




Special Section on Management of Feral Equids

# Estimating Abundance and Simulating Fertility Control in a Feral Burro Population

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**ABSTRACT** Overabundant populations of feral equids are negatively affecting rangelands in the western United States. To better manage these populations, robust estimates of abundance and demographic rates and cost-effective methods of reducing abundance are necessary. From August 2015 to April 2017, we estimated the abundance of feral burros (*Equus asinus*) at the Fort Irwin National Training Center (NTC; California, USA) using a double-observer-sightability aerial survey method; captured, radio-collared, and inoculated female burros with porcine zona pellucida (PZP), an immunocontraceptive control agent; estimated female demographic rates; and used matrix population models to simulate how changes in demographic and PZP delivery rates would influence burro abundance. We estimated there were 690 (95% CI = 618–752) feral burros within the surveyed area, but these are part of a much larger population that is not geographically isolated from those in the survey area. Sighting probabilities ranged from 0.19–0.98 and were most strongly influenced by distance from observer and group size. We estimated age-specific demographic rates at the NTC and compiled mean rates across burro populations in arid environments from the literature. Mean fecundity varied from 0.17 to 0.58 foals/adult female with younger females having lower fecundity. Mean survival was 0.90 for foals, 0.98 for yearlings, and 0.96 for adults. The PZP vaccine treatment strategies that suppressed fertility for up to 10 years predicted that burro abundance would be reduced by 67–88% after 15 years (compared with no treatment), but none of these strategies resulted in population extirpation. Population growth rates shifted from increasing to decreasing at adult survival rates below 0.84 and the population was predicted to become extirpated when adult survival declined to <0.60. In the absence of other methods to reduce burro numbers, our findings indicate that current formulations of PZP immunocontraception, which require multiple doses, would be inadequate for controlling population growth rates at the NTC. Our fieldwork also highlighted the difficulty of administering PZP vaccination to large, free-ranging animals. Development of longer-term fertility reduction agents or more efficient vaccine delivery techniques would likely improve the efficacy of fertility control for overabundant ungulate populations. Lack of geographic closure (physical barriers to migration) further complicated efforts to reduce burro numbers. © 2021 The Wildlife Society.

**KEY WORDS** abundance estimation, California, *Equus asinus*, fecundity, feral burros, feral equids, immunocontraception, matrix models, population dynamics, survival.

Horses (*Equus caballus*) and burros (*E. asinus*) are not native to North America but have a long cultural relationship with Americans, having been used for work and transportation, sport and recreation, and even treated as companion animals (Scasta et al. 2018). As a consequence of the Wild Free-Roaming Horses and Burros Act (WFRHBA) of 1971 (Public Law 92-195), feral equids are now protected from capture, branding, harassment, or death on certain federal

lands, primarily those administered by the United States Bureau of Land Management (BLM) and the United States Forest Service (USFS). These protections were initially enacted because the public perceived a lack of humaneness in the treatment of feral equids (Garrott 2018) and because the animals were perceived to be declining on public lands, heightening concern that this cultural and naturalized symbol of the West could be lost. As a result of several congressional actions subsequent to passage of the WFRHBA, the situation has reversed and feral equids are causing economic and ecological strife and human-wildlife conflict (Beever et al. 2018, Garrott 2018).

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Feral equids roam across >18 million ha of rangeland in 10 western states and 2 Canadian provinces (The Wildlife Society 2016). The abundance of all feral equids on public lands in the United States was purported to have doubled during 2000 to 2019, with an estimated 133,000 individuals managed by the BLM, including roughly 45,000 horses in off-range corrals or pastures, along with an additional 7,500 on USFS lands, and >70,000 more free-roaming equids on tribal lands (U.S. Government Accountability Office [GAO] 2017; Beaver et al. 2018). Robust estimates of equid population size on BLM lands have been in widespread use only since the National Research Council (NRC) critiqued BLM's previous aerial survey methods (NRC 2013). Although recent estimates on BLM lands (BLM 2019) are based on estimators that account for imperfect detection (Lubow and Ransom 2016), the number of free-roaming equids in the United States is still most likely underestimated (NRC 2013).

The WFRHBA requires that feral equid populations inhabiting BLM- and USFS-administered lands to be managed "in a manner that is designed to achieve and maintain a thriving natural ecological balance on public lands" (Public Law 92-195:649). To comply with this directive, the BLM and USFS have attempted to control overabundant feral equid populations by gathering and removing them from the wild and placing them into short-term holding for later adoption, or into longer-term holding for those considered unadoptable (Norris 2018). The BLM Wild Horse and Burro Program is costly, with nearly \$370 million (US\$) spent during 2012 to 2016, with expenditures on off-range holding facilities representing >60% of this amount (Norris 2018). Garrott and Oli (2013) predicted that it would cost \$1.1 billion to maintain horses in BLM holding facilities up to 2030, with annual costs of \$67 million thereafter. These estimates, which reflect the direct cost of managing feral equids under current law, do not include costs associated with the displacement of other livestock and wildlife from rangelands or the degradation of western rangelands, both of which result from overpopulation of feral equids (Jakus 2018).

Feral equids in excess of allowable management levels can reduce rangeland quality for other livestock and wildlife by reducing forage cover, increasing soil erosion, altering hydrologic processes, and competing with native wildlife such as bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*; Berger 1985; Abella 2008; Marshal et al. 2008, 2012; Beschta et al. 2013; Crist et al. 2019). Feral equids negatively influence use of water sources by native species (Dunn and Douglas 1982, Ostermann-Kelm et al. 2008, Hall et al. 2018). Effects can be exacerbated if trampling of vegetation and soil compaction occur near water sources, which are typically scarce in desert ecosystems (Weaver 1974, Tiller 1997). In the Mojave Desert, feral burros have increased in numbers and affect fragile desert plant communities, reducing forage availability for wildlife and domestic livestock (Bastian et al. 1999, Abella 2008). Feral burros also seek forage and water near human habitation, which brings them into conflict with humans, including vehicular collisions.

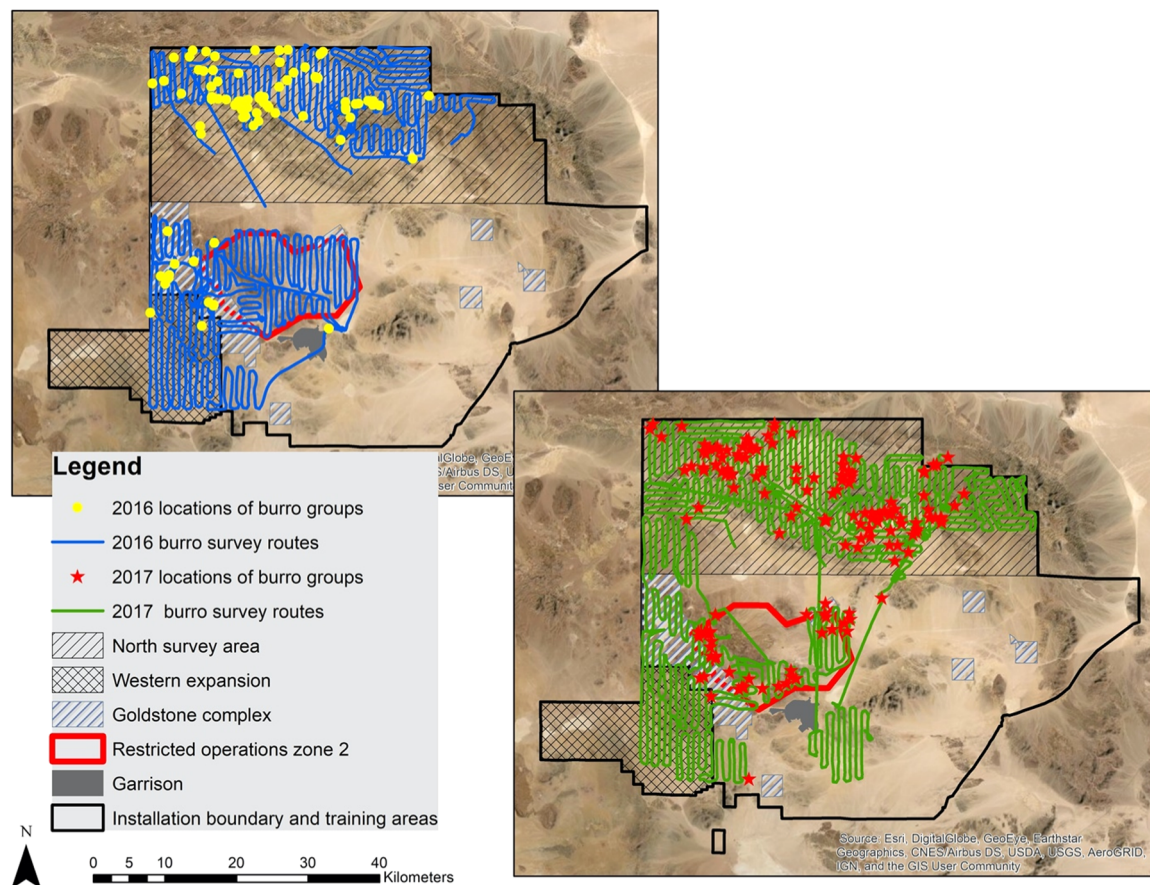
Because of the expense of managing feral equid populations in the United States and the effect they can have on western rangelands, controlling populations has become a management agency priority (BLM 2020). Developing, modeling, and evaluating an effective control strategy requires information on abundance and the sensitivity of population growth rate to changes in demographic rates. Congressional actions subsequent to the initial passing of the WFRHBA prohibit lethal control of feral equids; therefore, alternative non-lethal strategies for controlling overabundant populations must be explored (Norris 2018). Fertility-control vaccines (e.g., immunocontraceptives) have been infrequently used on BLM-managed lands to reduce population growth. The porcine zona pellucida (PZP) vaccine ZonaStat-H is an Environmental Protection Agency-approved immunocontraceptive that has been used to reduce fecundity in equids (NRC 2013, Roelle et al. 2017), and is considered a potential non-lethal alternative for population control (Fonner and Bohara 2017).

Our objectives were to estimate demographic rates and abundance of feral burros at the Fort Irwin National Training Center (NTC), California, USA. We then used matrix population models to simulate the practicality and efficacy of fertility reduction using PZP immunocontraception to reduce burro abundance.

## STUDY AREA

The NTC is a military training base located in the Mojave Desert approximately 60 km northeast of Barstow, California. The NTC encompasses 3,055 km<sup>2</sup> and is divided into 3 main regions: the garrison, the National Aeronautics and Space Administration Goldstone Deep Space Communication Complex (Goldstone Complex), and down-range training areas (Fig. 1). The garrison is a highly developed area with shade, irrigation, and sewage treatment ponds that covers 18 km<sup>2</sup> and is home to >8,000 people. West of the garrison is the Goldstone Complex, which has 3 active space antenna complexes with shade, forage, and water available to burros (Fig. 1). There are 2 large playas that provide an ephemeral source of water after rains, but there are no springs on the Goldstone Complex. There are also 8 springs near the garrison or down-range that have water for at least part of the year and multiple ephemeral playas that retain rainwater in the wet season and after summer monsoon rains.

Part of the down-range training areas located north and east of the garrison is relatively undisturbed and supports land-cover types typical of the Mojave Desert (Fig. 1). Creosote bush (*Larrea tridentata*)-white bursage (*Ambrosia dumosa*) desert scrub, and mid-elevation mixed desert scrub containing blackbrush (*Coleogyne ramosissima*), California buckwheat (*Eriogonum fasciculatum*), and Nevada ephedra (*Ephedra nevadensis*) were the dominant vegetation types (Thomas et al. 2018). Other mammalian fauna on base included mule deer (*Odocoileus hemionus*), desert bighorn sheep (*Ovis canadensis mexicana*), coyotes (*Canis latrans*), and black-tailed jackrabbits (*Lepus californicus*). The terrain is composed of alluvial valleys punctuated by rugged desert



**Figure 1.** Areas surveyed for feral burros, Fort Irwin National Training Center (NTC), California, USA, 2016–2017.

mountain ranges (145–1,875 m). Average daily high temperatures ranged from 40°C in July to 15°C in December and the average daily low temperatures ranged from 22°C in July to 1°C in December (Western Regional Climate Center 2016). Long-term (1948–2015) mean ( $\pm$ SD) annual precipitation was  $9.42 \pm 4.98$  cm and mean monthly precipitation ranged from 0.17 cm in May to 1.47 cm in January (Western Regional Climate Center 2016).

The NTC was estimated to be inhabited by approximately 1,000 burros (L. M. Aker, Fort Irwin, NTC, personal communication), some of which enter the garrison area and cause a variety of problems. Burros eat and trample vegetation around dwellings, defecate profusely, reduce traffic flow, and cause traffic accidents that damage vehicles and increase risk of personal injury. Burros also hinder base operations and military training. As a result, the Directorate of Public Works, Cultural and Natural Resources Division of the NTC was interested in reducing the abundance of burros using non-lethal methods. To address these objectives, we studied the burro population from August 2015 to April 2017.

## METHODS

### Capture and Handling

From August 2015 to July 2016, we captured 14 female burros using corral traps and 13 females by ground darting.

We darted these latter females from a vehicle using 3–4 mg of etorphine hydrochloride and 200 mg of xylazine, which we reversed with 150–200 mg of naltrexone and 400 mg of tolazoline. We freeze-branded captured burros with a unique identification number on each side of the rump using liquid nitrogen and numbered metal irons (Householder et al. 1999). We aged females trapped in corrals based on tooth eruption and wear and determined pregnancy status with a portable ultrasound. We fitted 10 females with global positioning system (GPS) collars programmed to record hourly locations (TGW-4500-3 store on board; Telonics, Mesa, Arizona, USA) and fitted 13 females with very high frequency (VHF) collars (Telonics MOD-500-2). All collars were equipped with a 6-hour mortality sensor. This study was approved by the New Mexico State University Institutional Animal Care and Use Committee (permit 2015-002).

### PZP Inoculation

Inoculation with a PZP vaccine reduces fertility in female equids (Turner et al. 1996, Ransom et al. 2011). Effective PZP immunocontraception typically requires an initial inoculation with the PZP antigen and an adjuvant to heighten immune response, followed by a booster dose of the vaccine within 1 month of the primer dose. This results in reduced fertility in the next reproductive year, with annual booster shots necessary to continue fertility suppression (Nuñez 2018). Without

annual boosters, fertility often returns to pretreatment levels in the following breeding season (Turner et al. 1996, Turner and Kirkpatrick 2002); however, following multiple consecutive boosters (e.g.,  $\geq 4$  doses), return to pretreatment fertility may be delayed (Kirkpatrick and Turner 2002, Nuñez et al. 2017).

We inoculated all captured females at the time of capture with liquid PZP vaccine (ZonaStat, Science and Conservation Center, Billings, MT, USA). They received an initial inoculation of 0.5 ml of Freund's Modified Adjuvant with 0.5 ml of PZP antigen administered via intramuscular injection in the hindquarters. The 2-week and annual booster shots consisted of 0.5 ml of Freund's Incomplete Adjuvant and 0.5 ml of PZP antigen. We held corral-trapped females until they received their 2-week booster of PZP vaccine, then we released them. We released darted females at their point of capture. We attempted to administer the 2-week booster to ground-darted females and annual boosters to all females by darting them from a vehicle with barbless darts. We used radio-telemetry to help locate the animals.

### Aerial Surveys

We used the recently developed and validated double-observer-sightability ( $M_{DS}$ ) aerial survey method to estimate feral burro abundance, which enabled us to account for burro detectability in relation to behavioral and environmental features (model  $M_D$  of Griffin et al. 2013, Lubow and Ransom 2016). This hybrid method combines features of traditional double-observer surveys (Caughley and Grice 1982, Potvin et al. 2004) with traditional sightability survey methodologies (Samuel et al. 1987, Unsworth et al. 1999, Gilbert and Moeller 2008, McIntosh et al. 2009), thereby reducing the limitations of each of these simpler and less reliable methods (Griffin et al. 2013). Because of flight restrictions, we conducted helicopter surveys across 32.5% of the NTC (992 km<sup>2</sup>) in March 2016 and 41.2% of the NTC (1,257 km<sup>2</sup>) in February 2017 (Fig. 1). We predetermined the flight plan to ensure complete coverage of the allowable survey area, with transects spaced at 0.8-km intervals. We subdivided the area into survey units that we searched visually, then we searched them again with VHF telemetry to ensure that we could relocate any radio-collared burros missed during the visual search as soon as possible (typically within ~30 min of having been missed during the visual search). The helicopter was a model Bell 206L4 (Bell Aircraft, Buffalo, NY, USA) with the doors removed to improve visibility. The visual search used a ground speed of 100–110 km/hour (55–60 knots), approximately 75–105 m above ground level.

During the visual search, 3 observers and the pilot independently searched for burros. One observer was in the front seat adjacent to the pilot and the others were in the rear seats. The front-seat observer oversaw the flight plan and checked for radio-collared animals after completion of the surveys in each survey unit. We combined any burros seen by the pilot with the front-seat observer's observations. The rear-seat observers primarily were restricted to seeing burro groups

out the sides of the aircraft and were not hindered by conducting other activities, except that 1 rear-seat observer recorded data on a paper data form and the other used a handheld GPS unit (GPSmap 76CSx, Garmin Ltd., Olathe, KS, USA) to record waypoints close to the locations where the crew detected burros. The rear-seat observers also switched seats among flights within the survey so that each spent roughly equal time on the same side as the front observer. To ensure all observations were independent, none of the survey crew alerted another to burros he or she detected until the rear seat of the helicopter was well past the group of burros (Quang and Becker 1999). The crew then noted which observers detected the burros—front (either pilot or observer), left rear, right rear, or both—and then circled back to obtain information on group size and age composition, vegetation type, percent vegetative cover, distance from the transect to the burro group (in 100-m increments), lighting, and burro activity at the time of initial observation. Upon completion of a survey unit, the survey crew relocated unobserved groups via radio-telemetry to determine the same set of covariate data, except that they determined distance from the group to the nearest transect using a geographic information system (GIS) based on the GPS location of the relocated group.

Our analytical approach generally followed methods presented previously (Griffin et al. 2013, Schoenecker and Lubow 2015, Lubow and Ransom 2016). Based on *a priori* expectations, we included a parameter for distance (from the group to the helicopter) in all models after finding overwhelming support (second-order Akaike's Information Criterion corrected for small sample size [ $AIC_c$ ] evidence ratio >49) for it in preliminary analyses. We also omitted models without an effect for back-seat observers (either common or individual) because of overwhelming support ( $AIC_c$  evidence ratio >8,200) for some effect of position. We also considered *a priori* that the following 6 effects were likely to influence the probability of a group of burros being observed: 1) group size, 2) activity (still or moving), 3) lighting (high contrast vs. shade or flat), 4) observations on the pilot's side (for front-seat sighting probability only), 5) primary front-seat observer identity (1 parameter), and 6) either a single parameter for position (front or rear seat) or 2 parameters identifying individual back-seat observers (both included in a model without a position effect or both excluded with a common position effect). We created a set of models for all combinations of the 6 effects listed above resulting in  $2^6 = 64$  models, and determined  $AIC_c$  scores and model weights for each model (Burnham and Anderson 2002). We computed abundance estimates from each model and used  $AIC_c$ -weighted model averaging to account for model selection uncertainty, resulting in a single estimate of abundance and uncertainty for each survey and survey unit (Table S1, available online in Supporting Information).

We fit  $M_{DS}$  models to the pooled observations made in 2016 and 2017 for the purpose of estimating sighting probability, although we computed abundance estimates separately for the 2 surveys. We fit  $M_{DS}$  models only to



burros observed by the survey crew without the use of radio-collars. Then we estimated abundance after setting sighting probability to 1 for all groups containing  $\geq 1$  radio-collared burros (regardless of whether they were observed during the unaided portion of the survey). In other words, we added the number of burros comprising groups with  $\geq 1$  radio-collar to the estimated number of burros based on observations of unmarked groups to derive the total estimate.

### Demographic Rates

We derived demographic rates and used them to model abundance of female burros at the NTC. We estimated survival of radio-collared females from August 2015 to April 2017 with Cox proportional hazards models (Cox 1972) in R 3.6.2 (R Development Core Team 2019) using the survival package (Therneau 2015) and calculated fecundity as the proportion of adult females with foals observed between July and October. We also surveyed peer-reviewed publications for survival and fecundity data from burro populations in arid environments (Table S2, available online in Supporting Information). To identify reproductive rates that best represented burro populations on arid lands, we included only studies that reported fecundity determined by observing foals with mothers or by evidence of lactation, and only those derived from observations of  $\geq 4$  females (Table S2). We calculated the mean and variance of survival and fecundity estimates across multiple populations (i.e., variation around demographic rates was not reported in these studies) and employed these rates in the burro abundance projection models (Table 1).

We compiled fecundity data from peer-reviewed publications for PZP-treated feral equids (i.e., we assumed the efficacy of reducing fertility would be similar in burros and horses). To simulate the projected effects of using PZP vaccine to reduce fertility in the herd, we calculated the mean and variance of these estimates across populations, and used these rates in a separate matrix in the time step following PZP treatment (Tables 1, S2).

### Abundance Projection Models

We developed age-structured matrix models (Caswell 2001) in R 3.6.2 (R Development Core Team 2019) to simulate burro population dynamics under varying PZP-control strategies. We modeled only females because they are the sex that most influences population growth in polygynous species (Geist 1971). We classified females as foal, yearling, young adult (2–3 yr), adult (4–9 yr), and old adult ( $\geq 10$  yr). We ran an elasticity analysis of our demographic matrix using the popbio package (Stubben and Milligan 2007) to determine which demographic parameter contributed most to population growth rate. To derive the initial age distribution, we calculated the mean proportions of foals, yearlings, and adults from burro populations in arid environments (Morgart 1978, Walker and Ohmart 1978, Seegmiller and Ohmart 1981, Rudman 1990). The mean foal:yearling:adult ratio was 17:14:69. We used this ratio to assign numbers of females to each age within age classes (i.e., based on our estimate of the number of females at the

NTC in 2017) using a truncated normal distribution (truncated at 0 and 11) that yielded a similar age structure. This was the estimated starting abundance and age structure used in our simulations.

Although burros are polyestrous and can breed throughout the year (Perryman and Muchlinski 1987, Grindler et al. 2006), they typically exhibit a defined breeding season (Norment and Douglas 1977, Morgart 1978, Ruffner and Carothers 1982, NRC 2013). In the southwest United States, breeding peaks from April through July (Moehlman 1974, Norment and Douglas 1977, Ruffner and Carothers 1982). Burro gestation is about 12 months (Moehlman 1974, Johnson et al. 1987), so the model time step was 1 year with reproductive events effectively occurring in spring-summer of each year when foals enter the modeled population. Female burros can breed in their second year (Woodward 1976, Morgart 1978, Ruffner and Carothers 1982) so we set the minimum age of reproduction at 2 years, and thus, females birth their first foal in their third year. Fecundity can remain high beyond 10 years (Ruffner and Carothers 1982, Johnson et al. 1987), so we did not include reproductive senescence in the models. Twinning is rare, and when it occurs, a second foal usually does not survive (Ransom et al. 2016), so we set the maximum number of foals that could be produced by a female in a year to 1. Although burros can live to  $\geq 15$  years (Woodward 1976, Morgart 1978, Ruffner and Carothers 1982), populations typically have very few females  $>10$  years (Woodward 1976, Seegmiller 1977, Johnson et al. 1987), so we assigned a survival of 0.50 to adults  $\geq 10$  years of age. We would expect higher variability in survival of older adults ( $\geq 10$  yr) than prime-aged adults, so we assigned the same variance for foal survival at the NTC to survival of females  $\geq 10$  years old (Table 1).

**Table 1.** Age class-specific demographic rates obtained from literature used in feral burro abundance projection models.

Demographic rate	Age class	<i>n</i> <sup>a</sup>	$\bar{x}$	Variance
Survival <sup>b</sup>	foal	7	0.90	0.016
	yearling	5	0.98	0.001
	2–9 yr	6	0.96	0.003
	$\geq 10$ yr	na	0.50	0.016
Fecundity				
	Unvaccinated <sup>c</sup>			
	2–3 yr	5	0.17	0.039
	$\geq 4$ yr	6	0.58	0.137
PZP vaccinated <sup>d</sup>	all adults	6	0.07	0.004

<sup>a</sup> Number of populations or studies from which we calculated means; na = assigned survival.

<sup>b</sup> Means calculated from Moehlman (1974), Ohmart et al. (1975), Morgart (1978), Seegmiller and Ohmart (1981), Rudman (1990), Choquenot (1991), and this study; we assigned mean survival rates for  $\geq 10$ -year-old females and assigned survival variance from foals at NTC to all  $\geq 10$ -year-old survivals.

<sup>c</sup> Means calculated from Moehlman (1974), Ruffner and Carothers (1982), Johnson et al. (1987), Wolfe et al. (1989), and NTC (unpublished data).

<sup>d</sup> We calculated porcine zona pellucida (PZP) vaccinated fecundity rates from Turner et al. (1996, 2007), Turner and Kirkpatrick (2002), Kirkpatrick and Turner (2008), and Ransom et al. (2011).

In each age class, we determined the number of foals produced and the number of females surviving according to the following Lefkovitch matrix (Lefkovitch 1965):

$$\begin{bmatrix} n_{\text{foal}} \\ n_{\text{yrl}} \\ n_{\text{YA}} \\ n_{\text{A}} \\ n_{\text{OA}} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & S_{\text{A}} F_{\text{YA}} & S_{\text{A}} F_{\text{A}} & S_{\text{OA}} F_{\text{A}} \\ S_{\text{foal}} & 0 & 0 & 0 & 0 \\ 0 & S_{\text{yrl}} & P_{\text{YA}} & 0 & 0 \\ 0 & 0 & G_{\text{YA}} & P_{\text{A}} & 0 \\ 0 & 0 & 0 & G_{\text{A}} & S_{\text{OA}} \end{bmatrix} \times \begin{bmatrix} n_{\text{foal}} \\ n_{\text{yrl}} \\ n_{\text{YA}} \\ n_{\text{A}} \\ n_{\text{OA}} \end{bmatrix}_t$$

Here,  $n_{\text{age}}$  is the age-specific number of females (yrl = yearling; YA = young adult; A = adult; OA = old adult),  $t$  is time step in years,  $F_{\text{age}}$  and  $S_{\text{age}}$  are age-specific fecundity and survival, respectively,  $P_{\text{age}}$  is probability of surviving and staying within the same age class, and  $G_{\text{age}}$  is probability of surviving and transitioning into the next age class (Crouse et al. 1987). This matrix represents the basic structure used in all model sets, and fecundity varies depending on whether a female has received PZP treatment (see descriptions of model sets below). We determined sex of foals by sampling from a binomial distribution with an equal probability of producing a male or female. We included all demographic rates and proportions of PZP-treated females in the models as stochastic variables by sampling from a beta distribution using moment matching, and determined the number of surviving females by sampling from a binomial distribution. This allowed us to simulate demographic variation by resampling values at each time step requiring the generation of new matrices for each year. We were not able to model the effects of environmental variation or burro density on burro demographic rates because this type of data was unavailable for burros. We ran models for 15 years with 1,000 iterations, with the mean abundance ( $\pm 95\%$  CI) of females estimated at each time step. We examined the change in female abundance (%) and absolute female abundance after 15 years.

In a free-ranging population, capturing and inoculating a large proportion of females or vaccinating them remotely with darts can be difficult, so delivery rates of  $<100\%$  are expected. We simulated PZP control by varying the proportion of females receiving initial inoculations (i.e., 0.25, 0.50, 0.75, and 0.90 of the entire female population) and annual boosters (i.e., 0.25, 0.50, 0.75, and 0.90 of females treated in the previous year). We assigned a variance of 0.01 to all of these proportions and included these terms in the models as stochastic variables. We simulated round-ups and corralling events by assuming that all females that received an initial inoculation also received their 2-week booster. We also assumed that PZP vaccine effectiveness was the same in booster-dose years as in initial years, and we made a conservative assumption that each PZP vaccine dose only conferred 1 year of effectiveness. We then simulated the following PZP-control strategies: 1 4-year course (initial inoculation + 3 annual boosters), 1 10-year course (initial inoculation + 9 annual boosters), and 3 3-year courses (initial inoculation + 2 annual boosters, then repeated twice; 9 years of treatment). We tested a strategy of repeated courses (i.e., strategy 3) because low delivery rates of PZP vaccination will

result in a rapid decline in the proportion of vaccinated females in the population over time, such that it would be unlikely that the PZP treatment would be successful in curbing population growth.

## RESULTS

### Aerial Surveys and Abundance Estimates

The first aerial survey occurred from 4–6 March 2016 but ended prematurely because of high winds (Fig. 1). Estimated abundance for the areas surveyed in 2016, based on the  $M_{\text{DS}}$  models, was 460 (95% CI = 367–644) burros (Table 2). A second, complete aerial survey occurred from 2–4 February 2017. The 2017 abundance estimate, also based on the  $M_{\text{DS}}$  models, was 690 (618–752) burros (Table 2). The latter estimate had a substantially lower coefficient of variation than the 2016 survey (2016 = 14.9%, 2017 = 6.6%) indicating higher precision in the estimate, which was also reflected in a lower estimated proportion of groups missed in 2017 (2016 = 26.8%, 2017 = 13.3%; Table 2). We found evidence of long-distance movements of burros across years; there were  $>2.5$  times as many burros estimated in the Goldstone Complex in 2017 than in 2016 (2016 = 45, 2017 = 117) and  $>20\%$  more estimated in the northern reaches of the survey area (2016 = 409, 2017 = 495). Foal:adult ratios (foals/100 adults) were higher in 2017 compared with 2016 (2016 = 12.0, 2017 = 16.0), as was the estimated number of foals (2016 = 49, 2017 = 85). We used only the 2017 abundance estimate as the basis for our simulations because the survey was incomplete in 2016 and precision was higher in 2017.

Estimated sighting probability ( $\hat{p}$ ) was low for many observations, despite narrow transects and highly skilled observers. For example,  $\hat{p}$  for all observers was  $<0.8$  for 77.6% of the observations and  $<0.5$  for 36.0% of burro groups. Estimated  $\hat{p}$  (AIC<sub>c</sub> model-weighted average) for the combined observers ranged across burro groups from 0.189–0.977. For front-seat observers, independent  $\hat{p}$  ranged from 0.196–0.873 and for rear-seat observers it ranged from 0.438–0.910 for groups available to them (i.e., excluding groups on the centerline, directly beneath the aircraft, which had  $\hat{p} = 0$  for rear-seat observers).

The  $M_{\text{DS}}$  modeling also provided insight into the importance of various conditions to sighting probability. The effect of burro group size received the most support (92.1% AIC<sub>c</sub> model weight; Burnham and Anderson 2002) and was substantial in magnitude (Tables 3, S1). There was moderate support for the effects of lighting (68.2%) and average rear-seat observer position (66.1%, vs. individual effects for rear-seat observers). Support was weak ( $<35\%$ ) for the other effects evaluated, including group activity, pilot side, and specific individual observers. Burro groups that were on the pilot's side, smaller, in flat lighting, or at a greater distance were less visible (Tables 3, S1). Aside from groups on the centerline, which were not visible to rear-seat observers, other groups were more visible under a given set of conditions for each rear-seat observer than for the front-seat team of pilot and observer (Tables 3, S1).

**Table 2.** Estimated feral burro abundance, lower (LCL) and upper (UCL) 95% confidence limits, standard error (SE), and coefficient of variation (CV) from 2016 and 2017 helicopter surveys at the Fort Irwin National Training Center, California, USA.

Area <sup>a</sup>	Age class	Estimated number of burros	95% LCL	95% UCL	SE	CV (%)	Number of burros observed	% missed	Number of groups	Group size ( $\bar{x}$ )	Observed foals/100 adults
2016											
ROZ 2 <sup>b</sup>	Total										
Goldstone	Total	45	22	71	12.5	28.0	34	23.8	13	3.3	7.2
WE	Total	7	2	11	2.2	31.3	6	14.1	2	2.8	0.0
North	Total	409	322	590	63.8	15.6	297	27.3	90	4.5	12.8
All areas	Foals	49	35	71	8.4	17.1					
	Adults	411	327	585	62.1	15.1					
	Total	460	367	644	68.8	14.9	337	26.8	106	4.3	12.0
2017											
ROZ 2	Foals	10	7	14	1.4	14.4					
	Adults	63	50	77	6.9	10.9					
	Total	73	58	90	7.9	10.9	65	10.5	16	4.4	15.8
Goldstone	Foals	20	10	25	3.6	17.9					
	Adults	97	64	112	12.6	12.9					
	Total	117	79	139	14.9	12.7	99	15.6	27	4.4	20.5
WE	Foals	0	0	0							
	Adults	5	0	5	1.6	31.4					
	Total	5	0	5	1.6	31.4	5	0.0	1	5.0	0.0
North	Foals	65	54	78	6.3	9.6					
	Adults	429	373	480	28.7	6.7					
	Total	495 <sup>c</sup>	430	554	33.3	6.7	429	13.3	136	3.6	15.2
All areas	Foals	95	82	108	7.0	7.3					
	Adults	594	531	646	33.1	5.6					
	Total	690	618	752	38.1	5.5	598	13.3	180	3.8	16.0

<sup>a</sup> Roz 2 = restricted operations zone 2 and vicinity; Goldstone = Goldstone complex and vicinity; WE = western expansion; North = north survey area.

<sup>b</sup> No burros observed in this area during 2016 survey.

<sup>c</sup> An estimated 16 burros were outside of the original planned survey area based on observations of 15 burros in 3 groups: a group of 8 seen enroute to the survey, a group of 3 located by radio-collar 0.8 km outside the planned survey area, and a group of 4 observed while investigating the radio-collared group.

We suspected lack of geographic closure of the survey area given the absence of sufficient natural and artificial deterrents to burro movement. The presence of radio-collars

**Table 3.** Effects of observers and sighting condition covariates on estimated percent of feral burro groups seen for front and rear observers from helicopter surveys, Fort Irwin National Training Center, California, USA, 2016–2017.

Variations in survey conditions	Sighting probability (estimated % seen)		
	Front observer	Back observer	Combined observers
Baseline <sup>a</sup>	30.3*	57.9*	70.7
Group size ( $n=1$ )	23.6	49.2	61.2
Active group	28.6	55.9	68.5
Distance (0–100 m)	48.9	75.3	87.4
High contrast lighting	40.6	68.6	81.3
Burros on pilot side	28.8	57.9*	70.0
Front observer (JC)	43.1	57.9*	76.1
Back observer (TK)	30.3*	59.3	71.7
Back observer (CR)	30.3*	56.5	69.7

<sup>a</sup> Baseline case (\*) is for observers in the indicated seat. We provide the baseline for burros on the primary observer's side (not the pilot's side), with observer PG in the front seat, a group size of 4 burros (the median value), stationary group, at a distance of 200–300 m (the most commonly observed value), low contrast lighting, and the average back seat observer effect. Other cases show the effect of changing the value of 1 covariate at a time, as indicated. Estimated percent seen for each row should be compared to the baseline (first row) to see the effect of the change in condition. Baseline values are shown with an asterisk whenever they occur. Estimates are calculated from the weighted average across all 64 models.

provided an opportunity to examine the extent to which the survey area encompassed a closed population of burros. Although the number of radio-collars was insufficient to provide precise abundance estimates comparable to the  $M_{DS}$  estimates, they can be used to get a rough indication of the extent to which the burros within the survey area are part of a larger, closed population. We used radio-collared burros as marked individuals ( $n_{2016}=25$ ,  $n_{2017}=21$ ) as input to Chapman's modification of the Lincoln-Peterson estimator (Chapman 1951) to generate an estimate of the larger population of which the radio-collared burros were a part:  $N_{2016}=975$  (95% CI=649–1,467) and  $N_{2017}=1,882$  (1,180–3,000) burros. Treating these as 2 independent estimates of population size (assuming the true population did not appreciably change in size between the surveys) yields a mean estimate of 1,428 (860–2,373).

The Chapman estimates are far less reliable than the  $M_{DS}$  estimates because of the small sample size (number of radio-collared burros), and the unjustifiable assumption that all groups of burros have equal sighting probability. We located 5 of the 21 functional radio-collars (24%) during the 2017 survey outside the study area, and did not hear 3 others, which could mean they had failed or that those burros had migrated even farther outside the study area. These observations and the data suggest that the total population may be much larger than the burros present in the survey area at the time of the surveys (1.25–3.4 times larger than the 2017  $M_{DS}$  estimate for only the surveyed area, using the 95% CI presented above).

### Demographic and PZP Vaccination Delivery Rates

Mean survival ( $\pm$ SE) of female burros at the NTC was  $0.667 \pm 0.192$  for foals ( $n=6$ ) and  $0.869 \pm 0.071$  for adults ( $n=25$ ), and fecundity was 0.20 foals/young adult female ( $n=5$ ) and 0.70 foals/adult and old adult female ( $n=20$ ; Table S2). Mean ( $\pm$ variance) survival for burros across populations on arid lands (i.e., including survival rates from the NTC) was  $0.90 \pm 0.016$  for foals ( $n=7$  populations),  $0.98 \pm 0.001$  for yearlings ( $n=5$  populations), and  $0.96 \pm 0.003$  for adults 2–9 years old ( $n=6$  populations; Tables 1, S2). Mean ( $\pm$ variance) fecundity of burros across populations on arid lands (i.e., including fecundity from the NTC) was 0.17 foals/young adult female ( $n=5$  populations) and 0.58 foals/adult and old adult female ( $n=6$  populations; Tables 1, S2).

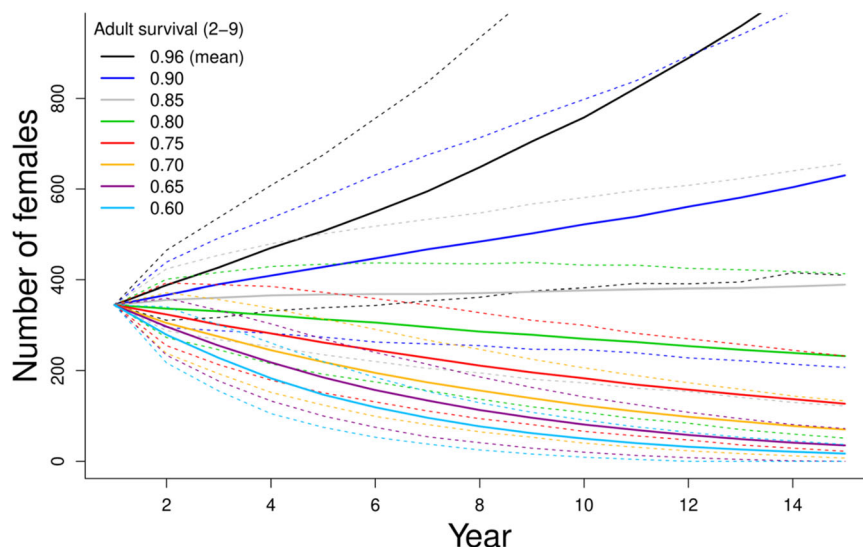
We administered an initial inoculation of PZP to 27 females at the NTC. All adult females that were captured in corrals received their 2-week booster, whereas we were able to administer the 2-week booster to only 67% of the females initially captured via ground darting ( $n=12$ ; 1 animal died <2 weeks after capture). Additionally, we were able to administer the annual booster to only 67% of inoculated females that were scheduled to receive an annual booster within the study period ( $n=18$ ), despite having marked and radio-collared animals. Mean fecundity ( $\pm$ variance) of PZP-treated feral burros and horses calculated from the literature was  $0.07 \pm 0.004$ , and thus, we applied this rate to vaccinated females in our models (Tables 1, S2).

### Abundance Projections

The initial female abundance in our models was set at 345 based on a population estimate of 690 burros in 2017 (Table 2) and assuming 50% females. Elasticity analysis

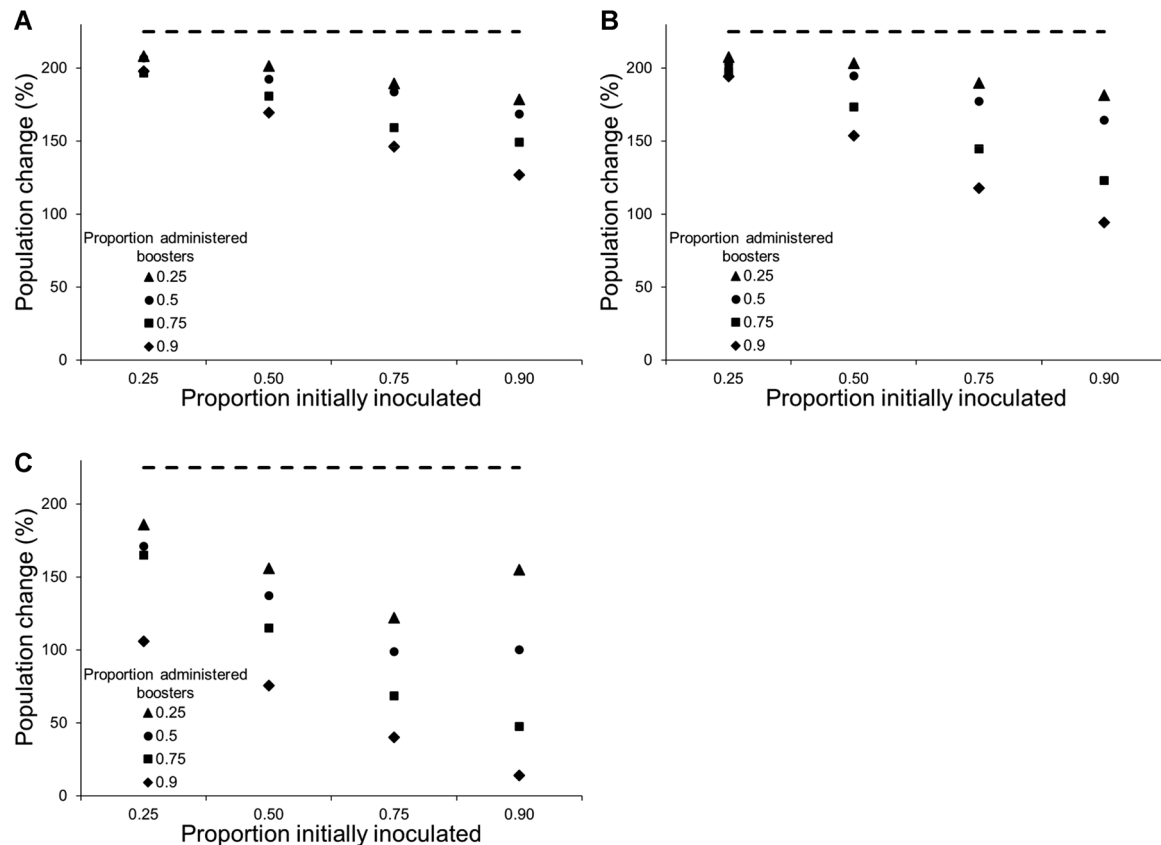
estimated that adult survival contributes 55% to population growth rate, whereas fecundity contributes only 16%. Therefore, we conducted a numerical sensitivity analysis by running models where we reduced adult survival from the mean of 0.96 to the survival rate required to extirpate females (i.e., we held fecundity constant at the mean of 0.17 foals/young adult female and 0.58 foals/adult and old adult female). Models predicted that each decrease in adult survival of 0.05 reduced female abundance by an average of  $45 \pm 4.7\%$  (SD) after 15 years. Abundance shifted from increasing to decreasing at a survival rate  $<0.84$  ( $\bar{x}$  [95% CI] after 15 years = 354 [101–607] females) and females were predicted to become extirpated when survival declined below 0.60 (17 [0–37] females; Fig. 2).

Models projecting burro abundance from demographic rates derived from populations on arid lands, predicted a positive population growth rate ( $\lambda=1.088$ ); female abundance nearly tripled to 1,120 [410–1,830] females over 15 years (Fig. 2). When compared with projections that had no fertility control, PZP treatment reduced female abundance at year 15 by 67–76% (4-year course), 68–79% (10-year course), and 70–88% (3 3-year courses); however, none of these PZP-control strategies were able to prevent population growth (Fig. 3). The lowest female abundance that could be achieved after 15 years was 393 [146–640] with 3 3-year courses of PZP control, where 90% of females were inoculated and received annual boosters (Fig. 3). But we have seen in this study, and in other studies (e.g., Kirkpatrick and Turner 2008), that with an initial abundance of 345 animals, inoculation of 75% of females followed by an annual booster rate of 75% may be more attainable, and this rate of delivery resulted in a 68–159% increase in female abundance over 15 years for the 3 strategies evaluated (Fig. 3).



**Figure 2.** Mean abundance (solid lines) and 95% confidence limits (dashed lines) of female feral burros projected from matrix population models. Mean survival is calculated across burro populations in arid environments and the other survival rates represent those simulated in our numerical sensitivity analyses. Fecundity is held constant at the mean across burro populations in arid environments: 0.17 foals/2–3-year-old young adult female and 0.58 foals/older adult and old adult female.





**Figure 3.** Changes in population size (%) of female feral burros based on simulations over a 15-year period with porcine zona pellucida (PZP) immunocontraception control for 1 4-year course (initial inoculation + 3 annual boosters; A), 1 10-year course (initial inoculation + 9 annual boosters; B), and 3 3-year courses (initial inoculation + 2 annual boosters, then repeated twice; 9 years of treatment; C). Panels show the proportion of females initially inoculated and the proportion of inoculated females administered annual boosters. Dashed line represents population change without PZP immunocontraception control.

## DISCUSSION

Reliable estimates of abundance and demographic rates are required to assess the dynamics of an animal population, and such data are required to better manage feral burro populations across North America (NRC 2013). We used a hybrid double-observer-sightability aerial survey method to estimate feral burro abundance at the NTC. This method allowed us to account for burro detectability in relation to behavioral and environmental features, yielding more precise estimates of abundance. We conducted simulation modeling of the NTC burro herd using demographic rates reported from burro populations in arid environments, which included rates we estimated at the NTC. Our abundance estimates indicated a significant burro herd size at the NTC, and our modeling predicted significant growth over the next 15 years. As a potential strategy to control burro abundance, we conducted further simulation modeling to examine the efficacy of PZP immunocontraception to reduce female burro fertility. These results indicated that the use of the current formulation of PZP immunocontraception on its own is not a viable method for controlling burro population growth.

Our modeling indicated that to achieve reasonable reductions in burro population growth, longer-term immunocontraception strategies with high vaccine delivery rates are necessary. Our models predicted that 90% initial inoculation and booster

delivery rates for 10 years or 75% initial inoculation and booster delivery rates for 3 3-year courses (i.e., with multiple corraling events) were required to prevent the simulated population from doubling in 15 years. Simulations of fertility control in other ungulates predicted a stable population only when >75% of females are treated (Hobbs et al. 2000, Gross 2000). It was reported that reductions in white-tailed deer (*Odocoileus virginianus*) densities with contraceptives were possible only if ≥90% of the females were treated for several consecutive years (Raiho et al. 2015). As an example of the intensity of PZP treatment required to affect population decline, all female feral horses on Assateague Island in Maryland, USA, were inoculated for 3 years once sexually mature, then inoculations were withheld from each female until a foal was produced, after which females were inoculated indefinitely thereafter (Ballou et al. 2008). An individual-based stochastic population model was then used to project a 13% annual population decline over 50 years (Ballou et al. 2008). Our results and these studies highlight the intensive effort and significant resources potentially required to implement an effective fertility-control strategy for ungulate populations.

Although PZP control agents can significantly reduce fecundity (Rutberg and Naugle 2008), the current Environmental Protection Agency-registered formulation of

the vaccine (ZonaStat-H) requires a booster shot within 1 month of initial inoculation and annual boosters to maintain infertility in females. Therefore, it is highly unlikely that a sufficient proportion of females could be repeatedly vaccinated for effective control. Factors such as the size of the area a population uses, topography, weather conditions, species targeted for control, animal temperament, and available resources all lead to high variability in vaccination delivery rates (Sharma and Hinds 2012, NRC 2013, Naugle and Grams 2013). There were also logistical issues in administering vaccinations in our study area (including limited access to military training sites) even though we had personnel working full time attempting to dart marked and radio-collared individuals that were relatively habituated to vehicles (i.e., our delivery success rate was only 67% for both the 2-week and annual boosters). This highlights the potential difficulties in tracking and administering booster shots to individuals that are already inoculated to ensure continued fertility suppression for an adequate proportion of the population. Initially vaccinating uncollared animals and subsequently locating them to administer booster shots would be even more difficult, especially if they inhabited more remote or roadless areas. Other investigators have reported similar difficulties in administering immunoconceptive vaccinations (Kirkpatrick and Turner 2008, Rutberg et al. 2013). Delivery of immunoconceptives is currently a major limitation to their effective use for controlling fertility of feral equids (Swegen and Aitken 2014).

Fertility control, especially PZP immunoconception, has shown promise as a non-lethal alternative for controlling overabundant ungulate populations that are small and occupy geographically closed areas (Kirkpatrick et al. 1997, Cooper and Larsen 2006, Kane 2018). For example, an insular feral horse population in Maryland that was growing 8% annually prior to PZP treatment ceased to grow during the first 10 years of treatment and then declined by 13% annually over the next 4 years of treatment (Kirkpatrick and Turner 2008). The PZP-treated insular populations of white-tailed deer in South Carolina and New York, USA, demonstrated annual reductions in density of 11% and 10%, respectively (Rutberg and Naugle 2008, Rutberg et al. 2013). The success in controlling these geographically closed populations (i.e., only bridges connect them to the mainland or adjacent islands) was at least in part, due to the small areas they occupy (910–16,000 ha). In contrast, the NTC burros occupy more than 750,000 ha and constitute only a portion of a larger metapopulation (NRC 2013) that occupies other protected areas (e.g., Mojave National Preserve, Death Valley National Park, China Lakes Naval Weapons Station) and BLM lands (Slate Range Herd Area, Panamint Herd Area), and this is typical of most feral equids in the western United States.

Our simulations predicted that logistically plausible PZP immunoconception strategies alone were insufficient to reduce burro numbers, even without considering the likelihood of immigration from other managed areas. The Chapman estimator suggested that the burros surveyed

are part of a substantially larger population. Our simulations assumed a closed population, but there is no effective fence or natural barrier to prevent movement of burros into or out of the NTC. If populations are not geographically closed, the efficacy of any control strategy would be compromised.

The logistics of delivering booster shots to free-ranging animals prevent many immunoconceptive compounds from being viable methods for controlling ungulate populations. Immunoconception formulations that can ensure longer-term infertility in females from a single inoculation event could significantly increase the practicality and efficacy of fertility agents (NRC 2013). Several vaccines have shown promise in causing multi-year infertility in equids from a single dose (Kane 2018). Despite the potential of single-dose immunoconceptive formulations, high adult survival in ungulates diminishes the utility of fertility agents for controlling populations in the absence of other methods of reducing herd sizes (e.g., animal removal operations). Our elasticity analysis indicated that adult survival influenced burro population dynamics much more strongly than fecundity, so significant reductions in fecundity may not have the capacity to override the influence of high survival on population growth. Indeed, our projected population sizes continued to grow under every PZP-control strategy we evaluated. Hobbs et al. (2000) drew similar conclusions from their population control models of ungulates. In our simulations, populations ceased growth and began declining when annual adult survival rates decreased below 0.84. Other burro populations have adult survival rates  $>0.84$  (Norment and Douglas 1977, Rudman 1990, Choquenot 1991). In contrast, several of the ungulate populations mentioned above where fertility control led to population declines had adult survival rates  $<0.84$  (Rutberg and Naugle 2008, Rutberg et al. 2013). Additionally, higher survival rates have been reported for infertile females (Kirkpatrick and Turner 2007), which could exacerbate the negative influence of high adult survival on reducing population size via fertility control. The high survival and long lifespan of feral equids may limit the value of using short-term fertility control methods to reduce herd size, unless those methods are used as part of a strategy that includes removing animals.

## MANAGEMENT IMPLICATIONS

More robust methods for estimating abundance of feral equids are needed. The high vaccination delivery rates necessary, repeated over many years, and the difficulty in administering PZP immunoconceptives to wide-ranging animals that are part of a large population that is not geographically closed, suggest that reducing burro numbers using only fertility control will be a difficult task. Combining immunoconceptives as part of a strategy that also includes animal removal may slow population growth, but in the absence of barriers to immigration, short-term management actions that have the long-term aim of reducing abundance will most likely be futile.

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