



Evaluating the benefit of captive breeding and reintroductions to endangered Sonoran pronghorn



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ABSTRACT

Sonoran pronghorn (*Antilocapra americana sonoriensis*), an endangered subspecies of American pronghorn, are of great conservation concern in the southwestern U. S. Following a dramatic population decline in 2002, the U.S. Fish and Wildlife Service (USFWS) began a captive breeding program that has subsequently been used to supplement the wild population. Additionally, in 2009 the USFWS proposed to establish another, self-sustaining population outside of their range at that time. We modeled Sonoran pronghorn population dynamics based on time-series of abundance and conducted a population viability analysis (PVA) to evaluate the benefit of these management actions. We found that rates of change in the Sonoran pronghorn population were closely tied to the amount of precipitation in the area but that viability was greatly enhanced by conservation actions including the maintenance of a captive population, as well as the establishment of two additional populations outside the current range.

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The Sonoran pronghorn (*Antilocapra americana sonoriensis*, Goldman, 1945), an endangered subspecies of North American pronghorn, is of great conservation and management concern. They are a desert-adapted subspecies that occur in areas with sparse rainfall and temperatures that commonly exceed 45 °C (deVos and Miller, 2005). Historically, Sonoran pronghorn ranged from Sonora, Mexico northward into southeastern California and southeastern Arizona, reportedly being relatively common in wide alluvial valleys of the Sonoran desert (Wilson et al., 2010a). Widespread decline in both distribution and abundance began in the mid- to late 1800s due to human settlement, unrestricted hunting, competition with domestic livestock, and habitat fragmentation by fences, railways, highways and canals. Sonoran pronghorn occur as three subpopulations, two in Sonora Mexico and one in the southern Arizona which is functionally separated from the Mexican subpopulations by a highway and agricultural developments (Wilson et al., 2010a). Additionally, in 2014, 23 Sonoran pronghorn were released into an area northwest of their previous range in the U.S. which may result in the establishment of an additional subpopulation in southern Arizona. The U.S. Fish and Wildlife Service (USFWS, 2010) estimated

the range in the U.S. to be about 7.6% of their original distribution, bordered by Highway 85 to the east, the Cabeza Prieta Mountains to the west, U.S. Interstate 8 to the north, and the U.S.–Mexico border to the south (Fig. 1). Sonoran pronghorn were federally listed as endangered under the Endangered Species Act of 1973 (USFWS, 1998).

After the decline in the late 1800s, population estimates in the U.S. ranged from ~100 individuals in the early 1900s to ~300 individuals in 1994 (Krausman et al., 2005, USFWS, 2010). However, during a prolonged and extreme drought in the early 2000s, the estimated abundance declined from 99 individuals in 2000 to 21 individuals in 2002 (Table 1). Due to increased concern over possible extinction of the subspecies, aggressive management actions were initiated, including creation of a captive breeding program as well as manipulation of forage and water availability (Wilson et al., 2010a). In the fall of 2003, a 2.6 km² captive pen was constructed on Cabeza Prieta National Wildlife Refuge (Cabeza captive pen) and initially populated with two males and 12 females during 2004–2006. Since the initial effort, the number of individuals in the Cabeza captive pen grew to ~70 individuals in 2009 and 2010, and releases of captive Sonoran pronghorn to the wild began with four males released during the winter of 2006–2007, followed by additional releases of males and females in subsequent years.

To further aid recovery, in 2009 the USFWS began a program to reestablish Sonoran pronghorn in two new areas (Areas A and

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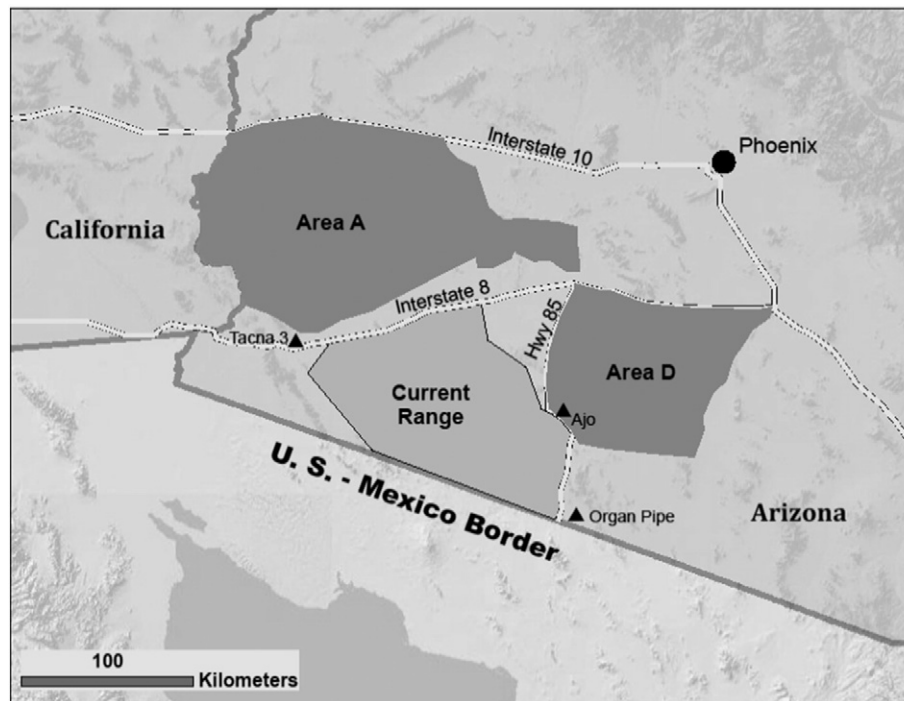


Fig. 1. Map of southwestern Arizona depicting the current range of wild Sonoran pronghorn in the U.S.; Areas A and D proposed for re-establishing new populations; and three weather stations (Tacna 3, Ajo, and Organ Pipe) used to characterize precipitation in the area. Major roads include State Highway 85 and U.S. Interstate Highways 8 and 10.

D) within the historic range but outside of the current range (USFWS, 2010; Fig. 1). The project would release individuals from the Cabeza captive pen into Area D and release individuals into Area A from a newly created 1.3 km² captive pen (Kofa captive pen) on the Kofa National Wildlife Refuge. The ultimate goal of this project is to establish a separate, self-sustaining population outside the current range and facilitate maintenance of a total population size of at least 300 individuals, both of which are criteria identified for downlisting in the Sonoran Pronghorn Recovery Plan (USFWS, 2003).

Ironically, in 2002 (the year of the dramatic population decline) Hosack et al. (2002) published a population viability analysis (PVA) of Sonoran pronghorn to determine extinction risks, identify model parameters whose estimation uncertainty had the greatest influence on estimates of viability, and evaluate changes in viability due to potential management actions. While the PVA of Hosack et al. (2002) was helpful in answering many of the outstanding questions that prompted their study, several changes, both naturally and due to

management, have affected Sonoran pronghorn and there is a need to re-evaluate viability following these changes. Furthermore, while both the captive program as well as the effort to reestablish populations outside the current range would certainly increase viability, managers are constantly being challenged to quantify the benefits of these programs such that the cost–benefit of alternative management actions can be evaluated.

The goal of this study was to evaluate population viability of wild Sonoran pronghorn with particular attention paid to (1) incorporating new information (i.e., empirical data on changes in the population before, during and after the severe drought of 2002) on the relationship between precipitation and population dynamics, (2) quantifying the benefits of the captive breeding program which serves as a source for releases into the wild population, and (3) evaluating the benefits of the USFWS recently enacted management plan to establish additional populations within their historic range. Additionally, it is becoming increasingly important for contemporary

Table 1
Changes in female abundance (N_C) of Sonoran pronghorn within the captive pen at Cabeza Prieta National Wildlife Refuge. Reconstructed from Sonoran Pronghorn Monthly Updates provided by Arizona Fish and Game and Arizona Antelope Foundation.

Year	Adults introduced	Reproduction	Fawn mortalities	Adult mortalities	Adults released	$N_{C,t}$	$N_{C,t+1}$	r_t
2004	6	5	3	0	0	6	8	0.287
2005	3	4	0	1	0	11	14	0.241
2006	3	7	0	0	0	17	24	0.344
2007	0	11	1	0	0	24	34	0.348
2008	0	14	2	5	7	34	41	0.187
2009 ^a	0	NA	NA	NA	NA	34	47	0.324
							$\hat{\mu} =$	0.289
							$\hat{\sigma}_C =$	0.064

^a We did not have detailed information on changes to the female population during 2009–2010 but were able to acquire $N_{2009} = 34$ and $N_{2010} = 47$ from Arizona Fish and Game (unpublished data).

viability assessments to quantify the full range of uncertainty in model predictions and assess whether the effects of management actions are significant enough to detect a change in viability despite this uncertainty (Ludwig, 1996, Reed et al., 2002). Therefore, we evaluated the effect of management actions on population viability while including all of the major sources of prediction uncertainty into our assessment. The approach and methods we used for incorporating uncertainty might be a valuable tool for other research seeking to assess the impact management efforts on recovery of endangered species, especially when viability is assessed using models based on time-series of abundance data.

1. Methods

1.1. Population viability model

Quantitative models of population dynamics are an important tool for assessing risk of extinction and evaluating potential management actions for species of conservation concern. Today’s stochastic models of population viability come in two general forms, those that are based on demographic data (e.g., means and variances of stage-specific survival and reproduction) and those based on general population growth models fit to counts of individuals through time (Morris and Doak, 2002, Mills, 2012), although integrated population models (IPM) that combine these two approaches are a recent alternative (Schaub and Abadi, 2011). While demographic-based models are generally used more often, we chose to evaluate viability using count-based models for several reasons, with the first being simply a matter of practicality. To properly model viability, it is important to capture the full range of temporal variation in population dynamics and a sufficiently long time series of estimates for key vital rates was not available for wild Sonoran pronghorn. In contrast, ~20 years of biennial abundance estimates existed for the wild population and, importantly, these estimates spanned the time period before, during and after the drought of 2002. Furthermore, the number of model parameters and complexity of demographic-based models can make rigorous propagation and assessment of uncertainty challenging (see Bakker et al., 2009) while the process is greatly simplified for count-based models. Lastly, because of the stochastic and multiplicative nature of population growth, simple models of population change often perform as well as, or better than, demographically-based models for predicting extinction risk (Holmes et al., 2007, Perretti et al., 2013). In principle, demographic and abundance data could have been combined in an IPM, however, temporal overlap in these datasets was generally lacking. For these reasons, we chose to proceed with a viability analysis based solely on the abundance data. Indeed, we were interested in whether management relevant questions could be answered based on simplified models of population dynamics derived from abundance data.

American pronghorn are polygynous (Byers and Moodie, 1990) and thus, population dynamics are largely driven by changes in female abundance, survival, and reproduction. Therefore, our population growth models reflect changes in female abundance of both wild and captive populations. Movement between the U.S. population and those in Mexico is assumed to be minimal (only a single male was observed moving from the U.S. into Mexico in 2008). Thus, Sonoran pronghorn in the U.S. functionally operate as a metapopulation of two populations (i.e., one wild and one captive) with human-managed movements of individuals between these populations. Individuals in captivity are mostly buffered from density dependent processes (e.g., predation and overutilization of resources) and environmental fluctuations via predator exclusion and irrigated forage as well as supplemental food and water (Wilson et al., 2010b). Thus, we modeled female abundance of the captive population(s) (N_C) by assuming a constant mean annual growth rate (μ_C) with annual variation in the realized growth rate

Table 2

Changes in biennial abundance of wild Sonoran pronghorn, population growth rates (r_t) and precipitation (Precip_t) from 1992 to 2010.

Year	Total abundance estimate	r_t	Precip _t
1992	179	0.455	47.63
1994	282	-0.774	16.74
1996	130	0.089	36.02
1998	142	-0.361	28.45
2000	99	-1.55	19.63
2002	21	1.02	40.13
2004	58	0.159	27.91
2006	68	0.000	33.45
2008	68	0.111	22.76
2010	76		

caused by stochastic events that perturb the realized growth rate away from μ_C . Thus, the stochastic growth model for the captive populations was

$$N_{C,t+1} = N_{C,t} \times \exp[\mu_C + Z_t\sigma_C] \tag{1}$$

where $Z_t \sim normal(0, 1)$. Parameters were estimated from previous data where $\hat{\mu}_C$ was the average of the observed instantaneous growth rates ($r_t = \ln[N_{C,t+1}] - \ln[N_{C,t}]$) and $\hat{\sigma}_C$ was the standard deviation of these growth rates (Dennis et al., 1991). We used monthly records of changes to the composition of the female population inside the Cabeza captive pen from 2004 to 2010 and calculated $N_{C,t}$ as the number of females in the pen in year t just prior to reproduction and $N_{C,t+1}$ as these females plus their female offspring that survived to the following year (Table 2). We obtained these data from Sonoran Pronghorn Monthly Updates provided by Arizona Game and Fish Department and Arizona Antelope Foundation.

Precipitation is a major factor influencing wild Sonoran pronghorn survival both through the availability of free water as well as indirectly by mediating forage growth (Bright and Hervet, 2005). In addition, there is the possibility that negative density dependence (i.e., lower population growth rates at larger population sizes) could also influence population dynamics. Therefore, we modeled the change in abundance of the wild population as a function of annual precipitation and density dependence. Because abundance of the wild population is estimated every other year, the stochastic growth model depicting biennial changes in abundance was

$$N_{W,t+2} = N_{W,t} \times \exp[\beta_0 + \beta_1 \times N_{W,t} + \beta_2 \times (\text{Precip}_t) + Z_t\sigma_W], \tag{2}$$

where β_1 measures the magnitude of density dependence, β_2 measures the relationship between precipitation and the population growth rate, and $Z_t\sigma_W$ represents residual or unexplained variation in population growth. The variable for precipitation (Precip_t) quantifies the amount of precipitation during the interval t to $t + 2$.

To estimate parameters of the growth model for wild Sonoran pronghorn, we used estimates of abundance (Bright et al., 2001; Table 1) derived from aerial line-transect surveys conducted in December by Arizona Game and Fish every other year from 1992 to 2010. For each year abundance was estimated, we measured Precip_t by first averaging total monthly precipitation from three weather stations (Organ Pipe Cactus National Monument, station 026132; Ajo, station 020080; Tacna 3, station 028396; Western Regional Climate Center) within and proximate to the current range of wild Sonoran pronghorn (Fig. 1) and then summing these averages over the following two years.

Because the presence and form of density dependence as well as the effect of precipitation on population dynamics were largely unknown, we fit various forms of the growth model (Eq. (2)) using multiple linear regression (Dennis and Otten, 2000) where Eq. (2) was reformulated as $\ln[N_{W,t+2}/N_{W,t}] = \beta_0 + \beta_1 \times N_{W,t} + \beta_2 \times (\text{Precip}_t) + Z_t\sigma_W$.

Table 3
Models of wild Sonoran pronghorn population growth.

Model description	Model	AICc	Δ AICc	AICc weight	R ²	Parameter estimates			
						β_0	β_1	β_2	σ_W
Log-precipitation	$r_t = \beta_0 + \beta_2 * \ln(\text{Precip}_t) + \varepsilon$	21.3	0	0.45	0.61	-4.189		1.686	0.433
Precipitation	$r_t = \beta_0 + \beta_2 * \text{Precip}_t + \varepsilon$	22.0	0.8	0.31	0.58	-1.788		0.142	0.451
Exponential growth	$r_t = \beta_0 + \varepsilon$	25.0	3.7	0.07		-0.095			0.736
Gompertz density dependence and precipitation	$r_t = \beta_0 + \beta_1 * \ln(N_t) + \beta_2 * \text{Precip}_t + \varepsilon$	26.0	4.7	0.04	0.71	-2.686	-0.360	0.124	0.376
Gompertz density dependence and log-precipitation	$r_t = \beta_0 + \beta_1 * \ln(N_t) + \beta_2 * \ln(\text{Precip}_t) + \varepsilon$	26.1	4.9	0.04	0.70	-4.592	-0.307	1.462	0.380
Gompertz density dependence	$r_t = \beta_0 + \beta_1 * \ln(N_t) + \varepsilon$	26.7	5.4	0.03	0.29	-1.707	-0.524		0.585
Ricker density dependence and log-precipitation	$r_t = \beta_0 + \beta_1 * N_t + \beta_2 * \ln(\text{Precip}_t) + \varepsilon$	27.9	6.6	0.02	0.64	-3.716	-3.073	1.564	0.419
Ricker density dependence and precipitation	$r_t = \beta_0 + \beta_1 * N_t + \beta_2 * \text{Precip}_t + \varepsilon$	27.9	6.7	0.02	0.63	-1.390	-4.610	0.1311	0.420
Ricker density dependence	$r_t = \beta_0 + \beta_1 * N_t + \varepsilon$	28.0	6.8	0.02	0.17	0.356	-7.811		0.632

We fit a total of nine candidate models with and without the effects of density dependence and precipitation, as well as models with log-transformed effects of abundance (i.e., Gompertz-type density dependence) and precipitation (Table 3). We used Akaike weights corrected for small sample size (AIC_c) to determine the best model for predicting future population dynamics of wild Sonoran pronghorn (Burnham and Anderson, 2002).

We modeled three scenarios that represented alternative management options for recovering wild Sonoran pronghorn in Arizona. Scenario 1 was created to depict management in which there is no captive breeding program, and thus, the wild population receives no immigration from a captive population. For this scenario, we projected future abundance of the wild population using

$$N_{W,t+2} = N_{W,t} \times \exp[\hat{\beta}_0 + \hat{\beta}_2 \times \ln(\text{Precip}_t) + z_t \hat{\sigma}_W] \quad (3)$$

where $\hat{\beta}_0$, $\hat{\beta}_2$, and $\hat{\sigma}_W$ were the estimated values fit to past abundance and precipitation data and z_t was a random deviate from a standard normal distribution. Values of Precip_t were drawn from a normal distribution with mean ($\hat{\mu}_{\text{Precip}}$) equal to 30.3 cm and standard deviation ($\hat{\sigma}_{\text{Precip}}$) equal to 10.0 cm based on the observed biennial precipitation from 1992–2010.

Scenario 2 represented management in which the current wild population receives individuals from the Cabeza captive pen. For this scenario, we projected future abundance using

$$N_{W,t+2} = [N_{W,t} + I_{C,t} + I_{C,t+1}] \times \exp[\hat{\beta}_0 + \hat{\beta}_2 \times \ln(\text{Precip}_t) + z_t \hat{\sigma}_W]. \quad (4)$$

The model was the same as Scenario 1 with the addition of $I_{C,t} + I_{C,t+1}$ which represented the number of females released into the wild population from the Cabeza captive population. To determine I_C , we projected future abundance of the captive population at each time step using

$$N_{C,t} = N_{C,t-1} \times \exp[\hat{\mu}_C + z_{t-1} \hat{\sigma}_C] \quad (5)$$

where $\hat{\mu}_C$, and $\hat{\sigma}_C$ were the estimated values fit to past abundance data. If the size of the captive population at t was greater than a fixed capacity for the enclosure (K_C) (set at 34 adult females for the Cabeza captive pen), then $I_{C,t} = N_{C,t} - 34$. The abundance of the captive population was then reset to 34, and this process was repeated for $t + 1$.

Scenario 3 projected future abundance of wild Sonoran pronghorn based on the recently implemented plan to reestablish two new populations to the north (Area A) and east (Area D) of the current population (USFWS, 2010). This management action would maintain the Cabeza captive pen to supplement the current wild population as well as reestablish and supplement a wild population

in Area D. The newly constructed Kofa captive pen would be used to reestablish and supplement a wild population in Area A. The population growth models governing these populations were the same as Scenario 2 with the following modifications. First, due to a smaller size, the capacity of the Kofa captive pen was set to half of the Cabeza captive pen (17 versus 34 adult females). Second, for the wild population in Area A, values of Precip_t were drawn from a normal distribution with mean equal to 34.2 cm and standard deviation equal to 10.9 cm which were derived from the observed biennial precipitation at the Kofa Mine weather station, located within Area A, during the period 1992–2010. Third, following guidelines of the proposed reestablishment (USFWS, 2010), when there were females within the Cabeza pen available for transfer (>34), they would be released into the current wild population if the estimated number of individuals in this population were <140. Otherwise, the individuals would be transferred to the wild population (current range or Area D) whose abundance was proportionally furthest from its assumed carrying capacity (see subsection *Estimating population viability* for methods of determining carrying capacities). Because Highway 85 and Interstate 10 function as a barrier to movement, we did not allow for movement of individuals among the wild populations.

1.2. Incorporating and evaluating prediction uncertainty

By their very nature, stochastic PVA models must accommodate some level of uncertainty in predicting future population dynamics. In general, uncertainty arises from five main sources: (1) effects of future management, (2) choice of an appropriate simplified model structure to characterize complex ecological processes and project future population dynamics (model selection), (3) unexplained or residual variation in population dynamics not accounted for in the model (process), (4) uncertainty in the future values of covariates that are included in the model (covariate), and (5) error in model parameters due to limited (estimation error) or inexact (observation error) empirical data. We included all of these main sources of uncertainty into our predictions. Our approach was based on uncertainty analysis (Saltelli et al., 2000) in which important components of prediction error are identified, empirical data are used to develop probabilistic distributions for uncertain inputs, and simulations are used to propagate these uncertainties and evaluate their influence on model predictions. We incorporated uncertainty due to management actions by evaluating the 3 alternative scenarios described previously. To accommodate model selection uncertainty, we randomly selected among the top population growth models with the probability of selection proportional to their respective AIC_c weights. To incorporate uncertainty due to parameter estimation error, we drew new values of model parameters for each replicate from their respective sampling distributions. Finally, to incorporate process variance we randomly selected values of z_t and Precip_t during each

time step. A more detailed description of this process as well as R code (R Development Core Team, 2008) used for the simulations are provided in Appendix A.

To guide future research and management, it is important to understand how each component of uncertainty contributes to overall prediction uncertainty. We evaluated the contribution to overall prediction uncertainty from each source by calculating the proportional reduction in total prediction uncertainty due to removing each source,

$$PR_s = \frac{[Sd(\text{total}) - Sd(\neq s)]}{Sd(\text{total})}$$

where $Sd(\text{total})$ is the standard deviation in final abundance with all sources of uncertainty and $Sd(\neq s)$ is the standard deviation in final abundance not including source (s). To exclude uncertainty due to model selection, we ran all simulations with the AIC_c -best model. To exclude uncertainty due to process variation, we ran simulations with $\hat{\sigma}_W$ and $\hat{\sigma}_C$ equal to zero. To exclude covariate uncertainty, we set $\hat{\sigma}_{\text{Precip}}$ equal to zero. Finally, to exclude uncertainty due to parameter estimation error, we used the original estimates of all model parameters for each replication.

1.3. Estimating population viability

Future abundance was projected for $t = 1$ to 10 time steps (years) and $j = 1$ to 2000 replicate trajectories. We set initial abundances for the captive ($N_{C,0}$) and wild populations ($N_{W,0}$) to the last observed abundance for each in 2010. Thus, $N_{C,0} = 34$ and $N_{W,0} = 46$ (assuming females constituted 61% of the wild population totaling 76 individuals). We used 61% as this is the average of the proportion of females in the population (62.5% and 58.8%) reported by Wright and deVos (1986) and Hughes and Smith (1990), respectively.

We placed two additional restrictions on all simulated population growth. First, we set a limit on the realized finite growth rate [N_{t+1}/N_t], excluding growth from immigration, equal to two. We derived this number from the highest observed finite growth rate in the captive population (1.86) and the highest reasonable biological limit (three) which assumes two fawns per doe and 100% survival of does and fawns. Because we could not reliably estimate a carrying capacity based on our models that included density dependence (see Results), our second restriction was a “ceiling” carrying capacity for the current wild and the proposed reestablished populations intended to exclude implausibly high abundances. The highest observed abundance of the current wild population was 282 individuals in 1994. To allow for exceptionally good range conditions, we set the ceiling capacity of the current wild population to 846 individuals (three times the highest observed in 1994) which, with an estimated 6312 km² of available habitat (O’Brien et al., 2005), results in a maximum density of 0.134/km². For the reestablished populations, we set the ceilings so the densities would also be 0.134/km². Based on 8977 km² and 3890 km² of available habitat (O’Brien et al., 2005), we set the carrying capacities at 1203 and 521 for Area A and Area D, respectively.

We evaluated viability of wild Sonoran pronghorn under each management scenario using three metrics. The first, mean final abundance, provided an estimate of the expected population size after 10 years. The second was the proportion of replications in which the final female abundance was <50, >183, and >250 which provided an estimate of the probability that wild Sonoran pronghorn would be (1) reduced to the point that drastic management actions would likely be warranted, (2) greater than the criteria set in the Sonoran pronghorn Recovery Plan to consider downlisting, and (3) well above the minimum criteria suggested for downlisting, respectively. Our final viability metric, accounting for the shape of the distribution of final abundances, was the probability that the

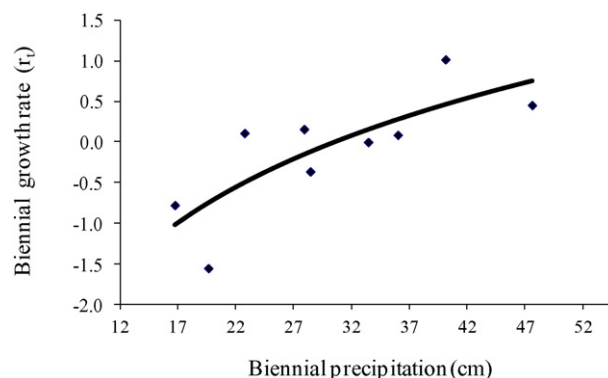


Fig. 2. Relationship between biennial growth rate of the wild Sonoran pronghorn population and biennial precipitation. Fitted line depicts a linear relationship between growth rate and log-precipitation. Zero growth is predicted at 30.5 cm.

final abundance from one management scenario (Y) would be greater than the final abundance under an alternative management scenario (X) which we estimated by calculating the proportion of replications in which the final abundance y was greater than the final abundance x .

2. Results

The AIC_c -best models indicated that changes in population abundance were dominated by the effect of precipitation ($R^2 = 0.61$). Under this model, the ‘equilibrium’ (no population growth) precipitation level was ~30.5 cm biennially. If precipitation were above this amount, we would expect the population to increase. Conversely, if precipitation were below this amount, we would expect the population to decrease. We found little support (AIC_c weights ≤ 0.04) for the models containing density dependent effects as most of the variation in growth rates was explained by biennial precipitation (Table 3; Fig. 2). However, there was some model selection uncertainty related to the form of the relationship between precipitation and population growth as well as some support for the model of exponential growth (AIC_c weight = 0.07).

For comparative purposes, we first present deterministic results of the population projections and their implications. Mean biennial precipitation of 30.3 cm from 1992 to 2010 was slightly below the precipitation level of 30.5 cm for which we would expect zero population growth based on the AIC_c -best model. Therefore, if future precipitation was held at its expected value and there was no

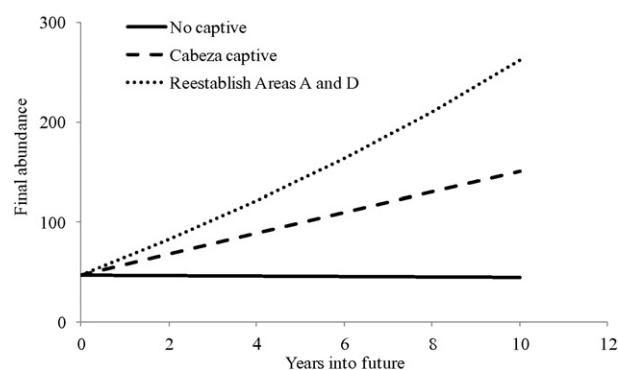


Fig. 3. Deterministic projections of the wild Sonoran pronghorn population 10 years into the future.

Table 4
Viability of wild Sonoran pronghorn under three alternative management scenarios. Population viability^a of wild Sonoran pronghorn is based on 2000 replicate simulations. N_{final} is the final female abundance after 10 years.

Management option	Mean final abundance	$P\{N_{\text{final}} < 50\}$	$P\{N_{\text{final}} > 183\}$	$P\{N_{\text{final}} > 250\}$
No captive program(s)	84	0.62	0.14	0.10
Cabeza captive pen	192	0.19	0.39	0.29
Reestablish Areas A and D	372	0.05	0.62	0.50

^a Population viability was measured as the average final abundance across replications, and the probability that the final abundance was greater or less than the specified abundance $P\{N_{\text{final}}\}$.

immigration from the captive population, the current wild population would be expected to undergo a slight decline in abundance from an estimated 46 females down to a final abundance of 43 (Fig. 3). For Scenarios 2 and 3 in which the wild population(s) received immigrants from the captive population(s), the final population size of the wild population without reestablishment of an additional population was 151 and with reestablishment was 262 (Fig. 3).

After including all major sources of prediction uncertainty, we found that mean final abundance was ~2 times larger under the current management (Scenario 2) than the scenario in which there is no supplementation of the wild population from the captive pen (Scenario 1), and there is a 0.77 probability that the final abundance would be larger under Scenario 2 versus Scenario 1 (Table 4). A similar increase in the expected final abundance was observed under the scenario of reestablishment (Scenario 3) as there is a 0.68 probability that the final abundance would be larger under Scenario 3 versus Scenario 2. Without any supplementation of the wild population from a captive pen, there is a high likelihood that wild Sonoran pronghorn would drop below 50 individuals ($P\{N_{\text{final}} < 50 = 0.62\}$). However, this probability decreases to 0.19 with supplementation from the Cabeza captive pen and further decreases to 0.05 if the reestablishment proceeds. Conversely, without any supplementation of wild populations, there is little chance that wild Sonoran pronghorn would meet or exceed the recovery goal in 10 years, yet this probability improves significantly with supplementation and reestablishment of additional populations (Table 4).

Covariate uncertainty (i.e., future precipitation) was the dominant contributor to overall prediction uncertainty accounting for 36% of the variation in final abundance (Table 5). Parameter estimation error was the next largest contributor accounting for 16% of the variation, and process variation in the population growth models was the least significant contributor, accounting for 10% of the variation in final abundance. For our PVA, evaluating how model selection uncertainty contributes to overall prediction uncertainty requires an understanding of the various competing models in light of other important contributors to prediction uncertainty.

Table 5
Variation in the final abundance of wild Sonoran pronghorn^a and percent reduction due to the removal of various components of prediction uncertainty.

Component of uncertainty	Variation included in viability model	Standard deviation in final abundance	Percent reduction in all-sources variation
	All sources	334	
Covariate	Process, estimation and model selection	244	36
Parameter estimation	Process, covariate, and model selection	310	16
Process	Estimation, covariate, and model selection	328	10
Model selection	Process, estimation, and covariate	353 ^b	NA ^b

^a Results are for the management scenario including the reestablishment of an additional wild population and immigration from the captive populations.

^b Counterintuitively, removing uncertainty due to model selection actually increased the uncertainty in the estimated final abundance. This was because one of the competing models (exponential growth) included in “all sources” simulations did not include an effect of future precipitation (a major contributor to overall uncertainty), thus actually making predictions more certain.

Counterintuitively, removing model selection uncertainty from simulations actually *increased* our measure of prediction uncertainty. This was because predicted population dynamics based on one of the competing models (exponential growth) was unaffected by covariate (i.e., future precipitation) uncertainty. Because covariate uncertainty was a major contributor to overall prediction uncertainty, removing its effect via the exponential growth model actually reduced the uncertainty of predicting future abundance. Despite the counterintuitive result, it emphasizes the importance of future precipitation in predicting future population dynamics of Sonoran pronghorn.

3. Discussion

3.1. Implications for recovery of Sonoran pronghorn

Our model of wild Sonoran pronghorn population growth is in agreement with other studies (Wright and deVos, 1986, Bright and Hervet, 2005, deVos and Miller, 2005, Hervet et al., 2005) that suggest a strong link between precipitation and Sonoran pronghorn population dynamics. When this link is coupled with highly variable (spatially and temporally) levels of precipitation in the Sonoran Desert, we can expect local populations of Sonoran pronghorn to exhibit substantial fluctuations in population abundance, making them susceptible to local extinction. We suspect that for Sonoran pronghorn to have persisted as a viable subspecies in the past, they likely functioned as a type of metapopulation prior to the early 1900s. One possibility is that groups of Sonoran pronghorn were a collection of “patchy populations” (sensu Harrison, 1991) in which movement from patches of poor quality to those with better conditions was so high that the system was effectively a single extinction-resistant population. Alternatively, Sonoran pronghorn may have been one of the few species to behave as a classic metapopulation with the subspecies persisting in a balance between local extinction in areas where range conditions were poor and colonization of patches in areas where range conditions were good. Unfortunately, we may never know the true dynamics of the historic population of Sonoran pronghorn. However, it is clear that if Sonoran pronghorn

did function as either of these types of metapopulations, viability would be critically dependent on the ability to move among spatio-temporally variable patches of favorable habitat. This ability has been greatly diminished due to anthropogenic barriers (highways and irrigation canals) and conversion of much of the river valleys to agriculture. Our PVA indicates that without these movements, the viability of wild Sonoran pronghorn is substantially diminished whereas viability is significantly improved by the captive program and reestablishment of additional wild populations. We contend that these management actions may be restoring (albeit anthropogenically) historic metapopulation processes by facilitating movements among patches (via translocations) and creating a source population (the captive pens) to augment wild populations in danger of local extinction.

Our model focused on the impacts of captive releases and reestablishment of additional subpopulations. However, Sonoran pronghorn viability might also be enhanced by decoupling the relationship between highly variable precipitation and Sonoran pronghorn population dynamics. The most direct way to do this may be via forage and water enhancements that are part of contemporary Sonoran pronghorn management (Wilson et al., 2010b). Due to the timing of these management actions (i.e., most did not become established until the very end of our time-series of abundances), we did not include their effects on our models of population dynamics. However, research investigating the effects of these management actions should be a top priority in the future as they might offer an alternative to the continuation of a captive breeding program. While future research can address this important question, we stress that researchers will need to be patient as a true evaluation of their impact will only be possible if and when another drought such as the one in the early 2000s occurs.

Based on our PVA that used recent climatological regimes (i.e., mean biennial precipitation of 30.3 cm over the past ~20 years) to predict future population dynamics, wild Sonoran pronghorn persistence would be unlikely without the captive breeding program or additional management actions that decouple the relationship between population dynamics and precipitation (e.g., supplemental forage and water). It is important to note that our predictions are dependent on the assumption that past climatological observations are good indicators of future precipitation. We feel this assumption was justified for our analysis because of the relatively short (10-year) future time frame for which we made predictions. Nevertheless, our analysis also showed that most of the uncertainty in predicting future viability was due to our uncertainty in future precipitation, and this was without the additional uncertainty related to climate change. Indeed, climate shifts in the past 25 years have led to warmer, drier conditions (Weiss and Overpeck, 2005, Kimball et al., 2010) and climate projections for this region suggest that conditions will continue to be drier than average (Weiss and Overpeck, 2005, Seager et al., 2007). The implications of these observations are that the discrepancy in viability between no conservation action versus the current and proposed management actions might actually be greater than our PVA indicated. We believe this is an important area for future research that will be facilitated by additional years of abundance data as well as better models of climate change in southern Arizona.

Count-based PVAs such as the one we conducted are dependent on long-term estimates of abundance. Similarly, recovery goals for Sonoran pronghorn are based on criteria related to abundance and trend. However, a commitment to uninterrupted monitoring of population abundance can be difficult to justify to managing agencies. We recommend that monitoring Sonoran pronghorn abundance continue in order to track population trend as well as to measure the efficacy of recovery actions (captive breeding, water development, forage enhancement). At the very least, abundance estimates should be obtained in pairs, for example every two years in the case of Sonoran pronghorn, such that models of population growth rates can be fit to these data.

Additionally, continued monitoring will enable future research to update our models as well as investigate the impact of changes to environmental conditions. Such evaluations and updates will be important for researchers to place Sonoran pronghorn management within an adaptive management framework.

In the face of our changing world, examples of complete endangered species recovery are rare (Scott et al., 2005, Doremus and Pagel, 2008), and while the Sonoran pronghorn population has rebounded since its historic low in 2002, movements likely to have occurred prior to the early 1900s may be impossible to restore in this region and Sonoran pronghorn will continue to be at risk from other threats such as climate change, drought, and increased activity along the U.S.–Mexico border. Thus, it is unlikely that wild Sonoran pronghorn will be able to maintain a self-sustaining population without ongoing human involvement to address factors limiting viability (poor range conditions or the inability to access good range conditions). Accordingly, Sonoran pronghorn might be considered a “conservation-reliant” (Scott et al., 2010, Goble et al., 2012, Rohlf et al., 2014) subspecies, being unable to maintain a viable population without species-specific management actions (Goble et al., 2012). Our PVA supports continuation of the current and proposed management actions under the Sonoran Pronghorn Recovery Plan (USFWS, 1998) including the release of captive raised pronghorn into their historic range, establishment of additional populations outside the current range, development and operation of irrigated plots, and development of supplemental water sources (USFWS, 2003).

3.2. Concluding remarks on uncertainty and PVAs

Conservation strategies for species at risk of extinction rely on effective communication between biologists and managers about how various recovery actions affect species viability. For these communications to be effective, researchers must clearly convey the implications of management alternatives on species viability while at the same time presenting managers and policy-makers with an assessment of the uncertainty in these predictions. We recognize that the ultimate decision about whether or not to implement a particular conservation strategy is a normative decision, integrating societal values of acceptable levels of extinction risk (Vucetich et al., 2006) with social, political and economic considerations. However, part of this process should be an honest assessment of our certainty in how a species will fair under alternative conservation strategies.

Our framework for incorporating prediction uncertainty in count-based PVAs is similar to the approach described by Bakker et al. (2009) for demographic-based PVAs. However, one of the major benefits of count-based models, other than data availability, is that they require estimation of far fewer model parameters than demographic-based models and empirical field data used to estimate model parameters can often be collected more efficiently and for longer time periods. Combined, these characteristics suggest better estimation properties of model parameters which can significantly reduce the uncertainty in model predictions. Additionally, the transition from model specification and parameter estimation to projecting future population dynamics is quite straightforward with count-based PVAs. Thus, other researchers might find our approach and methods useful for providing a link between quantitative PVA, rigorous uncertainty analysis, and straightforward metrics of species viability such that alternative conservation actions can be evaluated for imperiled species.

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Appendix A. Approach for incorporating various sources of uncertainty into count-based PVA of endangered Sonoran pronghorn

We used Monte Carlo simulation of future population sizes to evaluate Sonoran pronghorn viability and evaluating alternative management actions while including major sources of prediction uncertainty into the projection model. A general description of the process as well as the specific steps we used for Sonoran pronghorn are described in the table below.

General approach	Specific steps for Sonoran pronghorn
1. Develop biologically plausible and management relevant models of (meta) population dynamics	<ul style="list-style-type: none"> • Determined potentially important drivers of metapopulation dynamics (i.e., density dependence, precipitation, captive breeding program) • Assembled time-series of abundance data for wild and captive populations of Sonoran pronghorn • Assembled time-series of precipitation data for wild Sonoran pronghorn range
2. Fit population growth models to time-series of abundance data and quantify major sources of prediction uncertainty	<ul style="list-style-type: none"> • Fit several models incorporating various combinations and forms of density dependence as well as relationships with precipitation • Evaluated competing models with information-theoretic criteria • Quantified uncertainty due to model selection, process variation and estimation error
3. Change model structure, parameter estimates, or covariate values to reflect alternative management or conservation strategies	<ul style="list-style-type: none"> • Modified model structure and emigration/immigration parameters in the projection model to represent three alternative management strategies involving the captive population and proposed re-establishment of additional wild populations
4. Propagate major sources of prediction uncertainty and predict future abundances	<ul style="list-style-type: none"> • Used Monte Carlo simulations to model future population dynamics of Sonoran pronghorn while incorporating uncertainty due to alternative management actions, model structure, process variation, estimation error, and future precipitation • Estimated probabilities of extinction under alternative management scenarios
5. Summarize predicted population dynamics to evaluate management alternatives, quantify the contribution to overall prediction uncertainty from each component, and place results within an adaptive management or structured decision-making process	<ul style="list-style-type: none"> • Quantified percent contribution of each source of uncertainty to overall prediction variance • Recommended strategies for future management and research on Sonoran pronghorn

Monte Carlo simulations of viability and the hierarchical structure of these simulations are described below and with the specific R code we used for Sonoran pronghorn thereafter.

A.1. Scenario loop

Incorporate management uncertainty by generating a separate estimate of population viability for each management alternative and associated models.

Replication loop. Given a particular management scenario, during each replication of the stochastic simulations:

- Incorporate model selection uncertainty by randomly selecting an approximating model with inclusion probabilities proportional to the likelihood of a particular model being the best predictive model
- Incorporate estimation error by randomly selecting model parameters, specific to the chosen model from the previous step, from their respective sampling distributions

Time-step loop. Within a replication, for each time step:

- Incorporate process variation by randomly selecting a new value of Z_t from its probability distribution (e.g., normal with mean = 0 and variance = $\hat{\sigma}^2$)
- Incorporate covariate uncertainty by randomly selecting a new value of each covariate C_t . Depending on availability of previous data, values of C_t can be drawn from past values sampled randomly with replacement (e.g., Dennis and Otten, 2000) or from parametric models fit to past data (e.g., Rothery et al., 1997).

To incorporate uncertainty due to parameter estimation error, we drew new values of model parameters for each replicate from their respective sampling distributions. Thus, for the captive population, a new value of $\hat{\mu}_C$ was drawn for each replicate from a normal distribution with mean equal to $\hat{\mu}_C$ and standard deviation equal to the estimated standard error of $\hat{\mu}_C$. Similarly, a new value of $\hat{\sigma}_C$ was drawn for each replicate from

$$V \frac{\hat{\sigma}_C^2}{q-1} \quad (6)$$

where q = number of observed rates of change (five for our captive population) and V was a random deviate from a chi-square distribution with $q - 1$ degrees of freedom (Dennis et al., 1991). For the wild populations, we used a parametric bootstrap with past abundance and precipitation data to obtain new estimates of $\hat{\beta}_0, \hat{\beta}_2$, and $\hat{\sigma}_W$ for each replication (Dennis and Otten, 2000). Thus, for each replicate we simulated a new time-series of past abundance data from 1992 to 2010 using Eq. (3). We set the initial abundance to the observed abundance in 1992 and values of Precip_t equal to those observed from 1992 to 2010. For each bootstrapped time-series of past abundance, we refit the model (Eq. (2)) using this new time-series coupled with the natural logarithm of past precipitation to obtain new estimates of $\hat{\beta}_0, \hat{\beta}_2$, and $\hat{\sigma}_W$.

R code for conduction a population viability analysis of Sonoran pronghorn based on time-series of abundance data and incorporating major sources of prediction uncertainty.

```

# Simulation Setup
#####
library(MASS)

NoModelError = F           #Model selection uncertainty
NoParamEstError = F       #Parameter estimation error
NoPrecipError = F         #Covariate uncertainty
NoResidualError = F       #Process uncertainty
IncludeAreaD=T            #If included, when CurrentWild_N>140, emigrants are send to AreaD

IACaptCab = 34             #Number of females in Cabeza captive pen in 2009 (34); set to 0 for Scenario 1,
terminate captive program
IACaptKof = 17             #Number of females in Kofa captive pen once established (17); set to 0 for Scenarios
1 and 2, status quo - no additional populations

NumReps = 2000            #Set to 1 for deterministic projections, 2000 otherwise
NumTimeSteps = 10

WildSexRatio = .61        #Female/(Females+Males) sex ratio

IAWildC = 76              #Number of individuals in wild population in 2010
IAWildC = round(IAWildC*WildSexRatio) #Number of females in wild population
IAWildD = 0               #Intitial abund. of reestablished population in Area D
IAWildD = round(IAWildD*WildSexRatio)
IAWildA = 0               #Initial abund. of reestablished population in Area A
IAWildA = round(IAWildA*WildSexRatio)

lambdamax = 2             #1.86 highest observed in captive population; 3 highest biological = 2
fawns:doe, 100% survival adults and fawns
CaptCab_K = 34
CaptKof_K = 17
WildC_K = round(846*WildSexRatio)    #Highest observed abundance in current wild population was 282
WildD_K = round(521*WildSexRatio)    #Based on proportional area of habitat compared to current range using
CART model
WildA_K = round(1203*WildSexRatio)   #Based on proportional area of habitat compared to current range using
CART model

WildsCorr_C_D = 0         #Correlation between current wild and Area D in residual variance
(excluding relationship with precip.) #of growth models
WildsCorr_A = 0           #Correlation with Area A in residual variance (excluding relationship with
precip.) of growth models

PrecipIntercept_CandD = 11.93 #avg. biannual precip from Organ Pipe, Tacna3, Ajo (1993-2010) used for
current wild and AreaD
PrecipBetaYear_CandD = 0     #linear trend in precipitation
sdPrecip_CandD = 3.95        #residual error in precip. model

PrecipIntercept_A = 13.4     #avg. biannual precip from Kofa (1993-2010) used for AreaA
PrecipBetaYear_A = 0         #linear trend in precipitation
sdPrecip_A = 4.29           #residual error in precip. model
CorrPrecip_A = .75          #correlation between precip in AreaA and precip used for current wild and
areaD; data from 1981 - 2010

#Akaike model weights
Model1_LnPrecip = 0.45
Model2_Precip = 0.31
Model3_Exp = 0.07

M1_Params = c(-4.189, 0, 1.686, 0.433) #B_0 + B_1*N(t-1) + B_2*ln(Precip) + sigma*Z(t)
M2_Params = c(-1.788, 0, 0.142, 0.451) #B_0 + B_1*N(t-1) + B_2*(Precip) + sigma*Z(t)
M3_Params = c(-0.095, 0, 0, 0.736)     #Exponential

ModelParams = matrix(0,3,4)
ModelParams[1,] = M1_Params
ModelParams[2,] = M2_Params
ModelParams[3,] = M3_Params
Wild_SE_mu = sqrt(M3_Params[[4]]^2/9)

WildC_Nt = c(179,282,130,142,99,21,58,68,68) #Abundance data from wild pop.
Precip = c(18.75,6.59,14.18,11.2,7.73,15.8,10.99,13.17, 8.96) #Biennial precipitation
#####
#End User-defined model parameters
#####

```

```

#-----
#Create random deviates for future precipitation
#-----
if (NoPrecipError==T){
  sdPrecip_CandD=0
  sdPrecip_A = 0
}
Covariance = matrix(c(1,CorrPrecip_A,CorrPrecip_A,1),2,2)
DevsPrecip_CandD_A = mvrnorm(n=NumReps*NumTimeSteps,mu = rep(0,2),Sigma=Covariance)
#standard normal deviates
PrecipDeviat_CandD_t=matrix(DevsPrecip_CandD_A[,1],NumReps,NumTimeSteps)
PrecipDeviat_A_t = matrix(DevsPrecip_CandD_A[,2],NumReps,NumTimeSteps)
PrecipDeviat_CandD_t = PrecipDeviat_CandD_t*sdPrecip_CandD
PrecipDeviat_A_t = PrecipDeviat_A_t*sdPrecip_A

#-----
#Initialize arrays and matrices
#-----
Time_t = 0:NumTimeSteps
NumAbund = NumTimeSteps+1
CaptCab_N = matrix(0,NumReps,NumAbund)
CaptKof_N = matrix(0,NumReps,NumAbund)
WildC_N = matrix(0,NumReps,NumAbund)
WildD_N = matrix(0,NumReps,NumAbund)
WildA_N = matrix(0,NumReps,NumAbund)

CaptCab_Emigrants = matrix(0,NumReps,NumAbund)
CaptKof_Emigrants = matrix(0,NumReps,NumAbund)

CurrentPrecip_CandD=matrix(0,NumReps,NumAbund)
CurrentPrecip_A = matrix(0,NumReps,NumAbund)

CaptCab_lambda = matrix(0,NumReps,NumTimeSteps)
CaptKof_lambda = matrix(0,NumReps,NumTimeSteps)
WildC_lambda = matrix(0,NumReps,NumTimeSteps)
WildD_lambda = matrix(0,NumReps,NumTimeSteps)
WildA_lambda = matrix(0,NumReps,NumTimeSteps)

#For bootstrap estimates of relationship between abundance and precipitation
BootBeta_0 = array(0,NumReps)
BootBeta_InN = array(0,NumReps)
BootBeta_Precip = array(0,NumReps)
bootsigma = array(0,NumReps)

#-----
# Estimate Growth Parameters for Captive Populations (Cabeza and Kofa) from Cabeza data
#-----
CaptCab_Nt = c(6,11,17,24,34,34) #Female abundance data from CPNWR captive
pop.
CaptCab_NtPlus1 = c(8,14,24,34,41,47)
CaptCab_rt = log(CaptCab_NtPlus1/CaptCab_Nt)

CaptCab_mu = mean(CaptCab_rt) #Exponential Growth Model
CaptCab_sigma = sd(CaptCab_rt)
CaptCab_SE_mu = sqrt(CaptCab_sigma^2/length(CaptCab_rt))

#-----
# Create random deviates for captive populations' growth rate parameters (for parameter estimation error)
#-----
if (NoParamEstError==T) CaptCab_SE_mu=0
CaptCab_mu_rep = matrix(rnorm(NumReps,CaptCab_mu,CaptCab_SE_mu),NumReps,1)

CaptCab_sigma_sq_devs = rchisq(n=NumReps,df = (length(CaptCab_rt)-1))
CaptCab_sigma_rep = matrix(sqrt(CaptCab_sigma_sq_devs*CaptCab_sigma^2/(length(CaptCab_rt)-1)), NumReps,1)
if (NoParamEstError==T) CaptCab_sigma_rep = matrix(CaptCab_sigma, NumReps,1)

#-----
# Create random deviates for captive populations' growth rates (for process variation); independence assumed
#-----
CaptCab_E_t = matrix(rnorm(NumReps*NumTimeSteps,0,1),NumReps,NumTimeSteps) #Standard normal deviates
for Cabeza captive growth rate
if (NoResidualError==T) CaptCab_E_t = matrix(0,NumReps,NumTimeSteps)
CaptKof_E_t = matrix(rnorm(NumReps*NumTimeSteps,0,1),NumReps,NumTimeSteps) #Standard normal deviates
for Kofa captive growth rate
if (NoResidualError==T) CaptKof_E_t = matrix(0,NumReps,NumTimeSteps)

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```

#-----
# Create random deviates for wild populations' growth rate parameters of exponential model (for parameter estimation
error)
#-----
if (NoParamEstError==T)Wild_SE_mu=0
Wild_mu_rep = matrix(rnorm(NumReps,M3_Params[[1]],Wild_SE_mu),NumReps,1)

Wild_sigma_sq_devs = rchisq(n=NumReps,df = (9-1))
Wild_sigma_rep = matrix(sqrt(Wild_sigma_sq_devs*M3_Params[[4]]^2/(9-1)), NumReps,1)
if (NoParamEstError==T)Wild_sigma_rep = matrix(M3_Params[[4]], NumReps,1)

#-----
# Create random deviates for wild populations' (Current, AreaD, AreaA) growth rates (for process variation); correlations
not used
#-----
if (NoResidualError==T)WildC_sigma=0
Covariance = matrix(c(1,WildsCorr_C_D,WildsCorr_A,WildsCorr_C_D,1,WildsCorr_A,WildsCorr_A,WildsCorr_A,1),3,3)
Devs_C_D_A = mvrnorm(n=NumReps*NumTimeSteps,mu = rep(0,3),Sigma=Covariance)
WildC_E_t = matrix(Devs_C_D_A[,1],NumReps,NumTimeSteps) #Standard normal deviates for
current wild population
WildD_E_t = matrix(Devs_C_D_A[,2],NumReps,NumTimeSteps) #Standard normal deviates for AreaD
wild population
WildA_E_t = matrix(Devs_C_D_A[,3],NumReps,NumTimeSteps) #Standard normal deviates for AreaA
wild population

#=====
# Population Projection
#-----
WildPopsNumTimeSteps = NumTimeSteps/2

for (repj in 1:NumReps){
  CaptCab_N[repj,1]=IACaptCab
  CaptKof_N[repj,1]=IACaptKof
  WildC_N[repj,1]=IAWildC
  WildD_N[repj,1]=IAWildD
  WildA_N[repj,1]=IAWildA

#-----
#Get random model for each replication (incorporates model selection uncertainty)
#-----
if (NoModelError==F){
  rand_mod = rmultinom(n= 1, size= 1, prob= c(Model1_LnPrecip,Model2_Precip,Model3_Exp))
  Model = which(rand_mod[,1]==1)
} else {
  Model = 1}

#-----
#Get parameter estimates for each replication (incorporates estimation error)
#-----
#Captive Population
mu_j = CaptCab_mu_rep[repj,1]
sig_j = CaptCab_sigma_rep[repj,1]

if (NoParamEstError==F){

  #Wild Population
  if (Model==3){ #exponential growth model
    B_0 = Wild_mu_rep[repj]
    B_1 = 0
    B_2 = 0
    W_sigma =Wild_sigma_rep[repj]
  } else { #Parametric bootstrap time series to refit growth model (lnPrecip) for wild pops. growth parameters
    NormDev = rnorm(length(WildC_Nt))
    BootTimeSeries = array(0,length(WildC_Nt)+1)
    BootTimeSeries[1]=WildC_Nt[1]

    if (Model==1){
      for (ti in 1:length(WildC_Nt)){
        lambda =
exp(M1_Params[[1]]+M1_Params[[2]]*(BootTimeSeries[ti])+M1_Params[[3]]*log(Precip[ti])+NormDev[ti])*M1_Params[[
4]])

```

(continued).

```

        BootTimeSeries[ti+1]=BootTimeSeries[ti]*lambda
    }
    BootNt_2=BootTimeSeries[1:length(BootTimeSeries)-1]
    BootRt_2=log(BootTimeSeries[2:length(BootTimeSeries)])-log(BootNt_2)
    BootPrecipFit = lm (BootRt_2~log(Precip))
    B_0 = coef(BootPrecipFit)[[1]]
    B_1 = 0
    B_2 = coef(BootPrecipFit)[[2]]
    BootQ = length(BootRt_2)-df.residual(BootPrecipFit)+1
    W_sigma = sqrt(anova(BootPrecipFit)[(BootQ-1),2]/length(BootRt_2))
} else{ #Precip model (not log)
    for (ti in 1:length(WildC_Nt)){
        lambda =
exp(M2_Params[[1]]+M2_Params[[2]]*(BootTimeSeries[ti])+M2_Params[[3]]*(Precip[ti])+NormDev[ti]*M2_Params[[4]]
)

        BootTimeSeries[ti+1]=BootTimeSeries[ti]*lambda
    }
    BootNt_2=BootTimeSeries[1:length(BootTimeSeries)-1]
    BootRt_2=log(BootTimeSeries[2:length(BootTimeSeries)])-log(BootNt_2)
    BootPrecipFit = lm (BootRt_2~(Precip))
    B_0 = coef(BootPrecipFit)[[1]]
    B_1 = 0
    B_2 = coef(BootPrecipFit)[[2]]
    BootQ = length(BootRt_2)-df.residual(BootPrecipFit)+1
    W_sigma = sqrt(anova(BootPrecipFit)[(BootQ-1),2]/length(BootRt_2))
} # end if for which precip model

BootBeta_0[repj]= B_0
BootBeta_Precip [repj]= B_2
bootsigma [repj]= W_sigma

} #end if statement for which model is used
} else { #end if for whether there is parameter estimation error
    B_0 = ModelParams[Model,1]
    B_1 = ModelParams[Model,2]
    B_2 = ModelParams[Model,3]
    W_sigma = ModelParams[Model,4]
}
}
#-----
#Project Wild and Captive Pops.
#-----
if (NoResidualError==T)W_sigma=0
for (t in 2:NumAbund){

#Grow Cabeza Prieta Captive
    CaptCab_lambda[repj,t-1] = exp(mu_j+sig_j*CaptCab_E_t[repj,t-1])
    if(CaptCab_lambda[repj,t-1]>lambdamax)CaptCab_lambda[repj,t-1]=lambdamax
    CaptCab_N[repj,t] = round(CaptCab_N[repj,t-1]*CaptCab_lambda[repj,t-1])
    if(CaptCab_N[repj,t]>CaptCab_K){
        CaptCab_Emigrants[repj,t]=CaptCab_N[repj,t]-CaptCab_K
        CaptCab_N[repj,t]=CaptCab_K
    } # end if Cabeza Captive > K

#Grow Kofa Captive
    CaptKof_lambda[repj,t-1] = exp(mu_j+sig_j*CaptKof_E_t[repj,t-1])
    if(CaptKof_lambda[repj,t-1]>lambdamax)CaptKof_lambda[repj,t-1]=lambdamax
    CaptKof_N[repj,t] = round(CaptKof_N[repj,t-1]*CaptKof_lambda[repj,t-1])
    if(CaptKof_N[repj,t]>CaptKof_K){
        CaptKof_Emigrants[repj,t]=CaptKof_N[repj,t]-CaptKof_K
        CaptKof_N[repj,t]=CaptKof_K
    } # end if Kofa Captive > K

#Grow Wild populations only in odd years
if (t %% 2==1){

    #Set abundances in case there is no immigration
    WildC_NtPlusE = WildC_N[repj,t-2]
    WildD_NtPlusE = WildD_N[repj,t-2]
    WildA_NtPlusE = WildA_N[repj,t-2]

```

(continued).

```

#-----
#MetaPop Dynamics move individuals among populations
#-----
  if (IncludeAreaD==F){WildC_NtPlusE = WildC_N[repj,t-2]+CaptCab_Emigrants[repj,t-
1]+CaptCab_Emigrants[repj,t]}
  if (IncludeAreaD==T){
    #If Current wild is <140 then send emigrants to CurrentWild
    if (WildC_N[repj,t-2]<140*WildSexRatio){
      WildC_NtPlusE = WildC_N[repj,t-2] + CaptCab_Emigrants[repj,t-1]+CaptCab_Emigrants[repj,t]
    } else {
      #Send to whichever one is furthest (as a proportion of K) from their K
      PropWildC = WildC_N[repj,t-2]/WildC_K
      PropWildD = WildD_N[repj,t-2]/WildD_K
      if (PropWildC<PropWildD){
        WildC_NtPlusE = WildC_N[repj,t-2] + CaptCab_Emigrants[repj,t-
1]+CaptCab_Emigrants[repj,t]
      } else {
        WildD_NtPlusE = WildD_N[repj,t-2] + CaptCab_Emigrants[repj,t-
1]+CaptCab_Emigrants[repj,t]
      }
    }
  }
  WildA_NtPlusE = WildA_N[repj,t-2]+CaptKof_Emigrants[repj,t-1]+CaptKof_Emigrants[repj,t]
#-----
#Grow Wild populations
#-----

  # Get precipitation for Wild populations (Current, AreaD and AreaA)
  CurrentPrecip_CandD[repj,t] = PrecipIntercept_CandD +
PrecipBetaYear_CandD*(t+2007)+PrecipDeviat_CandD_t[repj,t-2]
  if (CurrentPrecip_CandD[repj,t]<0)CurrentPrecip_CandD[repj,t]=0.01
  # Get precipitation for Wild population AreaD
  CurrentPrecip_A[repj,t] = PrecipIntercept_A + PrecipBetaYear_A*(t+2007)+PrecipDeviat_A_t[repj,t-2]
  if (CurrentPrecip_A[repj,t]<0)CurrentPrecip_A[repj,t]=0.01

  if (Model==1){
    CurrentPrecip_CandD[repj,t] = log(CurrentPrecip_CandD[repj,t])
    CurrentPrecip_A[repj,t] = log(CurrentPrecip_A[repj,t])
  }

  #Grow Current Wild Population
  WildC_lambda[repj,t-2] = exp(B_0+B_2*CurrentPrecip_CandD[repj,t]+WildC_E_t[repj,t-2]*W_sigma)
  if (WildC_lambda[repj,t-2]>(lambdamax^2))WildC_lambda[repj,t-2]=(lambdamax^2) #wild pop grows every
2 years

  WildC_N[repj,t] = WildC_NtPlusE*WildC_lambda[repj,t-2]
  if (WildC_N[repj,t]>WildC_K)WildC_N[repj,t]=WildC_K
  if (WildC_N[repj,t]<1)WildC_N[repj,t]=0

  WildC_N[repj,t-1]=mean(c(WildC_N[repj,t],WildC_N[repj,t-2])) #For smooth plots interpolate abundance in
between 2-year counts

  #Grow AreaD Wild Population
  WildD_lambda[repj,t-2] = exp(B_0+B_2*CurrentPrecip_CandD[repj,t]+WildD_E_t[repj,t-2]*W_sigma)
  if (WildD_lambda[repj,t-2]>(lambdamax^2))WildD_lambda[repj,t-2]=(lambdamax^2) #wild pop grows every
2 years

  WildD_N[repj,t] = WildD_NtPlusE*WildD_lambda[repj,t-2]
  if (WildD_N[repj,t]>WildD_K)WildD_N[repj,t]=WildD_K
  if (WildD_N[repj,t]<1)WildD_N[repj,t]=0

  WildD_N[repj,t-1]=mean(c(WildD_N[repj,t],WildD_N[repj,t-2])) #For smooth plots interpolate abundance in
between 2-year counts

  #Grow AreaA Wild Population
  WildA_lambda[repj,t-2] = exp(B_0+B_2*CurrentPrecip_A[repj,t]+WildA_E_t[repj,t-2]*W_sigma)
  if (WildA_lambda[repj,t-2]>(lambdamax^2))WildA_lambda[repj,t-2]=(lambdamax^2) #wild pop grows every
2 years

  WildA_N[repj,t] = WildA_NtPlusE*WildA_lambda[repj,t-2]
  if (WildA_N[repj,t]>WildA_K)WildA_N[repj,t]=WildA_K
  if (WildA_N[repj,t]<1)WildA_N[repj,t]=0

  WildA_N[repj,t-1]=mean(c(WildA_N[repj,t],WildA_N[repj,t-2])) #For smooth plots interpolate abundance in
between 2-year counts

} #end if odd years
} #end time loop
} #end replication loop

```

(continued).

```

if (IACaptCab == 0 & IACaptKof==0 & IncludeAreaD==F){
  Wild_C_NoCaptives = WildC_N}

if (IncludeAreaD==F & IACaptKof==0){
  Wild_C_Cab = WildC_N}

if (IncludeAreaD==F){
  Wild_CwithCA_CabKof=WildC_N
  Wild_AwithCA_CabKof=WildA_N
  Wild_CA_CabKof = WildC_N+WildA_N}

if (!IACaptCab == 0 & !IACaptKof==0 & !IncludeAreaD==F){
  Wild_CwithCAD_CabKof = WildC_N
  Wild_DwithCAD_CabKof = WildD_N
  Wild_AwithCAD_CabKof = WildA_N
  Wild_CAD_CabKof = Wild_CwithCAD_CabKof+Wild_DwithCAD_CabKof+Wild_AwithCAD_CabKof
}

CaptiveCab = CaptCab_N
CaptiveKof = CaptKof_N

```

(continued).

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