Estimating survival and abundance of the endangered Sonoran pronghorn

CLIMAS Environment and Society Graduate Fellows Program Final Report

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EXECTUTIVE SUMMARY

Large herbivores are in decline around the globe. Understanding the impacts of climate change, human activity, and habitat fragmentation on large herbivore populations is essential to facilitate recovery of endangered species such as the Sonoran pronghorn (*Antilocapra americana sonoriensis*), a subspecies of American antelope unique to the Sonoran Desert. Wildlife managers with limited resources, including the Arizona Game and Fish Department (AZGFD), U.S. Fish and Wildlife Service, U.S. National Park Service, U.S. Air Force, and U.S Marine Corps, face the problem of accurately estimating basic population parameters such as abundance and survival of Sonoran pronghorn. Without quality estimates, managers struggle to accurately assess the effects of climate change, human activity, and habitat fragmentation on Sonoran pronghorn recovery, as well as the efficacy of costly recovery efforts implemented after a year of severe drought in 2002. To address these challenges, I collaborated with AZGFD, one of the main stakeholders in Sonoran pronghorn recovery, to improve estimates of abundance and survival.

Since 1992, AZGFD has led biennial, range-wide aerial surveys to estimate the size of the Sonoran pronghorn populations in the U.S. and Mexico, adjusting for the effect of group size on detection probability with a sightability model. Important parameters such as population growth rate can be calculated from abundance estimates and then related to climatic variables. I assessed the relationship between biennial population growth rate (as caluclated with abudance estaimtes from aerial surveys) and the natural logarithm of biennial precipitation before and after the implementaiton of recovery efforts. Before recovery projects, biennial population growth significantly increased with biennial rainfall. Post recovery projects, population growth was not significantly relatead to rainfall. However, managers are concerned about biased abundance estimates due to the effects of additional variables on detection rate. Given the costs of range-wide aerial surveys, they become an impractical means of surveying all pronghorn in the U.S. as the experimental populations increase in distribution and abundance.

Currently, AZGFD estimates annual survival as the number of radio-collared individuals that survive from one year to the next. This method is biased due to the small sample size and because most

radio-collared individuals were released from the captive breeding pen. Managers have no method to estimate fawn survival.

Given the challenges and limitations posed by the current methods for estimating surival and abundace, the most powerful technique for surveying Sonoran pronghorn in both the U.S. and Mexico may be the combination of noninvasive genetic sampling and capture recapture methods (NGS-CR). In NGS-CR, individuals are captured, marked, and released, and then managers perform additional captures after set time periods. The proportion of marked individuals that are recaptured can be used to estimate the size of the population being sampled. When this process is repeated for two or more years, researchers can estimate individual survival. For NGS-CR, individuals are "captured" by the collection of fecal samples, both opportunistically and at supplemental water and feed stations, and "marked" via the genetic identification of unique individuals from DNA extracted from the collected fecal samples. Analysis of five years of data (2013-2017) estimated fawn survival at 57.2% (95% CI: 40.4% to 72.5%) and adult survival at 81.7% (95% CI: 74.8% to 87.0%). Annual abundance estimates from NGS-CR are more precise than the estimates obtained during range-wide aerial surveys. Although NGS-CR estimates may be biased towards pronghorn utilizing waters and feed stations, this method could be a cost-effective way to expand sampling to include the other Sonoran pronghorn populations.

Next steps include improving the current sightability model, determining whether additional data types can be incorporated into the NGS-CR model, and presenting my findings from the NGS-CR analysis at the next Sonoran Pronghorn Recovery Team meeting. After updating my analysis based on feedback provided by wildlife managers, I will share the R script used for analysis with AZGFD and develop the results into a manuscript for publication, with AZGFD personnel as coauthors. The manuscript will also be included as a chapter in my dissertation.

REPORT

Introduction

Large herbivores are in decline around the globe. Understanding the impacts of climate change, human activity, and habitat fragmentation on large herbivore populations is essential to their conservation and management, especially the recovery of endangered species. The Sonoran pronghorn (Antilocapra americana sonoriensis) has been listed as endangered since 1967 in the United States (32 Federal Register 4001) and since 1994 in Mexico (NOM-059-ECOL-1994). A subspecies of pronghorn unique to the Sonoran Desert, Sonoran pronghorn differ from other subspecies in their small size, distinct cranial features, and lighter pelage (Goldman 1945). Historically, Sonoran pronghorn ranged over 142,450 km² from the Imperial Valley of California and Bahia Kino east to Hermosillo and north to Interstate 10 or Bill Williams River (USFWS 2016). Sonoran pronghorn are currently restricted to less than 12% of their historic habitat, surviving on 17,224 km2 as five geographically isolated populations-three in the United States and two in Mexico (USFWS 2016). In the U.S., the essential, endangered population (the Cabeza population) ranges on 7,122 km2 administered by the Department of Defense and the Department of the Interior, including the Barry M. Goldwater Range (BMGR), Cabeza Prieta National Wildlife Refuge (CPNWR), and Organ Pipe Cactus National Monument (ORPI; USFWS 2010; Figure 1). Through reintroductions to 6,045 km² of historic habitat, two additional nonessential, experimental populations were established in the United States under section 10(j) of the Endangered Species Act (1973): one on Kofa NWR in 2012 (the Kofa population), and one on BMGR-East east of Highway 85 in 2015 (the Sauceda population; USFWS 2016). The Pinacate and Quitovac populations of Sonoran pronghorn, managed by the Comisión Nacional de Áreas Naturales Protegidas (CONANP) and Comisión de Ecología y Desarrollo Sustentable del Estado de Sonora (CEDES), are found on 4,057 km² in northwest Sonora, Mexico across the U.S.-Mexico border from the Cabeza population (USFWS 2016).

Throughout the vast landscapes that comprise their range, Sonoran pronghorn persist at relatively low densities. These areas are also some of the hottest and driest parts of North America, presenting numerous logistical challenges to research and monitoring efforts. Wildlife managers, including the Arizona Game and Fish Department (AZGFD), U.S. Fish and Wildlife Service, U.S. National Park Service, U.S. Air Force, and U.S Marine Corps, thus face the problem of accurately estimating basic population parameters such as survival and abundance with limited resources. Without quality estimates, managers struggle to accurately assess the effects of climate change, human activity, and habitat fragmentation on Sonoran pronghorn recovery, as well as the efficacy of costly recovery efforts implemented after a year of severe drought in 2002. Recovery efforts include a captive breeding program, the irrigation of vegetation in important summer habitat, and the provision of supplemental water and forage at designated stations when range conditions are poor. To address the need of wildlife managers for improved estimates of survival and abundance, I collaborated with AZGFD, one of the main stakeholders in the recovery of Sonoran pronghorn (hereafter, also "pronghorn"). The Arizona Game and Fish Department employs the world's leading experts on Sonoran pronghorn; John Hervert and Jill Bright have almost 50 years of combined experience working with this endangered species. Their knowledge and experience has been invaluable to the recovery of Sonoran pronghorn. The products of this collaboration will be presented to the Sonoran Pronghorn Recovery Team (SPRT), which includes AZGFD, to inform management decisions.

Abundance

Once relatively common throughout their range, Sonoran pronghorn started decreasing in distribution and abundance during the mid- to late-1800s. The U.S. population stabilized at 100 individuals in the 1920s and ranged from 50-100 through the 1980s (USFWS 2016). With the implementation of biennial, range-wide aerial surveys in 1992, 130-282 pronghorn were estimated in the U.S. during the 1990s (USFWS 2002; Figure 2). In 1998, wildlife managers at AZGFD developed the current sighting probability model (also known as a sightability model) on which all population sizes are currently based. This model accounts for imperfect detection of pronghorn during the survey by adjusting for group size, thereby providing a more accurate estimate of abundance (Bright et al. 1999). Managers started conducting biennial, range-wide surveys of the Mexican populations in 2000. In 2007, wildlife managers transitioned to conducting surveys in the U.S. during even years and in Mexico during odd

years due to the extensive time and effort required to successfully plan and implement each survey. Aerial surveys of the Cabeza population generally require 7 days of 3 planes flying twice daily (morning and evening) to cover the entire range. Surveying the two Mexican populations requires 4 days of 3 planes flying twice daily. Typically, the survey plane is a Cessna carrying two observers in addition to the pilot. Occasionally the survey plane is a Supercub carrying a pilot and one observer.

Despite their cost, surveys provide extremely valuable information on abundance. For example, after a year of severe drought in 2002, the U.S. population dropped from 99 in 2000 to a record low of 21 individuals (Bright & Hervert 2005), motivating the implementation of previously planned recovery efforts. Important parameters such as population growth rates can be calculated from abundance estimates and then related to climatic variables. Biennial population growth rate significantly increases with biennial rainfall (Horne et al. 2016), but AZGFD requested that I determine whether this relationship has changed since the implementation of recovery efforts in 2004.

The Arizona Game and Fish Department is also concerned about the limitations of the aerial surveys. Because data were limited during the development of the current sightability model, it describes detection as a function of only one variable: group size. Confidence intervals are fairly large, approximately 20% of the calculated abundance (USFWS 2016). Based on experience, managers believe additional variables, including habitat type, cloud cover, time of day, and observer position in the aircraft, affect the detection rate, contributing to high level of imprecision. As the experimental populations of Sonoran pronghorn increase in distribution and abundance, range-wide aerial surveys become an impractical means of surveying all pronghorn in the U.S. The Arizona Game and Fish Department is thus interested in both an improved sightability model and a more cost-effective method for estimating abundance of Sonoran pronghorn. The combination of noninvasive genetic sampling and capture-recapture methodology (NGS-CR) has been successfully applied to estimating abundance and survival of Sonoran pronghorn (Woodruff et al. 2016). A partnership between the University of Idaho and the University of Arizona, including myself as one of the main collaborators, has collected and analyzed NGS-CR data for the Cabeza population annually from 2013 through 2018. Improvements in

methodologies suggest NGS-CR may be a promising new tool for estimating both abundance and survival of Sonoran pronghorn throughout its range.

Survival

Currently, the Arizona Game and Fish Department estimates annual survival as the number of radio-collared individuals that survive from year t to year t + 1. From 1994 through 2001, survival averaged 80%, with a low of 62% in 1996. In 2002 after a year of severe drought, adult survival was 17% (Bright & Hervert 2005). The latest population viability analyses indicate extinction risk is most sensitive to the survival of adult females (USFWS 2016). Assessing the efficacy of costly recovery efforts and extinction risk thus necessitates accurate estimates of survival. The method AZGFD currently uses to estimate survival is heavily biased due to the small sample size and reliance on radio-collared individuals, most of which have been released from the captive breeding pen. As mentioned above, methodological advances suggest NGS-CR may be a promising tool for accurately estimating abundance and survival of Sonoran pronghorn.

Methods

Abundance: population growth before and after implementation of recovery efforts

I compared biennial rainfall with the biennial population growth rate of the Cabeza population of Sonoran pronghorn (Horne et al. 2016). From 1992-2018, I obtained monthly precipitation data from the National Oceanic and Atmospheric Administration (NOAA) for weather stations in Tacna (Index # 8396), Ajo (0080), and Organ Pipe Cactus National Monument (6132). For each month, I averaged the amount of precipitation across all three sites. If a site's weather station failed to collect data for ten or more days during one month, I excluded the month's entry from analysis. I calculated biennial precipitation for year t as the sum of average monthly precipitation at the three weather stations from January of year t+1through December of year t+2 (NOAA 1993-2018). Abundance estimates were computed according to the sightability model based on count data obtained during biennial aerial surveys of the wild SOPH population in the United States (USFWS 2016, J. Hervert personal communication). I calculated r_t , the growth rate for year *t*, as the natural logarithm of the total abundance estimate for year t+2 (N_{t+2}) divided by the total abundance estimate for year *t* (N_t).

$$r_t = \ln\left(\frac{N_{t+2}}{N_t}\right)$$
 (Equation 1)

I performed simple linear regression analysis in R (R Development Core Team 2007) to assess the relationship between population growth rate and the natural logarithm of biennial rainfall for two time periods: 1) 1992-2002 (pre-recovery efforts) and 2) 2004-2016 (post-recovery efforts). The regression equation from the 1992-2002 data was used to calculate the amount of annual rainfall at which r = 0 before the implementation of habitat enhancements.

Abundance and Survival: NGS-CR

The noninvasive genetic sampling and capture-recapture combination method allows for estimation of abundance and survival by capturing individuals, marking them, releasing them, and then performing additional captures after set time periods. The proportion of marked individuals that are recaptured can be used to estimate the size of the population being sampled. When this process is repeated for two or more years, researchers can estimate survival of individuals. For NGS-CR, individuals are "captured" by the collection of fecal samples and "marked" via the genetic identification of unique individuals from DNA extracted from the collected fecal samples. Fecal samples were collected by applying a targeted sampling approach according to Pollock's robust design (Pollock 1982; Woodruff et al. 2015). From 2013-2017, fecal samples were collected at supplemental waters and feed stations during June, when pronghorn congregated around these areas and probability of capture was highest. Each year was considered a primary sampling session, including up to three secondary sampling sessions. Between primary sampling sessions, the pronghorn population was assumed to be open to emigration, immigration, birth, and death. Within a primary session, i.e., among secondary sessions of a single year, closure was assumed, i.e., no pronghorn were lost to emigration and death or gained due to immigration and birth. At low-use, remote sites, we conducted only one secondary sampling session. We implemented three (2013 and 2014) or two (2015-2017) secondary sampling sessions, separated by oneweek intervals, at high-use sites. During each sampling session, we collected as many fecal samples as three times the number of pronghorn estimated to be visiting the site based on information collected during management visits or flights to locate radio-collared individuals via telemetry. From 2014-2017, we collected fecal samples opportunistically from pronghorn located away from waters and feed stations as determined by visual scanning of the landscape from elevated observation points, e.g., hills, and by pronghorn observed during telemetry flights. Following genetic identification of fecal samples by the University of Idaho (Woodruff et al. 2014), I used the R (R Development Core Team 2007) package RMark (Laake 2013) to construct and compare models for estimating abundance and survival in program MARK (White and Burnham 1999). Models followed Huggins' robust design with full heterogeneity allowing for the inclusion of individual covariates (age and sex) and the estimation of apparent survival (ϕ) and apparent detection probability (p). To account for unknown sources of variation in individual detection probabilities, we considered a mixture model in which individual pronghorn essentially belonged to one of two groups or "mixtures", with the probability of belonging to one mixture equal to π and the probability of belonging to the other mixture equal to $(1 - \pi)$ (Pledger et al. 2003). The model also included two parameters for estimating the probability an individual was not available for sampling: γ' and γ'' . Given an individual was not available for sampling during the primary sampling session of year t and survived to year t + 1, γ' was the probability of not being available for sampling again in year t + 1. Given an individual was available for sampling during the primary sampling session of year t and survived to year t + 1, γ'' was the probability of not being available for sampling in year t + 1. I combined single and multisession sites in the same model. Including individual covariates, I compared all combinations of the following models: survival equal for males and females but varying by age (adult versus fawn); survival varying by both age and sex; detection probability varying by secondary session; detection varying by session and mixture; and detection varying by age, session, and mixture. I used the Akaike Information Criterion corrected for small sample size (AIC_c) to determine the best model for estimating abundance and survival of Sonoran pronghorn (Symonds & Moussalli 2011).

Results and Outputs

Abundance: population growth before and after implementation of recovery efforts

Population growth rate and biennial precipitation were determined for 1992 through 2016 (Table 1). Population growth rate has a significant, positive relationship with the natural logarithm of biennial precipitation from 1992-2002, pre-recovery efforts ($F_{0.05(1),1,4} = 13.85$, p = 0.0205; Figure 2). This relationship is described by

$$\hat{Y}_i = 2.093X_i - 7.347$$
 (Equation 2)
(0.562) (1.934)

in which Y_i is the biennial population growth rate for year *i* and X_i equals the natural logarithm of biennial precipitation for year *i*; the standard error of the coefficients are shown in parentheses. Setting Equation 2 equal to zero, when biennial rainfall equals 33.5 cm, r = 0, meaning the average annual rainfall must be 16.7 cm for r = 0. Since the implementation of habitat modifications, no relationship was observed between population growth rate and biennial rainfall ($F_{0.05(1),1,3} = 0.482$, p = 0.5184; Figure 2). I shared these results with AZGFD in July 2018.

I digitized data collected during the U.S. aerial surveys from 2000 through 2016, including all wildlife detections. After I obtain and enter data from the surveys conducted in December 2018, I will share the data with AZGFD and the rest of the Sonoran Pronghorn Recovery Team by May 2019. *Abundance and Survival: NGS-CR*

The best model for estimating abundance and survival of Sonoran pronghorn included survival varying by age and detection probability varying by secondary session and mixture. The small sample size prevented me from accurately estimating the parameters γ' and γ'' . Examining preliminary estimates, however, suggested a null model in which $\gamma' = 1$ and $\gamma'' = 0$, where individuals do not move between being unobservable and observable. In other words, individuals are either always available for sampling or always unavailable for sampling. I used this model to estimate annual abundance from 2013-2017 (Figure 3). I estimated fawn survival at 57.2% (95% confidence interval: 40.4% to 72.5%) and adult survival at 81.7% (95% confidence interval: 74.8% to 87.0%).

Discussion and Next Steps

Abundance: population growth before and after implementation of recovery efforts

The absence of a significant relationship between biennial population growth rate and rainfall after the implementation of recovery efforts suggests that recovery actions may be positively affecting survival and/or recruitment. Excluding 2016, the population of Sonoran pronghorn increased every year post-implementation from 2004 – 2014, even though biennial precipitation fell below the threshold value at which r = 0 (33.5 cm) for four out of seven two-year periods (Figure 2). However, the biennial population growth rate would have been positive in 2016 had a group of 17 pronghorn been available for detection during the 2018 survey. Because aerial surveys can take up to a week to complete, pronghorn occasionally move from an unsurveyed block to a surveyed block and are thus unavailable for detection. Wildlife managers are concerned about such movements biasing population counts, as well as the ability to implement range-wide surveys for the experimental populations of Sonoran pronghorn. With the digitized aerial survey data, I will be able to simulate different methods for surveying the Cabeza pronghorn population to determine if a different sampling approach, e.g., distance sampling, could reduce bias while increasing precision. After feedback from the SPRT, I will develop the results of simulations into a manuscript for publication, with AZGFD personnel as coauthors. Having recently received copies of the paper records from the aerial surveys in Mexico, I will be digitizing these data to share with AZGFD and the rest of the Sonoran Pronghorn Recovery Team by May 2019.

Abundance and Survival: NGS-CR

The most powerful technique for surveying Sonoran pronghorn in both the U.S. and Mexico may be NGS-CR. By continuing research started by the University of Idaho, I have helped demonstrate that NGS-CR can produce useful estimates of both abundance and survival, especially when sampling opportunistically in addition to at waters and feed stations. Abundance estimates from NGS-CR are more precise than the estimates obtained during range-wide aerial surveys. Furthermore, NGS-CR abundance estimates increase in precision the longer the study is conducted as marked individuals undetected in one year are detected in subsequent years. Due to the relatively low cost of NGS-CR methods, especially in terms of personnel time, sampling can be conducted annually, thus providing annual estimates as opposed to the biennial estimates obtained from aerial surveys. Most importantly, NGS-CR can estimate survival of Sonoran pronghorn. Survival estimates from NGS-CR are both less biased and more precise than estimates from collared individuals, most of which have been released from the captive breeding pen.

Considering the increase in the distribution of Sonoran pronghorn with the two experimental populations, NGS-CR may be a cost-effective way to expand sampling to include the Kofa and Sauceda populations, which have waters and feed stations that would allow for both targeted and opportunistic sampling following the established methods. Because the Sonoran pronghorn populations in Mexico lack waters and feed stations for targeted sampling, the current NGS-CR methods for estimating abundance and survival are not directly applicable to the Pinacate and Quitovac populations. However, after discussions with collaborators at the University of Idaho and University of Arizona, I started collecting fecal samples from Sonoran pronghorn on El Pinacate y Gran Desierto de Altar Biosphere Reserve in 2016. Based on the results of genetic identification, we have been discussing the appropriate study design for surveying the Pinacate population. Within the next month, I am planning on traveling to the Pinacate to collect additional fecal samples for analysis.

One disadvantage of NGS-CR, however, is that even with opportunistic sampling, estimates are likely biased in favor of pronghorn that use supplemental waters and feed stations. If data collection continues into the future, however, greater sample size may allow managers to effectively model pronghorn availability for sampling. The current data set supports a null model in which observable pronghorn are always observable and unobservable pronghorn are always unobservable (i.e., $\gamma' = 1$ and $\gamma'' = 0$) because the sample size is too small to accurately estimate the parameters γ' and γ'' . Within the next couple weeks, I will determine if information from additional data types, e.g. telemetry flights and photographs taken at NGS-CR sampling sites, can be included in the model to improve accuracy. For example, some individuals with physical marks (ear tags and radio collars) have been linked to a specific genetic identification. Because pronghorn with physical marks have been regularly located during the

NGS-CR study period, sometimes on a daily basis, I may be able to incorporate additional information on individual availability for detection into the existing model.

I will present my findings from the NGS-CR analysis, including information from additional data types, to the SPRT during the next quarterly meeting on Tuesday, 19 Feb 2019. After updating my analysis based on feedback provided by SPRT members, I will share the R script I used for analysis with AZGFD and develop the results into a manuscript for publication, with AZGFD personnel as coauthors.

REFLECTION

As a former employee of the Arizona Game and Fish Department who worked exclusively with Sonoran pronghorn, I participated in efforts to collect some of the data analyzed in this report. I assisted with three range-wide aerial surveys, two in the U.S. (2010 and 2012) and one in Mexico (2011), and conducted numerous telemetry flights to locate and monitor radio-collared individuals. I have worked with many members of the SPRT for more than 10 years, including John Hervert and Jill Bright (AZGFD), both of whom were former supervisors. As an inexperienced wildlife biologist, I questioned some of the conclusions drawn by knowledgeable and experienced SPRT members, only to have my own experience and analysis lead to similar conclusions. I have seen members of academia pursuing datasets for analysis overlook partnerships with the wildlife managers who actively collected the data, as well as wildlife managers avoid collaboration with academics who would have gladly conducted analyses that could help inform management decisions. Given the understanding of the conflicts that can arise between academia and management agencies, I hope to help bridge this gap and build lasting partnerships between managers and researchers.

Based on stakeholder engagement, including attendance at quarterly SPRT meetings and monthly phone updates with John Hervert (AZGFD), I shifted the focus of my original proposal for analyzing abundance and survival of Sonoran pronghorn. I responded to AZGFD's request to assess the efficacy of recovery efforts by comparing population growth rates before and after the implementation of recovery actions. Although I had originally hoped to improve abundance estimates by developing a new sightability model, I also encountered several challenges in obtaining all of the necessary data. Initial receipt of the photo-copied datasheets took longer than expected. Furthermore, the survey datasheets did not include data on all groups missed during the surveys, information essential to developing a sightability model. The Arizona Game and Fish Department is currently working on locating this information, with the intent to share the data when located so I can continue my efforts to improve abundance estimates from aerial surveys. Stakeholders expressed explicit interest in the NGS-CR data during June 2018, causing me to redirect my focus on survival analysis to developing appropriate models for the NGS-CR dataset.

Overall, I believe collaboration with AZGFD has helped prepare me for future partnerships. I have more realistic expectations for project timelines. Given the challenges faced by managers during the 2018 aerial survey, I hope the information I present during the next Sonoran Pronghorn Recovery Team meeting on NGS-CR will allow managers to make more informed decisions about monitoring Sonoran pronghorn. Through joint publications with AZGFD, I anticipate sharing important progress on conservation challenges commonly faced by researchers and managers around the world.

FIGURES

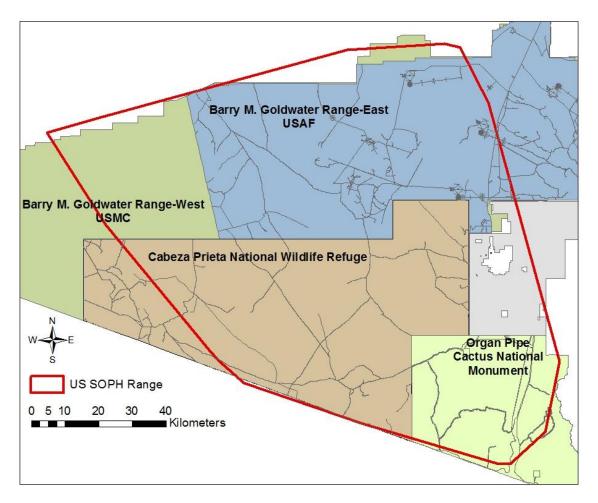


Figure 1 The essential, endangered population of Sonoran pronghorn in the United States ranges on 7,122 km² of Sonoran Desert. The U.S. Marine Corps (USMC) and U.S. Air Force (USAF) administer the Barry M. Goldwater Range-West and -East, respectively. The U.S. Fish and Wildlife Service manages the Cabeza Prieta National Wildlife Refuge (CPNWR), and the National Park Service administers Organ Pipe Cactus National Monument (ORPI).

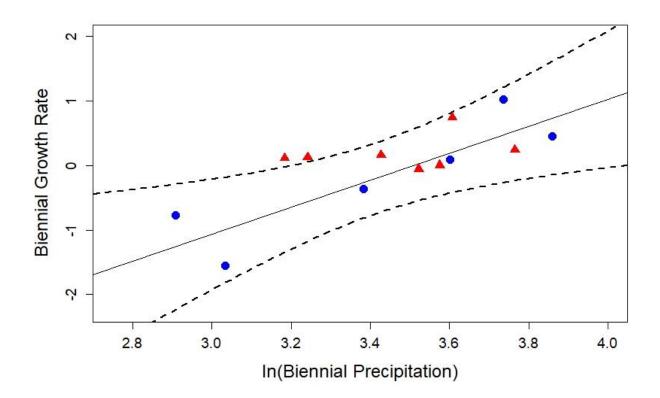


Figure 2 Before recovery efforts, biennial population growth rate was directly related to the natural logarithm of biennial precipitation ($F_{0.05(1),1,4} = 13.85$, p = 0.0245). The blue circles represent biennial growth rates pre-recovery projects. The black line represents the least squares regression equation, $\hat{Y}_i = 2.0929X_i - 7.3467$, and the black dashed lines show the 95% confidence band. The red triangles are biennial growth rates post-recovery projects. Although five of the seven points fall within the 95% conditionce band, these seven points exhibit no relationship between biennial growth rate and precipitation ($F_{0.05(1),1,5} = 0.482$, p = 0.5184).

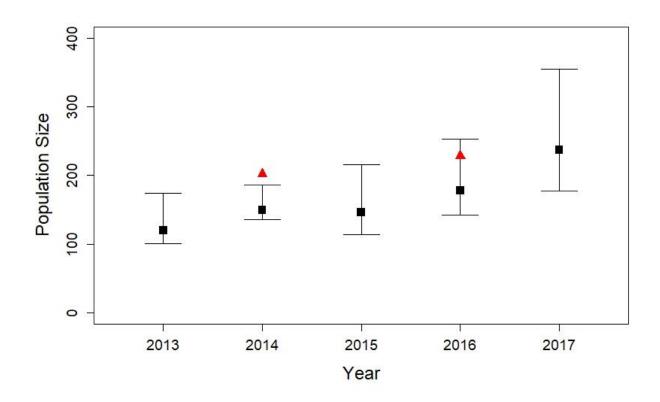


Figure 3 Estimated abundance of the U.S. population of endangered Sonoran pronghorn. The black squares represent estimates from noninvasive genetic sampling and capture-recapture (NGS-CR), shown with 95% confidence intervals. The red triangles are the biennial aerial survey counts adjusted for variation in sighting probability according to group size.

TABLES

Year (t)	Total abundance estimate (<i>Nt</i>)	Growth rate (rt)	Biennial precipitation (cm)
1992	179	0.455	47.4
1994	282	-0.774	18.3
1996	130	0.0883	36.7
1998	142	-0.361	29.5
2000	99	-1.55	20.8
2002	21	1.02	42.0
2004	58	0.159	30.8
2006	68	0.00	35.7
2008	68	0.111	24.1
2010	76	0.738	36.9
2012	159	0.239	43.2
2014	202	0.121	25.6
2016	228	-0.0587	33.9
2018	215		

Table 1 Biennial growth rates calculated from total abundance estimates.

LITERATURE CITED

- Bright JL, Hervert JJ. 2005. Adult and fawn mortality of Sonoran pronghorn. Wildlife Society Bulletin **33**:43–50.
- Bright, JL, Hervert JJ, Piest LA, Henry RS, Brown MT. 1999. Sonoran pronghorn 1998 aerial survey summary. Nongame and Endangered Wildlife Program Technical Report. Arizona Game and Fish Department, Phoenix, Arizona.

Goldman E. 1945. Proceedings of the Biological Society of Washington 58:3-4.

- Horne JS, Hervert JJ, Woodruff SP, Mills LS. 2016. Evaluating the benefit of captive breeding and reintroductions to endangered Sonoran pronghorn. Biological Conservation **196**:133–146.
- Laake, JL. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Pledger S, Pollock KH, Norris JL. 2003. Open capture-recapture models with heterogeneity: I. Cormack-Jolly-Seber model. Biometrics **59**:786–794.
- Pollock KH. 1982. A capture-recapture design robust to unequal probability of capture. The Journal of Wildlife Management **46**:752.
- Symonds MRE, Moussalli A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology **65**:13–21.
- U.S. Fish and Wildlife Service. 2002. Recovery Criteria and Estimates of Time for the Recovery Actions for the Sonoran Pronghorn: A Supplement and Amendment to the 1998 Final Revised Sonoran Pronghorn Recovery Plan. U.S. Department of the Interior Fish and Wildlife Service, Albuquerque, New Mexico, USA.

- U.S. Fish and Wildlife Service. 2010. Final Environmental Assessment for Reestablishment of Sonoran Pronghorn. U.S. Department of the Interior Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- U.S. Fish and Wildlife Service. 2016. Recovery plan for the Sonoran pronghorn (*Antilocapra americana sonoriensis*), Second Revision. U.S. Fish and Wildlife Service, Southwest Region, Albuquerque, New Mexico, USA.
- White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46**:S120–S139.
- Woodruff SP, Adams JR, Johnson TR, Waits LP. 2014. Rapid species identification of Sonoran pronghorn from fecal pellet DNA: Species ID of Pronghorn and Mule Deer Pellets. Wildlife Society Bulletin 38:842–848.
- Woodruff SP, Johnson TR, Waits LP. 2015. Evaluating the interaction of faecal pellet deposition rates and DNA degradation rates to optimize sampling design for DNA-based mark-recapture analysis of Sonoran pronghorn. Molecular Ecology Resources **15**:843–854.
- Woodruff SP, Lukacs PM, Christianson D, Waits LP. 2016. Estimating Sonoran pronghorn abundance and survival with fecal DNA and capture-recapture methods. Conservation Biology 30:1102– 1111.