DISSERTATION

POPULATION ECOLOGY OF FERAL HORSES IN AN ERA OF FERTILITY CONTROL MANAGEMENT

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ABSTRACT

POPULATION ECOLOGY OF FERAL HORSES
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Management of wildlife often requires intervention to regulate growth of populations that would otherwise become overabundant. Controlling fecundity using contraceptives has become an increasingly popular tool for attempting to manage locally overabundant wildlife species, but the population-level effects of such applications are largely unknown. Contraceptive treatments can produce unexpected feedbacks that act on births, survival, immigration, and emigration. Such feedbacks may considerably influence our ability to regulate populations using fertility control. I followed feral horses (*Equus caballus*) in three intensively managed populations to assess longitudinal treatment effects on demography. The transient contraceptive porcine zona pellucida (PZP) produced longer duration of infertility than intended. Repeated PZP vaccinations of females extended the duration of infertility far beyond the targeted management period, with time to first post-treatment parturition increasing 411days for every annual inoculation received. When these animals did conceive and give birth, parturition was later in the year and temporally asynchronous with forage abundance. An average of 30% (range=11–77%) of females were contracepted annually during the treatment period in all three populations and apparent annual population growth rate was 4–9% lower in the post-treatment years as compared to pretreatment years. Population growth was positive, however, and increased steadily every year that a management removal did not

occur. The observed number of births was 33% fewer than the expected number of births, based on number of treated females, individual efficacy of treatment, and number of untreated females and their age-specific fecundity rates. Only half of this difference was explained by the apparent residual effect of treatment. Birth rate in the youngest untreated females (age 2–5 years old) was reduced in years when their conspecifics were treated, enhancing the effects of treatment at the population-level. This was partially offset by increased survival in adults, including a 300% increase in presence of horses ≥20 years old during the post-treatment period. In closed populations of feral horses, the positive feedbacks appear to outweigh the negative feedbacks and generate a larger contraceptive effect than the sum of individual treatments. The role of fertility control is uncertain for open populations of many wildlife species, with broad consensus across a synthesis of research that negative feedbacks on fertility control performance are occurring, and in many cases increased survival and increased immigration can compensate entirely for the reduction in births attributed to treatment. Understanding species' life-history strategies, biology, behavioral ecology, and ecological context is critical to developing realistic expectations of regulating wildlife populations using fertility control.

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DEDICATION

Dr. Ronald H. Tali

February 17, 1930 – November 26, 1992

This dissertation is dedicated to the memory of Dr. Ronald H. Tali, who greatly expanded my childhood view of the world and inspired me with his love of travel, family, the arts, and academia. I hope this work bridges his passion for mathematics and my passion for the natural world. Ron contributed 19 years to the study of music and mathematics at McGill University, but left the world before my intellectual evolution could fully explain the dead porcupine I loaded into the trunk of his new car on the back roads of Quebec. Science, like love, may be blind, but on such paths we discover truth.

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Chapter 1: Introduction

Forty years have passed since feral horses (*Equus caballus*) were first granted protection in the United States through the Wild Free-Roaming Horses and Burros Act of 1971 (Public Law 92–195, as amended), which declared that "wild free-roaming horses and burros are living symbols of the historic and pioneer spirit of the West" and that these animals "shall be protected from capture, branding, harassment, and death." Since that time, the primary custodial agency, the US Bureau of Land Management (BLM), has struggled to find effective non-lethal management tools for controlling horse populations and meet their directive of maintaining a "thriving natural ecological balance" on the public lands they manage. This is primarily because the genesis of protective legislation arose from a deeply emotional human perspective and the realities of resource management also demand an ecological perspective.

Approximately 38,500 feral horses currently roam 12.8 million hectares of public lands in the US, and provided federal protection and largely unchecked by predators, populations can increase 15–25% annually (Eberhardt et al. 1982,Wolfe 1986, Garrott et al. 1991). Survival of adults is high, ranging 92–97%, and individuals may live >20 years (Roelle et al. 2010). The BLM has historically managed these populations by capturing and removing surplus animals from the range and placing them in private homes through an adoption program; however, less than half of the captured animals are placed, leaving additional animals for the government to care for in captivity. At the end of 2011, there were approximately 47,000 unadopted feral horses in captivity, whose care

cost American taxpayers over $35,700,000 per year (US Department of the Interior 2012). The management strategy is unsustainable.

Decreasing population growth rates of free-roaming wildlife requires either regulating births or survival. Fertility control may be a promising management tool for regulating birth rates, but little is known about how such treatment influences population ecology and demography in wildlife species. The clinical efficacy of many fertility control agents has been demonstrated in controlled environments, but the effect of their application on recruitment and survival may be considerably different in natural systems where feedbacks from behavioral adaptation, ecology, and physiology introduce potentially important influences that determine the population-scale outcome of such management. Effective administration of a fertility control program to maintain a target population that can survive catastrophic population reducing events and maintain genetic viability requires knowledge of age and sex specific reproductive rates, survival rates, and population growth rates (Garrott 1991). Once fertility control has been applied, it is critical for managers to know the rate at which contracepted animals return to fertility and how phenology of parturition affects survival. Unfortunately, most studies of wild horse populations in the western U.S., with some notable exceptions (Berger 1986, Garrott and Taylor 1990), have been too short in duration (< 5 years) to provide enough data on population dynamics and demography to understand how management strategies might influence ecology of these systems. Only one longitudinal study has been conducted that examines population-scale effects of immunocontraception in feral horses and it involves a small island population (Kirkpatrick and Turner 2008), which may or may not be effective in interpreting such management schemes in western systems. Before fertility

control can be widely used to regulate populations, its effects on population dynamics and ecology must be better understood.

Feral horses are non-territorial and generally form long-term cohesive social groups (bands) consisting of a polygynous male with a harem of females, and their offspring (Klingel 1975). These harems typically include 1 to 3 mature females (Feist and McCullough 1975, Berger 1986, Goodloe et al. 2000, Roelle et al. 2010). Bands with two or more stallions also occur and are generally associated with larger numbers of females (McCort 1984). The proportion of bands with multiple stallions may be related to population density and sex ratio, with a greater ratio of males to females leading to the formation of multiple-stallion bands (Kirkpatrick and Turner 1986). Regardless of number of stallions present, these bands are maintained by a suite of behaviors consisting of reproductive, herding, agonistic, and defensive expressions initiated by the polygynous male(s) in the band, as well as hierarchical dominance relationships among females (Feist and McCullough 1976, Klimov 1988, Pickerel et al. 1993, Linklater et al. 1999, Ransom and Cade 2009). The stability of such bands has direct implications toward reproductive success, with females residing in a stable harem producing offspring at a higher rate than those who moved bands or were taken over by a new stallion (Berger 1986, Kaseda et al. 1995, Goodloe et al. 2000). Males up to age 5 or 6 years old, as well as the extremely old, occur outside of bands in populations, and these bachelors may remain independent or form ephemeral bachelor groups (Berger 1986, Kaseda and Khalil 1996, Asa 1999).

The collection of feral horse bands and bachelors occurring in geographic isolation from other horses comprises a population. Three populations were chosen for this longitudinal study; horses inhabiting Little Book Cliffs Wild Horse Range, Colorado,

McCullough Peaks Herd Management Area, Wyoming, and Pryor Mountain Wild Horse Range, Montana. These areas represent a wide variety of habitats occupied by feral horses in the western US, and include desert, sage steppe, piñon-juniper woodland, coniferous forest, and montane environments. Each population experiences typical BLM management practices, including capture and removal, intentional sex-ratio skewing, and fertility control applications. Fertility control treatments were initiated at Pryor Mountain in 2001, at Little Book Cliffs in 2002, and at McCullough Peaks in 2004, as part of a large field trial designed to investigate the effects of the immunocontraceptive porcine zona pellucida (PZP) at the individual level (see Ransom et al. 2010, Ransom et al. 2011). Those treatments included conventional PZP (designed for 10-12 months efficacy) applied to females only once, or consecutively for 2, 3, 4, or 5 years, and PZP-22 (a time-release pellet form of PZP designed to provide 22-months of efficacy).

A fertility control application, such as PZP, that changes reproductive capacity of an individual has the potential to induce individual behavioral changes that can cascade to alterations in family group structure, changes to interspecific and intraspecific interactions, and ultimately influence population dynamics in unforeseen ways. Fertility control has been associated with changes in immigration (Ramsey 2005, Merrill et al. 2006), decreased group fidelity (Nuñez et al. 2009, Madosky et al. 2010), increased survival (Caughley et al. 1992, Kirkpatrick and Turner 2007, Williams et al. 2007), and altered reproductive behavior (Nuñez et al. 2010, Ransom et al. 2010). Attempting to understand these shifts is profoundly difficult, and the challenge of separating the influences of multiple population growth controls can be daunting (Sibly and Hone 2002).

In this dissertation, I examine the longitudinal effects of PZP treatment and include data from 2000–2011 at Little Book Cliffs, 2003–2011 at McCullough Peaks, and 1993–2011 at Pryor Mountain. My objectives were to 1) determine the rate at which females return to fertility (so-called "reversibility") following different durations of PZP treatment, 2) investigate the birth phenology from post-treated females and determine if the health and survival of those offspring were compromised by treatment, and 3) determine if indirect effects of PZP treatment can influence population growth disproportionately to the sum of individual direct effects, and if so what demographic parameters are being altered. Lastly, I aimed to synthesize my findings with the broader scientific literature in an attempt to improve our understanding of how life-history strategies, biology, and behavioral ecology in fertility-controlled populations influence population growth, and thus our ability to regulate populations.

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Chapter 2: Contraception can create trophic asynchrony between birth pulse and resources

Phenology of biological phenomena is reflected in traits evolving to maximize fitness. When humans perturb this process by affecting abiotic influences or intervening in biotic influences such as reproductive cycles, the ecological consequences may be profound. Trophic mismatches between birth pulses and resources in large mammals may cascade toward decreased survival and threaten the viability of small populations. I followed feral horses (*Equus caballus*) in three intensively managed populations for a longitudinal study of porcine zona pellucida (PZP) immunocontraception, and found that repeated PZP vaccinations extended the duration of infertility far beyond the targeted period. When these animals did conceive and give birth, parturition was later in the year compared to untreated females, and the births were temporally asynchronous with forage abundance. These results demonstrate surprising physiological plasticity for temperate latitude horses, whose reproductive cycles are thought to be strongly associated with sunlight and temperature. There is some evidence that within two years, the powerful underlying physiological constraints driving the biological rhythms of conception and birth in this species may correct the altered phenology.

Keywords birth seasonality, *Equus caballus*, horse, phenology, porcine zona pellucida, PZP, wildlife contraception

Phenology of nearly all biological phenomena is influenced by natural abiotic events, but human actions have the potential to perturb such patterns (Forrest and Miller-Rushing 2010). Intervening in reproductive cycles of large mammals by controlling their fertility, for example, has emerged as a potentially valuable alternative to lethal methods of population control. However, the transient nature of many fertility control agents and variation in individual responses to those agents introduces uncertainty to the timing of births that occur after treatment (Asa and Porton 2005). Trophic asynchrony between birth pulses and seasonal peaks in resources can have profound effects in the population ecology of wildlife species (Thomas et al. 2001, Stenseth and Mysterud 2002, Edwards and Richardson 2004, Post and Forchhammer 2008). Observed changes in such phenology and their implications have garnered much attention in climate change science (Walther et al 2002, Parmesan and Yohe 2003), but more direct anthropogenic influences, such as fertility control, remain almost completely unknown.

Births of many large mammal species occur in annual pulses that are regulated by seasonal cues such as photoperiod and temperature. Increasing sunlight and temperature that accompanies the transition from winter to spring can trigger a physiologic response in the pineal gland that initiates reproductive receptivity (Reiter 1977, Grubaugh et al. 1982, Goldman 2001). This ultimately influences when females may conceive and when offspring are born. For example, feral horses (*Equus caballus*) in the northern hemisphere typically begin estrus in early spring and return to anestrus in early winter; consequently, we may posit that conception should naturally peak near the longest day of sunlight (summer solstice) and parturition should peak 335–342 days later (equine gestation: Card and Hillman 1993). This pattern results in synchrony of the birth pulse

with spring, when climate and forage availability for the dam can contribute to increased neonate survival.

Wildlife populations that become locally overabundant can deplete resources and alter natural communities (Hone 2007). As a result, resource managers are increasingly considering nonlethal control, such as transient contraceptives to limit growth (Kirkpatrick et al. 2011). These agents are appealing to managers of protected species and small populations because fertility of treated individuals may return when the transient contraception wears off (Kirkpatrick and Turner 2002). While many studies have investigated the individual-level efficacy of such contraceptive agents (see Chapter 4), far less is known about longitudinal effects on fertility and birth phenology after the targeted years of infertility. Transient contraceptive effects that diminish toward the end of a physiologically-constrained fertility window may shift birth phenology and lead to decreased neonate survival. Unintended treatment effects such as prolonged infertility and out-of-season births may compromise the ability of populations to recover after deleterious stochastic events and may influence viability of small populations. Such effects also introduce ethical questions toward regulating populations with tools that may broadly alter ecology of the species.

The immunocontraceptive porcine zona pellucida (PZP) is becoming an increasingly popular management tool and has been used in at least 76 animal species worldwide (Kirkpatrick et al. 2011). This transient contraceptive may last 10–22 months per application, depending on the formulation and species (Liu et al. 1989, Kirkpatrick et al. 2011, Ransom et al. 2011). The appeal of this agent is not only that it can reduce fertility in females, but it is relatively easy to apply and has few known immediate

contraindications (Gray and Cameron 2010, Ransom et al. 2010). Population-level contraindications are more uncertain, but some evidence suggests decreased fecundity among untreated females and increased survival in adults can occur in populations containing PZP-treated females (see Chapter 3).

The individual-level efficacy of this immunocontraceptive was investigated in three free-roaming feral horse populations in the western U.S (Ransom et al. 2011). I have now followed each individual female in these same populations past their targeted infertile years to further evaluate their return to fertility, changes in birth phenology, and survival of their offspring. I hypothesized that due to the expected individual response variability to treatment and the unknown and variable duration of treatment, post-treated females would give birth later in the year compared to untreated females, and those births would be asynchronous with forage availability. I expected that parturition timing would be constrained by photoperiod and temperature and that offspring born toward the end of this temporal window would have decreased survival.

Methods

Free-roaming female feral horses were treated with PZP for 1–5 years and every individual horse was directly observed and followed at Little Book Cliffs Wild Horse Range, CO, McCullough Peaks Herd Management Area, WY, and Pryor Mountain Wild Horse Range, MT, USA (Ransom et al. 2011). I defined post-treatment as beginning two full parturition seasons after the final inoculation of conventional PZP or after the single inoculation using PZP time-released pellets. For example, if a female received a conventional PZP inoculation in autumn 2004, then she was presumably contracepted in

2005. This meant she should not produce an offspring, but could conceive at some time in 2006. The first post-treatment year would then be 2007. If that 2004 inoculation was time-released PZP, then the first post-treatment year could have been as early as 2007 depending on the month of application.

I followed post-treated mares from 2005 at Little Book Cliffs and Pryor Mountain and from 2007 at McCullough Peaks until they died, were removed, were treated again by managers, or the end of 2011, whichever came first. I omitted data for one female from the Little Book Cliffs and six females from McCullough Peaks because they produced offspring in every treatment year and thus were never effectively contracepted. Females that produced offspring during treatment years, but not in every year, were retained because contraception could have occurred. The untreated female group consisted of all individuals in each population that had never been inoculated with PZP and were at least 4 years old at the first year of this study period. The youngest a post-treated female could have been at that time was 4 years old. The resulting data arose from observations of 88 post-treated females (age 4–24 years) and 119 untreated females (age 4–23 years) (Table 2.1).

Observation protocols followed Ransom et al. (2011) for all three sites. For the Pryor Mountain site in 2010–2011, I also used data provided by the Pryor Mountain Mustang Center, WY, USA, and these were collected under the same protocols. Throughout the study, 96.1% of all females and offspring (when present) were located at least weekly from April to October of each year. At Little Book Cliffs, 6–8 females were difficult to access weekly, but were located at least once per month. A single band containing two females at McCullough Peaks was not located weekly, but was observed

at least monthly during 2007–2010. In 2011, that band was found only once and both females were observed with neonates. At Little Book Cliffs, I also used motion-activated infrared trail cameras at remote water points to provide supplemental observations. Observations during the winter were irregular and sometimes constrained by weather. It is possible that some offspring were born and died without being observed during the course of this study; however, given the intensity of observations, I believe this rarely occurred. I also did not assess the potential impacts of management removals on fecundity, but all treated animals were exempt from removal and no effects of removals on population growth rate were detected (see Chapter 3). I matched all neonates with dams based on observations of attachment (e.g., nursing, general proximity) during the early days and weeks of a neonate's life (Waring 2003). I did not attempt to assess pregnancy in females that may have visually appeared pregnant but did not produce a viable offspring. Parturition probability was thus estimated from the frequency of live births per cohort as detected by direct observation.

Neonate data were collected at the first sighting of a neonate in the field and its general activity state was categorized as vigorous, lethargic, or immobile at that time. If neonates were resting when first observed, they were continually observed until the band became active again and neonate activity could be classified. Body condition of each dam was visually classified using the Henneke et al. (1983) index, where the score increased discretely from 1 through 9 by increasing fatness. Neonate date of birth was estimated subjectively by observing presence of an umbilicus, level of activity, and by the time elapsed since the dam was previously observed pregnant. The median time elapsed before a neonate was detected was only six days during the post-treatment observation years (*n*

= 328 neonates).

Study Areas

The Little Book Cliffs Wild Horse Range, located in Mesa County, Colorado, USA (latitude 39°12’N, longitude 108°25’W), consisted of approximately 14,600 ha of sloping plateaus, sagebrush (*Artemisia* spp.) parks, and 4 major canyon systems. Elevations ranged from 1,500 m to 2,250 m. The study area was characterized by dense stands of Colorado piñon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*). Population size varied from 131–179 horses from 2005–2011 and was distributed in bands of 2–9 horses. Mean annual temperature was 11.5°C (range= -26.7– 41.1°C). Mean total annual precipitation was 235.4 mm (range=184.4–300.2 mm) and this typically fell in a monsoonal pattern of late summer rains.

McCullough Peaks Herd Management Area in Park County, Wyoming, USA (latitude 44°35’N, longitude 108°40’W), consisted of 44,400 ha of primarily open sagebrush steppe. Elevations ranged from 1,200 m to 1,964 m. Population size ranged from 169–236 horses in bands of 2–17 individuals during 2007–2011. Mean annual temperature was 8.0°C (range -30.0– 37.8°C) and mean total annual precipitation was 271.2 mm (range=168.9–389.1 mm).

The Pryor Mountain Wild Horse Range, located in Bighorn County, Wyoming and Carbon County, Montana, USA (latitude 45°04’N, longitude 108°19’W), consisted of roughly 16,000 ha of low desert, foothill slopes, forested montane slopes, steep canyons, and isolated grassy plateaus. Elevations ranged from 1,190 m to 2,625 m. Vegetation types varied greatly from lower to higher elevations of the range with lower elevations dominated by sagebrush communities, mid elevations dominated by curl-leaf

mountain mahogany (*Cercocarpus ledifolius*) and Utah juniper communities, and high elevations dominated by limber pine (*Pinus flexilis*), subalpine fir (*Abies lasiocarpa*), and alpine bluegrass (*Poa alpina*). Elevation ranged from 1,190 m to 2,625 m, with mean annual precipitation of 161.4 mm (range = 96.7–233.4 mm). Mean annual temperature was 7.1°C (range -33.9– 40.0°C). The population ranged 171–233 during the study and was arranged in bands of 2–12 individuals.

Data Analysis

I used mixed-effects logistic regression models to estimate parturition probability, phenology, and offspring survival in the maximum likelihood framework (Harville 1977). Individual female was used as a random effect on the intercept term to account for the repeated observations (multiple years) of individuals over time. This was necessary to account for variation that may be present among individuals who were sampled repeatedly, though not always equally over time. Such variation may arise from the many biotic and abiotic factors that may affect conception, pregnancy, parturition, and neonate care. I also used population as a random effect on the intercept term to account for variation attributed to location and treatment regimen. I used the lmer(·) function in the lme4 package in R version 2.14.1 (R Development Core Team 2011) to obtain mixed-effects model estimates.

Parturition rates of feral horses typically increase for the first few years after females reach sexual maturity, remain high through middle age, and decrease in old age (Ransom et al. 2011); therefore, I included linear and quadratic effects of age in models of parturition probability. I rescaled age in the quadratic effect by subtracting the mean age of horses (9.98 yr across all populations), so the intercept term of the model

corresponded to probability of parturition at mean age. Total annual precipitation for the biological year prior to parturition (spring of conception to spring of parturition) was used as a proxy for forage abundance, and thus potential body condition at the year of conception. Daily surface climate data were obtained from the National Climate Data Center (http://www.ncdc.noaa.gov) for Grand Junction, CO (Station 53488, about 13 km southwest of Little Book Cliffs), Cody, WY (Station 481840, about 32 km west of McCullough Peaks), and Lovell, WY (Station 485770, about 21 km south of Pryor Mountain) for all years of the study. Parturition was known history (binomial response of the female producing at least one offspring in the past or not) from direct observation of all females <12 years old at Little Book Cliffs and Pryor Mountain, and all females < 9 years old at McCullough Peaks. All older females were documented giving birth at least once within that same time period. The complete model of parturition probability included the fixed effects of age, treatment, conception year total precipitation, and parturition history. I performed a secondary analysis (using the same model structure) for only the post-treated females that produced offspring in order to investigate the influence of age at first treatment and number of treatments received (1–5 annual inoculations).

I hypothesized that photoperiod and temperature were the critical factors influencing phenology of conception, and thus phenology of parturition. Consequently, the model of parturition phenology included treatment and temperature at the approximate conception date as fixed effects, and individual and population as random effects on the model intercept. A supplemental model was considered for post-treatment females at Little Book Cliffs and Pryor Mountain to assess the interaction of last treatment date and number of consecutive annual treatments as a fixed effect, also using

individual and population as random effects.

Survival was a binomial response attributed to persistence of a neonate from parturition until the following year April observation or death during that time period. Managers removed 30 neonates from the range during their birth year, and those animals were not included in modeling survival. I hypothesized that survival was a function of treatment, dam age, dam body condition, mean winter temperature (Nov 1–Mar. 31), and the temporal difference between birth date and spring peak available forage. I used Normalized Difference Vegetation Index (NDVI) data obtained from the National Aeronautics and Space Administration (http://modis.gsfc.nasa.gov) and reconciled using ArcGIS software (Esri, Redlands, California) for assessing temporal variation in forage availability. The phenology product from Tan et al. (2011) was used to generate date of maximum NDVI in each year for each study area. NDVI was used as a temporal indicator of forage availability, but not forage abundance because tree presence and distribution can strongly influence this metric.

Table 2.1. Parturition data from untreated and porcine zona pellucida (PZP) treated female feral horses (*Equus caballus*) at Little Book Cliffs Wild Horse Range, CO, Pryor Mountain Wild Horse Range, MT, and McCullough Peaks Herd Management Area, WY.

	Little Book Cliffs WHR (2005–2011)	Pryor Mountain WHR (2005–2011)	McCullough Peaks HMA (2007–2011)
No. untreated females	41	44	34
No. untreated females never producing offspring	6	11	15
Age of untreated females	4–23 yr	4–15 yr	4–21 yr
No. post-treated females	22	38	28
No. post-treated females never producing offspring	15	18	15
Age of post-treated females	6–21 yr	4–24 yr	4–20 yr
Observed parturition range for untreated females	Feb. 23–Sep. 1	Feb. 21–Sep. 3	Jan. 15–Sep. 7
Observed parturition range for post-treated females	Mar. 5–Dec. 22	Apr. 5–Sep. 29	Feb. 20–Aug. 4
Estimated parturition peak for untreated females	May 10 (Apr. 28–May 22)	May 14 (May 4–May 24)	May 19 (May 8–May 30)
Estimated parturition peak for post-treated females	Aug. 24 (Jul. 18–Sep. 29)	Jun. 18 (May 31–Jul 6)	May 4 (Apr. 14–May 24)
Estimated difference in peak parturition date (95%CI)	105.9 (69.7–142.1) days	34.8 (17.0–52.3) days	None

Results

Fertility

During the seven years of observation at Little Book Cliffs and Pryor Mountain, 20% of untreated females and 55% of post-treated females never produced offspring (Table 2.1). Similarly, in the 5 years of observation at McCullough Peaks, 44% of untreated and 53% of post-treated females never produced offspring. Of all post-treated females in the study, 91% had successfully produced offspring prior to PZP treatment and 92% of all untreated females had successfully produced offspring prior to the observation period.

The probability of producing offspring was related to treatment (odds ratio = 5.20, 95% CI = 3.3–8.2), fertility history (odds ratio = 0.06, 0.01–0.27), and age (odds ratio =1.07, 1.02–1.13), but not to total annual precipitation during year of conception (odds ratio = 0.92, 0.84–1.01). At mean age and mean precipitation, the estimated parturition probability for post-treated females was 25.6% (17.8–35.2%) and untreated females was 64.1% (53.1–73.9%) if they had produced offspring in any year previous to this study, but only 2.1% (1.3–3.2%) for post-treated females and 10.7% (7.0–15.9%) for untreated females that had never previously produced offspring. Population contributed to a small amount of variation in the model (σ =0.33) but individual identity was more influential (σ =0.82).

Of the 52 females that received 1–5 annual injections of conventional PZP (Little Book Cliffs and Pryor Mountain), 27 females produced at least one offspring post-treatment. The length of time between last inoculation and first parturition ranged 565–2,971 days and was strongly influenced by the total number of years a female was treated

(t =5.176, P<0.001). Estimated time to parturition increased 411.3 (246.5–576.0) days per year of consecutive treatment (Fig. 2.1). Neither age at first treatment (t =-1.04, P=0.309) nor fertility history (t =0.01, P=0.991) influenced the length of time to parturition. The secondary model was not run for McCullough Peaks, where all 36 females were treated with the 22-month time-released PZP pellets on the same day. Thirteen post-treated females in that population produced an offspring during the 5 years of observation and the observed length of time between inoculation and first parturition ranged 530–2,000 days.

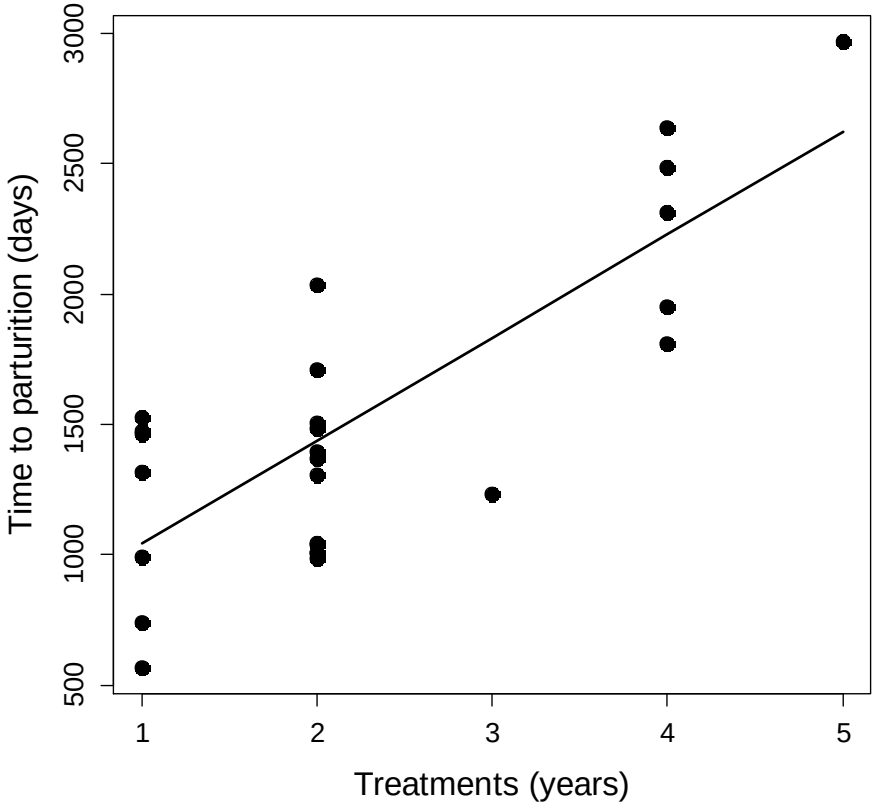

Figure 2.1. Time between final inoculation and first parturition from feral horse (*Equus caballus*) females at Little Books Cliffs Wild Horse Range, CO, and Pryor Mountain Wild Horse Range, MT, as a function of the consecutive annual porcine zona pellucida (PZP) treatments, 2005–2011.

Phenology

Parturition phenology for all untreated females increased in frequency near the summer solstice and decreased toward the winter solstice, and these trends corresponded with temperature and NDVI (Fig. 2.2). Parturition from untreated females was similar by location, with births ranging from Jan. 15– Sep. 7 (Table 2.1). After controlling for temperature at conception date, parturition from post-treated females ranged Feb. 20 – Dec. 22, and the estimated peak was 31.5 (17.0–46.0) days later than from untreated

females. The treatment effect varied considerably between populations and PZP form (Table 2.1, Fig. 2.2).

The date of final PZP inoculation ranged Feb. 25–Oct.11 at Little Book Cliffs and Aug.4 –Oct.14 at Pryor Mountain. The secondary model included only the first birth from each post-treated female at these two sites. The interaction of final treatment date with number of consecutive treatments in this model failed to explain the observed difference in phenology between treatment groups (t= -0.46, P=0.65). Three females at Little Book Cliffs gave birth in multiple post-treatment years as did 11 females at Pryor Mountain. These additional post-treatment births from the Little Book Cliffs females occurred after a one year gap from their first post-treatment birth, and the date of parturition for these was earlier in the year (83 days, 111 days, and 249 days) (Fig. 2.2A). This trend was less clear at Pryor Mountain where two post-treated females that skipped a year between births gave birth earlier for the second offspring (145 days and 111 days), and the other female gave birth later (99 days). Eight post-treatment mares gave birth in consecutive years and second offspring came earlier (1–36 days) for 3 of these females, later for 4 females (13–29 days), and on the same day for one (Fig. 2.2B).

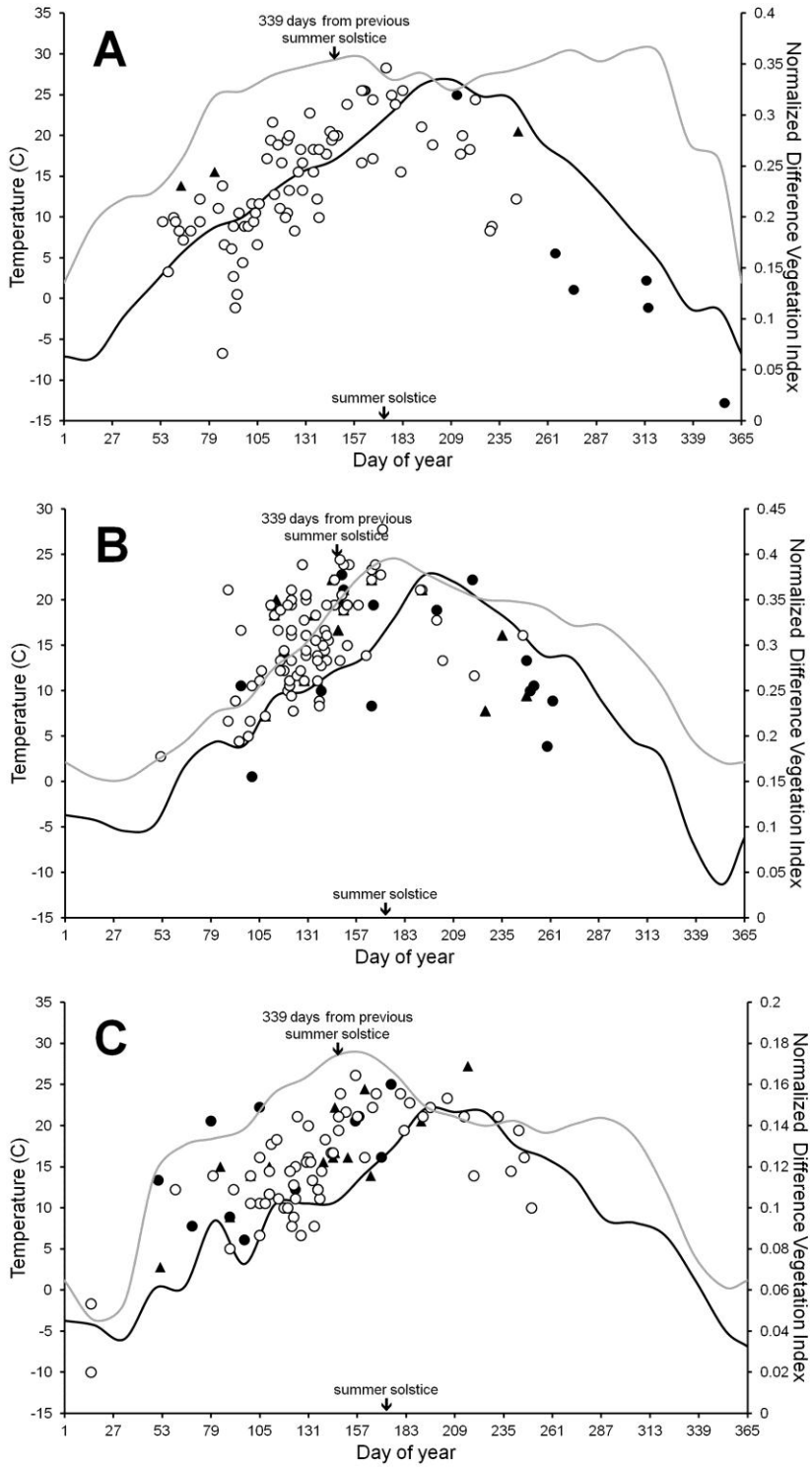

Figure 2.2. Phenology of parturition from feral horse (*Equus caballus*) untreated (○) and post-treated (● = first post-treatment birth, ▲= birth subsequent to ●) females as a

function of temperature at approximate conception date for populations at Little Book Cliffs Wild Horse Range, CO (A) and Pryor Mountain Wild Horse Range, MT (B), 2005–2011, and McCullough Peaks Herd Management Area, WY (C), 2007–2011. Mean Normalized Difference Vegetation Index (grey line) represents temporal availability of forage. Mean annual temperature is shown as the black line.

Survival

Nearly every neonate born was observed in vigorous activity, with the exception of four that were immobile (one to a post-treated female) and two that were lethargic (none to post-treated females). All six of these neonates died before the following spring. Body condition of dams ranged 3–9 (mean = 5.73, 5.61–5.84) at first observation of neonates. Eighty-five percent of neonates were observed alive the following spring. Dam body condition (odds ratio = 2.63, 1.11–6.23) and temporal relationship between date of birth and spring peak NDVI (odds ratio = 1.01, 1.01–1.02) contributed to offspring survival, and treatment (odds ratio = 2.15, 0.78–5.91), band size (odds ratio = 0.96, 0.85–1.08), dam age (odds ratio = 1.07, 0.95–1.21), and mean winter temperature (odds ratio = 0.92, 0.98–1.03) did not. The survival probability of a neonate born to a dam in mean body condition at spring peak NDVI was 79.9% (67.9–85.4%). This probability decreased 11.4% (10.7–12.0%) with each 1-unit decrease in body condition. Survival declined 1.4% (1.4–1.5%) for every 10 days after the peak in NDVI.

Discussion

The probability of producing an offspring for females previously treated with annual injections of conventional PZP was 38.5% lower than for untreated females after controlling for differences due to age, precipitation during conception year, and fertility

history. This effect of treatment on apparent fertility was largely explained by the number of years a female had been treated: the length of time to parturition increased an estimated 411.3 days per year of consecutive treatment. The return to fertility rates observed were highly variable and this may in part be due to the disparate abilities of individual females to raise therapeutic-level antibodies against PZP and the length of time those antibodies persisted above threshold concentrations (Liu et al. 1989, Turner et al. 2002, Lyda et al. 2005). This finding concurs with results from Assateague Island National Seashore, MD and VA, USA, where 68.8% of 32 female horses treated for three consecutive years with conventional PZP became pregnant 1–4 years after the last treatment (Kirkpatrick and Turner 2002). Only 3 horses were vaccinated for four consecutive years in that study: one became pregnant 3 years after the last treatment, another became pregnant after 4 years, and the third became pregnant after 8 years. Some of those horses experienced ovulatory failure, which is not the targeted physiological response of PZP vaccination (Powell and Monfort 2001). That effect was highly variable between individuals due to the episodic nature of ovulatory failure, as opposed to a chronic condition (Powell and Monfort 2001). Other studies have demonstrated atrophic changes in ovarian morphology, folliculogenesis, and reproductive endocrine function, indicating that prevention of sperm binding may not be the only mechanism acting on infertility in PZP-inoculated animals (Wood et al. 1981, Mahi-Brown et al. 1985, Dunbar et al. 1989, Stoops et al. 2006).

Parturition phenology for North American feral horses has been widely shown to peak during May (Berger 1986, Garrott and Siniff 1992, Kirkpatrick and Turner 2003, Nuñez 2010). My results for untreated females concur with earlier observations but my

findings for PZP-inoculated females demonstrated a markedly different phenology. I estimated parturition by untreated females peaked May 10–19 across the 3 populations, which was 22–43 days before spring forage availability began to decline and placed conception roughly 7–15 days before the longest day of sunlight (or 323–332 days from previous summer solstice). This phenology appears synchronized with the most abundant forage during the parturition period while females' metabolic needs are elevated from late term pregnancy and lactation (National Research Council 2007). The estimated peak in parturition from post-treated females at two sites (Aug. 24 at Little Book Cliffs and Jun. 18 at Pryor Mountain) occurred as spring forage availability began to decline; however at Little Book Cliffs where births were latest, the monsoonal rains provided a bimodal distribution in forage availability (Fig. 2.2A). The second peak in NDVI arrived November 1, which was 69 days after estimated peak in parturition from post-treated females.

At Shackleford Banks, North Carolina, USA, feral horse females vaccinated annually with PZP for 1–6 years gave birth 3.36 months later than untreated females (Nuñez et al. 2010). That study posited that consecutive annual inoculations may lead to irregularity in decline of antibodies, and this process may contribute to the phenological shift to later births. Kirkpatrick and Turner (2002), Nuñez et al. (2010), and this study all suggest that in a longitudinal time scale, additional annual PZP inoculations extend the temporal efficacy of contraception beyond the targeted period. I found no statistical evidence that timing of the final PZP inoculation influenced the date of first post-treatment parturition, but given the variable individual immune responses expected, temporally variable antibody persistence, and uncertain additive nature of consecutive

annual vaccinations, this is unsurprising.

To elucidate the proximate mechanisms influencing birth phenology in feral horses, I must clearly define the term ‘seasonality’, which has clouded debate over fertility control and birth phenology. I define the temperate equine parturition season simply as a unimodal distribution ranging from the earliest known birth to the latest known birth in a year, with a well-defined peak that appears to center approximately on May. Across the 3 populations I studied, the parturition season thus ranged 229 days for untreated females and 305 days for post-treated females, or nearly the entire year for all females (341 days). This suggests surprising plasticity in birth phenology of temperate latitude feral horses; nevertheless, 81.4% of the 328 documented births in this study occurred between March 1 and June 21, in concert with increasing temperature and photoperiod (Fig. 2.2). These abiotic inputs influence physiology in many ways that contribute to the plasticity observed. Follicular activity of the estrous cycle during the first half of the breeding season is characterized by more numerous large follicles and greater incidence of anovulatory waves (Ginther et al. 2004). Gestation length is variable and has been attributed to seasonal variations that influence nutrition of females (Howell and Rollins 1951). The annual rhythm of luteinizing hormone (LH) secretion is partially regulated by photoperiod, but also has a strong endogenous component (Palmer and Guillaume (1998). Age and fertility history of females can strongly influence the occurrence of a winter anovulatory period (Palmer and Driancourt 1982), as can melatonin sensitivity of individuals (Goldman 2001). This litany of influences is compounded by the known variations in PZP immunocontraception efficacy and duration, as well as the uncertain mechanism of action that may be confounded with

ovarian pathologies.

High variability in parturition seasons within taxa and biomes is not uncommon, but there is considerable support for the importance of climate on the physiology driving those patterns (Rutberg 1987). The lengthier breeding seasons of PZP-vaccinated females found in my study, as well as by Nuñez et al. (2010), largely reflect that horses who would normally conceive during their first or second estrous cycle of the year continue to cycle throughout the year and then only conceive when contraception sufficiently decays. This inherently extends the breeding season, but not the physiological constraints largely regulating fertility. This is evident in the birth phenology observed for post-treated horses at Little Book Cliffs and Pryor Mountain. Those horses gave birth late in the year, did not give birth the following year, and then produced offspring the next spring in concert with warming temperatures and lengthening photoperiod. This 'self-correcting' trend provides additional support for the importance of such abiotic factors in birth phenology, but also illustrates that phenological shifts associated with the uncertainties surrounding immunocontraception may be short term. The changing nature of abiotic factors such as temperature introduces a broader consideration for birth phenology and like Nuñez et al. (2010) observed warmer years in concert with later post-contraception births, changing temperature is being attributed to phenological shifts across taxa and biomes (Walther et al 2002, Parmesan and Yohe 2003).

The ultimate consequence of changes in birth phenology is survival. Survival of neonates in my study was 79.9%, estimated at mean body condition of the dam at spring peak NDVI, and this did not differ between treatment groups. This probability predictably decreased with decreasing dam body condition and with temporal distance

between date of birth and spring peak NDVI. The secondary peak in forage availability at Little Book Cliffs ameliorated the potential effect on survival for the neonates born late in the year at that site. Overall, survival of all neonates in my study was consistent with the mean survival rate (73.9%) derived from 12 historic studies on feral horse neonate survival (Roelle et al. 2010:21).

Conclusion

The tools we use constantly introduce a multitude of uncertainties into our understanding of systems, and humans are increasingly attempting to manage the planet's wildlife and habitats. Yet to avoid catastrophic mismanagement of resources, we must strive toward a deeper understanding of natural processes and ultimately improve our management tools. The growing need for humane, non-lethal, population control measures such as PZP demands we understand their short and long term influences at both individual and ecological scales. This study demonstrates that infertility resulting from repeated PZP vaccinations in feral horses can extend the duration of infertility far beyond the targeted period and that caution may be warranted for extensive treatments, especially in small populations or conservation populations maintained as refugium. It has also shown that PZP can alter phenology of birth in seasonal polyestrous species at temperate latitudes. This effect appears to be short term due to the powerful underlying physiological constraints driving the biological rhythms of conception and birth in this species. It remains unknown how such changes may manifest in other species treated with PZP or even how the observed changes may affect long-term population dynamics and viability.

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Chapter 3: Demographic feedbacks of fertility control in feral horse populations

Management of wildlife often requires intervention to regulate growth of populations that would otherwise become overabundant. Fertility control has become an increasingly popular tool for managing locally overabundant species because it allows for nonlethal regulation. Few studies have investigated the longitudinal population-level effects of fertility control, and I hypothesized that individual-level estimates of efficacy would not scale to the population-level outcomes because indirect demographic feedbacks from treatment would influence growth. I evaluated three populations of feral horses (*Equus caballus*) where porcine zona pellucida (PZP) was applied to an average 30% (range=11–77%) of females annually during the treatment period. Apparent annual population growth rate was 4–9% lower in the post-treatment years as compared to pretreatment years; however, population growth was positive and still increased steadily every year that a management removal did not occur. The observed number of births averaged 33% less than the number expected based on number of treated females, individual-level efficacy of treatment, and age-specific fecundity of their untreated conspecifics. Fifty-nine percent of this difference was explained by an apparent residual effect of treatment in females after their targeted infertility period. Controlling for climate, birth rate in the youngest females (age 2–5 years old) was reduced in years when their conspecifics were treated with PZP, indicating a potential population-level behavioral feedback from treatment. Survival of 1–19 year olds was 3% higher during the post-treatment period after controlling for climate, and there was 300% increase in presence of horses ≥20 years old during the same period. Climate had some influence on

the demography I investigated, but predation was also implicated in reduced survival in one population. The practicality of inoculating enough females in a population to actually reduce its size over the short term makes the utility of fertility control questionable for aggressively managing growth, but considerable economic gain may be realized for managing closed feral horse populations with even modest application. The role of fertility control is uncertain for open populations of other wildlife species, where lethal removal is an option and the fiscal costs of long term captive care are irrelevant. In such cases, understanding behavior and life-history strategies is essential to forming realistic expectations of fertility control performance at the population level.

Keywords demography, *Equus caballus*, fertility control, horse, porcine zona pellucida, population dynamics, PZP, wildlife contraception

Wildlife populations are regulated by births, deaths, immigration, and emigration, and these processes are increasingly shaped by human actions (Sanderson et al. 2002, Morrison et al. 2006). Many wildlife populations must be regulated to prevent the habitat damage and resource depletion that can arise from overabundance (Hone 2007). Such regulation can be achieved by reducing survival with hunting or culling, or by reducing birth rates with fertility control. The latter has become an increasingly popular tool because it circumvents many of the problems associated with managing survival of wildlife in urban or protected areas (Hobbs et al. 2000, Porton 2005). Techniques for controlling fertility of wildlife include hormone applications, immunocontraceptive vaccines, mechanical devices, and surgical alteration of reproductive organs (Asa 2005).

Many fertility control tools are expensive to use, impractical for application at a

large scale, or are ethically controversial (Kirkpatrick and Frank 2005). Immunocontraceptive vaccines incorporating antigens such as porcine zona pellucida (PZP) or gonadotropin-releasing hormone (GnRH) may be among the most favorable because they can be relative easy to apply, have high expected efficacy and duration, and are anticipated to lack serious side-effects (Gray and Cameron 2010, Kirkpatrick et al. 2011). Managers have inoculated individuals of at least 76 species around the world with PZP. Example applications to populations have occurred in white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), feral horses (*Equus caballus*), and African elephants (*Loxodonta africana*) (Kirkpatrick et al. 2011). At the individual level, reported efficacy of PZP is about 75–100% in these species; however, few studies have reported estimates of efficacy that account for age-specific fecundity. There are few empirical observations of the effects of PZP treatments on population growth rates.

There are several underlying reasons for the lack of research on efficacy of fertility control at the population-level. The most important impediment is the difficulty of separating the influences of multiple controls on population growth (Sibly and Hone 2002). These controls are often confounded in observational data. Moreover, longitudinal studies at the population level are expensive and time consuming. It is therefore generally more convenient for scientists to draw inferences on small individual-level trials of fertility control agents, where individual fecundity can be measured. The assumption that individual-level effectiveness of a contraceptive directly scales to population-level effectiveness may not be valid, however: fertility control has been associated with changes in immigration, decreased group fidelity, increased survival, and other behavioral changes that may influence population growth (Caughley et al. 1992,

Ramsey 2005, Merrill et al. 2006, Williams et al. 2007, Nuñez et al. 2009). To complicate the population-level question further, scientists have argued that reducing and maintaining wildlife populations using fertility control will require intense management effort that includes contracepting a large proportion of a population over a long time period (Garrott 1991, Hone 1992, Garrott 1995, Seagle and Close 1996, Hobbs et al. 2000).

Perhaps no large mammal in North America has been managed as intensively as feral horses since the enactment of the Wild Free-Roaming Horses and Burros Act of 1971 (Public Law 92–195, as amended). Approximately 38,500 feral horses currently roam 12.8 million hectares of public lands in the U.S. Provided federal protection and largely unchecked by predators, populations have been known to increase 15–25% annually (Eberhardt et al. 1982, Wolfe 1986, Garrott et al. 1991). The Bureau of Land Management (BLM) has historically managed this growth by artificially controlling survival through a capture and removal process that takes excess animals from the range and places them in private homes or in long-term holding facilities. There are currently 47,000 horses in long-term holding facilities at an annual care cost of about $35,700,000 (U.S. Department of the Interior 2012). These costs illustrate that controlling growth by removals is not sustainable. Managers have now attempted to supplement this removal process by using PZP to control births.

Individual-level efficacy of PZP in three populations of feral horses in the western U.S. has been assessed through an intensive effort that followed each individual feral horse through time (Ransom et al. 2011). I continued observing these same populations with the objectives of determining the effects of the three different PZP-treatment

regimens on population growth rate and identifying potential demographic feedbacks of treatment on birth and survival rates. I hypothesized that population growth would decrease during treatment periods but would never reach zero, and that increased survival and increased birth rates would partially compensate for the targeted reduction in births.

Study Areas

I observed feral horse populations at the Little Book Cliffs Wild Horse Range in Mesa County, Colorado, (latitude 39°12'N, longitude 108°25'W), McCullough Peaks Herd Management Area in Park County, Wyoming, (latitude 44°35'N, longitude 108°40'W), and Pryor Mountain Wild Horse Range in Bighorn County, Wyoming and Carbon County, Montana, (latitude 45°04'N, longitude 108°19'W). Little Book Cliffs was characterized by dense Colorado piñon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) woodlands and complex topography, whereas McCullough Peaks was a predominantly flat sagebrush (*Artemisia* spp.) steppe ecosystem. Pryor Mountain habitat ranged from desert lowlands rising to montane mixed conifer forest and subalpine tundra. Area, elevation, and climate varied between the sites, but no extreme stochastic weather events were recorded during the study (Table 3.1). Mountain lions (*Puma concolor*) were present at all three locations, but depredation on horses was only directly observed at Little Book Cliffs and Pryor Mountain. Coyote (*Canis latrans*) were commonly observed at all three sites and black bear (*Ursus americanus*) were occasionally observed at Little Book Cliffs and Pryor Mountain. Though scavenging was common, no direct evidence of depredation on horses by coyotes or bears was recorded.

Table 3.1. Characteristics of feral horse (*Equus caballus*) habitats and mean annual climate at Little Book Cliffs Wild Horse Range, Colorado, USA 2000–2011, McCullough Peaks Herd Management Area, Wyoming, USA, 2003–2011, and Pryor Mountain Wild Horse Range, Montana, USA, 1993–2011.

Location	Area (ha)	Elevation (m)	Temperature (C)	Minimum Temperature (C)	Maximum Temperature (C)	Precipitation (cm)
Little Book Cliffs	14600	1500–2250	11.8	-19.0	39.7	22.3
McCullough Peaks	44400	1200–1964	8.5	-28.0	35.4	24.7
Pryor Mountain	16000	1190–2625	7.2	-29.2	40.0	17.9

Methods

The empirical data used for this study were collected by direct observation of all individual horses comprising the study populations. Observations at Little Book Cliffs from 2000–2011, McCullough Peaks from 2003–2011, and Pryor Mountain from 1993–2011, included approximately 125–400 person-days per year of effort, excepting observations at Pryor Mountain 1993–1994 that only included approximately 30 person-days. Some informal observation data from Little Book Cliffs 1973–1999 were available, but were only used for establishing age of individuals extant in 2000–2011 whose births were previously documented. Observations were concentrated from March/April through September/October, when nearly all bands were located at least weekly and most were located several times per week. Reduced effort in the winter usually resulted in less than one observation per week per band. Observations were made from the ground along roads and trails that traversed the study areas. These were augmented with aerial surveys (4 at Little Book Cliffs, 4 at McCullough Peaks, 8 at Pryor Mountain), as well as a minimum

of 20–25 days per year of horseback surveys during some years (Little Book Cliffs 2002–2006, McCullough Peaks, 2003–2009, Pryor Mountain 2003–2009).

Each horse was individually identified based on pelage color, markings, and sex, and was assigned a unique identification number. Age of individuals was known from birth records for 71.7% of the 1,779 animals that were present in the populations during the study years. Age of 66 horses at Pryor Mountain during the early years of the study were estimated subjectively based on morphology and anecdotal historical evidence of years the animals were on the range. Ages of 6 horses at Little Book Cliffs and 134 horses at McCullough Peaks were also estimated subjectively and were never confirmed because all were removed or died in the first 2 years of study. Ages of all remaining horses were estimated by experienced veterinarians based on tooth eruption and wear (Martin 2002). Death year was determined by identification of the carcass; if an individual was not observed for two consecutive years, the animal was considered to have died in the year it went missing. All of the populations were geographically isolated from other feral horse populations and neither natural immigration nor emigration was considered plausible for these analyses. Nevertheless, 15 domestic horses were illegally released by the public into the populations (2 at Little Book Cliffs, 11 at McCullough Peaks, and 2 at Pryor Mountain). These included one domestic male horse introduced at Little Book Cliffs that was present 2003–2004, as well as one female 2005–2009, one female 2009–2010, one female 2009–2011, and six females 2010–2011 at McCullough Peaks. All other domestic introductions were removed by managers in the year they were introduced and thus did not directly contribute to the calculations of population growth. Four of the introduced females at McCullough Peaks contributed offspring to the

population during the study.

Female horses at Little Book Cliffs and Pryor Mountain were inoculated annually for 1–5 years using conventional PZP and female horses at McCullough Peaks were inoculated using a single injection 22-month time-released form of PZP (Ransom et al. 2011). A total of 51 individual horses at Little Book Cliffs, 62 horses at Pryor Mountain, and 47 horses at McCullough Peaks were treated and potentially contracepted during the study years. The total number of treated individuals present in a population during any given year varied due to individual treatment dates, deaths, and demonstrated return to fertility after individually prescribed treatment periods (see Ransom et al. 2011, Chapter 2). Animals that were inoculated between autumn 2010 and the end of 2011 were considered untreated for these analyses because the first year their birth rate could have been impacted was after 2011.

Data Analyses

I directly calculated apparent annual population growth rate (λ_A) based on biological years, which I defined as beginning before the annual birth pulse in spring to the same time the following year. I used the expression

$$\lambda_{At} = \frac{N_t}{N_{t-1} - R_{t-1}}$$

where λ_{At} is the growth from year t–1 to year t, N is the population size, and R_{t-1} is the number of animals removed in the period t–1 to t. This calculation reflects apparent population growth had horses not been removed by management (Garrott and Taylor 1990). I defined pretreatment period as every year before the earliest treatment could have impacted parturition, and post-treatment as every year after that. I did not include

2003 at Little Book Cliffs as a post-treatment year because treatment could have only affected birth from one female in that year. Births were tabulated as presence/absence of a neonate for each female in each population each year, and birth rates were calculated as the mean number of births in each age cohort for each year. Survival was calculated by dividing the number of individuals present in a given cohort alive at the end of the year by the number present at the beginning of the year. Management removals occurred after the annual birth pulse, and thus did not affect calculation of birth rates; however, removals did occur before the conclusion of biological years and removed animals were therefore not included in calculations of survival for those years.

I used mixed-effect linear regression to model λ_{At} , birth rate, and survival in the maximum likelihood framework (Harville 1977). Population was used as a random effect on the intercept term to account for variation attributed to location and treatment regimen. I modeled λ_{At} as a function of treatment period, total spring precipitation (March–June) of the previous year (as an index of forage production around the time of conception and early pregnancy), mean of average monthly maximum summer temperature (April–September) (as an index of heat stress), and mean of average monthly minimum winter temperatures (December–February) (as a sink for energy demands). I also looked for evidence of density dependence in population growth rate using a stepwise linear regression of annual population size on λ_A. I used R version 2.14.1 (R Development Core Team 2011) to obtain all estimates.

Birth rates in feral horses are typically lower in young and old horses and peak when females are around 8–10 years old (Ransom et al. 2011). Because I hypothesized that birth rates among untreated females may increase, and fecundity typically varies with

age, I stratified my analyses into 2–5 year old, 6–14 year old, and ≥15 year old age cohorts. I modeled birth rates for each of these cohorts as a function of treatment period, total spring and summer (March–September) precipitation (as an index of forage production from conception through midterm pregnancy), mean of the average monthly minimum temperature for the biological year leading up to parturition (as a potential energy sink throughout pregnancy), and total winter precipitation (December–February) (as a constraint on forage availability and thus body condition). I compared observed births with the number of expected births by summing the product of number of targeted PZP-treatment females and their birth rates, and the product of all other females and the age-specific birth rates for untreated females.

I stratified survival analyses into three age cohorts because survival of neonates is typically much lower than adults and is also expected to be low in extremely old animals (Roelle et al. 2010). I modeled survival of <1 year olds, 2–19 year olds, and ≥20 year olds as a function of treatment period, spring precipitation (March–June), average of monthly maximum summer temperature (April–September), and average of monthly minimum winter temperature. Abiotic covariate metrics for all analyses were compiled from daily surface climate data obtained from the National Climate Data Center (http://www.ncdc.noaa.gov) for Cody, WY (Station 481840), Lovell, WY (Station 485770), and Grand Junction, CO (Station 53488).

Results

Population growth

Apparent annual population growth in years preceding any fertility control treatment ranged 0.972–1.236 across the three populations (*n*=19 years). The percent of treated

females present during the post-treatment period (n=18 years) ranged 10.8–76.6%, with a mean of 32.2% (95% CI = 23.9–40.4%). The highest λ_A in each population occurred during the pretreatment period, and the lowest λ_A observed in each population occurred during the first year of the post-treatment period (Fig. 3.1). Treatment period strongly influenced population growth (t=-3.358, P=0.002), but previous spring precipitation (t=0.612, P=0.545), average maximum summer temperature (t=0.132, P=0.896), and average minimum winter temperature (t=-1.375, P=0.179) did not. Variance attributed to population identity was negligible in this model (σ = 0.002). The estimated pretreatment λ_A of all populations at the mean of each climate metric was 1.156 (1.111–1.201) and the post-treatment mean λ_A was 1.082 (1.037–1.127).

Density dependence on λ_A was not evident in any population across the years of study (Little Book Cliffs, t = 0.934, P = 0.375; McCullough Peaks, t = 0.247, P = 0.813; Pryor Mountain, t = -1.353, P = 0.195). Predation may have strongly influenced population growth at Pryor Mountain, where λ_A generally declined from 1993–2004, and some direct evidence of mountain lion depredation was observed. Three mountain lions were removed by hunters from that location during the winter of 2004–2005 (U.S. Department of the Interior 2006), and then λ_A increased steadily through 2010 (Fig 3.1C). There were 10 large management removals across the populations and λ_A decreased from the year prior to removal in 6 occurrences and increased from the year prior to removal in 4 (Fig. 3.1).

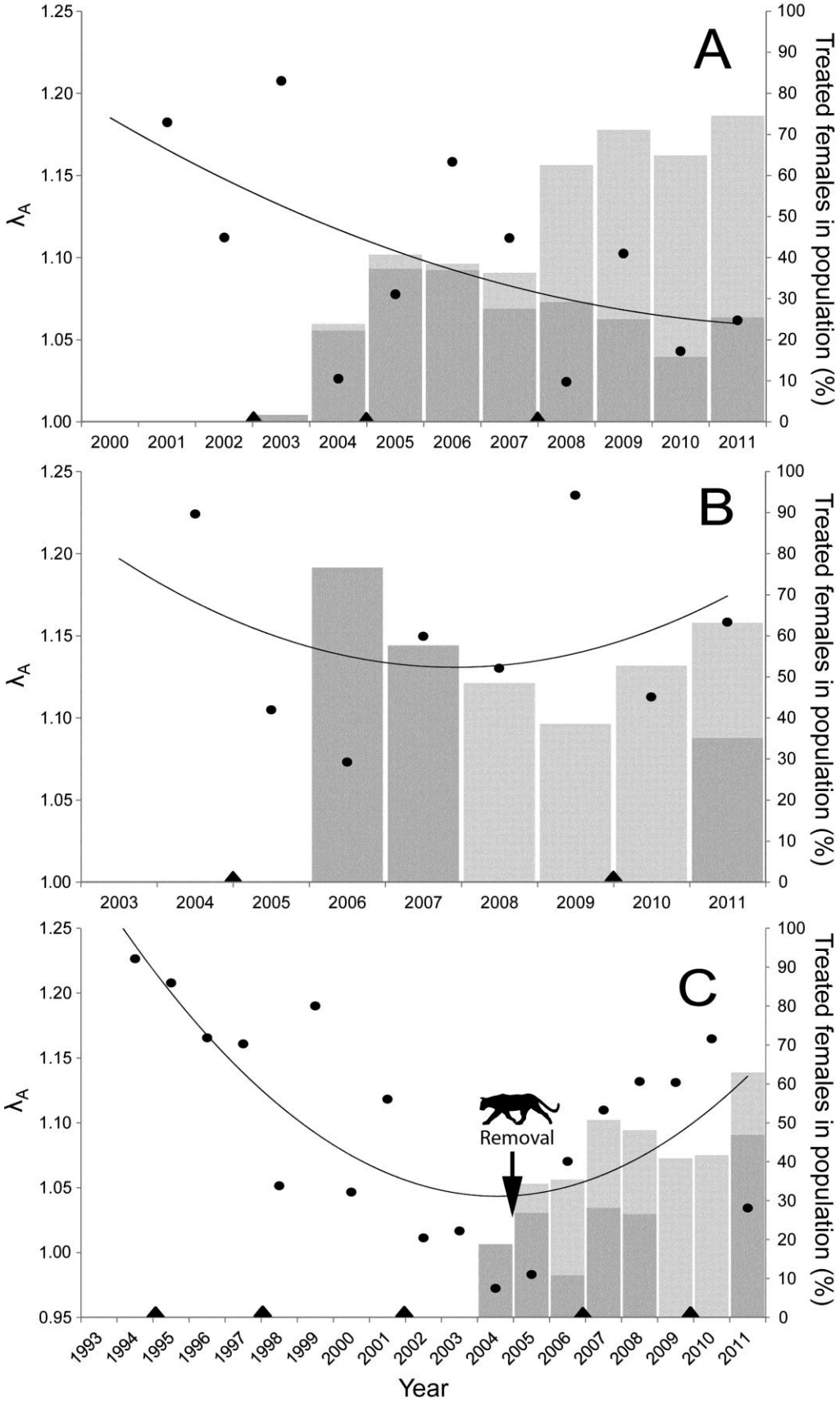
A
B
C
λ_A
Treated females in population (%)
Removal
Year

Figure 3.1. Apparent annual population growth rate (λ_A) and percent of female feral horses (*Equus caballus*) treated with porcine zona pellucida (PZP) for populations at Little Book Cliffs, Colorado, USA (A), McCullough Peaks, Wyoming, USA (B), and Pryor Mountain, Montana, USA (C). Treated females are represented in dark grey for the years of intended impact on birth. Previously treated females no longer targeted for infertility, which may or may not be infertile, are shown in light grey. The time series trend of λ_A is shown as a polynomial to reflect periodicity of PZP treatments (A: $y=0.001x^2-0.022x+1.206$, B: $y=0.003x^2-0.037x+1.230$, C: $y=0.002x^2-0.046x+1.322$) and large removal events are shown as ▲.

Birth rate

Age-specific fecundity for 2 to ≥20 year old untreated females across the three populations ranged 0.15–0.80 (Table 3.2). The observed number of births averaged 33.0% (27.7–38.3%) less than the predicted number of births across all three populations in the post-treatment period (Fig. 3.2). The number of births contributed by females after their target infertility period only represented 58.6% (34.6–82.6%) of the difference between observed and expected numbers of births. Precipitation during March–September of conception year explained 21.9% (R^2) of this variation.

Table 3.2. Age-specific birth rates ± SE for female feral horses (*Equus caballus*) at Little Book Cliffs Wild Horse Range, Colorado, USA, 2000–2011, McCullough Peaks Herd Management Area, Wyoming, USA, 2003–2011, and Pryor Mountain Wild Horse Range, Montana, USA, 1993–2011. Some females were treated with porcine zona pellucida (PZP) and infertility was expected in targeted years (treated females), but persisted beyond those years (post-treated females).

	Untreated females				Treated females		Post-treated females	
Age (yr)	N	Pretreatment period	N	Post-treatment period	N	In targeted infertility years	N	After targeted infertility years
2	176	0.15 ± 0.03	104	0.21 ± 0.04	1	0 ± --	--	--
3	151	0.48 ± 0.04	64	0.50 ± 0.06	21	0.05 ± 0.05	1	1 ± --
4	145	0.50 ± 0.04	41	0.44 ± 0.08	32	0.25 ± 0.08	4	0 ± 0
5	113	0.63 ± 0.05	35	0.51 ± 0.09	23	0.26 ± 0.09	20	0.25 ± 0.10
6	98	0.61 ± 0.05	30	0.63 ± 0.09	26	0.15 ± 0.07	26	0.42 ± 0.10
7	88	0.60 ± 0.05	32	0.72 ± 0.08	21	0.10 ± 0.07	32	0.31 ± 0.08
8	80	0.65 ± 0.05	36	0.67 ± 0.08	19	0.32 ± 0.11	35	0.29 ± 0.08
9	75	0.63 ± 0.06	39	0.74 ± 0.07	21	0.29 ± 0.11	30	0.23 ± 0.08
10	64	0.77 ± 0.05	39	0.67 ± 0.08	19	0.21 ± 0.10	29	0.21 ± 0.08
11	51	0.57 ± 0.07	36	0.67 ± 0.08	18	0.06 ± 0.06	24	0.25 ± 0.09
12	49	0.67 ± 0.07	27	0.78 ± 0.08	14	0.14 ± 0.10	18	0.28 ± 0.11
13	40	0.60 ± 0.08	22	0.73 ± 0.10	17	0.24 ± 0.11	17	0.47 ± 0.12
14	30	0.50 ± 0.09	18	0.72 ± 0.11	20	0.35 ± 0.11	16	0.19 ± 0.10
15	22	0.68 ± 0.10	12	0.67 ± 0.14	18	0.06 ± 0.06	14	0.07 ± 0.07
16	15	0.53 ± 0.13	6	0.50 ± 0.22	17	0.29 ± 0.11	18	0.17 ± 0.09
17	7	0.57 ± 0.20	6	0.50 ± 0.22	18	0.33 ± 0.11	13	0.08 ± 0.08
18	5	0.20 ± 0.20	6	0.33 ± 0.21	10	0.20 ± 0.13	14	0.36 ± 0.13
19	5	0.80 ± 0.20	5	0.20 ± 0.20	7	0 ± 0	9	0.22 ± 0.15
≥20	10	0.30 ± 0.15	10	0.40 ± 0.16	14	0.14 ± 0.10	24	0.08 ± 0.06

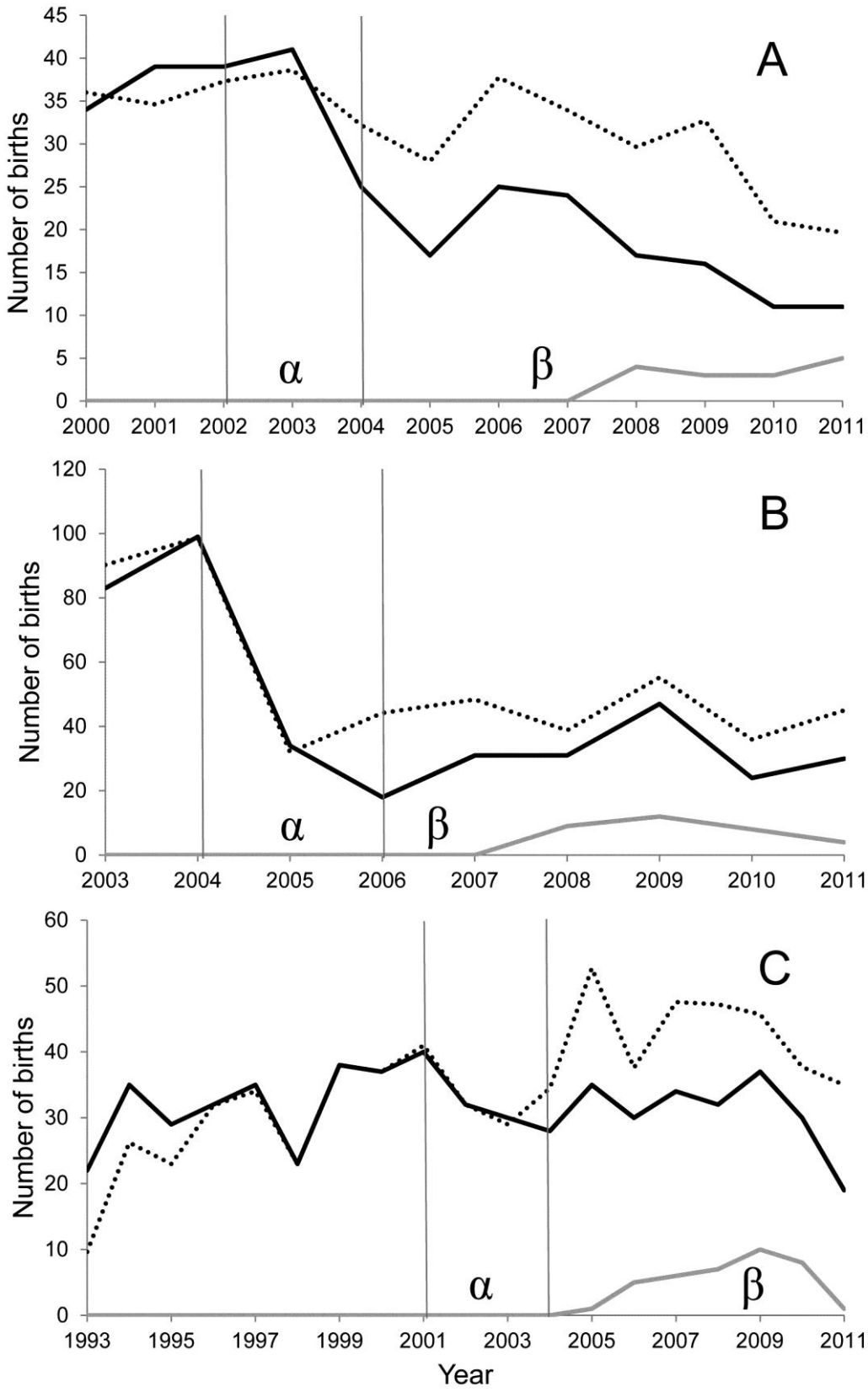
A
B
C
Number of births
Year
α
β
45
40
35
30
25
20
15
10
5
0
120
100
80
60
40
20
0
60
50
40
30
20
10
0
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011

Figure 3.2. Observed (solid black line) and expected (dotted line) number of offspring born each year at Little Book Cliffs Wild Horse Range, Colorado, USA (A), McCullough Peaks Herd Management Area, Wyoming, USA (B), and Pryor Mountain Wild Horse Range, Montana, USA (C). The α period represents PZP presence in the population before a contraceptive effect could influence births and the β period represents when the effect of PZP on births could be observed. The gray line is observed number of offspring born to post-treated females after their individually targeted fertility control period.

At mean previous spring/summer precipitation (13.95 cm), mean total winter precipitation (0.24 cm), and mean monthly minimum temperature (1.66°C), an estimated 48.8% (37.8–59.9%) of 2–5 year old untreated females gave birth during the pretreatment period and 35.2% (24.2–46.3%) gave birth during the post-treatment period. None of the climate measures I considered contributed to birth rate in this age cohort, but treatment period had a strong effect (t = 2.495, P = 0.020). Birth rates in this cohort differed between populations (σ = 0.022), ranging from 21.3% (10.2–32.3%) during the post-treatment period at Pryor Mountain to 60.5% (49.4–72.6%) during the post-treatment period at McCullough Peaks.

Birth rates were highest in the 6–14 year old cohort, and at mean previous spring/summer precipitation, mean total winter precipitation, and mean monthly minimum temperature, an estimated 65.4% (54.3–76.5%) of untreated females gave birth during the pretreatment period and 69.8% (58.7–80.9%) gave birth during the post-treatment period. As in the 2–5 year old cohort, birth rates for 6–14 year olds also varied by population (σ = 0.035). The lowest rate of 46.8% (35.7–57.9%) occurred during the

pretreatment period at Little Book Cliffs and the highest rate of 84.9% (73.4–95.9%) occurred during the post-treatment period at McCullough Peaks.

Birth rates in the ≥15 year old cohort were extremely variable. At mean previous spring/summer precipitation, mean total winter precipitation, and mean monthly minimum temperature, an estimated 46.6% (16.0–77.2%) of untreated females gave birth during the pretreatment period and 68.4% (37.8–98.9%) gave birth during the post-treatment period. Both mean monthly temperature (t= -1.968, P = 0.057) and total winter precipitation (t = 1.944, P = 0.056) influenced births in this cohort, but treatment period had a much weaker effect (t = -1.461, P = 0.099). Some of the variance around these estimates was attributed to differences between the populations (σ = 0.018), with 77.3% (46.7–100%) of ≥15 year olds at McCullough Peaks giving birth during the post-treatment period and only 41.4% (10.5–71.7%) giving birth at Little Book Cliffs during the pretreatment period.

Survival

Observed mean annual survival of neonates from birth to the following spring was 0.947 (0.925–0.969) at Little Book Cliffs, 0.953 (0.935–0.970) at McCullough Peaks, and 0.765 (0.733–0.797) at Pryor Mountain. Across all populations, foal survival did not differ between pretreatment and post-treatment periods, and at mean spring precipitation (9.12 cm), mean maximum summer temperature (24.81°C), and mean minimum winter temperature (-9.71°C), estimated neonate survival during the pretreatment period was 0.858 (0.794–0.991) and during the post-treatment period was 0.794 (0.661–0.926). The slight random effect variance of σ = 0.003 arose from lower foal survival at Pryor

Mountain. Spring precipitation was the most important effect in this model (t = 2.087, P = 0.045) and each centimeter of precipitation from March–June increased foal survival by 1.5%.

Observed mean annual survival of horses 1–19 years old was uniformly high across populations at 0.957 (0.945–0.970). Estimated survival for this age cohort at mean spring precipitation, mean maximum summer temperature, and mean minimum winter temperature was 0.946 (0.919–0.973) during the pretreatment period and 0.971 (0.944–0.998) during the post-treatment period. Climate did not measurably effect the estimates, but treatment period had some influence (t = 1.917, P = 0.064).

There were 66 horses in the populations during the study that were ≥20 years old, including the oldest male at 27 years old and the oldest female at 29 years old: both of which were still alive in 2011. The oldest female to produce an offspring was 21 years old at the time of parturition. Observed mean annual survival for the ≥20 year cohort was 0.794 (0.690–0.899) across the populations. Estimated survival for these animals at mean spring precipitation, mean maximum summer temperature, and mean minimum winter temperature was 0.768 (0.550–0.987) during the pretreatment period and 0.812 (0.753–1.000) during the post-treatment period. As with the foal cohort, survival in the oldest cohort was influenced by spring precipitation (t = -2.054, P = 0.049), but average minimum winter temperature may have also contributed (t = -1.711, P = 0.098). Although only 2 animals in this age cohort were removed during the pretreatment period and 2 were removed during the post-treatment period, there was an average of 2.39 (1.17–3.61) individuals present per year in the pretreatment period and 7.18 (5.22–10.14) present per year in the post-treatment period (Fig. 3.3).

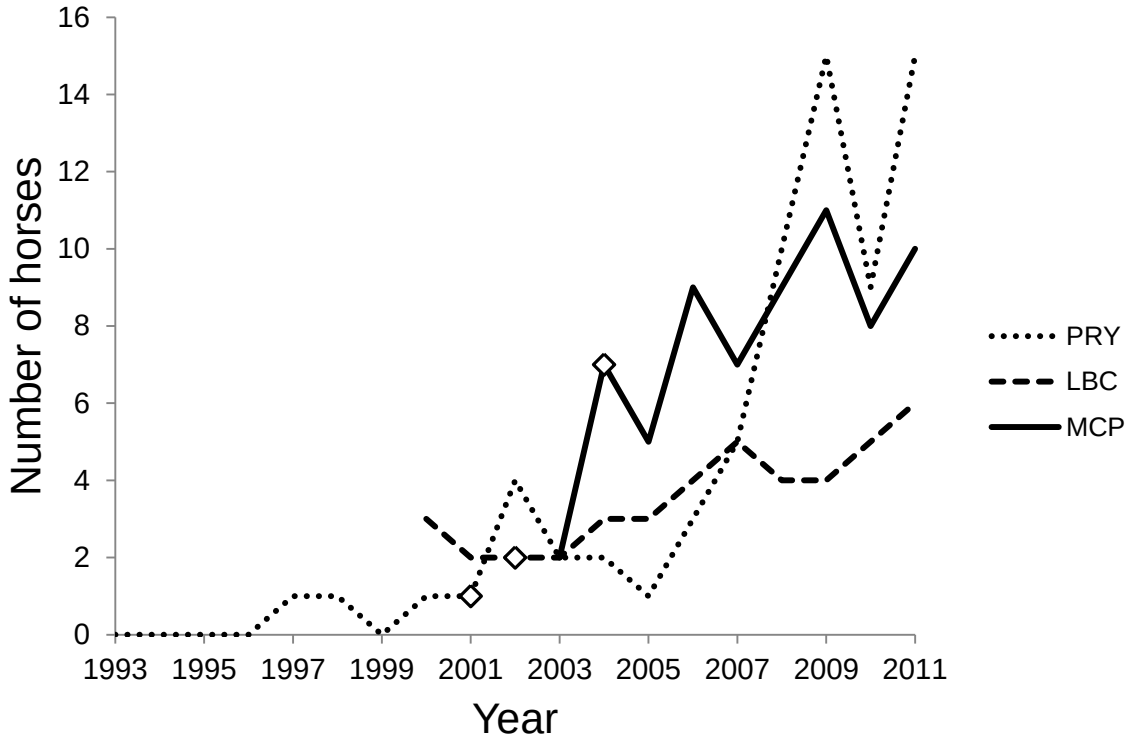

Figure 3.3. Number of horses ≥20 years old present at Little Book Cliffs Wild Horse Range Wild Horse Range, Colorado, USA (LBC), McCullough Peaks Herd Management Area, Wyoming, USA (MCP), and Pryor Mountain Wild Horse Range, Montana, USA (PRY). Porcine zona pellucida (PZP) applications began in each population at the ◊ marker on each time series.

Discussion

The ultimate purpose of applying a fertility control agent to wildlife is to decrease population growth rate (Hone 1992). Quantifying this relationship clearly in free-roaming wildlife populations is profoundly difficult. Even in the case of this study, where three populations of feral horses were known at the individual level, the population

growth rates observed could not be viewed solely as a function of contraception, independent of removals, predation, and environmental stressors.

I attempted to draw some insight into these relationships by calculating apparent annual growth rates and comparing λ_A in pretreatment and post-treatment periods: estimated post-treatment λ_A was 7.4% lower than pretreatment λ_A. This trend temporally coincided with percent of females treated in Little Book Cliffs and McCullough Peaks across the years of study, but only coincided at Pryor Mountain in the final year (Fig. 3.1). The long-term treatment strategy at Little Book Cliffs resulted in an average of 27% of females treated per year across the post-treatment period with mean λ_A of 1.076. The periodicity between removal operations extended through time and even four years after the last removal, λ_A was still 11% lower than during the pretreatment period mean (Fig. 3.1A). The very different management approach at McCullough Peaks was characterized by a large removal (74% of the population) at the beginning of the study, followed by an intended 2 year fertility control period when 58–77% of females were treated (Fig. 3.1B). The lowest λ_A ever recorded at this site coincided with the year when 77% of the population was treated, but the decrease was brief and λ_A reached a record high 3 years later. Lastly, the treatment regimen at Pryor Mountain appears to have had no effect on λ_A until nearly 50% of the females were contracepted in 2011. It is unclear from this single data point if the reduction in λ_A is a result of the PZP treatment, especially given the apparent strong influence of predation that obfuscates any potential contraceptive effect in the first year of treatment (Fig. 3.1C).

Despite the reductions in population growth rate, the populations continued to grow steadily every year that a removal did not occur with the exception of the known

stochastic predation period at Pryor Mountain, 2004–2005. This directly corresponds to earlier theoretical modeling that concluded 90–95% of females in a population must be sterile in order to reduce a population; and to have the same effect as culling, a contraceptive must last more than 2–5 years if density dependence is not acting (Hobbs et al. 2000). If the maximum rate of reduction based on fertility control regulation is simply the natural mortality rate (Hobbs et al. 2000), then we could expect a population decline in my study of only 3–6% annually, if all females were treated and PZP efficacy was around 90–95%. In contrast, removals reduced my study populations by as much as 32–74% in a single year. It should be noted, however, that the apparent demographic feedbacks in my study increased the efficacy of PZP at the population-level through a residual contraceptive effect in treated animals and reduction in birth rates in untreated animals. The simultaneous increase in survival did not completely compensate for this difference. My estimates of population growth imply that a 24% reduction in annual growth might be achieved if 100% of females were treated, indicating that reduction of populations may be achieved more quickly than simulations suggest.

The range of apparent population growth observed during the pretreatment period was comparable to the historic accounts of 15–25% growth for feral horse populations (Eberhardt et al. 1982, Wolfe 1986, Garrott et al. 1991). Although this range has been debated over the decades (Roelle et al. 2010), all of my study populations experienced years where growth exceeded 20%. The effect of removals on population growth rate has also been deliberated through time, positing that large sudden reductions in population size may lead to compensatory reproduction or increased fetal loss subsequent to the events (Swenson 1985, Kirkpatrick and Turner 1991, Boyce et al. 1999, Williams 1999).

In a comparison of two groups of feral horses on a barrier island, there was some evidence annual neonate removal from one group led to subsequently increased birth rates (Kirkpatrick and Turner 1991), and uncaptured females in another study had a higher birth rate following capture and release in one year, but not in another (Ashley and Holcombe 2001). There was no difference in birth rates from uncaptured females as compared to captured and released females or captured and removed females in two other populations (Hansen and Mosley 2000). Similarly, there was no difference in positive versus negative change in apparent population growth rates prior to removal as compared to post-removal in my study.

Other potential abiotic influences on population dynamics of ungulates include climate and predation (Saether 1997, Post and Forchhammer 2002, Vucetich and Peteron 2004, Owen-Smith et al. 2005). I found little evidence of climate strongly influencing the vital rates I modeled, but this is unsurprising given that no catastrophic stochastic climate events occurred and I found no evidence that density dependence was acting on population growth rate in any of the populations. The apparent absence of density dependence is also unsurprising because managers must consider multiple-use mandates that affect how horses and other resources are managed on the landscape. Compliant management action mitigates the resource-limiting effects of climate for most years and thus allows populations to grow at their maximum rates, given the constraints of contraception, removal, and predation (Garrott 1991).

There is compelling evidence that predation influenced population growth at Pryor Mountain, but there are few quantitative measures of predator abundance or prey selection to draw further inferences from. Mountain lion predation on feral horses has

been known to strongly influence neonate survival in some horse populations, such as at Montgomery Pass Wild Horse Territory, where the predation constraint on neonate survival was released following a decrease in the mountain lion population, much like in my study at Pryor Mountain (Turner and Morrison 2001). Influence of mountain lion predation was also found at the Nevada Test Site (now the Nevada Wild Horse Range) where the average population growth rate over 10 years was -7% (Greger and Romney 1999). A current study on prey selection by mountain lions has demonstrated that diet can be very individualized, with some lions selecting entirely for horses year round, some selecting horses only seasonally, and others selecting for different prey species when horses are available (Andreasen 2012). Such selection would explain the dramatic change in annual population growth of horses after three lions were removed at Pryor Mountain in 2004–2005. At Little Book Cliffs and Pryor Mountain, lion depredation on neonates and yearlings was directly evident from cached remains at kill sites, and one attempted depredation of a neonate was witnessed in progress. Perhaps more surprising is that attempted depredation of adult stallions was observed on 3 occasions for animals ranging 5–12 years old.

Survival of neonates at Pryor Mountain was observed as 18% lower than in the same age cohort at the other sites, but survival of 1–19 year olds across all populations was very high at 0.957. This is comparable to historical reports of adult feral horse survival that range from 0.923 (Goodloe et al. 2000) to 0.975 (Siniff et al. 1986). After controlling for climate, survival of 1–19 year olds was about 3% higher during the post-treatment period compared to the pretreatment period. Survival in the oldest age class was quite high at 0.768–0.812 after controlling for climate, but the estimated survival was

extremely variable due to the small number of animals present to draw inference from. However, there were about 3 times as many animals in this age cohort during the post-treatment period as compared to the pretreatment period, even though the number of animals in the cohort removed by time period was equal. Greater longevity for PZP-treated female horses was reported at Assateague Island and was explained by the reduction in metabolic costs of pregnancy and lactation that often decreases body condition in aging females (Kirkpatrick and Turner 2007).

The potential feedbacks from PZP treatment itself have rarely been considered when evaluating efficacy (see Chapter 4). I detected some evidence that birth rates decreased among untreated 2–5 year olds when PZP was acting to reduce fertility in treated conspecifics. Adult males in these populations directed 55% more reproductive behavior toward treated females, which may have resulted in less reproductive effort directed at the already less fecund young cohort (Ransom et al. 2010). Similar behavior was also observed in coastal feral horse populations, where increased estrous cycling was correlated with decreased band fidelity (Nuñez et al. 2009, Madosky et al. 2010, Nuñez et al. 2010). Both increased estrous behavior and decreased band fidelity can result in stallions pursuing, defending, and tending treated females more than untreated females. In addition to this indirect effect of treatment, PZP is also known to present a residual contraceptive effect after repeated inoculations. The duration of infertility in this residual period increases with number of consecutive year treatments (Chapter 2), and this effect appears to have contributed to 59% of the difference between number of offspring expected and produced.

Conclusion

Wildlife managers have been using adaptive management practices for decades, and they will likely implement them even more frequently as climate and other ecological factors become increasingly uncertain (Walters 1986, Lawler et al. 2008). Such strategies will undoubtedly be necessary for managing wildlife using fertility control. Population-level effects of fertility control applications are far less certain, and while annual population growth rate may be lowered by managing reproduction, most populations can only practically be reduced in the short term through culling or removal. PZP in a single application, long-lasting form is currently limited to the 22-month time-released pellet (Turner et al. 2008) and the liposome-encapsulated form of PZP, SpayVac®, which has only been tested in only a small number of horses (Killian et al. 2008). Managers would need to treat nearly every female in a population with a multi-year agent in order to realize true population reduction, so application remains challenging at the population scale.

Even though some feedbacks detected operated synergistically with PZP treatment to enhance the reduction in fertility, this study supports conclusions of some previous simulations that posit reduction of most wildlife populations solely using fertility control may be extraordinarily difficult (Garrott 1991, Seagle and Close 1996, Hobbs et al. 2000). However, it has been achieved under special circumstances, such as with feral horses at Assateague Island (Kirkpatrick and Turner 2008). Fertility control remains an important tool to aid in management of overabundant populations, nonetheless. The treatments in my study did extend the period between needed removals, thus reducing management cost and effort. Based on the observed birth rates of treated

females and the number of females treated annually (Table 3.2), we might deduce that the births of roughly 215 horses were likely prevented over the course of my study. At an average neonate survival rate of 87% and current adoption rate of 32%, 127 of those 215 horses would have been placed in long-term care at the approximate cost of $760 per year (calculated from U.S. Department of the Interior 2012). Assuming a conservative average of 15 years of lifetime care and $21,552 in total PZP cost, managers potentially saved $1,426,248 using the different treatment approaches in my study. This scale of fiscal savings roughly concurs with early simulations of the economics of fertility control (Bartholow 2007). This simple thought experiment illustrates the value of even modest fertility control programs for populations of feral horses, regardless of the scale of population-level effects. The role of fertility control is far more uncertain for open populations of other wildlife species, where lethal removal is an option and the fiscal costs of long term captive care are irrelevant. In such cases, understanding behavior and life-history strategies is essential to forming realistic expectations of fertility control performance at the population level.

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Chapter 4: Can nature overcome contraception in the race for fitness?

Natural systems and processes are stressed by anthropogenic pressures and ever-fragmenting landscapes, and the need for regulating wildlife populations is increasing. Controlling wildlife fecundity using fertility control applications has been considered for almost four decades, but nearly all research has been conducted on individual-level efficacy of treatments. Our ability to regulate populations by manipulating fecundity is largely unknown. Feedbacks from treatment can produce unexpected changes in birth rates, survival, immigration, and emigration that may considerably reduce the ability of fertility control to regulate populations. Here, I move toward a synthesis of population-level fertility control literature and compare some of those outcomes with individual-level reports of efficacy. Most population-level studies demonstrate that negative feedbacks on fertility control performance are occurring, and in many cases increased survival and increased immigration can compensate entirely for the reduction in births attributed to treatment. Nearly all available simulated and empirical data suggest that growth in closed populations might be regulated if the population is first reduced and a large percentage of females are treated. Understanding species' life-history strategies, biology, behavioral ecology, and ecological context is critical to developing realistic expectations of regulating populations using fertility control. I propose a progressive quantitative approach for formal accumulation of evidence toward understanding the complex states and processes present in fertility-controlled wildlife populations.

Keywords Behavior, demography, ecological process, fertility control, modeling, population ecology, wildlife contraception, wildlife management

Humans have been attempting to control animals for over 13,000 years (Diamond 2002). While the need to regulate domestic animals has persisted throughout these millennia, we have also attempted in more recent centuries to regulate wild animal populations using a complex set of management techniques (Bolen and Robinson 1995, Decker et al. 2001). These efforts have historically involved controlling survival through lethal hunting and culling strategies. Nonlethal strategies of regulating births through fertility control applications are becoming more common as wildlife management needs change (Hobbs et al. 2000, Porton 2005). This trend can be attributed at some level to an increasingly mutualistic societal view arising from abundance of wildlife in suburban and urban areas (Teel and Manfredo 2009). In such circumstances, perception of wildlife may become less as a natural resource and more as part of our social environment (Leong 2010). The balance of human perception and wildlife abundance is precarious though, because as highly adaptive species increase in density, wildlife-human conflicts increase and society can then be stuck in the dichotomy of desire for protection and relief from conflict (Knuth et al. 2001, Lauber and Knuth 2004, Lauber et al. 2007, Hadidian 2009).

The practice of using fertility control to manage reproduction in wildlife emerged over 40 years ago (Asa and Porton 2005). We look now to such tools when animals threaten our lives, livelihoods, or property, when they cause declines in species we prefer, and when densities are high enough to increase disease transmission or disrupt ecosystem function (Caughley 1981). The vast majority of empirical knowledge about wildlife fertility control comes from individual-level studies of efficacy and contraindications, and we know relatively little about how fertility control influences populations (Garrott

1995, Kirkpatrick et al. 2011). Do the individual-level fertility control findings scale up to effective reduction in population growth or can nature provide mechanisms to compensate for individuals' reduction in fitness?

Many types of fertility control have been applied to wildlife and include hormone applications, immunocontraceptive vaccines, mechanical devices, and surgical techniques (Asa 2005). All of these methods may prevent births, but they also may induce unintended changes to behavior and physiology (Nettles 1997, Gray and Cameron 2010). It is unsurprising that hormonal applications such as melengestrol and levonorgestrel effect behavior (Gray and Cameron 2010), but it is surprisingly uncertain how variable such behavioral changes are, even within similar taxa. Stumptailed macaques (*Macaca arctoides*), for example, can become markedly more aggressive toward conspecifics when treated with a synthetic progestin (Linn and Steklis 1990), but hamadryas baboons (*Papio hamadryas*) can become more passive when treated with a similar progestin (Portugal and Asa 1995). Such uncertainties have driven a shift in wildlife fertility control toward immunocontraceptives, whose mechanisms of action target natural pathways by immune response rather than using hormones to fundamentally change reproductive physiology (Kirkpatrick et al. 2011).

Any fertility control application that changes reproductive capacity of an individual has the potential to induce individual behavioral changes that can cascade to alterations in family group structure, changes to interspecific and intraspecific interactions, and ultimately influence population dynamics in unforeseen ways. Fertility control has been associated with changes in immigration (Ramsey 2005, Merrill et al. 2006), decreased group fidelity (Nuñez et al. 2009, Madosky et al. 2010), increased

survival (Caughley et al. 1992, Kirkpatrick and Turner 2007, Williams et al. 2007), and altered reproductive behavior (Nuñez et al. 2010, Ransom et al. 2010). Attempting to understand these shifts is profoundly difficult, and the challenge of separating the influences of multiple population growth controls can be daunting (Sibly and Hone 2002). To exacerbate these problems, the longitudinal studies needed to detect and quantify population-level effects of fertility control treatments can be expensive and time consuming.

Insights into population-level fertility control effects have largely been accomplished through efforts that simulate population dynamics using statistical models (Caughley et al. 1992, Hone 1992, Hobbs et al. 2000, Davis and Pech 2002, Merrill et al. 2006). Simulation models can be very cost-effective and informative for gaining insights into management techniques; however, widespread behavioral and demographic changes in fertility-controlled animals may subvert the underlying assumptions of demographic parameters in naive predictive models. The assumptions of many fertility control population models could be wrong if the vital rates informing them are based on the wealth of a priori ecological knowledge about species and systems before fertility control was applied. In such cases, the true posterior distributions may be quite different than predicted. What might be viewed as stochastic behavioral noise and relegated to a single error term could in fact be fundamentally new process paradigm (see Caughley et al. 1992, for example).

I attempt here to synthesize the population-level literature on wildlife fertility control and compare some of those outcomes with individual-level reports of efficacy. I specifically investigate the behavioral components from wildlife fertility control studies

to ask the question of what feedbacks, and what magnitude of feedbacks, might be influencing population-level outcomes of fertility control strategies. I attempt to identify some of the underlying processes in order to help inform modeling efforts and future design for empirical population-level fertility control studies, and ultimately I try to determine if, in fact, nature can overcome our control efforts at a scale that makes fertility control ineffective as a wildlife management tool.

The feedback dilemma

The importance of considering animal behavior in broad ecological and conservation contexts is critical to understanding population ecology (Sutherland 1998, Buchholz 2007); yet, lack of rigorously quantified behavior data often inhibits our understanding. At the individual level, wildlife contraceptive studies have illuminated a wide array of behavioral changes attributed to fertility control applications (Nettles 1997, Gray and Cameron 2010). The impetus behind many of these studies is an effort to control agonism in captive populations, while others have focused on how behavior is altered in free-roaming wildlife populations (Asa et al. 2005). All of these studies provide clues to population level effects of fertility control, and ultimately we can categorize our thoughts into the vital rates that drive population dynamics; birth, survival, immigration, and emigration. The many potential feedbacks on population growth rate include both negative and positive sources, and these may vary with the ecology of the species in question.

Fertility control is designed to act on individual birth rate, so it should be expected that fecundity of treated animals will directly differ from untreated animals;

however, indirect effects make the broader influence of treatment on birth rates less clear. Unintentionally prolonged contraception has been attributed to physiological changes in ovarian function after fertility control treatments (Kirkpatrick et al. 1995, McShea et al. 1997, Nettles 1997, Stoops et al. 2006). Such residual effects were found in feral horses (*Equus caballus*) repeatedly treated with porcine zona pellucida (PZP), and were further complicated by shifts in the seasonal birth pulse when fertility resumed (Nuñez 2009, Chapter 2). Increased frequency of reproductive behavior has been observed in PZP and gonadotropin releasing hormone (GnRH) treated females, and has the potential to focus attention of breeding males away from fertile females and toward the attractive, but sterile, females (Shumake and Wilhelm 1995, McShea et al. 1997, Heilmann et al. 1998, Ransom et al. 2010, Powers et al. 2011). This could decrease fitness of males and untreated females and result in a higher net contraceptive effect at the population level (Chapter 3). In sharp contrast, fecundity of untreated female mice increased when fertility controlled females were present, creating a lower net contraceptive effect (Chambers et al. 1999). The effects of fertility control on biochemical and olfactory communication are virtually unknown, but have been implicated in disrupting intraspecific interactions in a primate (Crawford et al. 2010) and could lead to greater uncertainty about fecundity at the population level.

Fidelity to family groups has decreased in conjunction with fertility control applications (Fayrer-Hosken et al. 2000, Nuñez et al. 2009, Madosky et al. 2010), and time spent with conspecifics or potential mates has also changed (Bertrand et al. 1996, Poiani et al. 2002, Harrenstien et al. 2004). Territoriality increased for pikas (*Ochotona curzoniae*), and the increase was related to decreased litter size (Liu et al. 2012). These

types of changes can affect time budgets such that basic maintenance behaviors of feeding and resting are decreased, resulting in lower body condition (see Ji et al. 2000, for example). Increased or decreased agonism between conspecifics has also been attributed to some contraceptive applications (Linn and Steklis 1990, Portugal and Asa 1995, Penfold et al. 2005, Snape et al. 2011), and these behaviors can alter dominance hierarchies and thus access to resources (Dublin 1983, Schulte et al. 2000, Creel 2001). More directly, some deer treated with hormonal applications lost body condition or stopped eating altogether (Bell and Peterle 1975, White et al. 1994). Low body condition arising from any of these processes can decrease birth rate because the nutrition requirements needed to support pregnancy and parturition are not met at some life stage (Cook et al. 2004, Rhind 2004).

Apart from the many potential direct and indirect effects of fertility control on births, some applications may influence survival as well. When the costs associated with competition and reproduction decrease, body condition and longevity can increase. Such has been the case in a population of feral horses treated with PZP (Turner and Kirkpatrick 2002). Survival was higher among fertility-controlled rabbits (*Oryctolagus cuniculus*) (Twigg et al. 2000, Williams et al. 2007), coyotes (*Canis latrans*) and foxes (*Vulpes vulpes*) (McCallum 1996, Bromley and Gese 2001), and feral horses (Chapter 3) when compared to untreated animals. When adult survival is increased, a negative feedback on population-level fertility control performance occurs. Survival of neonates born late to formerly contracepted females was the same as those to untreated females in a study of birth phenology in this context, but such asynchrony may not be as forgiving in other species or different climates (Chapter 2). In one study of possums (*Trichosurus*

vulpecula), disease transmission was 28% higher in populations with sterile females, indicating a potential mechanism for decreased survival in fertility-controlled populations (Caley and Ramsey 2001).

Perhaps the most confounding issue in understanding indirect fertility control effects occurs in open populations, where birth and survival are not the only vital rates operating. Behavioral changes resulting from fertility control can result in individuals arriving into populations or dispersing out of populations. Male possums, for example, increased in frequency at sites where females were contracepted (Ji et al. 2000), and in one study, the rate of immigration equaled the rate of reduction in births attributed to fertility control (Ramsey 2005). A similar feedback was also observed in deer (Merrill et al. 2006), and may be a result of disassociation between males and fertility-controlled females (see Miller et al. 2001, for example). In a rat (*Rattus argentiventer*) population, fertility-controlled females had larger ranges than fertile females (Jacob et al. 2004), and a similar finding in koalas (*Phascolarctos cinereus*) was explained by absence of range-limiting dependent young (Hynes et al. 2011).

For nearly all of the side-effects discussed here, there are almost as many cases where no effects occurred when a different fertility control method was used or a different species was studied (Gray and Cameron 2010: Fig. 2). Such variation in individual and species response emphasizes the need for careful consideration of species biology, reproductive system, behavioral ecology, population biology, and ecological context when considering fertility control management for any population.

Population-level effects of fertility control

Despite a call for population-level study of wildlife fertility control nearly two decades ago (Garrott 1995), scientific progress has been slow. I reviewed 479 papers in the scientific literature on wildlife fertility control from 1980–2011, and found that 90% focused only on individual effects (Fig. 4.1). Half of the papers reviewed were published in the last decade, reflecting an increasing interest in wildlife fertility control. There was an increasing trend in population-level studies, but still only 10% of the papers reviewed addressed population-level effects.

Only 6.5% of all papers I reviewed considered behavioral or indirect demographic effects in population-level assessment of fertility control (Table 4.1), and only half of those quantitatively considered such effects in modeling population dynamics with fertility control (Table 4.2). This is surprising given that such a large number of individual-level studies describe the potential for indirect effects to influence fertility control efficacy at the population level (Nettles 1997, Gray and Cameron 2010).

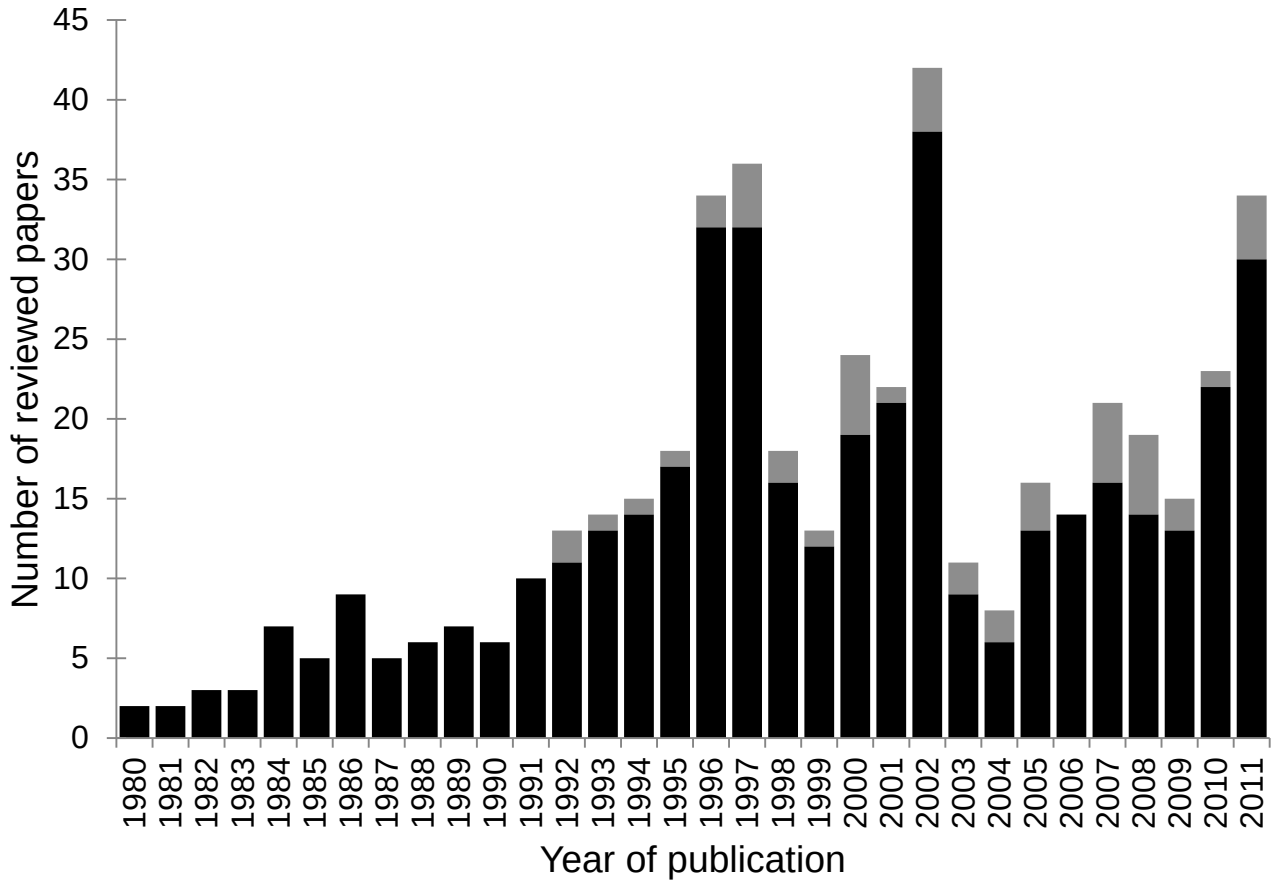

Figure 4.1. Trends in publication (*n* = 479 papers) for research on fertility control in wild and feral fauna from 1980 to 2011. Proportion of each bar in grey depicts investigations that included empirical or simulated population-level effects.

Table 4.1. Number of reviewed scientific publications from 1980–2011 that included population-level effects of fertility control on wild or feral animals in theoretical, simulation, or empirical contexts, and number of those publications that considered behavioral or indirect demographic feedbacks on population-level effectiveness of the application.

	Type of study			**Feedback on fertility control efficacy**		
Fauna type	Theoretical	Simulation	Empirical	Negative	Positive	Not Considered
Ungulate	1	10	6	4	0	13
Rodent	2	2	6	6	1	3
Marsupial	0	1	3	4	0	0
Pachyderm	2	2	1	2	0	3
Carnivore	0	3	1	0	0	4
Fish	1	0	0	1	0	0
Non-specific	4	3	0	4	0	3
Total	10	21	17	21	1	26

Table 4.2. Population-level effects of fertility control in simulated (S) and empirical (E) studies that explicitly incorporated demographic feedbacks into analyses.

Source	Taxa	Data	Individual treatment efficacy	Percent of population treated	Population effect	Feedback	Mechanism
Caughley et al. 1992	gregarious, stratified by dominance structure	S	Non-specific:100%	0-100% in social groups of up to 5 females	If female loses dominance at treatment, productivity increases	Negative	Increased births from subordinate females
Hone 1992	a: long-lived, low fecundity b: short lived, high fecundity	S	Non-specific:100%	20-100% of original fecundity of females	curvilinear response: for b, 80% fertility reduction ≈ 50% abundance reduction	Negative	Increased survival
Seagle and Close 1996	White-tailed deer (*Odocoileus virginianus*)	S	Non-specific:100%	0-100% of females	no reduction at <50% of females treated in open population	Negative	Increased immigration
Barlow 1997	a: monogamous and, b: polygamous	S	Non-specific: 100%	0-100% of females and/or 0-100% of males	greatest effect in (a) with both sexes treated; less effect in (b)	Negative	increased survival; increased births in b
Twigg et al. 2000 Williams et al. 2007	European rabbit (*Oryctolagus cuniculus*)	E	Tubal ligation: 100%	0%, 40%, 60%, 80% of females	After 4 years, no difference in population size between treatments	Negative	Increased survival, increased immigration, decreased emigration
Singleton et al. 2002	House mouse (*Mus domesticus*)	E, S	Tubal ligation & ovariectomy: 100%	67% of females	75% density reduction after 11 weeks, but compensation by 20-24 weeks	Negative	Increased births per female
Davis and Pech 2002	Based on red fox (*Vulpes vulpes*)	S	Non-specific: 100%	0-100% of females	absent density dependence, density increased with up to ~50% treatment	Negative	Increased survival

Table 4.2 continued

Merrill et al. 2006	White-tailed deer (*Odocoileus virginianus*)	S	Non-specific: 100%	30%, 45%, 60% of females	No population reduction if movement rates were >25% of observed and treatment was <45%	Negative	Increased immigration
Ramsey 2005	Brushtail possum (*Trichosurus vulpecula*)	E	Tubal ligation: 100%	0%, 50%, 80% of females	60% recruitment for 50% treated/74% for 80% treated: no population effect	Negative	Increased immigration, increased survival
Kirkpatrick and Turner 2008	Feral horse (*Equus caballus*)	E	PZP: 0-8% birth rate in females	42-76% of females	Population decreased 22.8% in 11 years	Negative	Increased survival
Jacob et al. 2008	Ricefield rat (*Rattus argentiventer*)	E	Tubal ligation, progesterone: 100%	up to 76% of females	no population effect in open population	Negative	Increased births, increased survival
Budke and Slater 2009	Feral cat (*Felis catus*), closed population	S	surgical or contraception: 100%	0-30% of females	91% of adult females need to be sterile to stop population growth	Negative	Increased survival
Ransom (Chapter 3)	Feral horse	E	PZP: 8-34% birth rate in females	11-77% of females	4-9% reduction in annual population growth	Positive, Negative	Decreased births in untreated females, increased survival

A broad consensus among both empirical and simulated studies is that in most free-roaming wildlife populations, a majority of the animals present in one or both sexes must be infertile to realize a meaningful reduction in population growth, and reduction in abundance typically requires long temporal horizons and aggressively maintained treatment (see studies in Table 4.2). Depending on life-history strategies, this can conservatively mean >50% of females must be treated in closed populations of long-lived, low fecundity species to achieve moderate reduction in growth (Hone 1992, Hobbs et al. 2000), and perhaps >90% of females must be treated in open populations where immigration can compensate for birth reductions (Merrill et al. 2006). Controlling populations of short-lived, high fecundity animals is even more daunting because the high recruitment rates require fertility control treatments to be applied frequently (Singleton et al. 2002, Williams et al. 2007, Jacob et al. 2008). In some applications, the lag time between treatment and effect on birth rates can result in too many new fertile females being recruited into the population for treatment strategies to be efficiently applied, even in long-lived, low fecundity species (Nielsen and Porter 1997, Whyte et al. 1998). Achieving population goals using fertility control for highly promiscuous breeders may not be feasible (Caughley et al. 1992).

Most simulations have concluded that the response of a population to fertility control is non-linear, and if survival increases as fecundity declines then survival is more influential on population growth than births (Hone 1992, Sinclair 1997, Hobbs et al. 2000, Merrill et al. 2003). The logical conclusion to this is that fertility control is generally more effective at maintaining populations than actually reducing them, and thus effective use of fertility control first may require culling (Hone 1992, Barlow et al. 1997,

Hobbs et al. 2000). Perhaps most alarming is that many of these simulations assume 100% sterility, which is generally only achieved using surgical applications. In practical management terms, physically treating such large numbers of animals may be fiscally and operationally prohibitive. This is not the end of the story, however, because some empirical studies on population level fertility control illustrate a more encouraging outcome.

Feral horses have a long life span and females can potentially produce offspring annually for up to 20 years of their life. A fertility control study at Assateague Island, USA, achieved zero population growth in only 2 years, with 42–76% of adult female feral horses treated annually with PZP (Kirkpatrick and Turner 2008). Actual population decline began in 8 years and by year 11 it had decreased nearly 23%. This sharply contrasts most simulation predictions, and clues to the discrepancy lie in the indirect effects of treatment, the population parameters, and life history strategies of the species, as well as the management options available. This example reflects a relatively small, closed population of a polygynous species with strong dominance hierarchies, so lack of immigration and potentially reduced fecundity in subordinate females may act to supplement the effects of fertility control at the population level. Survival, however, appears to have increased in older females, which acts against the effects of fertility control. In another study of feral horses using the same contraceptive, residual effects of treatment and suppression of births in subordinate females contributed to a 33% difference in expected and realized births (Chapter 3). This complex system of feedbacks demands a deeper understanding of the influences acting on vital rates in populations we propose to control, and before we categorically dismiss the use of fertility control to

functionally reduce populations, we must carefully consider how those feedbacks are operating.

A thoughtful quantitative approach

Stochasticity happens. The question then is how much stochasticity can we embrace in explicit modeling efforts and how much is noise that detracts from general conclusions about systems? Perhaps a more compelling question is when does assumed stochasticity become routine system behavior and how informative are our models when such underlying assumptions are compromised? In addressing such problems, traditional statistical techniques may fall short because hypotheses are chosen to match long-accepted, but often narrow, analytical methods rather than robust statistical methods being chosen to match complex ecological questions (Hobbs and Hilborn 2006). Historically, statistical models such as regression and ANOVA have been used to evaluate population dynamics, primarily because technology and computation ability have constrained more complex analyses. Such statistical approaches often have difficultly considering multiple sources of stochasticity and pool both observation and process error into a single term of uncertainty (Clark 2003). In the case of fertility-controlled wildlife populations, the feedbacks that may arise from cascading behavioral and demographic changes related to such treatment may warrant fully stochastic hierarchical state-space Bayesian models that explicitly consider both process and observation error. This would allow variation among individual survival and recruitment rates, as well as other attributes, to be incorporated through the hierarchical model forms. As computational capacity becomes increasingly greater, advanced techniques such as

Markov Chain Monte Carlo (MCMC) analyses become more accessible and can help avoid misleading conclusions that may arise from consolidating observation and process error into one term (Calder et al. 2003, Freckleton et al. 2006).

Likelihood and Bayesian techniques can use multi-model inference to look for support in the data for multiple hypotheses and generate more informed estimates of multiple parameters (Hobbs and Hilborn 2006). A true strength of Bayesian models is that we can also use a wealth of prior information about species and systems to inform our models, but here is where we must exercise considerable caution in the realm of fertility-controlled populations. Informative priors may misinform our estimates if multiple parameters, such as birth, survival, immigration, and emigration are being influenced and our hypotheses are focused only on births. In such cases, uninformative prior distributions may be more useful if prior distributions from other fertility control studies on like species and systems are unavailable. These approaches can help facilitate a formal accumulation of evidence toward understanding the complex states and processes present in fertility-controlled wildlife populations. Without formally incorporating some of this 'noise' we are missing important ecological parameters and are thus more likely to arrive at misinformed predictions of population dynamics (Calder et al. 2003). Furthermore, advances in quantitative tools for addressing such questions have never been so powerful or available, and confronting models with empirical individual-level long-term population data can provide deep insights into wildlife ecology and form more realistic predictions as to how fertility management influences population growth.

Conclusion

Study of individual effects of fertility control applications is, and will always be, an important step toward technology development and discovery of potential wildlife management tools, but understanding the ecological effects of our actions is paramount to good natural resource management and stewardship. Natural systems and processes are strained under anthropogenic pressures and ever-fragmenting landscapes, so actions such as population-level fertility control demand that practitioners weigh ethical and biological costs to prevent mismanagement. To begin to reach this goal, more empirical research is desperately needed on population-level effects of fertility control. Such tools may be very effective at regulating abundance in some species and systems, but quite ineffective in others. Feedbacks from fertility control application may vary widely and produce quite unexpected results. In some cases, changes to births, survival, immigration, and emigration clearly could provide a formidable barrier to effective fertility control management of populations. As scientists, managers, and practitioners, we must strive to understand the complex and often confounding nature of the actions we implement. We must ask if the cascading perturbed trophic effects of fertility control are fundamentally changing ecological systems, and we should be obligated to answer those questions using rigorous science. Our best chance at understanding such complex issues is to combine the data from in depth individual empirical studies, thoughtful simulations, and longitudinal empirical population studies to determine how demographic parameters behave in fertility-controlled wildlife populations.

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APPENDIX

Study Area Maps

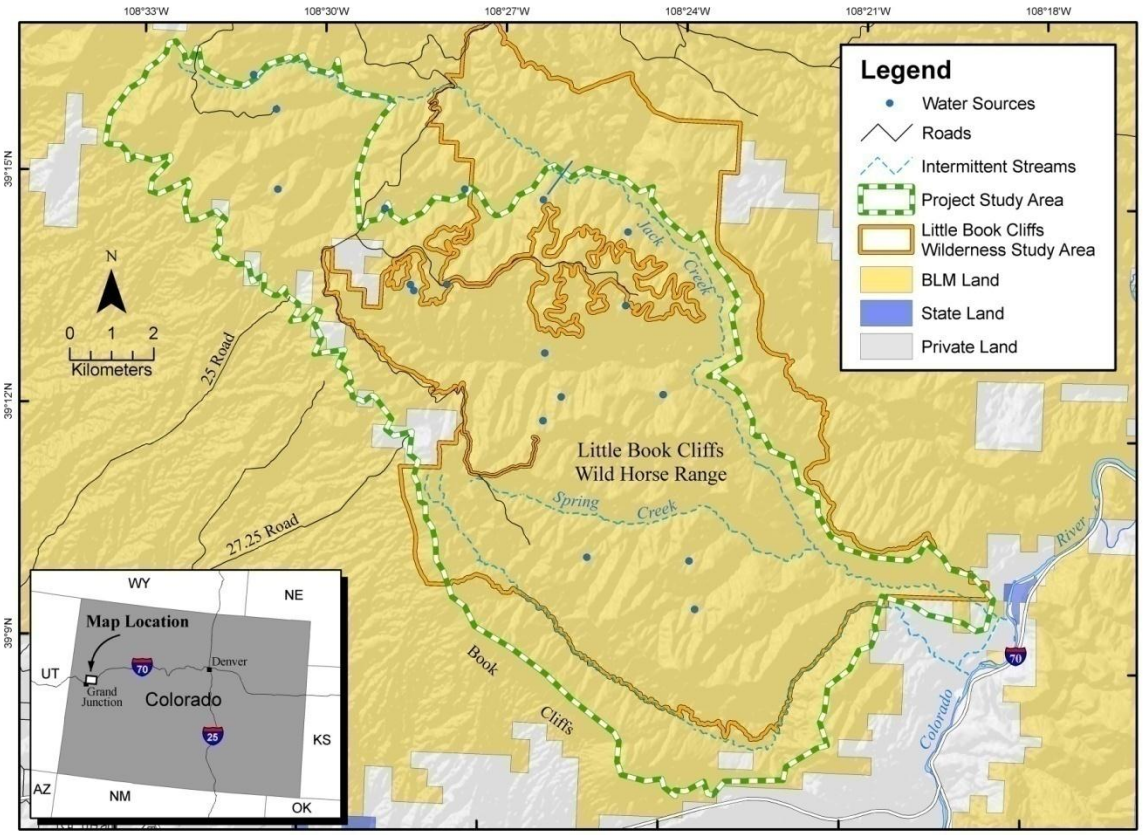

Figure A.1. Location of the Little Book Cliffs Wild Horse Range and study area boundaries.

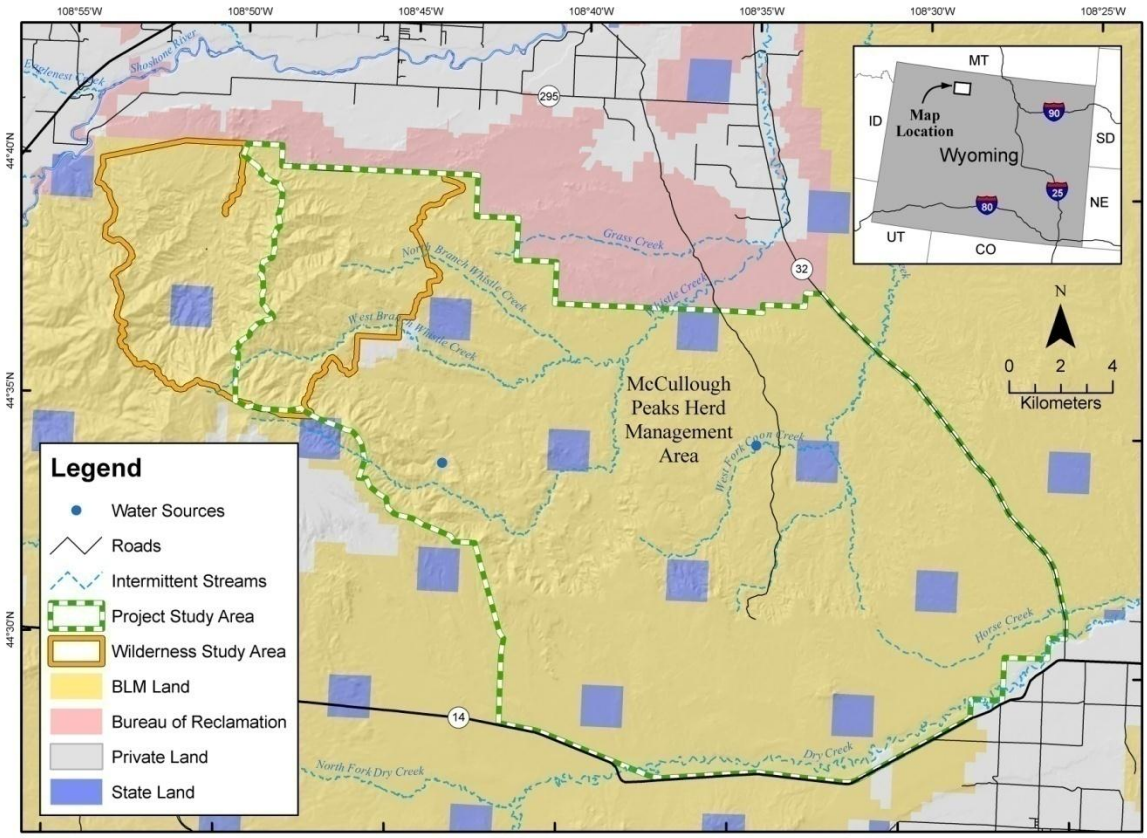

Figure A.2. Location of the McCullough Peaks Herd Management Area and study area boundaries.

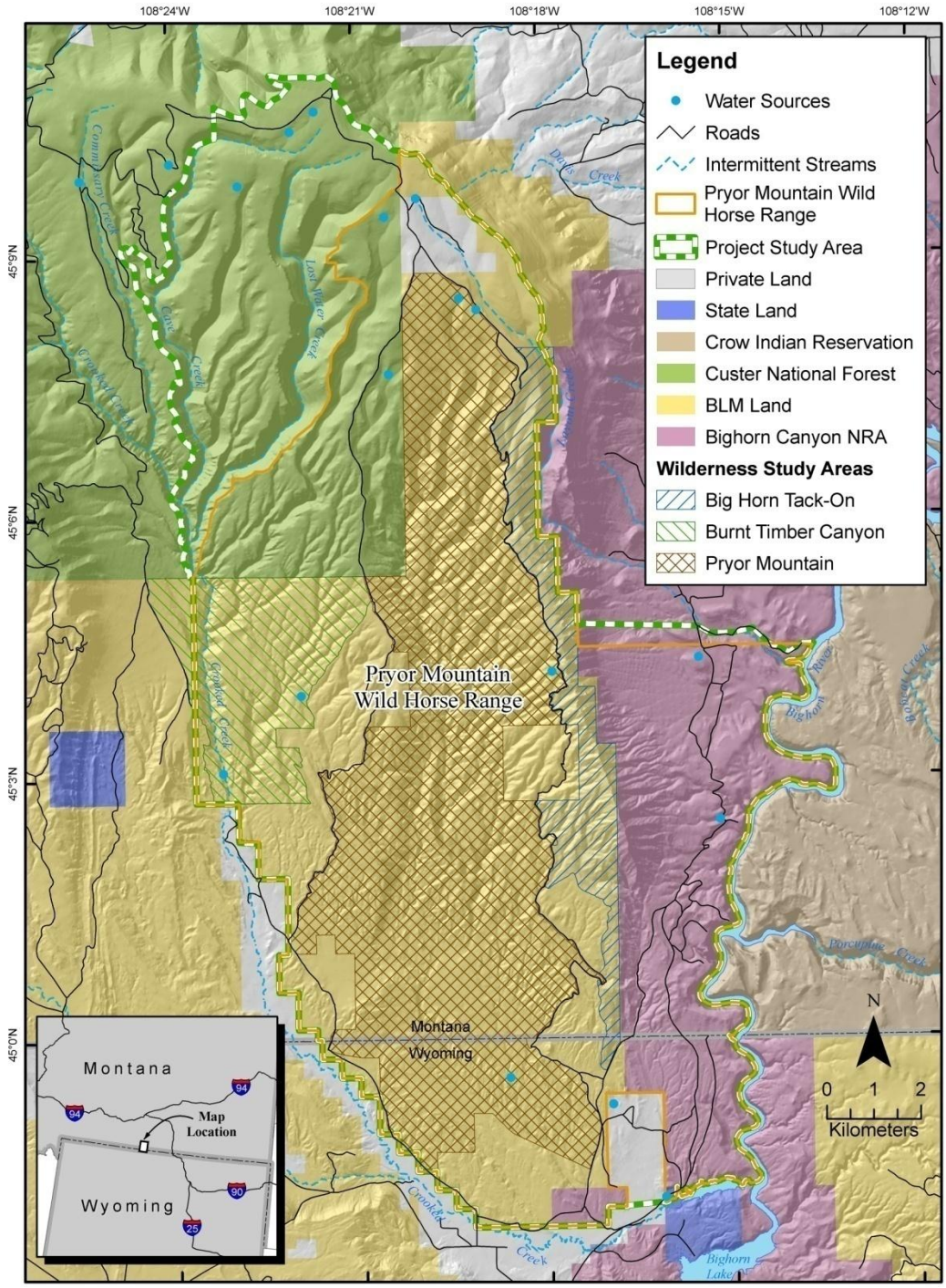

Figure A.3. Location of the Pryor Mountain Wild Horse Range and study area boundaries.