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Achieving population goals in a long-lived wildlife species (*Equus caballus*) with contraception

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Abstract. The ultimate goal of any wildlife contraceptive effort is some alteration of the target population, either through a slowing of growth, or stabilisation or reduction of the population. Early population models suggested that short-term contraceptive agents applied to long-lived species would not achieve significant population changes. Native porcine zona pellucida antigen (PZP), a short-term contraceptive vaccine, was applied to a herd of wild horses inhabiting Assateague Island National Seashore, MD, USA, over a 13-year period, with an immediate goal of achieving zero population growth, a secondary goal of reducing the population from 175 to 150 and a tertiary goal of reaching 120 individuals, all without the physical removal of animals. Contraceptive efficacy ranged from 92 to 100% on an annual basis (96.28 ± 2.49%), and the percentage of adult females that was treated on any given year ranged from 42 to 76% (67.78 ± 18.21%). The goal of zero population growth was achieved in 2 years, an initial decline in the population became apparent in 8 years and by Year 11, the population declined to 135, a decrease of 22.8%. The lengthy period required for achieving a population decline was caused by increasing body condition scores, reduced mortality and significantly increased longevity among treated females.

Additional keywords: equids, fertility control, horses, immunocontraception, population, zona pellucida.

Introduction

Contraceptive research aimed at managing populations of wild horses did not begin until the late 1970s (Kirkpatrick *et al.* 1982; Turner and Kirkpatrick 1983). These early and subsequent studies (Plotka *et al.* 1988; Kirkpatrick *et al.* 1990, 1991; Eagle *et al.* 1992; Willis *et al.* 1994; Daels and Hughes 1995; Goodloe *et al.* 1997; Turner *et al.* 1996; Turner *et al.* 1997, 2001, 2002; Cameron *et al.* 2001; Stafford *et al.* 2001; Killian *et al.* 2004) were all directed at testing the efficacy and safety of various antifertility compounds, vaccines, devices and delivery systems and/or the effects on social behaviour.

The actual management of wild horse populations by means of fertility control was initiated in 1995, on Assateague Island National Seashore (ASIS), MD, and represented the first attempt at actually altering an entire population and attempting to achieve a discrete population goal exclusively with fertility control. Shortly thereafter, additional attempts at managing entire populations were initiated on Carrot Island, NC, for the Rachel Carson National Estuarine Reserve, on the Shakleford Banks of Cape Lookout National Seashore, NC, and Return-to-Freedom Wild Horse Sanctuary, CA, and are ongoing. Two smaller and limited trials for the contraceptive management of wild horse populations were initiated in 2001 and 2002, on the Pryor Mountain National Wild Horse Range, MT and the Little Book Cliff National Wild Horse Range, CO respectively. The antifertility agent of choice for these initial attempts at population management was porcine zona pellucida (PZP) vaccine, first described as an inhibitor of fertility in horses by Shivers and Liu (1981) and Liu *et al.* (1989) and first applied to free-ranging wild horses by Kirkpatrick *et al.* (1990).

The onset of serious wildlife contraceptive efforts, in the early 1980s prompted the growth of population modelling with which to assess the theoretical effectiveness of contraceptive efforts. Several models were developed with which to determine the various levels of effort and the concomitant effects of contraceptive management on entire populations of large ungulates, and specifically, wild horses (Garrott 1991; Garrott and Siniff 1992; Hobbs *et al.* 2000). These various models examined possibilities within the parameters of (1) duration of contraceptive effect, (2) reproductive rates, (3) mortality rates and (4) contraceptive efficacy. The early predictions, although interesting, lacked a sound empirical database derived from actual population management trials, yet provided some direction for researchers in the field (McCullough 1997). For example, before the late 1990s, most models suggested that contraception would only be effective in species with short life spans and high reproductive rates (Hone 1992). Other models suggested that only contraceptives with multi-year life spans (Garrott 1991*a*) or actual sterilising agents (Garrott 1995) would be effective in population management. Still other complicating factors in early models included reproductive and growth rates of herds. Garrott (1997) suggested that only herds with less than 15% growth rates and the application of contraceptives with pharmacological life spans of 3–10 years

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would lend themselves to successful contraception. Almost all, however, made it clear that generalisations based on data that were not site specific with regard to herd age class profile, reproductive and mortality rates were fraught with risk.

The purpose of this research report is to provide empirical data regarding the management of a wild horse population exclusively by means of contraception, from which even more accurate models might be developed, and for other ungulate species that are candidates for contraceptive management. The hypotheses put forth at the beginning of this study were, that contraceptive management of a herd of barrier island wild horses, using a remotely-delivered short-term fertility control agent, could (1) stabilise the population rapidly and (2) reduce the herd size from ~175 animals to 150 over a longer period of time, and in a second phase, further reduce the population to 120, without the need to remove animals. The time elements necessary to achieve these goals were undefined at the initiation of the study.

Methods

Population

The study population consisted of wild horses inhabiting ASIS. The species has inhabited the island for 330 years and originated from 28 wild horses inhabiting the Maryland portion of the island (16 085 ha) at the time of the creation of the national seashore, in 1968. This population expanded to a high of 175 in March of 2001. The nature and circumstances surrounding this population, and the need for managing it in a manner ensuring acceptable ecological impacts and the maintenance of a healthy and viable herd have been described in detail elsewhere (Kirkpatrick 1995; Kirkpatrick and Turner 2007).

In 1988, the managing authority for horses, the National Park Service (NPS), authorised research aimed at evaluating the use of immunocontraception as a potential population management tool, and from 1988 through 1993, 46 different mares were intermittently treated with PZP vaccine (Kirkpatrick *et al.* 1990). Research during this period showed that the vaccine was effective and safe (Kirkpatrick *et al.* 1990, 1991, 1992, 1995). Beginning in 1994, with the herd size at 166, the NPS authorised actual management of the ASIS herd through PZP contraception. In phase I, and under the provisions of a written management plan and required environmental assessment, every untreated mare 2 years or older and which had never been treated before was given a single 'primer' dose of PZP. The purpose of this phase was to cause antigen recognition in the herd and thereby create a 'one-inoculation' population that would only require a single booster inoculation in subsequent years. In 1995, with the March herd size at 166 and the environmental assessment completed, phase II of the management plan was initiated, with an immediate goal of stabilising the population, a secondary goal of reducing the population to 150 animals and a tertiary and subsequent goal of reaching 120. For the first 3 years, the management plan allowed the inoculation of all 2-year old mares and booster inoculations with PZP at ages 3 and 4, followed by withdrawal of treatment until the mare produced three living offspring or a second generation, after which the mare would be treated with the PZP annually until her death. The underlying philosophy behind this plan provided for a delay in the reproductive age of mares, but a continuous contribution of genes from all mares on the island. This plan was modified in 1998 to allow only two foals after withdrawal from treatment, and again in 2000 to allow only a single foal, largely because there was no apparent decrease in the population as a result of contraception. This plan was maintained through 2007.

Vaccine application

The vaccine was prepared according to the modified method of Dunbar *et al.* (1980) at the University of California, Davis from 1988 through 1997 and at the Science and Conservation Center thereafter. Delivery of the vaccine was by 1.0 cc Pneu-Darts, at doses of 100 µg, along with an appropriate adjuvant, as described by Kirkpatrick *et al.* (1990, 1991), at ranges of 10–55 m and authorised under the Food and Drug Administration Investigational New Animal Drug Exemption File 8857-G0002. From 1994 to 2001 the adjuvant used for all initial inoculations was Freund's complete adjuvant (FCA), and since 2002, Freund's modified adjuvant has replaced the use of FCA. All booster inoculations for the entire duration of this study utilised Freund's incomplete adjuvant. No horses were captured or handled during the course of this study.

Data collection

All animals in the Assateague population are monitored every 2 months by an ASIS employee (AT) and data collected include: (1) identification of individual animals by unique markings; (2) band affiliation; (3) band location; (4) band habitat; and (5) dates of births and deaths. Numbers presented in this study are not estimates, but actual numbers based on bi-monthly data collection.

Results

The ASIS wild horse population profile is illustrated in Fig. 1. Systematic and regular population counts were initiated in 1975 and the period between then and 1987 indicates a growth curve that represents an approximate 8% annual increase. The dramatic drop between 1987 and 1990 was associated with the initiation of contraceptive research, which removed 26 mares from the reproductive pool, and an epidemic of eastern equine encephalitis (EEE) that caused, at a minimum, the death of at least another 14 horses. By 1997, 2 years after the initiation of management-level contraceptive control, the population was stabilised and continued within a range of nine animals over the ensuing 7 years. The March population began a decline to 158 animals in 2005, 138 in 2006 and 135 in 2007. During the 11 years following the initiation of management-level contraception, foaling rates dropped to $6.9 \pm 2.30\%$ annually (an approximate 88% reduction) for mares 3 years or older. Thus, the first two population goals of stabilisation and a reduction to 150 were achieved and significant progress has been made towards the goal of 120.

The age profile of the herd changed coincident with the intensive contraceptive control and is illustrated in Fig. 2, which provides a comparative view from 1990, before management, to April 2007. This change in age profile is characterised by (1) fewer young animals, (2) an increase of animals in older age classes and (3) the appearance of entirely new older age classes, primarily among mares. Sex ratio also changed

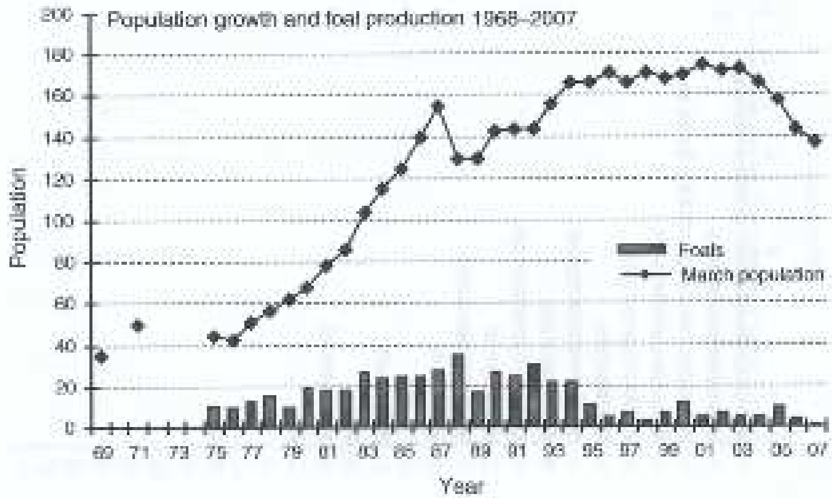

Fig. 1. Population changes of the Assateague Island National Seashore (ASIS) wild horse herd over a 38-year period. Contraceptive management began in 1995.

during the contraceptive management of the herd. Historically, the ASIS sex ratio has been ~1 : 1, but after 12 years of contraceptive management, the ratio has changed to 51 stallions : 84 mares, or 1 : 1.68 (Keiper and Houpt 1984).

The effort required, and the contraceptive efficacy necessary to bring about this level of population change, in this particular herd, is shown in Table 1. The percentage of adult mares treated annually ranged from a low of 52% to a high of 95% (67.78 ± 18.21). The latter high figure represents an effort in 1994, the year before the actual management effort went into effect, to treat all previously untreated mares with a 'primer' inoculation, not for purposes of contraception that year, but rather to establish the population as a 'one-inoculation' herd thereafter. The annual efficacy of the contraceptive vaccine ranged from a low of 92% to a high of 100% (96.28 ± 2.49). As time increased, so did the amount of time necessary to dart the target mares. Table 2 indicates this trend.

Discussion

The application of a short-acting immunocontraceptive to certain wild horse herds has the potential to reduce populations of long-lived wild horses given sufficient time; however, the application must be fairly intense over time. The change in population associated with contraceptive management provides some cause for optimism with regard to wider applications elsewhere. Mortality, outside of episodic disease and weather catastrophes, has been historically low in this population, yet the attainment of near-zero population growth was possible in only a few years.

At the outset of this research, historic data for population dynamics of this herd included a 57.1 ± 3.9% foaling rate (among adult mares), an annual 5% mortality rate and an overall annual 8% population growth rate (Keiper and Houpt 1984). The average age of a mare in 1994, before management-level contraception, was 8.19 ± 5.6 (s.d.) years. The 88% reduction in foaling rate during the 11 years following the initiation of management-level contraception, for mares 3 years or older, was expected; however, mortality rates also dropped until recently. From the onset of contraceptive management, in 1995, to 2003, the annual mortality rate was 3.3 ± 1.0% and the average age of mares increased to 14.8 ± 6.4 years. This was a period of population stabilisation characterised by an ever-increasing longevity among treated mares (Kirkpatrick and Turner 2002, 2007). As treated mares reached a new 'age of mortality', from 2004 to 2006, the mortality rate increased to 9.0 ± 1.0%. The increased longevity has previously been shown to be directly related to contraceptive treatment (Kirkpatrick and Turner 2007), with the average age at death reaching >20 years for mares treated for 3 years or more.

In a recent critique of immunocontraception in wildlife, Cooper and Larsen (2006) suggested that it may be impossible to evoke a strong enough immune response against the contraceptive antigen to cause contraception in a large enough proportion of the target animals for effective population control. Much earlier, Seal (1991) suggested that any effort to successfully manage free-ranging populations would require an agent with 100% efficacy. The concept embedded in that concern confuses two elements of wildlife contraception. Virtually all contraceptives have differing efficacies (see Asa 2005; Frank *et al.* 2005), but the more important question of relevance in wildlife contraception is to what proportion of the target population the contraceptive can be delivered. It is intuitive that a contraceptive with an overall efficacy of 92–100%, as in the case of PZP and wild horses, or any contraceptive for that matter, would not be acceptable for human contraception. However, if a 92% effective contraceptive was applied to 48 to 76% of the human population, as it has been in the ASIS horses, there would be a significant decrease in fertility rates of humans. Obviously, the more effective the contraceptive, the more effective is the population control that can be achieved, but efficacy alone is not the determining factor in achieving success with wildlife.

The dramatic increase in the average age of the female population would be expected as a result of fewer young animals; however, those average ages alone mask the more significant trend of a shift to older age classes. In 1994, the

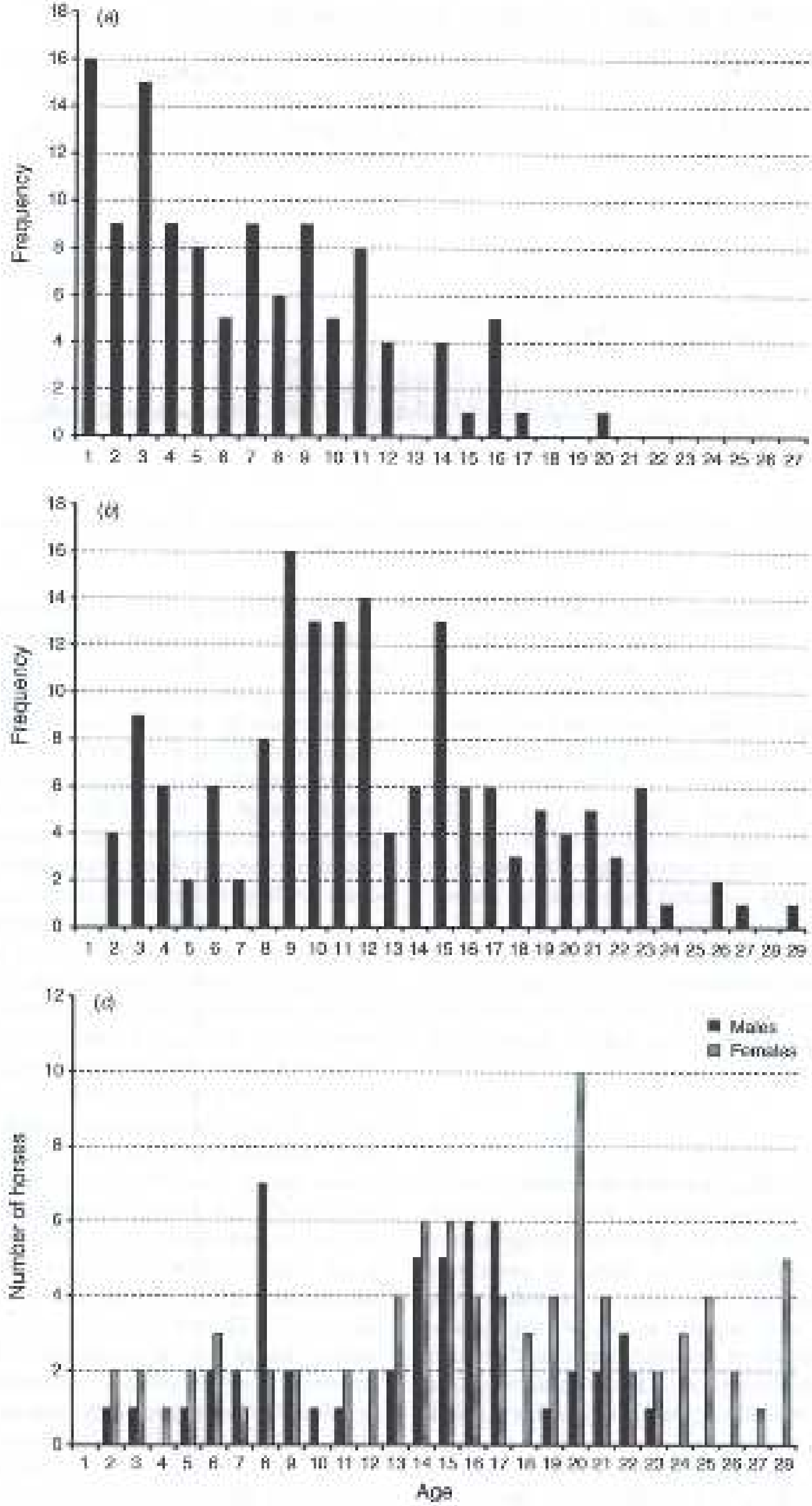

Fig. 2. Age-class structure for the Assateague Island National Seashore (ASIS) wild horse herd in (*a*) 1990, (*b*) 2002 and (*c*) 2007. Part (*a*) describes the age-class structure before contraceptive management, and it reflects a 'typical' structure profile for most wild horse herds. Part (*b*) indicates a shift in the structure after 7 years of management-level contraception, with increasing longevity being the major feature. Part (*c*) gives the structure for both males and females after 12 years of contraceptive management, reflecting the major increase in longevity among females.

Table 1. Percentage of mares treated and contraceptive efficacy, 1993–2006

Year	Spring population	Mares treated (%)	Foals	Foals from treated mares	Foals from untreated mares	Efficacy
1993	156	15 (20)	22	4	18	94%
1994	166	76 (95)	22	0	22	100%
1995	166	68 (83)	10	1	9	99%
1996	171	72 (84)	5	2	3	97%
1997	166	54 (59)	7	2	5	97%
1998	171	49 (52)	3	1	2	98%
1999	168	48 (52)	7	3	4	94%
2000	170	64 (68)	11	1	10	98%
2001	175	75 (79)	5	0	5	100%
2002	172	66 (69)	7	5	2	93%
2003	173	66 (70)	5	4	1	94%
2004	166	74 (76)	5	3	2	95%
2005	158	69 (71)	9	5	4	93%
2006	143	65 (71)	4	3	1	96%

Table 2. Number of days spent darting, 1994–2007

Year	No. of mares treated	Total days darting
1994	76	15
1995	68	14
1996	72	12
1997	54	17
1998	49	16
1999	48	17
2000	64	20
2001	75	25
2002	66	25
2003	66	28
2004	74	26
2005	69	34
2006	65	29
2007	55	25

percentage of mares between the ages of 15 and 19 years and >20 years were 9.8 ± 1.8% and 3.7 ± 0.9% respectively. By 2006, those same age-class cohorts had increased to 26.1 ± 2.7% and 23.8 ± 2.5% respectively. Thus, historic population dynamic data alone will not provide the necessary information to develop a sound and effective contraceptive management plan. Normally, 20 years represents an extreme old age among wild horse herds. Eberhardt *et al.* (1982) considered 20 years the maximum age for wild horses inhabiting ranges in Oregon, and Garrott *et al.* (1991) found that among 14 788 wild horses across Nevada, only 115 (0.007%) were older than 20 years. Linklater *et al.* (2004) found that among New Zealand's Kaimanawa wild horses, only an average of 1.0% would reach 20 years. Thus, the dramatic departure from these age restrictions among the ASIS horses represents a new understanding of the effects of contraception.

A major effect of the shift to older age classes among mares on ASIS is the change in the sex ratio from the historic 1 : 1 (male : female) to 1 : 1.67, post-contraception. This change is clearly the result of mares living longer than before contraceptive management. There is no expectation that this change will widen in favour of mares, as mortality rates have now increased, once the mares reach a new 'age of mortality'. Normally, sex ratios for foals among most wild horse herds is near parity but in some cases it changes in favour of males in older age classes (Garrott 1991*b*), but this is not a hard and fast rule. The male : female sex ratio for a Nevada wild horse herd was 0.78 : 1.0 (Greger and Romney 1999). Indeed, a National Academy of Sciences study found a wide range of sex ratios among wild horses (NAS 1982). Other management options that involve removal of animals may also skew sex ratios. In the Pryor Mountains of Montana, the adult sex ratio in 1970 was close to 1 : 1 (48 males : 52 females) (Feist and McCullough 1975), but within the ensuing 8 years, the ratio changed to 1 : 2, largely because of the bias in removing males through removal programs (Perkins *et al.* 1979). Given the stabilisation of the sex ratio on ASIS, as a result of more mares dying now, the current sex ratio should pose no serious problem and should shift back towards parity.

Used to slow or stabilise population growth among a long-lived species such as the horse, rather than to decrease numbers, PZP immunocontraception can have a rapid and significant effect. A reduction in growth rates and stabilisation of the population can occur in as little as 2 years if the intensity of the treatment is high enough. Indeed, such stabilisation of population growth has even been reported for African elephants treated with PZP (Delsink *et al.* 2006, 2007). If the management goal is reduction in herd size, on the basis of contraception alone the time necessary will be significantly longer and, it is now clear, even longer than historic models predicted, based on historic foaling and mortality rates. Both of the latter parameters, foaling and mortality rates, will change as the length of treatment time for individual animals increases, as a result of significantly lower mortality, increased body condition and increased longevity. Thus, population models will have to account for these changes in population dynamics, or contraceptive management must be flexible and adaptive.

Some concern might arise over the genetic effects of intense contraception. Studies were conducted on the genetic diversity of the ASIS population (Eggert *et al.* 2005) using faecal mtDNA haplotypes and nuclear genotypes at eight polymorphic loci. The results indicated that the relative genetic contributions of the founder animals were well represented and consistent with a high level of nuclear genetic diversity. Even at numbers as low as 100 horses, the population will not accumulate significant loss of genetic diversity sufficient to result in any inbreeding depression effects, nor will kinship increase, over time, and lead to line breeding potential (CBSG 2006).

Despite these empirical data, concerns about genetic effects of wildlife immunocontraception persist in some quarters (Nettles 1997; Cooper and Larsen 2006). In the case of the ASIS population, contraception has eliminated the use of gathers and removals for population control. As conducted by other agencies, for other wild horse herds, gathers and removals most often focus on young horses that are popular for adoption by the public. These removed animals have never bred or entered the gene pool, thus it is intuitive that the potential for genetic effects of the alternative management approach is far greater than from a simple delaying of reproduction and decreasing the number of foals produced by each mare.

It is now clear that contraception is associated with significant downward population trends and changes in long-lived wildlife species. The requirements for achieving these changes are both species specific and site specific, but careful analysis of all demographic and contraceptive parameters for any given species and agent, based on the data derived from the Assateague studies, suggests that this approach is viable and can be effective.

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