Seasonal mountain lion predation on a feral horse population

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A population of feral horses (*Equus caballus*) was studied from 1986 to 1991 to determine the demographic impact of predation by the mountain lion (*Felis concolor*). The population, inhabiting a 600-km^2 area on the central California – Nevada border comprised approximately 162 individuals >1 year old, with an average of 9 yearlings, 8 two-year-olds, and 144 adults. Numbers of horses varied by only 4–8% and showed no consistent trend. The parturition peak spanned May and June, when 80% of foaling occurred. One-third of the average annual cohort of 33 foals was missing by July and only half of the cohort remained by October. The mean first-year survival rate estimated from the differential incidence of foals and yearlings in successive years was 0.27, which was less than one-third of the foal survival rate reported for other feral horse populations. A minimum of four adult mountain lions used the study area each year between May and October. Of 28 foal carcasses located from May to mid-July, at least 82% were the result of mountain lion kills. No evidence of predation on older horses was observed, but mountain lions preyed on mule deer (*Odocoileus hemionus*) during winter. We conclude that the growth of this horse population is limited by predation.

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Une population de chevaux sauvages (*Equus caballus*) a été étudiée de 1986 à 1991 dans le but de déterminer l'impact démographique de la prédation exercée par le Couguar (*Felis concolor*). La population, qui habite une zone d'environ 600 km^2 à la frontière Californie–Névada, comptait, au moment de l'étude, environ 162 individus >1 an, soit une moyenne de 9 individus de 1 an, 8 de deux ans et 144 adultes. Ces nombres n'ont varié que de 4–8% et ne suivaient pas de tendance définie. La période principale de parturition s'étalait sur mai et juin, alors que 80% des poulains étaient mis au monde. Un tiers de la cohorte moyenne annuelle de 33 poulains manquait en juillet et seulement la moitié de cette cohorte était encore présente en octobre. Le taux moyen de survie la première année, estimé d'après la différence entre le nombre de poulains et le nombre de jeunes chevaux de 1 an au cours des années successives, était de 0,27, une valeur inférieure au tiers du taux de survie des poulains mesuré chez d'autres populations de chevaux sauvages. Au moins quatre couguars adultes ont utilisé la zone étudiée chaque année entre mai et octobre. De 28 carcasses de poulains retrouvées entre mai et la mi-juillet, au moins 82% avaient été la proie de couguars. Aucun cas de prédation de chevaux adultes n'a été observé, mais les couguars attaquaient des Cerfs mulets (*Odocoileus hemionus*) au cours de l'hiver. Nous concluons que la croissance de cette population de chevaux est limitée par la prédation.

[Traduit par la rédaction]

Introduction

Large felids are predators of some wild equids. Predation on onagers (*Equus hemionus*) by lions (*Panthera leo*) and leopards (*Panthera pardus*) is reported in central Asia (Solomatin 1973). In Africa, lions and spotted hyenas (*Crocuta crocuta*) are common predators of zebras (*Equus burchelli*) (Schaller 1972; Kruuk 1972), and these predators may limit or regulate some zebra populations (Sinclair and Norton-Griffiths 1982).

In North America the mountain lion is an effective predator of several ungulate species, mule deer and elk (*Cervus elaphus*) constituting its most common large prey (Hornocker 1970; Iriarte et al. 1990). Mountain lion predation on feral horses has been reported (Robinette et al. 1959; Ashman et al. 1983), but is considered incidental or uncommon (Berger 1986). One exception is in the Montgomery Pass Wild Horse Territory (MPWHT) on the central California – Nevada border. A moratorium on mountain lion sport hunting since 1972 in California, and limited hunting pressure in Nevada, have led to a high density of mountain lions there (Kutilek 1981; Fitzhugh and Gorenzel 1986).

Aerial surveys and ground counts conducted during the past 12 years on the MPWHT have indicated that this feral horse population is numerically stable or slowly declining (USDA Forest Service and USDI Bureau of Land Management 1979, 1988). By contrast, studies of horse populations in other western states have revealed annual rates of increase of 9–20% (Garrott and Taylor 1990; Wolfe et al. 1989; Turner and Kirkpatrick 1986; Eberhardt et al. 1982). Historical reports (Mennick 1979) and field data suggest that mountain lion predation may contribute to a reduced foal survival rate in the MPWHT. This study examines the demographic impact of mountain lions on the feral horse population of the MPWHT.

Methods

Study period

Data on the mountain lion and feral horse populations of the MPWHT were collected between May 1986 and July 1991, mostly during May and June, 2 weeks in September, and 1−2 weeks in January. Day visits were made during other months. May through June was the peak period for locating freshly killed foals and differentiating predation from scavenging. Moreover, many horse bands were concentrated in the 60-km^2 summer grazing area at that time.

Study area

The MPWHT encompasses a remote area of 600 km^2 (38°00′, 118°30′) on the California−Nevada border, where elevations range from 1600 to 2600 m. Vegetation on the study area is composed largely of shrub−steppe communities with sagebrush (*Artemisia* sp.), rabbitbrush (*Chrysosamnus* sp.), and bitterbrush (*Purshia tridentata*) dominating. Areas of pinyon pine (*Pinus edulis*) were present at higher elevations. During the study period the area received an average precipitation of 25 cm at 1500 m elevation, with increasing amounts (mostly as snowfall) at higher elevations. Free water was available from five permanent springs scattered throughout the study area.

Horse population

The MPWHT is inhabited by approximately 162 horses >1 year old with a harem band social structure (Turner et al. 1981; Turner and Kirkpatrick 1986). Individual horses were identifiable by coloration, face and leg markings, and band association (Berger 1986; Turner et al. 1981). Data were collected from bands and individuals by means of photographic or videotape records.

The summer range included a central high point with a 360° view of ridges and valleys radiating out and downward for 5−7 km. As much as 70% of the population utilized this area from May to October. The interval between successive observations of bands in this area was rarely more than 2 days, and the remainder of the herd was observed at intervals of 3−7 days. Thus, during the peak foaling period (May−June) we usually documented the presence of new foals and the subsequent disappearance of foals within 7 days. Some foals may have been killed by lions during their 1st week of life, although this was never observed in the case of foals (n = 19) for which the birth date (±1 day) was known. Foal carcass counts made from May to October in a given year included carcasses present from the previous November to May.

Systematic aerial surveys (3−4 h each) with a replicable flight pattern were conducted from May−October, 1 or 2 surveys being made by helicopter (Bell Jet Ranger) and 4−6 surveys by fixed-wing aircraft (Piper Super Cub). In 1987 and 1988, fixed-wing surveys were also flown in January. The same two experienced observers conducted all fixed-wing surveys and one participated in all helicopter surveys. Population sizes were calculated from fixed-wing aerial survey data for 1 May − 1 July (1987−1990), using the bounded-counts method (Seber 1982), in which abundance excluding foals is calculated as $n = 2N_m - N_{m-1}$, where N_m is the maximum count and N_{m-1} is the next largest count.

We also conducted extensive ground-based surveys, averaging approximately 1600 h of observation time annually, for the years 1987−1991. The methods employed were similar to those described previously (Turner et al. 1981).

Due to the rugged terrain of the study area, it was useful to locate horse bands from the air initially and plot their position on a topographical map. When on the ground we minimized intrusion on the horses and their daily activities by use of cover and distance. Foals were frequently lying in the brush and it was necessary to remain long enough to observe a band move several hundred metres, causing foals to move. Our best estimate of the number of horses present in a given season was the cumulative total of identifiable bands and individuals derived over several weeks' enumeration. We believe that these counts approach a total enumeration of the population.

Survival rates for various age-classes were calculated both age-specifically (i.e., horizontally) and time-specifically (Seber 1982).

TABLE 1. Aerial counts of feral horses in the Montgomery Pass Wild Horse Territory

Year	Count		N	95% CL[a]	No. of counts
	Max.	Second highest			
1987	111	108	114	111−168	3
1988	104	99	109	104−199	4
1989	109	99	119	109−199	5
1990	114	112	116	114−152	4

NOTE: Counts were made during approximately 3 h air time from a Piper Super Cub by two experienced observers. Counts did not include foals.
[a]CL, confidence limits: $N_m < N < [N_m - (1 - \alpha) N_{m-1}]/\alpha$.

The two approaches will yield comparable results if population size and composition remain stable over time (Caughley 1977). Incremental foal survival rates were calculated as the quotient of the number of foals remaining at the end of three time intervals (May−June, July−September, and October−April) and those alive at the beginning of the respective intervals. Age-specific estimates of the annual foal survival rates were obtained by dividing the number of foals alive at the end of a biological year (30 April) by the size of the initial cohort. Time-specific estimates were based on the differential incidence of foals and yearlings in the population at the beginning of a given biological year. Estimates of yearling and adult (>2 years old) survival rates were also calculated horizontally.

Mountain lions

Data on lions were obtained from track measurements, feces, tracking with and without hounds, kill-site locations, and visual identification of lions put at bay during tracking. The extremely limited availability of water ensured that mountain lion tracks would be found regularly near springs if animals were present in the area. Track counts revealed seasonal variation in numbers or activity of mountain lions (VanDyke et al. 1986). In 1987 and 1988, lion tracks were counted while the same 20 km of dirt roads in the MPWHT was travelled 7 mornings over a 2-week period. The tracks were obliterated during each transit. Vehicular frequency on these roads was about two per week. In addition to track frequency, detailed track analysis was employed to assist in identifying specific lions present in the spring and summer. Track measurements were based on standard procedures (Fjelline and Mansfield 1990). Three front center-pad imprint widths were measured from a given set of tracks. An average pad-width difference of ≥3 mm in soil of the same condition was considered sufficient to distinguish individuals.

Evidence of mountain lion predation was based on (*i*) canine tooth punctures in the neck and (or) throat area of the carcass; (*ii*) claw rake marks on the carcass; (*iii*) canine tooth punctures on the leg and skull bones of defleshed carcasses; (*iv*) drag marks associated with the carcass; (*v*) covering of the carcass with brush and debris; (*vi*) the presence of tracks; (*vii*) the presence of lion "scratch" marks nearby; and (*viii*) the presence of lion feces containing horse hair. Any one of *i*−*iii* was considered minimum definitive evidence of mountain lion predation, and any three of *iv*−*viii* was considered evidence of carcass use by lions. Aging time of carcasses was estimated by regularly observing, for up to 6 months, several kills that had been located within 1 day of death. Scavenging by golden eagles (*Aquilla chrysaetos*) and coyotes (*Canis latrans*) was common, and dismemberment of the carcass occasionally occurred within 1 month.

Results

Estimates of the MPWHT horse population (excluding foals) obtained from aerial surveys by applying the bounded-counts method varied from 109 to 119 between 1987 and 1990 (Table 1). These estimates accounted for 65−76% of the total population, based on accumulated ground and aerial surveys

TABLE 2. Size and composition of the feral horse population in the Montgomery Pass Wild Horse Territory from 1986 to 1991, based on accumulated ground and aerial counts made from 1 May to 1 July

Age-class	Number of horses						
	1986[a]	1987	1988	1989	1990	1991	Weighted mean[b]
Yearlings	7 (8.5)	10 (6.7)	8 (5.1)	8 (4.8)	11 (6.8)	9 (5.1)	9 (5.6)
Two-year-olds	7 (8.5)	8 (5.3)	8 (5.1)	8 (4.8)	9 (5.6)	8 (4.5)	8 (4.9)
Adults	68 (82.9)	132 (88.0)	140 (89.7)	149 (90.3)	142 (87.6)	158 (90.3)	144 (88.9)
Base population total	82	150	156	165	162	175	162
Foals	15	34	35	34	30	29	32

NOTE: Values in parentheses are the percentage of the total number of horses in each age-class.
[a]Partial count (see text).
[b]Excluding 1986.

TABLE 3. Foal losses and incremental foal survival rates in the Montgomery Pass Wild Horse Territory feral horse population

	Biological year[a]				
	1987–1988	1988–1989	1989–1990	1990–1991	Mean
No. of foals born	34	35	34	30	33[b]
No. of foals remaining					
July	23	21	25	20	22
Oct.	17	13	20	15	16
Apr.	8	8	11	9	9
Incremental foal survival rates[c]					
May–June	0.68	0.60	0.74	0.67	0.67
July–Sept.	0.74	0.62	0.80	0.75	0.73
Oct.–Apr.	0.47	0.62	0.55	0.60	0.56

[a]May–April.
[b]Does not include foals born in the 1991–1992 biological year.
[c]Survival rates calculated as the number of the cohort alive at the end of a given biological year divided by the initial cohort size, i.e., at the beginning of that biological year.

(Table 2). The latter estimates of the base population ranged from 150 to 175 (mean 162) for the same period, with a variation of 4–8% between consecutive years.

The enumeration–identification data from 1986 represented a partial count, derived from ca. 300 h of observation and covering approximately 60% of the summer-range area. However, the fractional occurrence of the respective sex and age classes was similar in subsequent years. Yearlings and 2-year-old animals averaged 5.6 and 5.1% of the base population, respectively. Males composed 57.3% of the adult segment.

Annual foal production was calculated as the number of foals observed in a given year divided by the number of females >2 years old. These rates were 0.54, 0.61, 0.59, 0.54, 0.50, and 0.44 for the years 1986–1991, respectively, and resulted in an average annual cohort of 32 foals. The sex ratio among 62 sexed foals was 52 M : 48 F and did not differ from unity.

A major portion (80%) of the foals were born during May and June. During the period of the study <10 foals were born between July and September. Foaling later than this was rare.

Age- and time-specific estimates of mean annual foal survival rates produced nearly identical results: 0.27 and 0.28, respectively. One-third of the 1987–1990 average annual foal cohort (mean 33) was missing by 1 July, and only 49% of the foals born remained by 1 October (Table 3). Mean foal survival during the period October–April was 0.56. Annual survival rates among foals, yearlings, and adults averaged 0.27, 0.95, and 0.96, respectively, for the period 1987–1991 (Table 4).

Of 48 foals lost between 1 May and 1 July over 4 years (1987–1990), 58% were found as carcasses, and 82% of those satisfied the criteria for having been killed by mountain lion (Table 5). Twelve of these 23 carcasses were fresh or well-fleshed and bore well-defined claw-rake marks and tooth-puncture wounds, usually on the head, neck, and shoulders. The remaining carcasses ranged from moderately defleshed to completely defleshed and partially dismembered. Coat color, facial markings, and lower leg markings usually remained recognizable for several months after death. When scavenger activity was not extensive, markings and portions of the skin and hair remained for at least 1 year. There was no evidence of other predation or predation on horses (n = 11 carcasses) older than foals.

Twenty lion scats ranging from fresh to partly dehydrated were examined for horse hair. Hard, dry samples were not included. Of 16 scats found in May, June, or September, 62% contained horse hair. None of 4 scats found in January contained horse hair. Determination of the number of lions using the MPWHT between 1986 and 1990 was not possible, but seasonal variation in lion track frequency was apparent (Table 6). Mean (±SE) track frequencies (tracks/10 km) for May and June were 0.55 ± 0.26 and 0.61 ± 0.23, respectively, while counts for January averaged 1.28 ± 0.28. Janu-

TABLE 4. Annual foal, yearling, and adult survival in the Montgomery Pass Wild Horse Territory feral horse population

	Biological year[a]				
	1987–1988	1988–1989	1989–1990	1990–1991	Mean
Foal survival rate[b]	0.24	0.23	0.32	0.30	0.27
Yearling survival rate[c]	0.80	1.00	1.00	0.73	0.89
Adult survival rate[c]	1.00	1.00	0.90	1.00	0.97

NOTE: Survival rates were calculated as the number of the cohort alive at the end of a given biological year divided by the initial cohort size, i.e., at the beginning of that biological year.
[a]May–April.
[b]Based on data from Table 3.
[c]Based on data from Table 2.

TABLE 5. Summer foal losses and mountain lion predation on foals in the Montgomery Pass Wild Horse Territory between 1 May and 1 July

Parameter	1986[a]	1987	1988	1989	1990	1986–1990 Weighted mean	1986–1990 %
Foals of initial cohort missing	4/15	11/34	14/35	9/34	10/30	48/148	32
No. of missing foals found as carcasses	2/4	9/11	8/14	4/9	5/10	28/48	58
Carcasses showing uses by lions	2/2	7/9	7/8	4/4	5/5	25/28	89
% of foal carcasses documented as kills	2/2	6/9	6/8	4/4	5/5	23/28	82

[a]Partial count (see text).

TABLE 6. Frequencies (tracks/10 km) of mountain lion tracks in the Montgomery Pass Wild Horse Territory

	Lion track frequency		
	1987	1988	Mean
January	1.35±0.22	1.19±0.33	1.25±0.14[a]
May	0.71±0.28	0.39±0.23	0.54±0.14
June	0.57±0.21	0.66±0.24	0.61±0.15
September	0.35±0.20	0.55±0.30	0.45±0.17

NOTE: Values are given as the mean ± SE. Frequencies are based on seven morning counts in 2 weeks on the same 20 km of dirt roads.
[a]Different from all others ($p < 0.05$, Tukey's test).

ary counts differed ($p < 0.05$) from those in other months (ANOVA with Tukey's test; Zar 1984). For the years 1986, 1987, and 1988, the minimum number of adult lions regularly utilizing the MPWHT from May to October was two males and two females. One female was accompanied by two yearlings in summer 1987, and the other had a kitten in 1988.

The areas of use differed between the two males, which had tracks of 56.1 ± 3.0 and 62.3 ± 2.7 (SE) mm (front center pad width), based on 19 and 18 sets of track recordings, respectively. The areas of use were also different for the two females, which had tracks of 35.1 ± 1.9 and 39.4 ± 2.4 mm, based on 25 and 19 sets of track recordings, respectively. The area of use of one of the males regularly overlapped that of the females. Although pad-size and location data collected in January 1987 and 1988 suggested the continued presence of these four lions, the increase in frequency of tracks and the variety in track size at that time precluded definitive conclusions.

The remains of 30 mule deer were found between 1987 and 1990. Mountain lion use was indicated for 14 of these carcasses, and 11 met the criteria for having been killed by lions. Most of the carcasses resulted from deaths during the winter and were discovered between May and July, often precluding conclusive confirmation of predation. Three fresh deer carcasses were found between May and October in 1987–1990, two of which showed evidence of lion predation.

Discussion

The population estimates obtained from aerial and ground counts, although yielding quantitatively different results, both indicated a virtually stable horse population. Siniff et al. (1982) reported that aerial counts of feral horses conducted in conditions similar to those prevailing on the MPWHT (i.e., dissected terrain with tree cover) might account for only 40–70% of the animals actually present. This is consistent with the discrepancy between our aerial surveys and combined aerial and ground counts. The combined approach has been shown to yield fairly accurate results (Bashore et al. 1990). The fact that the horse population was not increasing numerically probably accounts for the equivalence of foal survival rates computed dynamically and time-specifically.

The estimates of foal survival and evidence of predation by mountain lions suggest that predation has a significant impact on the demography of the MPWHT population. The estimated incidence of predation was very likely conservative. Of the foals known to be missing in May and June between 1987 and 1990, 48% were killed by lions. However, only 58% of the foals lost in May and June were found as carcasses. Conceivably, a comparable fraction of the carcasses of the foals killed by lions should have been found. Lions frequently cover their kills with brush, so the percentage may be even lower. Furthermore, though definitive evidence of predation was found on only 23 of 28 foal carcasses, the remaining deaths may have been due to predation.

Annual foal survival in the MPWHT is less than one-third of that reported (range 0.72 – 0.97) for other horse populations studied to date (Perkins et al. 1979; Wolfe 1980; Berger 1986; Garrott and Taylor 1990). If predation contributes to the foal losses in these populations, it is not of the magnitude observed in the MPWHT.

On Assateague Island, Keiper and Houpt (1984) reported a foaling rate of 0.74 in a herd experiencing annual removal of most of the foals compared with 0.57 in a separate, unmanaged herd on the same island. The foaling rate in the MPWHT was within the range reported for several other western horse populations, including those in the Red Desert in Wyoming (0.53, Boyd 1979), Stone Cabin Valley (0.50, Green and Green 1977) and Granite Range (0.71, Berger 1986) in Nevada, the Challis Range in Idaho (0.37, Kirkpatrick and Turner 1986; 0.67, Seal and Plotka 1983), and the Pryor Mountains in Montana (0.43, Feist and McCullough 1975; 0.49, Garrott and Taylor 1990). Predation on foals was not reported in those horse ranges. However, the numbers of foals reported in our study do not acocunt for foals that were born and died without being observed. Also, young adults (included in our data) have lower fecundity (Wolfe et al. 1989). Thus, the foaling rates calculated for MPWHT are conservative.

The horse population apparently was not limited by forage availability. In 1987, provisional calculations indicated a summer-use carrying capacity of 280 – 350 horses for the MPWHT summer range (USDA Forest Service and USDI Bureau of Land Management 1988). Horses were the only large grazing animal using the MPWHT during the study period, and the summer range was the site of greatest use.

With one exception all foals documented as lion kills were <6 months old and 70% were <3 months old. Almost half of the annual foal losses occurred by early July. Thus, the lions utilized a window of vulnerability in killing foals, the period of peak predation extending from late May through June. This coincides with the peak foaling period in May and early June in the MPWHT. This period is similar to that reported for other ranges (reviewed by Kirkpatrick and Turner 1986, 1983).

Although 66% of the annual foal losses occurred between 1 May and 1 October, lions were present in the MPWHT throughout the year. In fact there was either a higher density or greater activity of lions in winter than in summer. Lions apparently utilize prey other than foals between October and April. Mule deer are important prey, and the Casa Diablo mule deer herd, numbering ~500, migrates in late October and November from summer ranges in the Sierra Nevada Mountains into the MPWHT (Thomas 1986), where it winters, usually vacating the area in April. Of 23 mule deer equipped with radio collars on this winter range in 1985, 22% were killed by mountain lions within 2 years (Taylor 1988).

Of 30 deer carcasses encountered incidentally in spring and summer during the present study, 37% bore definitive evidence of having been killed by mountain lions. The degree of decomposition of 90% of the carcasses suggested that death had occurred prior to spring. Only two fresh deer carcasses showing signs of predation were found between May and October over 3 years. These observations suggest that the mountain lion population utilizing the MPWHT may exhibit seasonal prey switching. From May to October foals constitute the primary prey, while mule deer serve as an important prey during winter. Prey switching has been reported for other ungulate-based predator – prey systems (Bergerud and Elliot 1986).

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