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The Feral Horse

Reviewed

COMPARATIVE REPRODUCTIVE BIOLOGY OF NORTH AMERICAN FERAL HORSES

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ABSTRACT

Recent studies have suggested that various aspects of reproductive biology are strikingly different among the many herds of feral horses and ponies (*E. caballus*) in North America. The greatest differences include (1) sharply seasonal versus year-round mating and foaling patterns, (2) mare behavior at the time of parturition, (3) forced copulation and incest, (4) exclusive breeding by a single harem stallion vs breeding by two or more stallions, and (5) fecundity. The causes for these differences are discussed in terms of genetic origins of the various herds, the length of time each herd has been in a free-roaming state and subject to the forces of natural selection, the ecology of the ranges inhabited by these horses, population density, and sex ratios.

There is no record of scientific studies of the North American feral horse (*Equus caballus*) prior to 1970, despite large numbers of the animals, particularly in the western U.S. In the early 1970's developing interest in the preservation of these horses led to protective legislation, and a new awareness of the feral horse situation stimulated numerous studies of feral horse biology. Since 1970 at least fourteen different feral horse herds have been studied with sufficient care and breadth to provide some understanding of the social organization, behavior, and reproductive biology of feral horses.

Attempts have been made to structure management policies around the available biological data, but a failure to view these data in a comparative context has largely obscured the diverse nature of the feral horse herds. This has led to confusion and disagreement among those who make policy. Similarly, the increase in interest in these horses has spawned a proliferation of popular literature, which, while interesting, is often without sound scientific foundation. Finally, the origin of most feral horse herds is unknown and speculative at best. There is little reliable data to document how long these animals have been in a free-roaming state and subject to the forces of natural selection.

Klingel[22] reviewed the comparative social organization of wild equids and in a later paper[21] made the first attempt to examine the comparative biology of North American feral equids. This latter review included data from six feral horse ranges, and it suggested that the feral horse herds of North America represented a wide spectrum of social organization, behavior and biology. McCort[23] reviewed the comparative behavior of North American feral horses on a more comprehensive level and also suggested that there were differences among the animals from different herds and ranges. Many aspects of the evolution and the present patterns of reproductive biology remain unaddressed. It is the purpose of this review to examine the comparative reproductive biology of feral horses from 14 different and genetically isolated herds in North America. The data were taken from 37 different studies. A summary of herd locations and references is given in Table 1. Specifically, this review will examine reproduction as a function of seasonality, age, and the social structure of the band, as well as fecundity, forced copulation, incest, and the behavior of mares during foaling.

Seasonality: The majority of studies indicate that feral horses are sharply seasonal with respect to breeding and foaling. Horses from the Pryor Mountain herd[9,10,18], Winnemucca (Hall, unpublished data), Stone Cabin Valley[12], Red Desert[4], Carson National Forest[29,20], Alberta[35], and horses on Assateague Island[16,17], all have a well defined breeding and foaling season. Among these horses breeding commences in March and ends in August, with peak activity in May and early June. Foaling after August 31 is very rare and is best characterized by the Assateague horses, where 13% of 86 foals born over an eight year period

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TABLE 1

Herd Identification and Reference

Herd Location	Reference
Pryor Mountain (Montana)	Feist, 1971; Hall, 1972 Perkins, *et al*, 1979; Turner, *et al*, 1979, 1981; Kirkpatrick & Turner, 1983; Feist & McCullough, 1975; Kirkpatrick, *et al*, 1977; Angle, *et al*, 1979
Western Alberta	Salter, 1978
Red Desert (Wyoming)	Miller, 1979, 1981, 1983 Miller & Denniston, 1979 Denniston, 1979; Boyd, 1979, 1980
Stone Cabin Valley (Nevada)	Green & Green, 1977
Wassuk Range (Nevada)	Pellegrini, 1971
Carson National Forest (New Mexico)	Nelson, 1978, 1980
Grand Canyon (Arizona)	Berger, 1977
Granite Range (Nevada)	Berger, 1983
Winnemucca (Nevada)	Hall (unpublished)
Assateague Island (Maryland)	Keiper, 1976, 1979; Keiper & Houpt, 1984; Zervanos & Keiper, 1979; Houpt & Keiper, 1984; NPS, 1985
Shakelford Island (North Carolina)	Rubenstein, 1981
Sable Island (Nova Scotia)	Welsh, 1975
Challis (Idaho)	Turner & Kirkpatrick, 1982 Kirkpatrick, et al, 1982 Seal & Plotka, 1983
Beaty's Butte (Oregon)	Eberhardt, *et al*, 1982

appeared in April, 52% in May, 22.6% in June, 10.4% in July, and less than 1.0% in August and September[17]. Salter [35] reported that 97.3% of foals were born by June 31, in Alberta. Seasonal foaling patterns for three different herds are illustrated in Figure 1.

There are, however, a few notable exceptions to this seasonal pattern. Although, as noted above, the Carson National Forest horses showed a seasonal foaling pattern consistent with other herds, Nelson[30] witnessed mating activity throughout the year. Berger[3] also witnessed year-round mating activity among horses in the Granite Range of Nevada. In these two cases foaling was seasonal, from March to August, despite the occurrence of year-round mating. Welsh[43] on the other hand, reported both breeding activity and foaling throughout the entire year among the Sable Island horses despite peak activity for both parameters in the late spring.

The seasonal breeding and foaling pattern seen among most herds is most likely a function of mare reproductive physiology. Kirkpatrick and Turner[18] examined the incidence of ovulation and behavioral estrus among Pryor Mountain mares of proven fertility. Estrus cycles with proven ovulation occurred exclusively from April to August, although anovulatory behavioral estrus did occur occasionally from August to November. Since Nelson[30] and Berger[3] witnessed fall and winter mating without subsequent foaling during these seasons, this activity was most likely a result of the anovulatory behavioral estrus described above.

Why the Sable Island horses should breed successfully year-round, in the face of strict seasonality elsewhere in North America— and particularly when one considers the severity of North Atlantic winters— deserves more intense research but remains unanswered at the moment. It is noteworthy that the sharp seasonality of feral horses is in contrast to a less seasonal picture in domestic horses, where the incidence of ovulation ranges from 60% in September to about 20% in December.[11,42,36,31] It is doubtful that nutritional differences account for the disparity in the reproductive seasonality between feral and domestic horses. Kirkpatrick and Turner[18] placed captive feral mares from the Pryor Mountain herd on a relatively high plane of nutrition but ovulation still failed to occur after August. Kirkpatrick and Turner[18] speculated that natural selection has resulted in

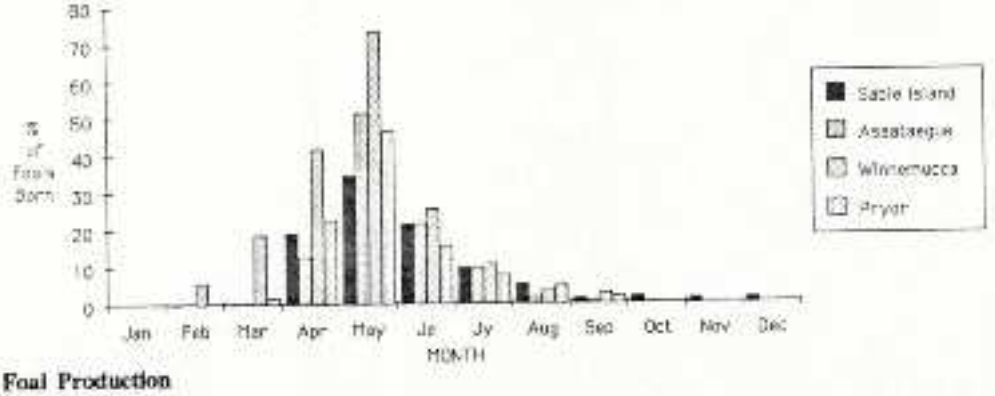

Figure 1. Seasonal Foal Production

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a highly seasonal reproductive pattern which limits foaling to the period most favorable for survival of foals.

Sexual Maturity: Three years appears to be the age when foaling is first successful. In the Pryor Mountains mares did not foal until age three[13,10,33]. Among the Assateague horses, mares came into estrus during the second summer and mares younger than three never foaled[17]. In Alberta, Salter[35] commonly observed the breeding of two-year-old mares, but only one ever foaled as a result of these breedings. Welsh[43] noted essentially the same situation among mares of the Sable Island herd. The youngest sexually mature mare was two years old and the youngest successfully parturent mare was three. Boyd[4] also noted some sexually mature two-year-old mares breeding in the Red Desert, but no mares aged less than three ever foaled.

It also appears that three years is the critical age for successful reproduction among feral stallions in the Pryor Mountain herd[9,10,33,1] and the Sable Island horses[43]. However, Boyd[5] claimed that stallions became sexually mature at age two among Red Desert horses. Although Feist[9] reported occasional attempts by male foals in the Pryors to mount mares, as often as not the attempts to mount were made upon the mares' flanks, demonstrating the inexperience of the foal and bringing into question whether this behavior was actually sexual in nature.

Parturition: Normally the harem stallion will not permit mares to stray from the band, but an exception to this rule is seen at the time of parturition. At this time the mare will wander some distance from the band, usually to a secret or sheltered spot where she will foal. From one to three days later she will rejoin the band. This pattern has been reported in the Pryor Mountains,[9,10,13] the Wassuk Range,[32] Stone Cabin Valley,[12] Alberta[35] and Sable Island[43]. On Sable Island one mare was reported to use the exact same birth site for three years in a row.

The one exception to this pattern is seen among horses of the Red Desert[5] where mares seldom left their bands to foal, but rather simply laid down next to the band and gave birth. Boyd speculated that this behavior resulted from a lack of cover and simply the inability to find an isolated or hidden location. This seems unlikely, since there is considerable sage and greasewood on the Red Desert.

Forced Copulation and Incest: Few studies have directed any attention to these topics. Berger[3] reported that when new stallions assumed control of a harem in the Granite Range, it was common to see them harass mares already pregnant by the previous stallion. The harassment consisted of persistent and aggressive biting and chasing until abortion was presumably induced. Following abortion, the stallion forced copulation. The author, however, cited no evidence that pregnancy had been diagnosed in the mares studied, nor was any clear proof of abortion provided, thus these data must be viewed with caution. Welsh[43] reported witnessing a few forced matings among the Sable Island horses although he reported nothing comparable to the induced abortions described by Berger[3] nor were new harem stallions involved in the forced matings.

Hall[13] reported that stallions were never witnessed breeding their daughters in the Pryor Mountains. Welsh[43] however, reported a single incidence of a stallion breeding a daughter on Sable Island. In contrast, Keiper (personal communication) reported that 25% of the mares on Assateague Island remained with their fathers' bands and many were successfully bred.

Single vs Multiple Male Breeding: Perhaps no aspect of feral horse reproduction is more confusing or controversial than the issue of single male breeding versus multiple male breeding. McCort[23] has provided an excellent overview of the subject. In general, most breeding is carried out by a single sexually mature stallion and the pattern is remarkably consistent among horses of different herds. Herds in which the majority of bands have a single sexually mature stallion have been described in the Pryor Mountains,[9,13,33] the Wassuk Range,[32] Assateague Island,[35] the

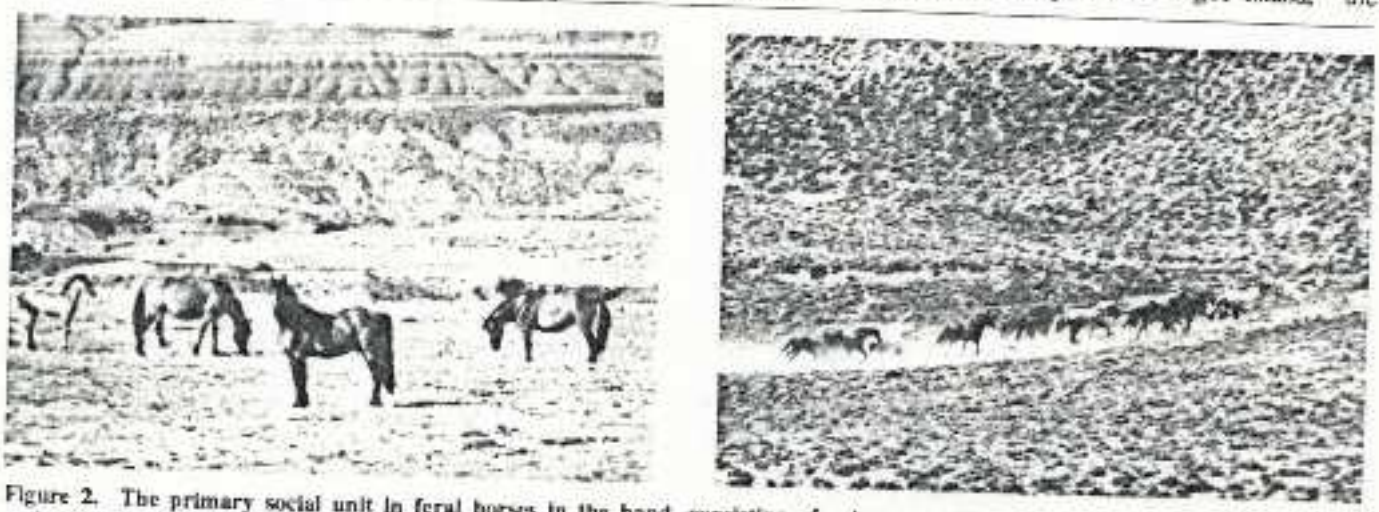

Figure 2. The primary social unit in feral horses is the band, consisting of a harem stallion, mares and their offspring (left). Bands usually move independently, being intolerant of the close proximity of other bands. However, in some instances, especially when fleeing danger, several bands may move as a single group (right).

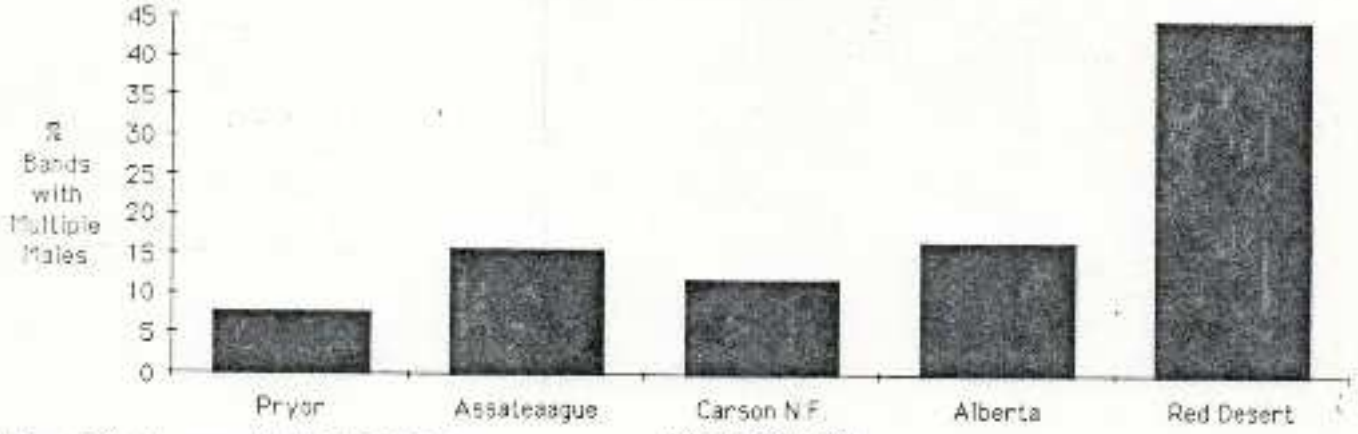

Figure 3. Single versus Multiple-Male Bands

Grand Canyon,[2] Carson National Forest,[30] Winnemucca, (Hall, unpublished data), Shakelford Island,[34] Alberta,[35] Sable Island,[43] and Challis[39].

Despite the predominance of single male bands in the Pryor Mountains, Hall[13] and Perkins *et al*,[35] reported a few instances where bands had two adult stallions. In these exceptional cases, however, the bands were usually large and always in excess of 10 horses. In 1971 Hall[13] gave the mean age of breeding stallions in the Pryors as 7.8 years while Perkins *et al*[35] described a range of 8-20 years with a mean of 12.8 (± 4.0 years) for Pryor harem stallions between 1974 and 1978. Of 17 bands described by Keiper[15] on Assateague Island, 12 possessed a single sexually mature stallion, four had more than one stallion, but most were sexually immature, and one herd had three young stallions of unknown age or maturity. Among the five multiple male bands there were no dominant stallions and they ruled by co-dominance. In 1985, the National Park Service[28] reported that Assateague Island held 107 horses, arranged in 14 bands, 12 of which were harem bands (two were bachelor bands). Among the 12 harem bands, only two had more than one stallion, and both were sons of the harem stallions. In Carson National Forest, Nelson[30] described 116 horses in 17 bands, fifteen of which had a single sexually mature stallion. Among the horses of Alberta, Salter[35] reported subordinate second males in only four of 23 bands.

A possible exception to the rule of single male bands was reported by Green and Green[12] at Stone Cabin Valley. Of 53 bands, 24 were described as having more than one stallion, but the investigators were careful to point out that there was no way of knowing the age of these animals or whether they were in fact sexually mature. The one clear exception to the single male rule is found amoung the horses of the Red Desert. Miller[24] reported that 23% to 45% of all bands in the Red Desert, observed between 1976 and 1979 were multiple male bands. These bands ranged in size from 3-17 horses, with a mean size of about 9.5, while single male bands ranged in size from 2-21 horses with a mean size of about six horses. The multiple male bands possessed 2-5 stallions with one always demonstrating dominance. In these multiple male bands, mating was accomplished 49% of the time by the dominant stallion, 42% of the time by the sub-dominant stallions, and 9% of the time by stallions from other bands. Equally unusual was the observation that in three instances mares in single male bands were bred by stallions from other bands, a condition not seen in any other herds. Also, 22 observations were reported of mares, in both single male and multiple male bands being mounted by more than one stallion.

Miller[24] also describes "feeding groups" of 50-150 horses within a one square mile area, in which individual bands cannot be distinguished from one another. This condition has not been witnessed in any other herd. Differences in single versus multiple-male bands, between herds can be visualized in Figure 3.

Why the Red Desert horses should present such a unique pattern among the continent's feral horses is a puzzle, however, Denniston[7] and Miller and Denniston[27] present three interesting theories for the development of multiple male bands. They first suggest that the herd is a loose aggregation of bands which represents a structured social unit. This would allow for some interaction between stallions of different bands, possibly resulting in a less rigid social structure. Thus it is possible that too much emphasis has been placed on the band as the primary social unit, and that subtle relationships between bands have gone unnoticed or unstudied.

These investigators also suggest that in some cases young males choose not to leave their bands and are not, for some reason, driven off by the band stallion. There is, however, little evidence to support this idea. A third possibility is the gradual loss of dominance by a band stallion, in a manner so slow and subtle that the interloper is never challenged. In this latter case a bachelor stallion will trail a band for some length of time and gradually join it, in degrees. This bachelor will follow closely, join in driving off other intruders, and finally join in mating. There may be a gradual increase in recognition of this bachelor by the band, and at the same time a gradual sense of acceptance by the band stallion. The fact remains, however interesting those theories, that the mating patterns of Red Desert horses are unique among the continent's feral equids.

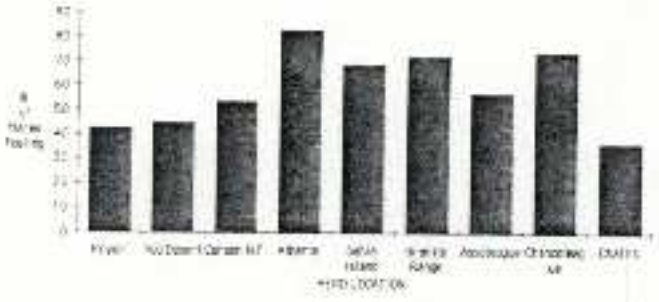

Figure 4. Fecundity by herd

A more probable cause for differences in the incidence of multiple male bands might be found in simple population density differences between herds, or the differences in sex ratios between different herds. Although these parameters are largely unstudied with respect to the issue of single versus multiple male bands, there are indications that they may profoundly affect band composition. Between 1979 and 1983, multiple male bands were extremely rare in the Challis, Idaho herd[19]. The incidence of multiple male bands has increased through 1985, perhaps as a result of round-ups which remove more mares than stallions, thereby increasing the competition for the position of band stallion.

Fecundity: Fecundity, measured by the index of foals/sexually mature mares must be viewed with caution. First, as has already been discussed, the age when mares reach sexual maturity may vary from herd to herd. Second, the reliability of age data provided by numerous investigators from widely disparate herds, using different methodologies, suggests room for a wide margin of error. Nevertheless, an examination of some available data indicates a very variable pattern from herd to herd.

Feist[9] and Feist and McCullough[10] reported that 43.2% of mature mares foaled during the 1970 season in the Pryor Mountain herd. In the Red Desert, Boyd[5] reported that 53% of mares three years or older foaled and 54.5% of mares four years or older foaled. Similar foaling rates were recorded at Stone Cabin Valley, 50%[12] and Carson National Forest, 53.8%[30]. In Alberta, however, Salter[35] reported a foaling rate of 83% and Welsh[43] reported an average foaling rate of 68.5% for the Sable Island horses.

In the Granite Range, Berger[3], made a distinction between fecundity in bands in which there was no change of band stallion (stable bands) and those in which band stallions had recently been replaced by new males (unstable bands). Among horses in unstable bands, Berger witnessed harassment of pregnant mares— which he claimed led to abortion - and 14 subsequent forced copulations with unreceptive mares. The foaling rate among the stable bands was 72 foals from 88 mares (81.8%) while the unstable bands produced only 9 foals from 24 mares (37.5%). Taken together, the Granite Range herd foaling rate was 72.3%.

Over an eight year period Keiper and Houpt[17] reported a 57.1% (±3.9%) foaling rate among the Assateague horses. The foaling rates were age-group specific and indicated that 23% of three-year-old mares foaled, 46% of four-year-olds, 53% of five-year-olds, and 69% of six-year-olds. On the adjoining Chincoteague refuge, just to the south of the Assateague range, the foaling rate was 74.4% (±2.4%).

Among mares in the Challis herd, Seal and Plotka[37] assessed pregnancy in 137 mares by measuring plasma progesterone, luteinizing hormone or pregnant mares serum gonadotropin, and estradiol-17 beta. Age specific pregnancy rates ranged from 35% among two-year-olds to 100% among 15-30 year-olds, with a collective 67.7% pregnancy rate for all mares age two to thirty. However, when foaling rates were determined a year later, among 35 mature mares in eight bands on the same range, Kirkpatrick *et al* [20] reported only 13 foals, or a rate of 37.1%.

Among Red Desert horses, Boyd[4,5] believes that consecutive year foaling is the rule, interrupted only by particularly severe winters. In 1978 she reported a foaling rate of 86 foals per 100 sexually mature horses (not just mares), but a year later, after a severe winter, the rate dropped to 54%. In support of this idea, Keiper[16] reported that only 10.2% of the Assateague ponies foaled on an alternate year basis, and Salter,[35] in Alberta, observed that among 12 mature mares with foals only 17% had not foaled the previous year. A similar pattern was described by Welsh[43] on Sable Island, where 26.7% of mature mares foaled three times in three years, 44.4% foaled two times/three years, and 8.9% did not foal once in three years. Welsh[43] also noted that 51% of parturient mares had conceived during foal heat and another 24% by the end of the next estrus. He interpreted this to mean that lactation does not suppress ovulation. Finally, the pregnancy rate study of Seal and Plotka[37] indicated that 52 of 85 mares had foals by their sides, or a 61.1% consecutive year pregnancy rate, although as has been pointed out earlier, it is unlikely that foaling rates were as high as pregnancy rates. These data suggest a significant embryonic loss over the winter months. Among horses from two different herds in Oregon, Eberhardt *et al*[8] reported 24.7 and 26.8 foals per 100 sexually mature adults, and an approximate 20% increase in herd size annually, between 1969 and 1980. Differences in foaling rates for different herds can be visualized in Figure 4.

One difference between foaling rates among horses of different herds can be explained by the physiological stress created by lactation and subsequent embryonic loss during severe winters. While no direct support for this hypothesis currently exists for feral horses, Keiper and Houpt[17] offer some strong circumstantial evidence. While the unmanaged horses of Assateague showed a 57.1% foaling rate, their counterparts on the Chincoteague refuge showed a 74.4% foaling rate. This latter herd has the foals weaned and removed in July of each year, removing the stress of lactation from the parent mares. Thus, among unmanaged herds it is logical to assume an inverse relationship between foal survival and foaling rates.

The major factor, however, in explaining differences in fecundity from herd to herd is most likely the differences in age structure between herds. The data from studies by Feist[9,10], Hall[13], Boyd[4,5], Welsh,[43] Reiper,[16] and Nelson[29,30] indicate that fecundity increases with the age-class of mares in the herd, thus, herds with older age structures will tend to have higher fecundity rates.

DISCUSSION

It is clear that there is variability among the reproductive parameters studied thus far in North American feral horses. At least five major forces may be assumed to influence reproduction to varying degrees. These forces include (1) the genetic origins of a given herd, (2) the ecology of the ranges inhabited by these animals, (3) population density, (4) age structure of the herd, and (5) sex ratios.

The genetic origins of the many herds are almost entirely unknown. The reintroduction of the horse to North America in 1519 and throughout the century which followed involved animals which have been described as Barbs and Andalusians, yet it remains pure speculation as to whether any of the contemporary herds are descendents of these horses. By the 1800's there were an estimated two million horses inhabiting North America[38]. Certainly the possibility that the original Barb and Andalusian genotypes may still exist, at least to some degree, cannot be dismissed. Empirical data also show modern domestic affinities exist in the contemporary feral horse herds. The largest infusion of these modern breeds undoubtedly occurred in the 1930's during the Great Depression, when thousands of horses were simply turned loose to fend for themselves.

At the present time only a single genetic study has been completed but certain genetic differences are obvious. Color patterns vary widely from herd to herd, as do average sizes and weights. The seasonal cyclic activity of feral mares, described here earlier, also varies greatly from breed to breed among domestic horses,[31] and points to the importance of genetics when examining biological differences between herds.

An alternative theory to significant genetic differences is epigenesis. Behavioral plasticity and adaptational flexibility are possible, without genetic change of populations. However, until comprehensive genetic studies are carried out, both theories have little substantive evidence to support them.

Habitat differences may have an important effect upon the reproductive biology of the feral horse. Availability of high quality grass, water sources, protective topography, size of the range (and therefore herd density), and weather patterns are but a few factors which may also dictate reproductive patterns and success. The best example here is the difference between foaling behavior of the Red Desert mares, where the mare simply foals next to the band, and that of mares from all other ranges, where they wander off to some hidden location to foal. Boyd[5] attributes this behavior to the open country of the Red Desert and the lack of suitable habitat in which to hide. Rubenstein[34] finds a correlation between geographical features of Shakelford Island— areas where the land was extremely narrow and visibility unrestricted— and the existence of territorial behavior.

In addressing the importance of the above forces in moderating reproduction, population density probably plays as large a role as any. The rodent studies of Christian[6] certainly support this view. In terms of horses it can logically be assumed that nutritional planes and population density will be inversely related and that reproductive success will depend upon adequate nutrition. In addition, the stability of band structure can be assumed to be inversely related to population density. Herd densities in turn may be a function of the age-class profile of the herd. A herd with larger numbers of older mares will have a higher fecundity rate and will increase at a faster rate than a herd with fewer older age-class mares.

Sex ratios may also alter band stability between herds even if overall density is the same. Larger numbers of sexually mature stallions would create increased competition for the position of band stallion, and the work of Berger[3] suggests that band instability leads to lower fecundity rates.

It is most logical, however, to examine the comparative reproductive biology of the continent's feral horses as a function of all five factors mentioned above. Genetics provides the foundation or starting point from which to examine any biological variation, and certainly reproductive biology. Horses with older genotypes might be assumed to take less time to reach equilibrium with their environment than those of a more modern lineage. Habitat and a multitude of other environmental conditions will in turn drive the process of natural selection and the more hostile the environment, the more dramatic the results of selection. Finally, fluctuations in population densities, age-class, and sex ratios, whether man-caused or natural, can bring about rapid changes which can impinge upon reproductive biology.

A few of the differences among the reproductive parameters discussed above-age at sexual maturity, and reproductive success— may represent nothing more than normal-curve variability that would be expected in any biological system, particularly since considerable variation occurs within a given herd of horses. Consequently it is difficult to place too much weight on the importance of genetic differences and natural selection. However, some variability between herds is so striking— parturition behavior, seasonality, forced copulation and incest, and single versus multiple male breeding— that normal-curve variability cannot explain the differences. This suggests a genetic influence and change through natural selection.

Information about the reproductive biology of North American feral horses has increased significantly since 1971, and it should be apparent from this review that considerable diversity exists from herd to herd. At least five factors must influence the reproductive biology of these animals, and the need exists for a model which integrates all relevant factors and seeks the correlations with reproductive parameters.

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