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February 22, 1990

Dawn Lappin - WHOA
15640 Sylvester Rd.
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Dear Ms. Lappin:

Enclosed is a copy of my recently completed report on the population dynamics of wild horses in the western United States. This work was funded by BLM through a contract with the University of Minnesota and could not have been accomplished without the cooperation of BLM personnel throughout the West. Since your organization is actively involved in the complexities of managing wild horse populations I thought you may be interested in the results of this study. If you have any questions or comments about this report please feel free to contact me.

Best regards,

Bob Garrott

Bob Garrott

3/1990

DEMOGRAPHY OF FERAL HORSE POPULATIONS IN THE WESTERN UNITED STATES

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

ROBERT ANDREW GARROTT

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

MARCH 1990

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ABSTRACT

The demography of feral horse (Equus caballus) populations in the western United States was investigated by consolidating information routinely gathered by Bureau of Land Management personnel. Records from the Pryor Mountain herd in Montana provided the only direct measures of survival. In this population annual survival was usually high, 0.93-0.99, however, severe winter conditions resulted in survival rates of 0.49 and 0.87 during 2 of the 11 years data were available. Examination of age-specific sex ratios calculated from >60,000 horses removed from public lands suggests survival rates of young males (0-3 years) may be lower than survival of young females while survival of adult males (>3 years) is higher than adult females. Two independent sources of reproductive data, serum hormone assays and lactation status, indicated that in most populations some 2-year old females foaled. The proportion of females foaling increased through age 6 with the highest rates in the 6-15 year age class and a gradual decrease in foaling rates thereafter. Log-linear regression estimates of finite annual growth rates of 12 herds ranged from 1.15-1.27 with a mean of 1.21. Population simulations using age-specific fecundity and survival schedules derived from this study corroborated these high growth rates and suggests that most feral horse populations are increasing at or near their biological maximum.

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I thank my committee members, Kinley Larntz, David Smith, Don Siniff, Tony Starfield, and John Tester for their support and advise throughout my graduate program. Special thanks to my advisor Don Siniff, who gave me the freedom to pursue my ideas and supported all aspects of my research and education. Conversations with Tom Eagle about horse biology, management, and politics were instrumental in the formulation of my dissertation topic. His constant assistance, encouragement, and hospitality are very much appreciated. I frequently called on John Tester's experience and advice and he critically reviewed early drafts of each paper. I am grateful to Francie Cuthbert and David Andersen for performing various committee duties when appointed committee members were not available.

Special thanks to Lee Eberhardt who took an interest in my research from its inception and tutored me on many of the complexities of population dynamics. His frequent reviews of my work were a constant source of constructive criticism. Tony Starfield introduced me to population modelling and aptly demonstrated its utility on many occasions and Kinley Larntz provided many hours of interesting conversations and advice on data analysis. Ed Plotka provided serum hormone data and instructed me on reproductive physiology.

I am indebted to the many BLM employees in district offices throughout the West who provided access to their files and shared their knowledge of horse biology. The data provided by Lynne Taylor of the Billings, Montana BLM office, was particularly valuable and he is to be commended for his diligent work with the Pryor Mountain Herd. Funding for this project was provided by BLM contract USDI-AA852-CT5-29.

INTRODUCTION

The demographic characteristics of feral horse populations in the western United States has been a subject of much speculation and controversy since the mid-1970s. Claims of population growth rates approaching 20% annually have been criticized as biologically unrealistic. Little empirical data have been published on the dynamics of horse populations despite 15 years of conflict over the management of the species on federal land. I initiated this study in 1986 on the premise that some insights into the dynamics of horse populations could be gained by consolidating and analyzing data routinely collected by the Bureau of Land Management, the primary agency responsible for wild horse management. This volume contains the results of these investigations organized into 5 papers that are intended for submission to various journals.

The order in which the papers are presented was dictated by the need to reference data and conclusions in subsequent studies. The first paper in this volume deals with the population dynamics of the Pryor Mountain herd and contains the only herd-specific data on all 3 major demographic parameters, reproduction, survival, and population growth. The short paper on aging bias documents limitations of current aging techniques, which influences analysis of age-specific reproduction and sex ratio data in the following 2 papers. The final paper estimates population growth rates from aerial count data. This paper also uses the results of the previous 4 papers to construct population simulations in order to determine if the reproductive and survival data available support the growth rate estimates.

DYNAMICS OF A FERAL HORSE POPULATION IN MONTANA

Abstract: The dynamics of an isolated feral horse (*Equus caballus*) population were studied by analyzing data routinely collected by the Bureau of Land Management from 1970 to 1986. All animals in the population were individually identifiable by 1976, and all but 4 animals had been captured, sexed, and aged by 1978. Annual survival was usually high, ranging from 0.93-0.99, however, increased mortality due to severe winter conditions in 1977 and 1983 resulted in annual survival rates of 0.49 and 0.87, respectively. Adult female survival was significantly higher than adult male with most mortality occurring in animals ≥15 years old. Females did not begin to reproduce until 3 years old. Annual foaling rates of reproductive age females ranged from 36-65%. The highest foaling rates occurred after a 51% reduction in the population, suggesting a density dependent response. The reproductive history of multiparous females the previous year had no effect on probability of foaling, however, primiparous females were less likely to reproduce the following year. The adult sex ratio was consistently skewed approximately 2 to 1, in favor of females and was attributed primarily to the removal of disproportionate numbers of males during herd reduction programs. Excluding the year when half the population died because of abnormally severe winter conditions, the population grew at a mean rate of 18% annually.

Introduction

Prior to 1971, feral horses occupying rangelands in the western United States had no status with respect to ownership or management. Horses were left to roam both public and private rangelands with their numbers controlled by commercial "mustangers" who usually sold the animals for slaughter (Symanski 1985). Passage of the Wild and Free-Roaming Horse and Burro Protection Act in 1971 established federal ownership of feral horses occupying public lands and gave the animals complete protection (Wagner 1983). Concerns about conflicts between livestock interests and growing horse populations led to the passage of the Public Rangelands Improvement Act in 1978, which facilitated the federal agencie's power to manage horse populations through the removal of excess animals (Boyles 1986). Effective management of western feral horse populations, however, has been hindered by a lack of essential information on biology, behavior, and population dynamics (National Research Council 1980, 1982).

In a review of current knowledge of feral horses and burros, the National Research Council (1980) depended heavily on studies of domestic horses and feral herds occupying coastal islands along the Atlantic seaboard. Information on populations in the arid rangelands of the western United States was limited to a few studies involving one or two field seasons (National Research Council 1980).

Although there has been considerable controversy about the dynamics of feral horse populations, with the exception of the 5-year study by Berger (1986), little empirical data on this important topic have been published in the last decade.

Progress in understanding the population dynamics of long-lived large mammals such as horses is difficult because granting agencies seldom support studies extending longer than 2-3 years. Smith and Fowler (1981) suggested overcoming this problem by identifying and analyzing historical data sets collected by agencies responsible for routine monitoring of populations within their jurisdiction. The Bureau of Land Management (BLM) has been collecting detailed information on an isolated population of horses in southcentral Montana since 1970. The information includes histories of every animal in the population for an 11-year period and may represent the most complete and long-term data on a feral horse population in existence. This paper presents a synthesis of these data and discusses survival, reproduction, sex ratios, age structure, density dependent mechanisms, and growth rates of the population.

Study Area

The Pryor Mountain Wild Horse Range (PMWHR) was created in 1968 primarily for the protection and management of the local horse population (Bureau of Land Management 1984). The PMWHR consists of 148 km^2 of designated land with the horse herd using an additional 41 km^2 of adjacent land.

Approximately 71 km^2 of this area is considered unsuitable for horse grazing because of a lack of vegetation and a preponderance of rock and bare soil. Annual precipitation normally ranges between 12 and 50 cm. Elevations within PMWHR range from 1300 to 2600 m with diverse topography including moderately sloped foothills, steep canyons, and isolated plateaus. By the mid-1970's the horse population was confined to the area by boundary fences that also prohibited entry of domestic stock. Current management objectives are to maintain a population of 121 horses, excluding the current year's foal crop. Periodic round ups are conducted to remove excess animals (Bureau of Land Management 1984).

Four plant communities are found on PMWHR, segregated along elevational gradients. Subalpine meadows are found at the highest elevations and are composed of perennial forbs, grasses, and sedges with scattered stands of subalpine fir (Abies lasiocarpa). Mid-elevations support conifer stands composed primarily of Douglas fir (Pseudotsuga mienziessi) with snowberry (Symphiorcarpus spp.) and ninebark (Physocarpus malvaceus) as the primary understory shrubs. Unforested areas are dominated by big sagebrush (Artemisia tridentata) and shrubby cinquefoil (Potentilla fruticosa). A mountain shrub community, found at lower elevations, is comprised of Utah juniper (Juniperus osteosperma), mountain mahogany (Cercocarpus ledifolius), big sagebrush, black sage

(Artemisia nova), rabbitbrush (Chrysothamnus nauseosus), and a variety of grasses and forbs. A salt-shrub community occurs at the lowest elevations with the majority of the vegetation composed of saltbushes (Atriplex spp.).

Methods

Data on the demographic characteristics of the PMWHR population were derived from 2 sources, the periodic capture of a portion of the population in conjunction with herd reductions, and ground observations by BLM personnel familiar with the identity of individual horses. Capture programs were initiated in 1970 and have involved a variety of methods. An initial attempt was made to capture horses using immobilizing drugs in 1970 and 1971. Although 65 adults were captured, the technique was abandoned in favor of corral trapping. The most common trapping technique has been to employ men on horseback to drive small groups of horses into permanent corral traps erected in advantageous locations throughout PMWHR. During very dry periods horses have been captured in corral traps erected around the few permanent sources of water. Individual horses eluding corral traps or of particular interest have been roped by experienced wranglers (Bureau of Land Management 1984).

Once trapped, horses were restrained by roping the head and hind legs in a procedure known as "heading and heeling". Animals were sexed and aged by tooth eruption and wear (Amer. Assoc. Equine Practitioners 1981). Horses not selected for removal were lip tattooed with a unique number, and the color and distinctive head and leg markings were recorded. General capture location and other animals the horse was associated with at the time of capture were also recorded. All animals in the population were individually identifiable by 1976, and all but 4 animals had been captured, sexed, aged, and tattooed by 1978.

Ground observations were conducted at all seasons of the year; however, most data were collected during the summer and fall. Since 1976 annual records have been maintained on all animals in the population. Determination that a horse had died was usually dependent upon failure to locate the animal after repeated ground searches. It was common for horses not to be resighted for months at a time; thus animals were classified as dead only after they had not been seen for an entire year. This relatively infrequent sampling resulted in some imprecision on assigning time of death, hence, minor errors may be present in data presented on an annual basis.

Annual survival rates were calculated for the period between midsummer of one year and the next. This time interval was selected because almost all mortalities occurred during the winter or spring seasons. Survival was calculated as the proportion of animals alive at the beginning of the interval that were alive at the end of the interval, excluding all animals that were removed from the population by BLM personnel. For the sake of simplicity, annual survival rates are reported for the calendar year the interval started; hence, the 1976 survival rate describes survival from mid-summer of 1976 to mid-summer 1977.

Annual reproduction was assessed each field season by observing all harem groups to locate foals. The unique markings of each foal were recorded when first observed and each was given a number that permanently identified the animal. Foals were normally sexed with the aid of binoculars or a spotting scope, but some animals were not sexed until captured. Foals were not always captured and sexed during their first year, occasionally remaining uncaptured as long as 2 years. Data on age-specific foaling rates of females were obtained by observing each foal's interactions with members of its band until the foal's dam could be identified. Some foals were undoubtedly missed due to early post-partum mortality; therefore, reproductive data must be considered minimum estimates.

Contingency tables were constructed to explore differential survival and reproduction of various segments of the population and departures of sex ratios from parity. These data were tested using the Chi-square statistic (Fienberg 1980). Age specific survival rates were calculated by pooling data across all years except 1977. An l_x schedule was calculated from these data (Caughley 1977) and was fit to the survivorship model used by Siler (1979) and Eberhardt (1985):

$$l_x=\exp[-F-Gx-D\{\exp(Ex)-1\}].$$

The equation notation follows that of Eberhardt and Siniff (1988) and models a 3-component hazard function (Siler 1979). The early hazard component (F), is a coefficient representing survival from birth to age of maturity, which was considered to be 1 year ($F=-\ln[Surv_{0-1}]$). The second component (G), describes a single survival rate for prime age adults ($G=-\ln[Surv_{adults}]$). The third component of the function represents senescence and is composed of 2 coefficients, D and E, which can be interpreted as coefficients describing the modal age of senescence (T), and its standard deviation (S_t), respectively. The relationships between D and T and E and S_t are

$$D=\exp(-T/S_t) \text{ and } E=1/S_t.$$

Estimates of the 4 coefficients of the survivorship model (F, G, D, and E) were obtained using the SAS non-linear least squares procedure NLIN (SAS Institute 1985).

Results

The identification of all animals in the population and the establishment in 1976 of a rigid program of record keeping for each horse provided an excellent data base to study the population dynamics of the herd. Data presented in this paper were drawn primarily from these records for an 11-year period from 1976-1986. Annual records were accumulated on 403 horses, representing 1564 horse years.

Additional information available prior to 1976 included annual foal counts and sex ratios from 1972-75 and limited data on horses removed during herd reduction programs.

Removals and Survival

BLM personnel removed 143 horses from the population between 1976-86. The maximum number of horses removed in any year was 48, representing approximately 25% of the population (Table 1). Animals selected for removals were not representative of the population as both sex and age biases were detected. Removals favored males (17%, n=389) over females (12%, n=676) ($\underline{P}<0.025$) and 1 to 2 year old animals (29%, n=299) over foals (6%, n=202) and horses $\geq$3 years old (7%, n=578) ($\underline{P}<0.001$). Three additional removals were conducted prior to 1976. These removals involved 16 foals and 28 adult males in fall 1971, 45 animals of unknown sex and age in spring 1973, and 15 adult males and 12 adult females in spring 1975.

Between 1976 and 1986, 121 horses were known to have died or were no longer seen and assumed to be dead. Few animals died during most years with annual overall survival rates ranging from 0.93 to 0.99 (Table 1). Two exceptions to this pattern of high annual survival occurred in 1977 and 1983. The winter of 1977-78 was extremely severe with alternating periods of heavy snow accumulations followed by abnormally warm temperatures creating several layers of ice within a deep layer of snow. Such snow conditions made

Table 1. Post-foaling population data, numbers of animals removed by man, deaths, survival rates, and annual growth rates (λ) of a feral horse herd in Montana, 1976-86.

Year	Total[1]	Adult Male	Adult Female	No. Anim. Removed[2]	No. Deaths[3]	Surv.[4]	Annual λ[5]
1976	147	41	80	0	2	0.986	
1977	171	48	96	26	74	0.490	1.163
1978	86	23	48	0	5	0.942	0.593
1979	104	24	57	0	7	0.933	1.209
1980	123	29	68	1	1	0.992	1.183
1981	150	38	77	6(6)	3	0.980	1.230
1982	181	53	94	48	6	0.955	1.207
1983	155	46	80	22(2)	18	0.867	1.165
1984	142	43	76	13	2	0.984	1.052
1985	153	47	78	27	1	0.992	1.186
1986	152	38	82	0	2	0.987	1.206
Totals	1564	430	836	143	121		

1 includes foals and adults of unknown sex

2 numbers in parenthesis are subset of horses removed in spring instead of the usual summer-fall period

3 includes all animals that died through the following foaling season

4 calculated as 1-(no. deaths/pop.-no. removed)

5 calculated as pop. time t/((pop. time t-1)-no. removed from t-1 to t)

foraging exceedingly difficult, resulting in the loss of 51% of the population. Thirteen percent of the population died during winter 1983-84 when snowfall was also above normal, however, accumulations were not as deep as winter 1977-78 and there were no ice barriers.

Due to the small number of animals that died each year, data were pooled across all years to compare the survival rates of males and females. Data from 1977 were excluded and analyzed separately because of the unique nature of the mortalities in that year. Overall survival of females was 0.97 (n=679), which was significantly higher than the 0.94 survival rate of males (n=321)($\underline{P}<0.05$). The relatively large number of mortalities during the 1977-78 winter provide adequate samples to explore the possibility of differential survival for various segments of the population subjected to unusually severe conditions. There was no significant difference in survival rates of males (0.52, n=44) and females (0.52, n=93)($\underline{P}>0.20$). Survival of females that produced foals in 1977 and were, therefore, lactating at the onset of winter (0.50, n=22) was nearly identical to non-lactating females (0.52, n=71)($\underline{P}>0.20$). Foal survival (0.31, n=26), however, was significantly lower than survival of horses $\geq$1 year old (0.56, n=105)($\underline{P}<0.05$). Ten of 14 horses of unknown age died for a survival rate of 0.29, which is not significantly different from the 0.49 survival of the population ($\underline{P}>0.20$).

An excellent fit of the survivorship equation (Siler 1979, Eberhardt 1985) to the observed l_x schedule was obtained using non-linear least squares (Fig. 1). Estimates of the 4 coefficients were F=0.0467 (S.E.=0.0218), G=0.0164 (S.E.=0.0032), D=0.0001 (S.E.=0.0001) and E=0.4226 (S.E.=0.0560). Biological interpretations of these coefficients are, juvenile survival $Surv_{0-1}$=0.954, adult survival $Surv_{1-15}$=0.984, modal age of senescence T=21.38, and standard deviation of the age of senescence S_t=2.366.

Reproduction

Data on the number of foals observed in the PMWHR population are available for a 15-year period, 1972-86. During this time a total of 349 foals were recorded with annual foal crops ranging from 11-35 (Table 2). The sex of all foals born from 1980-83 was known; however, the sex of a small number of foals was undetermined in the other 7 years (Table 2). Only foal crops in 1974 and 1978 had sex ratios significantly different from parity ($\underline{P}<0.05$). However, data pooled over all years indicated a general disparity in sex ratio, 0.66M:100F ($\underline{P}<0.001$)(Table 2). The percent of females foaling in various age classes is also presented in Table 3 in order to standardize for annual variations in age and sex composition. These ratios could not be calculated for 1972-75 because the sex and age composition of the population were unknown.

Approximately 35% of all females $\geq$1 year old foaled

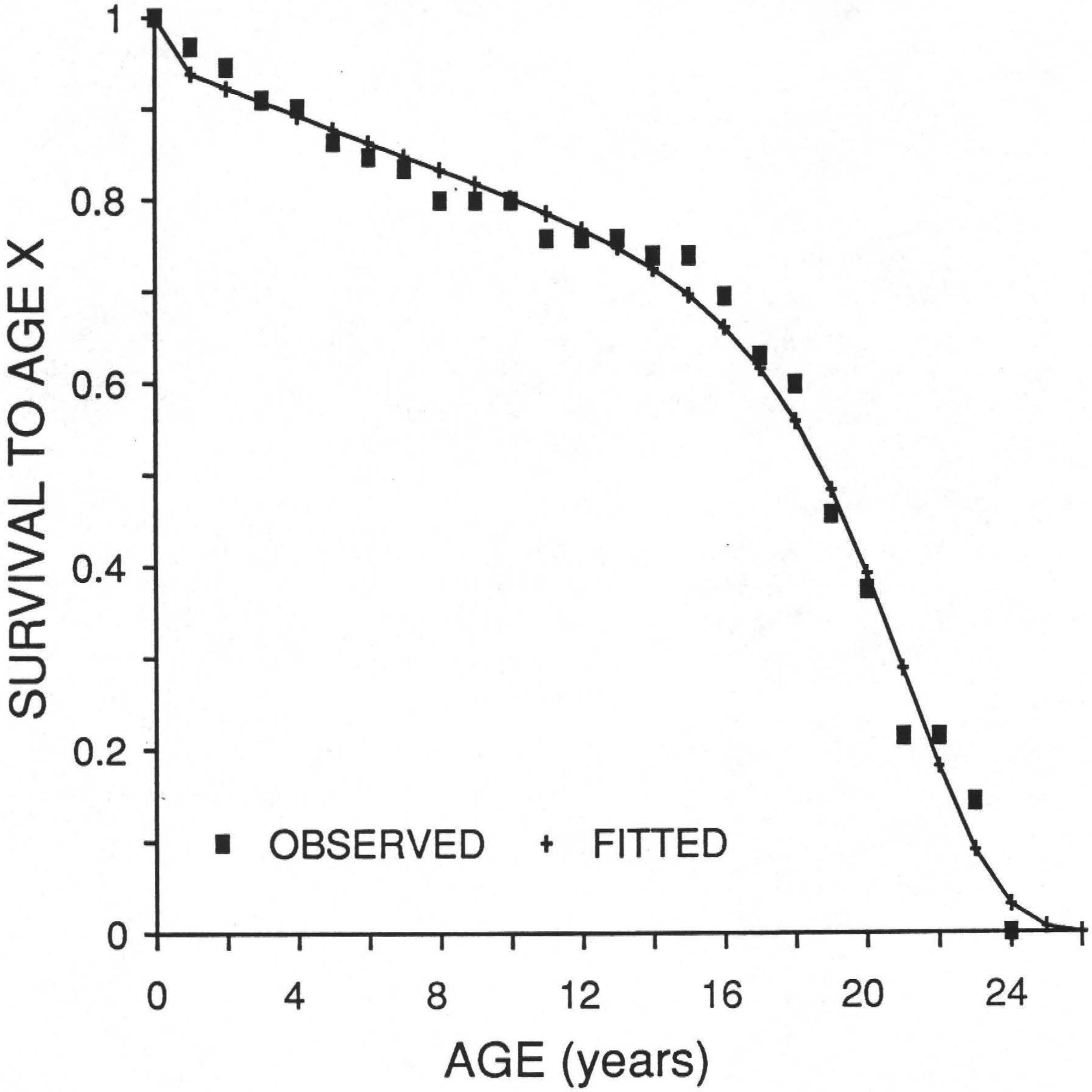

Figure 1. Survivorship of a feral horse herd in Montana derived from data collected between 1976-86 (squares), and a curve fitted to the observed data (crosses) using non-linear least squares and the 3-component survivorship model used by Siler (1979) and Eberhardt (1985).

Table 2. Number of foals and the percent of females in various age classes foaling annually in a feral horse herd in Montana, 1972-86. Numbers in parenthesis indicate sample sizes.

	No. foals			Percent females foaling annually			
Year	Total[1]	Female	Male	≥3 yr	3-5 yr	5-10 yr	>10 yr
1972	14	8	6	-	-	-	-
1973	11	5	6	-	-	-	-
1974	20	17	3	-	-	-	-
1975	11	6	5	-	-	-	-
1976	26	17	8	42(62)	20(10)	52(29)	33(15)
1977	26	12	7	36(73)	20(20)	42(26)	32(19)
1978	15	12	1	41(37)	25(8)	44(18)	50(8)
1979	23	13	9	59(39)	50(10)	75(16)	55(11)
1980	26	14	12	57(46)	38(13)	71(17)	57(14)
1981	35	19	16	65(54)	65(20)	83(12)	50(20)
1982	34	18	16	54(63)	48(27)	57(14)	65(20)
1983	30	18	12	53(57)	36(22)	50(12)	68(22)
1984	25	11	13	50(50)	39(18)	50(14)	44(18)
1985	26	15	8	46(56)	61(18)	43(21)	24(17)
1986	27	14	9	43(63)	29(24)	55(22)	35(17)
Total	349	199	131	58(600)	41(190)	55(201)	47(181)

[1] includes foals of unknown sex

from 1976-86. Known age dams were identified for 275 of the 293 foals born, providing information on age-specific reproductive rates (Table 3). Females did not begin to reproduce until 3 years old, with an overall foaling rate of 49% for females $\geq$3 years old. The percent of females foaling for the first time at ages 3, 4, 5, and 6 was 41 (n=82), 25 (n=56), 15 (n=39), and 6 (n=32), respectively. Peak foaling rates of 78 and 71% were observed in 9 and 14-year-olds, respectively (Table 3). The maximum age at which a female was observed with a foal was 23.

Foaling rates did not remain constant during the 11 years from 1976-86 ($\underline{P}<0.05$). Reproduction was lowest from 1976-78, increased substantially in 1979, reaching a peak in 1981, and then declined gradually through 1986 (Table 2). The onset of the increase in reproduction corresponded to a 51% reduction in the population due to abnormally severe winter conditions in 1977-78. The 60% foaling rate for the first 3 years after the population reduction (1979-81) was a 54% increase over the 39% foaling rate for the 1976-78 period ($\underline{P}<0.01$). Most of this increase in reproduction was caused by an approximately 2.5-fold increase in the foaling rates of 3 to 5 year old females, from 21% prior to the population reduction to 53% for the 3 year period after the population reduction. In contrast, foaling in females $\geq$6 years old only increased from 43 to 64% during the same time periods. These age specific foaling rates are slight

Table 3. Age-specific survival and fecundity rates of a feral horse herd in Montana, 1976-86. Mortality data from the winter of 1977-78 were excluded due to the unusually severe winter conditions.

	Survival				Fecundity			
Age	N	Deaths	Estim.	SE	N	Births	Estim.	SE
0	249	8	0.968	0.011	-	-	-	-
1	173	4	0.977	0.011	135	0	0.000	0.000
2	132	5	0.962	0.017	101	0	0.000	0.000
3	98	1	0.990	0.010	83	35	0.422	0.054
4	73	3	0.959	0.023	62	23	0.371	0.061
5	52	1	0.981	0.019	45	19	0.422	0.074
6	64	1	0.984	0.016	51	23	0.451	0.070
7	48	2	0.958	0.029	50	25	0.500	0.071
8	42	0	1.000	0.000	37	23	0.622	0.080
9	40	0	1.000	0.000	32	25	0.781	0.073
10	39	2	0.949	0.035	31	14	0.452	0.089
11	37	0	1.000	0.000	30	16	0.533	0.091
12	36	0	1.000	0.000	28	17	0.607	0.092
13	40	1	0.975	0.025	26	14	0.538	0.098
14	36	0	1.000	0.000	24	17	0.708	0.093
15	33	2	0.939	0.042	19	4	0.211	0.094
16	32	3	0.906	0.052	20	6	0.300	0.102
17	20	1	0.950	0.049	13	1	0.077	0.074
18	17	4	0.765	0.103	7	3	0.429	0.187
19	11	2	0.818	0.116	5	2	0.400	0.219
20	7	3	0.571	0.187	3	2	0.667	0.272
21	4	0	1.000	0.000	3	2	0.667	0.272
22	3	1	0.667	0.272	2	0	0.000	0.000
23	1	1	0.000	0.000	1	1	1.000	0.000

underestimates as 10 and 3 foals could not be assigned to known age females during the 1976-78 and 1979-81 periods respectively.

The complete foaling histories of females for 11 years provided data to test for differences in the probability of foaling given a female's reproductive history from the previous year. To reduce variability due to age-specific reproductive differences, an initial analysis was conducted using only parous, prime-aged females (5 to 15 years old). The probability of foaling was found to be independent of foaling history the previous year ($\underline{P}>0.25$). The probability of foaling given a female had foaled the previous year was 0.55 (n=163), while females that had not foaled the previous year had a 0.60 (n=86) probability of foaling. A comparison of primiparous and parous females, however, revealed significant differences ($\underline{P}<0.025$). The probability of foaling the year after a female's first foal was 0.33 (n=45) while parous females had a 0.55 (n=163) probability of foaling in consecutive years.

Adult Sex Ratios, Age structure, and Population Growth

With the exception of 5 animals, the sex of all horses ≥ 1 year old in the population each year was known. One yearling died in 1977 during the winter before it could be captured and sexed. Another horse born in 1984 was not captured and sexed during the study and was, therefore, a yearling in 1985 and a 2-year-old in 1986. The sex of 3 additional yearlings in 1986 was also undetermined. The sex ratio of adults in the population averaged 52M:100F and was consistently skewed toward females during all years from 1976-86 ($\underline{P}<0.01$)(Table 1).

Three hundred forty one of the 403 horses with individual records were born between 1970 and 1986, hence, their ages were known. The ages of 47 horses were estimated when they were first captured and an additional 15 horses died before they could be captured and aged. Twelve of the 15 horses that were not aged died during the winter of 1977-78. After 1978 animals of undetermined age never comprised more than 3% of the population.

The annual age structure of the PMWHR population was dynamic during the 11-year period, with relatively major shifts in the proportion of animals in the younger age classes (Fig. 2). From 1976-78, approximately 35-45% of the population was comprised of 1 to 5 year old horses. Beginning in 1979, the proportion of 1 to 5 year olds steadily increased, with a high of 64% in 1982. During this same interval the proportion of 6 to 10 year olds decreased from approximately 30-35% of the population before 1979, to 13% by 1982. After 3 years of stability (1982-84), the relative proportions of these 2 age classes began to reverse, with 1 to 5 year olds decreasing and 6 to 10 year olds increasing. The annual proportion of 11 to 15 year olds remained relatively stable, usually ranging from 12-

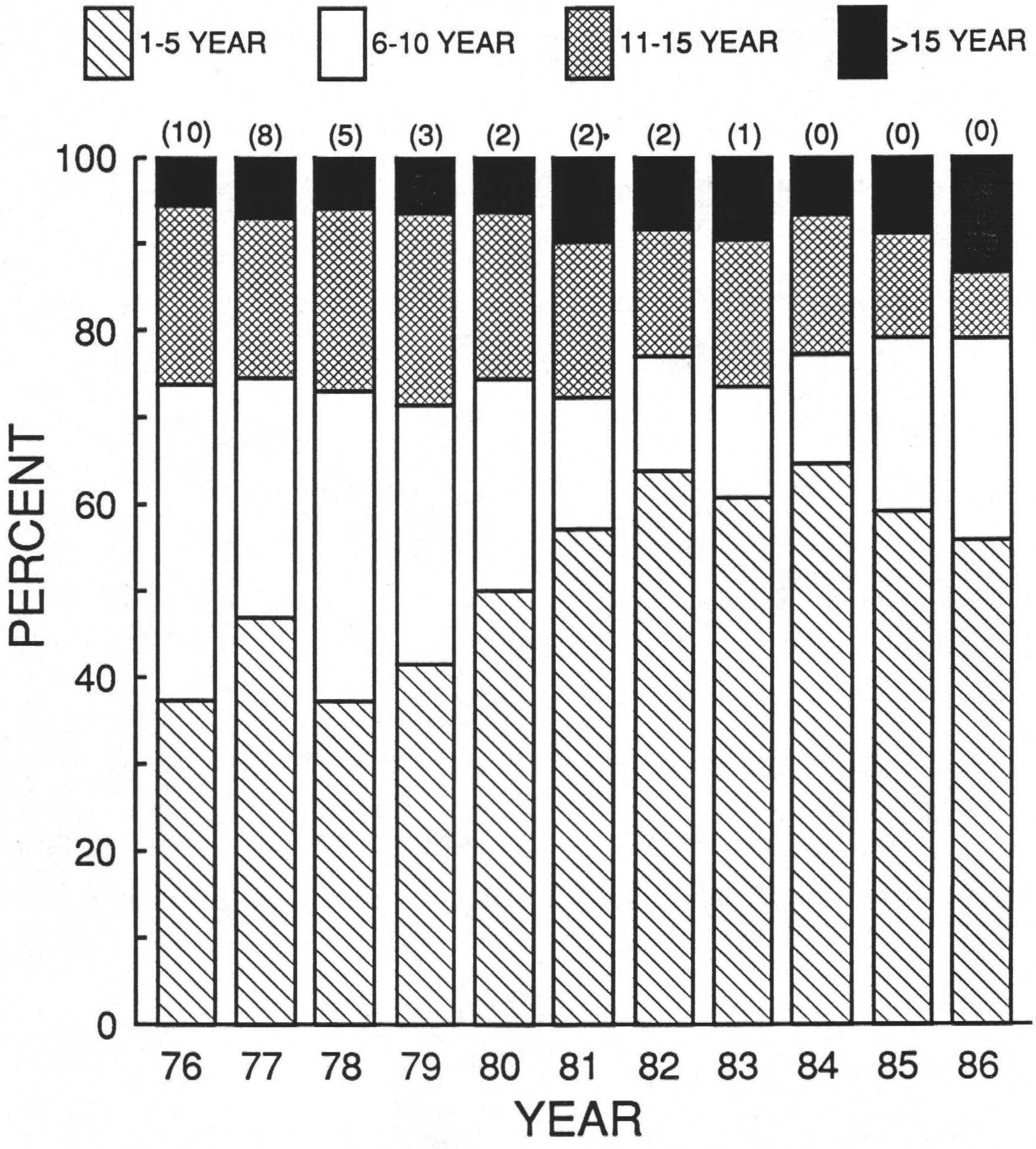

Figure 2. The annual age structure of a feral horse herd in Montana from 1976-86. The percent of horses in the population each year with unknown ages are given in parenthesis.

20%. Horses >15 years old were rare and, with the exception of 1986, never comprised more than 10% of the population. No horses lived beyond 23 years.

Annual population growth rates (λ) were variable during the 11-year study period (Table 1). The population grew in all years except 1978, when reproduction could not offset low survival rates due to an unusually severe winter. Survival during the winter of 1983-84 was also slightly lower than normal and resulted in only a 6% annual increase in the population. In all other years the population grew a minimum of 16% annually. Excluding 1978, the mean growth rate of the population between 1976 and 1986 was approximately 18%.

Discussion

Survival

Results from this study indicate that annual survival of adult horses on PMWHR is usually very high, with a pooled survival rate (1976-86, excluding 1977) of 0.97. Berger (1986:81), studying a herd in northwest Nevada, reported adult survival during a 5-year study of 0.95. These survival rates are comparable to rates of 0.87-0.97 calculated by National Resource Council (1980:52) for a number of observational studies. Wolfe (1980) used age distributions to calculate annual survival rates of 0.80-0.85 for 4 herds in Nevada. The Chapman-Robson (Chapman and

Robson 1960) segment method used in these calculations, however, assumes a stable population. If the population is increasing the survival rates are underestimates and must be corrected. Eberhardt et al. (1982) applied corrections to Wolfe's data and calculated an average survival rate of 0.94. Siniff et al. (1986) presented the only survival data based on telemetry. Radio-marked adult females in 2 herds in western Nevada had annual survival rates of 0.96-0.98 for the 2-year study.

In the present study, the pooled survival rate of adult males was found to be significantly lower than the survival rate of adult females. Differential survival of adult male and female feral horses has not been documented in previous studies, although National Research Council's (1980:53) review of data from several populations suggested that 1 to 6 year old males may have lower survival rates than females of the same age. Such differential survival has been documented for a wide variety of mammalian species (Ralls et al. 1980). Clutton-Brock et al. (1982:280) argue that under conditions of food shortage the increased nutritional requirements of males compared to females leads to higher male mortality. The timing and age composition of mortalities in this study supports Clutton-Brock's energetic hypothesis. Most deaths in the PMWHR population occurred during the winter when nutritional stress is likely to be most severe. Winter mortalities were also most common in young and old horses, which would be expected to have lower energy reserves than prime-aged animals. Berger (1986:102) suggested that higher male mortality may also result from injuries acquired during fights for mates.

The 0.97 estimate of foal survival to the yearling age class was nearly identical to the estimated survival of horses >1 year old. This figure is somewhat misleading because it does not represent survival of foals from birth to age 1. The primary foaling season in PMWHR is mid-April through June (Feist and McCullough 1975, Kirkpatrick and Turner 1983), but many foals each year were not observed for the first time until mid-summer and occasionally even later. Hence, foals that died before the entire area had been thoroughly searched would have gone undetected. Numerous investigations have found foal mortality to be highest during the first 1-2 months of life (Welsh 1975, Boyd 1979, Keiper 1979, Berger 1986). The 0.97 foal survival rate, therefore, must be considered a maximum and is, in all likelihood, an overestimate. The extent of early mortality that was undetected could not be assessed. The high survival rate for those foals that were detected indicates that foals normally experienced little mortality during the fall and winter.

Feist and McCullough (1975) intensively studied the PMWHR population from May to October 1970 and reported 4 of 35 foals dying for a 0.89 survival rate. Foal survival rates calculated from a variety of data sources led the National Resource Council (1980:49) to conclude that "75 to 80 percent survival rates might not be uncommon". The authors, however, discussed a variety of problems and weaknesses in the data including small sample sizes, varying periods of observations, and assumptions of uncertain validity. Berger's (1986) study, which involved very intensive observations throughout the spring and summer, probably provides the most reliable data available on foal survival. During the 5-year period from 1979-83, 120 foals were born in the Granite population with annual foal survival rates ranging from 0.90-0.93 (Berger 1986:82). Foal survival rates presented by Siniff et al. (1986) contrast markedly with the consistently high rates observed in this study and by Berger (1986). In the 2-year study by Siniff et al. (1986) the fate of foals observed with radio-collared females in 2 herd areas was followed throughout the spring and summer. Maximum foal survival in one herd was 0.85-0.90, but foal survival in the second herd varied from 0.67-0.92. These studies indicate that foal survival may be relatively high in most years, but considerable annual variation may exist.

Although timing of mortalities could not be determined precisely, most deaths in PMWHR appeared to occur during the winter when the combination of cold weather and decreased forage quantity and quality forced horses to deplete body reserves. Few horses died during most winters, however, the relatively high mortality rates that occurred during the winters of 1977-78 and 1983-84 represent 76% of all deaths recorded between 1976-86. Although most of the mortalities during both winters were undoubtedly caused by starvation and hypothermia, circumstances differed. The winter of 1983-84 was typical of above normal snowfall conditions experienced periodically throughout the intermountain West and resulted in a moderate increase in mortality. The snow and ice conditions prevalent during the winter of 1977-78, however, was unusual. Hence, these mortalities were excluded from all survival data pooled over years.

Berger (1986:86) also reported that most mortalities of horses ≥1 year old occurred during 2 winters when above normal snowfalls trapped the animals on high elevation ranges. He found a disproportionate number of skeletons above 2000 m, suggesting most mortalities in populations occupying mountainous areas may be due to entrapment at high altitudes during years of heavy snowfall. This hypothesis is supported by internal memos from numerous BLM districts throughout the West that discuss bands of horses perishing under similar circumstances (Garrott, unpublished data). Losses in the PMWHR population during winter 1977-78 were also heaviest in the segment of the population that routinely wintered on the highest ridges.

The important aspects of the survivorship curve presented in Fig. 1 are the high survival throughout the juvenile and prime age classes and the onset of senescence at approximately age 15. The influence of senescence on survivorship of PMWHR horses is conspicuous because of the very high survival rates through maturity (Eberhardt 1985). The proximate cause of senescence in large herbivores is probably due to progressive wear of the teeth (Laws 1981). Obtaining adequate data on the senescence portion of the survival curve is usually difficult because the proportion of a population in the older age classes is small and older animals are difficult to age accurately. Eberhardt (1985) suggests that in many management situations the investigator will frequently be limited to measuring the first 2 components of the survivorship curve, i.e., survival for the first year or 2 of life and survival of prime age animals. Many studies of population dynamics and investigations using population models, however, require complete l_x schedules (Caughley 1977, Starfield and Bleloch 1986). In these situations the senescence parameters presented here may be useful for approximating the impact of senescence on survivorship of the population of interest.

Reproduction

Annual foaling rates of reproductive age females (≥ 3 years)(Table 2) were related to changes in the number of animals in the population and may reflect intraspecific competition for limited forage. Feist and McCullough (1975) reported 38% of PMWHR females $\geq$3 years old foaled in 1970, and foaling rates presented in this study from 1976-78 averaged 39%. These rates are among the lowest reported in the literature and are far below the maximum horses can attain (Boyd 1979, Keiper 1979, Eberhardt et al. 1982, Berger 1986). Range conditions throughout the PMWHR were rated as extremely poor to poor during the early to mid-70's (Hall 1972). Hall (1972) attributed deteriorating range conditions to severe overgrazing that had caused a steady downward trend in forage availability in conjunction with increased soil loss, and invasion by exotic early successional plant species.

Prior to initiation of the first herd reduction program in 1971, Feist and McCullough (1975) estimated 270 horses in the PMWHR population in August 1970, which was triple the 85 animals Hall (1972) suggested as the appropriate stocking rate in 1972. The fragmentary evidence available indicates that from the establishment of PMWHR in 1968 through 1977 a minimum of 120-140 horses were present. Although it is difficult to define carrying capacity (Macnab 1985), this evidence suggests plant communities were severely impacted by herbivory with a scarcity of forage affecting horse reproduction.

Foaling rates abruptly increased in 1979, following the 51% population reduction during the 1977-78 winter, and remained high through 1981. Eberhardt (1977) and Fowler

(1981*a*) have suggested that density dependent responses in large mammal populations occur through a sequence of changes in juvenile survival, age of first reproduction, birth rates of adults, and adult survival. Foaling rates of all age classes increased following the population reduction demonstrating an increase in birth rates, foal survival, or both. A decrease in the average age of first reproduction may also have occurred as the largest increase in foaling rates was observed in 3 to 5 year old females. When the population had recovered to pre-reduction levels in 1982, foaling rates began a steady decline until reaching the relatively low rates observed prior to the herd reduction.

These data suggest that density dependent mechanisms are operating in the PMWHR horse population. This conclusion is based on 3 aspects of annual foaling rates that were related to changes in the horse population. First, foaling rates were extremely low initially and were associated with deteriorating range conditions attributed to heavy grazing. Second, foaling rates significantly changed in the predicted direction after a 51% reduction in the population. And finally, foaling rates showed a tendency to return to values observed prior to the reduction as the population increased to the pre-reduction level. Although conclusively demonstrating the existence of density dependent mechanisms is extremely difficult (Pollard et al. 1987), there is considerable evidence that such mechanisms operate in large mammal populations (Fowler 1981a, 1981b).

The minimum age PMWHR females were observed with a foal was 3 years, which agrees with observations of several other feral horse herds (Feist and McCullough 1975, Welsh 1975, Boyd 1979, Keiper 1979, Nelson 1979). Horses are capable of breeding as yearlings (Ginther 1979), however, the Granite Range population is the only feral horse herd where 2 year olds were reported to foal frequently (Berger 1986:79). Berger (1986:81) attributed the lower age of first reproduction to lack of competition with domestic animals and excellent range conditions.

Eberhardt (1985) suggested that age-specific reproductive rates can be modeled with a 3 component reproductive curve similar to the survivorship curve. The curve describes a gradual increase in foaling rates from the age of first reproduction to an asymptotic value that remains constant until senescence begins to reduce foaling rates in older animals. Both Speelman et al. (1944) and Berger (1986:79) present reproductive data for horses that conforms to Eberhardt's (1985) 3-component reproductive curve, as do the subsets of reproductive data presented in Table 3. Eberhardt's m_x equation (1985), however, could not be successfully fitted to the pooled reproductive data because trends in both early reproduction and reproductive senescence were not well defined. These problems were the result of the age-specific annual changes in reproduction, previously discussed, and extreme variability in reproductive rates of older females due to relatively small sample sizes (Table 3).

Several authors have suggested that foaling females may not be able to recover energy reserves depleted due to the demands of pregnancy and lactation quickly enough to breed in consecutive years (Tyler 1972, Boyd 1979, Nelson 1979). Results of this study, however, indicated that the reproductive history of parous females the previous year had no effect on probability of foaling. Additional evidence that foaling in consecutive years is common is provided by Seal and Plotka (1983) who found that 52 of 76 pregnant females were lactating or had a foal by their side. Although the probability of mature female horses foaling was not significantly affected by their reproductive history the previous year, primiparous females were less likely to reproduce the year following their first foal. This phenomenon is common in domestic animals and is attributed to breeding immature females that are still growing (Morrow 1986:336). Most horses are still physically immature when they become reproductively active as they are capable of breeding as yearlings (Ginther 1979), but continue growing until 4-5 years (Dawson et al. 1945). Hence, the combined energetic demands of maintenance, growth, and reproduction may be responsible for the decreased fecundity the year following a female's first foal.

Adult Sex Ratios, Age Structure, and Population Growth

Several authors have reported sex ratios of adult horses skewed toward females (Keiper 1979, National Resource Council 1980, Berger 1986). A preponderance of adult females has also been recorded for many other species of mammals and has been attributed to increased male mortality and emigration rates (Ralls et al. 1980). Three factors have been identified in this study that, singly or in combination, could act to skew the adult sex ratio toward a preponderance of adult females; differential survival of adult males and females, removal of a disproportionate number of males, and skewed foal sex ratios.

The initial cause of the skewed adult sex ratio in the PMWHR population appears to be the result of the first herd reduction conducted by BLM in 1971. Feist and McCullough (1975) studied the PMWHR population intensively the year prior to the initial reduction and reported the sex and age composition of the population. From these data I calculated an adult sex ratio of 88M:100F (n=235). Hall (1972) evidently did not have access to Feist and McCullough's data and "estimated" the sex ratio of adults in 1971 as "roughly 60% males and 40% females", i.e., 150M:100F. The only mechanism that could have caused such a dramatic change in the sex ratio in 1 year was the exclusion of 40 horses from the population in 1970 by the completion of a boundary fence (Feist and McCullough 1975). Feist and McCullough (1975) placed no significance on the exclusion so it might be assumed that the sex and age composition of these animals was reasonably representative of the population.

Based on Hall's (1972) apparently erroneous estimate of the adult sex ratio, a decision was made to "adjust" the sex ratio of the population. This was accomplished by removing 30 adult males during the initial herd reduction in October 1971 (Hall 1972). The impact of this removal can be estimated using data from Feist and McCullough (1975). If it is assumed that over-winter mortality between 1970 and 1971 was negligible and the 40 horses excluded by the boundary fence was a representative sample of the 1970 population, then the adult population in 1971 would have been 110 males and 120 females (92M:100F). The removal of 30 males would have resulted in a sex ratio of 66M:100F. Thereafter, the skewed sex ratio could be maintained or exaggerated by the 3 factors previously mentioned.

The age structure of the PMWHR population was dynamic throughout the 11-year study period. Although the proportions of older aged horses (>10 years) remained relative stable, the proportions of 1 to 5 and 6 to 10 year olds was variable. The variability in these younger age classes was the result of 2 factors; variable foaling rates and BLM removals. As was discussed in the previous section, foaling rates changed throughout the study. These changes resulted in recruitment of varying numbers of animals into the population each year. Removal programs tended to decrease the number of young animals as they were directed primarily at 1 to 2 year olds. The relatively large shifts in the proportions of 1 to 5 and 6 to 10 year old horses observed between 1978 and 1982 were due to the cessation of the removal program after the 1977-78 winter kill and the concurrent increase in foaling rates.

The 18% growth rate of the PMWHR population is slightly lower than the 20% rates reported by Eberhardt et al. (1982) and Berger (1986:77). The skewed adult sex ratio allowed the PMWHR population to maintain comparable growth rates to the herds studied by Berger (1986) and Eberhardt et al. (1982) despite lower foaling rates. Numerous investigators have questioned the validity of reported annual growth rates exceeding 10-15% in feral horse populations (Conley 1979, Frei et al. 1979, Wolfe 1980, National Research Council 1980). Frei et al. (1979) criticized census techniques and suggested that the high rates were an artifact of poor counts. Conley (1979), Wolfe (1980), and the National Research Council (1980:69) perceived the high survival and fecundity rates necessary to attain such growth rates as unrealistic. Results from this study, as well as those of Eberhardt et al. (1982) and Berger (1986), provide evidence that feral horse populations can attain unusually high growth rates and suggest that such growth rates may be common in the western United States.

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BIAS IN AGING FERAL HORSES

Abstract: Records from 60,116 feral horses (*Equus caballus*) removed from public rangelands in Nevada, Oregon, and Wyoming were used to investigate possible biases in estimating age based on the standardized dental criteria used by veterinarians. Estimates of ages up to 5 years based on incisor eruption and replacement appeared to be relatively unbiased. An exception was the under representation of yearlings in Oregon data that was apparently due to misclassification of yearlings with fully erupted third deciduous incisors as 2 year olds. Systematic biases were detected when estimating ages beyond 5 years and reflects the unreliability of using incisor wear to determine age. These results suggest that biologists developing age-specific demographic parameters based on dental characteristics should only use yearly increments through age 5 and group older animals into broader age classes in order to more accurately reflect the uncertainties of aging these animals.

Introduction

Controversy about the management of feral horse populations occupying public rangelands in the western United States has stimulated a number of studies that have reported age-specific data on a variety of demographic parameters (National Research Council 1980, Wolfe 1980, Seal and Plotka 1983, Berger 1986, Siniff et al. 1986, Plotka et al. 1988). Two of these studies have compiled age structure data (National Research Council 1980, Wolfe 1980) and both have detected anomalies that have raised concern about the validity of the aging criteria (National Research Council 1982). Aging criteria based on eruption and wear of incisors have been standardized and accepted by veterinarians commonly working with known-age domestic horses, however, literature documenting the accuracy of the technique are lacking.

Accuracy of aging techniques cannot be assessed without known-age animals (Dapson 1980), however, systematic biases may be detected by aging a large number of animals and examining the resulting age distributions. Between 1973 and 1987, over 88,000 horses were removed from public rangelands and aged by veterinarians or other qualified personnel (Bureau of Land Management, unpublished data). Since removals occurred throughout the western rangelands and over many years, irregularities in age distributions due to regional and temporal influences, which may affect natality and survival, are avoided. Hence, age distributions derived from these data should approximate a smooth curve with a progressively smaller number of animals in each successive age class. Deviations from this expected distribution would represent biases in the aging technique. The objective of this paper is to present the results of a study of age distributions derived from BLM's removal program and discuss possible biases in the technique used to age horses.

Methods

Records for 60,116 horses removed from public rangelands between 1975 and 1987 were collected from BLM sources in Nevada, Oregon, and Wyoming. Animals were captured by using helicopters to locate and herd bands of horses into corral traps. Captured horses were transported to centralized processing facilities in each state. Each animal was restrained in a padded squeeze chute and freeze branded with a unique number. Records for individual horses included sex, capture date and location, and date the animals was processed. Animals were aged by veterinarians or qualified BLM personnel using standardized dental criteria developed by the profession. The presence and absence of various deciduous and permanent incisors were used to determine age through 5 years, when the last permanent incisors are fully erupted. After age 5 aging becomes more subjective as it is dependent on various characteristics of tooth wear and form (Amer. Assoc. Equine Practitioners, 1981). Horses were aged to the nearest year, except in Wyoming, where no attempt was made to estimate the age of animals ≥12 years old.

Results and Discussion

Age distributions from all 3 states have a variety of peaks and troughs that deviate from the expected smooth distribution (Table 1). With the exception of an apparent

Table 1. The age distribution of feral horses removed from public rangelands in Nevada, Oregon, and Wyoming between 1978 and 1987.

	Nevada		Oregon		Wyoming	
Age	No.	Percent	No.	Percent	No.	Percent
0	5993	17.88	1881	20.27	2948	17.03
1	5092	15.19	960	10.34	2747	15.87
2	4140	12.35	1393	15.01	2614	15.10
3	3096	9.24	928	10.00	1559	9.00
4	2485	7.41	741	7.98	1495	8.63
5	1806	5.39	504	5.43	646	3.73
6	3098	9.24	765	8.24	759	4.38
7	2325	6.94	598	6.44	914	5.28
8	1375	4.10	389	4.19	802	4.63
9	558	1.66	213	2.30	536	3.10
10	514	1.53	284	3.06	393	2.27
11	251	0.75	203	2.19	375	2.17
12	493	1.47	82	0.88		
13	452	1.35	16	0.17		
14	203	0.61	56	0.60		
15	343	1.02	113	1.22		
16	116	0.35	16	0.17		
17	136	0.41	2	0.02		
18	160	0.48	10	0.11		
19	31	0.09	33	0.36		
20	483	1.44	80	0.86		
21	31	0.09	0	0.00		
22	39	0.12	1	0.01		
23	41	0.12	1	0.01		
24	57	0.17	4	0.04		
25	79	0.24	6	0.06		
>25	106	0.32	2	0.02		
Total	33521		9281		17314	

under representation of yearlings in the Oregon data, the number of horses assigned to each age class from foal to 5 years steadily decreases, as expected. Since the yearling deficiency is unique to the Oregon data, it cannot be attributed to the aging criteria, but must represent a problem peculiar to this state.

The National Research Council (1980) also noted under representation of yearlings in horse age distributions derived primarily from Oregon BLM data and attributed the problem to sampling bias, i.e., yearlings were not captured in proportion to their availability. This explanation seems questionable for 2 reasons. First, all 3 states used similar techniques for capturing horses. Any sampling bias associated with the capture technique, therefore, should also be present in data from Nevada and Wyoming. Second, yearlings are not spatially or socially segregated in horse populations, but are usually associated with harem or stallion bands (Berger 1986). The normal procedure when capturing horses is to consolidate several of these natural social groups and herd them as a unit into a corral trap. Thus, there is no obvious mechanism that would make yearlings less susceptible to capture.

An alternative explanation for the apparent deficiency of yearlings in the Oregon data is the systematic misclassification of yearlings into adjacent age classes. Discussions with Oregon BLM personnel revealed that horses were considered yearlings if the third or corner deciduous incisors were partially erupted, but if these incisors were fully erupted and in contact the animal was considered a 2 year old. Several references on aging horses, however, indicate that the corner incisors are in contact by 18-20 months (Ensminger 1977, Amer. Assoc. Equine Practitioners 1981). Hence, yearlings captured and aged in late fall or winter had a high probability of being misclassified as 2 year olds. The use of this criteria to distinguish between yearlings and 2 year olds is probably the primary reason for the under representation of yearlings in the Oregon data.

At 5 years of age all incisors are fully erupted and the criterion for estimating age for older animals is based primarily on incisor wear (Amer. Assoc. Equine Practitioners 1981). There appears to be a systematic bias at this transition point as the number of horses classified as 6 and 7 year olds exceeds the number of horses classified as 5 year olds in all three states (Table 1). Again, the most reasonable explanation for this bias is the misclassification of animals from adjacent age classes into the 6 and 7 year age groups. Caughley (1965, 1977) demonstrated considerable variation in the timing of tooth eruption and wear patterns between individual Himalayan thar (Hemitragus jemlahicus) and it is reasonable to assume similar variation exists in other large herbivores as well (Wiener and Donald 1955). This variation results in errors in estimating age of animals that can best be visualized as a probability distribution. An animal that is X years old may have a 0.50 probability of being assigned into the correct age class based on dental characteristics and a 0.25 probability of being assigned into either the X-1 or X+1 age classes. For example, some 5 year old animals will have greater than normal incisor wear and be classified as 6 year olds while the incisors of some 6 year olds will have less than normal wear and be classified as 5 year olds. These errors are obviously not compensating in the first several age classes that use incisor wear to estimate age. The reason for this is unclear, but it is clear from the data in Table 1 that aging errors are common and a distinct bias exists in these age classes.

The age distributions beyond 9 years old are erratic and undoubtedly reflect the uncertainty of estimating age based on tooth wear. The American Association of Equine Practitioners (1981) cautions that after all permanent teeth are fully erupted aging becomes increasing difficult and Ensminger (1977) states that horses cannot be accurately aged beyond 12 years. Data from Nevada and Oregon, where horses were assigned ages up to 30 years, provides evidence that aging older animals is quite speculative. The age distributions from both of these states show a strong bias toward ages divisible by 5. This bias is particularly noticeable for the 15 and 20 year age classes, but is also evident to a lesser extent in the 10 and 25 year age classes (Table 1), suggesting ages can only be roughly estimated beyond 10 years old.

Development of age-specific fecundity and survival schedules are important in order to understand the dynamics of feral horse populations and construct models to explore the consequences of various management programs (Caughley 1977, Eberhardt 1985, Starfield and Bleloch 1986). Data presented in this paper suggest that current techniques used for aging feral horses result in a variety of inaccuracies and biases that limit the application of age data derived from dental characteristics for demographic studies. In general, the use of incisor eruption and replacement to age horses up to age 5 appears to be relatively unbiased, allowing the development of age-specific parameters based on yearly increments. The use of tooth wear to estimate age beyond 5 years, however, is less reliable due to a variety of biases. Because of these problems I recommend abandoning the use of yearly increments beyond age 5 in favor of broader age classes such as 5 year increments that would more accurately reflect the reliability of age estimates based on tooth wear.

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AGE-SPECIFIC REPRODUCTION IN FERAL HORSES

Abstract: Two age-specific reproduction schedules were constructed for feral horses (Equus caballus) based on lactation status of 14,788 females captured during herd reduction programs and pregnancy rates of 667 horses determined by serum progesterone assays. The probability of detecting lactation progressively decreased for females captured further from the foaling season indicating that these data resulted in substantial underestimates of true foaling rates. A third reproductive schedule was, therefore, constructed based on a subsample of 1144 horses captured immediately after the foaling season in June. Characteristics common across all 3 data sets were first reproduction at age 2, an increase in the proportion of females foaling through age 6, highest foaling rates from 6-15 years, and a gradual decrease in foaling rates of females >15 years. Variability in the proportion of reproductively active females in each age class was detected among populations and among years within a population, however, the general trend was high reproductive rates with 80-90% of the prime age females foaling. Eberhardt's (1985) reproduction model provided a close mathematical approximation of the observed age-specific changes in foaling rates, providing a useful tool for the construction of reproduction schedules required for age-structured population models.

Introduction

Feral horses are an important component of the faunal community in the western United States with an estimated 40,000 animals present on public lands in 1988 (Bureau of Land Management 1989). Most of these animals live in the Great Basin, a geographic region covering much of Nevada and portions of Oregon, California, and Utah. Large numbers of feral horses also occur in the Red Desert of southwestern Wyoming with smaller populations scattered throughout the rest of the state. In addition, small, isolated populations are found in Arizona, Colorado, Idaho, Montana, and New Mexico (Bureau of Land Management 1989). Although feral horses have been present in the western United States since the 17th century (Zarn et al. 1977), they have received little scientific attention (National Research Council 1980).

Passage of several laws in the 1970's established public ownership of feral horses occupying federal lands and mandated the monitoring and control of populations by the appropriate federal agencies (Boyles 1986). Since that time, the management of feral horse populations has been hindered by conflicts between special interest groups that have been aggravated by a lack of data on the population dynamics. A primary point of contention has been the claim by some federal agencies that feral horse populations commonly increase 20% annually (Wagner 1983). Population modeling experiments have demonstrated that in order to attain such high growth rates both reproduction and survival of feral horses must be exceedingly high compared to other large mammals (Conley 1979, National Research Council 1980, Wolfe 1980, Eberhardt et al. 1982). The objective of this study was to determine age-specific reproduction in feral horses using several independent data sets and attempt to fit these data into a mathematical framework that would aid in the construction of population models.

Methods

Two sources of data were used to investigate age-specific reproduction. The most extensive information was obtained from records of 14,788 female horses ($\geq$1 year old) captured in Nevada during Bureau of Land Management (BLM) herd reduction programs. These records represent 66 reductions conducted on 38 horse management areas between 1979 and 1987. The number of horses captured during individual reductions varied from <50 to 2,221. Most horses were captured using a helicopter to herd groups of animals into corral traps. Captured horses were transported to a holding facility at Palomino Valley, Nevada. Each animal was restrained in a padded squeeze chute, sexed, aged, and freeze branded with a unique number. The lactation status of all females $\geq$1 year old was determined by visual examination of the udder. Lactation was considered evidence that the female produced a foal during the current reproductive season. In addition to presenting age-specific foaling rates for the entire data set, foaling rates for a subsample of animals captured immediately after the foaling season in June are also presented. These data represent 1144 horses removed from a single population (Nevada Wild Horse Range) over 3 consecutive years (1985-1987).

The second source of data was blood samples collected from 667 female horses ($\geq$1 year old) captured for research purposes between 1985 and 1987. Horses from 4 management units in Nevada were sampled, 78 from the Flanigan unit in December 1985, 59 from the Wassuk Mountain unit in January 1986, 144 from the Stone Cabin Mountain unit in August 1986, 83 from the Clan Alpine Mountain unit in September and October 1986, and an additional 240 from the Clan Alpine Mountain unit in August 1987. Seventy-three samples were obtained from the Beatty's Butte unit in southeastern Oregon in February 1986. Standard BLM procedures, as described above, were used to capture, handle, and age all horses. Blood samples were collected and handled as described by Plotka et al. (1988). Pregnancy status was determined from serum progesterone levels measured by radioimmunoassay (Plotka et al. 1975) with levels $\geq$2 ng/ml considered indicative of pregnancy (Wolfe et al. 1989). The gestation period of a horse is approximately 340 days (Ginther 1979), hence, a 3 year old female assessed as pregnant will produce the foal as a 4 year old. In order to make the pregnancy data comparable with data derived from BLM records the age of each female bled was incremented by 1 year to reflect her foaling status the following year, assuming no intrauterine mortality.

Horses from both groups were aged to the nearest year based on dental characteristics. Age estimates up to 5 years were based on incisor eruption and replacement with ages >5 estimated based on incisor wear (Amer. Assoc. Equine Practitioners 1981). Although accuracy of the aging technique has not been documented, an examination of the age distributions of captured feral horses indicated that age estimates through 5 years appeared to be relatively unbiased while age estimates of older horses were less reliable due to a variety of biases (Garrott 1990b). Age-specific reproductive data, therefore, are presented in yearly increments through age 5 and 5-year increments beyond age 5. Foaling rates for each 5-year age class were calculated as unweighted means and plotted at the center of the interval when fitting reproductive curves to the data.

Age-specific reproductive data were fitted to the equation developed by Eberhardt (1985) for long-lived vertebrates using the SAS nonlinear least squares procedure NLIN (SAS Institute 1985). This equation:

$$R_x=A\{1-\exp[-B(x-C)]\}\exp\{-D(\exp[Ex]-1)\}$$

models a 3-component curve where x is age, A represents the maximum reproductive rate, B is a parameter describing the rate of increase during the early reproductive years, C is the age prior to first reproduction, D and E are parameters that describe the decrease in reproduction in older age classes due to senescence, and R_x represents age-specific reproductive rates. The equation notation follows that presented by Eberhardt and Siniff (1988) with the exception of R_x, which was presented as m_x in both Eberhardt (1985) and Eberhardt and Siniff (1988). The m_x notation is traditionally used to denote age-specific reproductive rates expressed as number of female births or embryos per adult female (Caughley 1977). I choose to present age-specific reproductive data in this paper as the proportion of females foaling in each age class and, therefore, changed the notation to R_x to avoid confusion.

Results and Discussion

Sources of Error in the Data

There were 2 potential sources of error in the data presented in this paper, mistakes in aging the animals and misclassification of reproductive condition. One possible indication of aging error is the classification of 31 horses as having foaled as yearlings (Table 1). These are clearly errors since horses have a 340-day gestation period (Ginther 1979), which would have required breeding as foals. It is possible that some of these errors were due to misclassification of reproductive status, however, all 31 horses were judged to have distended udders and errors in

Table 1. Age-specific foaling rates derived from lactation status of feral horses captured during BLM herd reductions conducted throughout the year, reductions conducted during June only, and from pregnancy rates determined from serum progesterone levels of a sample of horses captured for research purposes. Numbers in parenthesis indicate the number of females that produced foals in each age class.

	Reduction-all		Reduction-June		Serum Prog.	
Age	N	% foaling	N	% foaling	N	% foaling[1]
1	2691	1.2 (31)	243	0.4 (1)		
2	2262	12.2 (275)	239	30.5 (73)	89	34.8 (31)
3	1698	26.3 (446)	133	51.9 (69)	73	67.1 (49)
4	1441	31.2 (450)	146	63.0 (92)	94	77.7 (73)
5	1047	34.8 (364)	59	66.1 (39)	65	73.8 (48)
6-10	4242	40.0 (1695)	251	78.5 (197)	219	88.6 (194)
11-15	864	41.7 (360)	40	80.0 (32)	78	93.6 (73)
16-20	428	37.9 (162)	26	76.9 (20)	44	86.4 (38)
>20	115	33.0 (38)	7	57.1 (4)	15	73.3 (11)
Total	14788	25.6 (3790)[2]	1144	46.0 (526)[2]	667	

[1] serum progesterone data measured pregnancy rates so ages were incremented by 1 year to reflect age female would produce foal

[2] does not include yearlings assigned as foaling

aging seem more probable. As discussed earlier, horses >5 years old were grouped into 5-year age classes in an attempt to minimize inherent biases in determining the age of older animals (Garrott 1990b). Although it is difficult to assess the frequency of aging errors without known age animals (Dapson 1980), errors in assigning horses into even these broad age classes still undoubtedly occurred. However, the impact of such errors on the reproductive data presented in this paper is believed to be minor. A more significant source of error for the data derived from females removed during the BLM herd reduction programs was apparently failure to identify reproductively active females.

The estimated foaling rate of all females ($\geq$1 year old) removed by BLM during herd reductions was 26% (Table 1), which is approximately half that reported for other feral horse herds throughout the western United States (Feist and McCullough 1975, Boyd 1979, Berger 1986, Siniff et al. 1986). These data suggest the criterion used to assess reproductive status failed to identify a large proportion of the females that foaled. A chi-square test of estimated foaling rates by month revealed that the proportion of females classified as foaling was related to the month they were captured ($\underline{P}<0.001$). The highest foaling rate was recorded for horses captured in June. Thereafter, foaling rates steadily decreased with the lowest rates recorded for females captured during the winter months (Fig. 1).

Reproduction in feral horses is strongly seasonal with most foals born from April through June (Feist and McCullough 1975, Boyd 1979, Berger 1986). The temporal trend in these data indicates that the probability of detecting lactation declines for females captured progressively further from the foaling season. Age-specific foaling rates derived from these data, therefore, will be substantial underestimates of the true foaling rates. Examination of foaling rates derived from the entire sample, however, is still useful for studying the general trends in age-specific reproduction, especially the senescence portion of the curve where adequate sample sizes are exceedingly difficult to obtain (Eberhardt 1985).

Foaling rates calculated from the subset of horses captured in June (immediately after the foaling season) undoubtedly provides a more accurate estimate of age-specific reproduction, however, misclassification errors are still probable. Numerous investigations have found that most foal mortality occurs during the first 1-2 months of life (Welsh 1975, Boyd 1979, Keiper 1979, Berger 1986). Females that loose their foals usually cease lactating within several weeks (Ginther 1979). Thus, females that had lost their foal a month or more prior to capture would not be classified as reproductively active. Females that did not foal during the current year may have continued to nurse the previous year's foal which could also result in

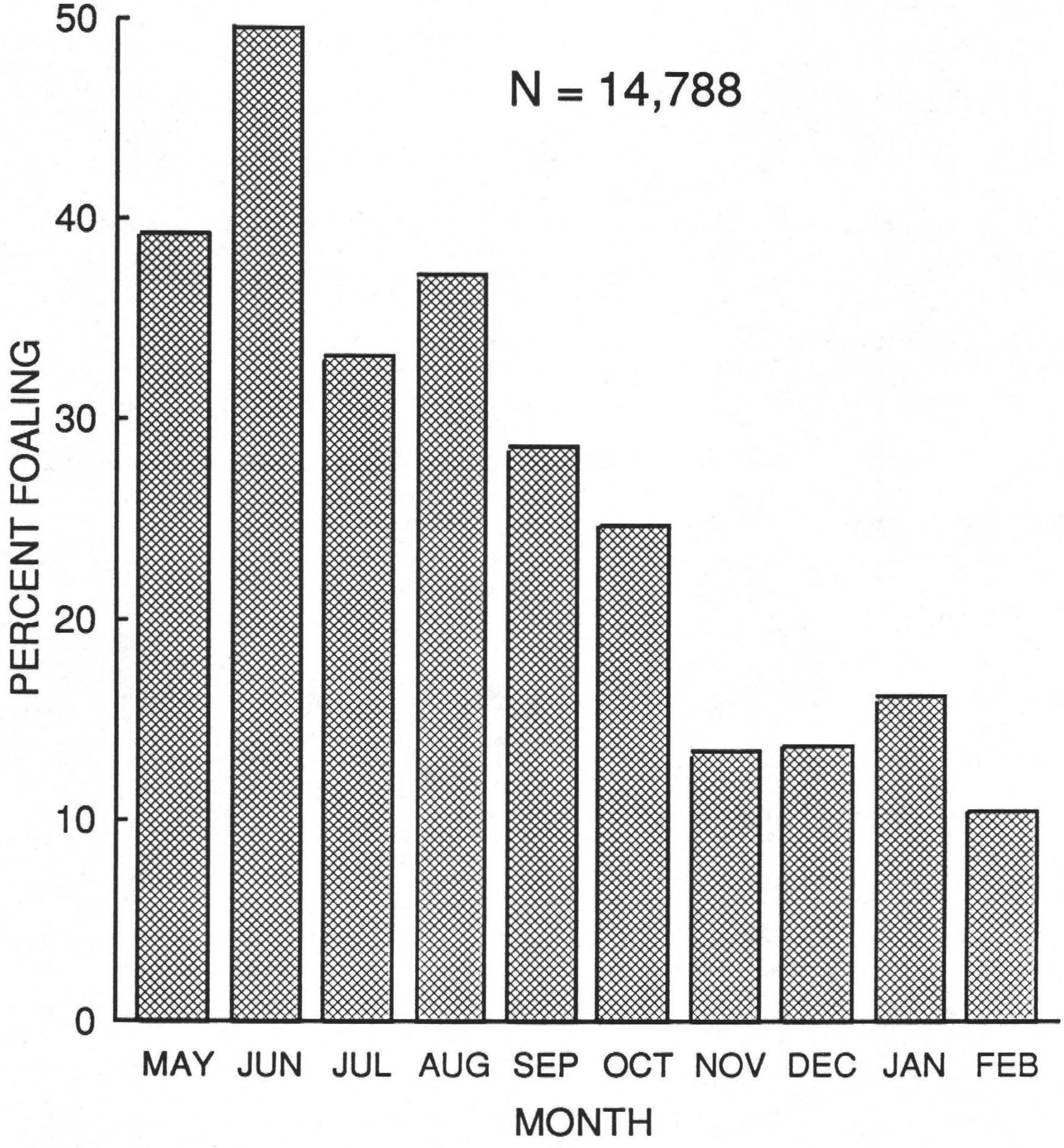

Figure 1. Monthly changes is the proportion of feral female horses removed from public rangelands in Nevada between 1979 and 1987 that were classified as lactating, indicating they had foaled during the year of capture.

classification errors. Such prolonged nursing, however, appears to be rare (Berger 1986), suggesting that foaling rates calculated from the horses captured in June are underestimates due to early foal mortality.

The accuracy of assessing pregnancy in feral horses based on serum progesterone levels was investigated by Wolfe et al. (1989) using horses that were rectally palpated by a veterinarian to determine pregnancy. Pregnancy status determined by the 2 techniques was in agreement for 82% of the 113 horses in the experiment. These data indicate that determination of pregnancy status based on serum progesterone levels is not without error, however, whether the technique is biased is uncertain as the authors did not distinguish between errors of omission and commission. An additional possible source of error is intrauterine mortality that would result in a smaller proportion of the females producing viable foals than indicated by pregnancy rates. Approximately 10-12% of domestic horses diagnosed as pregnant do not produce viable foals, with most losses occurring during the first several months of pregnancy (Ginther 1979). Errors in foaling rates due to fetal loss were probably not common since pregnancy status for most of the horses in this study was determined from blood samples collected in the fall or winter, after the period when most losses would be expected to occur.

Age-specific Reproduction

Characteristics common across all data sets are first reproduction at age 2, an increase in the proportion of females foaling through age 6, highest foaling rates from 6-15 years, and a gradual decrease in foaling rates in females $\geq$15 years old (Table 1, Fig. 2). This pattern of age-specific reproduction conforms closely to the general model developed by Eberhardt (1985) for long-lived large mammals, with non-linear least squares procedures producing relatively good fits to all 3 data sets (Fig. 2). With the exception of A (maximum reproductive rate), the coefficient estimates were similar for the foaling rates derived from horses removed in June and the serum hormone data (Table 2). The coefficient values for the curve fitted to foaling rates derived from all horses removed by BLM personnel differed markedly from the other 2 data sets, however, this was not surprising given the previously described limitations of these data.

Prior to 1980, all available data indicated that feral horses did not foal until they were at least 3 years old (National Research Council 1980) with recent studies by Seal and Plotka (1983) and Garrott (1990a) supporting this supposition. The 37% foaling rate for 2 year olds reported by Berger (1986) for a feral horse population in Nevada was the first evidence of significant foaling by feral horses <3 years old. Berger (19860 attributed the high reproduction

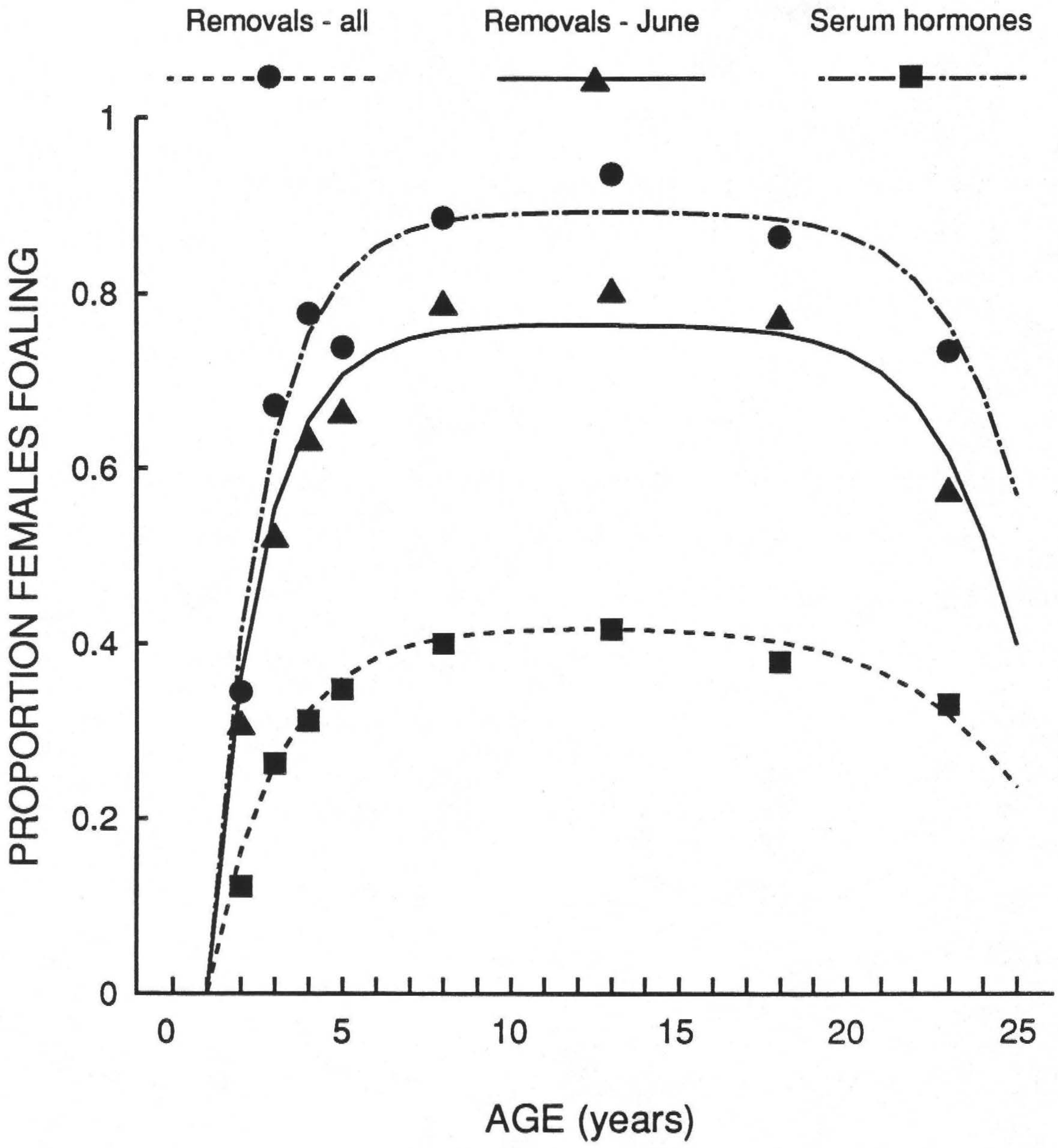

Figure 2. Curves fitted to feral horse reproductive data using non-linear least squares to estimate the coefficients of Eberhardt's (1985) equation for modelling age-specific reproduction in large mammals.

Table 2. Results of non-linear least squares procedures for fitting Eberhardt's (1985) equation for modelling age-specific reproduction to the 3 feral horse data sets presented in Table 1.

Coeff	Biological interpretation of coeff.	Coeff. Value		
		Reduc.-all	Reduc.-June	Serum Prog.
A	Maximum repro. rate	0.4140	0.7973	0.8945
B	Early rate increase	0.4672	0.5053	0.6178
C	Age prior 1st repro.	1	1	1
D	Senescence param.	0.00003008	0.00000132	0.00000082
E	Senescence param.	0.3926	0.5390	0.5294
T	Modal age senesc.	26.6	25.1	26.5
S_T	Modal age std. dev.	2.55	1.86	1.89
SSE	Sum square errors	0.0007	0.0014	0.0115

of this herd to unusually favorable foraging conditions caused by a recent range fire and removal of cattle from the area. Data from the present study as well as Wolfe et al. (1989), however, indicate that foaling by 2 year olds may be common.

Serum progesterone levels detected pregnant yearlings (therefore foaling as 2 year olds) in 4 of the 5 herds sampled in this study and 6 of 7 herds sampled by Wolfe et al. (1989), with the proportion pregnant varying from 10 to >50% among populations. Although the criteria used to detect foaling females in horses removed from rangelands substantially underestimated foaling rates, foaling 2 year olds were detected in 31 of the 38 herds sampled, providing additional evidence that foaling by 2 year olds is common. Foaling rates of 41% (n=143) and 17% (n=79) for 2 year olds removed from the Nevada Wild Horse Range during June of 1985 and 1987, respectively, indicates that foaling rates of 2 year olds may also vary significantly ($\underline{P}<0.001$) among years within the same population.

Substantial variability in age of first reproduction is common in long-lived large mammals. Variation in this demographic parameter cannot be attributed to any single factor, but is the result of complex interactions between physical and biological components of the ecosystem. Regional and annual differences in abiotic factors such as soils, precipitation, and growing season control primary productivity that dictates the quantity and quality of forage available for herbivory. The degree of intra and inter-specific competition then controls the amount of forage each individual can procure which, in turn, is reflected in the time needed for individuals to attain sexual maturity. Thus, the variation observed in the proportion of 2 year old horses foaling in various populations is to be expected.

Binomial estimates of foaling rates for prime age females (6-15 years old) were 40 (n=5106), 78 (n=300) and 90% (n=261) for all captured horses, those captured in June, and the serum hormone data, respectively (Table 1). Estimates of this same parameter based on the non-linear least squares fit of Eberhardt's (1985) model to each data set were 42, 76, and 89%, respectively (Table 2). The similarity of the non-linear least squares and binomial estimates of prime age foaling rates provides additional evidence of the suitability of Eberhardt's model for describing age-specific changes in feral horse reproduction. The differences in foaling rates calculated for the horses captured in June and the serum hormone data are probably more an artifact of the differences in the techniques used to assess reproductive activity than any inherent differences in reproduction between the populations sampled with each technique.

The most comparable data to this study are those presented by Seal and Plotka (1983) and Berger (1986) who reported similar prime-age reproductive rates of approximately 80-85%. A variety of other investigators have also reported age-specific reproductive rates for feral horse populations (Feist and McCullough 1975, Welsh 1975, Boyd 1979, Garrott 1990a, Wolfe et al. 1989), however, differences in sample size, methodology, and how the data were reported precluded direct comparisons. Despite these limitations, data presented by these investigators suggest that reproductive rates of prime-age females may vary considerably among populations as well as among years within the same population. Like age of first reproduction, variability in foaling rates of prime-age females is probably the result of both biotic and abiotic factors affecting the quantity and quality of forage individual horses procure.

Although reproductive senescence is evident in all 3 data sets, the rate of decline in the proportion of females foaling in the 15-25 year age classes is relatively gradual. Eberhardt's equation for modelling age-specific reproduction uses the Gompertz curve to model senescence (Eberhardt 1985). This curve, originally used by Siler (1979) to model senescence in survival, provides a very good representation of senescence in age-specific survival probabilities of a variety of large mammals (Siler 1979, Eberhardt 1985, Garrott 1990a). Application of the Gompertz curve to model reproductive senescence, however, has been more limited, with data from the northern fur seal (Callorhinus ursinus) the only example were the curve provides a uniformly good fit to the data (Eberhardt 1985). Conceptually, the Gompertz curve forces the probability of reproducing to zero in the oldest age class. While this is certainly appropriate when modelling survival, its applicability when describing reproductive senescence may be somewhat limited. There is increasing evidence for a variety of large-bodied mammals that reproductive senescence is not as precipitous as senescence in survival, with females in the older age classes continuing to produce young at relatively moderate rates until death (Clutton-Brock et al. 1988, Le Boeuf and Reiter 1988, Packer et al. 1988, Shaw and Carter 1989).

Despite the conceptual difficulty of applying the Gompertz curve to model reproductive senescence in feral horses, a good fit to each set of data was obtained by putting no bounds on the parameter values that could be selected with the non-linear least squares procedure and truncating the fitted curve at the oldest age class. Siler (1979) provided biological interpretations of the 2 senescence coefficients as $D=\exp(-T/S_t)$ and $E=1/S_t$, where T is an approximation of the modal age of senescence and S_t is the variance about the mode. Conversion of the coefficients for the feral horse data would result in estimates of the modal age of senescence of approximately 25-26 years with standard deviations ranging from 1.8 to 2.6 (Table 2).

Since feral horses do not appear to live beyond 25 years (Garrott 1990a), such interpretations appear to be inappropriate when using the Gompertz curve to model senescence in the manner presented in this paper.

The construction and use of population models has become an increasing common endeavor to explore ecological and demographic interactions and the consequences of various natural and man-made perturbations to populations (Starfield and Bleloch 1986). Two methods commonly used for modeling long-lived animals are Lotka's equations (1907) and Leslie matrix calculations (1945, 1948). Both of these techniques require age-specific reproduction schedules that, in practice, are seldom available for the population or species of interest. The early attempts at modeling feral horse population dynamics are good examples of this common problem (Conley 1979, Wolfe 1980).

In future modelling efforts this problem may be alleviated by using Eberhardt's (1985) reproduction model, as it provided a close mathematical approximation to age-specific changes in feral horse foaling rates documented in this study. In addition, the similarity of the model coefficients describing the rate of reproductive increase in early years (B) and senescence (D and E) derived from two independent data sets (June removals and serum hormone assays) suggests these coefficients may be relatively constant. If the coefficient values presented in this paper are accepted as representative of feral horse populations in general, then construction of age-specific reproductive schedules could be accomplished simply by varying the remaining 2 model coefficients, age prior to first reproduction (C) and foaling rate of prime age animals (A). In many situations when detailed age-specific data are not available or impossible to obtain it is often possible to estimate these 2 reproductive parameters.

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FERAL HORSE SEX RATIOS AND DIFFERENTIAL SURVIVAL

Abstract: Data were collected on 60,111 feral horses (*Equus caballus*) removed from public lands in Nevada, Wyoming, and Oregon between 1976-1987. Foal sex ratios differed significantly from parity ($P<0.05$) in samples from 9 of 75 management area, 7 in favor of females and 2 in favor of males. Adult sex ratios were skewed ($P<0.05$) in samples from 44 of 89 areas, 42 in favor of females and 2 in favor of males. No evidence of differential capture probability between adult males and females could be detected, therefore, the tendency for adult sex ratios to be skewed toward females was attributed to differential survival. Samples from all management areas within each state were combined to explore age-specific changes in sex ratios in an effort to identify possible mechanisms causing differential survival. Data from all 3 states showed a similar trend, with the proportion of males steadily decreasing from near parity in foals, to lows of 0.61-0.77 in the 4-5 year age classes. The trend then reversed with males becoming predominant (1.08-1.36) in the >10 year age class. Population simulations indicated that survival differentials of 0.05-0.07, favoring females through age 4, and 0.02-0.04 favoring males in older age classes were required to mimic observed age-specific sex ratio changes. In order to obtain the high proportions of males in the >10 year age class, onset of senescence also had to be earlier for females.

Causes for differential survival in the young age classes are uncertain, but may relate to behavioral or metabolic differences between the sexes. Lower survival of females in older age classes was attributed to the relatively high energetic costs of reproduction in females and spring breeding that allows males to recover lost body reserves before the onset of winter.

Introduction

Information on age and sex-specific differences in survival is important in our understanding of population dynamics (Caughley 1977, Eberhardt 1985) and sexual selection (Trivers 1972). Obtaining survival data directly is difficult and expensive as it requires individually identifying or radio tagging large number of animals and observing them for long periods of time to detect mortality (Clutton-Brock et al. 1982, Berger 1986, White and Garrott 1990). Survival can also be estimated indirectly with such techniques as the analysis of age distributions (Chapman and Robson 1960) and recovery of marked animals (Brownie et al. 1985).

Another indirect method of investigating differential survival between the sexes is the examination of sex ratios (Trivers 1972, Ralls et al. 1980). Although sex ratio data cannot provide direct estimates of survival, when used in conjunction with information on the age of the animals, insights into the timing and relative magnitude of differences in survival can be obtained. Obtaining such data in sufficient quantities to detect significant shifts in sex ratios, however, is extremely difficult (Trivers 1972). Over the past decade, large numbers of free-ranging horses have been removed from public lands in the western United States, providing an extensive data base for the study of sex ratios in this large herbivore. The purpose of this paper is to present the results of an investigation of differential survival between the sexes using these data.

Methods

Data in this study were obtained by consolidating Bureau of Land Management (BLM) records of horses removed from public lands in Nevada, Oregon, and Wyoming, the 3 states with the largest feral horse populations (Bureau Land Management 1989). Areas occupied by feral horses in the western United States have been divided into discrete management units, with horses within each unit managed as a population (Boyles 1986). In some regions, such as the insular mountain ranges of Nevada, management units may represent closed populations, however, in other areas, such as the Red Desert of Wyoming, horses move freely between management units. Populations are monitored by periodic aerial censuses and are allowed to increase until reaching a pre-determined maximum level, at which time a herd reduction in conducted (Boyles 1986). The proportion of the population removed during each reduction normally ranged from 35-70%, with most populations reduced several times since active management began. In addition, entire populations were occasionally removed in situations where the horses were infringing on the rights of private land owners. Between 1973 and 1987 this management program resulted in the capture and removal of a minimum of 89,000 horses (BLM, unpublished data).

Animals were captured by using helicopters to locate and herd bands of horses into corral traps. Captured horses were transported to centralized processing facilities in each state. Each animal was restrained in a padded squeeze chute and freeze branded with a unique number. Records for individual horses included sex, pelt coloration and markings, date, and capture location. Animals were aged by qualified veterinarians using standardized dental criteria developed by the profession (Amer. Assoc. Equine Practitioners, 1981). Horses were aged to the nearest year, except in Wyoming, where no attempt was made to estimate the age of animals beyond 12 years.

Sex ratio data are presented as number of males per female (ex. 0.86). Chisquare tests were used to test for significant departures from parity in sex ratios of foals (<1 year old) and adults ($\geq$1 year old) captured within each management unit (Fienberg 1980). Only samples with a minimum of 25 animals were used in the analysis. All horse records from each state were combined to explore age-specific changes in sex ratios. Criteria for aging horses up to 5 years was based on tooth eruption and replacement and appears to be relatively unbiased (Garrott 1990b). Sex ratios, therefore, were calculated for yearly age classes from foal (0) to 5 year olds. After 5 years, age was estimated base on subjective evaluation of tooth wear, the usefulness of which appears limited to assigning animals into general age categories (Garrott 1990b). Data beyond age 5, therefore, were grouped into 2 categories, 6-10 year olds and horses >10 years old. Log-linear analysis was used to test the effects of age and state on the proportion of males and females in each age category (Fienberg 1980).

Population simulations were conducted using a variety of age-specific survival schedules (p_x) for males and females in an effort to emulate age-specific changes in the sex ratios observed in the data. A deterministic, age-structured model using 26 age classes (0-25) was constructed using a commercial spreadsheet program. Reproductive data derived from 1144 horses examined for lactation status in June were used to construct a reproductive schedule using Eberhardt's (1985) model for age-specific reproduction (Garrott 1990c) This schedule remained constant for all simulations. The model assumed sex ratio at birth was parity. Simulations were conducted for a 20-year period in order to assure a stabilized age structure. Age-specific sex ratios were then calculated from the population at year

20. Finite rates of increase (lambda) were calculated as the population in year 20 divided by the population in year 19.

Results and Discussion

Data were collected on 60,111 horses, including 33,521, 17,309, and 9,281 animals from Nevada, Wyoming, and Oregon, respectively. These records represent 261 individual removals conducted on 89 different management units distributed throughout feral horse range in each of the 3 states. The number of animals captured during each removal range from <50 to 2,221, with a mean of 499, 131, and 152 for Nevada, Wyoming, and Oregon respectively. These records represent nearly all animals removed from public lands in Wyoming and Oregon since active management began in the mid-1970's until 1987. Records from an estimated 10,000+ horses removed in Nevada, however, could not be located.

Foal and adult sex ratios

Eighty-seven percent of the 74 management areas which had adequate data ($n \geq 25$) to test foal sex ratios showed no significant departure from parity ($P > 0.05$). Other studies of feral horse populations have also reported foal sex ratios near parity (Feist and McCullough 1975, Boyd 1979, Keiper 1979, Berger 1986), which is common for mammals in general (Clutton-Brock and Iason 1986). Of the 9 areas with significant differences, 7 were skewed in favor of females and 2 in favor of males ($P < 0.05$)(Table 1). When performing

Table 1. Summary of the results of chisquare tests for significant departures from parity in sex ratios of foals and adults captured within various BLM herd management units in Nevada, Wyoming, and Oregon between 1976 and 1987.

Age class	State	Total no. animals	No. mgmt. units	Median n	Signif. diff. M>F	Signif. diff. F>M	No signif. diff.
Foal	Nevada	5993	36	144	0	3	33
	Wyoming	2886	20	66	0	3	17
	Oregon	1863	18	71	2	1	15
	Total	10742	74	91	2	7	65
Adult	Nevada	28266	39	544	0	26	13
	Wyoming	14139	26	267	1	9	16
	Oregon	7527	24	252	1	7	16
	Total	49932	89	323	2	42	45

large numbers of statistical tests one would expect some significant test results when, in fact, there were no differences (Type I error). Thus, it is probable that a portion of the 9 data sets that showed significant departures from an even sex ratio occurred by chance. It is also important to understand that these results are not necessarily indicative of sex ratios at birth since removals occurred throughout the year, resulting in foal sex ratios measured at various time intervals after the peak foaling season in spring. Numerous investigators have found foal mortality to be highest during the first 1-2 months of life (Welsh 1975, Boyd 1979, Keiper 1979, Berger 1986). Foal sex ratios reported here, therefore, were undoubtedly influenced by early post-partum mortality.

Adult ($\geq$1 year old) sex ratios differed significantly from parity in 49% of the 89 areas sampled. Sixty-seven percent of areas in Nevada had significantly skewed adult sex ratios while only 39 and 33% of the areas in Wyoming and Oregon, respectively, had skewed adult sex ratios ($\underline{P}<0.05$). Of the 44 areas with skewed adult sex ratios, 42 favored females (Table 1). These results reflect the overall trend, as samples from 72 of the 89 areas showed a preponderance of females. The difference in the proportion of areas in the 3 states with significantly skewed sex ratios may be due more to sample size differences than actual differences in the populations. The smaller the sample size the poorer the power of the test and, hence, the higher the probability of a Type II error (i.e., failing to reject H_0 when it is false). Median sample size for tests of adult sex ratios in Nevada areas was twice that of the other 2 states and twice as many Nevada areas had significantly skewed sex ratios. In addition, the smaller the departure from parity the larger the sample size needed to detect the difference. The unweighted average sex ratio for the 89 samples was 0.82, hence, the larger sample sizes from Nevada areas had a higher probability of detecting such relatively small departures from parity.

The general conclusion that can be drawn from the results presented in Table 1 is that foal sex ratios tend to be close to parity while there is a trend toward a preponderance of females in the adult segment of the populations. The tendency toward a skewed adult sex ratio, therefore, is not a result of a skewed sex ratio at birth, but reflects either a disparity in survival rates between males and females or differential probability of capture.

Data from management units where the entire horse population was removed provided a means of exploring the possibility of differential capture probabilities between adult male and female horses. In the case of complete removals, the sex ratio of the population is known rather than estimated from a sample, hence, eliminating any bias associated with capture techniques. The approach was to compare the adult sex ratios derived from the complete removals for areas that had a history of previous removals and areas that had no prior history of removals. If adult females had a higher probability of capture than adult males (skewing samples toward females), than one would predict that the sex ratios of populations that had a history of removals would tend to be skewed toward males.

Table 2 presents data from the 8 management units where the entire population was captured. In both groups, females were prevalent in 2 herds while sex ratios were near parity or skewed in favor of males in the other 2 herds. Sex ratios were significantly different from parity in only 2 of the 8 herds (Table 2), however, given the problem of sample size and the relatively small differences in sex ratio previously discussed, interpretation of these test results is tenuous at best. The similarity of the sex ratios of herds with and without a history of removals suggests that any differential capture probability between adult males and females is slight and probably has had little impact on observed sex ratios. The tendency for adult sex ratios to be skewed toward females, therefore, can be attributed to differential survival, with females experiencing higher survival than males. This pattern appears to be common in native and feral equids (Berger 1983).

Although a preponderance of females is common in many mammalian species and has generally been attributed to

Table 2. Comparison of adult sex ratios of populations that have had a history of previous herd reductions and populations that had not been manipulated prior to the final removal program. The sex ratios were calculated from records of all horses captured during the final removal program that was aimed at eliminating each of the populations.

No history of removals			History of removals			
Herd	No. adults in final removal	Sex ratio	Herd	No. adults in final removal	Sex ratio	Total No. removed previously
NV-223	323	0.67*	NV-202	332	0.92	173
NV-304	865	0.85*	NV-207	267	1.04	292
OR-095	178	1.33	NV-224	502	1.04	1040
OR-096	81	1.00	NV-225	482	0.87	1304

* chi square test significant at $\underline{P}<0.05$ level

differential survival (Trivers 1972), numerous hypotheses have been presented to explain the mechanisms causing higher mortality in males (Ralls et al. 1980). One prominent explanation for polygynous species such as equids is that male-male competition for access to females during the mating season results in direct injuries and/or increased energetic costs that ultimately diminish survival (Trivers 1972, Ralls et al. 1980, Berger 1986). An alternative hypothesis is that males are more susceptible to nutritional stress due to greater nutritional requirements and increased protein catabolism due to the effects of androgens (Widdowson 1976, Ralls et al. 1980, Clutton-Brock et al. 1982).

One would expect mortality due to competition for mates to occur primarily in horses ≥5 years old as younger males are seldom successful at maintaining harems and do not escalate fights to gain access to females (Berger 1986). Mortality due to nutritional stress, however, should be expressed primarily in the immature age classes when animals require energy for growth as well as body maintenance (Case 1978). Examination of age-specific changes in sex ratios, therefore, provides a means of exploring the relative contribution of these 2 mechanisms to increased male mortality. If differential survival occurs in the immature age classes, sex ratios of yearlings should begin to diverge from parity and become increasingly skewed through age 4 or

5. If skewed adult sex ratios are due primarily to costs associated with harem maintenance and reproduction then sex ratios in the reproductively immature age classes (0-4) should remain close to parity and begin to become skewed toward females at approximately age 4 or 5.

Age-specific sex ratios

Sex ratios varied significantly with age and state ($\underline{P}<0.01$), however, data from all 3 states showed a similar trend (Figure 1). The proportion of males in samples from each state steadily decreased from the foal age class, which was near parity, to lows ranging from 0.61 to 0.77 in the 4 to 5 year age classes. The trend then reserved, with males becoming predominant in the >10 year age class. The only exception to this general pattern was the 1 year age class from Wyoming that had an exceptionally low proportion of males. This was due primarily to a scarcity of males in samples from 1979-82. Because the scarcity of males was restricted to samples from a specific time period and was not observed in older age classes, I feel the Wyoming 1 year old sex ratio may represent an aberration, possibly caused by some problem in maintaining records.

There are 2 potential biases that could have impacted these results, sampling bias due to heterogeneous capture probabilities of males and females in different age classes, and sex-specific aging biases. Capture bias may be present as sampling was not random because probability of capture

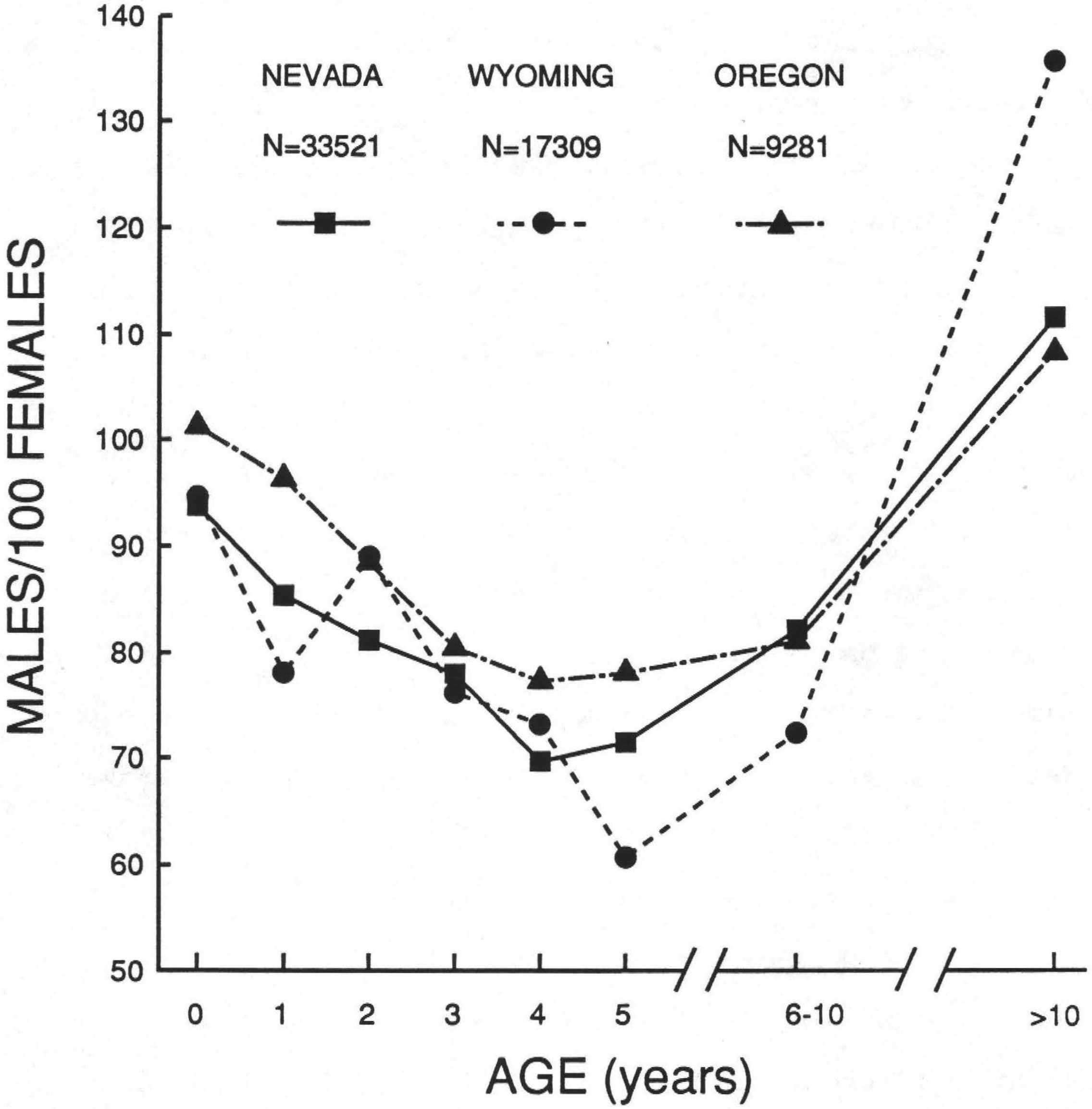

Figure 1. Age-specific changes in the sex ratio of feral horses captured from populations in Nevada, Wyoming, and Oregon between 1974 and 1987. Data were grouped in the older age classes due to uncertainties in aging techniques (Garrott 1990b).

was not independent (i.e., horses were captured in groups). Although sampling was not random, I feel the captured horses were relatively representative of their respective populations because herd reduction programs usually removed a large proportion of each population. In addition, there appears to be no spatial or social segregation that would result in one sex or age class of horses being more susceptible to capture than another. As discussed previously, capture procedures did not appear to disproportionately sample males or females. An examination of data from the 6 complete removals where age-specific sex ratios could be calculated revealed similar trends to those illustrated in Fig. 1, however, smaller sample sizes caused considerable variability. Pooling all 6 complete removal samples (n=3,461) yielded sex ratios of 0.94, 0.82, 0.72, 1.02, 0.78, 0.71, 0.95, and 1.08 for age classes 0, 1, 2, 3, 4, 5, 6-10, and 10+, respectively.

Accuracy of horse aging techniques has never been evaluated (Garrott 1990b), therefore, it is difficult to assess the possibility that sex-specific biases in aging caused the patterns observed in Fig. 1. Of particular interest is the apparent reversal of the sex ratio trend at approximately the same time when age estimation changes from a relatively objective criterion (tooth replacement) to subjective evaluation of tooth wear (Amer. Assoc. Equine Practitioners 1981). Although aging horses beyond 5 years is relatively imprecise (Garrott 1990b) and may involve unknown biases, consolidating all animals >5 years old into two age classes should have minimized the impact of possible biases on the results. Without any additional information, one can only conclude that there is no indication of sex-specific bias in the aging technique and assume the trends observed in Fig. 1 are not artifacts of the sampling and data collection procedures.

The pattern of increasingly skewed sex ratios in favor of females through age 4 or 5 implies that survival was lower for males than for females during this period. The apparent reversal in sex ratio trends in older age horses indicates that differential survival switches from favoring females in the immature age classes to favoring males in mature age classes. Quantitative data on horse survival is limited to several observational studies of relatively small populations (Berger 1986, Garrott et al. 1990a) and a short term telemetry study (Siniff et al. 1986) that provide little information on differential survival between the sexes for various age classes. Measures of survival could be obtained from the age distributions of captured animals (Chapman and Robson 1960, Seber 1982), however, uncertainties in the aging technique (Garrott 1990b) and sampling variability (Polacheck 1985) make application of such procedures questionable. Experimenting with simple population models provides one way of exploring differential survival and understanding how changing age and sex-specific survival rates influence sex ratios.

Population Simulations

The age-specific reproduction and survival rates presented in Table 3 represents what I perceive to be a realistic combination of values that mimic the observed age-specific changes in sex ratios. Although there were numerous combinations of male and female survival schedules that produced sex ratio changes similar to Fig. 1, several characteristics could not be modified without substantial departures from the data. In order to obtain the increasingly skewed sex ratios in favor of females through age 4, a survival differential of approximately 0.05-0.07 had to be maintained from 0 through 3 years of age. In addition, survival of 5-10 year old males could not exceed females by more than 0.04-0.05 without causing sex ratios to become disproportionately skewed toward males in the older age classes.

An additional manipulation of the survival schedules that appeared necessary to adequately skew the sex ratio in the oldest age class was to initiate senescence earlier in females than in males. In the example illustrated in Table 3 there is a 3 year difference in the onset of senescence between males and females, resulting in a 1.11 sex ratio for 11-25 year age class. The sensitivity of the sex ratio to this feature of the survival schedules is illustrated by

Table 3. Key parameters for an age-structured population model that simulates the age-specific changes in feral horse sex ratios observed for data collected in 3 western states. The reproduction and survival schedules in this table result in a population with a finite annual growth rate of 1.20.

		Survival rate		Sex ratios			
Age	Foaling rate	Male	Female	Model	NV	WY	OR
0	0.00	0.92	0.98	1.00	0.93	0.95	1.01
1	0.00	0.92	0.98	0.94	0.85	0.78	0.96
2	0.32	0.92	0.98	0.88	0.81	0.89	0.89
3	0.51	0.92	0.98	0.83	0.78	0.76	0.81
4	0.62	0.94	0.97	0.78	0.70	0.73	0.77
5	0.69	0.96	0.96	0.75	0.72	0.61	0.79
6	0.73	0.98	0.94	│	│	│	│
7	0.76	0.98	0.94	│	│	│	│
8	0.77	0.98	0.94	0.81	0.82	0.72	0.81[1]
9	0.78	0.98	0.94	│	│	│	│
10	0.79	0.98	0.94	│	│	│	│
11	0.79	0.98	0.94	│	│	│	│
12	0.79	0.98	0.94	│	│	│	│
13	0.79	0.98	0.92	│	│	│	│
14	0.79	0.98	0.89	│	│	│	│
15	0.79	0.98	0.85	│	│	│	│
16	0.79	0.97	0.80	│	│	│	│
17	0.79	0.95	0.75	│	│	│	│
18	0.78	0.92	0.69	1.11	1.12	1.36	1.08[2]
19	0.77	0.88	0.64	│	│	│	│
20	0.75	0.83	0.58	│	│	│	│
21	0.71	0.75	0.50	│	│	│	│
22	0.66	0.65	0.42	│	│	│	│
23	0.58	0.55	0.32	│	│	│	│
24	0.46	0.33	0.18	│	│	│	│
25	0.31	0.00	0.00	│	│	│	│

1 sex ratio for 5-10 year age classes
2 sex ratio for 11-25 year age classes

changing the senescence difference to 1, 2, and 4 years that results in sex ratios of 1.022, 1.058, and 1.180, respectively.

Although data on senescence are extremely difficult to obtain (Eberhardt 1985), there is indirect evidence to suggest the onset of senescence may not be the same for male and female horses. The proximate cause of senescence in large herbivores is believed to be the progressive wear of teeth (Laws 1981). Both Duncan (1980) and Berger (1986) found that reproductively active adult females spent more time feeding than adult males, suggesting that the teeth of females may wear more rapidly than males. Horses with badly worn teeth are probably less efficient foragers, which could result in higher mortality rates during the winter when forage quantity and quality are at their lowest. Females that are reproductively active would be the most vulnerable to mortality due to the additional energy demands of gestation and/or lactation. Although this scenario is certainly not conclusive it represents a biologically plausible mechanism that could cause the onset of senescence in female horses at an earlier age than males. Age-specific mortality rates of female red deer (Cervus elaphus) provide support for this thesis. Clutton-Brock et al. (1982) found that onset of senescence in reproductive or "milk" hinds occurred at 9-10 years of age while survival of non-reproductive hinds, which may be somewhat analogous to males, did not begin declining until age 13.

Causes of differential survival

Increased subadult male mortality has been documented in a variety of mammals (Ralls et al. 1980) and is common in ungulates (Taber and Dasmann 1954, Woolf and Harder 1979, Flook 1970, Bergerud 1971, Child 1972, Clutton-Brock et al. 1982). Most authors attribute the differences in survival rates to behavioral and/or energetic differences between the two sexes. In most mammals, immature males have a greater tendency to disperse than females, which exposes them to increased stress and risks of predation (Greenwood 1980), thus diminishing their chances of survival (Ralls et al. 1980). Energetic differences have been attributed to the presence of androgens in males. These anabolic hormones stimulate the conversion of dietary protein into muscle mass and are responsible for the higher growth rates and larger adult body size in most sexually dimorphic mammals (Mainwaring 1979). Other sex differences that have been proposed are increased metabolism (Hamilton 1948, Taber and Dasmann 1954, Trivers 1972), poorer thermoregulatory processes (Clutton-Brock et al. 1982), and less efficient utilization of protein and fat reserves in males (Widdowson 1976). All of these possible energetic differences would result in increased demand for dietary protein that would predispose males to increased mortality due to nutritional stress when forage is limited (Trivers 1972, Widdowson 1976, Ralls et al. 1980, Clutton-Brock et al. 1982).

Although these mechanisms may present plausible explanations for differential survival observed in immature males and females of other mammalian species, the applicability of several of these possible explanations appears questionable for feral horses. It is unlikely that dispersal was responsible for differential survival in immature horses because both sexes disperse as 2-4 year olds (Berger 1986) and there are no effective horse predators in the western United States. Horses are also monomorphic with both sexes growing at approximately the same rate and attaining similar body size (Dawson et al. 1945, Berger 1986) so differences in dietary requirements due to these factors should be minimal. Little data are available to evaluate the remaining mechanisms, hence, the causes for differential survival in young horses remain uncertain.

Differential survival in horses >5 years old appears to be a consequence of differences in the costs of reproduction for males and females. The primary reproductive costs to females are the relatively high energetic demands of gestation and lactation (National Research Council 1978). Duration of both of these processes is prolonged, with gestation normally lasting from 338-340 days (Ginther 1979) and lactation spanning from 9 to 16 months (Berger 1986). In addition, females commonly reproduce in consecutive years, incurring the energetic costs of both lactation and gestation simultaneously (Berger 1986, Seal and Plotka 1983, Garrott et al. 1990a, 1990c, Wolfe et al. 1989). Pregnancy rates are high as females may begin breeding as 1 or 2 year olds and continue to reproduce throughout their life (Seal and Plotka 1983, Berger 1986, Plotka et al. 1988, Garrott 1990c, Wolfe et al. 1989). Female horses, therefore, are constantly subjected in prolonged periods of elevated energy demands as a consequence of reproduction. Berger (1986) observed that lactating females emerged from the winter in the poorest condition, suggesting that these females suffered a severe energy deficit when forage quantity and quality were seasonally reduced. Such nutritional stress, if severe enough, may ultimately lead to decreased survival as Clutton-Brock et al. (1982) demonstrated for red deer.

Reproductive costs for male horses consist of the energetic demands associated with performance of reproductive behaviors such as harem maintenance, vigilance, and mate acquisition and costs directly related to intrasexual fighting (Berger 1986). In most ungulates and other polygynous mammals, males commonly fight for access to females during the breeding season and injuries are common (Murie 1944, Bergerud 1971, Geist 1971, 1978, Clutton-Brock et al. 1982). Berger (1986) found 96% of adult male horses in his study population had bite related wounds each year, however, injuries were rarely permanent and had no obvious effects on the welfare of the animals. In areas with large carnivores, even temporarily disabled animals may be susceptible to predation (Kruuk 1972, Schaller 1972), but predation is insignificant in feral horse populations in the western United States. Records of male horses dying as a direct result of combat injuries are limited to a few anecdotal accounts and 3 horses in Berger's study (1986) that either disappeared or died several months after being involved in fights. Combat related deaths have been documented in a variety of ungulates (Geist 1978). Such mortality, however, is relatively infrequent and probably has little impact on survival rates.

It is difficult to assess the energetic costs of reproductive behaviors in males. Berger (1986) estimated reproductive costs during the breeding season and found males with large harems required more energy than those with smaller harems. He noted considerable variability between males and estimated increased dietary requirements of 16-26% above maintenance in 7 of 11 males with harems. The higher winter mortality rates of mature males compared to females observed in a wide variety of ungulates has been attributed to their poor body condition at the onset of winter due to breeding activities (Robinette et al. 1957, Flook 1970). Most ungulates, however, breed in the fall while horses breed in the spring and have months to replenish depleted body reserves before winter. Significant male reproductive costs, therefore, appear to be limited to a short period in the spring while energetic demands on females are prolonged and occur throughout the year. I suggest that the differences in costs of reproduction between males and females is of sufficient magnitude to cause the differential survival suggested in the sex ratio data for horses >5 years old.

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FERAL HORSE POPULATION GROWTH RATES

Abstract: The growth rates of feral horse (Equus caballus) populations in the western United States were studied by consolidating aerial count records for 103 management areas administered by the Bureau of Land Management. Data from most areas could not be used because of free exchange of horses between neighboring areas and/or inadequate or incomplete data. Twenty-two areas provided data that could be used to assess the accuracy of aerial counts using the index-removal method. Aerial counts consistently detected a large proportion of the horses with 24 of 31 estimates ranging between 85-105%. Replicate index-removal estimates provided little evidence of progressively higher sighting probabilities that would inflate growth rate estimates and it was concluded that aerial counts could be used to obtain reliable estimates of population growth rates. Finite annual growth rates (λ) were estimated using log-linear regression as populations appeared to be growing geometrically. Estimates of λ for the 12 areas with adequate data ranged from 1.15-1.27 with a mean growth rate of 1.21. Population simulations using age-specific reproduction and survival data collected independent of this study resulted in a similar range of growth rates. It was concluded that many feral horse populations are currently being maintained at levels below which density-dependent

responses operate and are, therefore, increasing at or near their biological maximum.

Introduction

Equids became extinct in North America 8-11,000 years ago, but were reintroduced when the domestic horse arrived on the continent with european settlers. With the aid of the American indian, horses spread throughout the western United States during the 17th and 18th centuries and still persist in many areas (Zarn et al. 1977). There are currently about 50,000 feral horses occupying federal lands, primarily in the Great Basin of Nevada and southeastern Oregon, and the Red Desert of Wyoming (Bureau of Land Management 1989). Although substantial populations of feral horses have occupied these regions for centuries, they received almost no scientific attention until passage of the Wild and Free-roaming Horse and Burro Act in 1971. This law established federal ownership of feral horses, thus prohibiting the commercial exploitation that had limited their populations. Expanding horse populations soon created conflicts with the livestock industry, which demanded their numbers be controlled (Wagner 1983). The ensuing controversy about growth rates and management of feral horse populations found federal agencies, horse protection groups, and the livestock industry with little data to support their positions.

Most feral horse populations in the western United States reside on public lands administered by the Bureau of Land Management (BLM). After feral horses were given federal protection, the BLM began to monitor trends in horse populations by conducting periodic aerial surveys intended to count all horses within each management unit (Boyles 1986). Preliminary studies using BLM's aerial count data suggested that growth rates of many horse populations approached or exceeded 20% annually. These investigators questioned the quality of the aerial counts as the growth rate estimates appeared unrealisticly high (National Research Council 1980, Wolfe 1980). Using aerial count data extending over a 10 year period, Eberhardt et al. (1982) also estimated annual growth rates of 20% for 2 feral horse populations in southeastern Oregon, however, these authors cautioned that such high growth rates should not be regarded as typical. The objective of this study was to extend the studies of Eberhardt et al. (1982) to populations throughout the range of feral horses in the western United States in an effort to document typical growth rates and the amount of variability between various populations.

Methods

Data were collected by visiting BLM district offices in Nevada, Oregon, Wyoming, and Idaho and consolidating all records available for each horse management unit within the district. Data were normally recorded as memos documenting the two primary BLM management activities, aerial counts and the periodic removal of horses to control populations. Information on each aerial count consisted of dates of flights, areas surveyed, and number of horses counted, with some memos also including additional details such as type of aircraft used, time flown, number of observers, unusual counting conditions, and number of horses categorized as young of the year (foals). Data on population reductions consisted of dates and locations of capture operations and the number of adult male and female horses and foals removed. BLM personnel familiar with each management unit were also questioned about fences and horse movement patterns in an attempt to identify management units segregated enough to be considered closed populations. Only data from management units that were isolated or were believe to have little exchange with adjacent units are presented.

The periodic removal of large numbers of horses from many management units provided opportunities to employ the index-removal method to estimate the proportion of animals detected during aerial counts (Eberhardt 1982) and assess temporal and spatial variability of the counts. In order to use this technique 2 counts must be conducted, 1 prior to the removal and 1 after the removal. The "apparent" number of animals removed (difference between the counts) divided by the actual number removed represents the proportion of animals removed that were detected by the aerial counts.

This proportion should have the same relationship to the actual number of animals in the population and, hence, is an estimate of the proportion of animals counted during aerial surveys (Eberhardt 1982).

Two situations provided data that could be used for index-removal calculations. The first, when both counts were conducted within 1-2 months of the removal, allowing the apparent number of horses removed to be calculated simply as the difference between the 2 counts. The second situation was when post-removal counts were not conducted until after the foaling season the following year. In these cases the apparent number of horses removed was calculated as the difference between the total pre-removal count and the number of horses categorized as adults in the post-removal counts. Additional estimates of the proportion of horses detected during aerial counts were obtained when all animals were removed from a management unit. In these situations the proportion of animals detected was calculated as the number of horses counted prior to the removal divided by the number of horses removed.

A preliminary review of the count data indicated that growth of feral horse populations appeared to be geometric, hence, growth rates were estimated using log-linear regression. The basic model for geometric population growth is:

$$N_t=N_o\lambda^t$$

where N_o is the initial number of animals in the population, N_t is the number of animals in the population at time t, and λ is the finite population multiplier. Taking natural logarithms of this basic model yields:

$$\log N_t=\log N_o+t\log\lambda$$

which is the form of a linear regression model (Caughley 1977). The slope of a regression line fitted to a series of log transformed population counts conducted over a period of years, therefore, provides an estimate of instantaneous annual rate of increase (r), with the antilog of the regression coefficient yielding λ (Eberhardt 1987). The relationship between λ and population growth is easily understood as $N_t=N_{t-1}\lambda$. Thus, if $\lambda=1.00$ the population is stationary while a value of 1.20 would indicate that the population was increasing 20% annually.

The estimation of growth rates was complicated somewhat for populations that had undergone one or more removals. Eberhardt (1987) suggested use of the "ratio" method, however, this technique requires absolute measures of abundance. In order to meet this requirement, aerial counts would have to be corrected for the proportion of animals not detected (Eberhardt 1987). Although the index-removal method provides estimates of sighting probability, adequate data were not available for many of the herds. I chose instead to extend the log-linear regression analysis to these herds by utilizing weighted or pooled regression techniques that fitted lines with a common slope to each interval between removals (Zar 1974). The fit of the weighted regressions were compared to fitting each interval separately using an F-test (Zar 1974). The F-test employed a mean MSE for individual segments that was calculated by summing SSE of all individual regressions and dividing by the total number of degrees of freedom. Since the regression slopes are themselves estimates of average population growth over many years a better estimate of true growth rates of feral horse populations in general can be obtained using Empirical-Bayes techniques (Efron and Morris 1977). Procedures described by Efron and Morris (1973), therefore, were used to calculate an overall mean growth rate and shrink the individual growth rate estimates toward this mean.

Population simulations were conducted by constructing a variety of age-specific survival and fecundity schedules using data in the literature and equations presented by Eberhardt (1985). The survival equation is:

$$l_x=\exp[-F-Gx-D\{\exp(Ex)-1\}]$$

where l_x is defined as the probability of living to age x, F is a coefficient describing juvenile survival (birth to 1 year), G is a coefficient for adult survival, and D and E are senescence coefficients. Coefficients F and G can be converted to survival rates by taking the antilog of their negative values. For example, if $F=0.03252$ then the juvenile survival rate is $\exp(-0.03252)=0.968$, and conversely, if juvenile survival is 0.980 $F=-\ln(0.980)=0.0202$.

The fecundity equation is:

$$m_x=A\{1-\exp[-B(x-C)]\}\exp\{-D(\exp[Ex]-1\}$$

where m_x is the number of female young produce per year by females of age x, A is a coefficient describing the maximum reproductive rate, B is a coefficient describing the rate of increase during the early reproductive years, C is the age prior to first reproduction, and D and E are coefficients describing reproductive senescence. Garrott (1990<u>c</u>) reported that feral horse sex ratios at birth are near parity so reproductive rates reported in the literature as number of young produce per female where halved.

The population model used in the simulations was that derived by Lotka (1907) and modified by Cole (1954) for populations where births are concentrated in a short time interval each year. The basic equation is:

$$1=\sum_{x=a}^{w}\lambda^{-x}l_x m_x$$

where the summation ranges from the age of first reproduction (a) to the maximum age in the population (w), and λ is the finite annual rate of increase. Population growth rates were determined for various combinations of l_x and m_x schedules by solving the equation using a spreadsheet program.

Results and Discussion

Aerial counts and removal histories were compiled from 15 BLM administrative districts and included 23 management units in Oregon, 62 units in Nevada, 17 units in Wyoming, and 1 unit in Idaho. Of these 103 management units, 22 contained records that allowed the use of the index-removal method to estimate the proportion of horses observed on aerial counts and 12 units had adequate data to estimate growth rates using log-linear regression. The basis for exclusion of most management units from analysis was free exchange of horses with neighboring units. Although little data on movements of marked horses were available the general knowledge of district BLM personnel was usually corroborated by aerial count data that fluctuated erratically for management units where horses were believed to commonly move across boundaries. In contrast, aerial counts from units that were completely fenced or isolated from other horse populations usually displayed consistent trends that made biological sense. Inadequate or infrequent aerial count data was also a major problem that resulted in the exclusion of many management units from this study.

Accuracy and Precision of Aerial Counts

Results of the index-removal analysis indicated that a large proportion of the horses were normally observed during aerial counts with 24 of 31 estimates ranging between 85-105% (Table 1). Only 1 estimate fell below 70% (1978-79 Three Fingers, OR) and in this instance I strongly suspect that the number of horses removed included animals taken from a neighboring unit during the same time period. These data contrast markedly to average observability estimates of 30-66% reported for other large terrestrial herbivores such as white-tailed deer (Odocoileus virginianus)(Beasom 1979, DeYoung 1985, Beasom et al. 1986), mule deer (Odocoileus hemionus)(Bartmann et al. 1986), and moose (Alces alces)(LeResche and Rausch 1974). The reason for the high observability of horses was apparently the lack of tree cover and arid climate that allowed easy detection of horses and their dust trails. Management units in some mountainous areas contained substantial areas of pinyon (Pinus edulis)-juniper (Juniperus osteosperma) woodland that can substantially reduce observability of horses (Siniff et al. 1982), however, many districts only conducted aerial counts when horses were occupying low-elevation sagebrush (Artemisia sp.) winter ranges.

Eberhardt (1982) and Siniff et al. (1982) discussed a number of possible biases that could have affected the sighting probabilities presented in Table 1. Perhaps the

Table 1. Estimates of the percent of animals detected during aerial counts of feral horse management units in the western United States using the index-removal method suggested by Eberhardt (1982).

State	Mgmt. unit	Year	No. anim. remo.	Aerial counts		Est. % remo.	Est. % anim. detected
				Pre-remo.	Post-remo.		
OR	Paisley	76-77	235	307	100*	67	88
	Paisley	81	183	244	81	66	89
	Beaty But.	81	272	391	150	62	89
	Beaty But.	84	260	382	134	65	95
	Palomino	86	173	183	30	84	88
	3 Fingers	75-76	256	424	186*	56	93
	3 Fingers	78-79	342	244	103*	58	41
	Jackie But.	70-72	181	263	78*	70	102
	Jackie But.	76-77	137	280	145*	48	99
	Jackie But.	78-79	136	235	101*	57	99
	Monger	75	178	169		100	95
	Stockade	78	81	74		100	91
NV	Eugene Mtn.	85	346	349		100	101
	Buffalo H.	79-80	494	623	194*	69	87
	Sonoma Ran.	85	349	391		100	112
	Humboldt	85	665	609	5	99	91
	East Range	80-81	931	1044	252*	76	85
	Fox-Lake	86	478	913	493	46	88
	Flanigan	85	351	704	320	55	109
	Pah Rah	84-85	1139	1075	107	90	85
	Pine Nuts	86	208	437	273	38	79
	New Pass	86	783	1880	1105*	41	99
	Bald Mtn.	81-82	401	686	326*	52	90
	Fish Creek	80	600	907	293	68	102
WY	McCullough	83-84	307	459	208*	55	82
	McCullough	87-88	152	290	121*	58	107
	15 Mile	78-79	154	302	155	49	95
	15 Mile	84-85	360	429	94*	78	93
ID	Challis	79-80	148	650	545*	16	71
	Challis	80	309	617	319	48	96
	Challis	83-84	311	499	223*	47	89

* used the number of adults instead of total count to remove effects of foaling season between pre and post removal counts

most important potential bias in these data is the long time interval between many of the pre and post-removal counts as approximately half of the sighting probabilities were calculated from counts conducted nearly a year apart. Ideally, counts should be conducted close to the removal to reduce the possibility that additional animals are lost from the population due to undetected mortalities (Eberhardt 1982). Natural mortalities between the 2 counts would tend to inflate sighting probabilities, however, the magnitude of this bias is apparently not large as sighting probabilities from counts conducted a year apart were similar to those calculated from counts conducted close to the removal dates ($\underline{P}>0.20$). Available data on horse survival support this contention as most foal mortality occurs within the first 1-2 months (Welsh 1975, Boyd 1979, Keiper 1979, Berger 1986), prior to the time aerial counts were usually conducted, and adult mortality is typically low (Berger 1986, Siniff et al. 1986, Garrott 1990a).

Although other unknown or undocumented biases may have influenced the calculated sighting probabilities, these biases do not influence estimates of population growth rates derived from a series of aerial counts unless the magnitude of the bias changes in some consistent direction over time (Harris 1986, Gerrodette 1987). Several authors have suggested that increased observer experience, switching from fix-winged aircraft to helicopters, and the refinement of counting techniques has resulted in progressively higher sighting probabilities over time, which would result in inflated growth rate estimates (Frei et al. 1979, Wolfe 1980, National Research Council 1982). Studies of feral horse census techniques, however, do not provide strong support for these concerns. Siniff et al. (1982) found no difference in the ability of experienced and inexperienced observers to detect horses from an aircraft. In addition, comparisons of aerial counts conducted with helicopters (Bell B-2) and fix-winged aircraft typically used by BLM personnel (Piper Supercub, Cessna 180) found that both types of aircraft performed similarly in some areas while helicopter flights in other areas resulted in slightly higher counts (Siniff et al. 1982).

Although little information on number and experience of observers, types of aircraft used, flight patterns, etc., were available for many of the aerial counts, some indication of possible trends in counting proficiency can be gained from examining sighting probabilities for the 7 management units where data allowed multiple index-removal calculations (Table 1). Estimated sighting probabilities remained relatively constant for 4 of these management units (Paisley, Beaty Butte, Jackie Butte, and 15 Mile) while estimates for the Three Fingers, McCullough, and Challis units were inconsistent. As discussed earlier, the low 78-79 Three Fingers' estimate is believed to be an error in the records. The low 79-80 Challis sighting probability was probably due to the small number of horses removed (16%) as Eberhardt (1982) cautioned that index-removal estimates are unreliable when the proportion of the population removed is low. The 96% sighting probability calculated after approximately half the population was removed the following year also suggests the low 79-80 Challis estimate was due to the small number of animals removed. The McCullough data provide the only evidence to support the contention that counting proficiency increased over time, therefore I conclude that aerial counts conducted over a period of years can be used to obtain estimates of population growth rates.

Population Growth Rates

Plots of log-transformed aerial counts for each herd were approximately linear (Fig. 1), indicating the simple model for geometric or constant growth was appropriate. For those herds where removals interrupted population growth, fitting lines to the individual segments did not result in better fits than pooled regression techniques ($\underline{P}<0.05$), therefore, only results of the pooled regressions are presented. Estimates of lambda for the 12 management units with adequate data to perform log-linear regressions ranged from 1.15-1.27 (Table 2) with an unweighted mean of 1.21. Due to the close fit of each data set to the linear model, Empirical-Bayes estimates were very similar with an

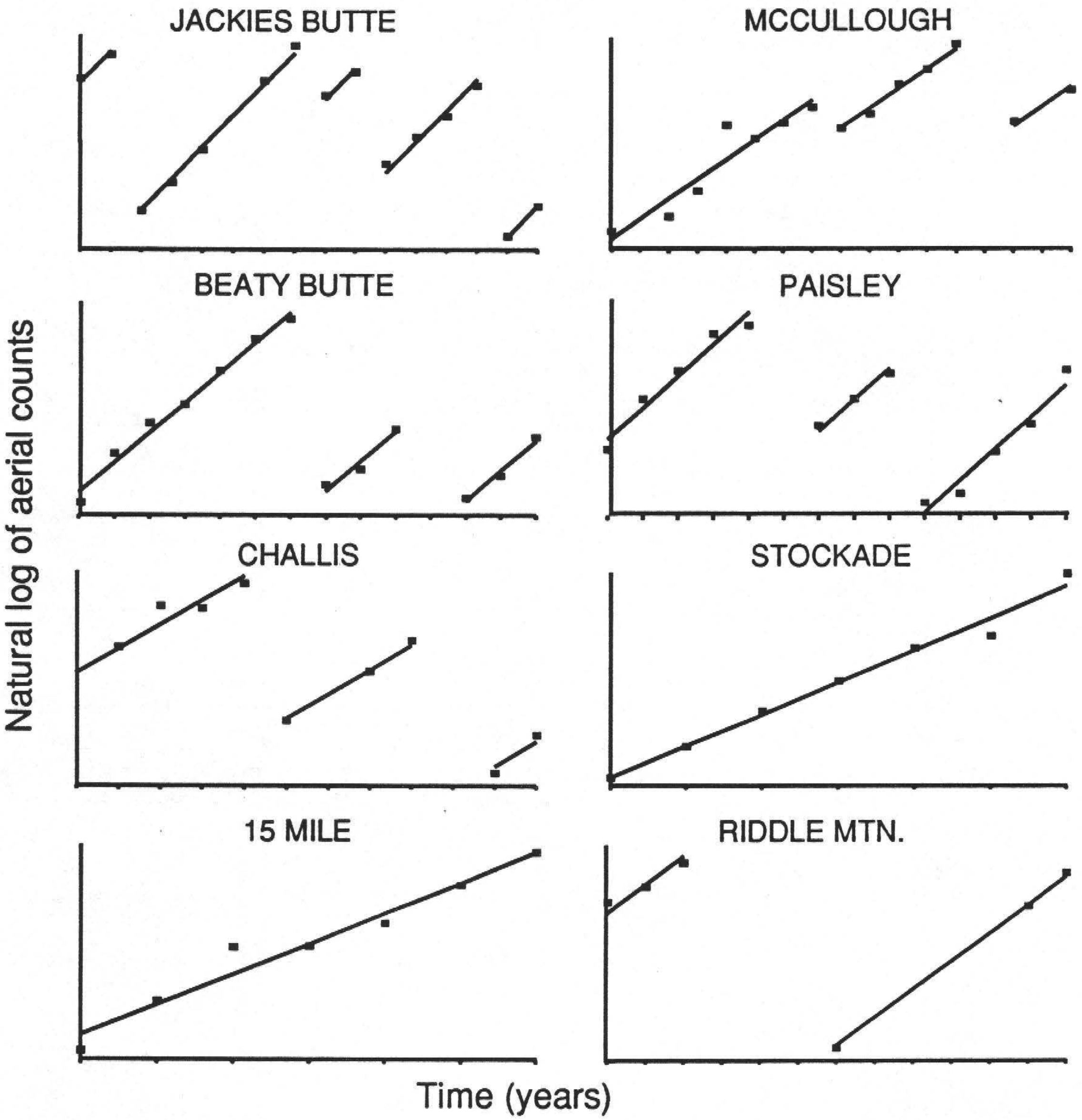

Figure 1. Plots of the apparent growth of 8 feral horse populations based on aerial counts conducted over variable time spans. Log-linear regressions were used to fit the lines and provided estimates of finite population growth rates (λ). Tick marks on x axis indicate yearly intervals, but scale of y axis varies for each plot.

Table 2. Estimates of finite annual growth rates (λ) of feral horse populations based on log-linear regression of aerial counts conducted over variable time periods. Where more than 1 line segment was fitted weighted regression techniques were used to obtain a single slope estimate. Lambda was calculated as the antilog of the regression slope.

Management Unit	No. counts	No. years	No. line segments	λ estimate	95% conf. interval
Jackie Butte	15	16	5	1.23	1.22-1.24
McCullough	14	17	3	1.22	1.20-1.24
Beaty Butte	13	14	3	1.24	1.23-1.25
Paisley	13	14	3	1.27	1.26-1.29
Challis	10	12	3	1.15	1.13-1.16
Stockade	7	7	1	1.16	1.14-1.19
15 Mile	7	7	1	1.17	1.13-1.21
Lander Complex	6	6	1	1.23	1.19-1.27
Riddle Mtn.	6	13	2	1.25	1.23-1.27
Cold Springs	5	7	1	1.18	1.09-1.28
Monger	5	5	1	1.21	1.16-1.29
Goshute	5	7	1	1.19	1.12-1.27

identical mean and slightly narrower range for the individual estimates (1.16-1.26).

Width of 95% confidence intervals ranged from 0.02-0.04 for estimates calculated using at least 10 counts, while regressions using only 5 counts resulted in confidence intervals in excess of 0.10. The confidence intervals presented in Table 2 are derived from the variance of the regression coefficient, which may underestimate the true variability of the trend lines. Although Harris (1986) and Gerrodette (1987) present alternatives for calculating confidence intervals that may be more appropriate, estimates of the coefficient of variation of the aerial counts are needed. Because such data are lacking for horse counts these techniques were not used.

Several authors have used log-linear regression to estimate feral horse population growth rates. The National Research Council (1980) calculated a weighted mean lambda of 1.16 for aerial count data from 25 management units in 5 states. Wolfe (1980) tabulated data from 12 management units representing 6 states and calculated lambdas ranging from 1.08-1.30 with an unweighted mean of 1.22. Both of these authors, as well as Conley (1979), conducted population simulations using modifications of the Leslie matrix (Leslie 1945, 1948) or Lotka's equation (1907) to determine the demographic characteristics needed to produce population growth rates similar to the log-linear regression estimates. Various combinations of fecundity and survival schedules were used that produced growth rates ranging from 1.04 to >1.20, however, all 3 authors concluded that the high reproduction and survival needed to produce growth rates approaching or exceeding 1.20 were not realistic. It was concluded, therefore, that the use of aerial counts to estimate population growth rates was unreliable (Conley 1979, National Research Council 1980, Wolfe 1980). However, data presented earlier in this paper on accuracy and precision of aerial counts indicate that the reliability of count data may not be as poor as these author's perceived.

At the time these early simulations were conducted females were thought to produce their first foal at 3-5 years, possibly only foaling in alternate years, and becoming reproductively senescent between 10 to 15 years old. Adult survival rates exceeding 0.90 were also believed to be unrealistic and foal mortality was assumed to be relatively high (Tyler 1972, Boyd 1979, Conley 1979, Nelson 1979, National Research Council 1980, Wolfe 1980). Recent reproductive studies, however, demonstrate that age of first foaling is usually 2-3 years with females commonly producing foals in consecutive years (Seal and Plotka 1983, Berger 1986, Siniff et al. 1986, Plotka et al. 1988, Garrott 1990a, 1990b, Wolfe et al. 1989). Females also remain reproductively active throughout their lives with only a slight reduction in foaling rates in the oldest age classes

(Garrott 1990b, Wolfe et al. 1989). In addition, studies by Berger (1986), Siniff et al. (1986), and Garrott (1990a) indicate that survival of both foals and adults is usually high, with annual survival rates of adults commonly exceeding 0.95.

Population Simulations

Previous efforts to model feral horse populations have lacked empirical data, compelling investigators to use generalized reproductive and survival parameters. Several studies have quantified age-specific reproductive and survival data for a variety of horse populations (Garrott 1990a,b) and fitted these data to survivorship (l_x) and fecundity (m_x) models presented by Eberhardt (1985). These papers provide a framework for constructing l_x and m_x schedules needed for conducting population simulations as well as estimates of reproduction and survival parameters based on data.

Population simulations were conducted using 4 l_x and 4 m_x schedules constructed using Eberhardt's (1985) models (Fig. 2). The l_x values used in Lotka's equation generally refer only to female survival, but the only age-specific survival data available in the literature combines both sexes (Garrott 1990a). Garrott (1990c) discussed age-specific changes in sex ratios that suggest that l_x schedules for males and females may differ substantially, however, for lack of any better empirical data, I chose to

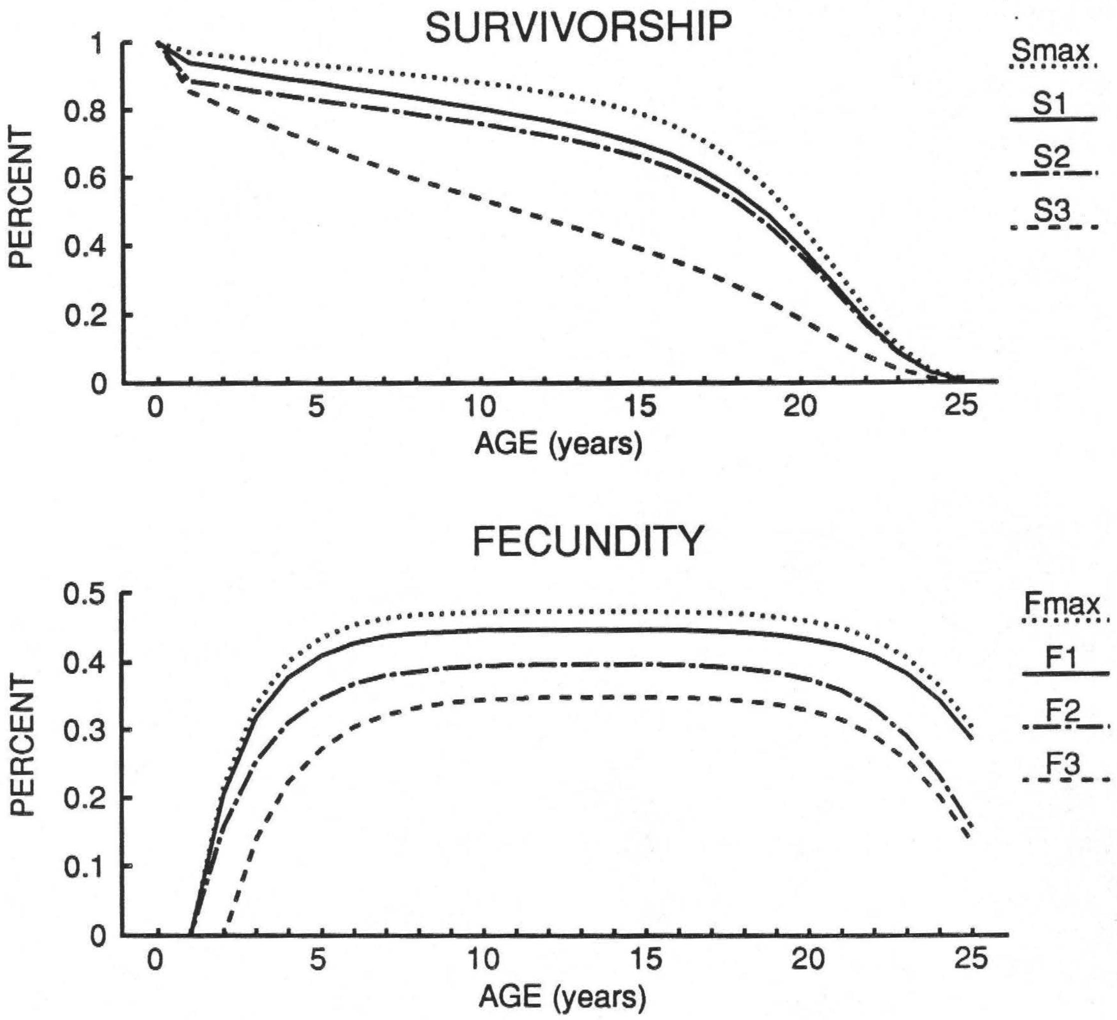

Figure 2. Four age-specific survivorship (l_x) and fecundity (m_x) schedules for feral horse populations. Curves were fitted using equations presented by Eberhardt (1985). The l_x schedule S1 and m_x schedules F1 and F2 are curves fitted to data presented by Garrott (1990a,b). The remaining schedules were produce by changing various parameters in the l_x and m_x equations to approximate both lower and higher survival and fecundity rates. The Smax and Fmax schedules are considered biological maximums for the species.

develop the 4 l_x schedules used in the population simulations from these data. The l_x schedule S1 was identical to the fitted schedule developed from 11 years of survival data from the Pryor Mountain herd in Montana (Garrott 1990a). The other 3 schedules were constructed by varying the coefficients for juvenile (F) and adult survival (G) to produce 1 schedule near the maximum survivorship possible (Smax) and 2 schedules where survival is lower than that observed for the Pryor herd. The senescence coefficients D and E derived from the Pryor data were used in all 4 schedules (Table 3). The coefficients used to generate m_x schedules F1 and F2 are those presented by Garrott (1990b) for reproductive rates derived from 2 independent sources of data. The Fmax schedule used the same coefficients as F1 with the exception that A was increased slightly while the F3 schedule used the same coefficients as F2 except for A, which was decreased, and C which was raised to 2 (Table 3). The Smax and Fmax were constructed to approximate what I feel would be the biological maximums possible for feral horses.

Simulations employing all possible combinations of the l_x and m_x schedules produced 16 values of lambda ranging from 1.11 to 1.27 (Table 4). The simulation results are similar to the range of growth rates derived from aerial counts (Table 2) and thus, corroborate the log-linear regression estimates. Such high annual growth rates appear

Table 3. The values of coefficients used to generate 4 survivorship (l_x) and 4 fecundity (m_x) schedules using models presented by Eberhardt (1985). The coefficients F and G can be interpreted as juvenile and adult survival rates of 0.98 and 0.99 for Smax, 0.95 and 0.98 for S1, 0.90 and 0.98 for S2, and 0.90 and 0.95 for S3, respectively.

Model	Coefficients values				
Survivorship	F	G	D	E	
Smax	0.0202	0.0101	0.00012	0.42265	
S1	0.0468	0.0164	0.00012	0.42265	
S2	0.1054	0.0164	0.00012	0.42265	
S3	0.1054	0.0513	0.00012	0.42265	
Fecundity	A	B	C	D	E
Fmax	0.48	0.6178	1	0.0000008	0.52910
F1	0.43	0.6178	1	0.0000008	0.52910
F2	0.40	0.5053	1	0.0000013	0.53908
F3	0.35	0.5053	2	0.0000013	0.53908

Table 4. Finite population growth rates calculated by solving Lotka's (1907) equation and all possible combinations of the 4 age-specific survivorship and fecundity schedules illustrated in Figure 2.

	Calculated lambda values			
	Survival schedules			
Fecundity schedules	Smax	S1	S2	S3
Fmax	1.27	1.26	1.24	1.20
F1	1.26	1.24	1.23	1.19
F2	1.22	1.21	1.20	1.16
F3	1.17	1.16	1.15	1.11

unusual for populations of long-lived vertebrates that experience delayed sexual maturity and produce only 1 young per reproductive cycle. However, growth rates approaching or exceeding 20% have been documented for colonizing populations of elk (*Cervus elaphus*) (Eberhardt 1987, Gogan and Barrett 1987, McCorquodale et al. 1988), bison (*Bison bison*) (Eberhardt 1987), and musk ox (*Ovibos moschatus*) (Reynolds 1989). Feral horse populations appear to be increasing at or near their biological maximum despite the fact that populations have existed in the western United States for hundreds of years (Zarn et al. 1977). It is apparent that many feral horse populations are currently being maintained at levels below which density-dependent responses in reproduction and survival operate.

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