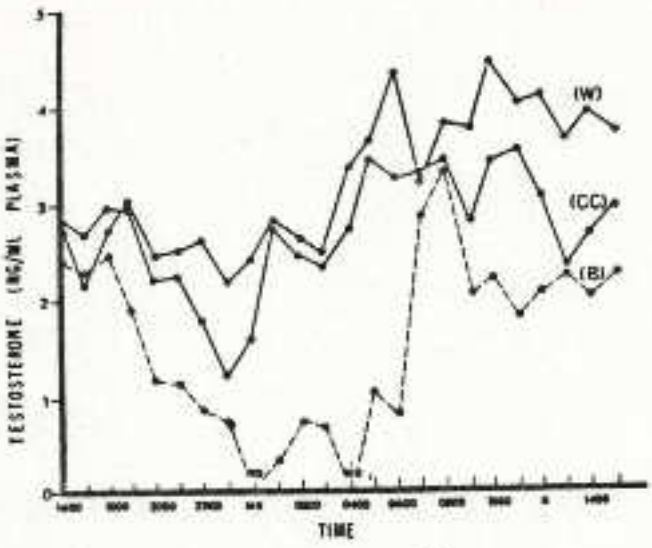

Figure 6. Individual diurnal patterns of plasma testosterone in three captive feral stallions (W, CC and B).

Male

In the male we were primarily interested in plasma testosterone levels. Since many hormones show a diurnal pattern of changing levels in the blood, ie. higher levels at some times of the day than at others, we measured plasma testosterone in samples taken via indwelling venous catheters at hourly intervals over 24 hours from three quietly standing tethered stallions. The details of this study have been previously reported by Kirkpatrick *et al* [6]. A definite diurnal pattern was evident (Figure 6), with the lowest values around midnight and highest values around 8AM. During the period from about 10AM to 4PM, values were plateaued, and all samples for the seasonal testosterone study were collected during this period. An additional consideration was the possible effect of capture stress on the levels of plasma hormones. In a separate study, Kirkpatrick *et al*[7] found no significant effect of capture by "heading and heeling" (the technique used in the testosterone study) on the blood levels of corticosteroids, hormones which are usually released from the adrenal gland in response to "significant" stress. It was therefore, unlikely that testosterone levels were affected in these studies, since testosterone release appears minimally responsive to acute stress. With this background data in hand, blood samples were collected from 34 stallions at different times of the year and assayed for testosterone.[5] The results are presented in Figure 7. These data demonstrate a definite seasonal pattern in plasma testosterone in feral stallions, with the highest average levels occurring during the breeding season. This seasonal pattern in testosterone was reminiscent of the seasonal pattern for stallion EMB, and when the two sets of data were placed on the same time scale, the curves were almost superimposable (Figure 8). Thus, there is a close correlation between plasma testosterone levels and incidence of EMB. Although no cause-effect relationship has been proven here, there is strong evidence in several other species that scent marking behavior is testosterone dependent.[11,12]

An additional opportunity to examine the testosterone-behavior relationship arose when we were able to obtain blood samples from 21 two-year-old males. Nineteen of these males had plasma testosterone levels well below the range for normal adult males (2-4 ng/ml). These nineteen

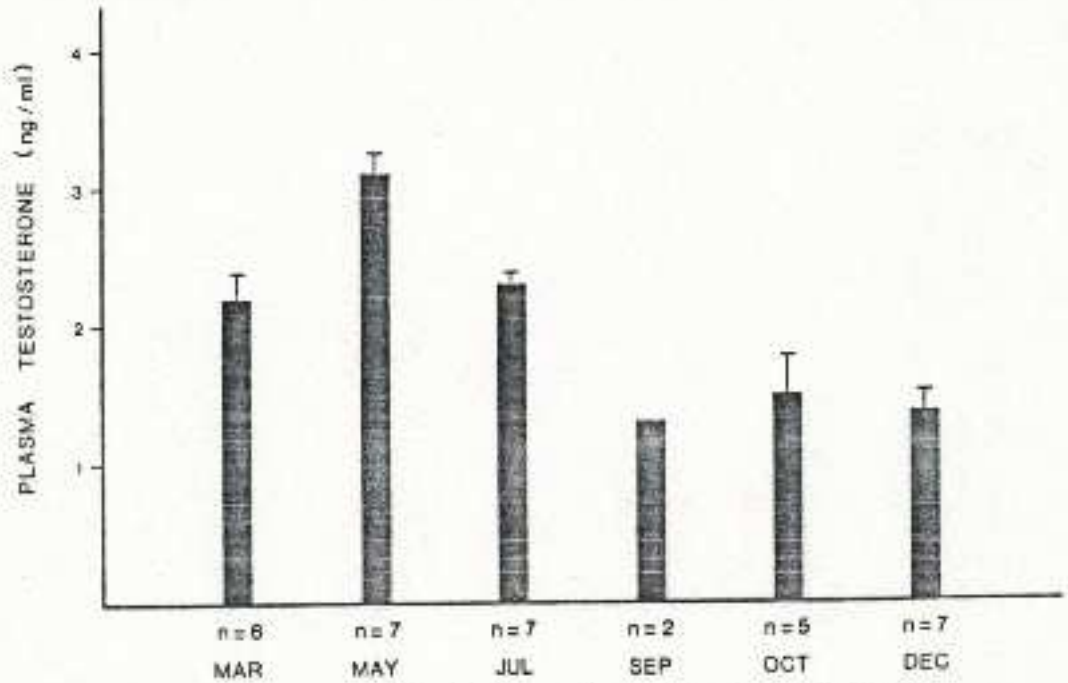

Figure 7. Seasonal pattern of plasma testosterone in feral stallions. The samples were collected from 34 feral stallions captured on their home range.

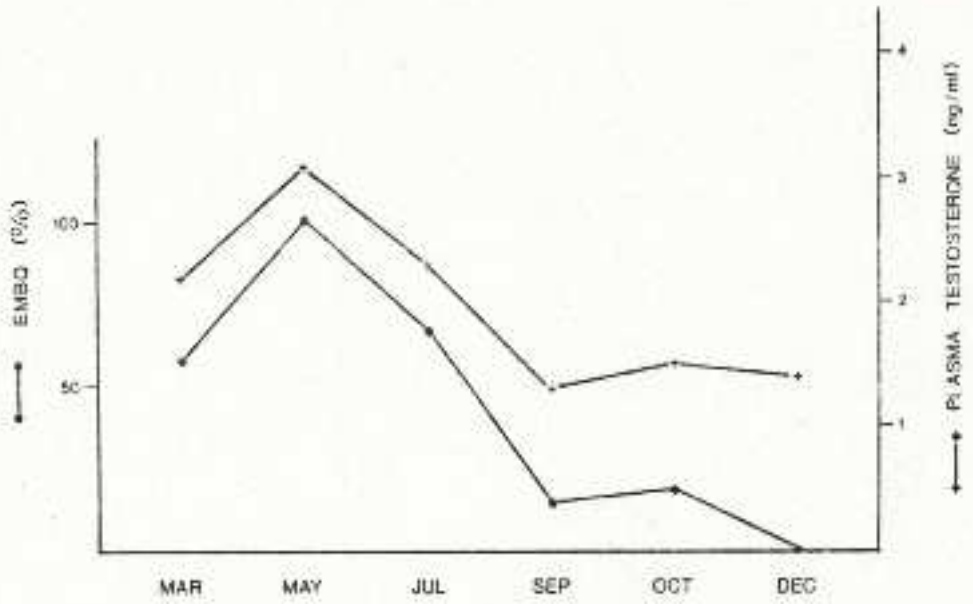

Figure 8. Comparison of seasonal pattern of plasma testosterone and elimination marking behavior quotient (EMBQ) in feral stallions

males also had undescended testes and had not yet been ejected from their respective harems (Table 3). In contrast two of these males had plasma testosterone levels in the normal adult range, had descended testes and had recently been ejected from their respective harems. Again, these data are consistent with the hypothesis of an important social behavior role for testosterone in male feral horses, but with only two horses in the ejected group no firm conclusion can be drawn. A final piece of evidence for this hypothesis was obtained in comparing the social status and plasma testosterone levels for three similarly aged adult feral males. As seen in Table 4, two of these males (Welfare and Crooked Creek) with plasma testosterone levels in the normal adult range were harem studs with a documented history of siring foals. In contrast, the third stallion (Black), showed testosterone levels in the immature male range despite being 8 years old. Interestingly, he was a bachelor and had never even attempted to gather a harem, which is quite unusual for a feral stallion.

Female

The critical factor determining the onset of breeding in feral horses is the entrance of the mare into estrus. On the basis of the hormonal studies already discussed, it appears

TABLE 3

Relationship of Social Status and Plasma Testosterone in 21 Maturing Feral Male Horses

SOCIAL STATUS	n	AGE RANGE (months)	PLASMA TESTO-STERONE (ng/ml)	TESTES
Ejected from Harem	2	23-24	3.35	Descended
Not Ejected From Harem	19	23-26	1.14±0.23	Undescended

TABLE 4

Relationship of Socio-sexual Status to Plasma Testosterone in Three Mature Feral Stallions

STALLION	AGE (years)	PLASMA TESTO-STERONE* (ng/ml)	SOCIO-SEXUAL STATUS 1972-1976
Crooked Creek	8	2.9±0.6	Harem Stud, Sired Foals
Welfare	9	3.2±0.7	Harem Stud, Sired Foals
Black	8	1.5±0.9	Bachelor, Never Attempted Harem Gathering**

* Diurnal average
** This is highly unusual for an adult stallion

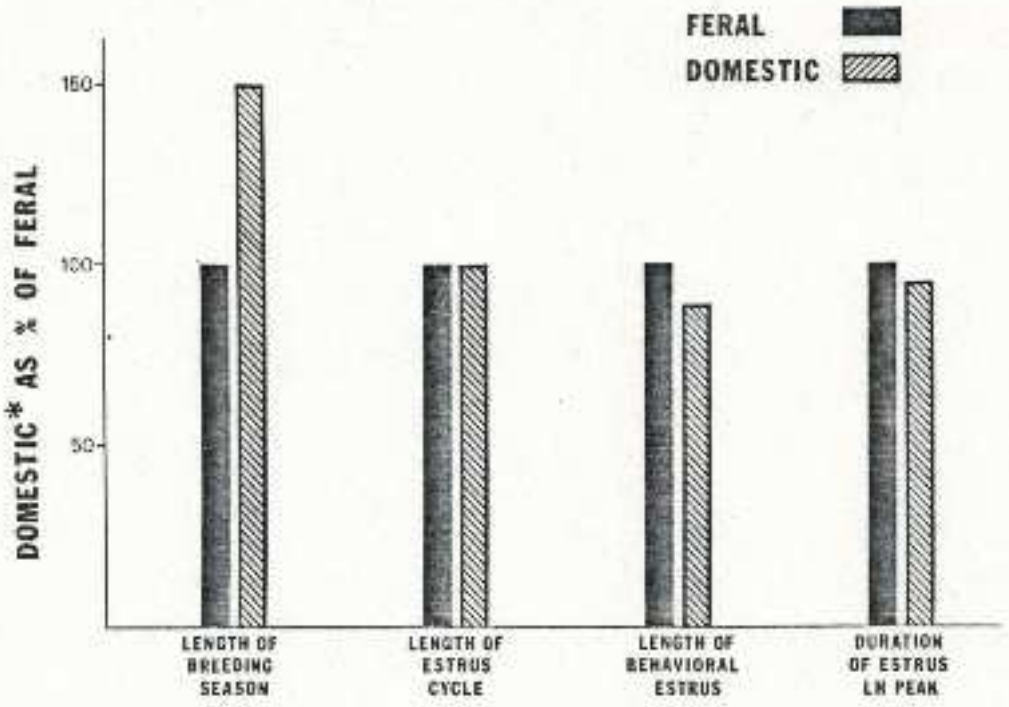

Figure 9. Comparison of aspects of the estrus cycle in feral and domestic mares.

likely that the stallion is capable of being sexually active prior to the onset of the breeding season. Thus an understanding of the factors which regulate the estrus cycle in the mare is important. Some insight can be obtained by observing estrus behavior and determining estrus patterns.

However, behavioral measures alone do not always give reliable information about female reproduction, since it is well known in several species that estrus can occur without ovulation (egg release from the ovary) and ovulation can occur without visible estrus, the latter called silent heat.

Fortunately, with BLM cooperation, we were able to perform a long-term study on reproductive hormone patterns in feral mares. Four feral mares captured in the Pryor Mountain horse range were maintained for 16 months in an outdoor enclosure (10,000m²) with wind shelter on one side. Alfalfa was provided and ad lib water was available when snow was absent. Small blood samples were taken every third day after 3 months acclimation for measurement of hormones. A Quarter Horse stallion kept in an adjacent enclosure served as a teaser for detection of estrus. Details of these protocols are available in a previous publication.[8]

The hormones measured in this study were luteinizing hormone (LH), progesterone and total estrogens. Although a brief review of the role of these hormones in mare reproduction must suffice here, complete books on the subject of domestic mare reproduction are available.[3]

The length of the estrus cycle in the horse is 20-22 days, with estrus (heat) comprising 5-8 days of this cycle. A summary comparing aspects the estrus cycle in domestic and feral mares is presented in Figure 9. One notable exception to the generally similar characteristics is the distinctly shorter length of the breeding season in the feral mares, who cycled only from mid-April through August. Estrus is the outward sign of cyclic changes occurring in the ovary. Estrus behavior occurs in response to increasing production of estrogen by the ovary. The estrogen made by the ovary also plays two other important roles. It helps prepare the ovary for ovulation, and it signals the brain and pituitary that the ovary is ready to ovulate. The response to this latter signal is a rapid release of a large amount of LH from the pituitary into the blood stream. The released LH reaches the ovary and causes biochemical changes there which result in the release of the egg (ovulation). Since the mare is in heat for several days before and after the ovulation, there is a good chance that she will be mated and that pregnancy will occur. Thus estrogen coordinates behavioral, ovarian and pituitary events, maximizing the opportunity for reproductive success.

Once ovulation has occurred, the ovary undergoes physical and biochemical changes over 24 hours resulting in a structure called the corpus luteum. The corpus luteum is the primary source of the hormone progesterone. If pregnancy occurs after ovulation, progesterone levels in the blood rise and remain elevated until birth. If pregnancy does not occur, progesterone levels rise and after approximately twelve days, the corpus luteum degenerates and progesterone levels

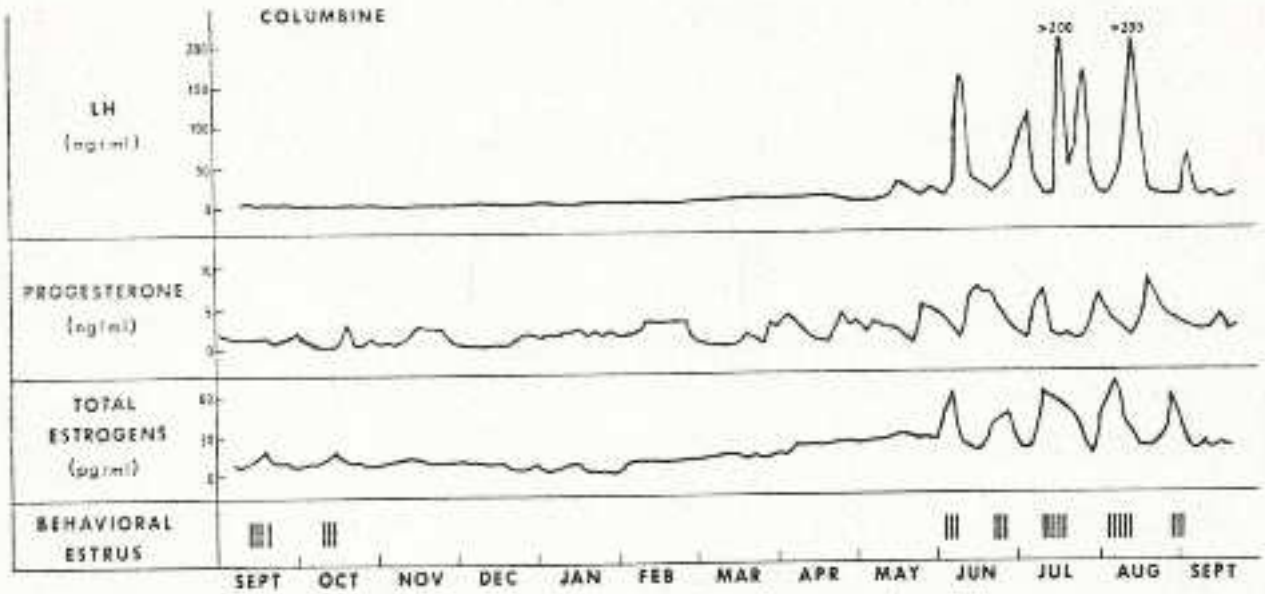

Figure 10. Seasonal pattern of behavioral estrus, LH, progesterone and total estrogens in a single feral mare. Blood samples were taken every third day throughout the year. Behavioral estrus was monitored using a teaser stallion living in an adjacent enclosure.

drop. A new cycle then begins.

Figure 10 shows the annual pattern of estrus cycling and reproductive hormones in one of the studied feral mares (Columbine), while Figure 11 is an expanded view of two cycles from a different feral mare (Sunflower) during the peak breeding season. It is notable in Figure 10 that ovulatory estrus cycles in this mare are confined to June, July and August. Combination of cycles for all 4 mares clearly showed that ovulatory cycles were present only from mid-April to the end of August, indicating a definite seasonality. This seasonality occurred despite the high quality of nutrition, a fact which suggests that reproductive seasonality is not dictated by inferior nutritional state. Furthermore, as is representatively seen in Figure 10, estrus behavior was sometimes observed in the absense of ovulation (see Figure 10, Sept.-Oct.). When ovarian cycle hormone levels in domestic and feral mares were compared, as shown in Figure 12, it was apparent that values were similar with the exception of the preovulatory LH surge, which was consistently larger in feral mares. The reason for the latter differences is unknown.

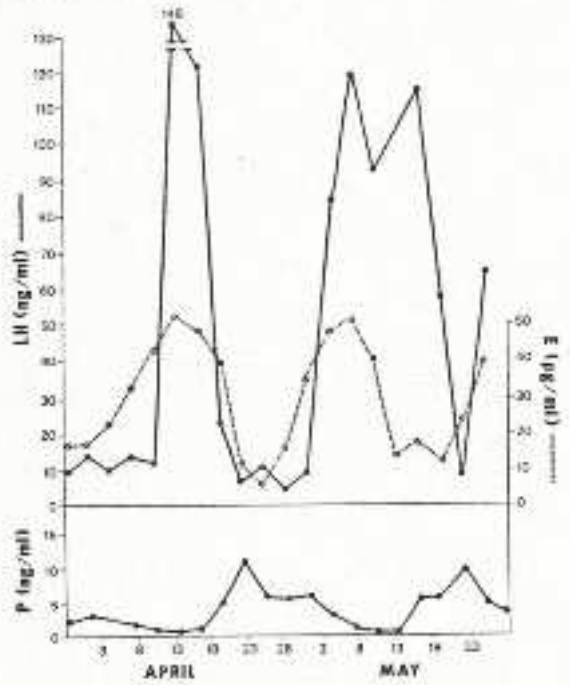

Figure 11. Example of hormonal changes across two ovulatory cycles during the breeding season in one feral mare.

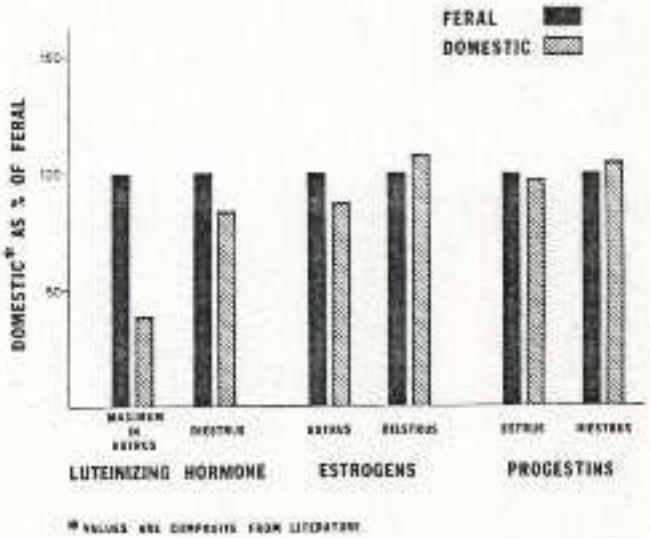

Figure 12. Comparison of feral and domestic mares in terms of plasma levels of several hormones during the estrus cycle.

As we noted earlier, it is difficult to draw firm conclusions from studies with a small number of animals. On the other hand, we were fortunate to have been able to collect even these data and we found no reason to believe these animals were unrepresentative. Thus, based on the above studies, several cautious statements may be made regarding feral mare reproductive physiology and behavior. Firstly, ovarian cycling occurred from mid-April through August, limiting foaling to the optimal survival period. Secondly, reproductive hormone patterns in feral and domestic mares were similar except that the LH peaks were larger in magnitude in feral mares. Thirdly, the LH peaks were consistently followed by a rise in progesterone, indicating association of these peaks with ovulation. Finally, behavioral estrus, despite its frequent use as behavioral measures, is not a reliable indicator of ovarian cycling.

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