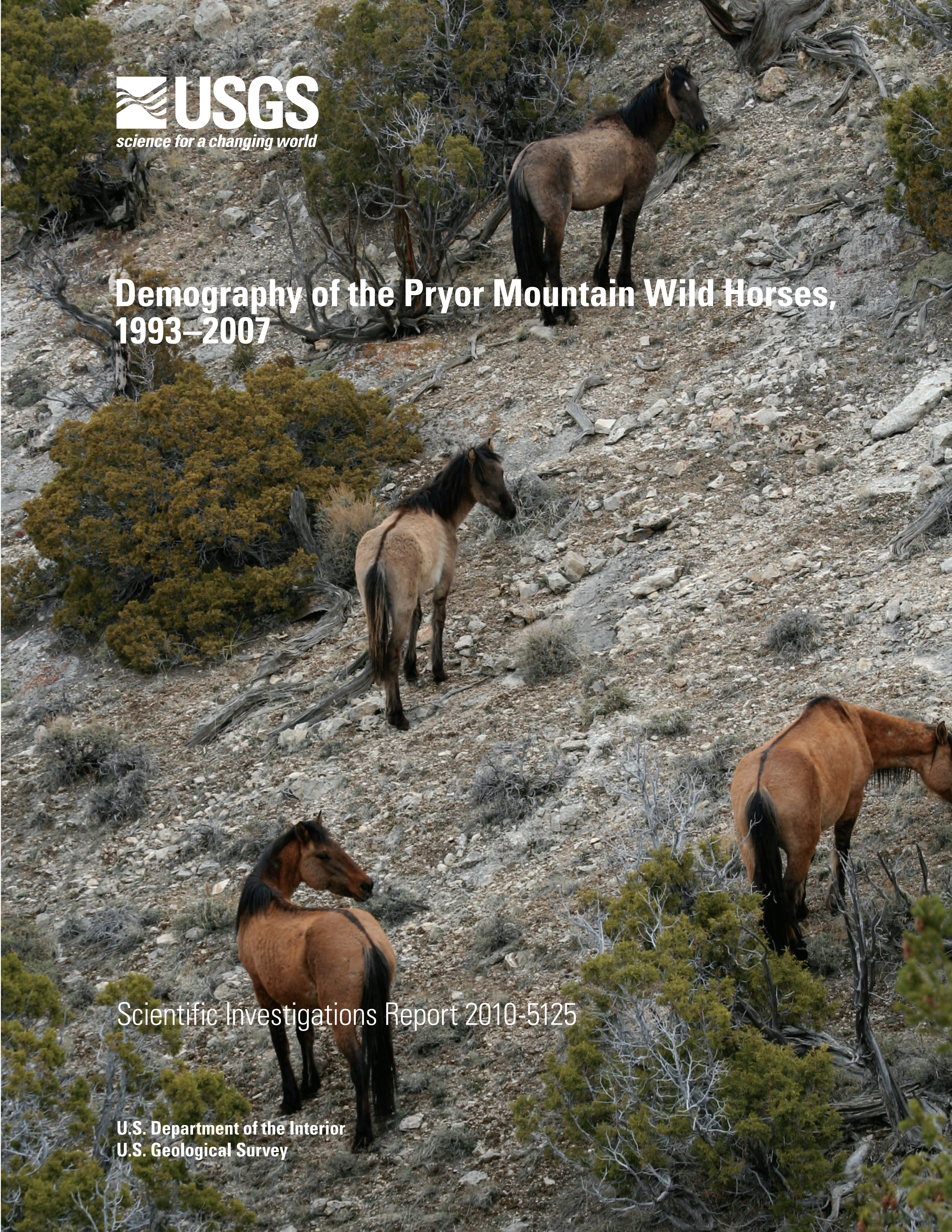
USGS
science for a changing world

Demography of the Pryor Mountain Wild Horses, 1993–2007



Scientific Investigations Report 2010-5125

U.S. Department of the Interior
U.S. Geological Survey

Front and back cover photographs. Jason I. Ransom, U.S. Geological Survey.

Demography of the Pryor Mountain Wild Horses, 1993–2007

By James E. Roelle, Francis J. Singer, Linda C. Zeigenfuss, Jason I. Ransom, Linda Coates-Markle, and Kathryn A. Schoenecker

Scientific Investigations Report 2010-5125

U.S. Department of the Interior
U.S. Geological Survey

U.S. Department of the Interior
KEN SALAZAR, Secretary

U.S. Geological Survey
Marcia K. McNutt, Director

U.S. Geological Survey, Reston, Virginia: 2010

For product and ordering information:
World Wide Web: http://www.usgs.gov/pubprod
Telephone: 1-888-ASK-USGS

For more information on the USGS—the Federal source for science about the Earth,
its natural and living resources, natural hazards, and the environment:
World Wide Web: http://www.usgs.gov
Telephone: 1-888-ASK-USGS

Suggested citation:
Roelle, J.E., Singer, F.J., Zeigenfuss, L.C., Ransom, J.I., Coates-Markle, L., and Schoenecker, K.A., 2010, Demography of the Pryor Mountain wild horses, 1993–2007: U.S. Geological Survey Scientific Investigations Report 2010-5125, 31 p.

Contents

Abstract 1
Introduction 1
Study Area 2
    Herd Behavior and Management 4
Methods 5
    Field Data Collection 5
    Analysis 5
Results 6
    Population Size and Growth 6
    Removals 7
    Sex and Age Structure 7
    Survival 8
    Foaling Rates 10
    Harem Stallions and Band Composition 13
    Bachelors 16
    Population Regulation 16
        Density Dependence 16
        Weather 17
Discussion 17
    Population Size and Growth 17
    Sex and Age Ratios 19
    Survival 20
    Foaling Rates 22
    Harem Stallions and Band Composition 24
    Bachelors 25
    Population Regulation 25
Acknowledgments 25
References Cited 27

Figures

1. Map showing location of the Pryor Mountain Wild Horse Range and study area 3
2-14. Graphs showing:
2. Trend in growth rate of the Pryor Mountain wild horse (*Equus caballus*) population, 1993–2007 7
3. Sex ratio of wild horse (*Equus caballus*) foals born in the Pryor Mountain herd, 1993–2007 8
4. Variation in the sex ratio of wild horse (*Equus caballus*) foals by age of dam in the Pryor Mountain herd, 1993–2007 8
5. Annual sex ratio of adult (≥1 year old) wild horses (*Equus caballus*) in the Pryor Mountain herd, 1993–2007 8
6. Average age of (*A*) male and (*B*) female wild horses (*Equus caballus*) in the Pryor Mountain herd, 1993–2007 9
7. Trend in annual survival of Pryor Mountain wild horses (*Equus caballus*) for adults and foals, 1993–2007 11
8. Age of wild horse (*Equus caballus*) stallions holding harems in the Pryor Mountain herd, 1996–2007 14
9. Age at which wild horse (*Equus caballus*) stallions first held a harem in the Pryor Mountain herd, 1996–2007 15
10. Frequency distribution of wild horse (*Equus caballus*) harem size in the Pryor Mountain herd, 1996–2007 15
11. Mean number of wild horse (*Equus caballus*) mares held relative to age of harem stallions in the Pryor Mountain herd, 1996–2007 15
12. Number of bachelor wild horses (*Equus caballus*) in the Pryor Mountain herd, 1996–2007 16
13. Age distribution of bachelor wild horses (*Equus caballus*) in the Pryor Mountain herd, 1996–2007 17
14. Relation of (*A*) survival and (*B*) population growth rate to the previous year's population for wild horses (*Equus caballus*) in the Pryor Mountain herd 18

Tables

1. Size and growth rate of the Pryor Mountain wild horse (*Equus caballus*) herd, 1993–2007 7
2. Removals of wild horses (*Equus caballus*) from the Pryor Mountain herd, 1993–2007 8
3. Annual survival rates of Pryor Mountain wild horses (*Equus caballus*), 1993–2007 10
4. Age-specific survival rates of Pryor Mountain wild horses (*Equus caballus*), 1993–2007 11
5. Annual foaling rates of Pryor Mountain wild horse (*Equus caballus*) mares, 1993–2007 12
6. Total foals born to Pryor Mountain wild horse (*Equus caballus*) mares, 1993–2007 12
7. Age-specific fecundity of Pryor Mountain wild horse (*Equus caballus*) mares, 1993–2007 13
8. Number of wild horse (*Equus caballus*) bands, mean age of harem stallions, mean harem size (mares ≥2 years old), and mean band size (all members) in the Pryor Mountain herd, 1996–2007 14
9. Results of stepwise multiple regressions between wild horse (*Equus caballus*) herd survival, foal survival, and foaling rate (mares ≥3 years of age) and various weather parameters for the Pryor Mountain herd 19
10. Survival rates reported for North American wild horse (*Equus caballus*) herds 21
11. Foaling rates reported for North American wild horse (*Equus caballus*) herds 23

Conversion Factors

Inch/Pound to SI

Multiply	By	To obtain
	Length	
inch (in.)	2.54	centimeter (cm)
foot (ft)	0.3048	meter (m)
mile (mi)	1.609	kilometer (km)
yard (yd)	0.9144	meter (m)
	Area	
acre	0.4047	hectare (ha)
square mile (mi^2)	259.0	hectare (ha)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$°F=(1.8\times°C)+32$$

Acronyms Used in Report

AML	Appropriate Management Level
APHIS	Animal and Plant Health Inspection Service
BLM	Bureau of Land Management
FS	Forest Service
HMA	Herd Management Area
NCDC	National Climatic Data Center
NPS	National Park Service
PMWHR	Pryor Mountain Wild Horse Range
RAWS	Remote Automated Weather Station
USGS	U.S. Geological Survey

Demography of the Pryor Mountain Wild Horses, 1993–2007

By James E. Roelle,[1] Francis J. Singer,[1,2] Linda C. Zeigenfuss,[1] Jason I. Ransom,[1] Linda Coates-Markle,[3] and Kathryn A. Schoenecker[1]

Abstract

Wild horses (*Equus caballus*) at Pryor Mountain were studied by direct observation from 1993 through 2007. All horses present were individually identifiable on the basis of coat coloration, head and leg markings, gender, and band associations. Of the 609 horses either present prior to foaling in 1993 or born since, ages were precisely known for 491 (observed as a foal). Ages for 52 horses were estimated through tooth eruption and wear patterns, and for the remaining 66 horses through body size, morphology, and anecdotal evidence concerning when they were present on the range. At varying intensities, never less than 30 days per year, all horses were inventoried and their band associations noted. Foals were paired with dams based on observations of attachment during the early days and weeks of life. Year of death was determined by identification of the carcass where possible. In the absence of finding a carcass, an animal that was not observed for 2 years was considered to have died in the year that it went missing. Animals that were removed from the herd and mares that were part of a contraception study were excluded from calculations of survival and foaling rates, respectively, as appropriate.

The average prefoaling population over the 15 years of the study was 148.8 animals (range = 120–187), and the annual foal crop averaged 32.1 (range = 23–40). Large removals (19–60 animals) in four years helped maintain the herd at this level; apparent growth rate (calculated as though removals had not occurred) was 9.6 percent annually ($\lambda = 1.096$, range = 0.977–1.220). This annual growth rate is relatively low compared to that for many western horse herds, at least in part because of a decline in foal survival. Sex ratio of the foal crop varied widely among years, but pooled across years did not differ from 50:50. Sex ratio in the herd changed mostly as a result of removals. The average age of both males and females in the herd increased during the course of the study. Annual survival of males did not differ from that of females, nor did gender affect annual survival of foals. Pooled across years, ages, and sexes, the annual survival rate was 0.899. Annual foal survival rate was 0.697 and declined through time, with a tendency toward recovery in 2005–2007. Foal survival was higher in larger bands, but did not differ between foals born to primiparous and multiparous mares. A few 2-year-old mares produced foals; foaling rate (excluding contracepted mares and foals they produced) increased through age 10, remained high through age 15, and declined thereafter. Overall foaling rate for mares ≥3 years of age was 0.576 foals per mare, with no apparent trend during the period of our study. Foaling rate in years following gathers was somewhat lower than in other years. There was a positive relation between foaling rate and band size. Primiparous mares were somewhat less likely to foal in the following year than were multiparous mares. Most stallions that acquired a harem did so at age 5 or 6, and the average age of harem stallions increased during our study. Most harems had 1–3 mares ≥2 years of age, but harem size varied with age of the stallion, increasing through about age 11 and declining thereafter. About 6 percent of bands had a satellite stallion (≥5 years of age), but the mean number of mares did not differ between single- and multistallion bands. Most stallions left their natal band at age 2 or 3, but 17 percent remained with their natal band until age 4 or 5.

Foal survival rate was positively related to precipitation, suggesting a possible link to forage production and availability mediated through mare fitness. There also was evidence for density-dependent population regulation, as both population growth rate and survival rate were negatively correlated with population size from the previous year. These and other factors were not sufficient to stabilize the population during our period of study, however, as evidenced by the necessity for large removals in several years.

Introduction

The Pryor Mountain Wild Horse Range was created in 1968 by order of the Secretary, U.S. Department of the Interior, who directed that wild horses (*Equus caballus*) be managed in “a balanced program which considers all public values and without impairment of the productivity of the land” (Federal Register, Document 68-11056, Sept. 11, 1969;

[1] U.S. Geological Survey, Fort Collins, Colorado.

[2] Deceased.

[3] Bureau of Land Management, Wheat Ridge, Colorado.

Bureau of Land Management, 2006, p. 5). The Bureau of Land Management (BLM) was designated as the lead agency for management of wild horses, though the range also contains lands administered by the U.S. Forest Service (FS; Custer National Forest) and the National Park Service (NPS; Bighorn Canyon National Recreation Area). The Wild Free-Roaming Horses and Burros Act of 1971 (P.L. 92-195) further directed the FS and BLM to manage wild horses at Pryor Mountain and wild horses and burros (*Equus asinus*) wherever they occur "in a manner that is designed to achieve a thriving natural ecological balance on the public lands."

While laudable as general management goals, the conditions implied by phrases such as "a balanced program which considers all public values without impairment of the productivity of the land" and "a thriving natural ecological balance" have proven difficult to achieve for many wild horse herds. With the protection afforded by the Act and a dearth of natural predators, many wild horse herds can increase at annual rates of 15–25 percent (Eberhardt and others, 1982; Garrott and Taylor, 1990; Garrott and others, 1991b; Singer and others, 2000), thus threatening to exceed the carrying capacity of their ranges. BLM has addressed this problem largely through a gather and removal program in which excess horses are removed from the range and offered to the general public for adoption or sale to good homes. While hugely successful by some measures (BLM has adopted out more than 220,000 horses since 1971; *http://www.blm.gov/wo/st/en/prog/wild_horse_and_burro/wh_b_information_center/Fact_Sheet.html*), supply has exceeded demand, leaving nearly 32,000 horses in BLM corrals and long-term holding pastures. This approach is not embraced by all members of the public. Wild horse advocacy groups often favor a policy of minimum disturbance and intervention, arguing that there are too few, rather than too many, wild horses and that the gather and removal process is detrimental to horse health and well-being. On the other hand, ranchers and conservationists often see wild horses as competing with domestic cattle (*Bos taurus*) and native wildlife for forage, and would thus prefer that BLM reduce the size of many horse herds.

Given the contentious nature of the issues involved, BLM has a continuing need for the best scientific information available on the ecology and demography of wild horse herds. Since creation of the range in 1968, information on wild horses has been gathered nearly continuously by trained investigators and volunteers, making the Pryor Mountain horses perhaps the most studied herd in the Western United States. Furthermore, all of the horses at Pryor Mountain are individually identifiable (unique color markings), and many are of known (observed as a foal) or closely estimated (tooth eruption and wear patterns) age, making the resulting data dependable. The first study of horses at Pryor Mountain was initiated in 1970 by J.D. Feist, who focused largely on behavior (Feist, 1971), but also gathered some information on demography of the population (Feist and McCullough, 1975). Shortly thereafter, Hall (1972) performed an assessment of the herd and possible management alternatives. Perkins and others (1979) studied population dynamics, age distribution, and band composition in the Pryor Mountain herd from 1974 through 1978. Garrott and Taylor (1990), using information gathered by BLM personnel, reported on many aspects of herd demography from 1972 through 1986. F.J. Singer and several colleagues began studies at Pryor Mountain in the early 1990s, broadening their scope to include vegetation dynamics and conservation genetics as well as demography (Singer and Schoenecker, 2000). Prior to his untimely death in 2005, Singer also participated in work at Pryor Mountain on contraception and population estimation.

Here we report on the demographics of the Pryor Mountain wild horse herd from 1993 to 2007. The results contained herein represent a more detailed analysis of the data presented by Singer and others (2000) and an extension covering the next decade. While specific to the Pryor Mountain herd, and thus not necessarily representative of the other 180 Herd Management Areas (HMAs) overseen by BLM, we hope that our results will provide wild horse managers with useful insights as they continue to meet the challenges of managing wild horse herds in the Western United States.

Study Area

During the period of our study, horses actually used an area larger than the Pryor Mountain Wild Horse Range as originally designated. The northwestern and northern boundaries of our study area are not well defined, as there are no natural or manmade barriers to horse movement in that direction. As shown in figure 1, however, the study area encompasses about 22,300 hectares (ha). The following description of the area largely follows Singer and others (2000) and Ricketts (2004).

The study area lies along the Montana-Wyoming border at approximately latitude 45°4'N and longitude 108°19'W, 76 kilometers (km) south of Billings, Mont., and 14 km north of Lovell, Wyo. (fig. 1). The area is topographically diverse, dominated by narrow canyons and steep cliff faces. Elevations range approximately from 1,175 to 2,670 meters (m), with corresponding variation in climate and vegetation. Temperatures range from 40 ºC in the summer to -34 ºC in the winter. Mean annual precipitation ranges from 15 centimeters (cm) at lower elevations to nearly 70 cm at higher elevations, with much of the annual total falling in April–June. Midelevation ridges and plateaus often remain snow free or accumulate <10 cm of snow as a result of winds and southern and western exposures. Higher elevations often have winter snow accumulations of 1 m or more. In water years 1993–1998 (water year 1993, for example, runs from October 1992 through September 1993), mean annual precipitation at Lovell, Wyo. (*http://www.wrcc.dri.edu/summary/climsmwy.html*), was 17.2 cm, essentially identical to the 30-year average (Bureau of Land Management and others, 2008). From 1999 to 2004, however, severe drought conditions prevailed (mean annual precipitation = 12.3 cm). Prolonged drought can decrease plant health

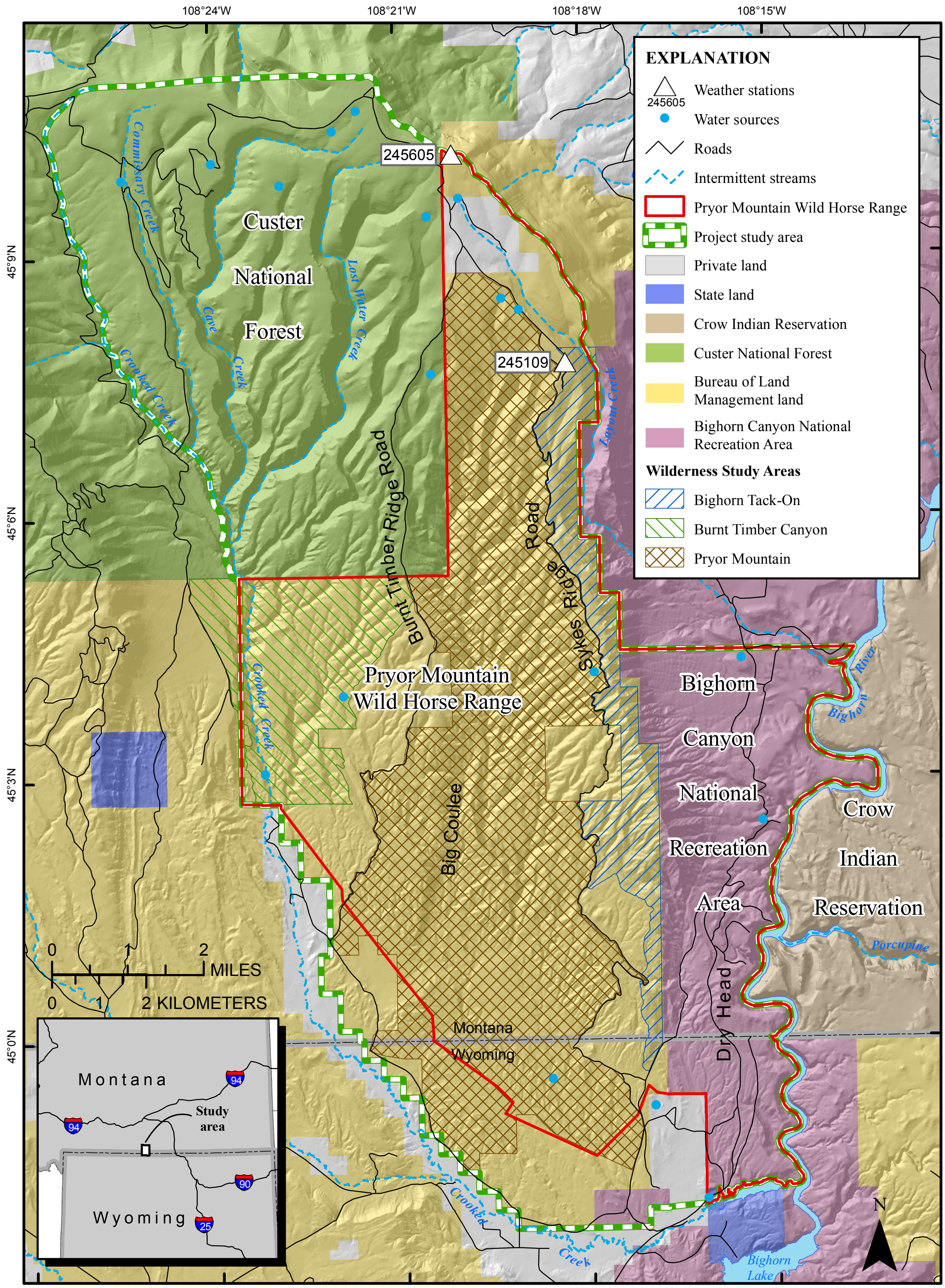


Figure 1. Location of the Pryor Mountain Wild Horse Range and study area.

and vigor and forage production. Temporary relief from the drought occurred in 2005 (annual precipitation = 21.2 cm) and 2007 (annual precipitation = 14.3 cm for 11 months, data missing for June) At least in 2005, greater precipitation probably resulted in improved forage production (Bureau of Land Management, 2006).

Vegetation in the study area changes dramatically with elevation. At the highest elevations, subalpine meadows (Idaho fescue, *Festuca idahoensis*; alpine timothy, *Phleum alpinum*; alpine bluegrass, *Poa alpina*; Ross sedge, *Carex rossii*; silky lupine, *Lupinus sericeus*) are interspersed with stands of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). At somewhat lower elevations, Douglas fir (*Pseudotsuga menziesii*) occurs with an understory of snowberry (*Symphoricarpos* spp.). Still lower is a shrub community dominated by big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Ericameria nauseosus*), shrubby cinquefoil (*Dasiphora fruticosa*), Utah juniper (*Juniperus osteosperma*), and curl-leaf mountain mahogany (*Cercocarpus ledifolius*) and a variety of grasses and forbs such as bluebunch wheatgrass (*Pseudoroegnaria spicata*), threeawn (*Aristida purpurea*), needle-and-thread (*Hesperostipa comata*), and blue grama (*Bouteloua gracilis*). For a more complete description of vegetation communities on the Pryor Mountain Wild Horse Range, see Ricketts (2004).

Herd Behavior and Management

The social structure of the Pryor Mountain wild horse population consists of bands that include a harem stallion, occasionally along with a satellite stallion, plus adult mares and yearlings and foals of both sexes. In general, we use the term band to refer to all members of the group and harem to refer to mares ≥2 years of age. Males older than yearlings that have not acquired a band usually are found in bachelor groups. Distribution and movements of the bands largely are restricted by topography to the west (Crooked Creek drainage) and east (Bighorn Canyon), and fences of varying integrity to the north and south (fig. 1). The wild horses occur in three more or less discrete subpopulations (Burnt Timber Ridge, Sykes Ridge, and Dryhead). These areas are separated by Big Coulee (a deep canyon) and a long, nearly vertical cliff face. However, the horses are able to move between these areas at high elevations and below Big Coulee, as well as occasionally by way of trails on the cliff face. Varying numbers of horses also use U.S. Forest Service land to the north and west of the original horse range boundary. Interchange of horses between subpopulations occurs regularly, but not with high frequency. The horses move with the seasons, spending winters at low and middle elevations where snow is less deep and summering at higher elevations. Distribution is restricted by available water in summer, when the horses tend to congregate near water sources. Water has less effect on distribution in winter, when the horses use snow to meet their water needs.

In the past, the herd has been managed consistent with national selective removal policy for the BLM Wild Horse and Burro Program, removing mostly young animals and conserving the core breeding component of the population. In general, BLM defines Appropriate Management Level (AML) as the number of adult wild horses (6 months and older) determined through the agency planning process to be consistent with the objective of achieving and maintaining a thriving natural ecological balance and multiple-use relation (Bureau of Land Management, 2006). Initially, the AML for the Pryor Mountain herd was set at 115–127, but was revised to 85–105 horses in 1992. However, based on genetic research (Cothran and Singer, 2000; Gross, 2000a,b), from 1996 to 2006 BLM attempted to manage the herd at an average of 140 adult horses to help conserve genetic diversity (Bureau of Land Management, 2006). More recently, BLM has determined that management at an AML of 90–120 adult horses is necessary to protect and improve rangeland health (Bureau of Land Management, 2009).

The BLM has managed the size of the Pryor Mountain herd primarily through a gather, removal, and adoption program. In 1994, wranglers on horseback attempted to capture the entire herd by moving horses into corral traps. In 1997 and 2001, a helicopter was used to move most of the family bands (individual bachelors typically were not gathered) into corral traps; approximately 125 animals were gathered in each of these years. Smaller gathers aimed at removing excess bachelor stallions and yearling females were conducted in 2003 and 2006. The 2003 gather involved a helicopter to move groups containing target horses into a corral trap. The 2006 gather was conducted using bait trapping to lure the horses into a trap, after which they were transported by vehicle to a holding corral.

Since 2001, some mares in the Pryor Mountain herd have received fertility control treatments using the contraceptive porcine zona pellucida [PZP; see Kirkpatrick and Frank (2005) for a recent review of contraception in equids and other free-ranging animals] as part of a cooperative research project between BLM, the U.S. Geological Survey (USGS), and the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (APHIS). In 2001, six mares (age 1–2) that had not yet reached breeding status were treated with PZP by hand injection during the gather. A booster inoculation was administered to three of these females in August 2002; the remainder had either died or could not be located to deliver the booster. Fertility control was subsequently applied to younger mares (age 1–2, 2002–2004) and older mares (>14 years, 2002–2004; >10 years after 2004) that had already contributed to the genetics of the population. After 2001, all inoculations (both primers and boosters) were delivered remotely by darting. Because of the timing of booster inoculations relative to the breeding season, the first contraceptive effects were expected in 2004. From 2004 through 2007, 20.0, 29.0, 10.8, and 30.8 percent of the mares (≥3 years old) in the herd were presumptively contracepted.

BLM also has attempted to manage the herd to adjust the sex ratio in favor of males (Bureau of Land Management, 2006) and occasionally has introduced a limited number of horses (both mares and stallions) from outside herds in order to supplement the herd genetically. Introduction of outside horses was discontinued in 1994.

Methods

Field Data Collection

All data reported in this study were gathered through direct observations of the herd by trained BLM and USGS employees and volunteers. From 1995 to 1997, efforts were focused on the peak foaling season, May 1 to June 30. From 1998 to 2007, daily observations were made during the peak foaling and breeding period, May 1 to August 30. This effort totaled approximately 100 hours of observation per week during 1995–1997 and 100–150 hours per week during 1998–2007. Semi-weekly to weekly observations were made March–April and September–November. Fewer observations were made during midwinter, and they were limited to accessible areas of the range, which varied from year to year. Observations were made from the ground during systematic surveys along roads and trails that traverse the study area. Ground observations were augmented with two helicopter flights each fall or winter, 1995–2001, and one flight in late 2006, as well as 20–25 days of horseback surveys throughout each year, 1995–2005.

Greater than 90 percent of the bands were located at least twice per week during the May–July period, and all bands usually were located at least once per week from April to mid-May and August to mid-October. Reduced effort in the remainder of the year resulted in less than one observation per week per band. Observers collaborated during the peak observation season to develop a weekly list of band composition and foal presence.

Wild horses were approached within 100–250 m and could be observed for periods of 2–6 hours with no apparent effect on their behaviors. All horses were identified individually based on color, markings, gender, and band associations since 1993. All stallions, mares, yearlings, and foals observed in bands, bachelor groups, or alone were recorded. Lead harem stallions were identified based on behavior as described in Feist and McCullough (1975), Oom and Santos-Reis (1986), and Berger (1986). Interchanges between bands by mares and stallions were recorded, as were returns to the original band.

Each horse in the population was assigned a unique number during data compilation. Of the 609 animals in the population from 1993 to 2007, horses whose birth year was known from foal records included 480 of the 481 foals born during 1993–2007 and 11 horses born prior to 1993. Ages of an additional 52 animals were estimated by a veterinarian based on tooth eruption and wear patterns (American Association of Equine Practitioners, 2002). Ages of the remaining 66 animals were based on body size and morphology and anecdotal evidence of years the animals were on the range. Death year was determined by identification of the carcass of the deceased individual or, if an individual was not observed for two consecutive years, the animal was considered to have died in the year it went missing. Number of foals produced was determined by observation as described above. It is possible that some foals were born and died without being seen; however, given the intensity of the observations, we believe that this was rare. Identification of an individual's dam was based on observations of attachment of foal to mare during the early days and weeks of the foal's life.

Analysis

We conducted all of our analyses on the basis of biological years, which we defined as just prior to foaling in one year to the same time the next year. Thus, the biological year 1993 encompasses the period from spring 1993 to spring 1994. Because we defined the biological year in this way, because we made no attempt to pinpoint when during a year a horse was born or died, and because we have the benefit of hindsight (other reported data were often projections), our data will in some cases not match exactly those presented elsewhere (for example, various Environmental Assessments prepared by BLM).

We calculated annual population growth using the expression $\lambda_t = N_t / (N_{t-1} - R_{t-1})$, where λ_t is the growth multiplier from year $t-1$ to year t, N is the population size, and R_{t-1} is the number of animals removed in the period $t-1$ to t. In this formulation, λ represents the apparent growth rate of the population had horses not been removed (Garrott and Taylor, 1990).

Survival rates were calculated as the number of animals present at the end of a year divided by the number present at the beginning of that year. Animals that were removed from the herd were excluded from survival calculations in the year they were removed. Foaling rates were calculated as the number of foals born (regardless of how long they lived) divided by the number of mares present. Mares that were presumptively contracepted and foals that they produced were excluded from calculations of foaling rate.

Band composition has been recorded on "horse lists" regularly (usually weekly) since 1996. These are lists of all the harem stallions present and all the members of their bands, plus lists of bachelor males and animals in transit between bands. To derive information on harem stallions and band composition, we used two of these lists for each year from 1996 through 2007, one from the breeding season (usually early June) and one from fall (September–November, usually the last list available for the calendar year). For each harem stallion present, we calculated the number of mares ≥2 years of age in the band for each of the two time periods and then took the maximum of those two values as the number of mares held in the harem in that year. We calculated total band size in an analogous manner, and we used these same lists to derive information on bachelors and satellite stallions, which we defined as ≥5 years of age. We defined a satellite stallion in this way in an effort to distinguish true multistallion bands from cases in which a male simply remained with his natal band longer than usual.

We looked for evidence of density dependence in foaling rate, herd survival, foal survival, and population growth rate in the Pryor Mountain wild horse population using stepwise multiple regression with the current year's postfoaling population and the previous year's postfoaling population as independent variables. For these analyses, we used data from Garrott and Taylor (1990) for 1976–1986 (foaling rate, herd survival, and population growth rate), as well as data from our study for 1993–2007. We excluded data from the winter of 1977–1978, during which 51 percent of the population died as a result of heavy snow and ice accumulations (Garrott and Taylor, 1990), from the analyses of density dependence in herd survival and growth rate. We also excluded data from 2004, when 96 percent of the foal crop was lost, from the analysis of foal survival. Foal losses in 2004 are suspected to have been the result of predation by mountain lions (*Puma concolor*). We believe that these exclusions are justified because the biological processes operating in these years were clearly different from those operating in other years.

It would be desirable to have consistent, long-term data on annual forage production for comparison with demographic parameters, but we are unaware of such data for the study area. As a possible surrogate, we examined weather records from a number of stations in the area, reasoning that forage production in this semiarid environment likely is related to precipitation, even though large elevation differences across the study area make it unlikely that any single station will be representative of the entire area. In terms of location, the best available data are from a Remote Automated Weather Station (RAWS; Wild Horse Montana, NWS ID #245605, elevation 2,675 m), which was operated in the study area from October 1991 to July 1997 (*http://raws.dri.edu/wraws/emtF.html*) (fig. 1). Unfortunately, overlap between this period of record and the period of our study is minimal. A National Climatic Data Center Station (NCDC #484770, elevation 1,170 m) at Lovell, Wyo., has a much longer period of record (1948–present; *http://www.wrcc.dri.edu/summary/climsmwy.html*), but its lower elevation caused us to question its relevance to higher elevations in the study area. For the 7 years of data in common, however, there was a strong correlation between the two stations for both total annual precipitation ($R^2 = 0.921$, $P = 0.0006$) and the minimum of the monthly average minimum temperatures ($R^2 = 0.763$, $P = 0.01$). We therefore used data from the Lovell station and stepwise multiple linear regression to analyze relations between weather and herd survival rate, foal survival rate, and foaling rate (mares ≥3 years of age). Data on annual herd survival and foaling rate were available from both our study and the work of Garrott and Taylor (1990), but data on annual foal survival were available only from our study. For the reasons cited above, we again excluded 2004 from the analysis of foal survival.

Other investigators (Heitschmidt and others, 2005; Smart, 2005) showed that spring precipitation (April–June) is related to annual forage production in the Great Plains. We therefore divided precipitation data into spring (April–June), summer (July–September), and winter (October–March). For each year, we also calculated the mean of the monthly average minimum temperatures (December–February) and the mean of the monthly average maximum temperatures (April–September) as indices of winter cold and summer heat.

For herd survival, we used the covariates winter precipitation in the previous year, spring precipitation in the current year, and summer precipitation in the current year (hypothesizing that all might have a positive relation with forage production in the current year), winter precipitation in the current year (potential negative effect of snow accumulation on forage availability in the current year), and average monthly minimum temperature in the current year (potential negative effect on ability to meet energy demands). For foal survival, we used the same set of covariates and added average monthly maximum temperature (possible effect of heat stress on more susceptible foals). For foaling rate, we used the covariates summer precipitation in the previous year (potential positive relation with forage production during early pregnancy), winter precipitation in the previous year (potential negative effect of snow accumulation on forage availability), average monthly minimum temperature (potential negative effect on ability to meet energy demands), and spring precipitation in the current year (possible positive relation with forage production during late pregnancy).

All data were entered into Microsoft Excel® spreadsheets (Microsoft Corporation, Redmond, Wash.). Analyses were conducted in SAS® v. 9.1 (SAS Institute, Cary, N.C.) using standard statistical techniques as noted in the Results section.

Results

Population Size and Growth

Prior to foaling in spring 1993, there were 128 horses ≥1 year of age in the study area. From 1993 to 2007, 481 horses were born; thus, our study encompasses 609 individual animals. During the period of study, the prefoaling population averaged 148.8 animals (range = 120–187), the foal crop (number born) averaged 32.1 (range = 23–40), and the postfoaling population averaged 180.9 animals (range = 149–227) (table 1). As we calculated it, the postfoaling population represents the maximum number of animals that could have been present at any time during the year, as it assumes no mortality of foals or adults during the foaling period. The number of deaths per year apparently increased during 1999–2006, while the foal crop remained relatively constant throughout

Table 1. Size and growth rate of the Pryor Mountain wild horse (*Equus caballus*) herd, 1993–2007.

[Growth rate (λ) is calculated based on the postfoaling population. —, not applicable; SE, standard error of the mean.]

Year	Prefoaling population	Foals born	Postfoaling population	Deaths	Removals	λ
1993	128	23	151	1	1	—
1994	149	34	183	3	60	1.220
1995	120	29	149	7	0	1.211
1996	142	32	174	7	2	1.168
1997	165	35	200	15	46	1.163
1998	139	23	162	7	1	1.052
1999	154	38	192	27	0	1.193
2000	165	37	202	15	0	1.052
2001	187	40	227	31	46	1.124
2002	150	32	182	28	0	1.006
2003	154	30	184	32	7	1.011
2004	145	28	173	38	0	0.977
2005	135	36	171	19	0	0.988
2006	152	30	182	16	19	1.064
2007	147	34	181	9	0	1.110
Total	2,232	481	2,713	255	182	—
Mean	148.8	32.1	180.9	17.0	12.1	1.096
SE	4.18	1.30	5.14	3.02	5.36	0.0228

the period of study. The mean annual apparent growth rate, calculated as though removals had not occurred, was 9.6 percent (λ = 1.096, range = 0.977–1.220), or 10.5 percent if the year (2004) of heavy foal loss is excluded. Although the growth rate rebounded somewhat in 2006 and 2007, there was a significant ($R^2 = 0.514$, $P = 0.004$) overall decline during the period of study as determined by linear least squares regression (fig. 2).

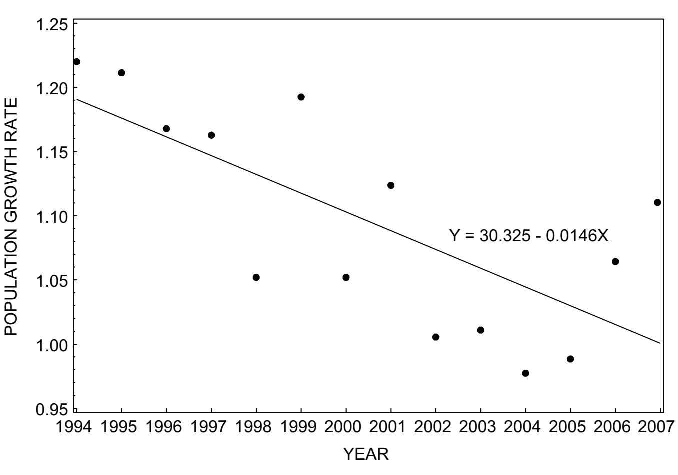


Figure 2. Trend in growth rate of the Pryor Mountain wild horse (*Equus caballus*) population, 1993–2007.

Removals

Major removals of wild horses occurred in 1994, 1997, 2001, and 2006, with smaller numbers of horses removed in four other years (table 2). For the entire period, adults (≥2 years of age) were removed most often (62.6 percent; $n = 182$), followed by yearlings (28.6 percent) and foals (8.8 percent). Across all age classes, slightly more males (56.6 percent; $n = 182$) were removed than females.

Sex and Age Structure

During the period 1993–2007, 477 foals of known sex were born; four foals disappeared before sex could be ascertained. Slightly more males (243) were born than females (234), but this difference was not statistically significant ($\chi^2 = 0.170$, $P = 0.68$). On an annual basis, however, the proportion of males in the foal crop varied widely (range = 34.8–71.9 percent) (fig. 3). The proportion of males produced also varied by age of mare, declining from age 3 through about age 10, and then increasing in older mares (fig. 4).

The sex ratio of animals ≥1 year of age varied only moderately during the period of study, ranging from a high of 55.2 percent males in 1997 to a low of 44.2 percent males in 2000 and 2007 (fig. 5). The largest interannual changes in sex ratio occurred as a result of removals in 1994 (27 males, 33 females

Table 2. Removals of wild horses (*Equus caballus*) from the Pryor Mountain herd, 1993–2007.

	Foals		Yearlings		Adults		
Year	**Males**	**Females**	**Males**	**Females**	**Males**	**Females**	**Total**
1993	0	0	0	0	1	0	1
1994	8	6	7	7	12	20	60
1996	0	0	0	0	2	0	2
1997	2	0	11	1	20	12	46
1998	0	0	0	0	1	0	1
2001	0	0	10	6	8	22	46
2003	0	0	1	0	6	0	7
2006	0	0	4	5	10	0	19
Total	10	6	33	19	60	54	182

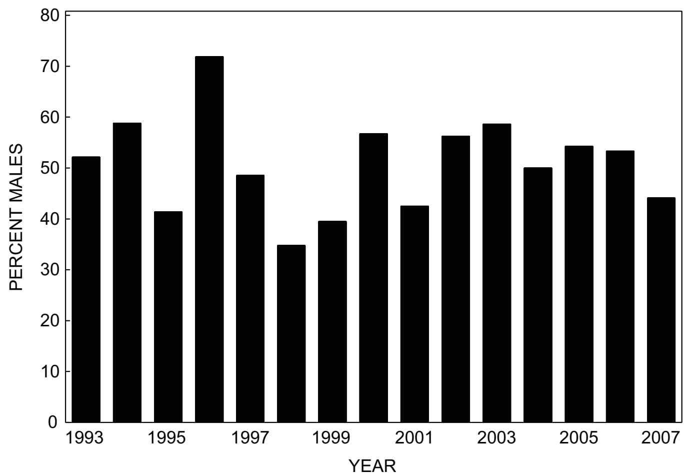


Figure 3. Sex ratio of wild horse (*Equus caballus*) foals born in the Pryor Mountain herd, 1993–2007.

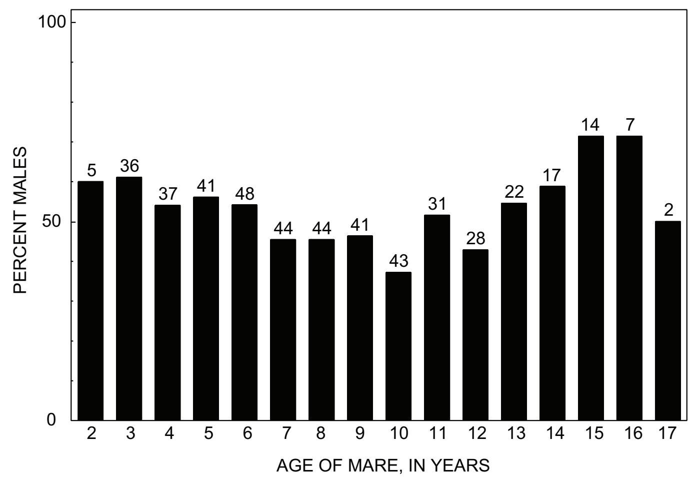


Figure 4. Variation in the sex ratio of wild horse (*Equus caballus*) foals by age of dam in the Pryor Mountain herd, 1993–2007. Values above the bars are number of foals born.

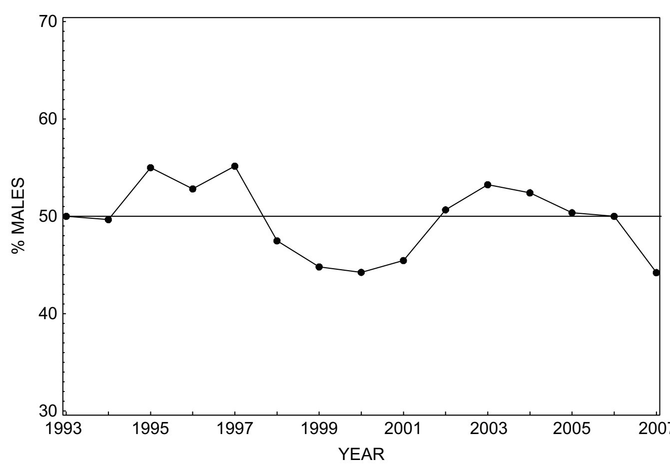


Figure 5. Annual sex ratio of adult (≥1 year old) wild horses (*Equus caballus*) in the Pryor Mountain herd, 1993–2007.

removed), 1997 (33 males, 13 females), 2001 (18 males, 28 females), and 2006 (14 males, 5 females).

The age structure of the Pryor Mountain wild horse herd, on the other hand, changed markedly between 1993 and 2007 (fig. 6*A*,*B*). In 1993, males in the herd averaged 4.4 years of age and females averaged 4.2 years. In 2007, the comparable values were 8.1 and 6.8 years, respectively. Both of these trends are statistically significant as judged by linear least squares regression (males, $P < 0.0001$, $R^2 = 0.911$; females, $P < 0.0001$, $R^2 = 0.832$).

Survival

Pooled across years, ages, and sexes ($n = 2{,}531$), the annual survival rate of horses on the study area was 0.899. Excluding four foals that disappeared before sex could be ascertained, survival of males (0.896, $n = 1{,}246$) did not differ from that of females (0.905, $n = 1{,}281$) ($\chi^2 = 0.486$,

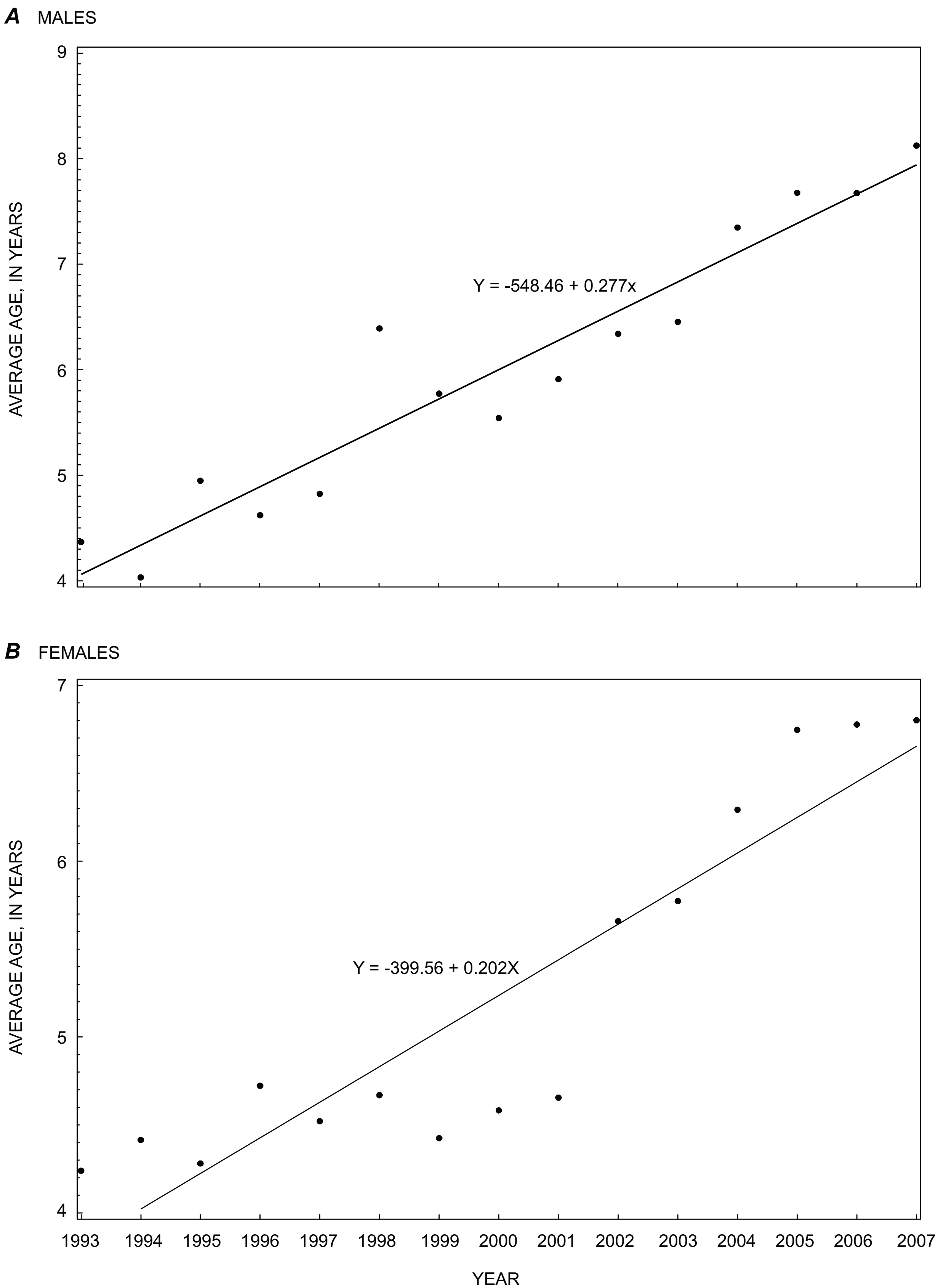


Figure 6. Average age of (*A*) male and (*B*) female wild horses (*Equus caballus*) in the Pryor Mountain herd, 1993–2007.

$P = 0.486$), nor was the difference between the sexes significant for foals ($\chi^2 = 2.500$, $P = 0.114$, $n = 461$). Data from both sexes were therefore pooled for calculations of survival by year.

Survival by year varied from a high of 0.993 in 1993 to a low of 0.780 in 2004 (table 3), when 27 of 28 foals were lost, with predation by mountain lions suspected as the cause (Bureau of Land Management, 2006). For the period of our study, there was a trend toward decreasing foal survival (fig. 7; $P = 0.020$, $R^2 = 0.353$), but there was no trend in survival of animals ≥1 year old ($P = 0.282$, $R^2 = 0.088$). Foal survival increased in the most recent three years of our study, however.

More than one half of the horses that died from 1993 to 2007 were foals, and annual foal survival pooled across years was 0.697 (table 4). Survival increased gradually from age 0 to age 3, remained high through age 15, and then declined gradually. Horses ≥18 years of age were pooled for this analysis because of small sample sizes in these age classes. The oldest animal recorded during the period of study was a male that died at age 26 in 2005. Nine horses lived to be 20 years of age or older, seven of which were males. Four horses (3 males, 1 female) age 20 and 21 were present on the range at the end of our study.

As judged by logistic regression, there was a positive relation between the probability of a foal surviving and the mean (average of summer and fall in a given year) number of members in the band ($n = 393$ foals in 1996–2007; Wald $\chi^2 = 14.964$, odds ratio = 1.244 with 95 percent CI = 1.114–1.390, $P = 0.0001$). Thus, for example, the regression yields a predicted foal survival rate of 0.457 (95 percent CI = 0.351–0.567) for a band size of two, and a predicted survival rate of 0.757 (95 percent CI = 0.688–0.815) for a band size of eight.

Table 3. Annual survival rates of Pryor Mountain wild horses (*Equus caballus*), 1993–2007.

[Horses that were removed were excluded from survival calculations in the year of their removal.]

Year	n	Deaths	Survival
1993	150	1	0.993
1994	123	3	0.976
1995	149	7	0.953
1996	172	7	0.959
1997	154	15	0.903
1998	161	7	0.957
1999	192	27	0.859
2000	202	15	0.926
2001	181	31	0.829
2002	182	28	0.846
2003	177	32	0.819
2004	173	38	0.780
2005	171	19	0.889
2006	163	16	0.902
2007	181	9	0.950
Total	2,531	255	0.899

We also examined survival of foals in relation to parity of their dams—primiparous (those giving birth to their first foal) compared to multiparous (those that had given birth one or more times). For this analysis, we excluded all mares born before 1993 (since parity could not be determined with certainty) and any foals they produced. We also excluded mares that were presumptively contracepted or were present postcontraception (hereafter referred to as treated and posttreated) and foals that they produced. For the remaining subset of foals, there was no difference in survival based on parity of the dam ($n = 189$, $\chi^2 = 0.957$, $P = 0.328$).

Foaling Rates

For ease of comparison with other studies, we calculated foaling rates of mares ≥2 years of age, ≥3 years of age, and ≥4 years of age. Treated and posttreated mares were excluded from these calculations, as were foals born to unknown dams. Pooled across years, productivity was 0.501 foals/mare (range = 0.254–0.705) for mares ≥2 years of age, 0.576 foals/mare (range = 0.300–0.795) for mares ≥3 years of age, and 0.597 foals/mare (range = 0.311–0.795) for mares ≥4 years of age (table 5). Regression analysis showed a slight increase in foaling rate of mares over time (for mares ≥3 years of age, $P = 0.088$), but variability was high ($R^2 = 0.208$).

From 1993 to 2007, 464 of the 481 foals produced in the study area were born to 118 known or highly probable dams (table 6), an average of 3.93 foals per mare. Many of the dams represented in table 6 are still producing foals; thus, the data represent only a single point in time. Twenty-seven dams that each produced seven or more foals accounted for a total of 237 foals, or 51.1 percent of the production by known dams. Of the 54 dams that have been monitored since birth (that is, those born in 1993 or later) and have not been contracepted, 6 (11.1 percent) first produced a foal at age 2, 29 (53.7 percent) at age 3, 14 (25.9 percent) at age 4, 3 (5.6 percent) at age 5, and 2 (3.7 percent) at age 7. The average age at first foaling for these dams was 3.4 years. Age-specific fecundity was 0.048 foals per mare for 2-year-old mares, increased nearly monotonically through age 10, remained high through age 15, and dropped rapidly thereafter (table 7). The maximum age at which any mare gave birth during the study period was 17 years, although that mare was presumptively contracepted and thus is not represented in table 7. A single set of twin foals (both females) was born during the period of our study, to a 6-year-old mare in 1994.

We used logistic regression to examine the probability of foaling in years following a gather as compared to other years for three age groups of mares: 2 years old, 3 years old, and ≥4 years old. Foal production (yes or no) was the dependent variable and year was the independent variable, and we used a specific hypothesis test (or contrast) to compare the mean probabilities of foaling. For this analysis we considered

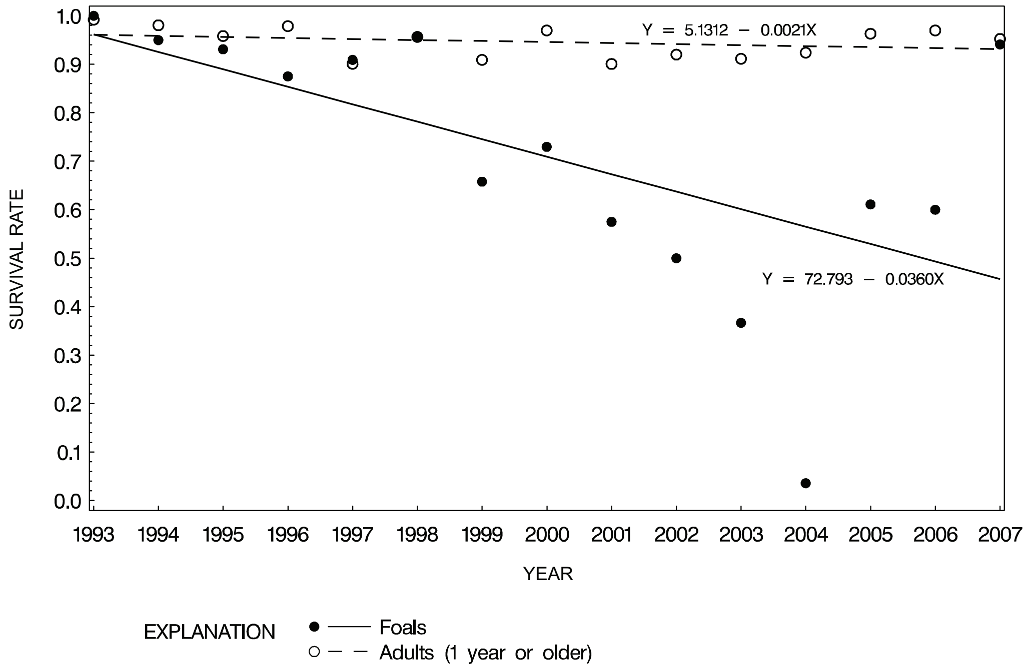


Figure 7. Trend in annual survival of Pryor Mountain wild horses (*Equus caballus*) for adults and foals, 1993–2007.

Table 4. Age-specific survival rates of Pryor Mountain wild horses (*Equus caballus*), 1993–2007.

[Horses that were removed were excluded from survival calculations in the year of their removal.]

Age	Males			Females			Total		
	n	Deaths	Survival	*n*	Deaths	Survival	*n*	Deaths	Survival
0	233	77	0.670	228	60	0.737	[1]465	141	0.697
1	115	9	0.922	137	12	0.912	252	21	0.917
2	91	5	0.945	108	9	0.917	199	14	0.930
3	77	3	0.961	89	2	0.978	166	5	0.970
4	72	1	0.986	84	5	0.941	156	6	0.962
5	70	1	0.986	87	4	0.954	157	5	0.968
6	67	4	0.940	76	3	0.961	143	7	0.951
7	60	2	0.967	73	0	1.000	133	2	0.985
8	60	1	0.983	69	0	1.000	129	1	0.992
9	56	1	0.982	65	1	0.985	121	2	0.984
10	53	0	1.000	57	4	0.930	110	4	0.964
11	49	3	0.939	48	3	0.938	97	6	0.938
12	38	2	0.947	40	5	0.875	78	7	0.910
13	34	1	0.971	32	4	0.875	66	5	0.924
14	33	1	0.970	27	1	0.963	60	2	0.967
15	30	1	0.967	22	2	0.909	52	3	0.942
16	30	1	0.967	18	4	0.778	48	5	0.896
17	26	4	0.846	9	2	0.778	35	6	0.829
≥18	52	12	0.769	12	1	0.917	64	13	0.797
Total	1,246	129	0.896	1,281	122	0.905	[1]2,531	255	0.899

[1] Includes four foals that disappeared before sex could be ascertained.

Table 5. Annual foaling rates of Pryor Mountain wild horse (*Equus caballus*) mares, 1993–2007.

[Treated and posttreated mares in 2004–2007 and foals that they produced were excluded, as were foals born to unknown dams.]

Year	Mares ≥ 2 years old			Mares ≥ 3 years old			Mares ≥ 4 years old		
	Foals	Mares	Foals/mare	Foals	Mares	Foals/mare	Foals	Mares	Foals/mare
1993	15	59	0.254	15	50	0.300	14	45	0.311
1994	32	64	0.500	32	59	0.542	30	50	0.600
1995	23	46	0.500	23	42	0.548	20	38	0.526
1996	32	51	0.627	30	44	0.682	27	40	0.675
1997	34	66	0.515	33	50	0.660	29	43	0.674
1998	23	55	0.418	23	48	0.479	22	43	0.512
1999	38	70	0.543	37	52	0.712	34	46	0.739
2000	37	76	0.487	36	61	0.590	27	44	0.614
2001	40	88	0.455	40	75	0.533	34	60	0.567
2002	32	63	0.508	32	57	0.561	28	53	0.528
2003	30	65	0.462	29	56	0.518	29	50	0.580
2004	28	52	0.538	28	48	0.583	28	48	0.583
2005	31	44	0.705	31	39	0.795	31	39	0.795
2006	23	42	0.548	23	42	0.548	23	37	0.622
2007	21	35	0.600	21	29	0.724	21	29	0.724
Total	439	876	0.501	433	752	0.576	397	665	0.597

Table 6. Total foals born to Pryor Mountain wild horse (*Equus caballus*) mares, 1993–2007.

[Includes only foals born to known dams. Many of the mares represented are still producing foals.]

Foals / Mare	Number of mares	Total foals	Percent of total foals
1	43	43	9.3
2	12	24	5.2
3	10	30	6.5
4	5	20	4.3
5	16	80	17.2
6	5	30	6.5
7	9	63	13.6
8	6	48	10.3
9	4	36	7.8
10	2	20	4.3
11	4	44	9.5
12	1	12	2.6
14	1	14	3.0
Total	118	464	100

only the gathers conducted in 1994, 1997, and 2001 in which most of the family bands were gathered; in 2003, only groups containing animals targeted for removal were gathered, and in 2006 a subset of the herd was captured by bait trapping. For mares 2 or 3 years old, the data were too sparse to allow calculation of the maximum likelihood estimate in the logistic regression (for example, in some years no mares in these age groups produced foals). For mares ≥4 years old the probability of foaling was lower in years following a gather than in other years ($P = 0.03$). The absolute value of this difference was small, however. The mean predicted foaling rate in years following a gather was 0.522 ($n = 3$ years, 134 mares) as opposed to 0.622 ($n = 12$ years, 531 mares) in other years.

We also used logistic regression to examine the probability of a mare foaling as a function of number of members in the band in summer and found a positive relation ($n = 577$ mare-years, Wald $\chi^2 = 24.122$, odds ratio = 1.254 with 95 percent CI = 1.146–1.372, $P < 0.0001$). As an example, the regression yields a predicted probability of foaling of 0.427 (95 percent CI = 0.347–0.511) with a band size of two, as compared to a probability of foaling of 0.743 (95 percent CI = 0.682–0.797) with a band size of eight.

Table 7. Age-specific fecundity of Pryor Mountain wild horse (*Equus caballus*) mares, 1993–2007.

[Treated and posttreated mares in 2004–2007 and foals that they produced were excluded, as were foals born to unknown dams. —, not applicable.]

Age	Number of foals	Number of mares	Foals/mare
0	0	234	0.000
1	0	156	0.000
2	6	124	0.048
3	36	87	0.414
4	34	81	0.420
5	37	72	0.514
6	43	69	0.623
7	41	68	0.603
8	44	70	0.629
9	42	69	0.609
10	43	59	0.729
11	31	48	0.646
12	28	40	0.700
13	22	30	0.733
14	14	23	0.609
15	14	20	0.700
16	4	9	0.444
17	0	4	0.000
≥18	0	3	0.000
Total	439	1,266	—

In addition, we compared the probability of foaling in the next year for primiparous and multiparous mares. Primiparous females were less likely to foal ($\chi^2 = 27.29$, $P < 0.0001$) in the year following their first foal (proportion foaling = 0.26, n = 43) than were multiparous females (proportion foaling = 0.72, n = 110). On the other hand, multiparous females were somewhat more likely to foal ($\chi^2 = 2.60$, $P = 0.107$) if they foaled in the previous year (proportion foaling = 0.72, n = 110) than if they did not foal in the previous year (proportion foaling = 0.61, n = 76).

Harem Stallions and Band Composition

During the 12 years (1996–2007) for which information was available, the number of bands varied from 29 to 38 (table 8), with an increasing trend through time (least squares regression, $P = 0.012$, $R^2 = 0.48$). There was no relation, however, between number of bands and band size (least squares regression, $P = 0.88$); that is, band size did not decline significantly as the number of bands increased. Bands were held by 64 different stallions during this period, the youngest being age 3 and the oldest being age 23 (fig. 8). The vast majority of bands, however, were held by stallions aged 5–17 (fig. 8; n = 399). A single stallion gained his first harem at age 3, but 18 of the 29 harem stallions (62.1 percent) for which we have records since birth (born in 1993 or later) acquired their first harem at age 5 or 6 (fig. 9). As might be expected from the increasing age of all males in the herd (fig. 6A), the average age of harem stallions also increased through time (table 8) (least squares regression, $P < 0.0001$, $R^2 = 0.82$).

Harems with as many as six breeding-age females (≥2 years old) were recorded occasionally, but more than 86 percent of the harems contained 1–3 breeding-age females (fig. 10; n = 399). Harem size varied by age of stallion, increasing from age 3 to about age 11 and declining thereafter (fig. 11; n = 399). There were four somewhat anomalous cases in which a male was listed as a harem stallion but the harem size was zero (fig. 10). In two of these cases there were no harem members at all when the observations were recorded. These represent harems in flux, with one or more mares sometimes with the stallion and sometimes not. In the other two cases the only band members were the harem stallion and a yearling female, and we counted only females ≥2 years old in our calculations of harem size.

Of 399 band-year combinations for which we have observations, only 25 (6.3 percent) involved satellite stallions, which we defined as a male ≥5 years old that was associated with a harem stallion. Three pairs of stallions that lived in the same band for 6, 6, and 5 years accounted for 17 of these 25 associations. The remaining eight associations lasted only 1 or 2 years. In only one case were three stallions involved, and that association was maintained for a year or less. Two of the long-term associations (≥5 years) involved stallions that were the same age (7 through 12 years of age) or 1 year apart (harem stallion 5 through 9 years of age; satellite stallion 6 through 10 years of age). The third long-term association included a harem stallion 17 through 22 years of age and a satellite stallion 7 through 12 years of age. The mean number of mares (≥2 years old) did not differ between single- and multistallion bands (2.2 mares in both cases), although 5 of the 25 multistallion bands had 4–6 mares.

Of the 180 male foals born from 1993 through 2003 (those born after 2003 would have been only 3 years old or younger at the end of our study), 124 died or were removed before reaching age 4 and thus had virtually no chance of becoming a harem stallion. An additional 17 died or were removed at age 4 or 5 and thus had a much reduced chance of becoming a harem stallion. Three died at age 6, and two were removed at age 7 without having held a harem. Of the original 180 male foals born, 29 became harem stallions. Of the remaining five animals, two were still bachelors at the end of our study (ages 4 and 6 in 2007), two briefly held harems (at ages 4 and 8) but reverted to bachelor status, and one was a satellite stallion in his natal band (at age 5).

Table 8. Number of wild horse (*Equus caballus*) bands, mean age of harem stallions, mean harem size (mares ≥2 years old), and mean band size (all members) in the Pryor Mountain herd, 1996–2007.

[—, not applicable.]

Year	Number of bands	Mean age of harem stallions	Mean harem size	Mean band size
1996	29	8.76	1.90	5.14
1997	31	9.68	2.06	5.23
1998	31	10.26	1.87	4.90
1999	31	10.71	2.68	5.74
2000	31	11.10	2.68	5.87
2001	38	10.71	2.39	5.24
2002	34	11.06	1.94	4.59
2003	36	10.89	2.06	4.53
2004	34	11.21	2.06	4.03
2005	35	12.11	2.11	4.20
2006	35	13.00	2.20	4.66
2007	34	11.97	2.38	5.18
Total	399	—	—	—

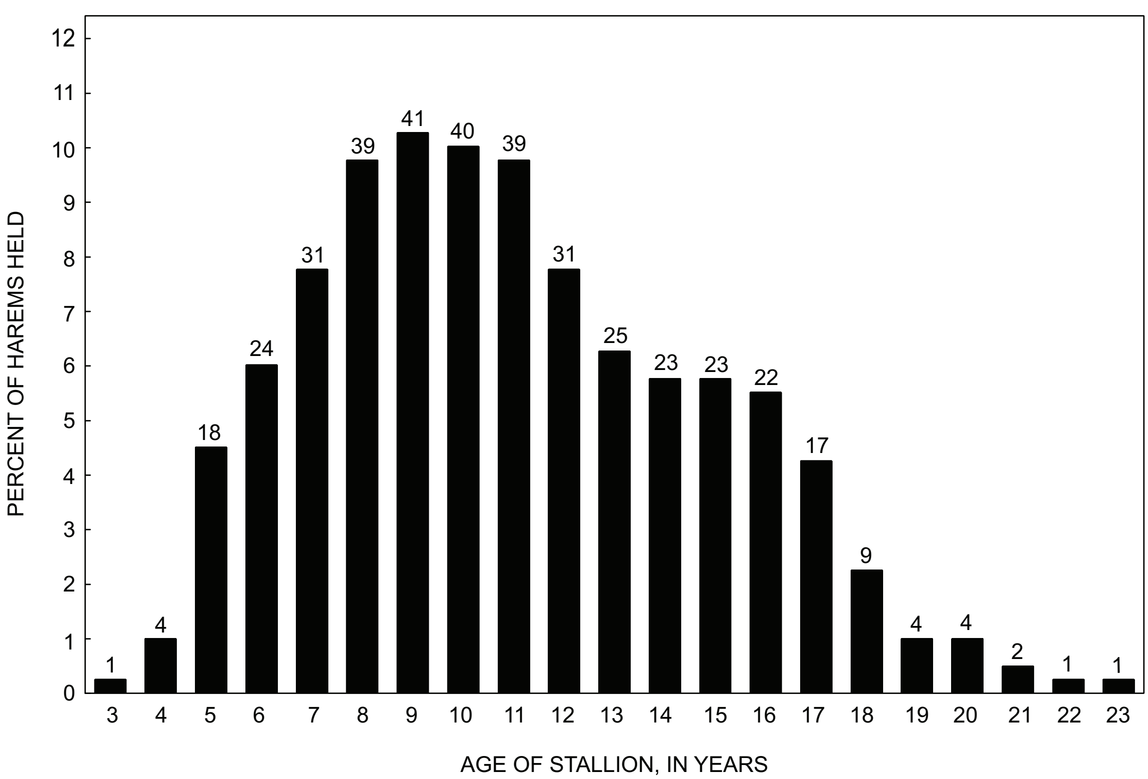


Figure 8. Age of wild horse (*Equus caballus*) stallions holding harems in the Pryor Mountain herd, 1996–2007. Values above the bars are number of harems.

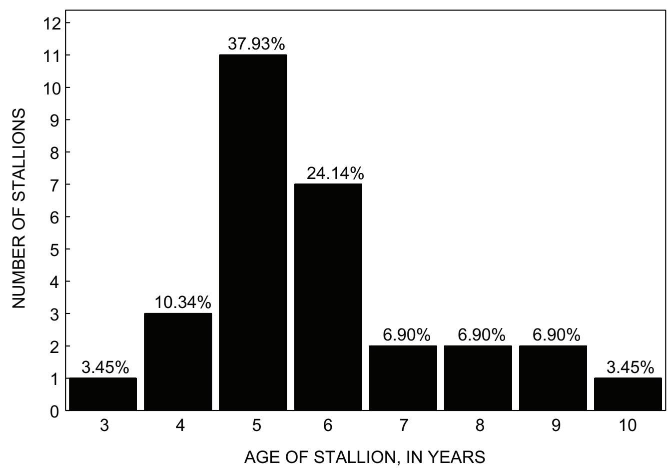


Figure 9. Age at which wild horse (*Equus caballus*) stallions first held a harem in the Pryor Mountain herd, 1996–2007. Values above the bars are percent of the total stallions represented on the chart.

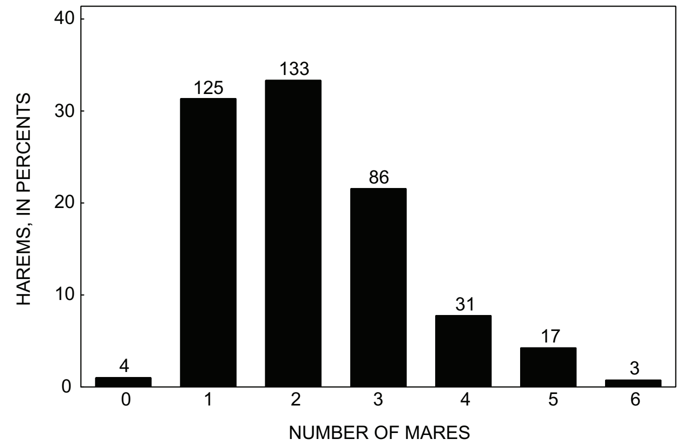


Figure 10. Frequency distribution of wild horse (*Equus caballus*) harem size in the Pryor Mountain herd, 1996–2007. Values above the bars are number of harems.

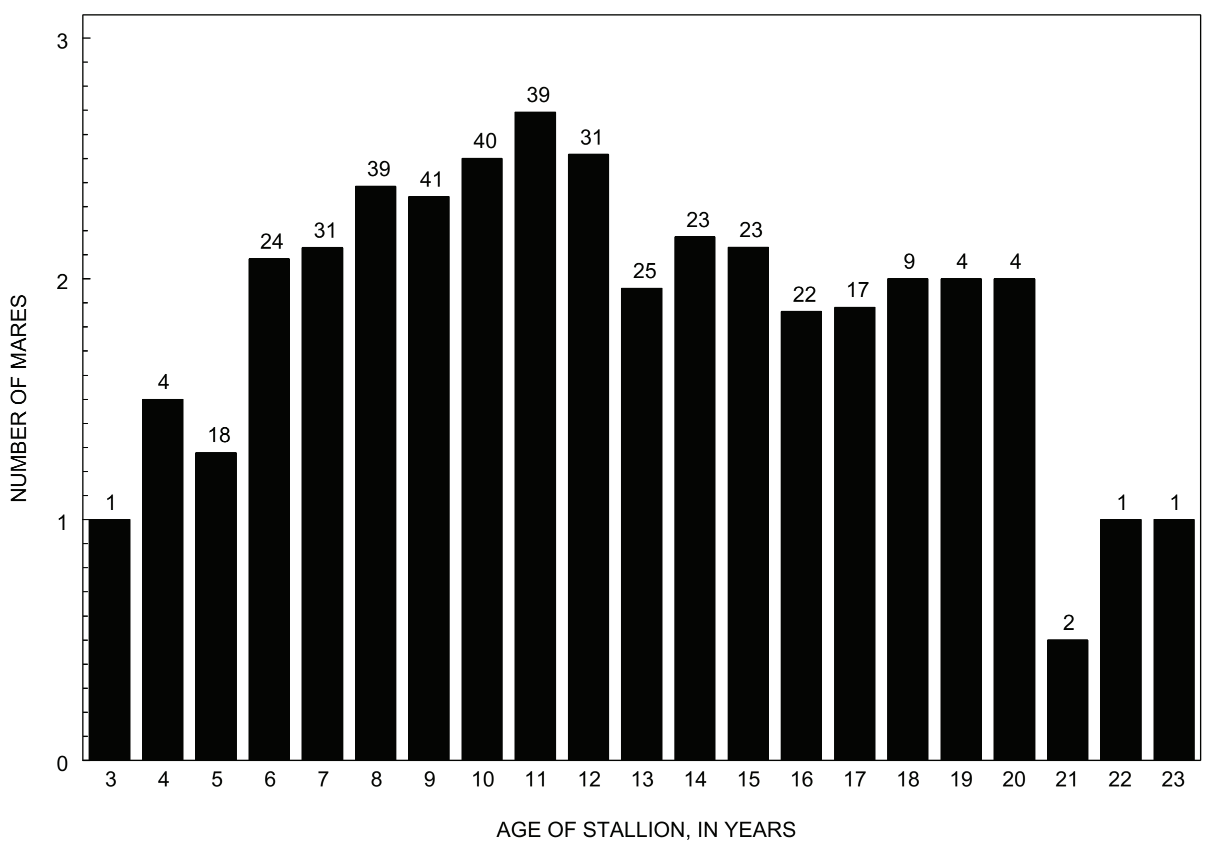


Figure 11. Mean number of wild horse (*Equus caballus*) mares held relative to age of harem stallions in the Pryor Mountain herd, 1996–2007. Values above the bars are number of harems.

Bachelors

The number of bachelor males in a wild horse herd changes through the course of a year, as young males are expelled from or leave bands, middle-aged males (formerly bachelors) gain bands, and older males gain and lose bands. In the Pryor Mountain herd, the number of bachelor males in summer (early to mid-June) varied between 16 and 36 during the period of study (fig. 12). The largest interannual change occurred between 1997 and 1998, in part because of the removal of 18 bachelors in fall 1997. In total, 40 bachelors were removed from the herd from 1996 through 2007. Pooled across years, 188 of 328 bachelors (57.3 percent) were 2 through 5 years of age (fig. 13).

To examine the question of when young stallions leave their natal bands and become bachelors, we used a subset of our data that included all males born in 1996 or later (thus ensuring that we had complete information on their band associations since birth). Of the 59 males that were born in 1996 or later and reached bachelor status (many died or were removed before becoming bachelors, others were born too late in the study period to have an opportunity to become bachelors), 4 (6.8 percent) became bachelors at age 1 (though one subsequently returned to his natal band), 32 (54.2 percent) at age 2, 13 (22.0 percent) at age 3, 7 (11.9 percent) at age 4, and 3 (5.1 percent) at age 5.

Population Regulation

Density Dependence

Regression analyses showed no relation between the foaling rate of mares ≥3 years of age and population size in either the current year or the previous year ($P \geq 0.143$). Foaling rate of 2-year-old mares may have declined somewhat with larger population in the previous year ($n = 13$ years, $P = 0.090$), but variability was high ($R^2 = 0.239$). Other young age classes (3–5 years) did not show similar relations, nor did combinations of these age classes.

Overall herd survival was related negatively to the previous year's postfoaling population (fig. 14A) ($n = 23$ years, $P = 0.006$), but there was a great deal of variability ($R^2 = 0.305$). Foal survival, however, was unrelated to population size ($n = 13$ years, $P > 0.15$). There also was a relation between population growth rate and the previous year's postfoaling population (fig. 14B) ($n = 23$ years, $P = 0.002$, $R^2 = 0.382$). This is perhaps not surprising, because survival rate is an important component of population growth rate.

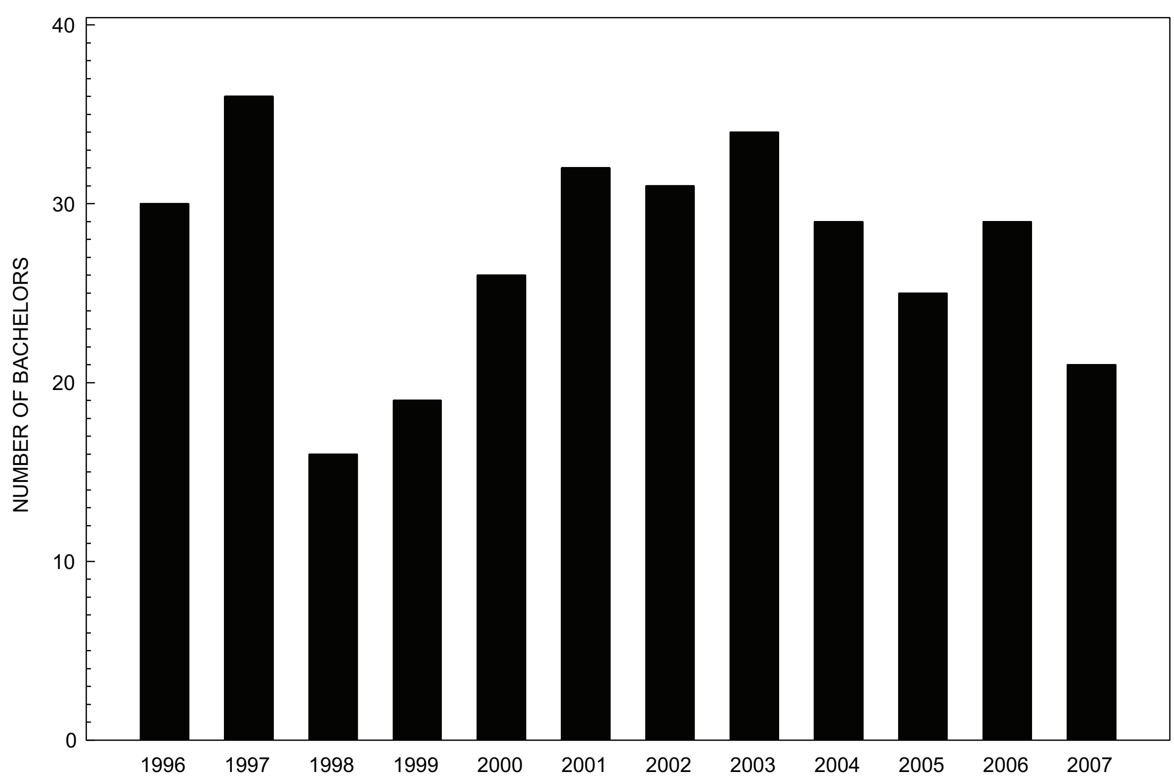


Figure 12. Number of bachelor wild horses (*Equus caballus*) in the Pryor Mountain herd, 1996–2007.

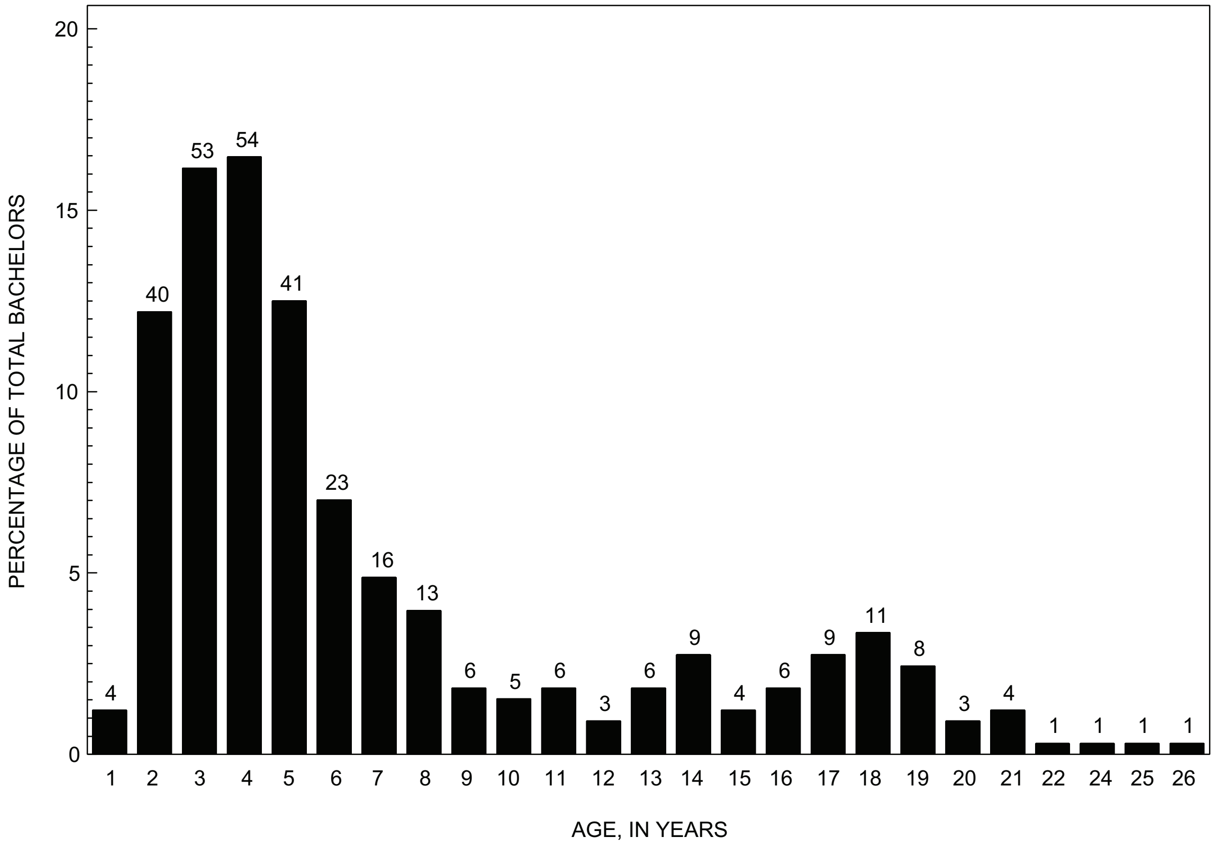


Figure 13. Age distribution of bachelor wild horses (*Equus caballus*) in the Pryor Mountain herd, 1996–2007. Values above the bars are number of bachelors.

Weather

None of the covariates that we used entered the stepwise multiple regression model for herd survival ($P > 0.15$; table 9). For foal survival, both summer and winter precipitation in the current year met the criterion for entry in the model ($P < 0.15$), and both were related positively to foal survival. In the case of winter precipitation in the current year, the positive relation was contradictory to our hypothesis. In combination, these parameters accounted for about 81 percent of the variability in foal survival. In terms of mare foaling rate, only the mean of the monthly average minimum temperature in the previous winter entered the model, and the relation accounted for only about 15 percent of the variability.

Discussion

Population Size and Growth

From 1993 to 2007, the prefoaling (adult) population averaged about 149 animals, only slightly more than the target population of ≈140 adults established on the basis of genetic considerations (Bureau of Land Management, 2006). Removals and a declining survival rate for foals appear to have been the primary factors keeping the population at this level. Contraception also may have played a role if it prevented the birth of any foals. However, it seems likely that the effect of the contraceptive program on population growth was small, given that relatively few mares were treated and that those mares were not in the most productive age classes.

The subject of population growth in wild horse populations has been controversial since early reports (for example, Cook, 1975) of rates as high as 30 percent annually. Other investigators challenged the accuracy of such estimates, and several used simulation modeling in combination with the scant data then available for wild horses and extrapolation of data from other ungulates to show that growth rates of 20–30 percent seemed highly unlikely given apparently reasonable assumptions about model parameters (Conley, 1979; Wolfe, 1980). Frei and others (1979) suggested that the apparently inflated growth rates might be an artifact of improved aerial census techniques and greater experience of observers.

As additional data were accumulated, however, it became apparent that initial assumptions regarding population parameters, particularly survival rates and age of mares at first reproduction, were probably conservative for many wild horse herds (Wolfe, 1986). Eberhardt and others (1982) calculated rates of increase of 20 and 22 percent for two herds

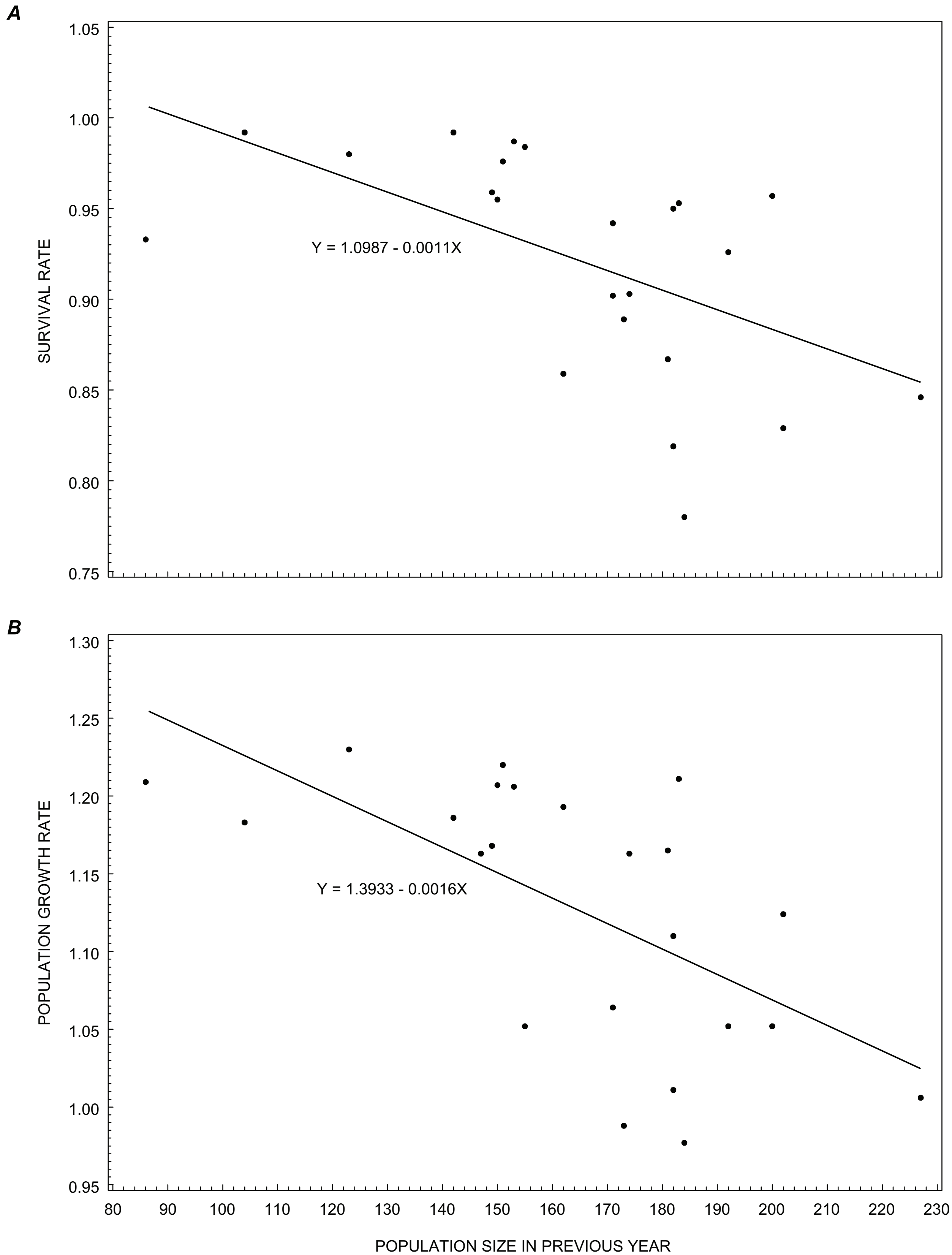


Figure 14. Relation of (*A*) survival and (*B*) population growth rate to the previous year's population for wild horses (*Equus caballus*) in the Pryor Mountain herd. Includes data from this study and from Garrott and Taylor (1990), excepting the abnormally severe winter of 1977–1978.

Table 9. Results of stepwise multiple regressions between wild horse (*Equus caballus*) herd survival, foal survival, and foaling rate (mares ≥3 years of age) and various weather parameters for the Pryor Mountain herd.

[Includes data from Garrott and Taylor (1990) and this study for herd survival and mare foaling rate, but only from this study for foal survival. *n*, sample size; SE, standard error of the estimate; R^2, coefficient of determination; *P*, probability; —, no variables entered the model; SUMP, summer precipitation in the current year; WINP, winter precipitation in the current year; LMNT, average monthly minimum temperature (December–February) in the previous year.]

Population parameter	*n* (years)	Covariate	Parameter estimate	SE	Partial R^2	Model R^2	*P*
Herd survival	19	—	—	—	—	—	—
Foal survival	10	SUMP	0.164	0.041	0.71	0.71	0.002
		WINP	0.117	0.059	0.10	0.81	0.090
Foaling rate	19	LMNT	0.008	0.005	0.15	0.15	0.105

in Oregon and, by comparing pre- and postremoval populations with known removals, showed that the aerial counts used to derive the growth rates must have been reasonably accurate. Berger (1986, p. 76), based on a 5-year study of horses in the Granite Range of Nevada, reported an average annual growth rate of 31 percent. [Note, however, that Berger (1986, p. 77) also reported an exponential growth rate of 0.188, which is equivalent to a finite growth rate of only 20.7 percent annually.] Wolfe (1986), using data from an unspecified number of BLM herds (>40,000 animals), calculated an annual growth rate of 14 percent for the period 1981–1983 and 15 percent for 1983–1985. Garrott and others (1991b) reported an unweighted mean growth rate of 21 percent (range = 15–27 percent) for 12 western herds. High rates of population growth are not limited to western horse populations. Franke Stevens (1990), for example, reported that the horse population at Rachel Carson National Estuary, made up of four small islands off the coast of North Carolina, increased from 44 animals in 1984 to 68 animals in 1986, from which we calculated an annual growth rate of 24.3 percent.

Reported growth rates of wild horse herds have not been universally high, however. Keiper and Houpt (1984), for example, stated that the horse population on Assateague Island National Seashore grew from 42 to 80 animals during the period 1975 to 1982, which represents an average annual growth rate of 9.6 percent. Goodloe and others (2000) found an average annual growth rate of 4.3 percent (range = 3.0–6.8 percent) for horses on Cumberland Island, Georgia, from 1986 to 1990 and suggested that the low rates likely were the result of density-dependent response to limited forage. Greger and Romney (1999), studying a horse population at the Nevada Test Site (now the Nevada Wild Horse Range), found an average growth rate of -7.0 percent, which they attributed to very low foal survival as a result of predation by mountain lions.

The first multiyear study of horses at Pryor Mountain was that of Perkins and others (1979). While they did not calculate population growth rates, they presented information sufficient to do so for two years. Based on information in their table 1, we calculated growth rates of 7.5 and 16.0 percent for 1976 and 1977, respectively, for the postfoaling population. Garrott and Taylor (1990) reported growth rates at Pryor Mountain for 1977–1986 with a mean of 11.9 percent, but 17.8 percent if a year with heavy winter mortality (51 percent of the population died) was excluded. Singer and others (2000) found a mean growth rate of 17.6 percent at Pryor Mountain from 1992–1997.

Our mean annual growth rate (9.6 percent; 10.5 percent if the year of heavy foal loss is excluded) for the period 1993–2007 is thus toward the lower end of the range reported for the Pryor Mountain and other herds. The declining trend in growth rate through time appears to be a result of decreasing survival of foals, though both foal survival (2005–2007) and growth rate (2006–2007) increased in recent years. Contraception also may have played a small role in reducing the average growth rate, though it is difficult to separate the effects of multiple factors.

Sex and Age Ratios

Studies at Pryor Mountain and elsewhere have found foal sex ratios favoring both males and females, with the pattern sometimes switching for the same herd in different time periods. At Pryor Mountain, for example, Feist and McCullough (1975) reported that 54.3 percent of 35 foals were males, Singer and others (2000) found that 58.3 percent of "surviving" foals were males (sample size not given), but Perkins and others (1979) found 48.5 percent males among 103 foals. Similarly, Keiper (1979) reported 52.6 percent males among 190 foals on Assateague Island, but Keiper and Houpt (1984) found 46.6 percent males in 103 foals born at the same location. In many of these studies with relatively small sample sizes, of course, the results did not differ significantly from parity, which also is true of most studies with larger samples, including ours. Speelman and others (1944), for example, found 49.4 percent males in 568 foals born to domestic mares raised under range conditions in Montana. Garrott (1991), who studied the sex ratio of more than 10,000 foals removed from 74 BLM herds, found no significant difference from parity in 65 of those herds; the foal sex ratio favored females in seven herds and males in two herds. Interestingly, one exception to this pattern is found in the study by Garrott and Taylor (1990) at Pryor Mountain, who reported a sex ratio of 39.7 percent males ($P < 0.001$) in a sample of 330 foals from 1972 to 1986. Garrott and Taylor offered no explanation for this result, but they did comment that other data from their study might suggest low forage availability. Other investigators have hypothesized that females in poor condition (as through low forage availability) should produce fewer male offspring (Trivers and Willard, 1973).

The foal sex ratio did not differ from parity during the course of our study, and there was no overall difference in survival between the sexes. Thus, apart from minor variations resulting from each foal crop entering the population, consistent departures from a 50:50 sex ratio are the result of removals. This is evidenced by the fact that the largest interannual changes in sex ratio occurred following the larger removals. The drop in the proportion of males in the herd in 2007 was because of the removal of 14 males and 5 females in 2006, but also because natural mortality in 2006 consisted of 13 males and only 3 females. The increasing age of the herd also is mostly explained by removals; for all animals removed during the period of study, the average age was 3.2 years for females and 2.7 years for males. This is in keeping with BLM's management strategy of retaining harem stallions and core breeding-age mares (6–10 years) on the range (Bureau of Land Management, 2006). Low survival of foals in 2003 (36.7 percent) and 2004 (3.6 percent) also reduced the proportion of young animals in the herd and thus increased the average age. To the extent that it prevented any mares from foaling, the contraceptive program also would have contributed to increasing age of the herd, but the magnitude of any such effect is unknown.

Survival

The most striking feature of the survival data from our study is the general decline in foal survival in 1993–2004, followed by an apparent increase in the next 3 years. It would be tempting to attribute at least the declining part of this pattern to increased observational effort and hence increased detection of neonatal loss. We do not believe this to be the case, however, because there was no trend in the number of foals produced through time (linear least squares regression, $R^2 = 0.06$, $P = 0.38$), and because all animals present in the herd in 1993 and all foals born since then have been accounted for. Predation by mountain lions is suspected as the cause of low foal survival in 2004 and perhaps in 2003, though only four foals were confirmed to have been taken by mountain lions (Bureau of Land Management, 2006). Three mountain lions were removed from the area by hunters in winter 2004–2005 (Bureau of Land Management, 2006), which might in part explain the increase in foal survival observed in 2005–2007. It also seems possible that predation began on a smaller scale much earlier than 2003, but we know of no evidence to support this hypothesis. Predation by mountain lions has been shown to be an important factor in foal mortality in at least one herd (Turner and Morrison, 2001) and has been implicated in others (Salter, 1979; Greger and Romney, 1999). Wolves (*Canis lupus*), when present, are also suspected of preying on wild horses (Salter, 1979; Oom and Santos-Reis, 1986). Another possible contributor to the observed pattern in foal survival is drought. The drought began in 1999, the same year as the first real drop in foal survival, and was somewhat ameliorated in 2005 and 2007, at which time foal survival increased. The results of our regression analyses between precipitation and foal survival would seem to support this explanation. On the other hand, the initial response to reduced forage availability would likely be a decline in body condition of mares and foals, and such a decline was not observed during the early years of the drought (LC-M).

Overall, survival rates from our study for 1993–2007 are similar to those reported by Perkins and others (1979), but lower than those reported by Garrott and Taylor (1990) and Singer and others (2000) for the same study area (table 10). The foal survival rate reported by Garrott and Taylor, however, probably is an overestimate because it covers the period from midsummer to midsummer; neonatal mortality, which often constitutes the majority of foal mortality (Boyd, 1979; Keiper, 1979; Berger, 1986; Monard and others, 1997; Goodloe and others, 2000), likely was missed. Age of the herd also may account for some of the difference between our survival rate and that calculated by Garrott and Taylor (1990). At the end of their study in 1986, about 22 percent of the herd was ≥11 years of age, whereas the comparable number for 2007 was 39 percent. Perkins and others (1979) and Singer and others (2000) did not provide sufficiently detailed age data to make similar comparisons. Survival rates from our study were also moderate compared to those reported previously for other horse herds in North America (table 10).

Relations between foal survival and band size have not often been reported in the literature on wild horses, and the few available results are equivocal. We found that foals from larger bands tended to survive better than those from smaller bands. Working on Camargue horses in France, Feh (1999) found that there was less foal mortality in bands with an alliance of two stallions (3.2 percent), than in single-stallion bands (22.0 percent). Multiple stallions often are associated with larger bands. Cameron and others (2003), on the other hand, found that among Kaimanawa horses in New Zealand more foals died in multistallion bands (survival = 80 percent, $n = 30$) than in single-stallion bands (survival = 94 percent, $n = 50$), but the difference was not quite significant ($P = 0.056$). Similarly, evidence for a relation between mare age or parity and foal survival is equivocal. We found no relation between foal survival and parity of the mare. Keiper and Houpt (1984) reached the same conclusion, but only 10 foals died in the course of their study. In contrast, Cameron and

Table 10. Survival rates reported for North American wild horse (*Equus caballus*) herds.

[Data are arranged in order of increasing foal survival. Sample size (n), when available, is given in parentheses. NA, data not available; PMWHR, Pryor Mountain Wild Horse Range.]

Source and location	Survival rate (n)				Comments
	Foals	Yearlings	Adults	Herd	
Greger and Romney (1999), NV	0.12	NA	NA	NA	Foal survival is a mean for 8 years and is a maximum estimate because some neonatal mortality probably went undetected.
Turner and Morrison (2001), CA and NV	0.32	0.88	0.92	NA	All data represent means for 10 years.
Goodloe and others (2000), GA	0.600 (105)	NA	0.923 (263)	NA	Adult rate is for mares only, probably ≥3 years old.
This study, (PMWHR)	0.697 (465)	0.917 (252)	0.949 (1,814)	0.899 (2,531)	
Perkins and others (1979), PMWHR	0.75	NA	NA	0.903 (579)	Foal survival is a mean for 4 years. Herd survival is a weighted mean calculated from Table 1, Perkins and others (1979).
Boyd (1979), WY	0.824 (51)	NA	NA	NA	Data for 1978 only.
Singer and others (2000), PMWHR	0.87	NA	NA	Males, 0.965 Females, 0.975	Not clear that data reported for the herd actually includes all animals.
Siniff and others (1986), Pine Nut, NV	0.875 (40)	NA	0.972 (72)	NA	Adult rate is a weighted mean for 2 years representing only mares, probably ≥2 years old
Siniff and others (1986), Pah Rah, NV	0.877 (73)	NA	0.975 (81)	NA	Adult rate is a weighted mean for 2 years representing only mares, probably ≥2 years old
Keiper and Houpt (1984), MD and VA	0.883 (86)	NA	NA	NA	Foal rate is a weighted mean for 8 years.
Pellegrini (1971), NV	0.905 (21)	NA	NA	NA	Data are for 1969. However, in 1968 no foals were observed, and in 1970 only one foal was observed.
Berger (1986), NV	0.917 (120)	0.969 (64)	0.951 (329)	0.945 (513)	Herd rate calculated from data on the three age groups.
Garrott and Taylor (1990), PMWHR	0.968 (249)	0.977 (173)	0.962 (865)	0.965 (1,287)	Excludes data from a severe winter. Adult and herd rates calculated from Table 2, Garrott and Taylor (1990). Foal rate measured from midsummer to midsummer and may be an overestimate.

others (2000) found significant differences in mortality of foals born to mares 3–5 years old (18 percent mortality), 6–8 years old (3 percent), and ≥9 years old (9 percent).

Foaling Rates

Foaling rates of mares at Pryor Mountain most often have been low to moderate when compared to those reported for other North American herds (table 11). In fact, the rate of 0.432 foals/mare for mares ≥4 years of age calculated from Feist and McCullough (1975) is among the lowest for any herd, although their study was primarily behavioral and lasted only 1 year. In addition, they attempted to classify mares aged 1, 2–3, and ≥4 years without the benefit of examining tooth eruption and wear, and they admit that some classification errors probably occurred. If there was a tendency to misclassify 3-year-old mares as being ≥4 years old, the resulting foaling rate would be biased low. Garrott and Taylor (1990), however, reported similarly low rates, and mares in their study were aged by dental characteristics. As noted above, Garrott and Taylor (1990) reported on foals present in midsummer; some neonatal loss likely was missed, which would tend to bias foaling rates low. Perkins and others (1979) did not report age-specific foaling rates of mares, but for the three years of their study for which data are complete (1975–1977), the foal crop was 15.1 percent of the prefoaling population (weighted average, n = 411 animals ≥1 year of age). The comparable value during our study was 21.6 percent (table 1, n = 2,232 animals). These values, of course, are affected by the sex and age structure of the herd. Similarly, Singer and others (2000) did not report age-specific foaling rates in sufficient detail to be included in table 11. They did, however, show rates of 0.107 foals/mare for mares of age 2, 0.54 for age 3, 0.67 for ages 4–11, and 0.46 for ages ≥12 in the period 1992–1997. Comparable values from our study (1993–2007) were 0.048, 0.414, 0.588, and 0.636, respectively. Thus, it appears that foaling rates at Pryor Mountain have varied considerably through time, with those from our study being intermediate.

Several investigators have suggested that forage availability can affect the condition of feral mares and thus foaling rates (Green and Green, 1977: Nelson, 1978; Berger, 1986; Siniff and others, 1986; Garrott and Taylor, 1990). Hall (1972) described range conditions at Pryor Mountain as being poor to extremely poor through much of the area. Feist and McCullough (1975) reported a low foaling rate in 1971, as did Garrott and Taylor (1990) in the first 3 years (1976–1978) of their study. Furthermore, Garrott and Taylor (1990) suggested that low foaling rates likely were a result of poor forage, also noting that the foaling rate increased markedly in 1979 following loss of 51 percent of the herd in the severe winter of 1977–1978. Singer and others (2000) reported somewhat higher foaling rates than were observed in the earlier studies and also noted that former managers who visited Pryor Mountain in 1997 remarked about the overall improvement in "plant condition." Again, our values for foaling rate appear to be intermediate. It also may be relevant that mean annual precipitation in the biological years covered by the study of Singer and others (17.55 cm; 1992–1997, all years included regardless of missing data) was greater than that for the remainder of our study (13.79 cm; 1998–2007).

In addition to its effects on foaling rates of adult animals, forage availability may affect age of first reproduction by mares. Feist and McCullough (1975), Perkins and others (1979), and Garrott and Taylor (1990) all worked at times when forage production may have been poor at Pryor Mountain and all found that mares first foaled at age 3. Singer and others (2000), on the other hand, at a time when forage production may have been somewhat better, found that 10.7 percent of 2-year-old mares produced foals; the comparable value from our study was 4.8 percent. First foaling at age 2 (Salter and Hudson, 1982; Berger, 1986; Lucas and others, 1991) and age 3 (Boyd, 1979; Keiper and Houpt, 1984; Goodloe and others, 2000) has been reported for other herds, with the rate for 2-year-olds varying both among herds and within herds in different years (Garrott and others, 1991a). In at least two studies, low foaling rates in young mares have been attributed to high rates of fetal and neonatal loss (Lucas and others, 1991; Linklater and others, 2004).

Other factors that have been shown or hypothesized to affect foaling rate include gathers, band stability, and parturition history of the mare. In the case of gathers, we found a small but statistically significant effect, with foaling rate being lower in years following gathers. It must be remembered, however, that we did not design an experiment specifically to test a hypothesis about the effect of gathers. In particular, we had to assume that the majority of mares were affected by the gather (either actually moved into a trap or significantly disturbed by helicopter activity) in each of the three years that we considered to be gather years. Given the nature of the gathers in those three years, we believe that such an assumption is reasonable. Other evidence for an effect of gathers on foaling rate is equivocal. Hansen and Mosley (2000) studied two herds, one in Idaho and one in Wyoming, and found no difference in foaling rate between mares ungathered, gathered and released, or gathered and adopted. The ungathered samples were small, however, consisting of only 14 mares in each herd. Ashley and Holcombe (2001), on the other hand, found that in one of the two years of their study, ungathered mares foaled at a higher rate than did those that were gathered and released or gathered and removed. They found no evidence for an effect of a gather in the other year.

Evidence for an effect of band stability on mare foaling rate is more consistent. Berger (1983) found that mares in bands with resident stallions produced foals at a higher rate than those in bands taken over by a new stallion. Kaseda and others (1995), working on Misaki horses in Japan, reported that mares in "stable consort relationships" had higher reproductive success than those that changed stallions. Similarly, Goodloe and others (2000) found that mares that changed bands had a lower probability of foaling than those that did

Table 11. Foaling rates reported for North American wild horse (*Equus caballus*) herds.

[To the extent possible, data are arranged in order of increasing production by mares ≥3 years old. Sample size (*n*), when available, is given in parentheses. NA, data not available; PMWHR, Pryor Mountain Wild Horse Range.]

Source and location	Foals/mare (*n*) Mares ≥2 years old	Mares ≥3 years old	Mares ≥4 years old	Comments
Siniff and others (1986), Pine Nut, NV	0.385 (104)	NA	NA	Combined data for 2 years. Age of mares inferred from other information.
Feist and McCullough (1975), PMWHR	NA	NA	0.432 (81)	Some animals may have been aged incorrectly. Includes two foals born to 3-year-old mares.
Greger and Romney (1999), NV	NA	0.360	NA	Unweighted mean for 5 years.
Garrott and Taylor (1990), PMWHR	NA	0.488 (600)	NA	Calculated from Table 3, Garrott and Taylor (1990).
Wolfe and others (1989), NV	0.432 (206)	NA	NA	Calculated from Table 5, Wolf and others (1989), for lactating mares.
Boyd (1979), WY, 1979	NA	0.526	0.545	Sample sizes not given.
Turner and others (1992), CA and NV	NA	0.537	NA	Unweighted mean for 6 years.
Keiper and Houpt (1984), MD	NA	0.571	NA	Unweighted mean for 8 years.
Nelson, (1978), NM	NA	NA	0.553 (38)	
This study, PMWHR	0.501 (876)	0.576 (752)	0.597 (665)	
Keiper (1979), MD	NA	0.614	NA	Unweighted mean for 5 years.
Salter and Hudson (1982), Alberta	0.521 (71)	0.621 (58)	NA	Calculated from Table I, Salter and Hudson (1982).
Seal and Plotka (1983), OR	NA	0.626 (99)	NA	Foaling rate based on lactating mares from Table 4, Ashley and Holcombe (2001).
Ashley and Holcombe (2001), Granite Range, NV, 1994	NA	NA	0.714 (28)	Calculated only for ungathered horses.
Ashley and Holcombe (2001), Granite Range, NV, 1997	NA	NA	0.741 (54)	Calculated only for ungathered horses. Age of mares inferred from other information.
Wolfe and others (1989), WY	0.535 (172)	NA	NA	Calculated from Table 5, Wolfe and others (1989), for lactating mares.
Garrott and others (1991a), NV	0.584 (901)	NA	NA	Foaling rate based on lactating mares gathered in June. Calculated from Table 1, Garrott and others (1991a).
Keiper (1979), VA	NA	0.744	NA	Unweighted mean for 4 years.
Ashley and Holcombe (2001), Garfield Flat, NV, 1997	NA	NA	0.824 (17)	Calculated only for ungathered horses. Age of mares inferred from other information.
Boyd (1979), WY, 1978	NA	0.781	0.863	Sample sizes not given.
Siniff and others (1986), Pah Rah, NV	0.670 (109)	NA	NA	Combined data for 2 years. Age of mares inferred from other information.

not. Data on mare interchanges are available from the Pryor Mountain herd, but have not yet been analyzed.

The question of whether parturition history of the mare affects foaling rate has been of interest since early investigators reported what they perceived to be a tendency to foal in alternate years (Green and Green, 1977; Nelson, 1978). This question has been addressed in a number of ways and results have varied. Seal and Plotka (1983) found that 68.4 percent (n = 76) of pregnant mares also had a foal at their side or were lactating, and Wolfe and others (1989) found no difference in pregnancy rates for lactating and nonlactating mares in six different populations. Neither of these studies, however, addressed the question of whether lactating and nonlactating mares are equally successful in bringing their pregnancies to term. On Assateague Island, 10.2 percent of 49 mares followed for 4 years foaled in alternate years, whereas 55.1 percent foaled in either 3 or 4 years (Keiper, 1979). Similarly, Keiper and Houpt (1984) could not see any tendency to foal in alternate years among 14 mares followed for 8 years. At Pryor Mountain, in both our study and that of Garrott and Taylor (1990), primiparous mares were less likely to foal in the next year than were multiparous mares. Cameron and Linklater (2000), on the other hand, found that the probability of foaling in a given year was reduced significantly if the mare had a foal in the previous year. Thus, while not universal, it appears that foaling in one year can sometimes reduce the probability of foaling in the subsequent year, particularly in primiparous mares.

Harem Stallions and Band Composition

Comparisons among band or harem sizes reported by various investigators are hampered by inconsistencies in defining what constitutes a harem member, or failure to do so at all. We defined harem members as mares ≥2 years of age, and found that the mean harem size was 2.2 mares with a range of 1.9 to 2.7 over 12 years; the number of bands ranged from 29 to 38. In other studies at Pryor Mountain, Feist and McCullough (1975) reported only average band size (5.0 including all members, not just mares), but they found 44 bands and 106 females ≥2 years of age, so the average harem size was likely somewhere near 2.4 mares. Note that the total population during the single summer of their study was about 225 animals, which probably explains the somewhat larger number of bands. Perkins and others (1979), working on a population that ranged from 95 to 168 animals (1974–1978), found 19–27 bands with a mean size of 4.9 (total animals), but did not report harem size in terms of number of mares. During a period (1992–1997) when the mean population was 161 animals, Singer and others (2000) reported an increase in the number of bands (18 to 31) and a decline in the number of mares (age unspecified) per harem from four to two. They attributed these trends to an increasing proportion of males in the population, death or waning vigor of a number of older males, and removal of members from the bands of several stallions aged 10–15 years. Investigators working on other herds have found similar or perhaps slightly larger average harem sizes. Mean harem size on Cumberland Island was 1.8 mares (Goodloe and others, 2000); the authors did not specify the age of mares included, but only mares ≥3 years old produced foals. Greger and Romney (1999) reported an average harem size of 2.4, which included all females ≥1 year of age, excluding daughters. Berger (1986, p. 130) found an average harem size of 3.1 mares with a range of 2.73–3.67 across years; age of mares was not specified but, because 2-year-old females reproduced, mares ≥2 years old may have been included. In Misaki horses (Japan), the annual average harem size ranged from 1.8 to 5.3 mares ≥2 years old; one stallion in one year had a harem of nine mares, and 55.0 percent of 60 harems (14 harem stallions) observed from 1979 to 1994 had four or more mares (Kaseda and Khalil, 1996).

In our study, 62.1 percent of harem stallions first acquired a harem at age 5 or 6. Other investigators have found comparable results: Berger (1986, p. 142), age 5–6; Kaseda and Khalil (1996), age 4–6; Asa (1999), age 5; Singer and others (2000), mean age = 6 years. In the last two years of our study, the mean age of harem stallions was 13 and 12 years, which is remarkably similar to the mean of 12.8 years reported at Pryor Mountain by Perkins and others (1979). Hall (1972), however, reported a mean age of 7.8 years, which is more similar to the data from the early years of our study. Age structure of removals is undoubtedly an important determinant of such results.

During our study, 6.3 percent of bands had multiple stallions. Feist and McCullough (1975) did not mention whether any of the 44 bands present during their study had multiple stallions. Perkins and others (1979) found only two multistallion bands in the 19–27 bands present during the 4 years of their study; if the mean number of bands present was, say, 23 per year, multistallion bands would have made up about 2.2 percent of the total. These percentages are lower than those reported for other herds: Goodloe and others (2000), 10.7 percent, n = 177; Nelson (1978), 11.8 percent, n = 17; Berger (1986, p. 129), 12 percent, sample size not given; Salter and Hudson (1982), 17.4 percent, n = 23; Asa (1999), 28 percent and 33 percent in 2 years, n = 18 and 9; Miller (1979), 23–45 percent for 3 years, n = 12–18; Bowling and Touchberry (1990), 39.1 percent, n = 69; Franke Stevens (1990), 50 percent, n = 12; Green and Green (1977), 45 percent and 54 percent in 2 years, n = 53 and 67, respectively. Kirkpatrick and Turner (1986) suggested that differences in proportions of bands with multiple stallions may be related to population density and sex ratio, with a greater ratio of males to females tending to lead to multistallion bands, and noted that some of the reported proportions may be high as a result of inaccurate aging of the animals based on body size [for example, Green and Green (1977)].

Bachelors

We have information on the total number of bachelors, but not on individual groups, which makes comparisons with other studies at Pryor Mountain difficult. Hall (1972) reported that the average size of bachelor groups was three, with individuals ranging in age from 1 to 5 years, and that older stallions usually lived alone after losing their harems. Feist and McCullough (1975) found 23 bachelor groups with a mean of 1.8 animals per group. Perkins and others (1979) found six bachelor groups, all with 2–3 individuals ranging in age from 3 to 8 years, as well as six older stallions that lived alone. With allowances for varying population size, our results do not appear to be greatly different from those found at other times at Pryor Mountain.

Most evidence suggests that males leave or are expelled from their natal band when they reach sexual maturity, which usually occurs at age 3 and occasionally at age 2 (Angle and others, 1979; Kirkpatrick and Turner, 1986). Our data show a somewhat different pattern. A few males left their natal band at age 1, most (54.2 percent) left at age 2, but 17 percent remained with their natal band until age 4 or 5. Of the three individuals that remained in their natal bands until age 5, two subsequently acquired harems and one was still a bachelor (6 years old) at the end of our study. Interestingly, one of these stallions took over his natal band, at which point his dam left the band for another. It seems possible that instances of stallions remaining with their natal band until age 4 or 5 account for some of the reports in other studies of a high proportion of multistallion bands.

Population Regulation

Several investigators have suggested a relation between forage availability and foaling rate, but few studies have been long enough and had sufficient variation in population size to allow detection of density-dependent effects. Berger (1986, p. 97) found little evidence for density dependence in his data from the Granite Range and suggested that the confounding effects of weather were responsible. He did, however, find some evidence for a decline in foaling rate with increasing population size in data from Keiper and Houpt (1984). Singer and others (2000) found that population growth rate at Pryor Mountain declined with increasing population size, but this result was clearly dominated by data from a single year [Singer and others (2000), fig. 5]. They did not find evidence for a density-dependent effect on either foaling rate or survival rate. Jenkins (2000) examined data from the Granite Range and Pryor Mountain herds, both having individually identified animals, as well as five additional herds where population size was estimated using aerial surveys. In all seven cases, he found that population growth rate decreased with increasing population size, but only one was statistically significant ($P \leq 0.05$). However, his meta-analysis of the entire data set indicated that the probability of the same result through chance alone was only 0.001.

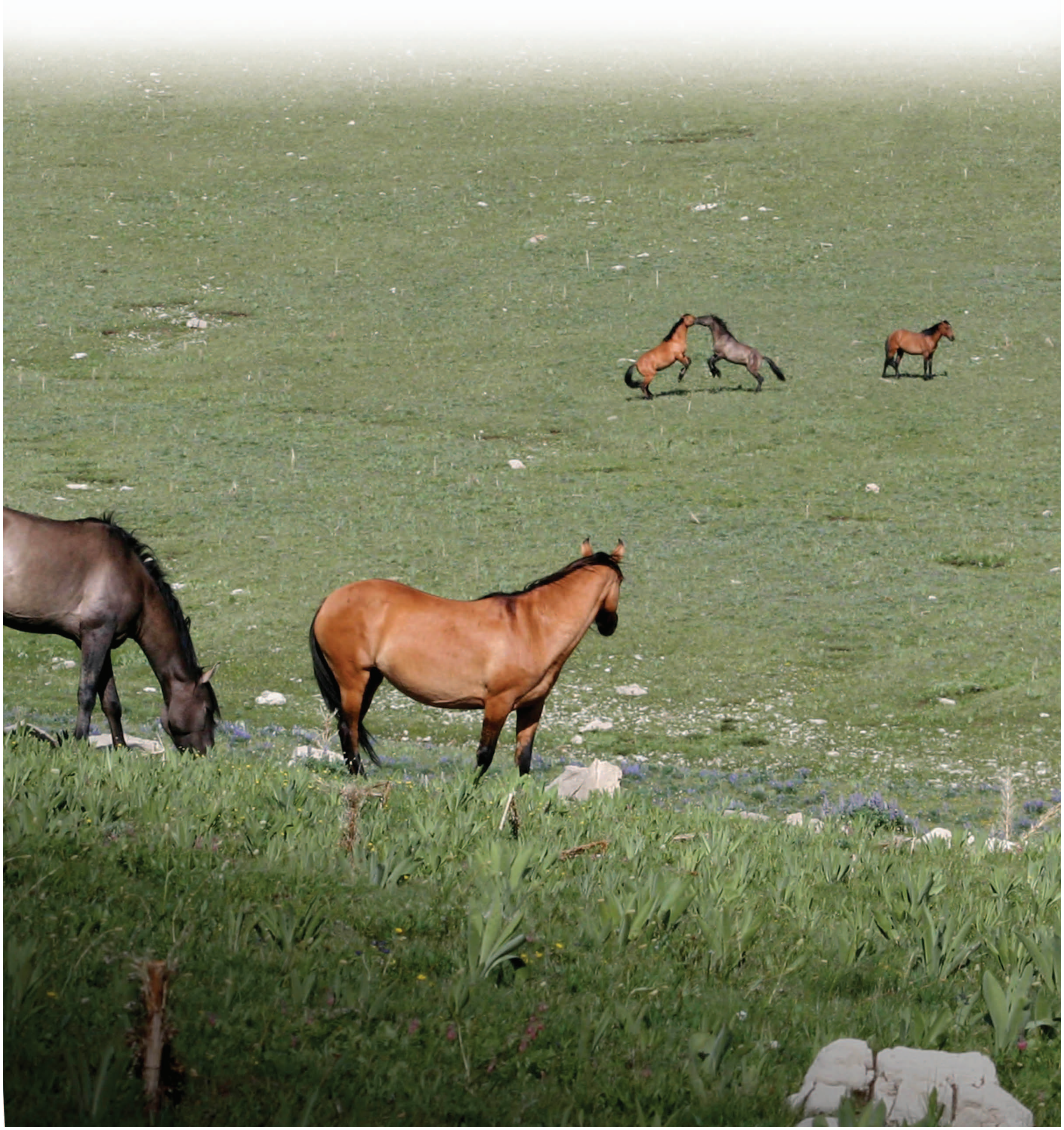
Our results are similar to those of both Singer and others (2000) and Jenkins (2000) in that we also found that population growth rate declined with increasing population size, albeit population size from the preceding year, which suggests that lag effects may be important. Furthermore, we found similar evidence for a negative relation between overall herd survival and population size, and perhaps some weaker evidence that the foaling rate of 2-year-old mares is affected by population size. We did not, however, find evidence for a density-dependent effect on foal survival, perhaps in part because Garrott and Taylor (1990), whose study encompassed a range of population sizes, did not provide annual foal survival rates.

We used population size as a surrogate for population density in these analyses, as did all of the authors cited in this section. In doing so, we made the implicit assumption that the area used by horses did not change significantly through the course of the study. In the case of the Pryor Mountain herd, however, horses probably made increasing seasonal use of Forest Service lands north and west of the original wild horse range. It seems likely that any density-dependent effects would have been more pronounced had this increase in use of Forest Service land not occurred.

In all cases where we found evidence for density dependence, variability was high, suggesting that other factors also may be important in regulating the Pryor Mountain wild horse herd. Assuming that the cause of mortality was correctly identified, mountain lion predation may have had a dramatic effect on foal survival in at least one year. In the latter years of our study, contraception also may have had some effect on foaling rate, though it seems likely that this effect was small given that relatively few mares were treated and that they were not in the most productive age classes. One of the most important regulatory mechanisms appears to be precipitation, which we found to be strongly related to foal survival. Both density dependence and precipitation effects are consistent with an interpretation of forage availability per individual as an important parameter. All of these factors combined, however, were not sufficient to stabilize the population during our period of study, as evidenced by the necessity for large removals in several years.

Acknowledgments

Thanks to the Bureau of Land Management's Billings Field Office for logistical support and making historical data available, and to the National Park Service, Bighorn Canyon National Recreation Area, for providing access and logistical support for field work on NPS lands. The integrity of long-term data for the Pryor Mountain herd can be partially attributed to the commitment and dedication of the late Reverend Floyd Schwieger, who graciously shared his work and answered many questions before his passing. Special thanks to the BLM and USGS field technicians who spent their summers following horses and accurately collecting the data: Hanem Abouelezz, Genie Amelung, Erin Anderson, Laura Caldwell, Steve Cordts, Kira Donnelly, Darla Dunaway, Jason Dungan, Melissa Esser, Jill Fanning-Rodgers, Don Galvin, Kayla Grams, Patti Grigsby, Susan Hahn, Christine Hardy, Heather Jensen, Martina Keil, Dan Kraemer, Megan Lallier, Samantha Lukas, Ian McCluskey, Sean Mead, Jessica Meredith, Jill Nannenga, Jane Nibler, Christopher Papouchis, Christina Petrandis, Justin Rodgers, Lisa Selner, Jennifer Severude, Aaron Swallow, Nani Teves, and Jamie Wages. Thanks also to Dan Baker, Jared Bybee, Bob Garrott, Al Kane, and Alan Shepherd for providing critical reviews of the manuscript, to Tammy Fancher for preparing the map of the study area, and to Jennifer Shoemaker for assistance with graphics.



References Cited

American Association of Equine Practitioners, 2002, Guide for determining the age of the horse (6th ed.): Lexington, Ky., American Association of Equine Practitioners, 39 p.

Angle, M., Swain, S., Kirkpatrick, J.F., Turner, J.W., Jr., Kenney, R.M., and Ganjam, V.K., 1979, Androgens in feral stallions, *in* Denniston, R.H., conference coordinator, Symposium on the ecology and behavior of wild and feral equids: Laramie, University of Wyoming, p. 31–38.

Asa, C.S., 1999, Male reproductive success in free-ranging feral horses: Behavioral Ecology and Sociobiology, v. 47, p. 89–93.

Ashley, M.C., and Holcombe, D.W., 2001, Effect of stress induced by gathers and removals on reproductive success of feral horses: Wildlife Society Bulletin, v. 29, p. 248–254.

Berger, J., 1983, Induced abortion and social factors in wild horses: Nature, v. 303, p. 59–61.

Berger, J., 1986, Wild horses of the Great Basin: University of Chicago Press, Ill., 326 p.

Bowling, A.T., and Touchberry, R.W., 1990, Parentage of Great Basin feral horses: Journal of Wildlife Management, v. 54, p. 424–429.

Boyd, L., 1979, The mare-foal demography of feral horses in Wyoming's Red Desert, *in* Denniston, R.H., conference coordinator, Symposium on the ecology and behavior of wild and feral equids: Laramie, University of Wyoming, p. 185–204.

Bureau of Land Management, 2006, Environmental Assessment for the Pryor Mountain Wild Horse Range, Population Control 2006, EA # BLM-MT-010-FY06-19: Billings, Mont., BLM Field Office.

Bureau of Land Management, 2009, Pryor Mountain Wild Horse Range/Territory Environmental Assessment, MT-101-08-24, and Herd Management Area Plan: Billings, Mont., BLM Field Office.

Bureau of Land Management, National Park Service, and Forest Service, 2008, Pryor Mountain Wild Horse Range evaluation: Billings, Mont., BLM Field Office.

Cameron, E.Z., and Linklater, W.L., 2000, Individual mares bias investment in sons and daughters in relation to their condition: Animal Behaviour, v. 60, p. 359–367.

Cameron, E.Z., Linklater, W.L., Stafford, K.J., and Minot, E.O., 2000, Aging and improving reproductive success in horses—declining residual reproductive value or just older and wiser?: Behavioral Ecology and Sociobiology, v. 47, p. 243–249.

Cameron, E.Z., Linklater, W.L., Stafford, K.J., and Minot, E.O., 2003, Social grouping and maternal behaviour in feral horses (*Equus caballus*)—the influence of males on maternal protectiveness: Behavioral Ecology and Sociobiology, v. 53, p. 92–101.

Conley, W., 1979, The potential for increase in horse and ass populations—a theoretical analysis, *in* Denniston, R.H., conference coordinator, Symposium on the ecology and behavior of wild and feral equids: Laramie, University of Wyoming, p. 221–234.

Cook, C.W., 1975, Wild horses and burros—a new management problem: Rangeman's Journal, v. 2, p. 19–21.

Cothran, E.G., and Singer, F., 2000, Analysis of genetic variation in the Pryor Mountain wild horse herd, *in* Singer, F.J., and Schoenecker, K.A., compilers, Managers' summary—ecological studies of the Pryor Mountain Wild Horse Range, 1992–1997: Fort Collins, Colo., U.S. Geological Survey, Midcontinent Ecological Science Center, p. 91–104.

Eberhardt, L.L., Majorowicz, A.K., and Wilcox, J.A., 1982, Apparent rates of increase for two feral horse herds: Journal of Wildlife Management, v. 46, p. 367–374.

Feh, C., 1999, Alliances and reproductive success in Camargue stallions: Animal Behaviour, v. 57, p. 705–713.

Feist, J.D., 1971, Behavior of feral horses in the Pryor Mountain Wild Horse Range: Ann Arbor, University of Michigan, Master's thesis, 129 p.

Feist, J.D., and McCullough, D.R., 1975, Reproduction in feral horses: Journal of Reproduction and Fertility, Supplement 23, p. 13–18.

Franke Stevens, E., 1990, Instability of harems of feral horses in relation to season and presence of subordinate stallions: Behaviour, v. 112, p. 149–161.

Frei, M.N., Peterson, J.S., and Hall, J.R., 1979, Aerial census of wild horses in western Utah: Journal of Range Management, v. 32, p. 8–11.

Garrott, R.A., 1991, Sex ratios and differential survival of feral horses: Journal of Animal Ecology, v. 60, p. 929–937.

Garrott, R.A., Eagle, T.C., and Plotka, E.D., 1991a, Age-specific reproduction in feral horses: Canadian Journal of Zoology, v. 69, p. 738–743.

Garrott, R.A., Siniff, D.B., and Eberhardt, L.L., 1991b, Growth rates of feral horse populations: Journal of Wildlife Management, v. 55, p. 641–648.

Garrott, R.A., and Taylor, L., 1990, Dynamics of a feral horse population in Montana: Journal of Wildlife Management, v. 54, p. 603–612.

Goodloe, R.B., Warren, R.J., Osborn, D.A., and Hall, C., 2000, Population characteristics of feral horses on Cumberland Island, Georgia and their management implications: Journal of Wildlife Management, v. 64, p. 114–121.

Green, N.F., and Green, H.D., 1977, The wild horse population of Stone Cabin Valley—a preliminary report, *in* Proceedings, National Wild Horse Forum: Reno, University of Nevada, Cooperative Extension Service, p. 59–65.

Greger, P.D., and Romney, E.M., 1999, High foal mortality limits growth of a desert feral horse population in Nevada: Great Basin Naturalist, v. 59, p. 374–379.

Gross, J.E., 2000a, Genetic and demographic consequences of removals and contraception on wild horses in the Pryor Mountain Wild Horse Range, *in* Singer, F.J., and Schoenecker, K.A., compilers, Managers' summary—ecological studies of the Pryor Mountain Wild Horse Range, 1992–1997: Fort Collins, Colo., U.S. Geological Survey, Midcontinent Ecological Science Center, p. 105–120.

Gross, J.E., 2000b, A dynamic simulation model for evaluating effects of removal and contraception on genetic variation and demography of Pryor Mountain wild horses: Biological Conservation, v. 96, p. 319–330.

Hall, R., 1972, Wild horse biology and alternatives for management—Pryor Mountain Wild Horse Range: Billings, Mont., Bureau of Land Management, no pagination.

Hansen, K.V., and Mosley, J.C., 2000, Effects of roundups on behavior and reproduction of feral horses: Journal of Range Management, v. 53, p. 479–482.

Heitschmidt, R.K., Klement, K.D., and Haferkamp, M.R., 2005, Interactive effects of drought and grazing on Northern Great Plains rangelands: Rangeland Ecology and Management, v. 58, p. 11–19.

Jenkins, S.H., 2000, Density dependence in population dynamics of feral horses: Denver, Colo., Bureau of Land Management, National Science and Technology Center, Resource Notes No. 26, 2 p.

Kaseda, Y., and Khalil, A.M., 1996, Harem size and reproductive success of stallions in Misaki feral horses: Applied Animal Behaviour Science, v. 47, p. 163–173.

Kaseda, Y., Khalil, A.M., and Ogawa, H., 1995, Harem stability and reproductive success of Misaki feral mares: Equine Veterinary Journal, v. 27, p. 368–372.

Keiper, R.R., 1979, Population dynamics of feral ponies, *in* Denniston, R.H., conference coordinator, Symposium on the ecology and behavior of wild and feral equids: Laramie, University of Wyoming, p. 175–183.

Keiper, R., and Houpt, K., 1984, Reproduction in feral horses—an eight-year study: American Journal of Veterinary Research, v. 45, p. 991–995.

Kirkpatrick, J.F., and Frank, K.M., 2005, Contraception in free-ranging wildlife, *in* Asa, C.S., and Porton, I.J., eds., Wildlife contraception—issues, methods, and applications: Baltimore, Md., The Johns Hopkins University Press, p. 195–221.

Kirkpatrick, J.F., and Turner, J.W., Jr., 1986, Comparative reproductive biology of North American feral horses: Equine Veterinary Science, v. 6, p. 224–230.

Linklater, W.L., Cameron, E.Z., Minot, E.O., and Stafford, K.J., 2004, Feral horse demography and population growth in the Kaimanawa Ranges, New Zealand: Wildlife Research, v. 31, p. 119–128.

Lucas, Z., Raeside, J.I., and Betteridge, K.J., 1991, Noninvasive assessment of the incidences of pregnancy and pregnancy loss in the feral horses of Sable Island: Journal of Reproduction and Fertility, Supplement 44, p. 479–488.

Miller, R., 1979, Band organization and stability in Red Desert feral horses, *in* Denniston, R.H., conference coordinator, Symposium on the ecology and behavior of wild and feral equids: Laramie, University of Wyoming, p. 113–128.

Monard, A-M., Duncan, P., Fritz, H., and Feh, C., 1997, Variations in the birth sex ratio and neonatal mortality in a natural herd of horses: Behavioral Ecology and Sociobiology, v. 41, p. 243–249.

Nelson, K.J., 1978, On the question of male-limited population growth in feral horses (*Equus caballus*): Las Cruces, New Mexico State University, Master's thesis, 68 p.

Oom, M.M., and Santos-Reis, M., 1986, Ecology, social organization and behaviour of the feral horses in the Peneda-Gerês National Park: Arquivos de Museu Bocage (sêrie A), v. 3, p.169–196.

Pellegrini, S.W., 1971, Home range, territoriality and movement patterns of wild horses in the Wassuk Range of western Nevada: Reno, University of Nevada, Master's thesis, 39 p.

Perkins, A., Gevers, E., Turner, J.W., Jr., and Kirkpatrick, J.F., 1979, Age characteristics of feral horses in Montana, *in* Denniston, R.H., conference coordinator, Symposium on the ecology and behavior of wild and feral equids: Laramie, University of Wyoming, p. 51–58.

Ricketts, M.J., 2004, Pryor Mountain Wild Horse Range survey and assessment: Bozeman, Mont., U.S. Department of Agriculture, Natural Resources Conservation Service, 146 p.

Salter, R.E., 1979, Biogeography and habitat-use behavior of feral horses in western and northern Canada, *in* Denniston, R.H., conference coordinator, Symposium on the ecology and behavior of wild and feral equids: Laramie, University of Wyoming, p. 129–141.

Salter, R.E., and Hudson, R.J., 1982, Social organization of feral horses in western Canada: Applied Animal Ethology, v. 8, p. 207–223.

Seal, U.S., and Plotka, E.D., 1983, Age-specific pregnancy rates in feral horses: Journal of Wildlife Management, v. 47, p. 422–429.

Singer, F.J., and Schoenecker, K.A., compilers, 2000, Managers' summary—ecological studies of the Pryor Mountain Wild Horse Range, 1992–1997: Fort Collins, Colo., U.S. Geological Survey, Midcontinent Ecological Science Center, 131 p.

Singer, F.J., Zeigenfuss, L., Coates-Markle, L., and Schwieger, Rev. F., 2000, A demographic analysis, group dynamics, and genetic effective number in the Pryor Mountain wild horse population, 1992–1997, *in* Singer, F.J., and Schoenecker, K.A., compilers, Managers' summary—ecological studies of the Pryor Mountain Wild Horse Range, 1992–1997: Fort Collins, Colo., U.S. Geological Survey, Midcontinent Ecological Science Center, p. 73–89.

Siniff, D.B., Tester, J.R., and McMahon, G.L., 1986, Foaling rate and survival of feral horses in western Nevada: Journal of Range Management, v. 39, p. 296–297.

Smart, A.J., 2005, Forecasting forage production, *in* Proceedings, The Range Beef Cow Symposium XIX: Rapid City, S. Dak., p. 101–106.

Speelman, S.R., Dawson, W.M., and Phillips, R.W., 1944, Some aspects of fertility in horses raised under western range conditions: Journal of Animal Science, v. 3, p. 233–241.

Trivers, R.L., and Willard, D.E., 1973, Natural selection of parental ability to vary the sex ratio of offspring: Science, v. 179, p. 90–92.

Turner, J.W., Jr., and Morrison, M.L., 2001, Influence of predation by mountain lions on numbers and survivorship of a feral horse population: The Southwestern Naturalist, v. 46, p. 183–190.

Turner, J.W., Jr., Wolfe, M.L., and Kirkpatrick, J.F., 1992, Seasonal mountain lion predation on a feral horse population: Canadian Journal of Zoology, v. 70, p. 929–934.

Wolfe, M.L., Jr., 1980, Feral horse demography—a preliminary report: Journal of Range Management, v. 33, p. 354–360.

Wolfe, M.L., 1986, Population dynamics of feral horses in western North America: Equine Veterinary Science, v. 6, p. 231-235.

Wolfe, M.L., Ellis, L.C., and MacMullen, R., 1989, Reproductive rates of feral horses and burros: Journal of Wildlife Management, v. 53, p. 916–924.

Publishing support provided by:
Denver Publishing Service Center

For more information concerning this publication, contact:
Center Director, USGS Fort Collins Science Center
2150 Centre Ave., Bldg. C
Fort Collins, CO 80526-8118
(970)226-9398

Or visit the Fort Collins Science Center Web site at:
http://www.fort.usgs.gov/

Roelle and others—**Demography of the Pryor Mountain Wild Horses, 1993–2007**—Scientific Investigations Report 2010–5125