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Alternate Population Limitation Strategies for Feral Horses

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ALTERNATIVE POPULATION LIMITATION STRATEGIES FOR FERAL HORSES

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ABSTRACT

The efficacy of various strategies for reduction of excess numbers and/or limitation of the growth rate in feral horses (Equus caballus) was investigated, primarily by means of computer simulation techniques. Strategies considered were: (1) sustained versus single or periodic removals; (2) age-specific removals; (3) sex-specific removals; and (4) fertility control measures. Sustained removals to maintain a population at a specific level are more costly than a single, large-scale removal because treatment must be repeated annually. However, in most cases, following one-time reductions of 60% or less and assuming an annual increase rate of 10-15%, the residual population will attain its original level in less than a decade. Age-specific removals offer only limited potential for manipulation of the population growth rate, but disparate female removals from a given population can effect at least a temporary depression in the rate of increase. Fertility control measures directed at either the female or male segment constitute neither logistically feasible nor permanent strategies of population limitation.

INTRODUCTION

This paper compares the efficacy of various population limitation strategies for feral horses. To avoid becoming involved in the emotional aspects of the wild horses issue, I shall proceed from three simplistic and I beleive largely incontrovertible premises, namely:

(1) That feral horse populations in the western United States are increasing, although the actual magnitude of the rates of increase remains the subject of considerable controversy: (cf. Cook 1975, Conley 1980, Wolfe 1980);

(2) that some degree of population control and/or reduction is needed to manage horses in coordination with other uses and the supporting vegetation;

(3) that the demographic effects of destructive removals, are identical to those of nondestructive removals e.g., gatherings, etc.

The concepts discussed below are not new, but merely constitute an attempt to apply certain aspects of conventional exploitation theory to control of feral horses.

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METHODS

The utility of the various population limitation strategies was compared primarily in terms of the results of a series of population simulations. The simulation trails were run by means of a computer model of a modified Leslie matrix (Leslie 1945, 1948). Operational details of model have been described by Innis (1980). Input variables in the simulations were derived primarily from provisional estimates of various demographic parameters from 18 feral horse populations in six states (Wolfe 1980). These data were supplemented by those from more intensive investigations of individual populations in Montana (Feist and McCullough 1975) and northern New Mexico (Nelson 1980). In simulation trials that entailed age-specific fecundity rates, values were taken from the results of an earlier investigation by Speelman et al. (1944) on the fertility of domestic horses raised on western ranges. The initial population employed in most of the simulations consisted of 500 animals, apportioned among 20 age classes in an approximate geometric distribution. In trials involving male removals, the initial sex ratio was set at unity; in other cases only the female segment was modeled. All simulations were run in a deterministic and density-independent mode.

Results of the various simulation trials discussed below were compared either in terms of the time required to return to the population level prior to treatment or the finite rate of population increase (λ). The latter value is a measure of a given population's rate of increase, expressed as a ratio of the number of animals present in two successive years (Caughley 1977). The relationship may be expressed in standard demographic notation as follows:

$$\lambda = \frac{N_{t+1}}{N_t}$$

where: N = numbers of animals

t = time (in years)

It is important to note the limitations of the matrix approach to population analysis and, in particular, the restrictive assumptions associated with the use of the finite rate of increase to express population growth. Strictly speaking, λ is hypothetical and asympototic quantity that describes the growth rate that a population will assume only after a fixed schedule of age-specific birth and death rates has been operative in the population for a period of several years. While this condition represents an abstraction, it constitutes a useful common denominator for comparing the potential effects of various removal strategies.

RESULTS AND DISCUSSION

Caughley (1977:168) defined "control" as "the treatment of a population that is too dense, or which has an unacceptably high rate of increase, to stabilize or reduce its density." Beyond this, it is important to distinguish between control measures that merely reduce the number of horses present in a given population and those, which actually depress or limit the future growth rate of the population. The latter strategy constitutes a more effective control measure. Accordingly 2 operational criteria of efficacy are used in the following discussion of control measures. Other factors being equal, more efficacious measures are those that: (1) effect the greatest reduction in the finite rate of increase for a given number of animals removed; and (2) maximize the period betwen treatments.

Possible population limitation strategies for feral horses encompass the following measures: (1) various removal strategies; (2) fertility control measures directed at either the male or the female population segment; and (3) habitat manipulation to the detriment of the horses. Caughley (1977:205) considered the latter strategy as the most sophisticated technique of population control. However, given the lack of habitat specificity in feral horses, the applicability of this approach to the species in question appears to be beyond the realm of our current state of the art.

REMOVAL STRATEGIES

Sustained Versus Periodic Removals

Reduction of an existing population can be accomplished either by continuous cropping (i.e., sustained removals) or by periodic removals. The former approach involves the removal (usually on an annual basis) of a specified fraction of excess animals to balance increments to the population from natality and immigration. Alternatively, single or periodic removals of greater magnitude may be executed to reduce the population to a predetermined level, whereupon it is allowed to increase again over a period of several years. The use of the latter strategy has been proposed by DeByle (1979) for elk (Cervus elaphus) in areas where high densities are causing damage to forest regeneration.

Both strategies have advantages and shortcomings. The application of sustained removals presupposes reasonably accurate estimates of the size and levels of recruitment and natural mortality for the population in question. From an economic standpoint, the logistics involved in the removal of a small number of animals on a sustained basis are likely more costly than a single large-scale removal. However, potential negative sociological consequences may render the latter strategy unacceptable. Moreover, if reproductive and survival rates in feral horse populations are subject to density-dependent influences, a drastic reduction of a given population could result in an acceleration in the annual rate of increase greater than that occurring prior to the reduction.

Sustained Removals

In theory, sustained removals equivalent to a given average rate of increase should maintain the population at a reasonably constant numerical level. Aside from methodological problems inherent in the determination of the "average" annual rate of increase and the confounding influences of stochastic variations, this relationship is subject to some semantic ambiguity. This can be shown by the following example.

Given a current population of 500 horses, increasing at an annual rate of 20%, the expected increment to the population will be 100 animals. Removal of an equivalent number of individuals from the present population would result in a net deficit of 20 animals. The appropriate removal for the population in question would be equal to the projected increment divided by the predicted new population or 16.7% of the existing population (i.e., 83 animals). The product of the residual population (417) and the finite rate of increase ($\lambda = 1.2$) will yield a new population of the same numerical strength as the original one. The balancing removal rate (BRR) can be expressed in more general terms as follows:

$$BRR = \frac{N_t - N_0}{N_t}$$

where: N_0 = present population

N_t = projected new population (i.e. $N_0 * \lambda$)

If births constitute the only increment to the population, the BRR is equivalent to the percentage of young animals in the projected new population in the absence of any removals. A series of removal rates corresponding to the spectrum of values for annual rates of increase that may be encountered in feral horse populations is given in Table 1.

Table 1. Annual removals (percentages) required to maintain populations subject to varying rates of increase at a constant level.

	Finite rate of increase (λ)				
	1.05	1.10	1.15	1.20	1.25
Balancing Removal Rate (%)[a]	4.8	9.1	13.0	16.7	20.0

[a]BRR represents the fraction of the current population that should be removed to maintain a constant numerical level (see text for further explanation).

Given the relatively low rates of increase in feral horse populations in comparison to those of more fecund species, the differences between the BRR values and rates of increase are minor, except where the latter parameter approaches biotic potential. In most cases, they probably fall within the range of sampling error that can be expected in estimates of the rate of increase.

Periodic Removals

Figure 1 shows the results of several simulation runs, designed to illustrate the effects of various one-time removals ranging from 10 to 90 percent of an initial population (in this case N = 500, $\lambda = 1.15$). A lambda value of 1.15 was chosen as a realistic upper limit for the rate of increase of most feral horse populations. The parallel lines represent population levels in successive years following the reduction. The figure shows that, following reductions of 50% or less, the residual population will attain its original level in at most 5 years. Even where reductions approach total removal (i.e., 80-90%), the recovery period is slightly more than a decade.

However, it can be shown that the cumulative number of horses that must be removed on a sustained basis to maintain the population at a prescribed level exceeds the number in a single removal required to keep the population below that level for a specified number of years. For example, in the hypothetical population considered in Figure 1, a single reduction of 250 animals (i.e., 50%) would require 5 years for the population to return to its pre-treatment level. By comparison the cumulative number of animals that would have to be removed under a sustained removal system (BRR = 13%) over a 5-year period would be 325 animals.

The slopes of the lines shown in Figure 1 are a function of the rate of increase and will hold proportionately for any given initial population. A more comprehensive summary of the effects of single reductions is given in Table 2. The table shows the years required for a population to equal or exceed its original level following one-time reductions of varying magnitude as a function of different increase rates. It can be seen that the only cases that might be considered as reasonably "permanent" reductions are those involving drastic removals from populations with relatively low rates of increase. Given a population that is increasing at a certain rate and the decision has been made that continuous cropping does not constitute a feasible alternative, the values in the table may be used as a frame of reference to determine the magnitude of reduction necessary to keep the population from exceeding a predetermined level for a desired time interval between successive treatments.

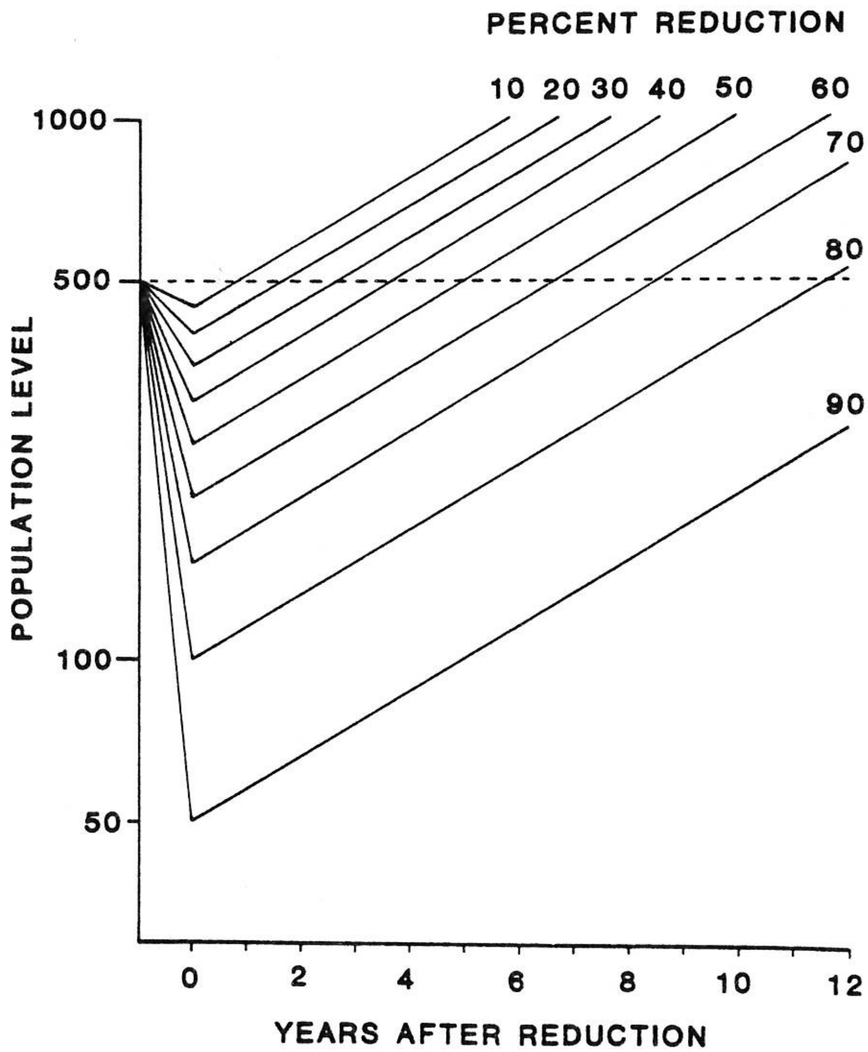

Figure 1. Years required for a population (N = 500) with a finite rate of increase (λ) of 1.15 to equal or exceed its original level following single reductions of varying magnitude.

Table 2. Years required for population to equal or exceed original level following a single (one-time) reduction of varying magnitude as a function of different rates of increase.

Percent Reduction	Finite Rate of Increase (λ) 1.08	1.10	1.12	1.14	1.16	1.18	1.20
10	2	2	1	1	1	1	1
20	3	3	2	2	2	2	2
30	5	4	4	3	3	3	2
40	7	6	5	4	4	4	3
50	9	8	7	6	5	5	4
60	12	10	9	7	7	7	6
70	16	13	11	10	9	8	7
80	21	17	15	13	11	10	9
90	30	25	21	18	16	14	13

Age-Specific Removals

Studies of other ungulates, such as white-tailed deer (Odocoileus virginianus) by McCullough (1979) and moose (Alces alces) by Lykke (1974), have demonstrated that the manipulation of the female age structure by means of age-selective harvest can be used to increase the maximum sustained yield of the population. Such harvest strategies involve disproportionately greater removals among the younger age classes, with the result that a greater fraction of older--and presumably more fecund--females remain in the population.

Conceivably, it should be possible to employ this strategy in reverse in the limitation of feral horse populations. Several simulation trials were conducted to test this hypothesis. Three hypothetical populations with differing rates of increase, obtained by varying fecundity schedules, were subjected to a series of sustained age-specific removals. In all cases survival was held constant at 90% across all age classes. Removals in the various age segments were numerically equivalent to the BRR that would need to be applied across all age classes in order to stabilize the respective populations. The removal strategies were as follows: (1) removals of foals only; (2) removals limited to the pre-reproductive age classes, including foals; (3) removals limited to the primary reproductive segment, i.e., age classes 3 or 4 to 9 years; and (4) removals limited to older age classes, i.e., 10-19 years.

Table 3. Effects of age-specific female removals on feral horse populations with varying rates of population increase.

Case (demographic parameters given below)[a]	Equivalent removal rates (%) and corresponding (λ) values				
	BRR (%)[b]	Foals only	Pre-reproductive (0-2 yr. olds)[c]	Primary-reproductive (3-9 yr. olds)	"Old age" (10+ years)
I (λ = 1.05)	4.8 (1.00)	24.0 (1.02)	9.6 (1.02)	11.9 (0.98)	48.5 (1.00)
II (λ = 1.13)	11.4 (1.00)	64.2 (1.01)	21.8 (1.02)	42.6 (0.97)	____[d]
III (λ = 1.17)	14.3 (1.00)	82.7 (0.97)	34.0 (1.00)	41.1 (0.98)	____[d]

[a]Explanation of demographic parameters for various cases:

I: Survival rates (SURV) for all age classes = 0.9; fecundity rates (FEC) = values given by Speelman et al. (1944)

II: SURV = 20*0.9; FEC = 3*0, 17*0.5; minimum breeding age = 3 years

III: SURV = 20*0.9; FEC = 2*0, 18*0.5; minimum breeding age = 2 years

[b]BRR: no age-specific selectivity

[c]In case II removals included 3-year old animals

[d]In cases II and III this strategy was not possible because the population did not contain sufficient numbers of "old-age" females for an equivalent removal.

The results of these simulation trials (Table 3) indicated that the potential depression in the rate of population increase that can be achieved by selective female removals from the primary reproductive setment is only 4-5%. Weighing this potential against the problems involved in age determination in adult horses, the advantages to be gained by such a removal strategy appear to be minimal. This is probably attributable to the fact that the maximum potential production of young per female in equids is more or less genetically fixed at 1.0.

Sex-Specific Removals

It is virtually intuitive that a disparate sustained removal of females from a given population will effect a greater depression in the rate of population increase than the removal of an equivalent number of horses distributed equally over both sexes. For example, given a current population of 100 horses with an even sex ratio and a finite rate of increase of 1.10, the BRR is 9.1% or 9 horses from the total population. Removal of the same number of females would constitute approximately 18% of the female segment, which would be sufficient to effectively limit the growth of the population at vittually all levels of fecundity below 1.0 foals per female of reproductive age (Table 4). An additional--albeit minor and temporary--limitation in the rate of increase might be achieved by selective removals from the primary reproductive age classes. It should be noted, however, that excessive female removals could result in a distortion of the sex ration to the point where aggression among the remaining adult males in the residual population might reach unacceptable levels (Waring 1980).

Table 4. Finite rates of population increase (λ values) in feral horse populations as a function of various combinations of fecundity and survival.

Fecundity (foals/breeding female)[a]	Survival Rate (%)						
	70	75	80	85	90	95	100
0.4	0.79	0.85	0.90	0.97	1.02	1.08	1.13
0.5	0.81	0.87	0.92	0.98	1.04	1.10	1.16
0.6	0.82	0.88	0.94	1.00	1.06	1.12	1.18
0.7	0.84	0.90	0.96	1.02	1.08	1.14	1.20
0.8	0.85	0.91	0.97	1.04	1.10	1.16	1.22
0.9	0.87	0.93	0.99	1.05	1.11	1.17	1.24
1.0	0.88	0.94	1.00	1.07	1.13	1.19	1.25

[a]Age at first breeding = 3 years.

Given the highly polygamous nature of horses, selective removals of males hardly appears to be a viable strategy of population limitation. As has been amply demonstrated by management studies of other polygamous ungulates, male removals will reduce the absolute number of animals present in the population at any given time. In order, however, to effect any lasting reduction in the rate of increase, a sufficient fraction of potentially breeding males must be removed on a sustained basis, so as to decrease the conception rate among reproductively mature females. The magnitude of such a sex-specific removal is determined by the number of females that can effectively serviced by a single male of a given age class. The program used in these studies contains an option to incorporate females serviced by one male which allows examination of the effects of changes in this parameter.

Lacking reliable empirical data on the number of mares serviced by a single male, the results of the simulation trials conducted to test the effects of varying levels of male removals probably have limited meaning. It was arbitrarily assumed that male foals are physiologically incapable of effective breeding, and that yearling males could breed five mares each. All older males were assumed to service 20 mares. Thus FSBOM = 0,5,18*20. Obviously, these input data make no provision for behavioral patterns, which may modify the breeding potential of individual males of differing social status.

Simulation runs were conducted to examine the effects of varying the levels of sustained non-age-specific male removals. The demographic conditions for the two cases simulated were as follows:

Case I: (λ with no removals = 1.07)
Fecundity = 2*0, 0.25, 17*0.6
Female survival = 0.8, 19*0.9
Male survival = 0.75, 19*0.85
Females serviced by one male = 0,5,18*20
Length of run = 10 years

Case II: (λ with no removals = 1.11)
Fecundity = 3*0, 17*1.0
Other variables - same as in Case I

The results of these simulations indicated that sustained removals (over a 10-year period) approaching 50% of the male segment were necessary to effect any appreciable depression in the rate of increase. By contrast, comparable results were obtained by application of sex-specific female removals of approximately 7 and 10%, respectively, for the 2 cases in question. Furthermore, simulated female removals resulted in an immediate depression of the rate of increase, whereas the male removals required a period of several years before the progressive distortion of the sex ratio could effect a limitation in fecundity rates by the FSBOM function.

FERTILITY CONTROL MEASURES

Permanent sterilization procedures applied to the breeding female segment are tantamount to a reduction of the fecundity rate (Table 4). In a population with a female survival rate of 90%, the fecundity rate must be reduced to less than 0.4 foals per potentially reproducing female in order to achieve a "no-growth" condition. The actual degree of fertility control that must be applied to obtain such a condition will depend upon the fecundity rates that are operative in the population in the absence of any control measures.

Fertility control among females cannot be considered as a permanent solution to population limitation. Unless all females (including reproductively immature animals) are treated, recruitment of younger mares into the reproductive segment will eventually negate the effects of such measures. Since such a drastic strategy probably represents an impractical alternative, control measures must necessarily be implemented periodically. The interval between treatments will depend upon the intensity of a given control effort (i.e., the fraction of the breeding female segment rendered sterile).

Fertility control, induced by means of either temporary or permanent sterilization of dominant harem stallions, has been proposed widely as a technique for limiting the growth rate in feral horse populations. The appeal of such a technique is obvious, since in theory it requires treatment of only a small number of animals in a given population. Nelson (1980) investigated in detail the potential for use of this strategy and examined several behavior requisites that must obtain for it to be effective. The primary assumptions are as follows: (1) only a fraction of the total male segment participates in the breeding; (2) this fraction is small relative to the pool of potentially reproducing females, such that many females are bred by a single stallion; (3) social groups are stable over time; and (4) if changes in band affiliation do occur, they involve primarily animals in the immature, pre-reproductive segment of the population.

The findings of Nelson's study indicated that the first 2 assumptions were met, but that contrary to the results of other studies of feral horse behavior (e.g., Feist and McCullough 1976) the premise of one male-many female reproductive units did not obtain. Nelson observed that a substantial fraction of the mature mares were involved in movements and reproductive activities outside their primary harem band. Furthermore, harem stallions were subject to an annual replacement rate of approximately 25%. Based on this evidence and the results of computer simulations, Nelson concluded that, even if the assumption of band fidelity was met, male-sterilization techniques would have to be implemented on an alternate-year basis, thus rendering this strategy impractical.

The present study afforded no opportunity to either corroborate or refute the validty of the behavioural observations in Nelson's analysis. It was, however, possible to replicate the population projections obtained by means of computer simulations in that study. Figure 2 shows the results of a series of three simulation runs, designed to evaluate the effects of male fertility control measures under varying demographic conditions.

All cases presupposed the execution of a fertility control program, such that all cominant harem stallions were permanently sertilized at 5-year intervals over a period of 15 years. Cases I and II incorporated Nelson's estimate of the turnover rate among harem stallions of 25% per year, while Case III involved an estimated annual replacement rate of half of that value. The initial population level was identical in all 3 cases. Likewise, survival rates were held constant at 90% for all cases and across all sex and age classes. Fecundity rates and corresponding λ values (in the absence of fertility control measures) for the respective cases were as follows:

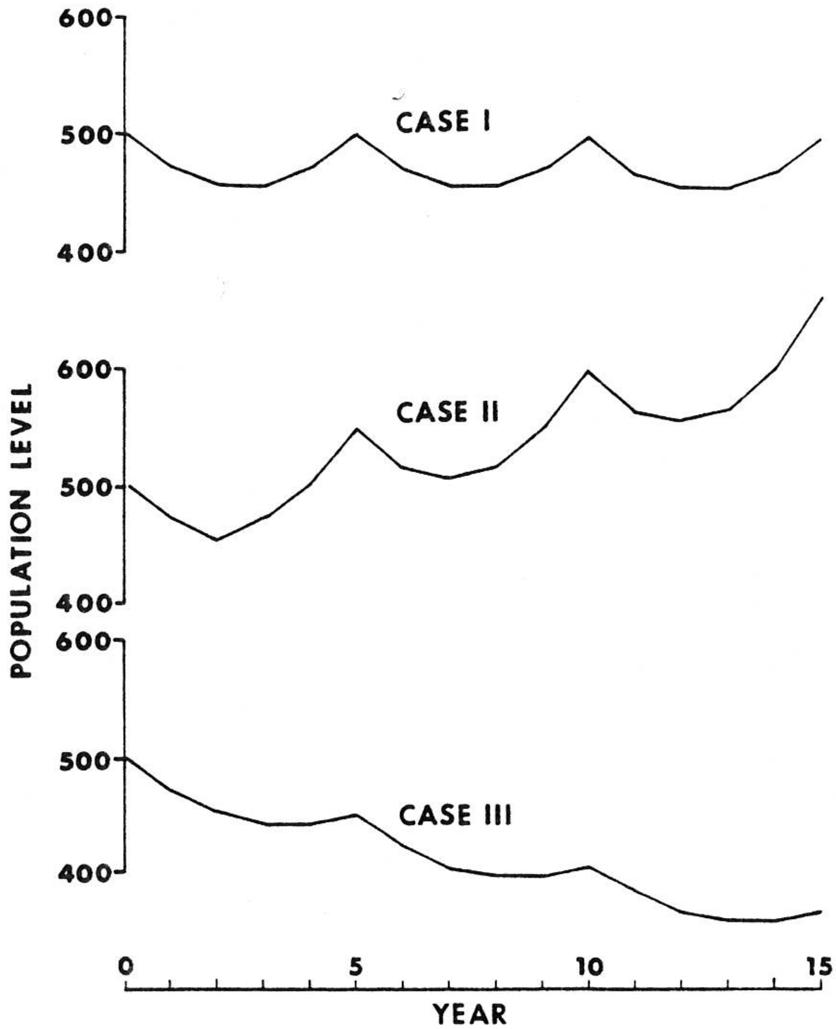

Figure 2. Simulated responses of three hypothetical populations subjected to male-sterilization procedures at 5-year intervals. See text for explanation of the various cases.

Cases I and III: Fecundity = 3*0, 17*0.6; $\lambda = 1.06$
Case II: Fecundity = 3*0, 17*0.8; $\lambda = 1.10$

The question of whether or not male fertility control measures can effectively limit the rate of increase in feral horse populations cannot be answered simply. The population response is subject not only to the behavioral constraints enumerated above, but also to intrinsic demographic parameters such as the survival and fecundity rates that are operative within a given population.

Although male fertility control measures alone probably are not practicable as a "large-scale" population limitation strategy, they might be employed in conjunction with significant numerical reductions to prolong the period between reductions. Conceivably, it should be possible to sterilize and return to the residual population a significant proportion of the stallions gathered in reduction operations, while most of the foals and females are given up for adoption.

CONCLUSIONS

Nelson (1980) recommended continuous cropping of a specified fraction of the population to maintain feral horse herds at prescribed levels. He proposed cropping of entire band units as a means to accomplish this objective while minimizing disruption to the social structure of the population. However, strict adherence to the efficacy criteria established above would argue for intermittent and reasonably large-scale reductions (i.e., at least 50-60% of the existing population). To the extent possible, the removals should involve a disproportionately larger fraction of females, particularly those in the primary reproductive age classes.

It may not be possible to apply operational criteria of efficacy without regard to behavioral and evolutionary considerations. For example, the residual populations remaining after large-scale reductions should be of sufficient size to avoid potential problems associated with small populations, namely: (1) the possibility of demographic extinction due to stochastic variation in birth and death rates; and (2) possible increased rates of allelic fixation or extinction as the result of genetic drift.

Given that the ratio of the crude death rate to the crude birth rate in feral horses is comparatively small, the former consideration should not constitute a problem in most situations. As an illustration, the probability of extinction is given by Krebs (1972:206) as:

$$\left(\frac{d}{b}\right)^{N_o}$$

where: d = death rate

b = birth rate

N_o = population size

If reasonably conservative values for crude birth and death rates (e.g., $d = 0.2$ and $b = 0.6$) are substituted into the above equation, it can be shown that the probability of extinction for a residual population (N_o)

of as few as 20 animals is only 1.1×10^{-8}.

Potential loss of genetic diversity in small residual populations constitutes an issue of greater complexity. In essence the scenario is analogous to the "bottleneck effect" described by Wilson and Bossert (1971), in which a population is intermittently reduced to a size sufficiently small to allow genetic drift to operate. Moreover, as pointed out by Bunnell (1978) the probability of allelic fixation or extinction will be increased where rank or harem mating systems are operative, roughly in proportion to the number of females serviced per male. A comparable phenomenon might occur in a residual population with a substantially distorted sex ratio as the result of disproportionately heavy female reductions.

I view the possible genetic constraints posed above as somewhat academic arguments for 2 reasons. Most feral horse populations are of relatively cosmopolitan genotypic origin. Moreover, given the "artificial nature" of the establishment of these populations in western North America, it should be possible to maintain or restore diversity (if necessary) by translocations of females drawn from other demographic units.

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