Species Status Assessment for the Sonoran Desert Tortoise (*Gopherus morafkai*)

Version 2.1
September 2021
U.S. Fish and Wildlife Service
Southwest Region
Albuquerque, NM

Arizona Ecological Services Office

Report Versions

Version 2.1 *is a draft report of the Sonoran Desert Tortoise Species Status Assessment (SSA) that incorporates feedback from peer and partner review.*

Version 2.0 *is a draft report for the Sonoran Desert Tortoise Species Status Assessment (SSA) and is meant exclusively to facilitate peer and partner review. Much of the report and analytical framework in this version remains the same as Version 1.0, but we have updated the data and information, including the spatial analysis and population model. As a draft document, this report should not be referenced or cited as an agency document.*

This report was prepared by biologists from the U.S. Fish and Wildlife Service: Jeff Servoss, Brian Wooldridge, Shaula Hedwall, Jim Dick, Mike Dick, Jacob Burkhart, Justin Bohling, Cristina Jones, and Nathan Allan. We received significant assistance from Tom Jones of the Arizona Game and Fish Department, and Elroy Masters and Codey Carter of the U.S. Bureau of Land Management.

Version 1.0 *of the SSA report was completed in 2015 (USFWS 2015) in support of the U.S. Fish and Wildlife Service's 12-month petition finding (80 FR 60321).*

Executive Summary

Background
This Species Status Assessment (SSA) report documents our use of the best available scientific information to characterize the biological status of the Sonoran desert tortoise (*Gopherus morafkai*). The purpose of the assessment was to inform the listing decision for the species under the Endangered Species Act and to serve as an information source to inform conservation efforts.

Species Biology and Needs
The Sonoran desert tortoise occurs in various habitat types, mainly mixed cactus-Palo Verde associations along rocky slopes of mountain ranges and, to a limited degree, in intervening lands, in parts of Arizona, United States (U.S.) and Sonora, Mexico. In general, and compared to many other animals, Sonoran desert tortoises have relatively low fecundity (females lay about 5 eggs on average every other year), are slow-growing (taking 18–20 years to reach sexual maturity), and long-lived (living more than 50 years in the wild). Individual Sonoran desert tortoises grow to sizes of about 15 inches (38 centimeters) in shell length. They feed on a variety of vegetation and spend the majority of their time in underground shelters, emerging mainly to drink, forage, and breed.

To maintain viability over the long term, the Sonoran desert tortoise requires populations of adequate size and distribution to support resiliency, redundancy, and representation. Populations need large numbers of individuals to improve the chances of withstanding stochastic events (a measure of resiliency). Resilient populations need to be spread across its range in both Arizona and Sonora, supported by suitable habitat quantity and quality, to provide for range-wide redundancy (species ability to withstand catastrophic events such as potential large-scale drought) and representation (species genetic and ecological diversity to maintain adaptive capacity). We analyzed the species status within two large analysis units corresponding to the range in Arizona and Sonora, respectively. These served as the two units we used to assess resiliency for the species. For redundancy and representation, we examined the distribution of suitable habitat across the range to guide our assessment.

Risk Factors
We reviewed the potential risk factors that could be affecting the Sonoran desert tortoise: 1) altered plant communities, primarily due to the invasion of nonnative vegetation; 2) altered fire regimes, also related to the changes in plant communities; 3) habitat conversion to human developed landscapes; 4) habitat fragmentation by the construction of permanent linear structures like highways and canals; 5) climate change as it relates to increases in the frequency, scope, and duration of drought conditions in the Sonoran Desert; and 6) human-tortoise interactions such as handling, collecting, and killing individuals intentionally or unintentionally (especially by vehicle strikes).

We evaluated each of these factors in detail for their potential to have population and species-level effects. While many of them could be having effects on individual Sonoran desert tortoises, or on localized areas (e.g., individual mountain ranges), because of the long-life span, relatively high abundance, and wide distribution, these effects would likely take many decades or longer to have measurable impacts on the species. In addition, many of these factors are ameliorated to

some degree by ongoing and future conservation efforts through land management, as about 72% of all Sonoran desert tortoise habitat is in either managed, multi-use or Tribal ownership, and a large portion of potential habitat in the U.S. is included in an interagency conservation agreement committing Federal land managers to continuing conservation efforts for the Sonoran desert tortoise. We did identify two threats, urbanization and drought, that have documented, quantified effects on Sonoran desert tortoise habitat and demography.

Current Conditions

The Sonoran desert tortoise currently occurs across much of its presumed historical range in Arizona and Sonora. According to our analysis, the range of the species covers roughly 68,500 sq mi (44 million ac, 18 million ha), about 62% of which is within Arizona, U.S. To our knowledge, the Sonoran desert tortoise has not experienced any measurable reduction in its overall range, and past population losses are presumed to be limited to areas that have been converted to urbanization or other permanent human development within historical habitat areas for the species.

We used habitat suitability models to categorize currently available Sonoran desert tortoise habitat into high, moderate, and low categories. Areas that lacked natural intactness, such as developed areas and agricultural fields, were removed from the models. The results provided an overall assessment of the current extent of potential suitable Sonoran desert tortoise habitat within the Arizona and Sonora analysis units. This resulted in an estimate of 49,222 sq mi (31.4 million ac, 12.7 million ha) of potential habitat across the species' range (Table ES-1). Of this total, 62% occurs in Arizona and 38% occurs in Sonora, and for both areas 24% is in the high class, 29% is in the moderate class and 47% is in the low class. The distribution of the high, moderate, and low classifications across the species' range is shown in Figure ES-1.

Table ES-1. Total area, in square miles, of suitable habitat of the Sonoran desert tortoise in Arizona and Sonora as categorized into three suitability classes.

Suitable Habitat Class	Arizona	Sonora	Range-wide Total
High	8,532	3,406	11,938
Moderate	9,116	4,945	14,061
Low	12,828	10,396	23,224
Total Habitat Area	30,475	18,747	49,222

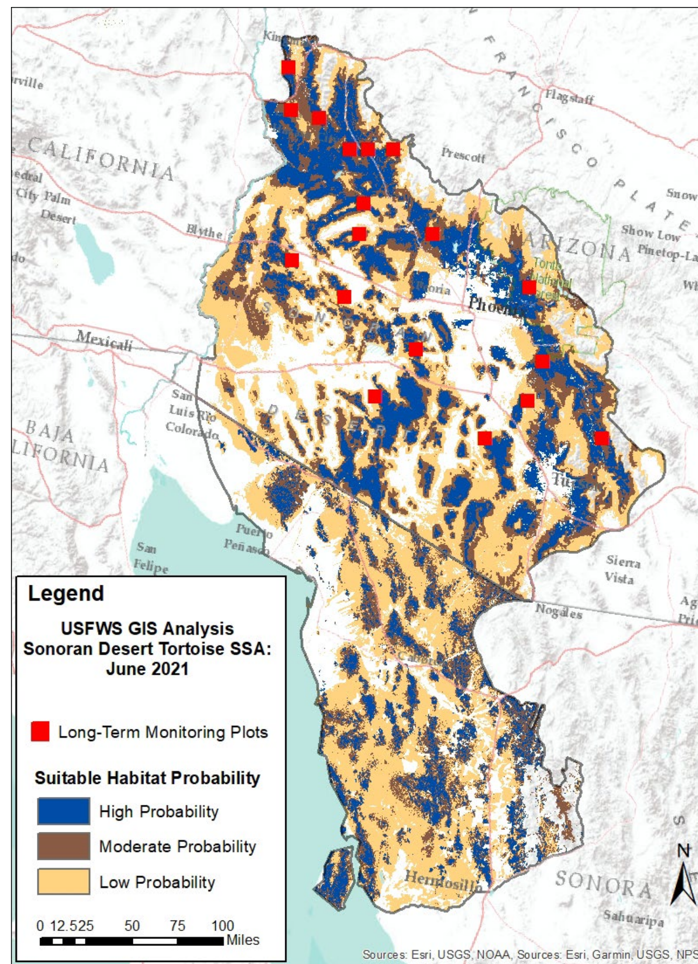


Figure ES-1. Suitable habitat for the Sonoran desert tortoise used in the species status assessment showing the current distribution of high, moderate, and low suitable habitats along with long-term monitoring plots (red points).

To further assess the current condition of the Sonoran desert tortoise we used our habitat suitability summaries to calculate an estimate of the potential Sonoran desert tortoise adult population sizes for Arizona and Sonora. To do this, we extrapolated reported population density estimates in high suitability areas (46 tortoises per sq mi; range: 6–155) using the long-term monitoring data (location of long-term monitoring plots are shown in Figure ES-1) and then elicited densities for moderate (25 tortoise per sq mi; range: 5–35) and low (6 tortoises per sq mi; range: 0–15) suitability habitat classes. We used these estimated density ranges multiplied by the available habitat in each class to reach an overall estimate of adult tortoises in each analysis area and range-wide. This approach resulted in mean estimates of current, adult Sonoran desert tortoise population sizes of 549,247 (range: 100,977–1,726,256) in Arizona and 273,013 (range: 47,346–782,140) in Sonora (Figure 18). Range-wide these estimates sum to 865,335 (range: 148,358–2,507,762) adult tortoises.

Future Conditions and Viability

We identified two threats, urban population growth and climate change, that are expected to affect Sonoran desert tortoise populations in the future. We used a habitat model to spatially project future conditions of the habitat of the Sonoran desert tortoise to serve as the basis to estimate population sizes and to conduct a simulation model to project future abundance and risks of quasi-extinction (defined as population simulations that drop to 2% or less of the starting population size). We projected future species' responses to climate change in two ways: changes in habitat suitability and decreases in survival rates in response to long-term increases in overall drought conditions. We also projected the effects of habitat loss due to urban growth and reduced survival around increasing areas of influence of larger future urban areas (Table ES-2). Our analysis of these future conditions (habitat suitability and demographic changes) provides a projection of resiliency, redundancy, and representation and the overall risk of extinction across our analysis areas for the species.

Table ES-2. Factors and assumptions made in the future scenarios used in the Sonoran desert tortoise status assessment.

		Low Effects Scenario (Upper Plausible Limit)	**High Effects Scenario (Lower Plausible Limit)**
Habitat	Climate Change	Future habitat suitability under RCP4.5 conditions	Future habitat suitability under RCP8.5 conditions
	Urban Growth	5-km buildout of Phoenix & Tucson metro areas (Eastern Cities) 1-km buildout on all other cities > 10k people (Western Cities & Sonora)	20-km buildout of Phoenix & Tucson metro areas (Eastern Cities) 5-km buildout on all other cities > 10k people (Western Cities & Sonora)
Demographic	Urban Influence	20-km influence on Phoenix & Tucson metro areas 10-km influence on all other cities > 10k people	
	Drought	No change in the average severity of drought compared to the last 30 years	Increase in the average severity of drought by 2080

Population resiliency at the analysis-unit scale was estimated with the population simulation model, projecting future abundance, population growth rates, and probabilities of the populations within the analysis areas falling below the quasi-extinction level. These projections of risk in terms of species abundance are largely influenced by the starting population size estimates. Because of the relatively large current estimated population sizes and the long-life span of these Sonoran desert tortoises, our simulation model suggests very low risks of quasi-extinction (< 1%) in the next 100 years of either the Arizona or Sonora analysis areas under either of the future scenarios even though slow population declines are projected (Table ES-3). When extended to 125 years, our simulation model suggests the risks of quasi-extinction remains very low under the "Low Effects" scenario but increases under the "High Effects" scenario to 7.8% and 5.3% in Arizona and Sonora, respectively. For the "High Effects" scenario, this increase in quasi-extinction risk was driven by the increased magnitude of change in survival rates due to drought and urban growth, leading to a substantial reduction in projected abundance at 125 years.

Table ES-3. Results of the population simulation model under different future scenarios, where N_0 is the median starting abundance of adult females; N_t is the median abundance (range) of adult females at time *t*; P_{Qet} is the median probability (range) of quasi-extinction at time *t*; and λ_{125} is the median population growth rate over 125 years; *% Change* is the percent change in abundance from initial values to 125 years.

Arizona, USA	*Initial Values*	*Results at 75 years*		*Results at 100 years*		*Results at 125 years*			
	N_0	N_{75}	P_{Qe75}	N_{100}	P_{Qe100}	N_{125}	P_{Qe125}	λ_{125}	% Change
Low Effects	**276,930** (*51,596–765,120*)	**242,807** (*45,903–670,127*)	**0.00%** (*0.00–0.10%*)	**233,109** (*43,894–651,161*)	**0.00%** (*0.00–0.40%*)	**225,604** (*42,831–633,273*)	**0.40%** (*0.00–1.30%*)	0.990	-18.5%
High Effects	**272,898** (*51,098–825,101*)	**123,817** (*24,012–371,681*)	**0.00%** (*0.00–0.30%*)	**72,057** (*14,164–214,663*)	**1.00%** (*0.20–2.10%*)	**35,972** (*7,139–107,355*)	**7.80%** (*5.20–10.80%*)	0.976	-86.8%

Sonora, Mexico	*Initial Values*	*Results at 75 years*		*Results at 100 years*		*Results at 125 years*			
	N_0	N_{75}	P_{Qe75}	N_{100}	P_{Qe100}	N_{125}	P_{Qe125}	λ_{125}	% Change
Low Effects	**127,998** (*24,969–375,443*)	**127,390** (*25,851–378,682*)	**0.00%** (*0.00–0.10%*)	**128,692** (*25,808–388,552*)	**0.00%** (*0.00–0.30%*)	**130,159** (*25,965–391,983*)	**0.20%** (*0.00–0.90%*)	0.991	1.6%
High Effects	**129,182** (*24,357–376,839*)	**68,546** (*12,651–205,731*)	**0.00%** (*0.00–0.20%*)	**42,173** (*7,705–127,165*)	**0.60%** (*0.00–1.50%*)	**22,483** (*4,176–67,582*)	**5.30%** (*3.20–7.90%*)	0.977	-82.6%

We assessed the redundancy (distribution of Sonoran desert tortoise populations) and representation (diversity) indirectly through projecting the suitability and quantity of habitat across the species range under different scenarios. Under the "Low Effects" scenario we project a 14% increase in the total amount of potential Sonoran desert tortoise habitat; specifically, the total amount of suitable habitat in Arizona increased from 30,475 sq mi (1.95 million ac, 7.89 million ha) to 34,883 sq miles (2.23 million ac, 9.02 million ha) of habitat by the 2080s (Table ES-4). Within this scenario for the Arizona analysis area, the model projected a 27% increase in high suitability habitat, a 50% increase in moderate suitability habitat, and a 19% decrease in low suitability habitat (Figure ES-2) (Table ES-4). The increase in the projected suitable habitat was largely tied to an increase in the suitability of mean winter temperatures. Although we did not explicitly project the future habitat suitability in Sonora, we assumed the same proportional change, and we projected an increase in total habitat from 18,747 sq mi (1.20 million ac, 4.86 million ha) of habitat currently to 20,119 sq mi (1.29 million ac, 5.21 million ha) of habitat in the 2080s (Table ES-4). While the amount of suitable habitat increased, the population growth rate at 125 years was slightly negative (λ_{125} = 0.990 and 0.991) which corresponded to the projected median female abundance changed by -18.6% in Arizona and 1.6% in Sonora (Table ES-3). Given that our "Low Effects" scenario assumes that the background rate of severe droughts does not increase into the future, a stable to slightly decreasing lambda is expected. Further, the slight decrease in abundance for the Arizona analysis area can also be described by the greater effect of urban areas on adult tortoise survival compared to Sonora. Given that the population growth rate was relatively stable through the simulation, there was a less than 0.5% chance for abundance dropping below our quasi-extinction threshold (Table ES-3).

Table ES-4. Current and future (2080s) suitable habitat estimates in square miles of suitable habitat of the Sonoran desert tortoise in Arizona and Sonora. Future projections include effects of climate change and urban growth.

Suitable Habitat Probability Class	Current	Low Effects Scenario		High Effects Scenario	
		Future	Proportion of Current	Future	Proportion of Current
ARIZONA					
High	8,532	10,852	127%	3,350	40%
Moderate	9,116	13,690	150%	13,776	151%
Low	12,828	10,341	81%	13,946	110%
Arizona Total	**30,475**	**34,883**	**114%**	**31,071**	**102%**
SONORA					
High	3,406	4,327	127%	1,328	39%
Moderate	4,945	7,422	150%	7,449	151%
Low	10,396	8,370	81%	11,227	108%
Sonora Total	**18,747**	**20,119**	**107%**	**20,004**	**107%**

Under the “High Effects” scenario, we projected a slight increase in the total amount of suitable habitat increased from 30,475 sq mi (1.95 million ac, 7.89 million ha) to 31,071 sq mi (1.99 million ac, 8.05 million ha) for Arizona in the 2080s and, by extension, from 18,747 sq mi (1.20 million ac, 4.86 million ha) to 20,004 sq mi (1.28 million ac, 5.18 million ha) for Sonora in the 2080s (Table ES-4, Figure ES-2). However, within this scenario for the Arizona analysis area, the changes correspond to a 61% decrease in the high suitability habitat class and increases of 51% and 9% for the moderate and low suitability habitat classes, respectively (Table ES-4, Figure ES-2). Although suitable habitat is projected to remain across the Sonoran desert tortoise’s range, the majority of the high suitability habitat is projected to be in the northern and eastern portions of its current distribution in Arizona (Figure ES-2). Under this scenario, the average population growth rates for the Sonoran desert tortoise population at 125 years were 0.976 for Arizona and 0.977 for Sonora, which corresponds to an approximately 2.7% annual decrease in the population. This growth rate corresponds to a projected reduction in the median population size of 86.8% in Arizona and 82.6% in Sonora over the next 125 years. Given these rates of decline, there was a less than 8.0% chance that the median abundance fell below the quasi-extinction threshold (Table ES-3). These long, slow declines are largely a result of the continual increasing effect of droughts that were assumed as part of this scenario. Population growth and survival rates are strongly influenced by drought with a mean estimated population growth rates of 0.97 (95% CRI: 0.92–1.00) when assuming severe drought conditions (Zylstra and Steidl 2021, pp. 5–8, 16). Additionally, we projected an increase in the rate of urban influence on the adult populations under our “High Effects” scenario. Although urban influence only affected adult survival and had a marginally smaller, and more variable impact than drought, there was also an annual increase in the proportion of the population subjected to that influence as population growth was projected into the future. Thus, the simulation model tracks an ongoing decrease in survival parameters as average drought conditions and the proportion of

the population subject to urban influence worsen over time.

Our projections indicate potential shifts in the range of the Sonoran desert tortoise that could affect overall redundancy and representation in the future, particularly under the "High Effects" scenario. The habitat models project that moderate and high suitability habitat will remain in varying amounts throughout the species distribution in Arizona. We are unable to posit where suitable habitat will remain within Sonora; however, we assume that suitable habitat will remain for the species within the Sonoran analysis unit into the future given the projected changes in habitat for Arizona under both future scenarios. Under the "Low Effects" scenario, the amount of habitat, including high quality habitat, increased and remained distributed across the species range (Figure ES-2). The spatial distribution of future habitat did not differ substantially from the current distribution of available habitat. Under the "High Effects" scenario, a substantial reduction in high suitability habitat is projected, with the remainder concentrated in the northern and eastern parts of the range in Arizona (Figure ES-2). Sonoran desert tortoise densities are generally currently higher in this portion of the species range, and estimated population growth rates and survival rates have been estimated to be higher in this portion of the species range as well. However, this portion of the range has an increased risk of wildfire and higher densities of nonnative invasive vegetation such as red brome and buffelgrass. The projected reduction in high suitability habitat within southern Arizona suggests some future reduction in tortoise abundances within that part of the range. High quality habitat under the "High Effects" scenario becomes aggregated in a large block on the southern Mogollon Rim (northeastern part of the tortoise's range), this would suggest a substantial reduction in high quality habitat. These effects are alleviated to some degree, however, by the increases in low and moderate suitability habitat areas throughout the remainder of the species' range. Distributional effects to tortoise habitat were not observed in the "Low Effects" scenario, as habitat is projected to increase under that scenario.

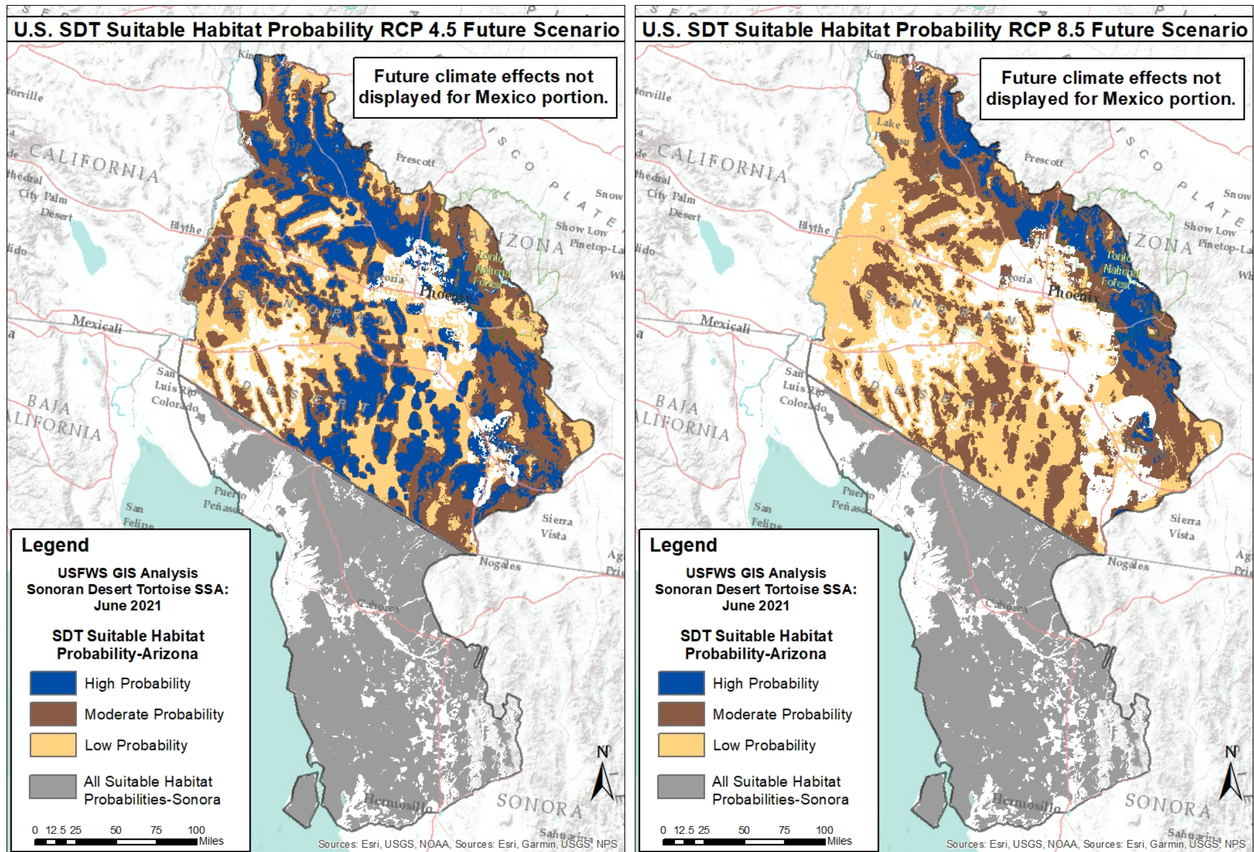


Figure ES-2. Projected future suitable Sonoran desert tortoise habitat under the "Low Effects" Scenario (left map) and "High Effects" Scenario (right map) in the 2080s. Future projections include effects of climate change and urban growth. Future suitable habitat was not modelled for Sonora.

Table of Contents

Executive Summary .... **iii**
Background iii
Species Biology and Needs iii
Risk Factors iii
Current Conditions iv
Future Conditions and Viability vi

Table of Contents .... **xi**

List of Acronyms and Abbreviations .... **xiii**

Chapter 1: Introduction **1**

Chapter 2: Species Biology and Needs **3**
2.1 Taxonomy 3
2.2 Species Description 3
2.3 Range 4
2.4 Life History 7
2.5 Resource Needs (Habitat) of Individuals 11
2.6 Defining Populations 14
2.7 Species' Range-wide Needs 17

Chapter 3: Risk Factors **19**
3.1 Altered Plant Communities (Nonnative Vegetation) 19
3.2 Altered Fire Regime 23
3.3 Habitat Conversion 29
3.4 Habitat Fragmentation 34
3.5 Climate Change and Drought 38
3.6 Human-Tortoise Interactions (Urban Influences) 40
3.7 Conservation Measures 43
3.8 Other Factors Considered 48

Chapter 4: Current Conditions **49**
4.1 Current Range 49
4.2 Current Habitat Suitability 49
4.3 Current Abundance Estimates 53

Chapter 5: Future Conditions and Viability **59**
5.1 Future Scenarios 59
5.2 Projected Habitat Change and Loss 60
5.3 Stochastic Simulation Model 65
5.4 Future Scenario Projections 71

Chapter 6: Summary of Viability and Uncertainties **76**
6.1 Viability Under Current Conditions 76
6.2 Viability Under Future Conditions 77
6.3 Uncertainty, Assumptions, and Models 79

Appendix A: Glossary **A-1**

Appendix B: Developing GIS Data Layers and Analysis for Sonoran Desert Tortoise (*Gopherus morafkai*) Species Status Assessment (SSA) **B-1**

Appendix C: Cause & Effects Tables C-1
Appendix D: Documentation of Conservation Activities Undertaken by Parties to the 2015 Sonoran Desert Tortoise CCA D-1
Appendix E: Stochastic Simulation Model Report for the Sonoran Desert Tortoise Species Status Assessment (SSA) E-1
Appendix F: Literature Cited for the Sonoran Desert Tortoise SSA Report v2.0 .... F-1

List of Acronyms and Abbreviations

ac- acre (1 ac = 0.0016 sq mi; = 0.04 ha)
Act- Endangered Species Act
AGFD- Arizona Game and Fish Department
AIDTT- Arizona Interagency Desert Tortoise Team
BLM- Bureau of Land Management
CCA- Candidate Conservation Agreement
cm- centimeter
ft- feet
GIS- Geographic Information Systems
ha- hectare (1 ha = 0.0039 sq mi; = 2.47 ac)
in- inches
km- kilometer
LTMP- long term monitoring plot
m- meter
mi- mile
mm- millimeter
PEP- Potassium Excretion Potential
REA SOD- Rapid Ecological Assessment for the Sonoran Desert
SDT – Sonoran desert tortoise
Service- U.S. Fish and Wildlife Service
SSA- Species Status Assessment
sq mi- square mile (1 sq mi = 640 ac; = 259 ha)
USFWS- U.S. Fish and Wildlife Service

Chapter 1: Introduction

The Sonoran desert tortoise (*Gopherus morafkai*) occurs in western, central, and southern Arizona and in northwest Sonora, Mexico, an area generally referred to as the Sonoran Desert. Prior to 2011, all tortoises in the Mohave and Sonoran Deserts were considered to represent a single species, the desert tortoise (*Gopherus agassizii*). Subsequent taxonomic revisions recognized the Sonoran desert tortoise to a unique species (*Gopherus morafkai*) (Murphy *et al*. 2011, p. 40). In 2008, the U.S. Fish and Wildlife Service (Service) was petitioned to list what is now recognized as the Sonoran desert tortoise as an endangered or threatened Distinct Population Segment (DPS) of the desert tortoise under the Endangered Species Act of 1973 (Act). The Service published a substantial 90-day finding on the petition on August 28, 2009 (74 FR 44335). On December 14, 2010, the Service found the species warranted for listing but precluded by higher priority actions, and the entity was added to the list of candidate species (75 FR 78094). After completing a SSA, the Service subsequently published a 12-month petition finding on October 6, 2015, determining that the Sonoran desert tortoise was not warranted for listing as endangered or threatened under the Act (80 FR 60321).

A complaint was filed on September 5, 2019, challenging the 2015 not-warranted finding for the Sonoran desert tortoise and alleging violations of the Act. The Service reached a settlement agreement with the petitioners, which was approved by the Federal Court on August 3, 2020, to reconsider our not-warranted finding and develop a new 12-month finding as to whether the Sonoran desert tortoise warrants listing as an endangered or threatened species. As a result of that agreement, the Service withdrew the 2015 12-month finding and returned the Sonoran desert tortoise to the candidate list. The Service agreed to submit to the Federal Register a new 12-month petition finding on the status of the Sonoran desert tortoise. This SSA report has been updated to inform that new 12-month petition finding.

The objective of the SSA is to thoroughly describe the viability of the Sonoran desert tortoise based on the best scientific and commercial information available. We developed this SSA report to summarize the most relevant information regarding life history, biology, and considerations of current and future risk factors facing the Sonoran desert tortoise. Through this description, we will determine what the species needs to remain viable, its current condition in terms of those needs, and its forecasted future condition. In conducting this analysis, we take into consideration the likely changes that are happening in the environment – past, current, and future – to help us understand what factors drive the viability of the species.

For the purpose of this assessment, we define **viability** as a description of the ability of a species to sustain populations in the wild within a biologically meaningful time frame. Using the SSA framework (USFWS 2016, entire; Smith *et al.* 2018, entire), we consider what the species needs to maintain viability by characterizing the status of the species in terms of its **resiliency**, **redundancy**, and **representation**.

- **Resiliency** is the ability of a species to withstand environmental stochasticity (normal, year-to-year variations in environmental conditions such as temperature, rainfall), periodic disturbances within the normal range of variation (fire, floods, storms), and demographic stochasticity (normal variation in demographic rates such as mortality and

fecundity). Simply stated, resiliency is the ability to sustain populations through the natural range of favorable and unfavorable conditions. We can measure resiliency based on metrics of population condition; in the case of the Sonoran desert tortoise, the primary indicators of resiliency are population abundance, population growth rates, and quasi-extinction risk.

- **Redundancy** is the ability of a species to withstand catastrophes. Catastrophes are stochastic events that are expected to lead to population collapse regardless of population health and for which adaptation is unlikely. Redundancy is about spreading the risk and can be measured through the duplication and broad distribution of resilient populations across the range of the species. The more resilient populations the species has, distributed over a larger area, the better chances that the species can withstand catastrophic events. For the Sonoran desert tortoise, we are using the geographic distribution of predicted potential habitat, as described by geospatial analyses and quasi-extinction risk, to measure redundancy.

- **Representation** is the ability of a species to adapt to both near-term and long-term changes in its physical (climate conditions, habitat conditions, habitat structure, etc.) and biological (pathogens, competitors, predators, etc.) environments. This ability to adapt to new environments--referred to as adaptive capacity--is essential for viability, as species need to continually adapt to their continuously changing environments. Representation can be measured through the genetic diversity within and among populations and the ecological diversity (also called environmental variation or diversity) of populations across the species' range. Theoretically, the more representation, or diversity, the species has, the higher its potential of adapting to changes (natural or human caused) in its environment. Quasi-extinction risk and geographic distribution of predicted potential habitat (via geospatial analyses) are also being used to describe representation for the Sonoran desert tortoise.

To evaluate the viability of the Sonoran desert tortoise both currently and into the future, we assessed a range of conditions to allow us to consider the species' resiliency, redundancy, and representation.

This SSA report does not result in, nor predetermine, any decisions by the Service under the Act. In the case of the Sonoran desert tortoise, the SSA report does not determine whether the species warrants protections of the Act, or whether it should be proposed for listing as a threatened or endangered species under the Act. That decision will be made by the Service after reviewing this document, along with the supporting analysis, any other relevant scientific information, and all applicable laws, regulations, and policies. The results of the decision will be announced in the *Federal Register*. Instead, this SSA report provides a strictly scientific review of the available information related to the biological status of the Sonoran desert tortoise.

Chapter 2: Species Biology and Needs

In this chapter, we provide basic biological information about the Sonoran desert tortoise, including its taxonomic history, range, morphological description, and known life history traits. We then outline the resource needs of individuals. Lastly, we provide our rationale for defining populations and outline the species' range-wide needs.

2.1 Taxonomy

The desert tortoise (*Gopherus agassizii*) was first formally described by Cooper (1863, pp. 118–123), and this taxonomic designation was applied to all tortoises found in the Mojave and Sonoran Deserts on both sides of the Colorado River. In 2011, genetic analysis supported elevating the Sonoran population of the desert tortoise as a unique species, Morafka's desert tortoise (*Gopherus morafkai*) (Murphy *et al.* 2011, p. 53), confirming the taxonomic distinction previously hypothesized (Lamb *et al*. 1989, p. 83; Lamb and McLuckie 2002, p. 74; Van Devender 2002, p. 24). The Sonoran desert tortoise taxonomy was further distinguished in the southern portion of its range with the description of its sister taxon, the Goode's thornscrub tortoise (*G. eygoodei*) (Edwards et al. (2016, entire), discussed below. To minimize potential confusion of acronym use with its sister species, the Mohave desert tortoise (*G. agassizii*), and adhere to long-used geographic references in the common name, Crother *et al.* (2017, p. 85) recommended retaining the common name of Sonoran desert tortoise for *G. morafkai*. The Sonoran desert tortoise is known in Mexico by the common names of "tortuga del monte," "Galápago de desierto," or the "xtamóosni" (Rorabaugh 2008, p. 35). The Sonoran desert tortoise, or "Komckud" in their native language, is the namesake for the Tohono O'odham Nation's capital, Sells, Arizona, where, from legend, the Sonoran desert tortoise became wedged between two mountain ranges, forming the community (Tohono O'odham Nation 2021, p. 3).

The currently accepted species classification is:

Class: Reptilia
Order: Testudines
Family: Testudinidae
Genus: *Gopherus*
Species: *morafkai*

2.2 Species Description

In Arizona, adult Sonoran desert tortoises (Figure 1) range in total carapace (straight-line top shell) length from 8 to 15 inches (in) (20 to 38 centimeters [cm]), with a relatively high domed shell (Arizona Game and Fish Department [AGFD] 2001, p. 1; Brennan and Holycross 2006, p. 54). The carapace is usually brownish or dark in color with a definite pattern and prominent growth lines (AGFD 2001, p. 1; Murphy *et al.* 2011, p. 56). The plastron (bottom shell) is yellowish and is not hinged (AGFD 2001, p. 1; Brennan and Holycross 2006, p. 54). The hind limbs are very stocky and elephantine; forelimbs are flattened for digging and covered with large conical scales (AGFD 2001, p. 1; Brennan and Holycross 2006, p. 54). Male Sonoran desert tortoises are differentiated from females by having elongated gular (throat) shields, chin glands visible on each side of the lower jaw (most evident during the breeding season), and a concave

plastron (AGFD 2001, p. 1). For a more detailed description of the species' holotype, see Murphy *et al.* (2011, pp. 55–56).

Figure 1. Image of a Sonoran desert tortoise in Arizona. (Jeff Servoss, USFWS)

2.3 Range

Traditionally, the range of the Sonoran desert tortoise has been defined as all areas occupied by tortoises east and south of the Colorado River in Arizona, United States, and south into Sonora, Mexico. Recent studies of tortoises along the northern and southern portions of this range, however, have refined the distribution of the species along the northwestern portion of the range (i.e., the Black Mountains) and the area east and south of Rio Sonora in Mexico (i.e., Sinaloa) to result in the range used in this SSA (Figure 2). These areas are described in more detail below.

Based on the range boundaries used for our analysis, the total area within the estimated range of Sonoran desert tortoise is about 68,600 square miles (sq mi) (about 44 million acres (ac), or 18 million hectares (ha)). This range includes about 42,800 sq mi (about 27 million ac, 12 million ha), or 62%, in Arizona, U.S., and about 25,800 sq mi (about 17 million ac, 7 million ha), or 38%, in Sonora, Mexico.

2.3.1 Black Mountains

Recent genetic analysis and modeling confirmed the work of McLuckie (1999, entire) that desert tortoises south, west, and north of the Black Mountains in Arizona are Mohave desert tortoises (*G. agassizii*) and further documented the extent of the range of this species in the area; this determination was further supported by habitat and topographical variables and modeling (Edwards *et al.* 2015, entire; Inman *et al*. 2019, Figure 5; Dolby *et al*. 2021, entire). Genetic admixture (hybridization) occurs between the Sonoran and Mohave genotypes in many areas east of the Black Mountains, including in the Hualapai Mountains and the White Hills area (Figure 2; Edwards *et al.* 2015, p. 2105). Genetic data suggest that hybridization of Sonoran and Mohave

desert tortoises is minimized farther east from the Colorado River (Edwards *et al.* 2015, p. 2107, Dolby *et al*. 2021, p. 20). The geographic distribution of hybrid individuals, and thus the hybrid zone, is likely a result of proximity to phylogenetic recontact zones (Edwards *et al.* 2015, p. 2107). Dolby *et al.* (2021, p. 19) further suggest that the introgression between these two species is a result of secondary contact during postglacial expansion in this region. There is a disproportionate distribution of hybrid classes spatially, with Mohave desert tortoise backcrosses dominant in the Black Mountains area and Sonoran desert tortoise backcrosses primarily distributed in the Hualapai Mountains (Edwards *et al.* 2015, p. 2107, Table 4). The data also suggest the Mohave desert tortoise genotype extends farther north into the White Hills (Edwards *et al.* 2015, p. 2105), which was confirmed by Dolby *et al.* (2021, p.15) with two Mohave desert tortoises being identified through genetics near Temple Bar in Lake Mead National Recreation Area.

Dolby *et al.* (2021, p. 15) documented hybridization between the two species south and east of Interstate Highway 40 (IH-40), including the Hualapai Mountains, as well as more extensive hybridization west of IH-40. Factoring these data and other genetic studies, we used the spine of the Black Mountains north and west of IH-40 to its junction with IH-40, then IH-40 westbound as our boundary for the Sonoran desert tortoise SSA. We used the spine of the Black Mountains, in conjunction with IH-40 as our boundary for separating the two tortoise species due to the predominance of Sonoran desert tortoises over Sonoran-Mohave hybrids on the east side of the Black Mountains, including in the Hualapai Mountains (Figure 2). Additionally, it is our understanding that there are no Sonoran desert tortoises west of the spine of Black Mountains. Therefore, we included the east side of the Black Mountains north and west of IH-40 in this Sonoran desert tortoise analysis. Since this is a hybrid zone, we acknowledge that our analysis area likely includes some Mohave desert tortoises. Rather than defining a boundary to exclude Mohave desert tortoises east of the spine of the Black Mountains, we set the boundary to be inclusive of areas predominately containing the Sonoran desert tortoise genotype.

2.3.2 Sinaloa

In Sonora, which is bisected by the Rio Sonora and characterized as largely Sinaloan thornscrub, desert tortoises are comprised of genetically and geographically distinct "Sonoran" and "Sinaloan" lineages (Edwards 2015, p. 68). Sinaloan thornscrub and tropical deciduous forest habitat in this region of Sonora represented a shifting, ephemeral boundary over geologic time that drove adaptations unique to both the core Sinaloan lineage found in tropical deciduous forest and the core Sonoran lineage, found in Sonoran desertscrub (Edwards 2015, p. 77). Despite the presence of a narrow contact zone of limited introgression between these tortoise lineages and incomplete reproductive isolation, the Sonoran and Sinaloan lineages of the desert tortoise are on separate evolutionary trajectories exhibited by deep divergence in their respective genotypes which is consistent with species-level divergence in other turtle and tortoise genera (Edwards 2015, p. 78). Subsequently, Edwards *et al*. (2016, entire) described a new species in the *G. morafkai-G. agassizii-G. berlandieri* (Texas tortoise) group, the Goode's thornscrub tortoise (*G. evgoodei*). This species is found to be strongly associated with Sinaloan thornscrub and tropical deciduous forest habitats in southern Sonora and northern Sinaloa, Mexico.

Although these two tortoise lineages hybridize south of the Rio Sonora, there is sharp genetic

cline that corresponds to marked habitat changes in the region (Edwards 2015, p. 78; Edwards *et al*. 2016, p. 133). Therefore, we used the Rio Sonora as the southern and eastern boundary of the Sonoran desert tortoise for this assessment (Figure 2). While we recognize the difficulty in identifying a boundary line on a map given the incomplete reproductive isolation resulting in the admixture of genetic lineages present on either side of an artificial boundary, we removed the area of the range south of Rio Sonora from our Sonoran desert tortoise analysis based subjectively on results from genetic research (Edwards 2015, pp. 67–101). Throughout the remainder of this SSA report, references to the range of the Sonoran desert tortoises refers to the analysis area as indicated in Figure 2.

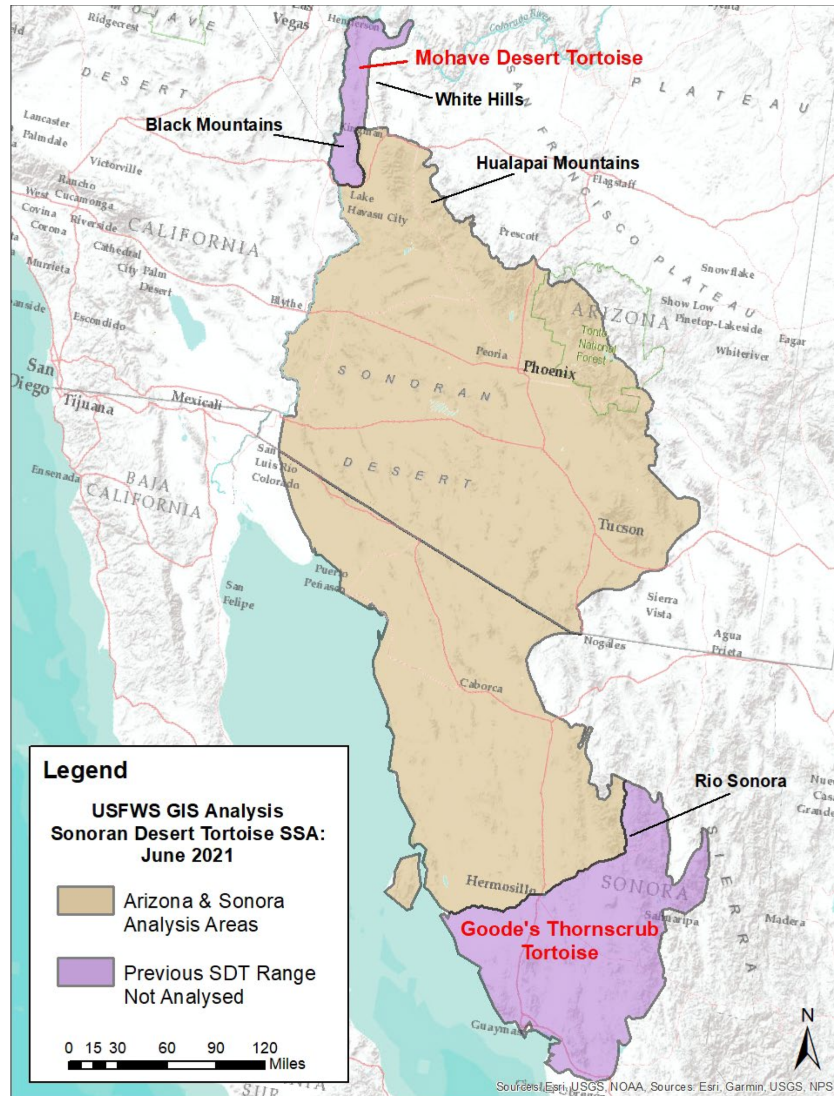


Figure 2. Sonoran desert tortoise range boundary used for this status assessment, showing areas that were previously included as portions of the Sonoran desert tortoise species range. Note that the ranges of the Mohave desert tortoises and Goode's thornscrub tortoises extend well beyond the areas identified on this map.

2.4 Life History

Sonoran desert tortoises are long-lived and grow slowly. In this analysis, we consider three life stages: young juveniles, older juveniles (or subadults), and adults (Figure 3). Time spent in each of these life stages is size-dependent. In the following paragraphs, we discuss each of these life stages.

The young juvenile size class includes hatchlings and very small juveniles. Sonoran desert tortoises generally remain in this size class for approximately 5 years. Eggs hatch in September and October (Averill-Murray 2002b, p. 295; Van Devender 2002, pp. 10–11), following the end of the monsoon season. The behavior and ecology of young juveniles is poorly understood because their small size makes them difficult to detect in the wild. Sonoran desert tortoises are most vulnerable to predation while in this age class, predominantly because of their small size and their softened shells, which provide little protection and are easily compromised until they ossify (harden) at approximately 4.3 in (110 millimeters (mm)) midline carapace length (MCL) (Nagy *et al*. 2011, p. 194). Gila monsters (*Heloderma suspectum*) may be a primary predator on Sonoran desert tortoise eggs (Barrett and Humphrey 1986, p. 262); coachwhips (*Coluber* (=*Masticophis*) *flagellum*) and gophersnakes (*Pituophis catenifer*) have been reported to consume young juvenile tortoises (Amarello *et al.* 2004, p. 178). Red-tailed hawks (*Buteo jamaicensis*) (Anderson and Berry 2019, p. 351) and American badgers (*Taxidea taxus*) (Emblidge *et al*. 2015, entire) are wide-ranging generalists that have been documented as predators of Mohave desert tortoise juveniles as well; although this has not been confirmed in the scientific literature, these species may consume Sonoran desert tortoises.

Once their shells are completely ossified (usually by the time they are 4.3 in (110 mm) MCL), Sonoran desert tortoises are considered to be older juveniles and they remain in this size class from approximately age 6–15 (or 18 years for males (Owens *et al.* 2019, entire)), depending on varying environmental conditions that affect individual growth rates and transition time to the adult stage. In one study examining Sonoran desert tortoise at 17 sites monitored multiple times between 1987 and 2020, survival rates during the older juvenile stage were estimated at 82% (Zylstra and Steidl 2021, p. 7) and varied from 70–89% in a spatially explicit hierarchical model (Campbell *et al.* 2018, p. 2060). Older juvenile survivorship is presumably higher than that of the young juvenile age class given their slightly larger size and completely hardened shells. Time spent in this size class ends when Sonoran desert tortoises reach sexual maturity, which typically occurs when their shells reach approximately 8.7 in (220 mm) MCL and is strongly influenced by precipitation trends (Averill-Murray and Klug 2000, p. 69; Averill-Murray *et al.* 2002b, p. 119; Bury *et al.* 2002, p. 100; Germano *et al.* 2002, p. 265). Minimum size at sexual maturity for males was documented at 8.3 in (210 mm) MCL for an individual approximately 18–19 years of age, based on established growth projection data (Owens *et al.* 2019, entire).

Generally, Sonoran desert tortoises transition to the adult size class around the ages of 16 (female; 8.7 in (220 mm)) to 18–19 (male; 8.3 in (210 mm)). Transition rates from juvenile to adult age classes were estimated to be between 7–13% across the range (Campbell *et al.* 2014, pp. 2, 14; Campbell *et al.* 2018, p. 2061; Zylstra and Steidl 2021, p. 6), which is consistent with a long-lived species that requires 16 to over 20 years to reach sexual maturity. Longevity of Sonoran desert tortoises in the wild is estimated to be 42–54 years (Curtin *et al*. 2009, p. 4), and

many are presumed to live longer. Annual survivorship for adult Sonoran desert tortoises in Arizona (based on long-term monitoring plot (LTMP) data from 1987–2020) has been estimated to average 96% for females and 95% for males (Zylstra and Steidl 2021, p. 6), which is well within values of survivorship that would be expected for long-lived species in general, and tortoises in particular (Heppell 1998, p. 370). Across the species' range in Arizona, adult survival rates varied from 85–95% with survival rates tending to be lower in the northwestern portion of the range and higher in the central and eastern portion of the range (Campbell *et al*. 2018, pp. 2060–2061). Adult tortoises are relatively protected from natural predation because of their size and hard shells. Sustaining the adult, reproductive age class within Sonoran desert tortoise populations is important because mortality rates of juveniles are high, and it takes a long time for a Sonoran desert tortoise to reach sexual maturity (Howland and Rorabaugh 2002, p. 339). Spatially quantified throughout their range in Arizona (based on a recruitment estimate of 0.32 females per female per year), the rate of population change (i.e., lambda) varied spatially from 0.94–1.03 and tended to be higher in the central and eastern parts of the range and lower in the southern and northwestern portions (Campbell *et al*. 2018, Figure 2, p. 2060). The overall range-wide rate of change was 0.99 (Table 1). A lambda < 1.00 indicates population decline, > 1.00 indicates population growth, and 1.00 indicates a stable population (no change).

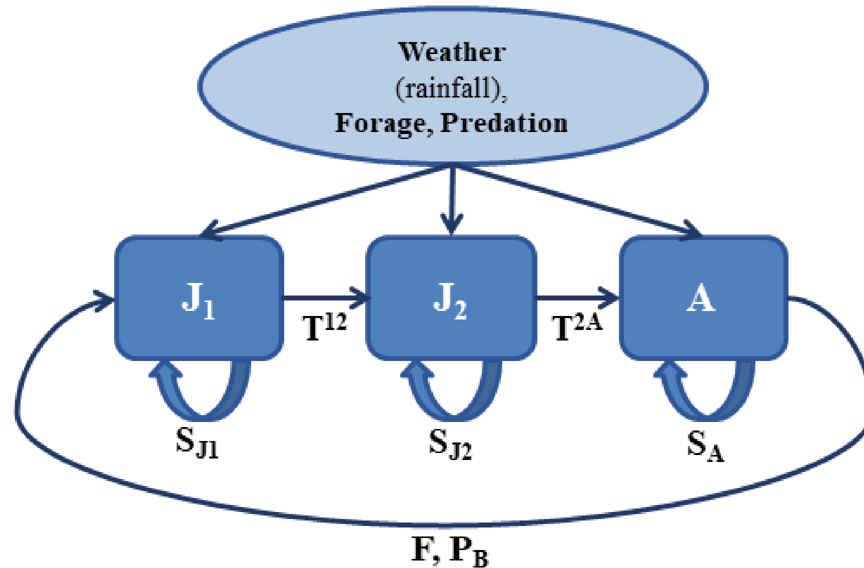
The Sonoran desert tortoise's breeding season generally occurs from July through October. Reproductive success is strongly influenced by environmental conditions (Averill-Murray *et al.* 2018, entire). In females, yolk deposition, or vitellogenesis, is typically initiated during the period of cold-season dormancy and continues during the spring until the process is complete (Averill-Murray *et al.* 2018, p. 41). Approximately half of the adult females in a population reproduce in any given year (Campbell *et al.* 2014, p. 2). Females may store sperm for up to two years, meaning that one year's mating could produce the following year's clutch of eggs (Palmer *et al.* 1998, pp. 704–705; Averill-Murray *et al*. 2002a, p. 141). Female Sonoran desert tortoises may lay one clutch of 1–12 eggs per year, usually around the onset of the summer rainy season (monsoon), although they may not produce a clutch every year (Averill-Murray 2002b, p. 295; Campbell *et al*. 2015, Table 2; Averill-Murray *et al.* 2018, pp. 38, 44). The average egg clutch size is 5.15 with a 61% hatch rate (Campbell *et al*. 2014, p. 2). Mean clutch size may vary considerably among years but does not appear to be related to rainfall, body size, or emergence date, but is directly influenced by body condition (Averill-Murray *et al.* 2018, p. 40).

Females occasionally lay two clutches per year if eggs have been retained from the previous year (Lovich *et al.* 2017, p. 319). Bimodal seasonal precipitation associated with the Sonoran Desert is hypothesized to select for late season hatching of smaller offspring (Ennen *et al.* 2017, entire). Extreme drought years can reduce or eliminate ovarian follicle development in the subsequent reproductive season (Averill-Murray *et al.* 2018, p. 37). When annual rainfall is below average, half of females that developed follicles of near-ovulatory size failed to reproduce that year. Reabsorption of follicles is suspected to occur when adequate forage is unavailable (Averill-Murray *et al.* 2018, p. 42).

Female Sonoran desert tortoises that survive to reproductive age can produce as many as 85 eggs over the course of their lives. While it has not been shown in other chelonian species, it is possible that females may undergo reproductive senescence at an unknown age, where egg development ceases indefinitely, but more research is required to test this hypothesis (Averill-

Murray *et al.* 2018, p. 42). However, given the survival rates for Sonoran desert tortoises, only two or three of those hatchlings produced over a female's life may survive to reproductive age (Van Devender 2002, p. 11). Modeling data reported herein considered three age classes of Sonoran desert tortoises (young juveniles, older juveniles, and adults). For an expanded treatment of reproduction and first-year survival of hatchling Sonoran desert tortoises, see Campbell *et al*. (2015, entire). Hatching success may be improved by nest defense behavior that has been observed in female Sonoran desert tortoises (Barrett and Humphrey 1986, pp. 261–262).

Sonoran desert tortoise behavior varies greatly among the seasons and at different elevations: tortoises at moderate to higher elevations exhibit the most notable surface activity during the early–mid spring, and again during the summer monsoon, spending the rest of the year in their shelters unless surfacing in response to precipitation (Sullivan *et al.* 2014, pp. 116–118) or other physiological needs. At lower elevations, Sonoran desert tortoises may emerge to bask any month of the year including November through March (Sullivan and Sullivan 2015, entire; Sullivan 2021, p. 3). Sonoran desert tortoise surface activity largely mimics the warm-season precipitation pattern (Averill-Murray *et al.* 2002a, p. 139; Van Devender 2002, p. 7). During the winter months from mid-November through mid-February, Sonoran desert tortoises are largely dormant within their shelters, although they may emerge to bask in response to thermoregulatory needs, to move between shelter sites, or to rehydrate during or after rainfall (Averill-Murray and Klug 2000, p. 66; Sullivan *et al.* 2014, pp. 116–118). A recent study found that 11 of 17 tortoises at one study site, affixed with radio transmitters, moved an average of 1,263 ft (385 m) from November through February, with more females than males moving, including longer distance movements of two female tortoises of 4,199 ft (1,280 m) and 3,281 ft (1,000 m) (Rubke and O'Donnell 2021b, p. 8). Opportunities to forage and rehydrate may be particularly important to Sonoran desert tortoises in their smaller size classes due to their limited capacity to build up energy reserves (Sullivan *et al.* 2014, p. 118; Sullivan and Sullivan 2015, entire). Periods of dormancy appear to vary greatly among populations and among years but appear to correlate with seasonal temperatures (Bailey *et al.* 1995, p. 367; Averill-Murray and Klug 2000, p. 66). During the spring, gravid (egg-bearing) females are typically the first to emerge and become surface active every year (Averill-Murray *et al.* 2002a, p. 138). The average date of emergence of reproductive females from winter shelter sites, was calculated from 10 years of data (1993 and 1997–2005) (Averill-Murray *et al.* 2018, p. 37). The average date of emergence for female tortoises that laid eggs that season was March 12, whereas the average date of emergence for females that were sexually mature but did not lay eggs that season was April 22 (Averill-Murray *et al.* 2018, p. 37). To acquire energy for egg development, females emerge during the spring to forage on spring annual plants generated by winter rains. While a small percentage of adult males may emerge during the spring, their primary surface-active season coincides with the summer monsoon (July through September), as it does for both sexes and all age classes (Averill Murray *et al.* 2002a, pp. 139–140). The Sonoran desert tortoise is diurnal (active during daylight hours) but may emerge at night to drink in response to rainfall (Sullivan and Sullivan 2015, p. 10). Availability of free-standing water, both spatially and temporally (for drinking) (Sullivan *et al*. 2014, entire), is thought to be critical to the survival of Sonoran desert tortoises. Sonoran desert tortoises can efficiently drink water from small, shallow catchments by using their nares (nostrils) and pulsating their throats to create a vacuum (Sullivan and Sullivan 2016, entire).



Where:

J_1 = Young Juveniles, from age 0–5 years (approximately 4.3 in (110 mm) MCL); the time in this stage is size-dependent and ends with firm calcification of the shell; stage includes hatchlings

J_2 = Older Juveniles from approximately age 6–15 years (approximately 8.3 in (210 mm) MCL); the time in this stage is size-dependent and ends with sexual maturity

A = Adults, from approximately age 16 years to death (greater than 8.3 inches (210 mm) MCL); life span is something beyond 50 years, as long as 100 years

S_{J1} = Survival rates during the Young Juvenile stage (Relatively Low)

S_{J2} = Survival rates during the Older Juvenile stage (Uncertain)

S_A = Survival rates during the Adult stage (Really High)

F = Fecundity, approximately 4 to 6 eggs per female, per breeding year; can vary; includes egg survival; only about 52% of females breed year

P_B = Probability of breeding

T^{12} = Transition rate from Young to Older Juvenile

T^{2A} = Transition rate from Older Juvenile to Adult

Weather (timing and amount of rainfall), **Forage Availability**, and **Predation** are the primary natural influences affecting all survival rates and fecundity.

Figure 3. The basic life history profile for the Sonoran desert tortoise.

2.5 Resource Needs (Habitat) of Individuals

Sonoran desert tortoises primarily inhabit rocky, steep slopes and bajadas of Mojave Desertscrub and the Arizona Upland and Lower Colorado River subdivisions of Sonoran Desertscrub (habitat definitions are from Brown 1994, entire; see Figure 4). Over 95% of all Sonoran desert tortoise records in Arizona are located between elevations ranging from approximately 0 to 5,000 feet (ft) (1,524 meters (m)). They most often occur in the paloverde-mixed cacti associations (Ortenburger and Ortenburger 1927, p. 120; Barret 1990, entire; deVos *et al.* 1983, p. 144; Vaughan 1984, p. 30); however, records have also been documented in Madrean Evergreen Woodland (Babb *et al.* 2013, entire), montane conifer forest (Aslan *et al*. 2003, entire), Semidesert Grassland, Interior Chaparral, Plains of Sonora, and Sinaloan Thornscrub habitats (Molina-Padilla and Van Devender 2019, entire). Habitat characteristics facilitate many life history needs for the Sonoran desert tortoise, including foraging, providing short- and long-term cover from exposure, providing concealment and protection from predators, offering thermoregulatory opportunities, facilitating movement, and providing opportunities for hydration. Telemetry research from one of the best studied locations suggests that Sonoran desert tortoises may select for vegetation type over any other habitat attribute including specific soil types, slope, or wash habitat in some areas (Leavitt *et al.* 2017, p. 6).

The Sonoran desert tortoise is an herbivore that has been documented to eat 199 different species of plants, including herbs (55.3%), woody plants (22.1%), grasses (17.6%), and succulents (5%) (Ogden 1993, pp. 1–8; Van Devender *et al.* 2002, pp. 175–176; Brennan and Holycross 2006, p. 54; Oftedal 2007, p. 21; Ernst and Lovich 2009, p. 562; Meyer *et al.* 2010, pp. 28–29, 44–48). Sonoran desert tortoises may also consume some species of nonnative plants which provide various degrees of nutritional benefit (Nagy *et al*. 1998, entire) but avoid consuming others (Gray and Steidl 2015, entire). Sonoran desert tortoises may obtain less of their metabolic water from their diet than previously thought, as Sullivan *et al*. (2014, entire) found a high proportion of telemetered Sonoran desert tortoises became surface-active to drink free-standing water in response to precipitation regardless of time of year. However, plant species eaten by Sonoran desert tortoises can directly affect their hydration-state. Many plant species contain potassium and Sonoran desert tortoises lose water in the process of metabolizing potassium (Oftedal 2002, p. 214). The potassium excretion potential (PEP) is an index of water, nitrogen, and potassium levels in a plant that affects the ability of all desert tortoises to efficiently excrete potassium. A positive PEP value for a plant species (preferred by Sonoran desert tortoises) means there is more water and nitrogen in the food than is needed to excrete potassium (water gained), and the opposite is true for a negative PEP value (water lost) (Oftedal 2002, p. 215). Sonoran desert tortoises have been documented selectively foraging on high PEP plant species (Oftedal 2002, p. 223; Oftedal 2007, pp. 3, 22). High PEP values can be found in certain species of primroses, filaree, legumes, mustards, and spurges (Ernst and Lovich 2009, p. 545), and access to high PEP plant species may be especially important for Sonoran desert tortoises to overcome the effects of drought (Averill-Murray *et al.* 2002a, p. 146; Ernst and Lovich 2009, p. 545).

A Sonoran desert tortoise's large, bi-lobed bladder is also critical for withstanding the effects of drought because it stores a high volume of water, dilutes excess dietary salts and metabolic wastes, and reabsorbs water into the bloodstream, allowing Sonoran desert tortoises to forage on dried vegetation while reducing the effect of dehydration (Averill-Murray *et al.* 2002a, p. 146;

Ernst and Lovich 2009, p. 545). When free-standing water for drinking becomes available, Sonoran desert tortoises drink to flush salts and reset the electrolytic balance in preparation for the next dry period (Averill-Murray *et al.* 2002a, pp. 140, 146).

In addition to using vegetation within these biotic communities for nutritional needs, the Sonoran desert tortoise uses vegetation (cover plants) for predator avoidance, thermal regulation, and in social behaviors (Avery and Neibergs 1997, p. 13; Grandmaison *et al.* 2010, p. 585).

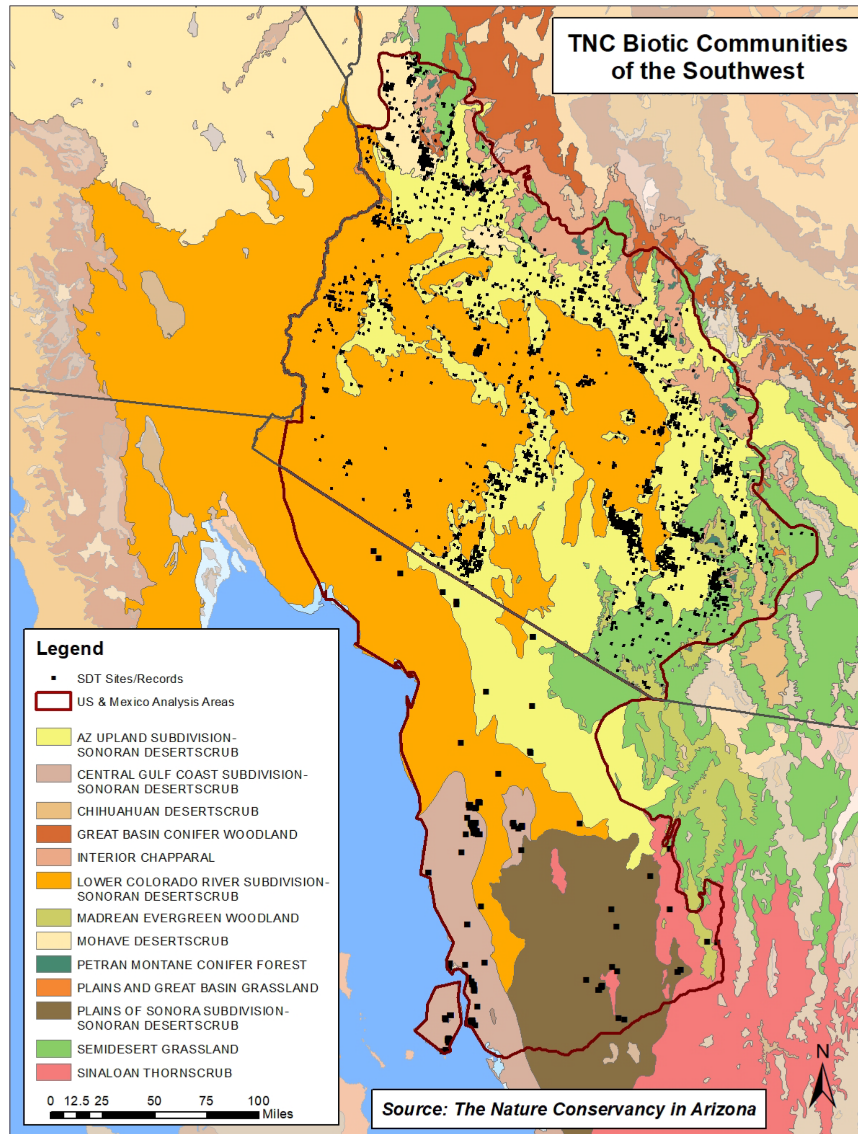


Figure 4. Biotic communities (from Brown 1994, entire) within the Sonoran desert tortoise's range encompassing portions of Arizona, U.S. and Sonora, Mexico, with tortoise records identified. Species records for Sonora were obtained from field investigations, museums, literature, and photo-vouchers as provided by Rosen *et al.* (2014a, Figure 1.2). Records for Arizona are from the Heritage Database Management System, provided as a courtesy of the Arizona Game and Fish Department.

In addition to herbivory, Sonoran desert tortoises are also geophagous, consuming bones, stones, and soil or mineral deposits for additional nutrient and mineral supplements, for mechanical assistance in grinding plant matter in the stomach, or to expel parasites in the intestinal tract (Sokol 1971, p. 70; Marlow and Tollestrup 1982, p. 475; Esque and Peters 1994, pp. 108–109; Stitt and Davis 2003, p. 57; Walde *et al.* 2007b, p. 148; Sullivan and Cahill 2019, entire). Both sexes and all age classes use these resources. For example, reproductive female Sonoran desert tortoises will regularly consume caliche fragments and mineral deposits during the spring and early summer months (April–June) to assist with the development of egg shells (Sullivan and Sullivan 2018, entire; Sullivan and Cahill 2019, entire). Sonoran desert tortoises are highly attracted to sites with exposed calcium carbonate and have been observed congregating at these sites year after year to eat these soils (Meyer *et al.* 2010, p. 11). Soil condition and quality are important to the Sonoran desert tortoise, not only for nutrients derived from eating soil, but also production and maintenance of vegetation that is consumed by Sonoran desert tortoises (Avery and Neibergs 1997, p. 13).

Sonoran desert tortoises spend a large proportion of their lives in shelters and appear to show strong shelter site fidelity among years and among seasons (Rubke and O'Donnell 2020c, p. 10). Adequate shelter is one of the most important habitat features for Sonoran desert tortoises (Averill-Murray *et al.* 2002a) and is correlated with population densities (Averill-Murray and Klug 2000, p. 69; Averill-Murray *et al.* 2002b, p. 126; Averill-Murray *et al.* 2020, entire). Shelters stay cooler in the summer and warmer in the winter than outside temperatures, providing opportunity for Sonoran desert tortoises to escape temperature extremes. Shelters are also used for nesting and protection from predators (Barrett and Humphrey 1986, p. 262; Bailey *et al.* 1995, p. 366; Zylstra and Steidl 2008, p. 752). Sonoran desert tortoises require loose soil in which to excavate shelters below rocks and boulders, beneath vegetation, on semi-open slopes, and within caliche caves of washes, or they may find refuge in rocky crevices (Burge 1979, p. 44; 1980, pp. 44–45; Barrett 1990, p. 205; Averill-Murray *et al.* 2002a, pp. 136–137; Grandmaison *et al.* 2010, p. 582). In lower bajada sites, caliche caves within incised washes provide critical sheltering opportunities during multiple seasons of the year (Sullivan 2021, p. 2) where surface soil types or a low abundance of rock structure limit other sheltering opportunities. These shelter sites may also provide the species with easy access to highly ephemeral water catchments that occur along wash bottoms after precipitation events. Sonoran desert tortoises have been observed using caliche caves as shelter sites, followed by above ground refuges such as woodrat (*Neotoma sp.*) middens and pallets under shrubs (Sullivan *et al.* 2016, p. 512). Caliche caves that offer particularly favorable microclimates will receive regular, seasonal use over years suggesting high shelter site fidelity by Sonoran desert tortoises, particularly females (Sullivan *et al.* 2016, pp. 513, 517).

In addition to steep, rocky slopes and bajadas, Sonoran desert tortoises also use inter-mountain valleys as part of their home ranges and for dispersal at all age classes (Averill-Murray and Averill-Murray 2002, pp. 16, 22), but particularly the juvenile age class (Averill-Murray *et al.* 2020, pp. 264, 266). In fact, 50% of juveniles dispersed outside their natal area over a 10-year period of study (Averill-Murray *et al.* 2020, pp. 264, 266). Infrequently, juvenile and adult Sonoran desert tortoises of both sexes will journey outside their home range for potentially one or more active seasons and subsequently return to their original core areas; this type of movement is referred to as a "sally", which may be mistaken for dispersal (Averill-Murray *et al.*

2020, p. 259). In some areas, desert washes may be more important for Sonoran desert tortoise movement but movements may be infrequent (Leavitt *et al.* 2016, pp. 7–9). Due to comparatively small effective population sizes of Sonoran desert tortoises, dispersal may play an important role in the long-term maintenance of populations, particularly in the event of drought or stochastic events (Edwards 2003, pp. 61–62). In the Ironwood Forest National Monument, researchers found Sonoran desert tortoises or their sign (such as scat (droppings) and shelters) up to 1 mile (mi) (1.6 kilometers [km]) away from the nearest slope, indicating that they occur in low densities in inter-mountain valleys (Averill-Murray and Averill-Murray 2005, p. 65). Sonoran desert tortoises have not been documented in broad, flat valleys in between mountain ranges in Sonora (Bury *et al.* 2002, p. 89), although, depending on the spatial extent of the area, they may use these areas for dispersal much as they do in similar areas of Arizona.

Drought conditions do not appear to affect home range size (Averill-Murray *et al.* 2020, p. 265). Sonoran desert tortoises often use a group of relatively closely located shelters as focal areas of activity in their home range and may develop movement patterns in their use of home ranges, exploiting resources (e.g., location of mates, water catchments, mineral licks, and shelter sites) (Berry 1986a, p. 113) where they are the most plentiful (Sullivan *et al.* 2014, pp. 116–118). Estimates for annual average home range sizes for males have varied from 0.04–0.10 sq mi (23–64 ac, 10–25 ha); females generally have smaller home ranges, with averages ranging from 0.01–0.09 sq mi (6–58 ac, 2–23 ha) (Barrett 1990, p. 203; Averill-Murray and Klug 2000, pp. 55–61; Averill-Murray *et al.* 2002a, pp. 150–151; Averill-Murray *et al.* 2020, p. 265). In the lower San Pedro River Valley, Sonoran desert tortoise home ranges varied between 0.07–1 sq mi (45–640 ac; 1–259 ha) (Meyer 1993, p. 99). Sonoran desert tortoises are known to exhibit high fidelity to their home ranges, with the exception of dispersal movements when they expand to new areas (Zylstra and Swann 2009, p. vi).

2.6 Defining Populations

An important step for understanding a species' status is identifying populations within the species' range. In Sonoran desert tortoise research and management, clustered, localized areas with inter-breeding individuals are generally treated as "populations," where individuals are more likely to breed with others in the same area. These areas are roughly defined by mountain ranges or other geographical features that support tortoise habitat. This is the scale of "populations" referred to in the analysis of risk factors potentially affecting the species (Chapter 3 and Appendix C). However, delineating geographically discrete units that form independent populations is a challenge for this species. First, Sonoran desert tortoises aggregate based on the presence of specific geological features (e.g., rocky slopes and bajadas) that may not be present on the landscape in consistent, easily definable ways. For example, isolated mountain ranges in southwestern Arizona may support discrete blocks of habitat and Sonoran desert tortoise populations that are demographically independent from others. Conversely, there are huge swathes of suitable habitat in places such as central Arizona likely function more as metapopulations with individuals moving between suitable habitat sites. These different scales and the tendency of Sonoran desert tortoises to move between them inhibits simple delineation of populations.

Second, genetic analyses have not identified significant genetic structuring across the species

range (Edwards *et al*. 2004, entire; Dolby *et al*. 2021, entire) suggesting historical gene flow between areas occupied by Sonoran desert tortoises. This is despite recent human alterations to the landscape that restrict Sonoran desert tortoise movement and could facilitate genetic differentiation due to fragmentation (see Chapter 3). However, given the long generation time for Sonoran desert tortoises, even in the absence of gene flow it could take centuries for genetic differentiation to be detected (Anderson *et al.* 2010, p. 3572; Kimble *et al.* 2014, pp. 6-7; McDougall *et al.* 2017, entire). In addition, with such long generation times even infrequent immigration events can facilitate sufficient gene flow to maintain connectivity and genetic similarities (Waples 1998, pp. 441–442; McDougall *et al.* 2017, entire). Therefore, genetic differentiation is not helpful in refining spatial population structure.

We considered using linear landscape developments, such as major interstates and large canals, which may act as barriers to movement, as population boundaries. However, while certain types of linear developments likely prevent or reduce tortoise movements on the landscape, there is uncertainty in how complete these barriers may be, and population connectivity may occur to some degree. Delineating populations based on the presence of barriers is thus hampered by our poor understanding of the effects of these structures and the lack of genetic data supporting their impermeability.

Due to the lack of support and difficulty in defining a smaller population structure within the Sonoran desert tortoises' range-wide distribution, we used the U.S.-Mexico international border as a division between the Arizona area of analysis and the Sonora area of analysis in this assessment. Dividing the range in this way was necessary to account for: the meaningful differences in the quality and level of information available about status and risk factors between the two areas; the differences in habitat quality due to differences in land management between the two countries; and the impermeable, artificial barriers preventing passage of dispersing Sonoran desert tortoises in some areas. Figure 5 illustrates these two analysis areas. However, our qualitative analysis of risk factors (Chapter 3: Risk Factors and Appendix C: Cause & Effects Tables) considers the potential effects of stressors at more localized scales consistent with the general concept of Sonoran desert tortoise populations.

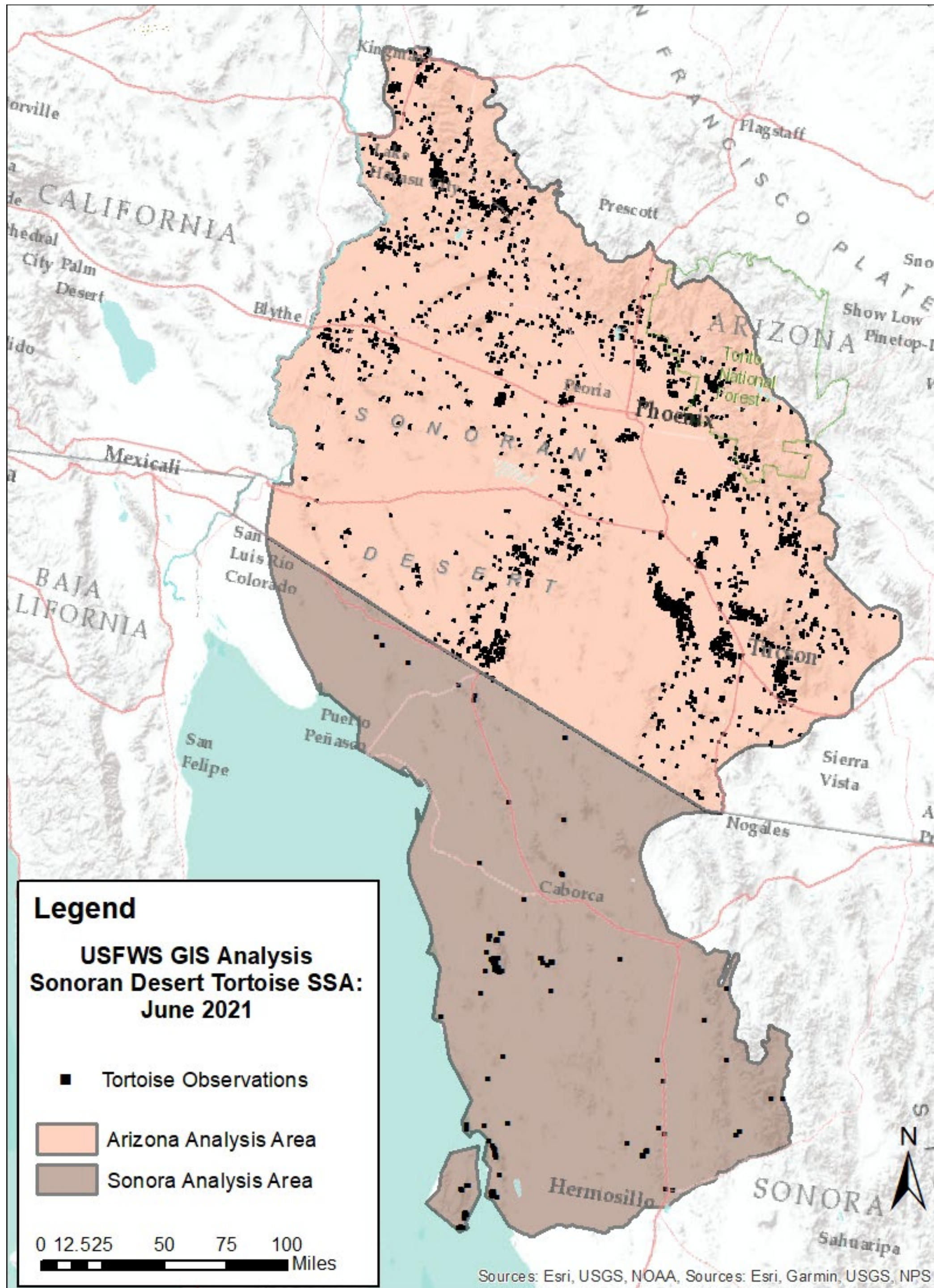


Figure 5. The extent of the Arizona, U.S. and Sonora, Mexico areas of analysis for the Sonoran desert tortoise with tortoise records identified. Species records for Sonora were obtained from field investigations, museums, literature, and photo-vouchers as provided by Rosen *et al*. (2014a, Figure 1.2). Records for Arizona are from the Heritage Database Management System, provided as a courtesy of the Arizona Game and Fish Department.

2.7 Species' Range-wide Needs

As described in Chapter 1, for the purpose of this assessment, we define **viability** as the ability of a species to sustain populations in the wild beyond a biologically meaningful time frame. Using the SSA framework, we describe the species' viability by characterizing the status of the species in terms of its **resiliency, redundancy, and representation** (the 3Rs). Using various time frames and the current and projected levels of the 3Rs, we describe the species' level of viability over time. To measure these factors, we have created a geospatial database that describes the suitability of potential habitat (see Appendix B) and a stochastic simulation model that forecasts abundance, population growth rates, and quasi-extinction risk for the areas of analysis (see Appendix E). This information is used to describe the current condition of the species and to forecast the species' condition into the future in Chapters 4 and 5 of this report, respectively.

2.7.1 Population Resiliency

For the Sonoran desert tortoise to maintain its viability, populations must be resilient and able to withstand stochastic events. For the quantitative analysis of population resiliency, we consider the full extent of the species' range in Arizona area of analysis and the full extent of the species' range in Sonora area of analysis to be separate "populations," as described above. To measure resiliency, we estimated the population abundance, population growth rates, and probability of quasi-extinction of both areas of analysis over 125 years (See Appendix E, Stochastic Simulation Model). In general, the higher the projected abundance and population growth rates and the lower the risk of quasi-extinction, the higher the resiliency of the Sonoran desert tortoise.

2.7.2 Species Redundancy and Representation

The Sonoran desert tortoise needs to have resilient populations (low quasi-extinction risk and high abundances) in the Arizona and Sonora analysis units and sufficient habitat quantity and quality throughout the species' range to provide for range-wide redundancy and representation. Because the available information did not support measuring populations on a smaller scale for the species and our simulation model was not spatially explicit beyond the large analysis areas, we are using the geographic distribution of predicted potential habitat suitability, as described below in Chapters 4 and 5, as measures of redundancy and representation.

For the Sonoran desert tortoise to have sufficient redundancy to withstand catastrophic events such as potential large-scale drought, it needs to have populations distributed across its range. While we did not define these populations, we were able to estimate current and future distributional patterns indirectly through the projection of the spatial location of habitats. A wider distribution of high and moderate suitability habitats throughout the species' range reduces the risk that entire species' range will be negatively affected by any catastrophic natural or anthropogenic event at any one time.

Key Assumption: We did not have sufficient information to conduct a spatially explicit demographic model of the Sonoran desert tortoise. Therefore, our measures of redundancy and representation are based on habitat. The assumption is that the abundance and distribution of tortoises are directly related to the quality and distribution of its habitat. This is a reasonable assumption given our understanding of the ecology of this species, but it is an important limitation in our analysis.

The Sonoran desert tortoise also needs to have sufficient representation to maintain genetic and ecological diversity for future adaptive capabilities to respond to changing environmental conditions. Genetic studies of the Sonoran desert tortoise in both Arizona (Edwards *et al*. 2004, entire; Dolby *et al*. 2021, entire) and Sonora (Edwards 2015, entire) suggest there is no genetic differentiation across the range that would support identifying particular parts of the range that are more important than others for long-term maintenance. The species occurs in a wide range of ecological conditions, such as elevational and precipitation gradients, and local adaptation to those conditions may be important for the species' long-term viability. Therefore, we assume that we can best reduce the risk of loss of any unidentified genetic or ecological diversity through maintaining a broad distribution of the species across its range. We are measuring this distribution indirectly through the spatial analysis of high and moderate quality habitats. The broader the distribution of these habitats, the higher the overall representation of the species and the more the adaptive potential for the species can be maintained.

Chapter 3: Risk Factors

> **Note:** This chapter contains **summaries** of the risk factors. For further information and more citations from the literature supporting these summaries, see the tables in **Appendix C**.

The following discussion provides a summary of the factors that are affecting or could be affecting the current and future condition of the Sonoran desert tortoise throughout some or all of its range. The full analysis of these factors is outlined in the attached cause and effects tables (see Appendix C) and some of the factors are further analyzed within our habitat analysis and population model (Chapters 4 and 5 and Appendix E). Although this is a range-wide analysis, the levels of information available for Arizona and Sonora remain significantly different. Where we had available data on any particular stressor for Sonora, we included it.

3.1 Altered Plant Communities (Nonnative Vegetation)

Nonnative invasive vegetation, including buffelgrass (*Cenchrus ciliaris*), red brome (*Bromus rubrens*), Mediterranean grass (*Schismus* spp.), Saharan (or Asian) mustard (*Brassica tournefortii*), fountain grasses (*Pennisetum* sp.), love grasses (*Eragrostis* sp.), stinknet (*Oncosiphon piluliferum*), and natal grass (*Melinus repens*), have spread on the landscape, have become naturalized in portions of the Sonoran desert tortoise's range (Bahre 1991, p. 155; D'Antonio and Vitousek 1992, pp. 65, 75; Brooks and Pyke 2001, pp. 3, 5; Esque *et al*. 2002, p. 313; Van Devender 2002, p. 16; Abella 2010, p. 1249; Jarnevich *et al.* 2020, p. 11; Webb 2020, p. 22). Proliferation of nonnative invasive plants is increasing across the Sonoran Desert, both in Arizona and Mexico, largely because of human disturbance, and research indicates it is a risk factor for desert tortoise habitat (Abella 2010, pp. 1249–1251; Carter *et al*. 2020, p 168). Invasive species occur in areas with disturbed soils and in areas of high human use (e.g., trails, roads, grazing allotments). Trails and roads facilitate nonnative plant introduction by serving as vectors for seeds to enter undeveloped or disturbed areas (Carter *et al*. 2020, p 168). In Mexico, available information suggests livestock growers continue to clear acreage for buffelgrass cultivation as livestock pasture (Franklin and Molina-Freaner 2010, p. 1664). When nonnative invasive plant species become established, native perennial and annual plant species may decrease, diminish, or die out (D'Antonio and Vitousek 1992, p. 65, 75). Nonnative grasses that invade desert tortoise habitat may not be as nutritious as the native forbs that typically comprise their diet (Hazard *et al*. 2010, pp 138–139; D'Antonio and Vitousek 1992, pp 68–71; Drake *et al*. 2016, pp. 7–9; Oftedal *et al*. 2002, pp. 344–347). Red brome, buffelgrass, and Mediterranean grass may pose more of a concern for the Sonoran desert tortoise (see section 3.2 Altered Fire Regime).

In the Mojave Desert, nonnative invasive annuals such as red brome and Mediterranean grass have short-lived seed banks, with red brome seed viability decreasing significantly after two years, and other brome species' seeds to last up to three years and susceptible to severe drought (Jurand *et al*. 2013, pp. 71–72). During a multi-year drought, red brome seeds may be outcompeted by native vegetation with long-lived seed banks; however, it is important to note that brome species can produce a high number of seeds per plant (Jurand *et al*. 2013, p. 72), and even a tiny percentage of the seed bank surviving can have an observable effect in plant

community composition. More recent research indicates vigorous stands of native perennial grasses are more likely to be resistant to invasion by red brome due to below-ground competition (Brooks *et al*. 2016, p. 20), although nonnative grasses can still compete with native grass species (which are used as food and cover by Sonoran desert tortoises) through competition for space, water, and nutrients, thereby affecting native plant species density and species composition within invaded areas (Stevens and Fehmi 2009, pp. 383–384; Olsson *et al.* 2012a, entire; 2012b, pp. 10, 18–19; McDonald and McPherson 2011, pp. 1150, 1152; Franklin and Molina-Freaner 2010, p. 1664; Germino *et al*. 2016, entire).

The effects of nonnative invasive vegetation on individual Sonoran desert tortoises can vary over time, largely as a function of the density of nonnative vegetation and the availability of free-standing water for drinking (different plant species may be more important when drinking water is not available). Effects can include (1) a reduction of forage availability, particularly of high-nutrition native plants; (2) a reduction in fitness of individual desert tortoises; and (3) an increase of time and energy spent in foraging activities, and, therefore, increased predation risk (Gray 2012, pp. 18, 47; Gray and Steidl 2015, p. 1986; Esque *et al*. 2003, p. 107; Rieder *et al*. 2010, p. 2436; Medica and Eckert 2007, p. 447; Hazard *et al*. 2010, pp. 139–145; Nagy *et al*. 1998, pp. 260, 263; Webb 2020, p. 22). Lower fitness due to inadequate nutrition may reduce reproductive potential in individuals, survival and recruitment of juveniles, and survival of adults. Stinknet germinates and grows in response to cool season precipitation and can form dense mats of ground cover in desert, thornscrub, xeric riparian areas, and disturbed areas. This causes potential threats to food sources of Sonoran desert tortoises (Webb 2020, p. 22). In high densities, buffelgrass may impede movement of small Sonoran desert tortoises and results in lower densities of native vegetation used for food and cover (Rieder *et al*. 2010, entire; Gray 2012, p. 48; Bracamonte *et al.* 2017, p. 55). A reduction in cover plants limit thermoregulatory opportunities and reduces periods of potential surface activity, making individuals more susceptible to dehydration and malnutrition, as well as increase predation risk when the individuals are surface-active (Gray 2012, entire).

The potential expansion or contraction of buffelgrass, through time, over the range of the Sonoran desert tortoise, may depend on climate change given that changes in temperature and precipitation associated with climate change were identified as significant drivers of buffelgrass distribution into the future (Suzart de Albuquerque *et al.* 2019, entire). Although increased temperatures and decreased precipitation are predicted to lead to contractions of buffelgrass distribution at 2050 and 2070 under all modelled climate scenarios (Suzart de Albuquerque *et al.* 2019, pp. 3342–3343), the projected distribution of buffelgrass corresponds with suitable Sonoran desert tortoise habitat throughout most of its range. Thus, buffelgrass is projected to be an ongoing threat in Sonoran desert tortoise habitat under various climate change scenarios.

The effect of nonnative vegetation on desert tortoise nutrition is minimally ameliorated by the fact that they can forage to some extent on nonnative grasses and forbs such as red brome, buffelgrass, and filaree (*Erodium cicutarium*) (Van Devender *et al*. 2002, entire), which could partially make up for losses in species composition and biomass of native forage species under certain circumstances. Nonnative filaree has been demonstrated to provide significantly more nutritional value than some native forbs, including providing more digestible energy and crude protein, and about the same amount of digestible water (Nagy *et al*. 1998, pp. 263–264). In

summary, the effects of nonnative vegetation on individual Sonoran desert tortoises are complex, but generally and cumulatively adverse as nonnative species continue to spread across the range of the Sonoran desert tortoise, outcompeting native forage species the tortoise evolved with and changing the fire regime (see section 3.2 Altered Fire Regime).

The status of nonnative invasive vegetation within high-density Sonoran desert tortoise populations is sparsely collected, although it may be observed in vegetation survey transects and noted in LTMP reports prepared for the AGFD and U.S. Bureau of Land Management (BLM). Information on their distribution and density is typically reported as being present. This underscores a generally poor understanding of the distribution, abundance, or diversity of nonnative invasive plant species (not associated with roads or highways) throughout the range of the Sonoran desert tortoise in Arizona. To illustrate the potential geographic scope of nonnative invasive vegetation, we used an existing spatial analysis conducted as part of the Rapid Ecological Assessment for the Sonoran Desert (REA SOD) completed by the BLM (Strittholt *et al*. 2012, pp. 89–92). The REA SOD modeled the predicted distribution in 2010 and included invasive riparian vegetation, and invasive upland vegetation including red brome, buffelgrass and Sahara mustard (Figure 6). Salt cedar (*Tamarix* sp.) and Saharan mustard are major drivers in the model and consequently disproportionately influenced the geographic distribution of nonnative invasive vegetation. Because of this, Figure 6 depicts a heavier influence of nonnative species towards the southwest portion of the species' range in Arizona, where nonnative grasses like red brome and buffelgrass may have a more pronounced effect in wetter, higher-suitability tortoise habitat along the northern and eastern areas of its range. Although this spatial analysis is dated, it shows the broad distribution of invasive vegetation across the species' range (Figure 6). While we do not have this information in Mexico, we presume that nonnative invasive vegetation is also widespread in that part of the species' range.

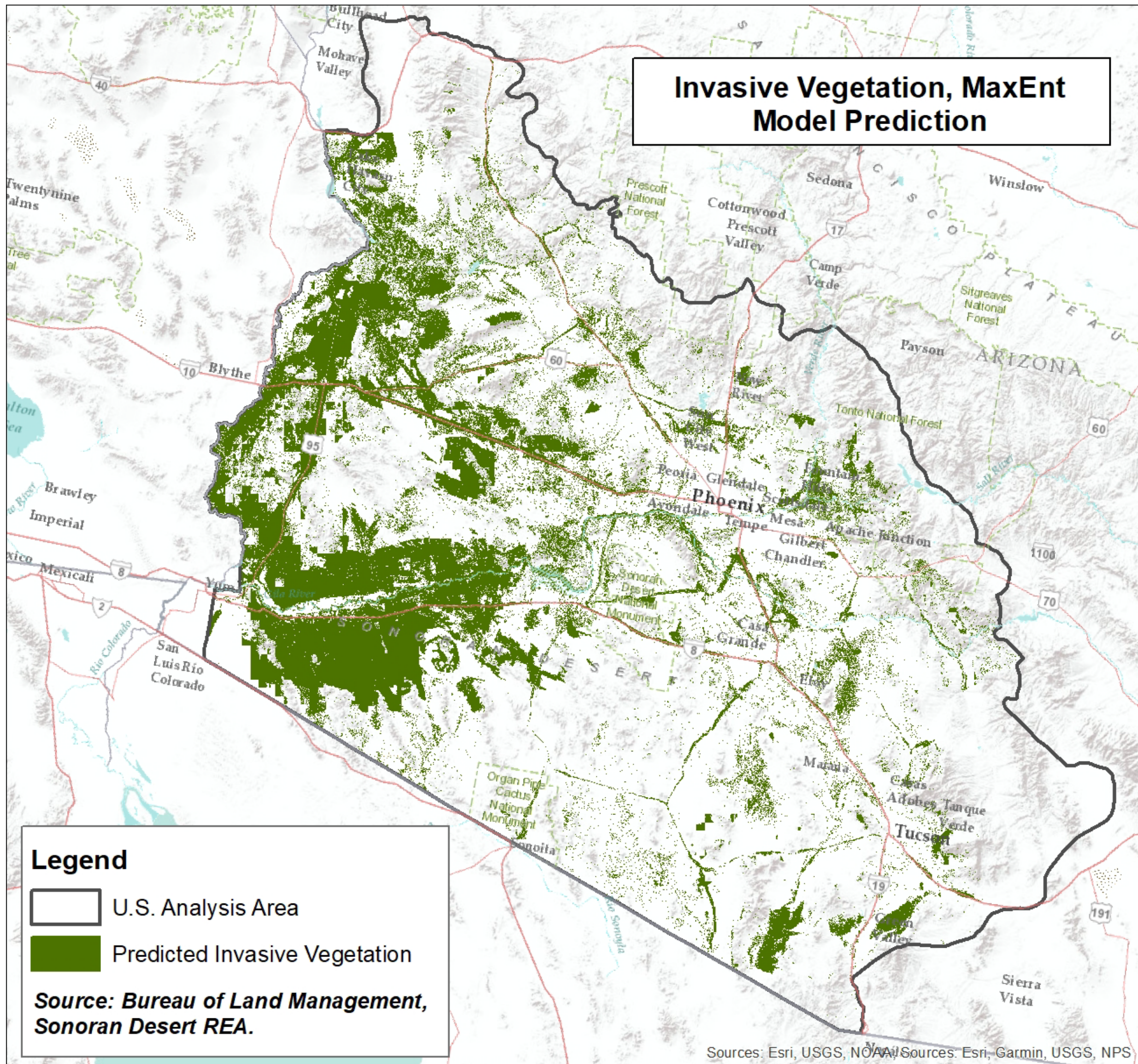


Figure 6. Distribution of modeled invasive vegetation within the range of the Sonoran desert tortoise in Arizona (based on REA SOD, Strittholt *et al*. 2012, pp. 89–92).

The varied effects of nonnative invasive vegetation on individual Sonoran desert tortoises may manifest in population-level effects over time and space. However, adverse population-level effects have not been identified through long-term monitoring (even though some species of nonnative invasive grass have occurred within the LTMPs for decades if not over a century), nor been documented in the literature. Without evidence of dramatic die-offs, population-level effects would only become discernable (with current research and monitoring methods) over an extremely long period of time (decades to centuries) due to the life history and longevity of the species. As stated above, some nonnative invasive vegetation can provide important nutrition (i.e., filaree) or suitable cover while surface active (i.e., buffelgrass). However, the preponderance of literature on this subject suggests that even these attributes are unable to ameliorate the overall, cumulative, adverse effects of nonnative vegetation invasions on the native vegetation forage base with which the Sonoran desert tortoise evolved.

3.2 Altered Fire Regime

While wildfire can occur within wholly native desertscrub communities, particularly after two or more consecutive wet winters that result in a build-up of native annuals as fuel (McLaughlin and Bowers 1982, p. 247), wildfire was never a significant factor influencing the evolution of Mojave and Sonoran desertscrub communities (Esque *et al.* 2002, p. 312). In desertscrub communities that are free of nonnative invasive vegetation, wildfire has a long return interval and is rarely able to carry itself over a spatially significant area due to the extent of bare ground between vegetated patches. Consequently, native plants, in particular cacti, trees, and shrubs, are ill-adapted to fire and generally fare very poorly in response to burns, although cacti still showed greater regeneration potential than trees or shrubs (Shryock *et al*. 2015a, p. 33).

In areas invaded by nonnative invasive vegetation, the density of fine fuels increases while open space between vegetation decreases, causing changes in fire behavior and, ultimately, in the fire regime; this has community-level effects of differing degrees that can last for several decades (Abella 2010, p. 1257; Pike *et al*. 2016, entire). Less is known about fire behavior in areas invaded by buffelgrass, but the higher biomass of buffelgrass (as compared to other nonnative grasses) and its higher burn temperatures (McDonald and McPherson 2013, entire) likely contribute to higher intensity wildfires with commensurately lower survival of native plants (Brooks *et al*. 2016, p. 20). Lightning is the only natural ignition source for wildfire in desertscrub, whereas human-caused ignition sources are varied and considered to be the most frequent cause for wildfire starts, both currently and in recent history (Alford *et al*. 2004, entire). Changes in fire regime have the potential to affect tortoises across the landscape; however, research suggests that habitat can recover to previous condition-states in the presence of altered fire regimes. A post-fire study in the Mojave and Sonoran deserts found that perennial plant cover can rebound to levels similar to undisturbed areas within 40 years and both species richness and cover rebound more rapidly than species composition, including within communities dominated by nonnatives (Abella 2010, p. 1273). Specifically, post-fire disturbance, without regard to native versus nonnative condition, the number of years predicted for desert vegetation communities to reach 100 percent of pre-fire cover ranged from 24–76 years; for plant species richness, the number of years ranged from 13–72 years (Abella 2010, Tables 1 and 2). Additionally, recent post-fire monitoring in Sonoran desert tortoise habitat indicates that topographically complex sites in central Arizona, invaded by red brome, require

much less time to meet the same pre-fire, red brome invaded conditions than what has been documented in the Mojave Desert (Abella 2010, p. 1273; Shryock *et al*. 2015a, p. 35).

Nonnative forbs, such as Sahara mustard (Dimmitt and Van Devender 2009, entire), and various thistle species (*Centaurea* and *Cirsium* species) are known to contribute to fires in many ecosystems (DiTomaso *et al*. 1999, entire; Lambert *et al*. 2010, entire). Native forbs, such as desert indianwheat (*Plantago ovata*) have also been documented contributing to fires in desert ecosystems (Esque *et al*. 2013, p. 224). Although these nonnative and native forbs occur in Arizona, they do not typically grow aggressively in the rocky habitat Sonoran desert tortoises typically occupy (DiTomaso *et al*. 1999, p. 233; Esque *et al*. 2013, p. 224; ASDM 2021, entire).

In the long-term, fire may decrease food availability, thermal refugia, and cover within Sonoran desert tortoise habitat (Esque *et al.* 2002, entire). Effects of wildfire and the post-burn recovery rate and potential has been shown to vary between Mojave and Sonoran desertscrub communities, particularly as influenced by environmental and abiotic factors (Abella 2010, entire; Shryock 2015a, entire). Specifically, within the Arizona Upland Subdivision of Sonoran Desertscrub invaded by red brome, factors such as elevation, aspect, precipitation, and topographic heterogeneity can ameliorate the negative effects of a single burn (Shryock *et al*. 2015a, pp. 34–35). Under certain conditions, Sonoran desert tortoise food plants can regrow in greater overall abundance than in unburned habitat (Shryock *et al*. 2015a, p. 26); however, cover plants such as trees, shrubs, and cacti have been shown to fare poorly in response to wildfire, regardless of conditions or habitat characteristics, although cacti have been shown to recover faster, as described above. One study found that long-term, post-fire vegetation assembly in the Sonoran Desert was influenced more by elevation and precipitation than time-since-fire (Shryock *et al*. 2015b, pp. 9–12). Specifically, vegetation structure recovered faster with increasing elevation and increasing average annual precipitation, but plant community composition showed less similarity to unburned control plots regardless of these same environmental factors (Shryock *et al*. 2015b, p. 12). Vegetation density increased in burned relative to unburned areas during the first decade following fire, but the difference was no longer apparent with longer times since fire (Shryock *et al*. 2015b, p 11).

The 2020 Bighorn Fire near Tucson burned approximately 15 sq mi (9,300 ac, 3,800 ha) of Sonoran desert tortoise habitat. Within the burn perimeter, approximately 9.1 sq mi (5,824 ac, 2,357 ha) (approximately 63%) burned with low severity effects, and approximately 4 sq mi (2,325 ac, 941 ha) (approximately 25%) burned with moderate severity effects (Dahlby 2021, entire). Other recent fires within the range of the Sonoran desert tortoise in Arizona that overlap suitable habitat include the 2020 Westridge Fire which burned over 3 sq mi (2,200 ac, 890 ha), and the 2020 Bush Fire which burned 300 sq mi (193,455 ac, 78,000 ha) (Arizona's fifth largest fire on record); however, not all of these burned acres occurred in Sonoran desert habitat. The Telegraph Fire burned for approximately one month from early June 2021 to early July 2021, burning approximately 282 sq mi (180,757 ac, 73,000 ha) and likely affected thousands of acres of Sonoran desert tortoise habitat (Inciweb; accessed: August 23, 2021). However, we do not know how many of these burned acres in 2021 fires contain Sonoran desert tortoise habitat. Due to the evolutionary history of these fire-adapted, nonnative invasive species, we expect nonnative invasive plants to continue flourishing in burned areas, potentially expanding their distribution and/or density. However, it remains possible that these burned areas may, over time, recover to

resemble their previous, nonnative-affected vegetation communities and continue to provide similar forage and shelter habitat for Sonoran desert tortoises (Abella 2010, entire; Shryock *et al.* 2015a, entire; Shryock *et al.* 2015b, entire).

Wildfires that occur in other types of Sonoran desertscrub, or in other biotic communities (e.g., Mojave Desertscrub), or areas invaded by nonnative vegetation other than red brome, may have different effects on Sonoran desert tortoise habitat. In Mexico, cultivated buffelgrass pastures are repeatedly burned to increase forage vigor for livestock use (Esque *et al.* 2002, p. 313). These pastures are primarily associated with the low valleys within the Plains of Sonora subdivision of Sonoran Desertscrub, geographically within the core of Sonoran desert tortoise distribution in Mexico, but generally outside habitat typically used by Sonoran desert tortoises. Sonoran desert tortoises generally do not occur in these lower valleys and may not be directly affected by burning pastures. Although most frequently documented in cultivated buffelgrass pastures in Sonora, repeated burns do occur in native Sonoran desert tortoise habitat, and baseline conditions of the vegetation community can be altered in such a manner that severe changes in species composition occur (also known as the grass-fire cycle) (D'Antonio and Vitousek 1992, p. 73).

Fire may also have direct effects on Sonoran desert tortoises by killing individuals through incineration, elevating body temperature, poisoning from smoke inhalation, and asphyxiation. Potential post-fire indirect effects to individuals include nutrient deficiencies (Esque *et al*. 2003, entire). Most wildfires in desertscrub communities occur during the spring and arid early summer (April–June) when relative humidity is low and ambient temperatures are high. This period of the year, particularly during April–May, is also important for adult female Sonoran desert tortoises to be surface active, consuming early annual growth as energy for subsequent egg development (Esque *et al.* 2002, p. 324). Therefore, adult female Sonoran desert tortoises may be at elevated risk of injuries or death associated with wildfire. Signs of tortoise activity identified during surveys along fire perimeters suggest that more tortoises survived fires than were located during surveys (Esque *et al*. 2003, p 107). In general, the mobility of adult Sonoran desert tortoises allows them to exploit microsites within a burn perimeter that support recovery of native forbs, grasses, and subshrubs, as well as use heterogeneous topography for thermal refugia. Therefore, many adult Sonoran desert tortoises may be able to persist in burned habitat (Shryock *et al*. 2015a, p. 39). However, juvenile Sonoran desert tortoises have less mobility to explore the landscape, less access to some food plants because of their short stature, and less thermal inertia, which may pose greater challenges in burned habitat and which may make them more susceptible to effects from wildfire than adults (Shryock *et al*. 2015a, p. 39).

A post-fire survey at the Four Peaks LTMP within the perimeter of the 2020 Bush Fire found 36 Sonoran desert tortoises that survived the fire, 29 of which had their heads visible to establish a body condition score (BCS). The BCS is established by evaluating the muscle mass and fat deposits in relation to skeletal features (Lamberski 2013, entire). All but one of those 29 individuals scored between 4 and 6 BCS (range is 1–9), which is within the "good" range (Lamberski 2013, entire). Researchers also established a control plot at the Sugarloaf LTMP in unburned habitat nearby. Preliminary BCS data indicate that Sonoran desert tortoises within the fire perimeter appeared to be in similar health than those Sonoran desert tortoises monitored outside of the fire perimeter (Jones 2021, entire). Approximately 97% of Sonoran desert tortoises within the Four Peaks LTMP which could be scored had a BCS between 4 and 6, while

approximately 96% of the Sonoran desert tortoises within the Sugarloaf LTMP control (unburned) plot had a BCS between 4 and 6 (Jones 2021, entire). Because the Bush Fire was fully contained in July 2020, and surveys occurred one to three months after, it is possible measurable effects of forage stress may not have been discernable. Furthermore, potential native and nonnative forage was documented sprouting shortly after the Bush Fire within the Four Peaks LTMP (burned) that was not sprouting within the Sugarloaf LTMP (unburned) (Jones 2021, entire).

To assess the potential scope of an altered fire regime within the range of the Sonoran desert tortoise in Arizona we considered the location of fires occurring since 1900 (Figure 7) and the potential location of high intensity fires based on landscape conditions and the ability to suppress fires in these areas (Figure 8). This information indicates that past fires and future fire risk to tortoise habitat are concentrated in the eastern portion of the species range in Arizona; the area generally considered to be high-suitability habitat (Figures 7 and 8).

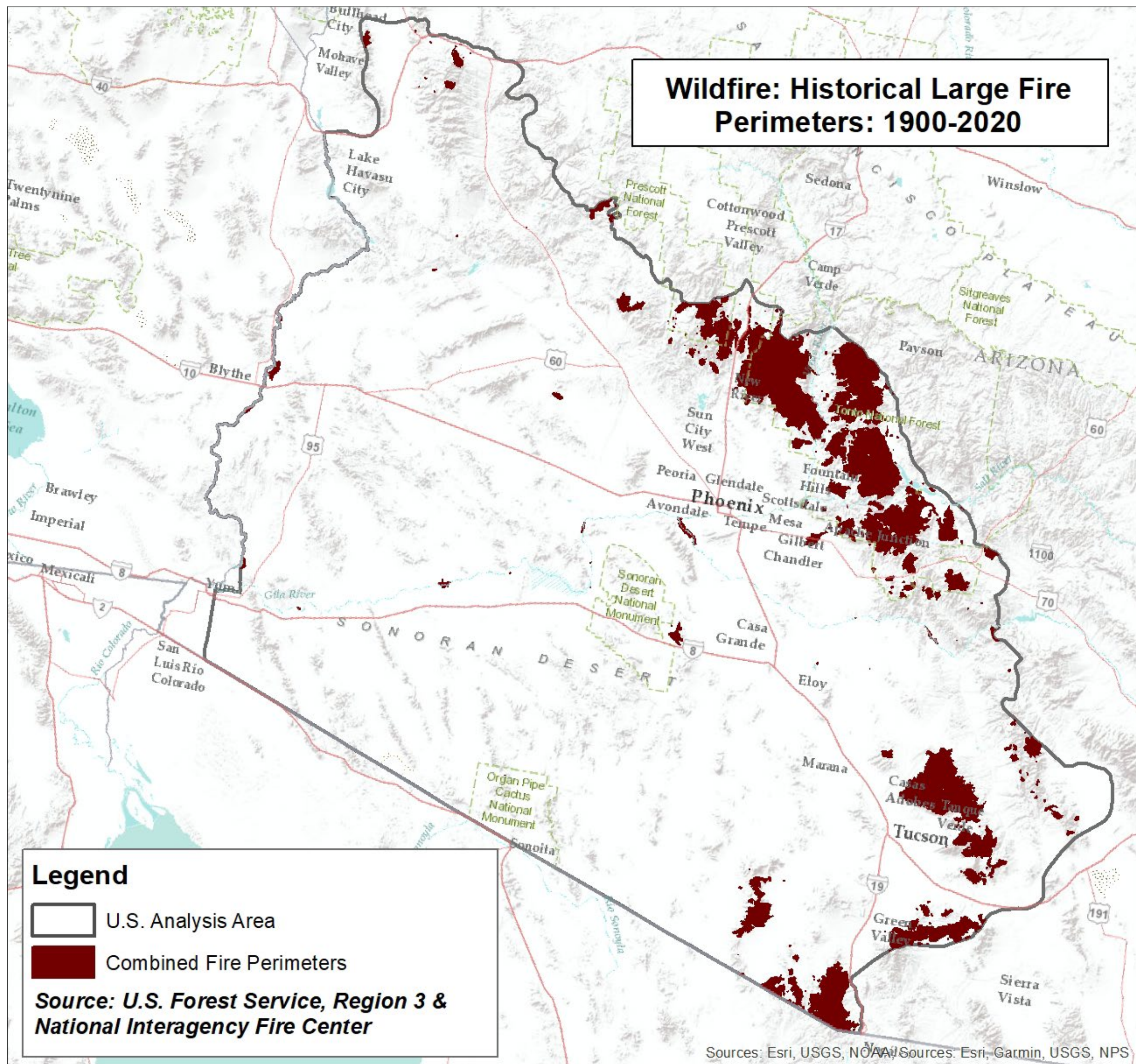


Figure 7. Location of burn areas showing perimeters of fires burned within the range of the Sonoran desert tortoise in Arizona on National Forest System lands since 1900 (https://www.fs.usda.gov/detail/r3/landmanagement/gis/?cid=stelprdb5201889, accessed June 2021), as well as on all lands since 2000 (https://data-nifc.opendata.arcgis.com/datasets/nifc::historic-perimeters-combined-2000-2018/about, accessed June 2021).

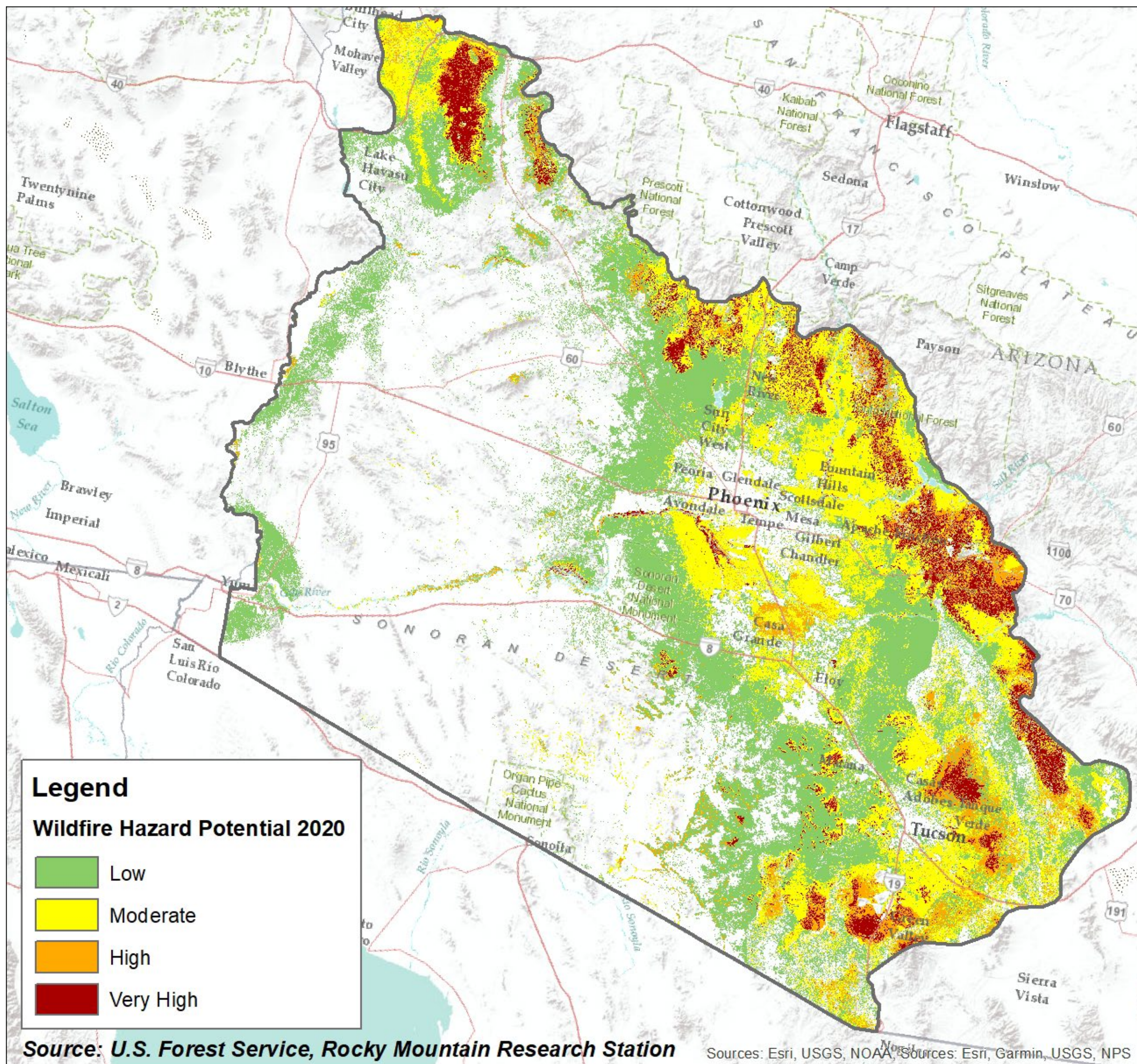


Figure 8. Wildfire hazard potential based on spatial estimates of wildfire likelihood and intensity within the range of the Sonoran desert tortoise in Arizona (https://www.firelab.org/project/wildfire-hazard-potential, accessed June 2021).

Wildfire ignitions occur annually in desertscrub communities within the range of the Sonoran desert tortoise. However, federal and state agencies implement wildfire suppression actions because these communities may contain or are adjacent to high value resources and assets. Wildfire suppression efforts from public land managers generally prioritize human life and property over all other factors. Because wildfire is supposed to be an ecological anomaly in desertscrub communities, there may be added emphasis to suppress every wildfire that occurs in the Sonoran Desert, governed only by the resources available and the number of fires burning at any given time. As a result of active fire suppression and other factors, the amount of suitable Sonoran desert tortoise habitat burned over the past several decades represents a relatively small proportion of the species overall range (Figure 7), but includes the highest suitability habitat for Sonoran desert tortoises within Arizona; areas critical to the species' adaptation potential for climate change effects. We expect that wildfire suppression policies will remain in place in Arizona and that these efforts will assist at minimizing the effects of wildfire. Therefore, we do not expect this stressor to have an appreciable effect on the species' overall resiliency, redundancy, or representation.

Key Assumption: Our assessment assumes that any changes in future wildfire regimes from possible nonnative grass expansion and increased human fire starts are not likely to have significant effects on populations of Sonoran desert tortoises because fire suppression efforts will prevent high numbers of large-scale fires and limit effects to native vegetation. Because of the uncertainty about the past, present, and future role of wildfire in the Sonoran Desert ecosystems and the ability for successful management suppression, we acknowledge the limitations in these assumptions.

We were not able to consider similar analyses in Sonora due to the lack of similar available information. Fires set intentionally in Sonora to benefit buffelgrass pasture could potentially affect adjacent Sonoran desert tortoise populations, but information is sparse in the literature, little research has been done on the effect of these fires on habitat in Sonora, and many of these pastures are located in areas where Sonoran desert tortoises are unlikely to occur based on their habitat preferences. We also do not have information suggesting that the effects from wildfire in Sonora will change in the near future.

3.3 Habitat Conversion

Over the past century as the human population has grown within the range of the Sonoran desert tortoise, areas of urban and agricultural development have replaced natural habitat. When habitat is replaced by urban and agricultural development, forage plants, cover plants, and shelter sites used by Sonoran desert tortoises are removed, often permanently. The alteration or removal of these habitat features removes the ability for Sonoran desert tortoises to adequately fulfill life history needs and can result in either immediate fatalities of individuals during construction or delayed fatalities from starvation, exposure, or predation should an individual survive the construction phase and/or be displaced from its home range. Additionally, habitat conversion also affects unaltered open space used by Sonoran desert tortoises to establish home ranges and facilitate short-, medium-, and long-distance dispersal movements. At larger scales, urban development causes significant changes or removes habitat altogether, removing high potential habitat areas and making regional and landscape movements by Sonoran desert tortoises

challenging, if not impossible. While some low-density urban developments may be permeable for Sonoran desert tortoises, effects associated with urban development, such as human interactions and human presence on the landscape (collection, road fatalities, predation by dogs, etc. [see Section 3.6 Human-Tortoise Interactions (Urban Influences)]), may mean these areas are functionally impermeable. Agricultural developments, while removing habitat characteristics needed to support several life-history functions, may be more permeable for Sonoran desert tortoise movements than urban developments. Mining operations, both large-scale and small-scale can lead to habitat conversion and death or injury to Sonoran desert tortoises, especially when vertical mine shafts are left un-remediated.

We report the results of our analysis of the current scope of habitat conversion and urban influences on the species in Chapter 4. The effects of future urban expansion and the resulting urban influences are evaluated in Chapter 5.

3.3.1 Urban Development

Landscape modeling has estimated that approximately 70% of desert tortoise (both Sonoran and Mohave) habitat has some level of development within 0.62 mi (1 km) and levels of development for the Sonoran desert tortoise were highest near cities such as Phoenix and Tucson, Arizona (Carter *et al*. 2020, p. 175). Both urban and agricultural developments generally occur on flat, or nearly flat, terrain, typically in valley bottoms where Sonoran desert tortoise densities are lowest or the species may be absent. Within our analyses, we consider these area as lacking natural intactness (Figure 9). Suburban housing developments, sometimes large-scale, can occur within lower bajadas, hillsides, and gently rolling hills where Sonoran desert tortoises may establish home ranges. Examples of these types of developments in Arizona include Gold Canyon and Anthem near the Phoenix metropolitan area, and Dove Mountain, Oro Valley, and the Catalina Foothills areas near Tucson. We think that developments in these types of areas may have a greater effect on Sonoran desert tortoise populations than developments found in valley bottoms.

Urban and suburban development, one of the primary factors driving Arizona's economy, is expected to continue into the future (Gammage *et al*. 2008, entire; 2011, entire). Projected development is expected to occur primarily within a zone referred to as the Sun Corridor Megapolitan, driven primarily by its association with major transportation routes and other existing infrastructure. In a northward direction from the U.S.-Mexico international border, this development zone occurs within the range of the Sonoran desert tortoise along Interstate Highways (IH)-19, IH-10, and IH-17 (Gammage *et al*. 2008 entire; 2011 entire), as well as the planned IH-11 (Lehman 2021, entire). Additional suburban development zones are expected to occur along IH-40 near Kingman and along State Route 93, which connects Wickenburg to Kingman, especially if the latter route is converted into an interstate highway (proposed IH-11). The majority of projected development in Arizona is not anticipated to occur in potential Sonoran desert tortoise habitat. Water availability influenced by climate change and increased water withdrawals associated with ongoing urban and suburban development may ultimately limit urban/suburban development in Arizona. However, we estimated potential future habitat losses due to urban development in Chapter 5.

3.3.2 Agriculture

The number of acres dedicated to irrigated agriculture has been on the decline in Arizona (U.S. Department of Agriculture 2009, p. 273). A current assessment and future projection of development in Arizona suggest agriculture will continue to be replaced by residential or commercial development (High Country News 2021, entire), or, rarely, left fallow for natural recovery. We predict that the observed trend associated with agricultural use will continue to decline in Arizona, unless farming practices or technology change, or a novel crop significantly influences market forces and reverses this trend.

Within the species' range in Sonora, Mexico, and according to recent reports, urban and agricultural development is also expected to continue into the future, but at a slower pace and smaller scale than Arizona. Hermosillo is the largest population center in Sonora (approximately 778,000 per the 2014 census) and could expand north and east which could potentially affect adjacent Sonoran desert tortoise populations (Rosen *et al.* 2014a, pp. 22–23). Limited urban expansion could also be predicted for a small number of other communities within Sonora (Rosen *et al*. 2014a, pp. 22–23). With respect to agriculture in Sonora, the majority occurs on large river deltas which are not occupied by Sonoran desert tortoises (Rosen *et al*. 2014a, pp. 22–23). Therefore, neither urban nor agricultural development is considered to be significantly affecting Sonoran desert tortoise populations over a large area in Sonora currently, or into the future.

3.3.3 Mining

In addition to urbanization and agriculture, large and small mining-related operations and artifacts can result in habitat conversion and death or injury of individual tortoises. New mine exploration and expansion of existing mine operations can also modify tortoise habitat. Similarly, mining development and activities may completely remove habitat. Recently, a 26 square-mile parcel of undeveloped land, likely containing some amount of Sonoran desert tortoise habitat near Bagdad, Arizona was purchased from the Arizona State Lands Department for mine tailings storage (Phoenix New Times 2021, entire). We do not know the extent of potential tortoise habitat within the expansion area. Of all mines, large-scale, open pit mines are expected to result in the greatest amount of habitat loss, while mines operated through smaller shafts will result in less habitat loss and, depending on the orientation of the mine shaft, may provide some level of benefit to Sonoran desert tortoises. Horizontal shafts may provide valuable respite for thermoregulation of Sonoran desert tortoises who enter them; however, vertical shafts can fatally entrap Sonoran desert tortoises.

While large-scale, commercial mines effect tortoises primarily through loss of habitat, small, vertical shafts and pits associated with old prospects and test pits are numerous and widespread across public lands. These vertical features, if left open and accessible, are likely to injure or kill more Sonoran desert tortoises over time and space than commercial operations. We do not know how many tortoises are affected or how this may affect population trends, nor do we know the distribution or abundance of these pits and/or shafts within various habitat suitability classes for the tortoise.

Many of these small mining artifacts occur on BLM-managed lands. The BLM is aware and actively working to address this threat to humans and wildlife alike. The BLM has remediated and retrofitted open pit mines, including using barriers to prevent Sonoran desert tortoise and other wildlife from being entrapped (BLM 2013a, p. 6) throughout their lands in Arizona. Specifically, the BLM restored approximately 10,000 acres (4,047 ha) of mine sites, monitored and maintained close to 4,000 restored abandoned mines, and addressed over 7,100 safety hazards associated with mines in 2011 (BLM 2013a, p. 8). These efforts are ongoing.

On the Tohono O'odham Nation, there are an estimated 17,000 mines or mining artifacts including exploration pits, mine tailings, caliche pits, and sand and gravel pits (Tohono O'odham Nation 2021, p. 3). None of these features have been closed and remain potential hazards to wildlife (Tohono O'odham Nation 2021, p. 3). In addition to known sites, there are additional mining features which remain undocumented (Tohono O'odham Nation 2021, p. 3).

In summary, without specific Mining Plans of Operations, it is difficult to assess how much habitat will be fragmented or lost to commercial mining operations in Sonoran desert tortoise habitat. It is possible that these mines will be developed in phases, leaving patches and islands of temporarily intact habitat for Sonoran desert tortoises. These mines will not likely remove a significant percentage of available suitable habitat for Sonoran desert tortoises across the species' range, however they could act as barriers to movement or trap Sonoran desert tortoises and increase the likelihood of fatalities. Because the expected habitat loss from mining activities is likely low compared to available suitable habitat across the species' range, and we do not know how many shafts and pits are within various habitat suitability classes for the tortoise, we have no data to show the threat of mining activities is a significant to the Sonoran desert tortoise.

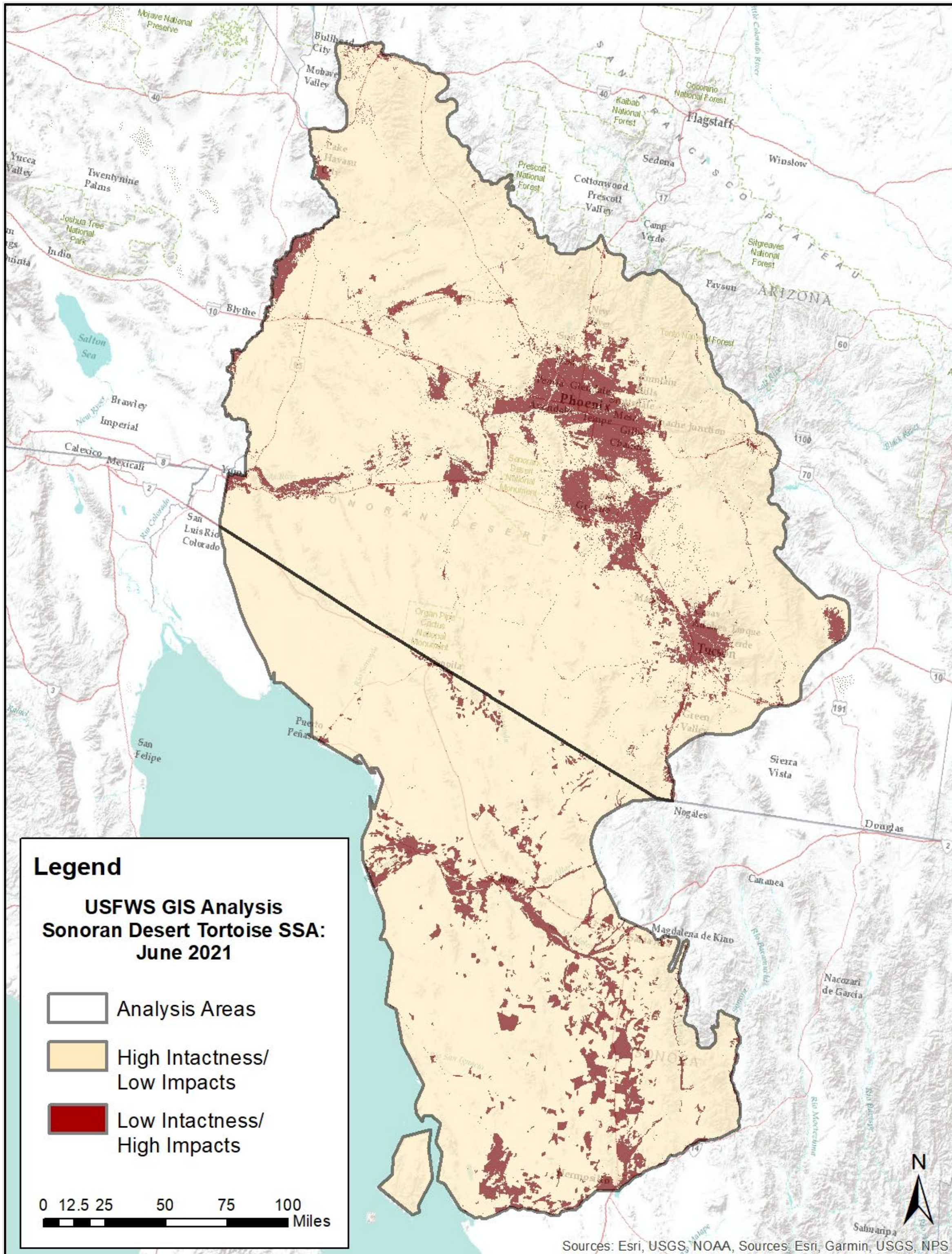


Figure 9. Areas within the Sonoran desert tortoise range with low intactness (i.e., developed areas and agriculture fields) that are impacted by land use changes.

3.4 Habitat Fragmentation

Habitat fragmentation is caused primarily by transportation infrastructure (e.g., roads, highways, interstates) as well as other forms of linear development such as canals, railroad tracks, and, in some sections along the U.S.-Mexico international border, pedestrian fences constructed to control cross-border human traffic. Recently new border security construction projects generally entailed improving existing barrier features or creating new barriers, whether human (30 ft (9.1 m) tall bollard fencing) or vehicle (Normandy-style barriers). Bollard fencing is generally considered impassible to subadult or adult Sonoran desert tortoises whereas vehicle barriers are considered passible for Sonoran desert tortoises of all size classes. We do not currently know the extent or location of either style of newly constructed barrier, but we do know where recent border barrier construction has occurred (Figure 10; description of suitable habitat is provided in Section 4.2).

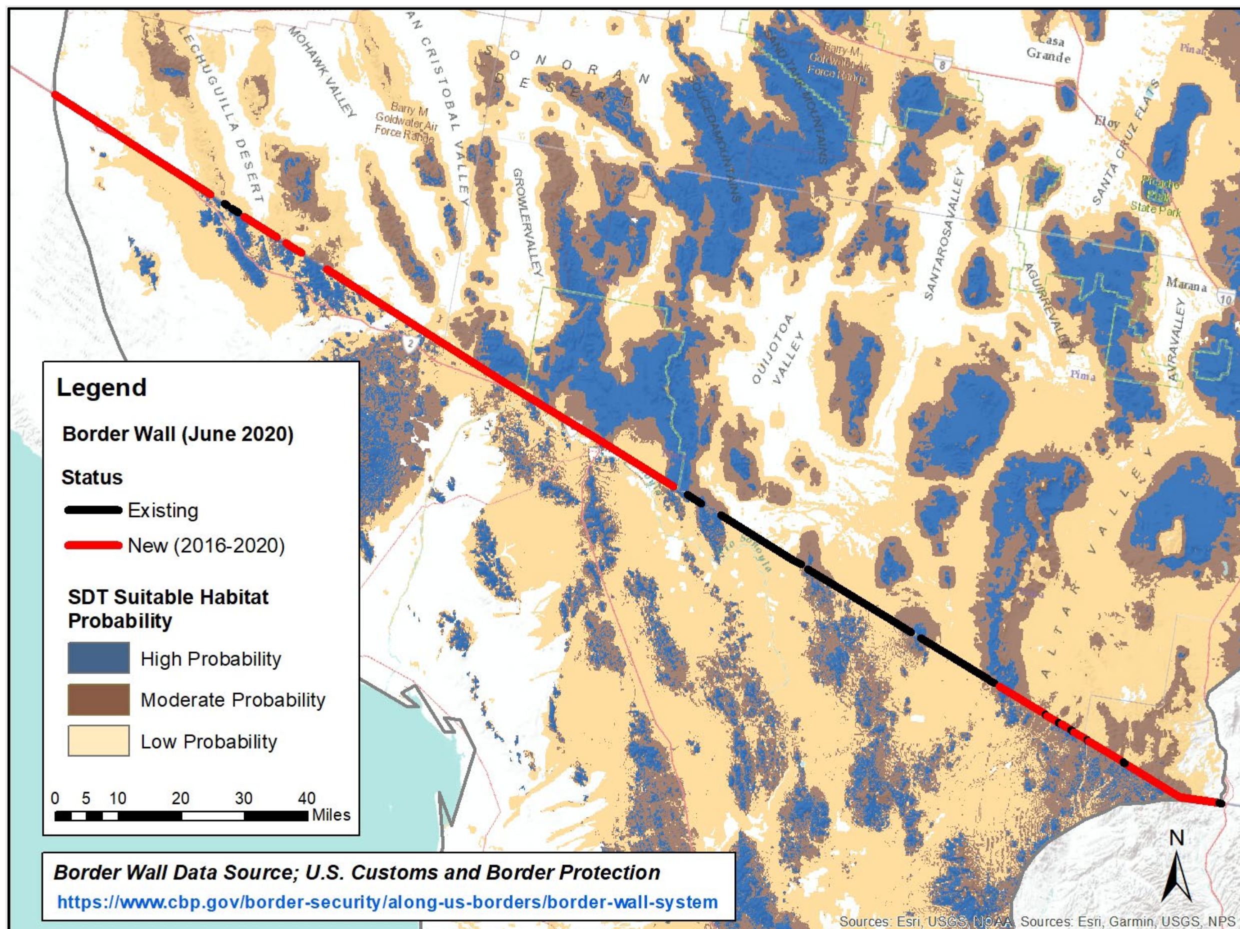


Figure 10. New border infrastructure construction or improvements within suitable Sonoran desert tortoise habitat from 2016-2020. Source: https://www.cbp.gov/border-security/along-us-borders/border-wall-system. Accessed June 15, 2021.

Considered permanent, these forms of linear development are ubiquitous (particularly roads) (Figure 11) across the range of the Sonoran desert tortoise and are necessary to facilitate the movement of commerce, people, and water. Where these forms of linear development occur within or adjacent to occupied Sonoran desert tortoise habitat, individual Sonoran desert tortoises may be injured, killed, collected (biologically dead to the population), or physically unable or reluctant to cross the development (Edwards *et al*. 2004, entire). Sonoran desert tortoises will regularly cross dirt roads but show reluctance to cross highways, based on over two decades of research on the species at the Florence Military Reservation (Rubke and O'Donnell 2018b, pp. 8–9; Rubke and O'Donnell 2019b, p. 10 and Figure A-10; 2020c, p. 10). Sonoran desert tortoises move within and outside their home ranges for different purposes depending on sex, age class, and size class. Sonoran desert tortoises will move to find preferred plant forage species that may be in season (Oftedal 2007, entire); to a different shelter site with a different exposure, depth, or substrate (Averill-Murray and Klug 2000, p. 62); or to search for potential mates (Averill-Murray *et al*. 2002a, pp. 139–144). Sonoran desert tortoises will also move to disperse outside of their home ranges, with distances ranging from a few hundred yards to several miles or more (Edwards *et al*. 2004, entire). When individuals are unable to complete these movements within their home ranges or on the landscape, basic natural history functions may be negatively affected.

The relative permeability of linear development to tortoise movement varies widely, with some structures considered impassible (i.e., some canals) and others easily traversed (i.e., infrequently used roads). Therefore, effects of linear development on individual Sonoran desert tortoises are not equal over space and time. For the closely related Mohave desert tortoises, variables that influence population genetics and connectivity on local scales are different than those influencing these factors on regional scales (Latch *et al*. 2011, entire). For example, not all roads have the same effect on Sonoran desert tortoise movements; dirt roads may actually attract tortoises to use them for various purposes including moving (short and long distance), resting, basking, and feeding (Sullivan 2021, p. 3). Primitive roadcuts through certain soil types may expose important mineral deposits for gastrointestinal health of tortoises or, depending on soil type, may also provide additional opportunities for drinking via compaction of the road surface trapping and holding water for longer than surrounding soils (Murray 2021, p. 5). Road width, road type (e.g., rugged, improved gravel, paved), speed limits, traffic volume, availability or location of washes or other means of crossing under roads, and quality of Sonoran desert tortoise habitat being transected have the greatest effect on Sonoran desert tortoise injury and mortality rates. In most cases, only Sonoran desert tortoises that are discovered dead on the road are reported (Lowery *et al*. 2011, p. 7, Grandmaison 2010, p. 5), but Sonoran desert tortoises that successfully cross are not. Telemetry research on the effects of roads on tortoises is limited, but suggests that depending on the type of road and frequency of traffic, Sonoran desert tortoises may use a road to bask or to facilitate unobstructed movement (Grandmaison *et al*. 2010, p. 587) or in some cases, may refuse to cross a road (AGFD 2012, pp. 19–46). U.S. Customs and Border Patrol has created new roads, potentially in Sonoran desert tortoise habitat on the Tohono O'odham Nation in southern Arizona (Tohono O'odham Nation 2021, p. 2). Additionally, unregulated access and new roads through one study site in the Union Hills on the northern edge of the Phoenix Metropolitan area has experienced a significant decrease in Sonoran desert tortoises during a 10–20-year period (Sullivan 2021, p. 2). We do not have similar data for other study sites.

Direct fatality and inhibited movements affect individual Sonoran desert tortoises and may manifest at local population-levels should they decrease survival, fecundity, or recruitment significantly. However, research has been limited in assessing the demographic consequences of these barriers on local populations. A broader consequence of barriers may be the restriction of gene flow across the landscape. Dispersal between populations facilitates gene flow that can maintain levels of genetic diversity. Restriction in gene flow can genetically isolate populations, facilitating the loss of genetic diversity in small populations through drift and inbreeding (Edwards *et al*. 2004, entire). In addition, should a stochastic event drastically reduce or effectively eliminate a given population that is isolated by linear development, natural recolonization from adjacent populations may be hampered or unlikely to occur (Edwards *et al*. 2004, p. 496). While population-level effects due to isolation may be occurring, there are no data available regarding the effects of linear development to Sonoran desert tortoises at the population level (Edwards *et al*. 2004, p. 496). Instead, Sonoran desert tortoises exhibit an "isolation by distance" population model, meaning that genetic exchange among populations is likely positively correlated by proximity (or nearness) to the next population (Edwards *et al*. 2004, entire). As indicated above, Sonoran desert tortoises can successfully traverse linear development, and even a few migrants per generation can be enough to facilitate gene flow (Waples 1998, pp. 441–442; McDougall *et al.* 2017, entire). Understanding whether linear development restrict gene flow is hampered by the biology of the species: because of the slow growth rates of Sonoran desert tortoises and their long generation times (approximately 25 years), it is difficult for genetic effects to be detectable. These trends unfold on a multi-decadal scale, if not over centuries; given such timeframes, it is well outside our ability to predict with reasonable certainty any trends likely to occur in the near-term future. Linear development may isolate certain populations and have a detrimental effect on their resiliency, or have disproportionate effects in certain portions of the species' range over others, but gene flow is likely present on a sufficient level to limit the potential for genetic effects to reduce species viability overall.

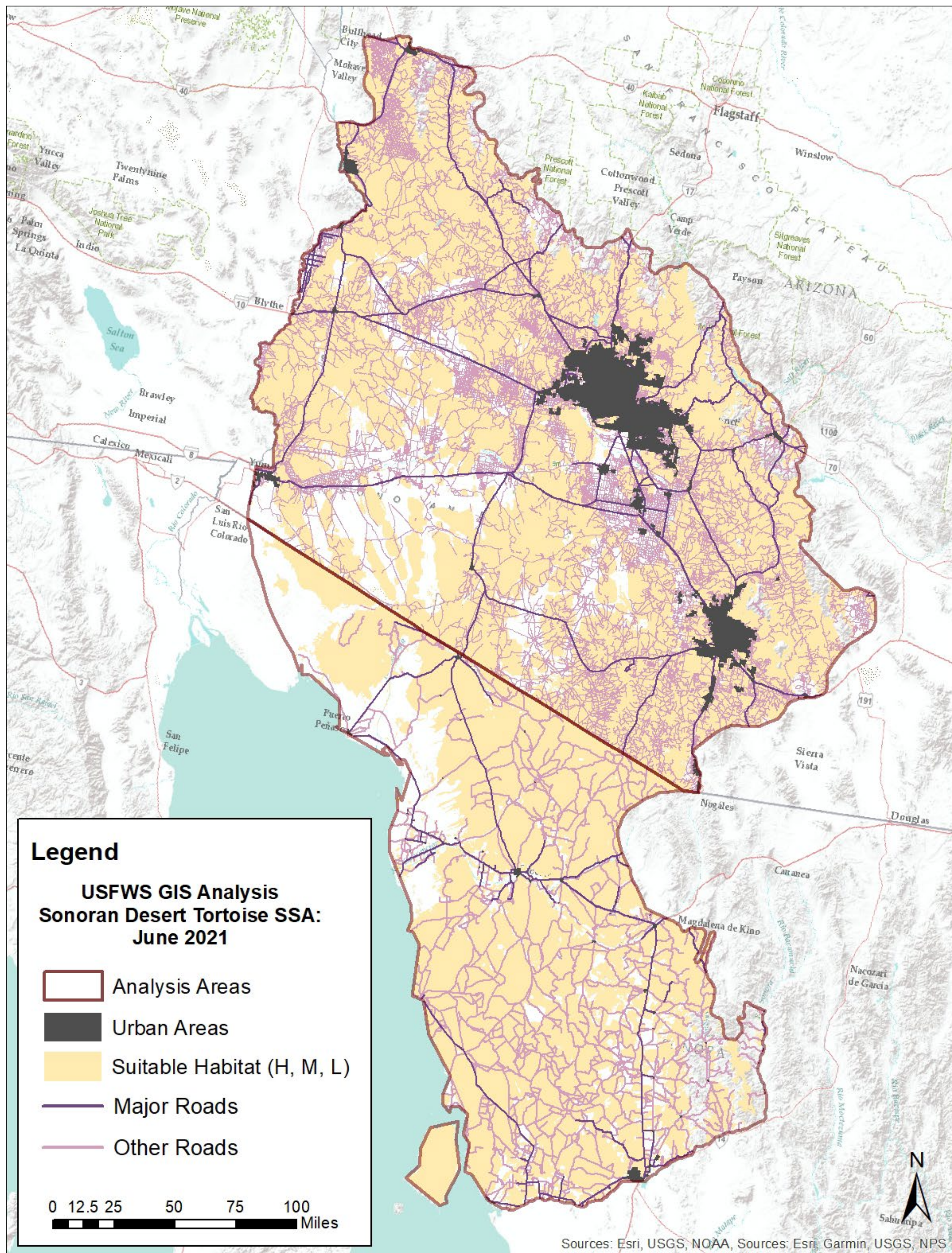


Figure 11. Roads within the range of the Sonoran desert tortoise.

3.5 Climate Change and Drought

Predicted temperature trends for the region encompassing the range of the Sonoran desert tortoise include warming trends during winter and spring, lowered frequency of freezing temperatures, longer freeze-free seasons, and higher minimum temperatures during the winters (Weiss and Overpeck 2005, p. 2075). In this same region, projections of changes in precipitation due to climate change are less certain, but climate scientists largely agree that annual precipitation totals are likely to decrease as compared to historical averages (Seager *et al.* 2007, entire; Cook *et al.* 2015, p. 4; Peters and Iverson 2016, Table 2.7). We expect climate change to influence biotic factors associated with invasive vegetation. Invasive grasses, such as red brome, may expand their distribution within Sonoran desert tortoise habitat (Bradley *et al.* 2016, p. 267). Climate models generally agree that winter and spring precipitation may be influenced by climate change, with predicted decreases in precipitation during these seasons. While modeling results generally vary considerably with respect to how climate change could affect summer (monsoon) precipitation in Arizona and northern Mexico, a recent study found that monsoon-related precipitation in Arizona and northwestern Mexico may be reduced by as much as 40 percent and that annual monsoon precipitation is expected decrease, but with the possibility of more extreme precipitation events (Pascale *et al.* 2017, entire; Pascale *et al.* 2018, entire). While annual precipitation totals are predicted to decrease, summer precipitation totals may increase (IPCC 2007, p. 20), with wide fluctuation in scope and intensity of summer precipitation events.

Climate change projections for the arid southwest indicate that drought frequency, severity, and duration are likely to increase over the next century (Gonzalez *et al.* 2018, entire). Sonoran desert tortoises evolved in arid conditions and have an array of physiological and behavioral tools to survive some degree of drought. However, because the principal effects of predicted climate change pertain to temperature and precipitation, the physiological ecology of Sonoran desert tortoises may be significantly compromised by changes in these climatic parameters, both directly and indirectly (Bagne and Finch 2012, entire). Drought associated with climate change can affect Sonoran desert tortoises directly by limiting the availability of freestanding water for drinking, either through a decrease in frequency of precipitation events or a decrease in precipitation totals per event. Availability of freestanding water is one of the strongest drivers of survivorship in Sonoran desert tortoises (Sullivan *et al.* 2014, entire). Drought can indirectly affect Sonoran desert tortoises through a reduction in biomass of forage and cover plant species used for food, thermoregulation, and protective cover. Persistent drought and its effects on the Sonoran desert tortoise's forage base can affect blood chemistry and water metabolism, reduce or eliminate the thymus and fat stores, and result in skeletal muscle and liver atrophy (Berry *et al.* 2002, pp. 443–446; Dickinson *et al.* 2002, pp. 251–252). Over time, drought and inadequate nutrition could result in lower growth rates, lower reproductive output, lower survivorship, and increased stress on bladder physiology. In Arizona, a reduction in average winter and spring precipitation is expected to disproportionately affect adult female Sonoran desert tortoises which depend on spring annuals as a key source of energy for egg development (Averill-Murray and Klug 2000, pp. 65–66). In other subdivisions of Sonoran Desertscrub and habitat types found in Sonora, relationships between winter and spring rainfall and annual plant responses are less clear.

Temperature increases associated with climate change directly affect Sonoran desert tortoises by

dictating the length of time and frequency of when they can be surface active and engaged in life history functions. Increased temperatures may also affect sex ratios during embryo development, as this process is temperature-dependent (Janzen 1994, p. 7488; Walther *et al.* 2002, pp. 393–394). The ability of tortoises to vary the timing of egg development and laying may buffer against predicted temperature rise associated with climate change, but more research is needed on developmental temperatures and nesting behavior to validate this hypothesis (Lovich *et al.* 2017, entire). Temperature increases can also indirectly affect Sonoran desert tortoises by increasing evapotranspiration rates in plants, which increases the plants' water demands and, therefore, vulnerability to drought. These climate change impacts can also contribute to an overall reduction in perennial and annual plant productivity, reduce the time available for tortoises to forage on green plants which are more nutritious, and result in a reduction of the forage base and cover plants used by Sonoran desert tortoises.

Of the various stressors associated with climate change, only drought has demonstrable effects on Sonoran desert tortoise population trends. Even short-term variability in precipitation can have sustained effects on Sonoran desert tortoises because of negative effects to reproduction, recruitment, and annual survival. As of June 2021, much of the Sonoran desert tortoise's range in Arizona is under extreme or exception drought status, with precipitation totals equaling less than half of average annual amounts (NOAA 2021a, entire; 2021b, entire). At the LMTP sites specifically, drought conditions have worsened over the 34-year survey period (Zylstra and Steidl 2021, pp. 6, 8). In the context of the tortoise, research has shown that in monitoring plots that experience localized, prolonged drought conditions, annual adult survival can decrease by 10–20%, and adult abundance may decrease by as much as 50% or more in local instances (Zylstra *et al*. 2013, pp. 113–114). Juvenile survival rates also decreased with increased drought severity and the effects of drought on survival rates for both age classes were most severe in populations in the most arid regions (Zylstra and Steidl 2021, p. 7). However, when drought conditions subsided, Sonoran desert tortoise numbers began to increase, reaching near pre-drought status, and the overall rate of change in population size was found to be greater than 1, indicating cumulative population growth over the range of the species in Arizona (Zylstra *et al.* 2013, pp. 112–114).

If climate change increases the magnitude and scope of drought in the future, effects to Sonoran desert tortoise survival rates could worsen. Current modeling suggests that adult survival rates could decrease by 3% during 2035–2060 due to climate change, as compared to the survival rates during 1987–2008 (Zylstra *et al*. 2013, p. 114). Sonoran desert tortoise populations that occur within the most arid portions of the species' range (western and southwestern Arizona and western-most Sonora) presently exist at lower overall densities and may, therefore, be particularly vulnerable to the effects of drought. Modeling suggests that Sonoran desert tortoise populations adjacent to higher elevation habitat may slowly migrate into higher elevation areas or more northerly as habitat suitability for Sonoran desert tortoises shifts over time and space (Van Riper *et al.* 2014, pp. 83–85). Another model predicted that the range of the Sonoran desert tortoise contracted by 2039, but then showed a slight reversal, predicting no effective long-term change in range by 2099 (Hatten *et al*. 2016, p. 17).

Our analysis of the future condition of the Sonoran desert tortoise incorporated the potential effects of climate change by using projected habitat suitability estimates that incorporated

climate changes in habitat variables and by assessing effects on increasing drought conditions on Sonoran desert tortoise survival rates (see Chapter 5).

3.6 Human-Tortoise Interactions (Urban Influences)

Human population centers of varying sizes occur throughout the range of the Sonoran desert tortoise. These cities and towns are sources of people who inadvertently or purposefully interact with Sonoran desert tortoises while engaged in various activities within occupied habitat. These types of effects are difficult to quantify although the literature is clear they occur and act collectively as a stressor on Sonoran desert tortoises. Examples of activities that could lead to human interactions with tortoises (when in occupied tortoise habitat) include the use of vehicles (Lowery *et al*. 2011, entire), off-highway vehicles and off-road vehicles (Bury and Luckenback 2002, entire; Ouren *et al*. 2007, entire; Switalski 2018, p. 87; Sullivan 2021, p. 3), or general recreation such as target shooting, hunting, hiking, rock crawling, trail bike riding, rock climbing/bouldering, and camping (Howland and Rorabaugh 2002, pp. 339–342; AGFD 2010, p. 9). These activities are also linked to human-caused wildfire ignitions within Sonoran desert tortoise habitat. In addition, pet dogs that escape captivity or are intentionally abandoned can form feral packs which have been shown to molest Sonoran desert tortoises (Zylstra 2008, entire). These are all examples of inadvertent interactions that can have incidental effects on tortoises that are not otherwise the intent or purpose of the activity itself. Other forms of human interaction are direct and intentional, such as collection, release of captive individuals into wild populations, or physical handling (Grandmaison and Frary 2012, entire). When a Sonoran desert tortoise is picked-up and physically handled by a human, it may void its bladder (a defensive mechanism) which depletes a critical source of its metabolic water. Depending on the season of year and likelihood of precipitation, simply voiding the bladder could result in a dehydrated state, decline in reproductive energy, and eventually death of a Sonoran desert tortoise (Averill-Murray 2002a, p. 430).

These types of human interactions with Sonoran desert tortoises occur at highest frequency in the wild-urban interface zone (where urban development contacts open, undeveloped space) and are thought to attenuate with increasing distance from human population centers (Zylstra *et al*. 2013, pp. 112–113). The likelihood of human interactions with Sonoran desert tortoises increases significantly with urban growth and the increase of highways, roads, and trails intersecting occupied habitat. Tortoises crossing roads can be seen by motorists who may do nothing, intentionally or unintentionally run them over, attempt to help them cross (by coaxing it to move or physically carrying it across the road), or collect them as pets (Grandmaison and Frary 2012, entire; Sullivan 2021, p. 3). The larger and more conspicuous the Sonoran desert tortoise is, the more likely it is to be noticed by motorists. Speed limits also influence the detection rate of Sonoran desert tortoises along roads; slower speed limits generally correlate with higher detectability of Sonoran desert tortoises and vice versa (Grandmaison and Frary 2012, pp. 265–266). Larger Sonoran desert tortoises are more apt to be seen and, therefore, more likely prone to direct human interaction and less likely to be injured or killed by a vehicle. Smaller Sonoran desert tortoises are presumed to be less likely to be noticed and, therefore, less prone to direct human interaction, but perhaps more prone to injury or death from vehicles.

Effects of human interactions on Sonoran desert tortoises are expected to occur when Sonoran

desert tortoises are surface active. Generally speaking, Sonoran desert tortoises are sedentary and fossorial by nature, spending a large proportion of their lives within their shelters to conserve energy and metabolic water reserves. However, basic life history functions such as foraging, reproducing, and dispersing all require some level of surface activity. Adult female Sonoran desert tortoises are most likely to be surface active during the spring and the summer rainy season. The peak surface activity period for all Sonoran desert tortoises, regardless of sex, age class, or size class, is the summer monsoon; however, all Sonoran desert tortoises will emerge from their shelters at any time of the year to drink free-standing water in response to precipitation (Averill-Murray and Klug 2000, entire; Sullivan *et al*. 2014, entire; Sullivan and Sullivan 2015, entire; Sullivan 2021, p. 3).

Population-level effects from human interactions are most severe when they affect adult tortoises because adult survivorship is the primary determinant of population status. The investment of time and energy required to achieve reproductive status is high and the likelihood of any particular Sonoran desert tortoise achieving adulthood is low (Howland and Rorabaugh 2002, p. 339; Zylstra *et al*. 2013, pp. 112–115; Campbell *et al.* 2014, pp. 2, 14). Further, negative effects to adult females may have a disproportionately larger effect on resident Sonoran desert tortoise populations because harassed adult females may have fewer clutches of eggs over their lifetime (Van Devender 2002, p. 11).

Current research found population-level effects from human interactions, as evidenced by high carcass-to-living-tortoise ratios such as in the population of Sonoran desert tortoise along Phoenix's southern boundary (Rubke and Leavitt 2017b, p. 10). Adult survivorship improves with increasing distance from urbanized areas; specifically, the odds of a Sonoran desert tortoise surviving one year, increases 13% for each 6.2 mi (10 km) increase in distance from a city of at least 2,500 people (Zylstra *et al*. 2013, pp. 112–113). Subsequent analysis found that the odds of a Sonoran desert tortoise surviving one year increases 8% for each 6.2-mi (10-km) increase in distance from a city center of at least 10,000 people (Zylstra and Steidl 2021, entire). We recognize that the data used by Zylstra *et al*. (2013) and Zylstra and Steidl (2021) to calculate the effect of distance to human population centers on survival rates came from 17 LTMP sites that are mostly located outside the zone of highest impact from Arizona's largest metropolitan areas such as Phoenix and Tucson. Thus, there is some uncertainty surrounding the precise impact of urban areas on Sonoran desert tortoise survival rates.

Effects from human interactions with Sonoran desert tortoises have not resulted in the documented extirpation of any known populations. However, in the case where Sonoran desert tortoise populations exist at low densities, are already threatened by persistent drought, or occur adjacent to areas of very high human population densities with commensurate levels of outdoor recreation and visitation, loss of adults may have a population-level effect. We included the influences of urban areas in our current and future condition analysis of tortoise population projections (Chapters 4 and 5). Figure 12 illustrates areas within 20-km of cities in the Phoenix-Tucson metropolitan areas and with 10-km of other cities with greater than 10,000 people (suitable habitat is described in Section 4.2).

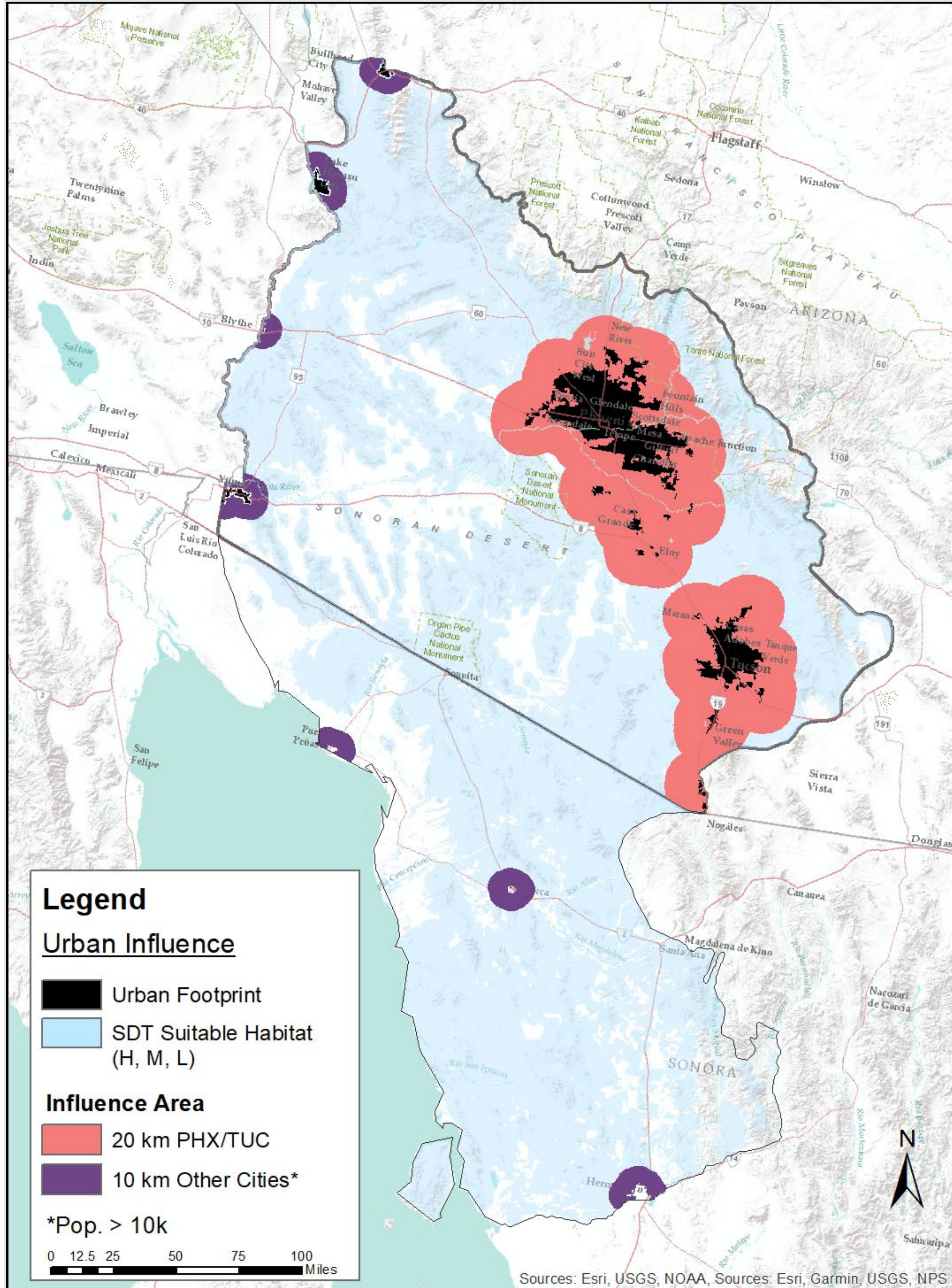


Figure 12. Distance from human population centers exhibited as 20-km rings around the footprint of urban areas in Phoenix/Tucson metropolitan areas and as 10-km rings around other cities with populations greater than 10,000 people.

3.7 Conservation Measures

3.7.1 Land Management

A large portion of the Sonoran desert tortoise range in Arizona is under public ownership, which provides various benefits to the species (Carter *et al.* 2020, entire). We categorized land management into five categories (Table 1, Figure 13) based on land ownership (Managed, Multi-use, Tribal, Unprotected (Private), and Other (State)) and the general benefits those ownerships may provide to tortoises. See Appendix B for more explanation of these categories. Those lands currently being “Managed” or protected for wildlife benefits that have high conservation value to the Sonoran desert tortoise and its habitat were considered to contribute most to habitat quality. Lands managed for wildlife benefits would reduce some potential stressors to the Sonoran desert tortoise through actions including, but not limited to, limiting the spread of nonnative plants, controlling fire, minimizing interaction with humans, and limiting the alteration of the natural vegetation community and geological structures that form the basis of Sonoran desert tortoise habitat needs. The areas identified as “Multi-use” include general conservation lands with at least an indirect benefit to wildlife and a moderate conservation value to the Sonoran desert tortoise. Livestock grazing management is an example of such use where best management practices are designed and implemented to reduce potential negative effects in some cases and provide direct benefits in others (see Ranching and Sonoran Desert Tortoise Working Group 2015, entire). Tribal lands were treated the same as multi-use lands but were identified separately. The Tohono O’odham Nation, located in south-central Arizona, represents a comparatively large proportion of the Sonoran desert tortoises’ range in Arizona (more than 4,000 sq mi), where the species is considered highly culturally significant to the O’odham people (Tohono O’odham Nation 2021, pp. 1, 3). “Unprotected” lands are primarily private lands with no indicated protection for wildlife or habitat, and “Other” lands are primary State of Arizona trust lands held for the purpose of generating funds. We calculated the amount of suitable Sonoran desert habitat within each of our suitable habitat classes (habitat suitability methodology described below in Section 4.2) (Table 1). Overall, about 72% of all Sonoran desert tortoise habitat is in either managed, multi-use or Tribal ownership.

Table 1. Summary of the amount of current Sonoran desert tortoise habitat in sq mi by suitability class and land management category in Arizona.

Land Management Category	Suitable Habitat Class (sq mi)			Total	Proportion of Total
	High	Moderate	Low		
Managed	2,535	2,523	3,641	8,699	29%
Multi-use	2,744	2,741	3,372	8,857	29%
Tribal	981	1,232	1,959	4,172	14%
Other/Unprotected	2,270	2,621	3,856	8,747	28%
Total	8,531	9,116	12,828	30,475	100%

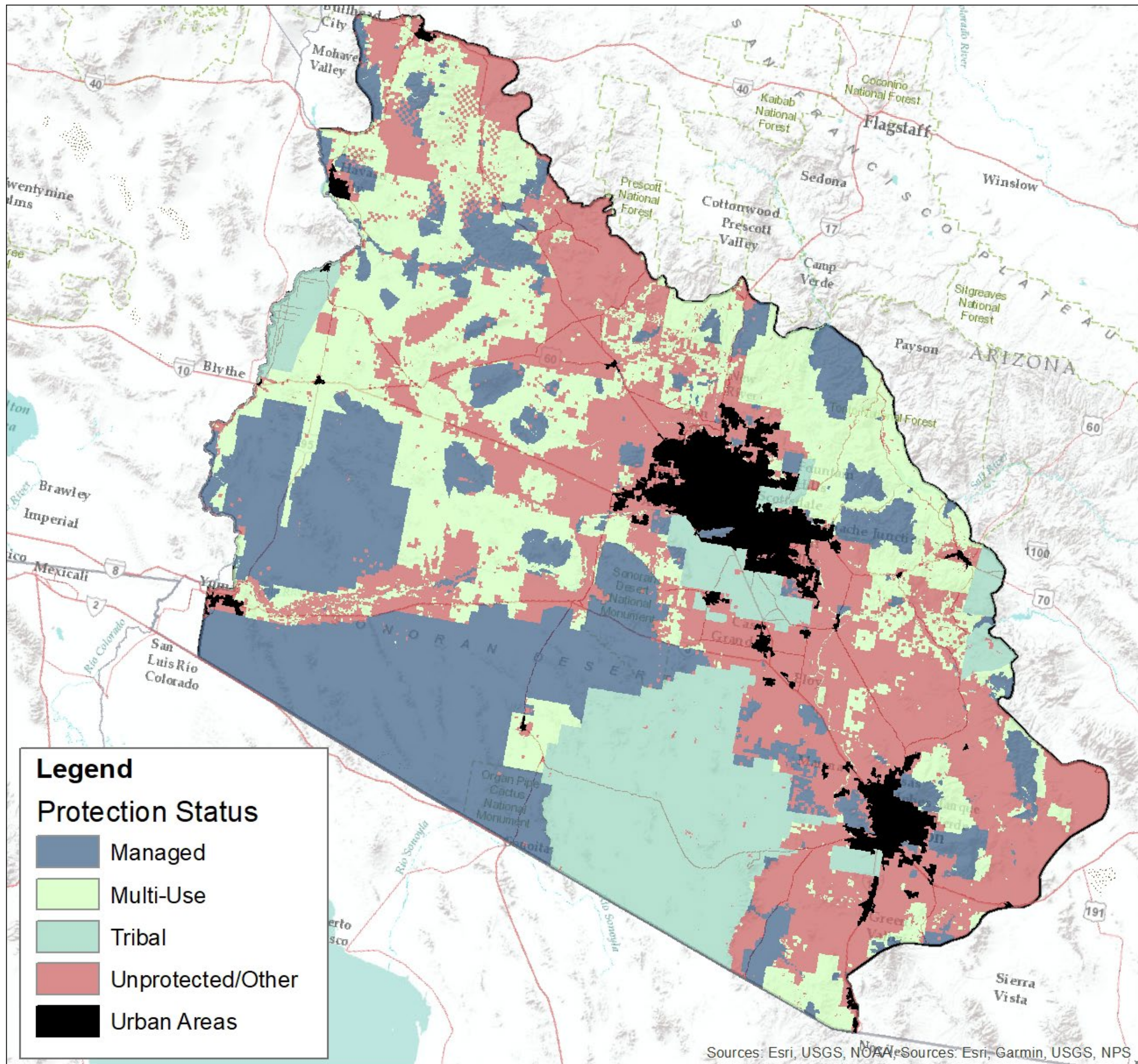


Figure 13. Land management and protection status within the range of the Sonoran desert tortoise in Arizona.

In Sonora, the World Database of Protected Areas identifies areas that are under some level of government conservation management, and we assumed there would be some benefits to the Sonoran desert tortoise in these areas (Figure 14). Although other non-governmental lands may provide benefits to the Sonoran desert tortoise and its habitats, we did not have information to further distinguish land management in Sonora.

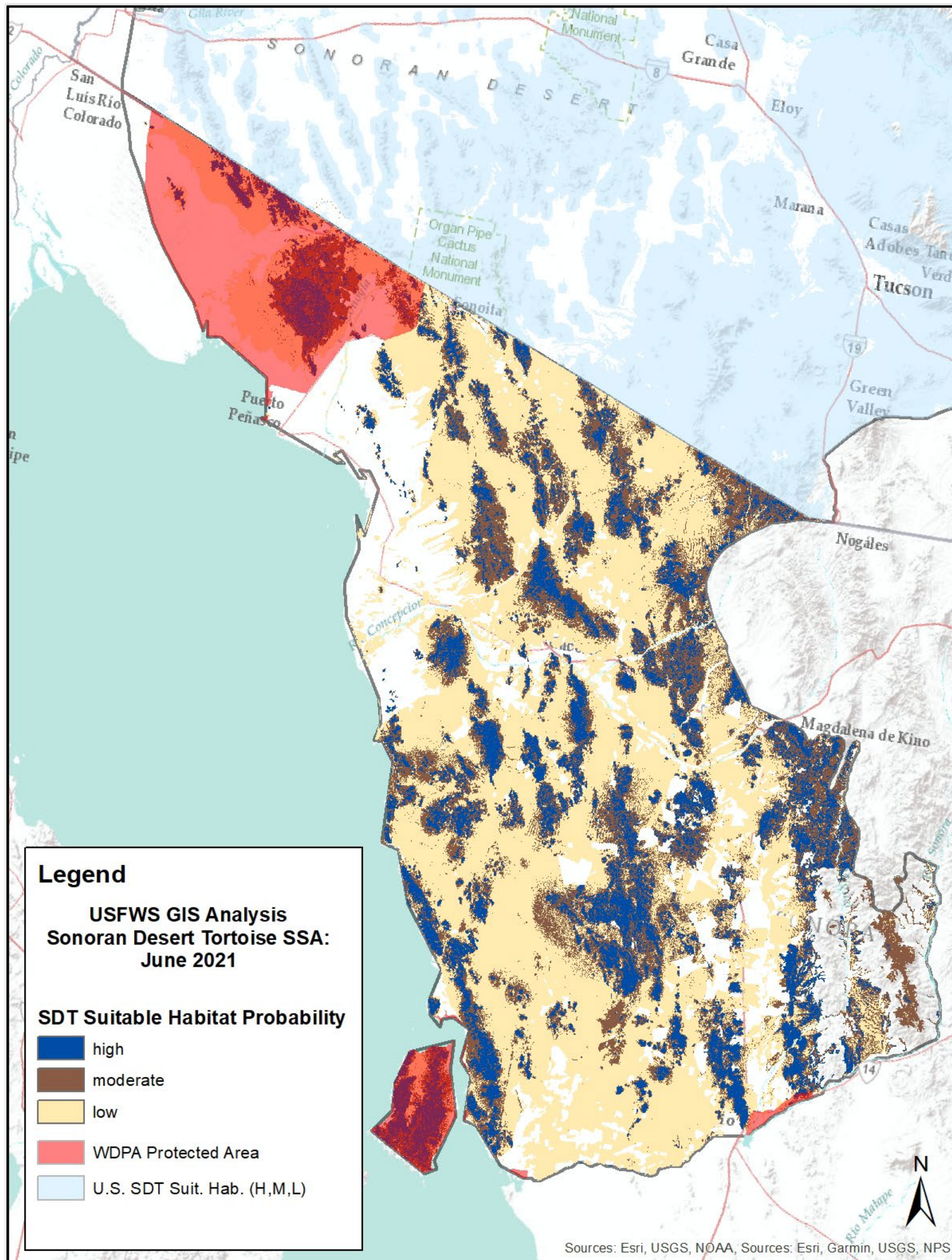


Figure 14. Location of designated management areas in within the Sonoran desert tortoise range in Sonora, Mexico, as identified by the World Database of Protected Areas. Habitat suitability is as described in Section 4.2.

3.7.2 Conservation Activities in Arizona

There are a number of conservation actions that have been implemented in the U.S. to minimize stressors and maintain or improve the status of the Sonoran desert tortoise, including most significantly a candidate conservation agreement (CCA; see AIDTT 2015, entire) with AGFD, BLM, Department of Defense, National Park Service, U.S. Fish and Wildlife Service, Bureau of Reclamation, Customs and Border Protection, U.S. Forest Service, Natural Resources Conservation Service, and Arizona Department of Transportation (collectively referred to as the "Parties"). CCAs are formal, voluntary agreements between the Service and one or more parties to address the conservation needs of one or more candidate species or species likely to become candidates in the near future. Participants commit to implement specific actions designed to remove or reduce threats to the covered species, so that listing may not be necessary. The CCA for the Sonoran desert tortoise was completed by the Parties in March 2015 and was signed by the final signatory, the Service, on June 19, 2015. The Parties have implemented the CCA across approximately 13,000 sq mi (8.3 million ac, 3.4 million ha) of Sonoran desert tortoise habitat in Arizona.

The CCA is designed to encourage, facilitate, and direct effective Sonoran desert tortoise conservation actions across multiple agencies and entities having the potential to directly influence species conservation in Arizona. Parties to the CCA identified existing tortoise conservation measures and efforts during the development of the agreement, while sharing conservation expertise and information across a broad range of organizations. This facilitated an organized conservation approach that encourages coordinated actions and uniform reporting, integrates monitoring and research efforts with management, and supports ongoing conservation partnership formation.

Through implementation of the CCA, all Parties continue to participate in range-wide conservation and management of the Sonoran desert tortoise by assessing and directing conservation measures in Arizona. The CCA is designed to provide a comprehensive conservation framework for applying effective Sonoran desert tortoise conservation and management actions, such that:

- Sonoran desert tortoise populations and habitats are more effectively identified, inventoried, and conserved through time;
- The Parties can develop and implement conservation measures aimed at maintaining or enhancing Sonoran desert tortoise habitat and populations; and,
- The ability of the Parties to monitor the response of the species to conservation and management actions is enhanced as a result of the cooperative/comprehensive framework provided through the CCA.

The 2015 CCA formalized existing management actions intended to conserve and protect the Sonoran desert tortoise and its habitat. Management actions in the CCA include, but are not limited to, reducing the spread of nonnative grasses, reducing or mitigating dispersal barriers, reducing the risk and impact of desert wildfires, reducing the impact of off-highway vehicles, population monitoring, and reducing illegal collection of Sonoran desert tortoises. A complete list of the stressor-specific conservation measures can be found in Appendix A of the CCA

(AIDTT 2015, pp. 56–128). Implementation of these conservation actions is being evaluated through ongoing monitoring of useful metrics to document that committed activities are being completed in a timely and thorough fashion. In addition, the Parties' commitments to continue research at the existing Sonoran desert tortoise LTMP sites throughout Arizona will increase the understanding of Sonoran desert tortoise population trends and management needs (see Chapter 4 for results of the long-term monitoring).

In order to meet the objectives of this CCA, the Arizona Interagency Desert Tortoise Team (AIDTT) has managed, administered, and periodically reviewed the implementation of species conservation outlined in the CCA. The AIDTT was formed in 1985 to coordinate research and management of Sonoran desert tortoise populations in Arizona. Co-chaired by representatives of AGFD and the Service, AIDTT cooperation is intended to: (1) ensure the perpetuation of the species and (2) prevent loss and improve quality of habitat in Arizona. As such, the AIDTT is uniquely qualified to manage and administer this program because its membership includes Sonoran desert tortoise experts and land/resource managers from across the range of the Sonoran desert tortoise in Arizona. Throughout this process, the AIDTT and other Parties recognize that the document needs to be updated to better focus on those conservation actions that alleviate the most significant threats and stressors described above in this chapter rather than focusing on all potential stressors identified in the December 2010, 12-Month Finding for the Sonoran desert tortoise (75 FR 78094), which served as the basis for the CCA.

Long-term management of Sonoran desert tortoise populations and habitat, as outlined in the CCA, is an important contribution to the conservation of the Sonoran desert tortoise. The initial term of the CCA is 10 years. Thereafter, the Parties agree that the CCA will be extended for additional 5-year increments until long-term habitat and population conservation of the Sonoran desert tortoise is achieved, as determined by the AIDTT. Not all Parties to the CCA have reported their conservation actions carried out under the CCA at this time; however, most of the Parties have reported their activities, and a summary of each of those Parties' activities since the CCA was signed is described in more detail in Appendix D.

3.7.3 Conservation in Mexico

Throughout Mexico, the Secretaria de Medio Ambiente y Recursos Naturales lists desert tortoises (i.e., Sonoran and Goode's thornscrub) as "Amenazadas," or Threatened (SEMARNAT; SEDESOL 2010, p. 77, entire). Threatened species are "those species, or populations of the same, likely to be in danger of disappearing in a short or medium timeframe, if the factors that negatively impact their viability, cause the deterioration or modification of their habitat or directly diminish the size of their populations continue to operate" (SEDESOL 2010, entire). With this designation take of the species is prohibited, unless specifically permitted, along with any activity that intentionally destroys or adversely modifies its habitat (SEDESOL 2010, entire). However, activities that unintentionally destroy or adversely modify their habitat do not appear to be specifically prohibited (e.g., cultivation of buffelgrass for livestock grazing). In 1988, the Mexican Government passed a regulation that mirrors the National Environmental Policy Act of the United States (42 U.S.C. 4321 et seq.). This regulation requires an environmental assessment of private or government actions that may affect wildlife or their habitat (SEDESOL 2010, entire).

Compared to Arizona, significantly less area within Sonora is set aside for officially designated conservation areas. About 556 sq mi (362,000 ac, 147,000 ha) of predicted potential habitat in Sonora, about 4% of the total, is within protected areas (USFWS 2015, p. 59). These primarily include El Pinacate y Gran Desierto de Altar Biosphere Reserve and Isla Tiburón.

3.8 Other Factors Considered

Because the Sonoran desert tortoise occupies such a large range, a wide variety of stressors, not discussed in detail in this SSA report, may affect individual tortoises. We evaluated these other stressors but did not include discussion of them because they do not represent operative stressors on the species into the future. These other factors may be historical (e.g., conversion to agriculture), or not known to have measurable population level effects (e.g., Upper Respiratory Tract Disease, Cutaneous Dyskeratosis, environmental contaminants, predation, grazing, large-scale mining operations). Some factors are narrow in scope in context of the relatively wide range of the Sonoran desert tortoise (e.g., trash, field research, human predation on tortoises, and target shooting), or are a combination of the above.

Chapter 4: Current Conditions

In this chapter, we describe the current condition of the Sonoran desert tortoise through analysis of habitat distribution and population size across its range. We analyzed the presumed historical range for current Sonoran desert tortoise habitat suitability (see further explanation in Appendix B). Using that information in addition to available data on stressors to the species, we then describe how we used population densities and our habitat quality analysis to make estimates of population abundance for the Arizona, U.S. and Sonora, Mexico areas of analysis.

Throughout our assessments of current and future condition, we leveraged information gathered from AGFD's and BLM's long-term monitoring plots (LTMP). There are currently 18 LTMP sites, 17 of which have been surveyed using capture-mark-recapture methods from 1987–Present. Each LTMP site is surveyed multiple times during the summer monsoon season (July–October) when Sonoran desert tortoises are most active using standard survey techniques to search for all age classes (Averill-Murray 2000; entire). On average, plots are surveyed every 5 years (Zylstra and Steidl 2021, p. 6), and surveys will increase in frequency when estimates of tortoise abundance indicate a significant decline between successive monitoring surveys (Rubke and O'Donnell 2019, p. 73). The monitoring data reports included information about Lincoln-Petersen abundance index estimates, survey effort, and other biotic and abiotic information relevant to Sonoran desert tortoises. For more detailed information about these data, refer to Appendix E and the most recent report for the LTMP sites (Woodman et al. 2009, entire; Dockens et al. 2011, entire; Hoffman et al. 2017, entire; Rubke et al.2017a, entire; Rubke et al. 2018a, entire; Rubke and O'Donnell 2019a, entire; Rubke and O'Donnell 2020a, entire; Rubke and O'Donnell 2020b, entire; Rubke and O'Donnell 2021a, entire).

4.1 Current Range

The presumed historical range of Sonoran desert tortoise covers roughly 68,500 sq mi (44 million ac, 18 million ha), about 62% of which is within Arizona (Figure 5). Although there has likely been some reduction in distribution within its range due to past habitat conversion (see Figure 9), we are not aware of any changes in the overall species' range or loss of populations within Arizona. Information on the historical versus current distribution of the tortoise in Sonora is less certain, but no large-scale changes in range are known or presumed.

4.2 Current Habitat Suitability

4.2.1 Habitat Assessment in Arizona

We collaborated with researchers at the University of Nevada-Reno and USGS to develop a model of potential Sonoran desert tortoise habitat suitability within the Arizona portion of the species distribution, (hereafter referred to as the "Ensemble Model"). Briefly, this modeling effort used known Sonoran desert tortoise occurrence records and a suite of 15 environmental covariates (i.e., topographic, climatic, and soil related predictor layers) to estimate areas of suitable tortoise habitat across the range of the species. The output of this modeling approach was an ensemble model of habitat suitability that was developed using four independent modeling algorithms (generalized boosted regression models [GBM], random forests, maximum

entropy [Maxent], and multivariate adaptive regression splines [MARS]). For more details on this modeling effort, refer to Appendix B.

To develop our base map of habitat suitability, we reclassified the Ensemble Model output, which provided probability surface of suitable habitat on a 0.0–1.0 scale, into four habitat classes: high suitability (0.71–1.0), moderate suitability (0.41–0.70), low suitability (0.11–0.40), or non-habitat (0.0–0.10). To define areas of high suitability habitat, we consulted with the tortoise biologists on the SSA team and looked at where the range of habitat suitability values for grid cells that correspond to the LTMP sites. Note that LTMP sites were originally selected for their apparent high-suitability for Sonoran desert tortoises with the expectation that individuals could be readily found when reading the plots. Given that the average habitat suitability value found within the LTMP sites was 0.70 or higher, we used 0.70 as our lower threshold for defining high suitability habitats. Similarly, we looked at the range of habitat suitability values for all known Sonoran desert tortoise occurrence records. Given that less than 2% of all known observations fell within grid cells with habitat suitability values of less than 0.10, we used 0.10 as our upper limit for the non-habitat class. Finally, we set the dividing threshold at 0.40 for the low and moderate habitat classes as this evenly divided the interval between the 0.10 and 0.70 thresholds. From there, we used the reclassified layer as the base model for predicted Sonoran desert tortoise habitat and overlaid additional impacts of urban areas and human development to remove areas of unsuitable habitat (i.e., areas that lacked natural intactness; Figure 9). More details are provided below or within Appendix B.

4.2.2 Habitat Assessment in Sonora

The Ensemble Modeling effort did not include estimates of habitat suitability for Sonora because of a lack of detailed environmental data for this portion of the Sonoran desert tortoise's distribution. As such, we generated a potential habitat model using GIS to provide a geospatial representation of the location and extent of predicted potential habitat for the Sonoran desert tortoise within Sonora. To estimate habitat suitability, we used a combination of three primary data layers: slope/ruggedness, vegetation type/land cover, and soils. For each layer, we reclassified the data based upon expert judgement of the range of values appropriate for the Sonoran desert tortoise. The resulting habitat model was then based on a union of these features. More detail on the data sources and analytical methodology can be found in Appendix B.

4.2.3 Current Habitat Suitability

After constructing these spatial models for both Arizona and Sonora to categorize habitat suitability as high, moderate, and low, we next removed any remaining areas that lacked natural intactness, such as developed areas and agriculture fields (see Appendix B for more information). The results provided an overall assessment of the current extent of potential suitable Sonoran desert tortoise habitat within the Arizona and Sonora analysis areas. This resulted in an estimate of approximately 49,000 sq mi (31.4 million ac, 12.7 million ha) of potential habitat across the species' range (Table 2). Of this total, 62% occurs in Arizona and 38% occurs in Sonora, and for both areas 24% is in the high class, 29% is in the moderate class and 47% is in the low class. The distribution of the high, moderate, and low classifications across the species' range is shown in Figure 15.

Table 2. Total areas, in square miles, of suitable habitat of the Sonoran desert tortoise in Arizona and Sonora as categorized into three classes.

Suitable Habitat Class	Arizona	Sonora	Range-wide Total
High	8,532	3,406	11,938
Moderate	9,116	4,945	14,061
Low	12,828	10,396	23,224
Total Habitat Area	30,475	18,747	49,222

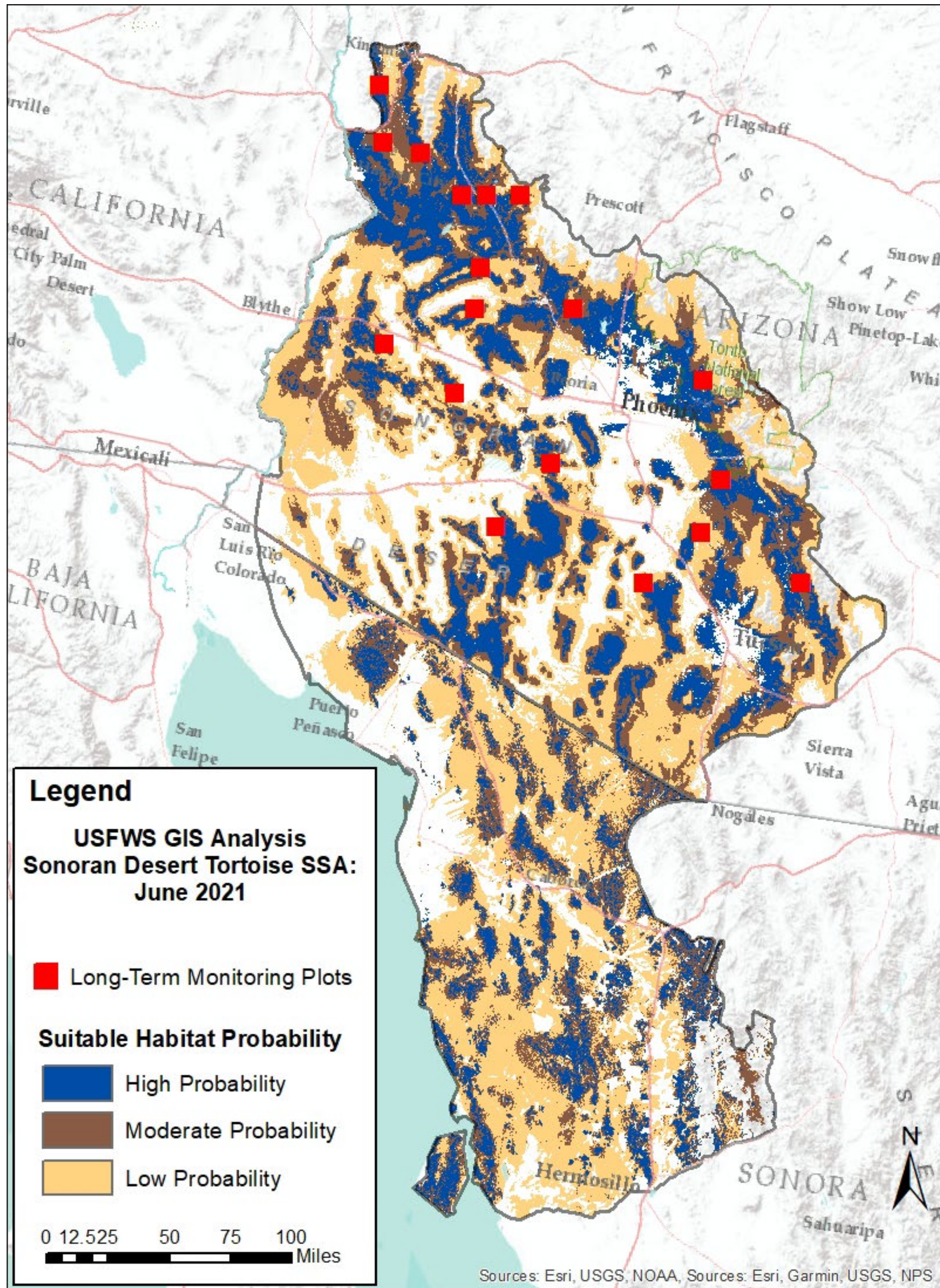


Figure 15. Suitable habitat probability for the Sonoran desert tortoise used in the species status assessment showing high, moderate, and low suitable habitats along with long-term monitoring plots (LTMP) (red squares).

4.3 Current Abundance Estimates

To further assess the current condition of the Sonoran desert tortoise we used our habitat suitability summaries to calculate a rough estimate of the potential Sonoran desert tortoise adult population sizes in Arizona and Sonora. To do this we calculated population density estimates from the long-term monitoring data for high suitability habitats and then elicited estimates of density from species experts on the SSA team for moderate and low suitability habitat classes. The density estimates within each class were represented by a distribution of plausible values. Then, we multiplied the density estimates by the suitable habitat in each class to reach an overall distribution of estimates for adult tortoises in each analysis area and range-wide.

4.3.1 Long-Term Monitoring Data and Density Estimates

We estimated the adult density of Sonoran desert tortoises in high suitability habitats by using the range of Sonoran desert tortoise densities observed at the 17 LTMP sites (Dockens *et al.* 2011, entire; Woodman *et al.* 2009, entire; Hoffman *et al.* 2017, entire; Rubke *et al.*2017a, entire; Rubke *et al.* 2018a, entire; Rubke and O'Donnell 2019, entire; Rubke and O'Donnell 2020a, entire; Rubke and O'Donnell 2020b, entire; Rubke and O'Donnell 2021, entire). All 17 LTMP sites are within areas we categorized as high potential habitat (Figure 15), and the plots have Lincoln-Peterson abundance estimates and survey effort for every survey during the monitoring period included within the reports (1987–present; Figures 16 and 17). We estimated density by dividing the abundance estimate by plot area (in sq mi) to obtain an estimate of tortoise density at each site for a given survey year.

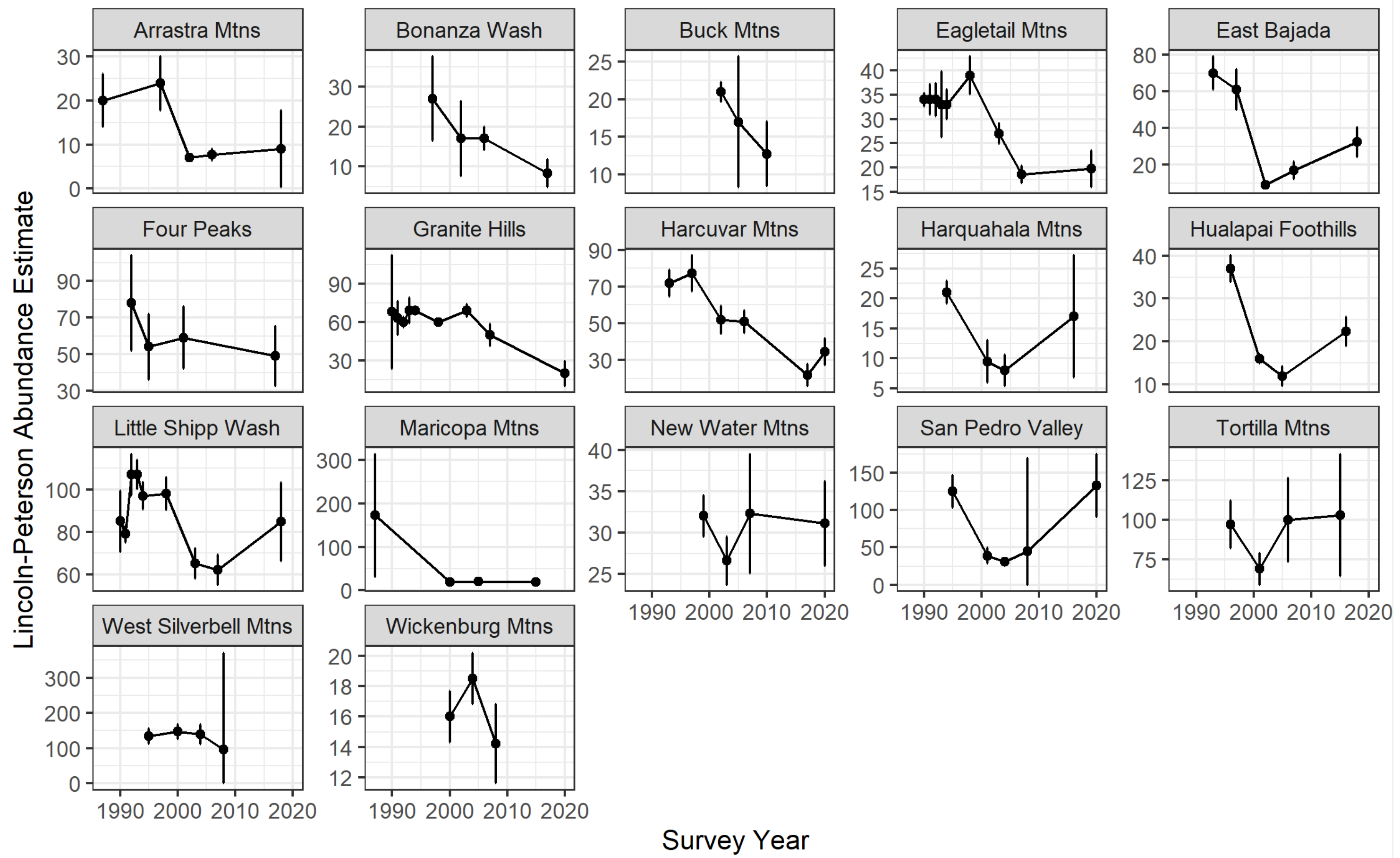
Across the entire monitoring period, the average adult density was 56 tortoises per sq mi (range 6–205 tortoises per sq mi). Although numbers have fluctuated over time, Lincoln-Petersen abundance estimates from the 30 years of monitoring at LTMPs have not shown a consistent decline or increase across all plots (Figure 16). Based on information from the LTMP plots, 9 plots appear to be stable and 8 appear to have decreased over the last 25-years; however, 8 plots appear to show increasing trends in the last decade, indicating that 14 of these plots appear to have remained stable or have increased in the last 10-years (Figure 16) and illustrating how detection of tortoises fluctuates over time. Three additional LTMPs are currently being surveyed in 2021; preliminary data indicate the population at one site is still increasing, one site remains stable, and the third site may have declined, but additional, ongoing field work is necessary before any conclusions can be drawn (Jones and Rubke 2021, entire). It is important to note that the confidence intervals associated with abundance estimates are large and overlapping, which makes trends difficult to tease out from Figure 16 alone. Because of this and the fact that there was not equivalent survey effort through time at each plot, we calculated catch per unit effort (CPUE) for each LTMP through time as an additional proxy for adult abundance. To calculate CPUE, we divided the number of unique tortoises captured in a survey season by the survey effort. Although there was some variability in CPUE through time and across LTMP sites, trends appear to be generally stable or slightly decreasing over the last 25 years, except for the West Silverbells and Wickenburg LTMPs (Figure 17). Specifically, 7 sites appear to be decreasing, 8 sites appear to be stable, and 2 sites appear to be increasing.

While not abundant, hatchling tortoises have been detected on six of 14 LTMPs in the last

decade. Although hatchling tortoises are exceptionally difficult to detect, in the last decade juvenile tortoises have been documented on almost all LTMPs surveyed, which indicates successful reproduction during this timeframe. Unmarked adults that continue to be found on most plots also suggest that some tortoises may have been missed previously or are recruited from adjacent sites off-plot. Whether or not that immigration includes hatchlings and juveniles is impossible to know. Juvenile tortoises are also difficult to detect and the lack of detections of individuals in these smaller size classes does not necessarily indicate a lack of younger tortoises on plot.

To derive an estimate of current abundance of Sonoran desert tortoises and to minimize the influence of survey effort on density estimates, we subset the monitoring data to include only surveys conducted 2000–present that had greater than 35 person days of effort. Using these thresholds, the average adult density was 46 tortoises per sq mi (range: 6–155 tortoises per sq mi), and this was used as the density estimate for areas in high habitat suitability.

To ascertain density estimates for the moderate and low suitability habitat classes, we elicited values from the tortoise biologists within the SSA team and used the range of elicited values to derive a distribution of plausible density estimates for each habitat class. Given that the distribution of density estimates from the long-term monitoring sites is best described by a gamma distribution, we assumed that the density estimates within the moderate and low suitability habitat classes also followed a gamma distribution. Using this approach, our estimates for average adult tortoise density were 25 tortoises per sq mi (range: 5–35 tortoises per sq mi) in moderate suitability habitat and 6 tortoises per sq mi (range: 0–15 tortoises per sq mi) in low suitability habitat. We used the same density estimates for both the Arizona and Sonora analysis areas. For more details on the density distribution modeling or expert elicitation approach, please refer to Appendix E.



Arrastra Mtns
Bonanza Wash
Buck Mtns
Eagletail Mtns
East Bajada
Four Peaks
Granite Hills
Harcuvar Mtns
Harquahala Mtns
Hualapai Foothills
Little Shipp Wash
Maricopa Mtns
New Water Mtns
San Pedro Valley
Tortilla Mtns
West Silverbell Mtns
Wickenburg Mtns
Lincoln-Peterson Abundance Estimate
Survey Year
1990 2000 2010 2020

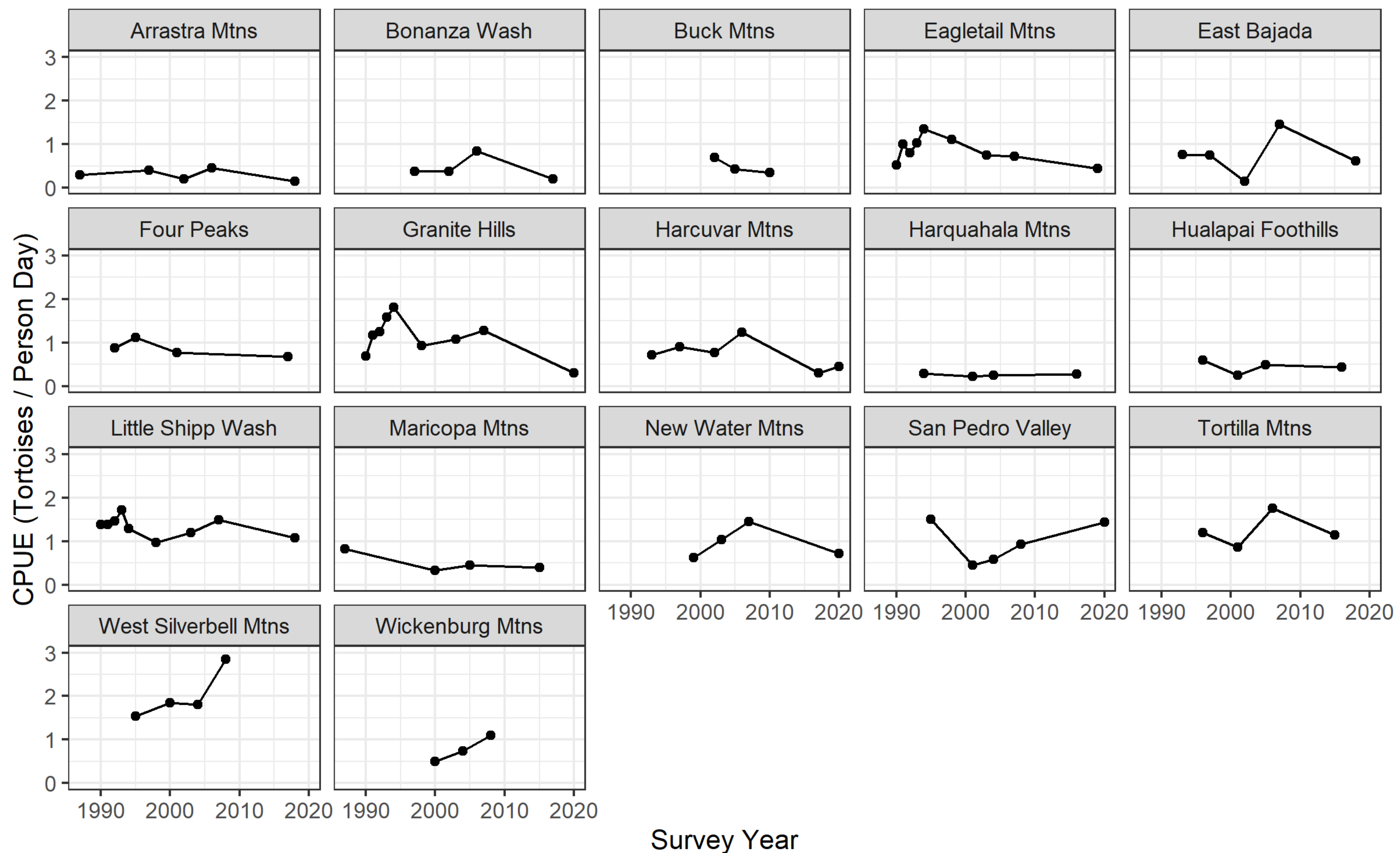


Figure 17. Adult Sonoran desert tortoise catch per unit effort (CPUE) across the 17 long-term monitoring plot (LTMP) sites in Arizona across all survey years. Points represent the total number of adult tortoises divided by the person days employed during a given survey period.

4.3.2 Total Tortoise Estimates

Because there is a large range in the density estimates, we built a distribution of potential current population sizes. More specifically, we took 100,000 random draws from our distributions of density estimate (outlined above) and multiplied those estimates by the current area estimates of habitat within each class. Because the density estimate distributions are slightly overlapping for each habitat class, we imposed the following constraints on the random draws: 1) the density estimate for a habitat suitability class must be less than the estimate drawn for the habitat class above it; and 2) the density estimate within a habitat class cannot exceed the maximum value for the class (high = 155, moderate = 35, and low = 15). Then, we multiplied each of the combinations of population densities by the three habitat classes to derive a distribution of population sizes. This approach resulted in mean estimates of current, adult Sonoran desert tortoise population sizes of 549,247 (range: 100,977–1,726,256) in Arizona and 273,013 (range: 47,346–782,140) in Sonora (Figure 18). Range-wide these estimates sum to 865,335 (range: 148,358–2,507,762) adult tortoises.

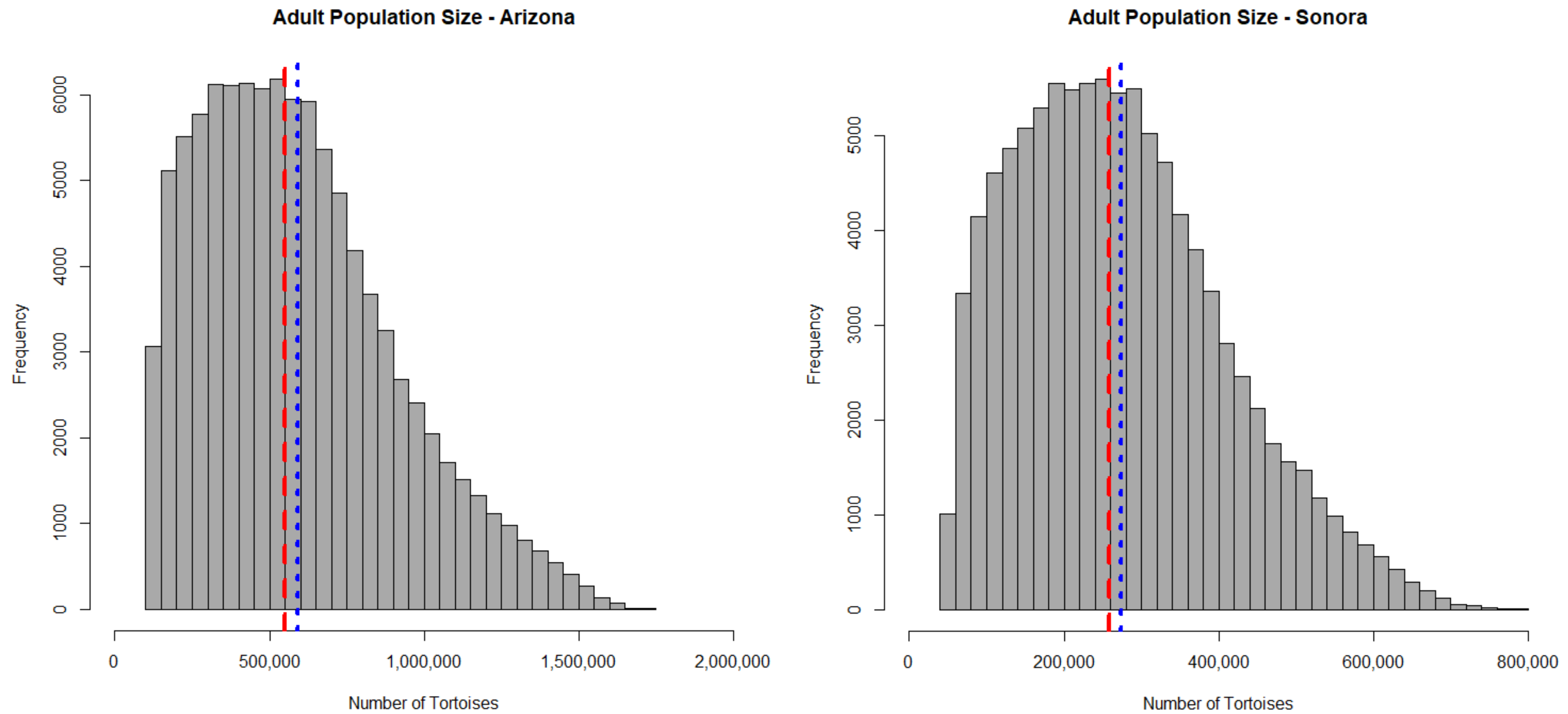


Figure 18. Distribution of potential current adult population sizes of Sonoran desert tortoises for Arizona (left) and Sonora (right) analysis areas. The red dashed line corresponds to the median potential adult population size, and the blue dotted line corresponds to the mean potential adult population size.

Chapter 5: Future Conditions and Viability

We have reviewed the ecological needs of the Sonoran desert tortoise, the current conditions of the species, and the risk factors and conservation actions that drive the condition of the species. We next turn to evaluating the potential future condition of the species to assess its viability. Because of the complexity of potential factors and the relatively large range of the Sonoran desert tortoise, we used several quantitative tools to assist us in characterizing the future habitat conditions and species responses in order to evaluate a range of plausible future scenarios. We used a spatial analysis of future habitat suitability under two scenarios of climate change and urban growth to estimate future carrying capacity. In addition, we accounted for future declines in vital rates of tortoise within areas of urban influence and in consideration of the long-term impacts of increasing drought conditions across the range of the Sonoran desert tortoise. The results provide an estimate of project abundances, growth rates and risk of quasi-extinction for both the Arizona and Sonora analysis areas under two future scenarios.

5.1 Future Scenarios

In evaluating the potential viability of the Sonoran desert tortoise, we considered two plausible future scenarios and assessed risks to the species from those scenarios (Table 3). These scenarios were developed to represent a range of conditions in order to consider the potential responses by the Sonoran desert tortoise to varying habitat and climatic conditions across its range. The scenarios help us account for a variety of key uncertainties in the information and in the analysis. We explain below the factors included in the scenarios.

Table 3. Factors and assumptions made in the future scenarios used in the Sonoran desert tortoise status assessment.

		Low Effects Scenario (Upper Plausible Limit)	**High Effects Scenario (Lower Plausible Limit)**
Habitat	Climate Change	Future habitat suitability under RCP4.5 conditions	Future habitat suitability under RCP8.5 conditions
	Urban Growth	5-km buildout of Phoenix & Tucson metro areas (Eastern Cities) 1-km buildout on all other cities > 10k people (Western Cities & Sonora)	20-km buildout of Phoenix & Tucson metro areas (Eastern Cities) 5-km buildout on all other cities > 10k people (Western Cities & Sonora)
Demographic	Urban Influence	20-km influence on Phoenix & Tucson metro areas 10-km influence on all other cities > 10k people	
	Drought	No change in the average severity of drought compared to the last 30 years	Increase in the average severity of drought by 2080

5.1.1 Time Frame

The length of time to consider in an assessment strives to incorporate enough generations of a species to be able to detect potential population and species-level responses to changes in environmental conditions. For the Sonoran desert tortoise this is particularly challenging because it has such a relatively long-life span and long time to maturity. We chose to run the simulation model we used to evaluate future species responses over a 125-year time frame. This length of time includes about two tortoise generations beyond the timeframes used in the habitat projections that incorporate climate change projections for the 2070–2100 (2080s) time period. This time period also represents about 5 generations for the Sonoran desert tortoise (assuming a 25-year generation time). Although this is a relatively small number of generations to identify changes in population parameters, it is a relatively long time over which to forecast changes in environmental conditions. We recognize there are large uncertainties associated with forecasting human behaviors, urban development, and climate change for this long of time frame.

5.2 Projected Habitat Change and Loss

We included two primary factors in evaluating future habitat conditions for the species: habitat change due to climate change and habitat loss due to urban growth.

5.2.1 Climate Change

We projected future habitat conditions across the range of the species in Arizona under two different climate change scenarios. We further collaborated with researchers at the University of Nevada-Reno and the USGS to develop these habitat projections, consistent with the methods used with the Ensemble Model for habitat assessment in the current condition (see Section 4.2). The analysis involved using down-scaled climate projection data for the 2080s timeframe (2070–2100) under the RCP4.5 and RCP8.5 climate scenarios and incorporated the changing climate variables to produce new probabilities of tortoise habitat across the range in Arizona. As we did with the current habitat conditions, we categorized the habitat into three suitability classes of high, moderate, and low to characterize future habitat conditions for the tortoise (see Appendix B for more information). The results indicate some modest increases in overall amounts of suitable tortoise habitat compared with current conditions; however, there was a substantial decline in high suitable habitat in the "High Effects" Scenario (Table 4; Figures 19 and 20).

We used these changes in habitat conditions as a basis for setting a future carrying capacity for each analysis area that is incorporated into the simulation model (see Section 5.3.1 below). For the Sonoran analysis area, we did not have similar data available to analyze the effects of climate change on habitat suitability. To project the effects of climate change, we adjusted the proportion of habitat in Sonora in the three habitat classes based on the projections for Arizona. In other words, projected changes in the total amount of high, moderate, and low habitat in Arizona due to climate change were applied to Sonora as well.

5.2.2 Urban Growth

We also accounted for potential future loss of tortoise habitat due to urban development expansion around existing cities in Arizona and Sonora. We did not find any available spatially explicit urban growth projection information that we could use in this analysis. Therefore, we made some general estimates of growth after considering population growth estimates and recent past urban growth areas. To account for the substantial uncertainty in these estimates we used a range of projections (Table 3). For the "Low Effects" scenario we assumed that urban growth by the 2080s would extend 5 km around the footprint of existing cities in the eastern part of the range (around the Phoenix and Tucson metropolitan areas) and 1 km around the footprint of existing cities in the western and Sonoran portions of the range. We assumed higher growth in the eastern part because of the continued and projected high population growth in the Phoenix-Tucson corridor (Gammage *et al*. 2008, entire). For the "High Effects" scenario, we assumed urban growth of 20 km around existing cities in the east and 5 km in the western and Sonoran portion of the range. For all of these projections, we assumed that the growth would occur only within areas with land ownership categories that are more likely to be developed: Unprotected (Private) or Other (State) categories (see Appendix B). We excluded areas identified as Managed, Multi-use, or Tribal from being lost to urban development in our projections. While this is a simplified assumption, as not all unprotected areas are likely to be developed and some protected areas could be developed over the next 50 to 80 years, it provides a reasonable way to estimate potential effects of future urban growth.

5.2.3 Future Habitat Projections

The results of estimating future habitat conditions considering two scenarios of climate change (Arizona only) and urban growth are reflected in Table 4 and Figures 19 and 20. The spatial distribution of the high, moderate, and low suitability habitats at 2080 under RCP4.5 and RCP8.5 are shown in Figure 19 (and quantified in Table 4) for Arizona and Figure 20 (and quantified in Table 4) for Sonora. For the Arizona analysis area, assessing future potential habitat conditions resulted in a range of 31% or 11% of all potential Sonoran desert tortoise habitat being in the high suitability class; 39% or 44% in the moderate suitability class; and 30% or 45% in low suitability class under the "Low Effects" and "High Effects" scenarios, respectively. In Sonora, this resulted in a range of 22% or 7% of all potential Sonoran desert tortoise habitat being in the high suitability class; 37% in the moderate suitability class; and 42% or 56% in low suitability class under the "Low Effects" and "High Effects" scenarios, respectively. These predicted proportions of habitat (calculated from projection totals reported in Table 4) and their spatial distribution (Figures 19 and 20) characterize the redundancy and representation by projecting the conditions and distribution of habitat for the Sonoran desert tortoise.

Table 4. Current and future (2080s) suitable habitat estimates in square miles of suitable habitat of the Sonoran desert tortoise in Arizona and Sonora. Future projections include effects of climate change and urban growth.

Suitable Habitat Probability Class	Current	Low Effects Scenario		High Effects Scenario	
		Future	Proportion of Current	Future	Proportion of Current
ARIZONA					
High	8,532	10,852	127%	3,350	40%
Moderate	9,116	13,690	150%	13,776	151%
Low	12,828	10,341	81%	13,946	110%
Arizona Total	**30,475**	**34,883**	**114%**	**31,071**	**102%**
SONORA					
High	3,406	4,327	127%	1,328	39%
Moderate	4,945	7,422	150%	7,449	151%
Low	10,396	8,370	81%	11,227	108%
Sonora Total	**18,747**	**20,119**	**107%**	**20,004**	**107%**

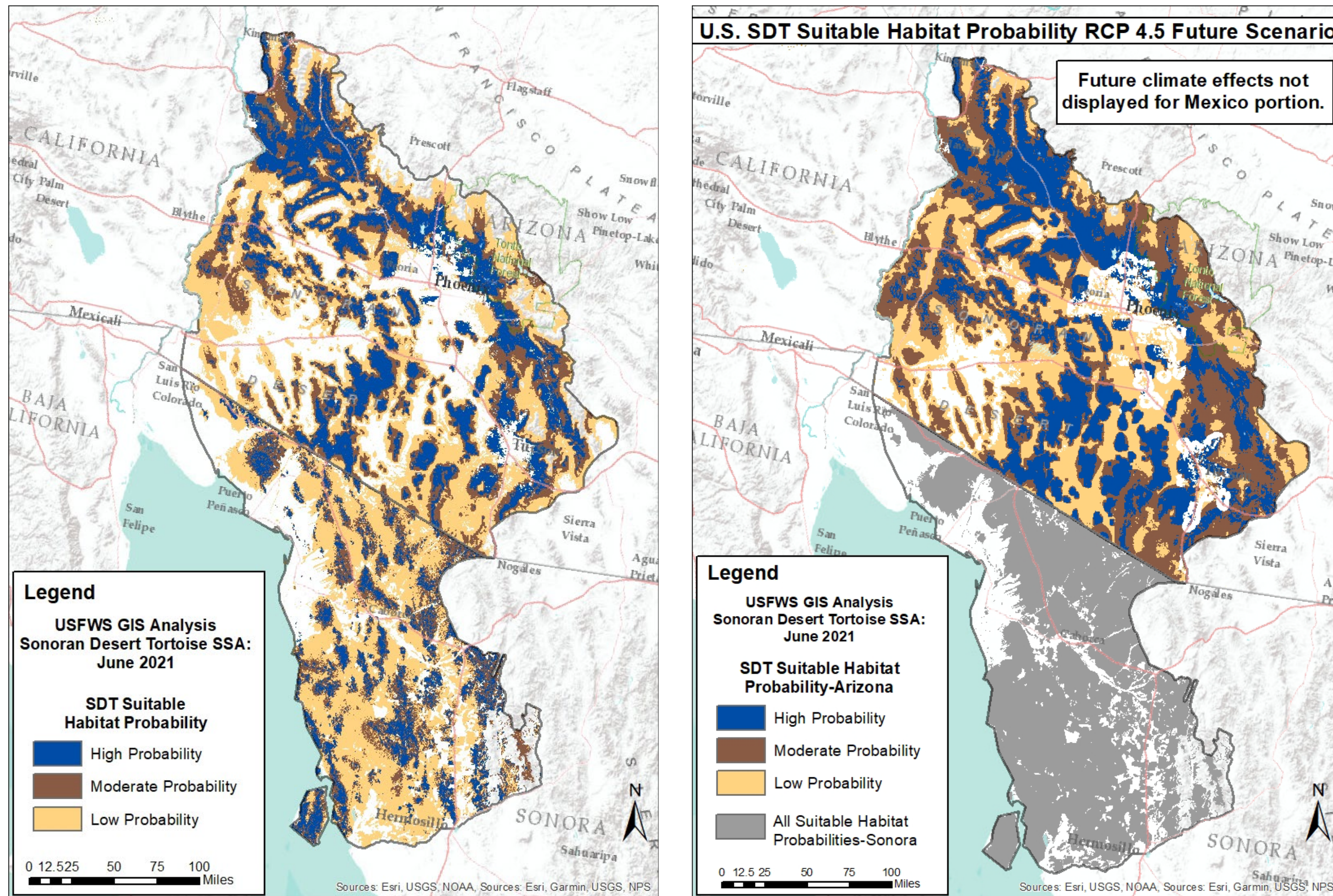


Figure 19. Current habitat suitability (left) compared to projected future suitable Sonoran desert tortoise habitat under the "Low Effects" scenario in the 2080s (right). Future projections include effects of climate change and urban growth. Future suitable habitat was not modeled for Sonora.

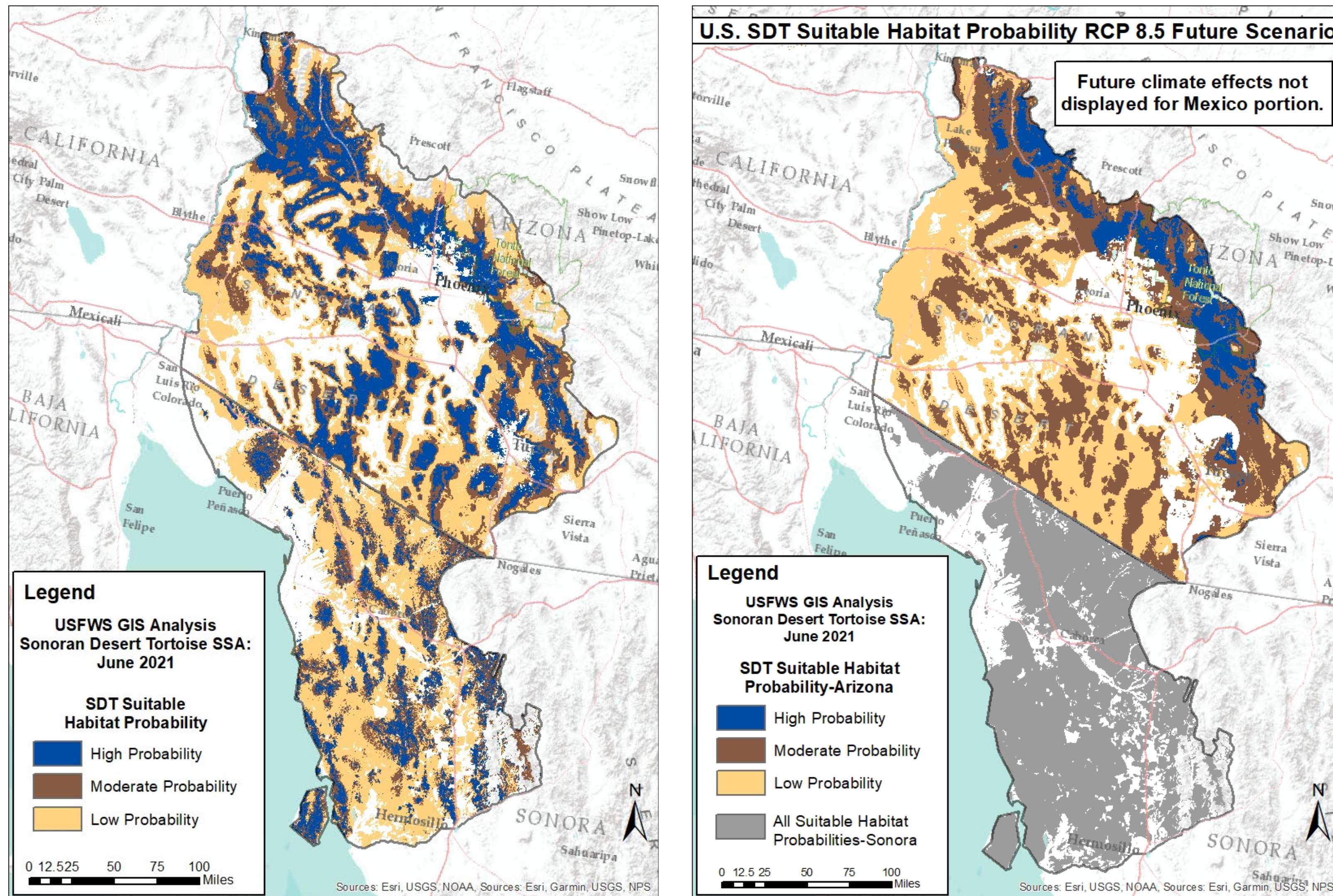


Figure 20. Current habitat suitability compared (left) compared to projected future suitable Sonoran desert tortoise habitat under the "High Effects" scenario in the 2080s (right). Future projections include effects of climate change and urban growth. Future suitable habitat was not modeled for Sonora.

5.3 Stochastic Simulation Model

We constructed a female-only, stage-structured matrix model to simulate the relationship of potential environmental conditions (habitat suitability) and species abundance to project the future risk of extinction of the Sonoran desert tortoise. After considering the potential causes and effects of stressors as they relate to habitat and the possible impacts on vital rates, two stressors (urban influence and drought) have been linked as factors that have direct effects on Sonoran desert tortoise demographic rates. Specifically, increased severity in drought has been linked to decreased survival of all age classes of Sonoran desert tortoise. Similarly, proximity to urban areas has been linked to decreased rates of survival through various human-tortoise interactions (see Section 3.6), which is accounted for within the urban influence metric. We constructed a simulation model with the following key parameters as inputs (described below): habitat suitability, starting abundance (or population size), average drought severity, urban influence proportion, maximum abundance, and vital rates. The model outputs are median abundance, probability of quasi-extinction over time, the average population growth rate (lambda), and the average survival rate. We ran the model under two different future scenarios representing key areas of uncertainty in the analysis. Below is a brief discussion of the model parameters. A more detailed explanation about how the simulation model incorporates these parameters is provided in Appendix E.

How does the simulation model work? Essentially the population simulation model takes a given starting abundance (estimated number of female tortoises) and calculates the future abundance over time by applying reproductive and survival rates (i.e., vital rates). These vital rates are the proportion of the total tortoises in a population that are surviving, being added to the population through reproduction, or being removed from the population each year. For example, an adult survival rate of 0.9 means 90% of the adult tortoises are surviving from one year to the next and 10% are dying. By calculating the number of tortoises being added to the population through reproduction and taken away from the population through death each year, it allows us to project the change in the abundance of tortoises over time based on those vital rates. Because there is natural variation in reproduction and survival rates, as well as uncertainty about those rates, the vital rates are not single set numbers but are a range of values based on available data and our understanding of the species. The computer runs the model 1,000 times, and in each model run, or replicate, randomly selects different annual vital rates within the given ranges. Therefore, the model results will vary between replicates based on which vital rates were randomly selected.

Each model replicate calculates the annual abundance of tortoises for each year for 125 years into the future, and we can use the median abundance of these 1,000 replicates as our estimate of the future abundance of the tortoise. The change in the median abundance estimates over time results in a population growth rate (lambda), where 1.0 is stable (no change in abundance), less than 1.0 is declining, and greater than 1.0 is increasing. With 1,000 replicates of annual population growth rate, we can calculate the average annual population growth rate.

Because of the variation and uncertainty in survival and reproductive rates, some of the abundance projections of those 1,000 replicates of the model will fall below a quasi-extinction level. The quasi-extinction level is a threshold number of individuals that we established prior to the analysis: 2% of starting population size. When the simulated abundance of a replicate drops below this threshold, we consider that replicate to be extinct. For example, if the population abundance falls below the quasi-extinction level in 10 of the 1,000 replicates over 100 years, then the quasi-extinction probability is 0.01 or 1% in 100 years. We ran the model independently for two different scenarios for the US and Sonora analysis areas and each scenario is replicated 1,000 times to produce the model results. The scenarios account for different future vital rates resulting from projected changes in environmental conditions.

5.3.1 Starting and Maximum Abundance

We used our density estimates of adult Sonoran desert tortoises in the different habitat qualities (see Section 4.3 Current Tortoise Abundance Estimates) to derive the starting abundance (or population size), maximum abundance (which represents the carrying capacity or population ceiling for the model), and quasi-extinction level (see below). For the starting abundance for the model simulations, we multiplied the estimated habitat area of each of the three habitat suitability classes by the population density estimates in those classes. However, the model uses half of this total number, as it is a female-only model and assumes a sex ratio of 1:1 (see Appendix E). For this evaluation, the population sizes estimated from the maximum density estimate for each class multiplied by the area of habitat within each class serves as a ceiling or carrying capacity to limit overall population growth in the simulation for scenarios not involving future loss of habitats due to urbanization. We calculated the maximum carrying capacity for our current and future habitat suitability maps. Then, we calculated the difference between the

current and future carrying capacity for each scenario to get an annual rate of change in carrying capacity such that carrying capacity increases or decreases through the simulation to match the presumed maximum population size after 125 years.

5.3.2 Vital Rates and Quasi-Extinction

We based our estimates for survival and transition rates at three life stages (Figure 3) on published literature to the extent possible and varied the rates around mean estimates (see Appendix E). Briefly, we used the demographic estimates calculated from the LTMP data (Zylstra *et al*. 2013, entire; Campbell *et al*. 2014, entire; Campbell *et al*. 2018, entire; Zylstra and Steidl 2021, entire) (Table 5). Where possible, we gave preference to the estimates from Zylstra and Steidl (2021, entire) as these estimates included the most up to date data from the long-term monitoring sites in Arizona. However, previous research did not include the young juvenile age class within their population modeling efforts; thus, we used the demographic estimates estimated by McGowan *et al*. (2017, p. 121).

Determining what the quasi-extinction threshold should be for this analysis for the Sonoran desert tortoise is an important choice because it influences the nature of the resulting quasi-extinction probability profile. It is important not to consider absolute extinction as a threshold because population dynamics that change once populations get very small are not accounted for in our model. And with a long-lived species such as the Sonoran desert tortoise, a population can persist for a long time with just a few individuals but be functionally extinct because no breeding is occurring (e.g., the Pinta Island tortoise population in the Galapagos archipelago which persisted for decades with just one individual). Instead using an absolute extinction threshold, we chose to use a higher quasi-extinction threshold which more appropriately reflects the genetic and ecological problems that could place the Sonoran desert tortoise at an unacceptable risk of extinction were the population size to fall below that threshold.

We chose 2% of the starting population size as the quasi-extinction threshold. For example, assuming a total estimate of Sonoran desert tortoises of 350,000 females in Arizona, this would put the quasi-extinction levels at 7,000 adult females in Arizona as the threshold below which the model would consider the population quasi-extinct. Given a current estimate of suitable habitat of approximately 30,475 sq mi (about 1.95 million ac, 7.89 million ha) in Arizona, these quasi-extinction levels would represent densities of 0.23 total adult Sonoran desert tortoises per square mile, regardless of habitat suitability class. These would represent very low densities, probably below densities at which Sonoran desert tortoises would be able to successfully find mates for sustaining reproduction. If the Sonoran desert tortoise was to actually decline this drastically, it is probably more realistic to envision that there would be a very small number of populations remaining within the highest quality habitats. This would represent a severe, unacceptable reduction in the redundancy and representation for this species. So, we used these levels as the metric for reasonable estimates by which we assessed the risk of quasi-extinction to the range of the species in Arizona and Sonora.

5.3.3 Urban Influence

The potential effects of urban areas were considered in our assessment of the future condition of

Sonoran desert tortoise habitat by identifying the portions of the analysis units to cities with at least 10,000 people (see Appendix B). We chose to use at least 10,000 people as our threshold to be consistent with Zylstra and Steidl (2021, entire) for this analysis, assuming that smaller towns with fewer people are less likely to have elevated effects on adult Sonoran desert tortoises due to a lesser opportunity of human interactions. For the same reasons, we also assumed that cities in the larger metropolitan areas in the eastern portion of the range near Phoenix and Tucson, Arizona, would have greater effects than would the smaller cities in the western portions of the range and in Sonora. Therefore, we calculated the amount of Sonoran desert tortoise habitat and the proportion the tortoises within 20 km of cities in the eastern portion of the range in Arizona and within 10 km of cities in the western portion of the range in Arizona and in all of Sonora (Figure 12).

To model the influence of urban areas on adult survival, we took a two-step approach. First, we calculated the proportion of the population influenced by urban areas for both our current and future habitat suitability layers under our two urban growth scenarios (Section 5.2.2). We then used the difference between the current and future areas of urban influence divided by the number of years simulated to obtain an annual rate of change in the proportion of the population influence by urban areas. Second, we used decreased survival rate for the proportion of the population that fell within the urban influence area. Within the model, survival became a weighted average of the animals that were influenced or not influenced by urban areas. The exact survival penalty for a given year was modelled as a uniform random number between 0.98 and 1.0 which approximates a 0 to 18% increase in the odds of survival for every 10km increase from a city center (Zylstra 2021, *pers. comm.*). We allowed this parameter to vary to represent a differing severity in the impact of urban influence in a given year. For more details, please refer to Appendix E.

5.3.4 Drought Severity

The pattern and extent of precipitation is a crucial variable that influences the abundance of Sonoran desert tortoise populations. And we expect climate-related variables to change in the future due to global climate change. We considered the extent and effect of drought (generally periods of time with below average precipitation and moisture conditions below at least moderate drought levels) as a key variable in the simulation model. While other potential changes in environmental conditions influenced the amount of suitable habitat and were incorporated into the model by limiting the maximum population size, the extent of drought was incorporated as a direct influence on the survival rates used in the model for adult and older juvenile life stages. We did not incorporate the influence of drought on young juvenile survival and transition rates as the survival rate for this class was already set to 0.01. Refer to Appendix E for more explanation of how drought was incorporated into the simulation model.

The simulation model incorporates two levels of potential increases in the extent of drought. Following the methods used in Zylstra and Steidl (2021, entire) we considered drought effects in terms of the Palmer Drought Severity Index (PDSI) over a 24-month period. PDSI values range from -4.0–4.0 where negative values indicate drought conditions and positive values indicate moist conditions; thus, an increase in PDSI values corresponds to a decrease in drought severity. The low climate change effects were considered in the "Low Effects" future scenario because we

think that some effects of climate change are already very likely to occur due to atmospheric conditions that have already changed. This low climate change effect was estimated to have no additional change in the average 24-month PDSI value (indicating an increase in moderate to severe droughts) from the values observed over the past 30 years. For the “High Effects” future climate change scenarios, we considered a decrease in the average 24-month PDSI value of one unit by the end of our simulation period of 125 years. Given that a 1 unit increase in the average 24-month PDSI increased the odds of adult survival by 62% (95% CI: 41–91%) and the odds of older juvenile survival by 45% (95% CI: 16–101%) (Zylstra 2021, *pers. comm.*), we imposed an annual decrease in the average annual survival rate of -0.01% for adults and -0.05% for older juveniles through the end of the century (Table 5).

Projecting future drought trends due to climate changes is challenging, particularly in the Southwest U.S. Climate models have shown wide variance of potential future drying trends, including no to small changes from recent current conditions (Peters and Iverson 2016, pp. 24, 30–32; Bradford *et al.* 2019, pp. 3909–3914). Thus, we think using recent drought conditions as a plausible future scenario is reasonable. Climate models do not use PDSI as a future variable because it oversimplifies the effects of future evapotranspiration, overestimates drying conditions, and does not perform well over time (Sheffield *et al*. 2021, entire). However, considering a one-unit decrease in the average PDSI—as is the case for our “High Effects” scenario—is a reasonable high climate effects scenario given related studies of drought related indices in the Southwest U.S that projected increases in severe and extreme droughts by the end of century under the most severe climate scenarios (Peters and Iverson 2016, p. 31). While these results are not directly comparable, our estimates for the population model that the average climatic conditions will decline from moderate to severe (i.e., a one unit decrease in average PDSI) is a reasonable estimate for our projections.

Table 5. Summary of input parameters for the simulation model for our "Low Effects" and "High Effects" future scenarios. *Urban Growth* corresponds to the percent of the overall habitat that is lost to human development and it influences carrying capacity. *Urban Influence* corresponds to the percent of the population that has a decreased survival rate due to human-tortoise interactions. *Drought Impact* is the annual percent decrease in survival rate due to a decrease in the 24-month average PDSI. N_0 is the median (range) of starting female population size, and P_{Qe} *threshold* is the median (range) quasi-extinction threshold, which is set at 2% of N_0.

	Habitat Class	Adult Density (# / sq. mi)	**2020** Habitat (sq. mi)	**2080** Habitat (sq. mi)	Urban Growth	Urban Influence	Drought Impact	Mean Survival **Initial**	Median N_0 (# of Females)	P_{Qe} Threshold (# of Females)
Arizona, USA										
Low Effects	High	**46** *(6–155)*	8,532	10,852	3.1%	24.0%	0.0%	Adult 0.960; Old Juv. 0.820	**276,930** *(51,596–765,120)*	**5,539** *(1,032–15,302)*
	Moderate	**25** *(5–35)*	9,116	13,690						
	Low	**6** *(0–15)*	12,828	10,341						
High Effects	High	**46** *(6–155)*	8,532	3,350	9.7%	36.0%	Adult -0.01%; Old Juv. -0.05%	Adult 0.960; Old Juv. 0.820	**272,898** *(51,098–825,101)*	**5,561** *(1,133–15,168)*
	Moderate	**25** *(5–35)*	9,116	13,776						
	Low	**6** *(0–15)*	12,828	13,946						
Sonora, Mexico										
Low Effects	High	**46** *(6–155)*	3,406	4,327	0.1%	1.4%	0.0%	Adult 0.960; Old Juv. 0.820	**127,998** *(24,969–375,443)*	**2,560** *(499–7,509)*
	Moderate	**25** *(5–35)*	4,945	7,422						
	Low	**6** *(0–15)*	10,396	8,370						
High Effects	High	**46** *(6–155)*	3,406	1,328	0.6%	1.9%	Adult -0.01%; Old Juv. -0.05%	Adult 0.960; Old Juv. 0.820	**129,182** *(24,357–376,839)*	**2,584** *(487–7,537)*
	Moderate	**25** *(5–35)*	4,945	7,449						
	Low	**6** *(0–15)*	10,396	11,227						

5.4 Future Scenario Projections

The full results of the analyses of future projections using simulation model for the Sonoran desert tortoise under our baseline and future condition scenarios are reported in Appendix E. These results (Figures 21 and 22; Table 6) show projected population growth rates, mean tortoise abundance, and quasi-extinction risk, and percent decline in median abundance over the 125-year timeframe of analysis.

Comparing the two scenarios, both projected a decline in population growth rate across both analysis areas (Table 6), but the "Low Effects" scenario projected an annual population decline <1% whereas the "High Effects" projected an annual decline around 2.3%. The probability of quasi-extinction varied between scenarios and time steps. At 75 and 100-year time steps, the mean probability of quasi-extinction did not exceed 1% for either scenario. For the "Low Effects" scenario, at no point in the 125-year projection did the mean probability of quasi-extinction exceed 0.5%. The exception was the "High Effects" scenario at 125 years, which projected a mean quasi-extinction probability of 7.8% for Arizona and 5.3% for Sonora.

The risk of quasi-extinction was heavily influenced by our selected 2% of starting population size threshold. Another way of expressing this threshold is that we considered a simulation to result in "extinction" is the population declined 98% relative to its starting size. Aside from the "High Effects" scenario, few simulations hit that threshold. However, the overall abundance of Sonoran desert tortoises was generally projected to decline. Under the "Low Effects" scenario, a decline of 18.5% was projected, while in Sonora a slight increase of 1.6% was projected. However, under the "High Effects" scenario, both analysis areas were projected to see a decrease of over 80% in Sonoran desert tortoises in 125 years.

Table 6. Results of the population simulation model under different future scenarios, where N_0 is the median starting abundance of adult females; N_t is the median abundance (range) of adult females at time *t*; P_{Qet} is the median probability (range) of quasi-extinction at time *t*; and λ_{125} is the median population growth rate over 125 years; *% Change* is the percent change in abundance from initial values to 125 years.

Arizona, USA	*Initial Values*	*Results at 75 years*		*Results at 100 years*		*Results at 125 years*			
	N_0	N_{75}	P_{Qe75}	N_{100}	P_{Qe100}	N_{125}	P_{Qe125}	λ_{125}	% Change
Low Effects	**276,930** (*51,596–765,120*)	**242,807** (*45,903–670,127*)	**0.00%** (0.00–0.10%)	**233,109** (*43,894–651,161*)	**0.00%** (*0.00–0.40%*)	**225,604** (*42,831–633,273*)	**0.40%** (*0.00–1.30%*)	0.990	-18.5%
High Effects	**272,898** (*51,098–825,101*)	**123,817** (*24,012–371,681*)	**0.00%** (*0.00–0.30%*)	**72,057** (*14,164–214,663*)	**1.00%** (*0.20–2.10%*)	**35,972** (*7,139–107,355*)	**7.80%** (*5.20–10.80%*)	0.976	-86.8%

Sonora, Mexico	*Initial Values*	*Results at 75 years*		*Results at 100 years*		*Results at 125 years*			
	N_0	N_{75}	P_{Qe75}	N_{100}	P_{Qe100}	N_{125}	P_{Qe125}	λ_{125}	% Change
Low Effects	**127,998** (*24,969–375,443*)	**127,390** (*25,851–378,682*)	**0.00%** (*0.00–0.10%*)	**128,692** (*25,808–388,552*)	**0.00%** (*0.00–0.30%*)	**130,159** (*25,965–391,983*)	**0.20%** (*0.00–0.90%*)	0.991	1.6%
High Effects	**129,182** (*24,357–376,839*)	**68,546** (*12,651–205,731*)	**0.00%** (*0.00–0.20%*)	**42,173** (*7,705–127,165*)	**0.60%** (*0.00–1.50%*)	**22,483** (*4,176–67,582*)	**5.30%** (*3.20–7.90%*)	0.977	-82.6%

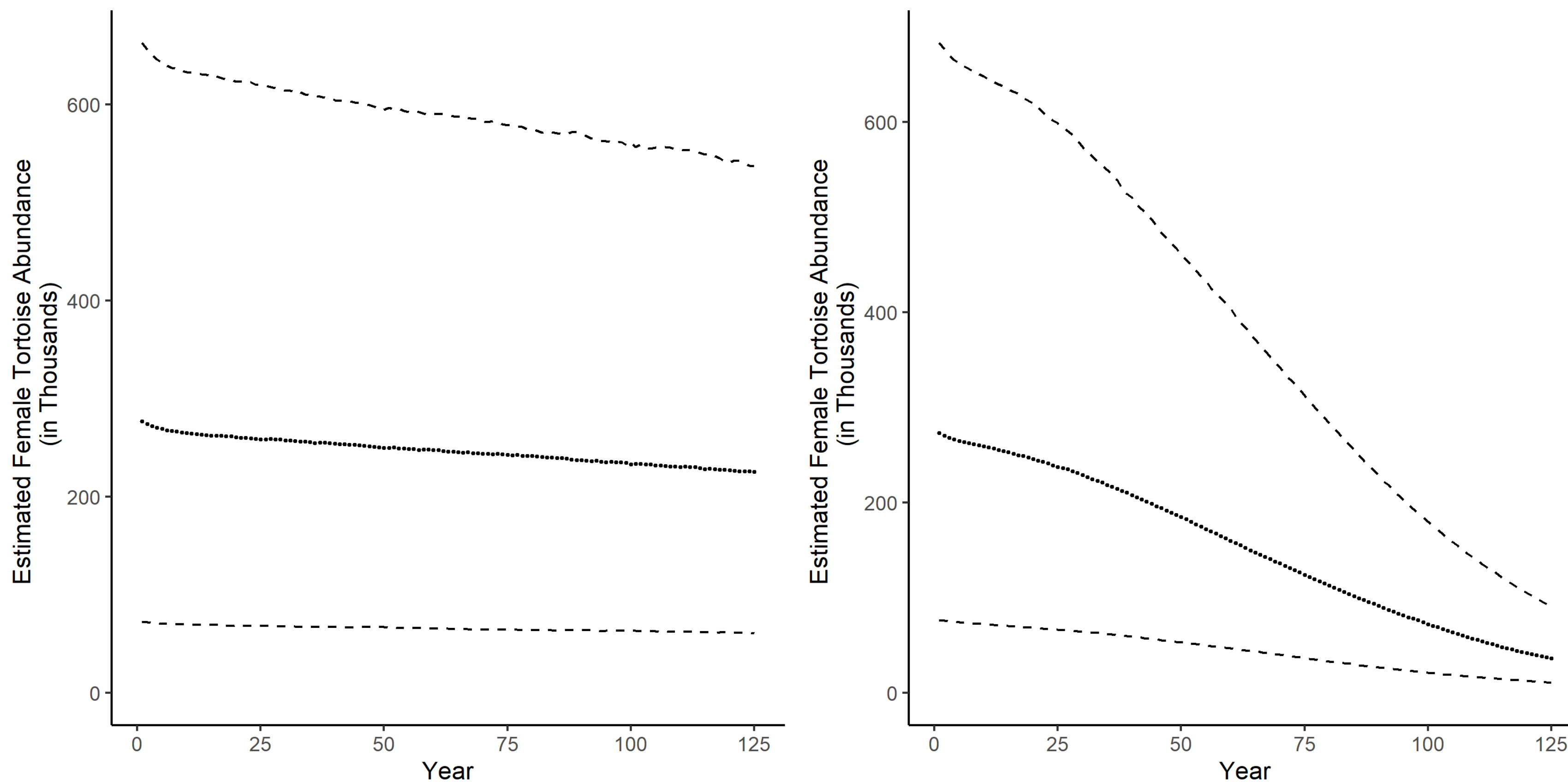


Figure 21. Projected trend of female Sonoran desert tortoise abundance through time under our "Low Effects" (left) and "High Effects" (right) future scenarios for the Arizona analysis area. Black points represent median female abundance across all simulations in a given year. Black dashed lines represent the 95% confidence intervals.

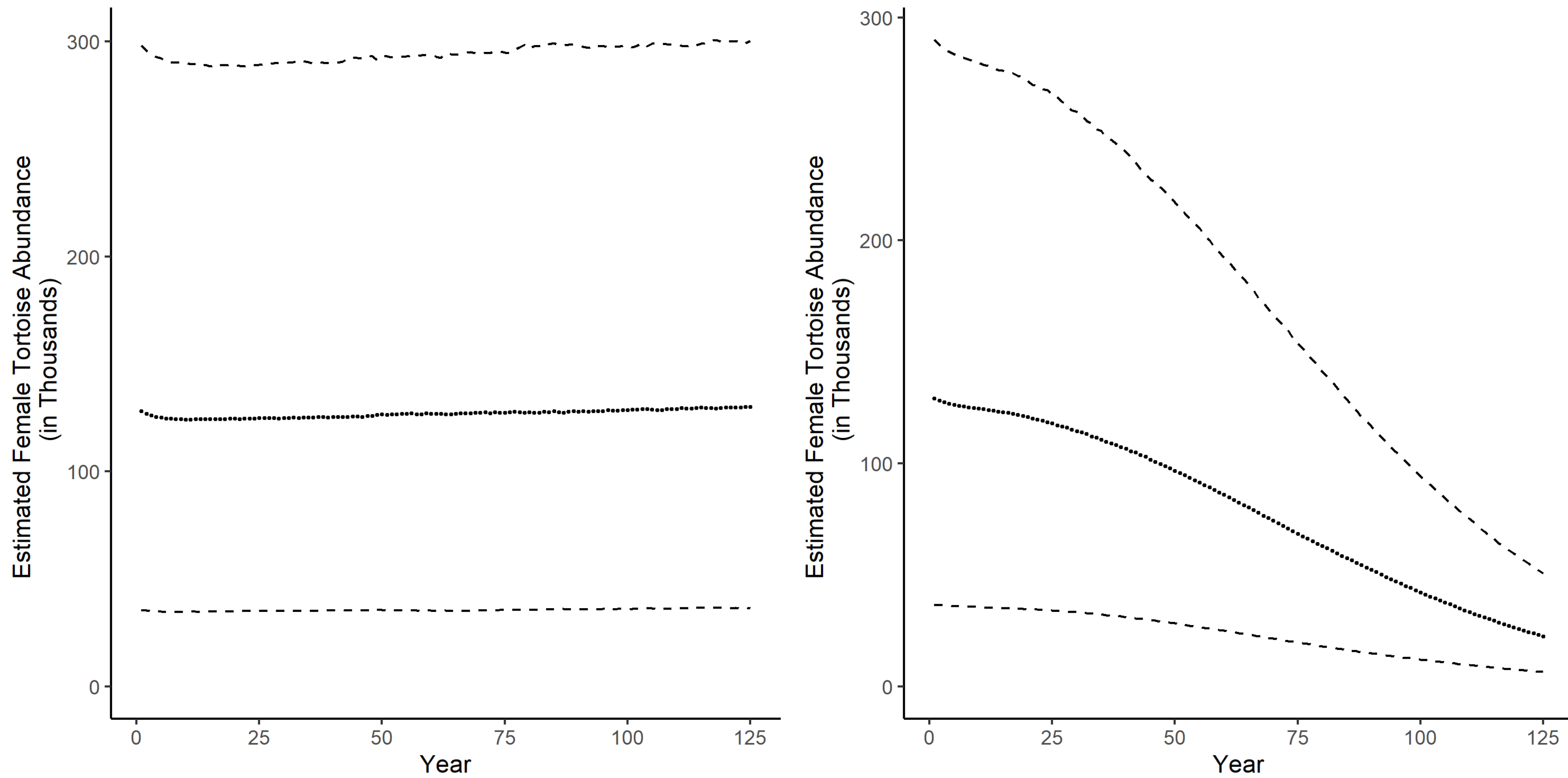


Figure 22. Projected trend in female Sonoran desert tortoise abundance through time under our "Low Effects" (left) and "High Effects" (right) future scenarios for the Sonora analysis area. Black points represent median female abundance. Black dashed lines represent the 95% confidence intervals.

The outputs of the simulation model include population growth rate, median abundance over time (with 95% confidence intervals), and the probability of the population falling below a quasi-extinction threshold (Table 6). The probability of quasi-extinction over time is based on running 1,000 simulations of the model with specific scenarios of input parameters and calculating the proportion of the simulations where the population size falls below a pre-determined abundance threshold. This probability (along with median abundance) is profiled on an annual basis and plotted over time to describe the resiliency as one unit of analysis under a specific scenario of model inputs.

Chapter 6: Summary of Viability and Uncertainties

This chapter synthesizes the results from our analysis of the current conditions and future scenarios and discusses the consequences for Sonoran desert tortoise viability. For the Sonoran desert tortoise to maintain viability, it needs to have resilient populations, capable of withstanding stochastic events and preventing local extirpations. The populations need to be distributed across its range in a way that reduces the chance that a catastrophic event is likely to lead to species extinction (redundancy). Moreover, the species needs to maintain ecological and genetic diversity in ways that preserves its adaptive capacity (representation). Our analysis of the future environmental conditions (habitat suitability and population changes) provides an indirect measure of these three concepts and the overall risk of extinction across our analysis areas in the face of current and ongoing threat factors.

6.1 Viability Under Current Conditions

To assess the current condition of Sonoran desert tortoise, we reviewed the available information on the status of the species range-wide, used a habitat suitability model, and generated our own abundance estimates for Arizona and Sonora. Sonoran desert tortoises occur across much of their historical range, based upon occurrence records collected in Arizona since 1905 and in Sonora since 1921 (Figure 5). Demographic estimates calculated from the LTMP sites show that population growth rates are relatively stable and both adults and older juveniles have high survival rates over the last 30 years (Zylstra and Steidl 2021, p. 7; Campbell *et al*. 2018, pp. 2059–2061). Within the species' range in Arizona, population growth rates and survival was higher in the central and eastern portions of the range and lower in the northwestern portion of the range (Campbell *et al.* 2018, pp. 2060–2061). However, both demographic estimates have a negative relationship with drought and will likely decline if the frequency and severity of drought increases (Zylstra and Steidl 2021, pp. 6–8).

The available information suggests that catastrophic events, such as wildfire and drought, have had localized effects on tortoises, but not at a scale to cause extirpations across the species range. Because young juveniles are difficult to detect, necessary data are not available to indicate that any particular age class has experienced significant declines or that there have been large-scale reproductive failures, either of which would reduce viability of the current populations. The best available information indicates that Sonoran desert tortoises are widely distributed across their historical range and have not experienced range-wide demographic collapses.

The habitat model also suggests that there are large swathes of the Sonoran desert tortoise range that contain high quality habitat. Following our review of species threats, we removed areas from the habitat model based upon the intactness model that factored in anthropogenic alterations to the landscape. Doing so is an acknowledgement that human disturbance has reduced the amount of habitat and thus the number of tortoises. In our review of threats, we considered whether other factors, such as nonnative invasive vegetation, recently burned areas, and mines have impacted the landscape sufficiently to cause reductions in the Sonoran desert tortoise population. Although the available information shows that these factors can affect individual Sonoran desert tortoises, we do not think the available information supports these factors being responsible for population-level effects that would result in large-scale declines for the species. Thus, we did not

penalize our estimation of Sonoran desert tortoise abundance based upon these factors.

Our estimation of the abundance of Sonoran desert tortoises in Arizona and Sonora was based on the habitat model and our decision to eliminate areas with significant human development. We estimated that the average range-wide adult abundance is about 865,000 with a large amount of uncertainty (range: 148,000–2,508,000). We included variation in our density estimates to generate a distribution of potential population sizes, instead of generating a single point value. This underscores the uncertainty in these estimates but also provides a robust approach to capture the potential true abundance.

Within the context of the 3Rs, we believe our analysis suggests the Sonoran desert tortoise currently has high resiliency. We considered redundancy and representation by assessing the distribution of moderate and high suitability habitat classes throughout the known range of the Sonoran desert tortoise. By having a broad distribution of suitable habitat throughout its range, the species is currently able to withstand catastrophic events (i.e., drought, wildfire) and to adapt to novel changes in the environment. Currently, there are large swathes of suitable Sonoran desert tortoise habitat distributed across the species' known range (Figure 15) in a variety of biotic communities (Figure 4), which represent a diversity of environmental conditions. Given the current high resiliency and wide distribution of potential habitat, our analyses suggest that the Sonoran desert tortoise currently has the ability to withstand catastrophic events and ability to adapt to novel changes.

6.2 Viability Under Future Conditions

We reviewed a number of potential factors that could be affecting Sonoran desert tortoise viability in the future. There are several threats that have varying effects on Sonoran desert tortoises, while there are also conservation actions being undertaken to alleviate some of those threats (Appendix D). While many of these factors (such as altered plant communities and fire regimes) could be having effects on individual Sonoran desert tortoises at localized or regional scales, we lack the data to conclude they have broad population-level effects across the species' range (Appendix C). These other factors may have population-level effects, but because of the long-life span, abundance, and wide range of the Sonoran desert tortoise, these changes would likely take many decades or longer to have measurable impacts on the species. In addition, many of these factors are ameliorated to some degree by ongoing and future conservation efforts through land management (Appendix D).

Based on our review of the threats acting on Sonoran desert tortoise, we identified two sources, urban population growth (permanent loss of habitat) and climate change (drought), that are expected to measurably affect Sonoran desert tortoise populations in the future. We used a habitat model to spatially project future conditions of the habitat of the Sonoran desert tortoise to serve as the basis to estimate population sizes and to conduct a simulation model to project future abundance and risks of quasi-extinction. Although the simulation model is not spatially explicit, it provides a robust, quantitative method to measure the potential effects of climate change and urban growth on the risk of extinction for Sonoran desert tortoises in Arizona and Sonora. We projected future species' responses to climate change at two levels: as changes in habitat suitability and as decreases in survival rates in response to long-term increases in overall drought

conditions. We also projected the effects of habitat loss due to urban growth and reduced survival around increasing areas of influence of larger future urban areas. As with our assessments of current conditions, we assessed the redundancy (distribution of tortoise populations) and representation (diversity) indirectly through projecting the suitability and quantity of habitat across the species range, which represents a diversity of biotic communities and environmental conditions.

Across both future scenarios, urban influence had a greater impact in Arizona than Sonora. Within Arizona, approximately 24–36% of adult tortoises experienced decreased survival rates due to human tortoise interactions under the "Low Effects" and "High Effects" scenarios, respectively (Table 5). In contrast, only approximately 1.4–1.9% of the adult tortoises under the "Low Effects" and "High Effects" scenarios, respectively, experienced decreased survival rates due to human tortoise interactions in Sonora (Table 5). Under the "Low Effects" scenario, the difference in the urban influence parameter is what underlies the projected stable to slightly increase in median abundance within Sonora versus the projected decrease in median abundance for Arizona. This suggests that within Arizona, even under more conservative urban expansion scenarios, the effect of urban areas could result in a decline in Sonoran desert tortoises regardless of the effects of other factors.

Sonoran desert tortoise survival is strongly influenced by drought, which was reflected within the output of the future projection models (Table 6). Unlike the urban influence factor, drought influenced the survival rate of the older juveniles and adult age classes. Under our "Low Effects" scenarios, which assumed a continuation of the ongoing rates of drought, we did not see large declines in the median abundance (Table 6). However, under our "High Effects" scenarios, which accounted for an increase in the average rate of severe droughts, median abundance was projected to decline by as much as -86% and approximately 5–8% of scenarios fell below the quasi-extinction thresholds (Table 6).

Overall, in the context of the 3Rs, resiliency of the Sonoran desert tortoise is projected to decrease into the future. Although the risk of reaching the quasi-extinction thresholds is relatively low within the 125-year timeframe analyzed, median abundance is projected to change across the Arizona analysis unit by -18.5– -86.8% in Arizona and the Sonora analysis unit by 1.6– -82.6%.

Regarding redundancy and representation, future scenarios differ in terms of projections to the amount of habitat and its distribution across the species range. The habitat models project that moderate and high suitability habitat will remain in varying amounts throughout the species distribution in Arizona. Under the "Low Effects" scenario, the amount of habitat, including high quality habitat, increased and remained distributed across the species range (Figure 19). The spatial distribution of future habitat did not differ substantially from the current distribution of available habitat. We are unable to posit where suitable habitat will remain within Sonora; however, we assume that suitable habitat will remain for the species within the Sonoran analysis unit under both scenarios given the observed changes in habitat in Arizona. Under the "High Effects" scenario, most of the high suitability habitat is projected to be found along the northeastern periphery of the distribution in Arizona (Figure 20). Sonoran desert tortoise densities are generally currently higher in this portion of the species range (Figure 16), and

estimated population growth rates and survival rates have been estimated to be higher in this portion of the species range as well (Campbell et al. 2018, pp. 2059–2061). However, this portion of the range is also at increased risk of wildfire (Figure 8) and higher densities nonnative invasive vegetation such as red brome and buffelgrass (Section 3.1). The projected reduction in high suitability habitat within southern Arizona suggests some future reduction in tortoise abundances within that part of the range. High quality habitat under the "High Effects" scenario becomes aggregated in a large block on the southern Mogollon Rim (northeastern part of the tortoise's range), with little high quality habitat in peripheral portions of the species range. This would suggest a substantial reduction in high quality habitat.

6.3 Uncertainty, Assumptions, and Models

Uncertainty is an inherent part of any biological analysis of the status of a species. We developed this SSA based on the best available scientific information for the Sonoran desert tortoise; however, although considerable in comparison to many other species, there is much that remains unknown. By its very nature, any status assessment is forward-looking in its evaluation of the risks faced by a species, and future projections will always be dominated by uncertainties, which increase as one projects farther and farther into the future. Some of the most critical unknowns are related to trying to predict how much environmental change is likely to occur in the future, and the likely response of the species to these changes. In the face of these and other uncertainties, we must make decisions about the species with the best information we have.

We addressed some of the unknowns and uncertainties by making reasonable assumptions about the species and its ecosystem based on other, similar systems, or basic ecological knowledge. We highlighted many of the key assumptions that we made as part of the analytical process in this SSA report. Two additional ways that we dealt with critical uncertainties were through using scenarios and generating distributional ranges for parameter values within our predictive models. In the case of tortoise abundance, we considered a range of plausible density estimates for each habitat suitability class in order to build a distribution of abundance estimates (Figure 18 and Table 5). Using a wide range of values helps account for the fact that the available empirical density estimates are derived from the LTMPs that were selected because they had a high number of tortoises, rather than a random sample. Similarly, we included different levels of habitat suitability to use in our analysis to evaluate a range of plausible future possibilities. For the overall analysis, we used two different scenarios in both the Arizona and Sonora analysis areas to capture a range of results for the risk to the species (Table 3). These scenarios attempted to bracket the range of uncertainty in the response of the Sonoran desert tortoise and the threats acting on the species into the future.

Another way we explicitly dealt with uncertainties in this analysis of a complex system was to use models to help us simplify the information. In general, quantitative models are useful if they help us make better decisions by incorporating large amounts of information and explicitly showing our assumptions (Starfield 1997, pp. 261–263). The two primary modeling systems we incorporated were the geospatial habitat analysis of both current and future conditions and the population simulation model to project the future changes in abundance of the Sonoran desert tortoise under different scenarios. While these models can output seemingly very specific quantitative results, they are only a simulation and by no means are intended to predict the future

with a high degree of certainty. For example, the actual amount of potential habitat or number of Sonoran desert tortoises on the landscape, both currently and in the future, are most likely different than what we report here (note that we only present the median and range of female abundance values for all time points). However, we built the models on our understanding of the ecological system that supports the Sonoran desert tortoises and the influences in that system. Therefore, the models represent our best understanding of these systems and the plausible implications of changing environmental conditions in the future in terms of the future risk of extinction to the Sonoran desert tortoise. The models do not give us a precise prediction, but rather the range of likely expected future status of tortoise populations given what we currently know, and do not know, about the species and the environmental conditions that will influence the future status of the species.

One other area of substantial uncertainty concerns the status of the species and its habitats in Sonora. We did not have the same level of information for Sonora as we had in Arizona. Importantly, we did not have the Ensemble Model of habitat for either current conditions or future projections. As a result, we developed a similar but separate model for current habitat conditions in Sonora (Appendix B), and we assumed that habitat conditions in Sonora would change in the future proportional to the changes projected for Arizona. Similarly, we did not have monitoring data in Sonora from which to calibrate tortoise densities in the suitable habitats, so we used the same densities developed for Arizona. While these are important limitations, our approach represents a reasonable use of the limited information available.

Appendix A: Glossary

Admixture: the mixing of genetic material from two different species
Annual: having a yearly periodicity; living for one year
Bajada: a broad alluvial slope extending from the base of a mountain range out into a basin and formed by coalescence of separate alluvial fans
Biotic community: a group of interacting species coexisting in a particular habitat
Carapace: the hard, upper part of the shell
Climate: prevailing mean weather conditions and their variability for a given area over a long period of time
Climate change: a change in one or more measures of climate that persists over time, whether caused by natural variability, human activity, or both
Cumulative effects: when several seemingly separate effects combine to have an effect greater than their individual effects
Drought: a prolonged period of abnormally low precipitation
Ecological diversity: the variation in the types of environmental settings inhabited by an organism
Extinction: the state or process of a species, family, or larger group disappearing from its entire range
Extirpation: the loss of a population or a species from a particular geographic region
Fallow: land that has undergone plowing and harrowing and has been left unseeded for one or more growing seasons
Fecundity: the potential reproductive capacity of an organism or population
Forage: to search for food or the food, itself
Fragmentation: the state of being broken into separate parts
Genetic diversity (genetic variability): the genetic measure of a tendency of individual organisms of the same species to differ from one another
Geophagous: to consume bones, stones, and soil for additional nutrient and mineral supplements, for mechanical assistance in grinding plant matter in the stomach, or to expel parasites in the intestinal tract
Gular shields: large, extended scales underneath the throat of male tortoises
Invasive species: a species that is not native to an ecosystem and which causes, or is likely to cause, economic or environmental harm or harm to human health
Introgression: the entry or introduction of a gene from one gene complex into another (as by hybridization)
Morphological: referring to the structure or form of an organism
Microsite: a small geographical area which exhibits markedly different ecological characteristic from the surrounding area.
Nonnative: originating in a different region and acclimated to a new environment
Ossify: to harden into bone
Potassium Excretion Potential (PEP): an index of water, nitrogen, and potassium levels in a plant that affects a tortoise's ability to efficiently excrete potassium
Plastron: the hard bottom or ventral part of the shell
Quasi-Extinction: the probability of abundance declining to less than a pre-determined abundance threshold
Redundancy: the ability of a species to withstand catastrophic events

Refugia: an area in which animals may escape from or avoid a predator or environmental conditions
Representation: the ability of a species to adapt to changing environmental conditions
Reproductive effort: the resources an organism devotes to reproduction, often simply measured as the number of offspring produced
Resiliency: the ability of a species to withstand stochastic events
Source: the human-produced or natural origins of a stressor; the mechanism of an impact or benefit to a species
Stochastic events: arising from random factors such as weather, flooding, or fire
Stressor: Any physical, chemical, or biological alteration of the environment that can lead to an adverse response by individuals or populations of a species
Taxon: a group of organisms classified by their natural relationships or genetics
Taxonomic: pertaining to the classification of animals and plants.
Thermoregulation: the process by which body temperature is established and maintained
Viability: viability is not a specific state, but rather a continuous measure of the likelihood that the species will sustain populations over time.

Appendix B
Developing GIS Data Layers and Analysis for Sonoran Desert Tortoise (*Gopherus morafkai)* Species Status Assessment (SSA)

Background Information

The Sonoran desert tortoise (*Gopherus morafkai*) is native to portions of Arizona, US, and Sonora, Mexico. Sonoran desert tortoises occur in eight distinct biotic communities but primarily on (often granitic rock) steep rocky slopes, bajadas (lower mountain slopes and alluvial fans) and in paloverde-mixed cacti associations, within the Arizona Upland and Lower Colorado River subdivisions of Sonoran desert-scrub vegetation types. Valley bottoms and washes may be used for dispersal.

Purpose

This analysis provides geographic/spatial data and models showing the extent of suitable habitat for the Sonoran desert tortoise and associated threats based on specific spatial criteria. Suitable habitat models were created by research partners from the University of Nevada-Reno and the U.S. Geological Survey (USGS) for the Arizona portion, and by the U.S. Fish & Wildlife Service (USFWS) for the Sonora portion. This appendix (Appendix B) will focus on the technical aspects of the GIS;

- Data types, acquisition, and applications related to Sonoran desert tortoise.
- Model construction and applications.
- Geoprocessing and GIS tools used in the analysis.

GIS Analysis Results

All results from the analysis, area summaries, and detailed discussions on data and models, as they apply to Sonoran desert tortoise current and future conditions, will reside in the main SSA report. A summary table of general area calculations will reside within this Appendix.

Analysis Area

The geographic extent of the GIS work and spatial modeling is a variation of the Sonoran desert tortoise distribution boundary initially developed by the Arizona Interagency Desert Tortoise Team, adopted from recent genetic research (Edwards *et al*. 2015; Edwards 2015; Dolby *et al.* 2021). For the current analysis, the boundary has been adjusted to better represent the known geography related to the Sonoran desert tortoise. This was accomplished through consultation with species experts on our SSA Core team. This boundary represents only our area of analysis (Figure B-1). Actual tortoise distribution may go beyond this area. As explained in the Species Status Report for the Sonoran Desert Tortoise (SSA Report), in the northern part of the study area, a genetic contact zone in and near the Black Mountains was adjusted to exclude areas predominately occupied by Mohave desert tortoises, and the southern part of the study area (a genetic contact zone) was reduced to exclude what are now considered to be a separate species, Goode's thornscrub tortoise. This boundary will be the extent for all for area calculations and analysis.

Data Limitations

All source datasets used were developed by entities outside the USFWS. Most datasets used are publicly available. Researchers from the University of Nevada-Reno and the USGS developed current condition and future projection statistical suitable habitat models (hereafter the Ensemble Models) for the Arizona portion of the analysis area. The quality and accuracy of these data (ecological and spatial) may vary. Remotely sensed data products and large national datasets may contain inherent errors of omission and commission. Current land cover status may differ from the data displayed in the analysis. Actual, on-the-ground, quality and/or condition of mapped cover types is not addressed. No field verification or reviews of ancillary datasets/aerial imagery were done to verify the accuracy of the data. Most of the source raster data has a minimum spatial resolution of 30 meters. Climate change data used for future condition

projections (https://adaptwest.databasin.org/pages/adaptwest-climatena/) will have its own limitations. This dataset, analysis, and all maps/products created from it are subject to change.

Projections and Transformations

For this project, all data was projected into North American Albers Equal Area Conic, North American Datum (NAD) 1983. Typically, the raster datasets are downloaded in WGS 84, or other geographic coordinate systems. The Ensemble Model Suitable Habitat Probability data was re-projected from North American 1927 Lambert Azimuthal Equal Area.

GIS Platform

All GIS analysis and mapping work was done using ArcGIS 10.6.1 and ArcGIS Pro 2.8.

Figure B-1. Sonoran Desert Tortoise Analysis Areas.

Current Condition: Suitable Habitat Probability Analysis (Arizona Portion)

Italicized information below provided by K. Nussear (University of Nevada-Reno), T. Esque (USGS), and C. Jones (AGFD).

Environmental Predictor Layers

A suite of 15 environmental variables were assembled that were hypothesized to be influential in describing tortoise habitat, including topographic, climatic, and soil related predictor layers (Table B-1). All raster layers for the environmental variables were re-sampled or downscaled to match the 250 m resolution of the soils data layers using a cubic spline interpolation method in gdalwarp (GDAP v 3.1.3; GDAL/ORG 2020). Model selection reduced the number of variables included in the model (see below).

Table B-1. Name of predictor variables identified for modeling and a brief description of the variable.

Name of Predictor	Units	Description
1. Winter Mean Precipitation	Millimeters (mm)	30 year normal of Winter Precipitation (Nov - April) obtained from PRISM
2. Winter Mean Precipitation SD	Millimeters (mm)	Standard Deviation of the 30 year normal of Winter Precipitation (Nov - April) obtained from PRISM
3. Summer Mean Precipitation	Millimeters (mm)	30 year normal of Summer Mean Precipitation (May - Oct) obtained from PRISM
4. Summer Mean Precipitation SD	Millimeters (mm)	Standard Deviation of the 30 year normal of Summer Mean Precipitation (May - Oct) obtained from PRISM
5. Winter Minimum Temperature	Degrees Celsius (°C)	30 year normal of Winter Minimum Temperature (Nov - April) obtained from PRISM
6. Winter Minimum Temperature SD	Degrees Celsius (°C)	Standard Deviation of the 30 year normal of Winter Minimum Temperature (Nov - April) obtained from PRISM
7. Summer Maximum Temperature	Degrees Celsius (°C)	30 year normal of Summer Maximum Temperature (May - Oct) obtained from PRISM
8. Spring Mean Temperature	Degrees Celsius (°C)	30 year normal of Spring Temperature (Mar - May) obtained from PRISM
9. Percent Clay	Percent (g/100g)	Proportion of clay in the first 0-5 cm obtained from https://soilgrids.org/
10. Percent Silt	Percent (g/100g)	Proportion of silt in the first 0-5 cm obtained from https://soilgrids.org/
11. Percent Sand1	Percent (g/100g)	Proportion of sand in the first 0-5 cm - obtained from https://soilgrids.org/
12. Percent Sand2	Percent (g/100g)	Proportion of sand from 15-30 cm - obtained from https://soilgrids.org/
13. Coarse Fragments	cm3/100cm3 (volume %)	Volumetric fraction of coarse fragments in the first 0-5 cm https://soilgrids.org/
14. Average Ruggedness	radians/m	Mean Topographic Ruggedness layer obtained from Carter et al. 2020
15. Topographic Position Index	NA	Mean Topographic Ruggedness layer per Inman et al. 2014

The environmental predictors were selected based on factors thought to represent elements containing habitat preferences, and potentially limiting influences on demographic processes and thus distributions of Sonoran desert tortoise (Nussear and Tuberville 2014). For example, they are known to occupy a range of habitats, but are known to be more prevalent in Arizona upland of the Sonoran Desert (represented by layers describing ruggedness and the Topographic Index – Table B-1). This shift toward inhabiting uplands is thought to be driven by temperature and precipitation influences (e.g., avoidance of flooding in lowland locations within the Sonoran Desert (Nussear and Tuberville 2014). The Lower Colorado subdivision of the Sonoran Desert is also characterized by extreme high temperatures combined with low precipitation, and high silt and sand fractions in the soils (modeled using the Sand, Sand and Clay fractions in the first horizon – Table B-1) resulting in lower plant diversity (Brown 1994; Van Devender 2002) than is found in more typical Sonoran desert tortoise habitat (Nussear and Tuberville 2014). The Sonoran Desert generally has a relatively high summer to winter precipitation ratio – thus both seasonal precipitation measures are of interest to modeling. In addition, summer precipitation, and temperature patterns typically provide a summer flora that stimulates foraging activity for Sonoran desert tortoise (Averill-Murray et al. 2002a), and provides additional opportunities for hydration (Esque et al. 2014), both of which likely influences reproduction potential for this species. Sonoran desert tortoises are known to live on rocky hillsides that provide the substrate for burrows and caves used for shelter (thus the inclusion of Coarse Fragments – Table B-1).

Habitat Suitability Model

We modeled Sonoran desert tortoise habitat incorporating four different algorithms: generalized boosted regression models (GBM; using thegbm package; v 2.1.8); random forests (RF; implemented in the R package randomforest, Liaw and Wiener 2002); maximum entropy (Maxnet; v 0.1.2); and multivariate adaptive regression splines (MARS; implemented in the mda package v 0.5-2) all executed using the biomod2 package (v 3.4.13, Thuiller et al. 2009) in R (v 4.04, R Core Team 2020). We used the ensemble modeling approach to reduce the biases, assumptions, or limitations of any individual algorithm, while broadening the types of environmental response functions that can be identified (Araujo and New 2007; Watling et al. 2015).

Species presence data were obtained from previous modeling efforts (Edwards et al. 2015; Carter et al. 2020), the Arizona Game and Fish Department (AZGFD), as well as research grade observations from iNaturalist (http://www.iNaturalist.org) for which locations were not obscured. Collectively this resulted in 45,564 occurrences in total. However, because presence points were spatially aggregated, which can lead to substantial bias in model predictions (Aiello-Lammens et al. 2015), we first rasterized the presence points to the modeling resolution (i.e., such that only one presence point could occur within each 250 m grid cell), and subsequently applied a geographically stratified re-sampling procedure, in which a maximum of four observations could be sampled from cells on a larger uniform grid (2000 m resolution). This grid sampling approach for spatial thinning of presence points can be effective at reducing spatial bias under a variety of conditions (Fourcade et al. 2014). This reduced the final number of localities used for modeling and evaluation to 5181.

True absence points were not available for this species: thus, we generated pseudo-absences (PA) to serve as constrained background points (Barbet-Massin et al. 2012) using the surface range envelope model 'SRE' option with a threshold of 0.3. We generated a 1:1 presence to PA ratio for use in modeling (Barbet-Massin et al. 2012). The presence/PA data were split into two datasets, 80% used for modeling and internal cross-validation, and 20% used for a blind, external validation set.

We used 65 iterations of each model algorithm with an 80/20% split for each internal evaluation run. Variable importance was assessed using 20 permutations. For purposes of model selection we used two

performance metrics calculated using the internal cross validation test data. The true skill statistic (TSS), which takes into account both omission and commission errors and is insensitive to data prevalence (Allouche et al. 2006), and the area under the receiver operator curve (AUC). The ensemble model of habitat suitability was produced using the top candidate models from each of the algorithm types. We selected the highest performing models from each algorithm choosing models for which the AUC of the cross-validation data were above the 50th quantile of AUC scores (0.859) for all models. This resulted in 43 GBM, 9 MARS, 12 MaxEnt (using the maxnet implementation), and 62 RF models used for the ensemble model. We created the ensemble model using a weighted average of all of the selected models for each algorithm based on the TSS score of each model, and a standard error map by dividing the standard deviation of the weighted maps by the square root of the number of maps selected (n=126).

We calculated several performance metrics for the ensemble model using the blind evaluation presence/PA localities, including AUC using the ROCR package (1.0-11), the True Skill Statistic (TSS;Allouche et al. 2006), Boyce Index (BI; Boyce et al. 2002), and the continuous Boyce Index (CBI; Hirzel et al. 2006) all using the ecospat package (v 3.1; Di Cola et al. 2017).

Note: USGS has plans to publish a detailed manuscript further describing the Sonoran desert tortoise modeling process.

Modelling Results and Geoprocessing

The output of the Ensemble Model was a continuous surface raster dataset, with probability values ranging from 0.0 to 1.0. These data were reclassified in ArcGIS with the Reclassify Tool (Spatial Analyst/Reclass), using a 10 class equal interval classification process. Results of this are shown below;

Table B-2. Continuous Surface Raster Reclassification

Classification Tool	Original Value Range	Reclass Value Integer
Class 1	0.0-0.1	0
Class 2	0.11-0.2	1
Class 3	0.21-0.3	2
Class 4	0.31-0.4	3
Class 5	0.41-0.5	4
Class 6	0.51-0.6	5
Class 7	0.61-0.7	6
Class 8	0.71-0.8	7
Class 9	0.81-0.9	8
Class 10	0.91-1.0	9

The reclassified values were then “binned” together to help focus species population/demographic modeling efforts;

Table B-3. Value groupings for USGS Suitable Habitat Probability data.

Bin Value Groups	Suitable Habitat Probability Ranking
0	No Value
1-3	Low
4-6	Moderate
7-9	High

Current Condition: Suitable Habitat Analysis (Sonora Portion)

Limited observation data and lack of similar layers (PRISM climate data) as used in the Arizona portion, led to the Sonora Suitable Habitat Analysis being done differently. For this GIS analysis, potential habitat for Sonoran desert tortoise was defined by a specific spatial relationship derived from available/public datasets. This spatial analysis was designed to provide a landscape-scale depiction of the relationship between several different spatial data layers that are relevant to Sonoran desert tortoise habitat. No attempt was made to define or describe actual, on-the-ground Sonoran desert tortoise habitat. We recognize that this was a very course habitat model for the Sonoran desert tortoise and many other physical factors would be included for a more robust intensive habitat model. However, for our purposes at the range-wide scale, this habitat analysis provides an adequate approximation of potential habitat on which to base our assessment.

Environmental Predictor Layers

A combination of three primary data layers were used for the Sonora Suitable Habitat Analysis;

Table B-4. Data Layers for Sonora analysis.

Predictor Layer	Source	Description
1. Slope/Ruggedness	USGS DEM, National Map	1 arc-second (30m) digital elevation model for North America. (https://apps.nationalmap.gov/downloader/#/)
2. Vegetation/Land Cover (LC)	Instituto Nacional de Estadística y Geografía-INEGI (The National Institute of Statistics and Geography)	2017 (Serie IV) 1:250,000 scale Uso de Suelo (Land Use) vector (polygon) digital map. (https://www.inegi.org.mx/)
3. Soils	ISRIC-World Soils Information/SoilGrids250m	World Reference Base (WRB) of 118 soil classes (https://files.isric.org/soilgrids/former/2017-03-10/data/TAXNWRB_250m_ll.tif)

Initial Geoprocessing

The three primary layers were reclassified and given a "ranking" (see Tables B 5-7). All layers were resampled to 250m pixel size (the size of the soils data). The vegetation vector data was converted to raster, then processed similarly. Slope/ruggedness were derived from the USGS DEM data using tools in ArcMap.

Table B-5. USGS DEM Slope reclassification for Sonora.

Slope Values (in degrees)	Description	Sonoran desert tortoise Slope Rank
0-1	Flat	Low
2-14	Moderate Slope	Moderate
15-50	High Slope	High
51+	Steep/Other	Low

Table B-6. Mexico INEGI Landcover data; Cover types for predicted potential habitat in Sonora.

INEGI Cover Type (Translated to English)	Sonoran desert tortoise Vegetation Ranking
Desert Scrub/Shrub (Tiny leaves)	High
Desert Scrub, Sarcocaule Scrub (copal, matacora, ocotillo)	High
Thorny Shrub Mix/Mesquite Xeric (Huisache/Palo Verde/Acacia Mix)	High
Desert Scrub, Crasicaule Thicket (Large Cactus/Sahuaro)	High
Desert Scrub, Mixed (Mixed Cactus)	High
Managed Pasture ("Induced" Grassland)	Moderate
Natural Grassland	Moderate
Desert Scrub/Shrub (Rosette leaves/agaves on gravely slopes)	Moderate
Mesquite Forest	Moderate
Secondary Grassland	Moderate
Secondary Scrub/Shrub (Thorny scrub mix, mesquite, xeric)	Moderate
Secondary Scrub/Shrub (Desert scrub, cactus)	Moderate
Secondary Scrub/Shrub (Desert scrub, tiny leaves)	Moderate
Oak Forest	Low
Secondary Scrub/Shrub (Oak Scrub)	Low
Riparian forest	Low
Barren/Non-vegetated	Low

Table B-7. WRB Soils Reclassification for Sonora.

WRB Soil Class (highest probability)	Description	Sonoran desert tortoise Soil Rank
Leptosols Values: 68, 70, 116	Shallow soil over hard rock. Steeper rocky areas.	High
Regosols Values: 99, 100, 104	Mineral soil in unconsolidated material. Hillsides.	Moderate
Calcisols Values:21/24	Desert soils from calcareous parent material, level to base of hills. Dry and stoney.	Low

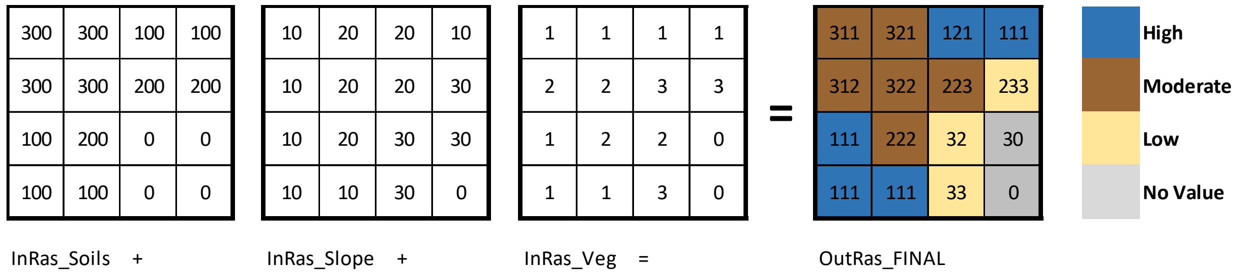
Habitat Suitability Model

Each of the new "Sonoran desert tortoise rankings" for the three data layers were given an integer value during their reclassification process. These values (see Table B-8) were combined to calculate an overall value using the Cell Statistics Tool in Spatial Analyst (ArcMap).

Table B-8. Model data structure/integer values for primary Sonora data layers.

Ranking	Soils	Slope	Vegetation/LC
High	100	10	1
Moderate	200	20	2
Low	300	30	3
No Value	0	0	0

Cell Statistics is a tool in ArcMap/Spatial Analyst which calculates the cell values of two or more rasters. Using the "SUM" function, the tool will add all cell values spatially overlaying each other (Figure B-2). Raster cells are set into alignment as they are reclassified or resampled, using the "SnapRaster" processing environment.



All possible final value combinations were ranked by the GIS team to High, Moderate, Low, or No Value based on the individual rankings discussed above, geographic setting, and the previous Sonoran desert tortoise model from the 2015 USFWS SSA document (USFWS 2015). Figure B-3 visually describes the rankings for each possible value combination. It should be noted that any "Vegetation" value of zero carried through to the final ranking. The vegetation/land cover layer were used to eliminate obvious non-habitat areas such as high elevation temperate forests/jungles and coastal sandy/dune areas. The combined values with only two integers represent slope and vegetation only, having a zero soils value.

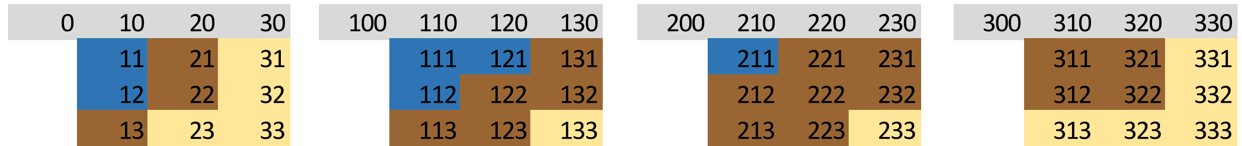


Figure B-3. Schematic of all possible Final Cell Statistics combinations and their overall ranking.

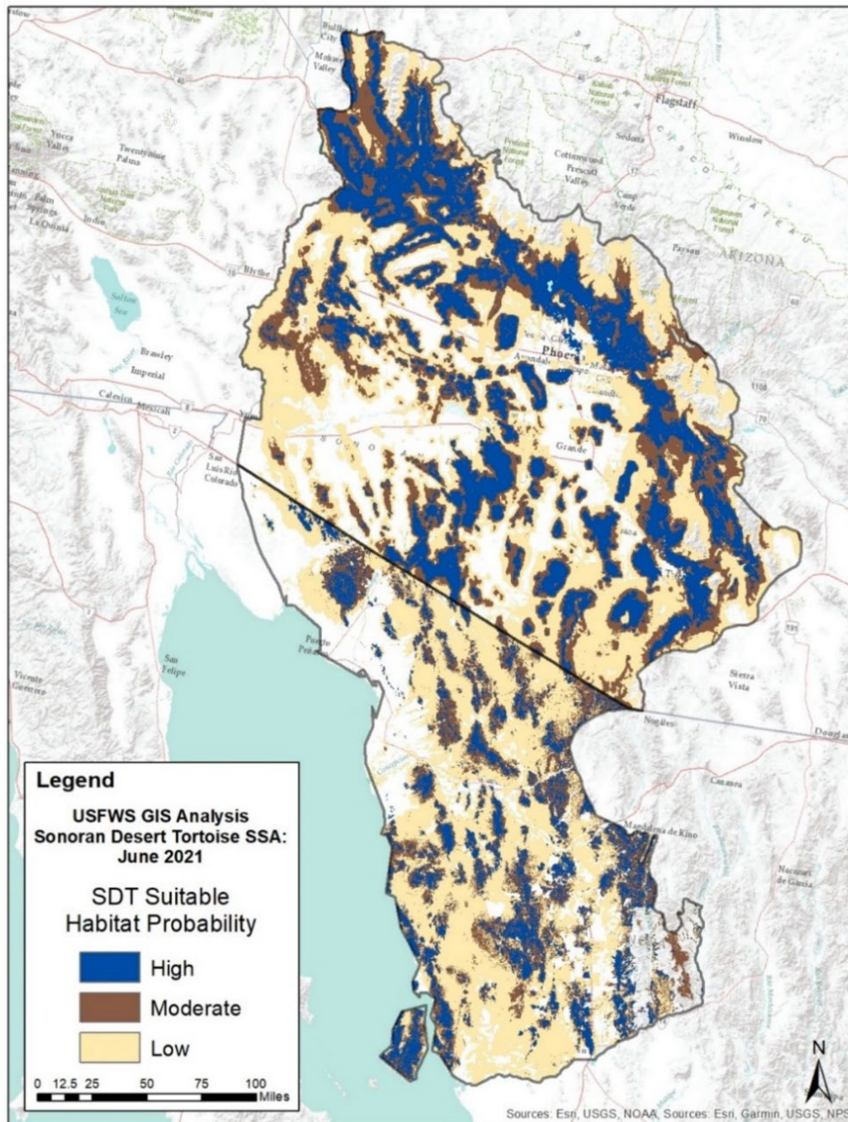


Figure B-4. Predicted potential Sonoran desert tortoise habitat from GIS analysis.

Current Condition: Human Development Effects on Sonoran desert tortoise Suitable Habitat (Arizona & Sonora)

Purpose

A data layer designed to show the effects of human development was created to identify areas of suitable habitat that may be affected by human influences. This was referred to as a *terrestrial intactness layer*, since it ranked land cover and impact features from natural (most intact/low impact) to urban/impervious surface areas (least intact/high impact). Once reclassified, the layer was resampled to a 250m pixel size (source data is 30m). The resampling used a “Majority” algorithm, reclassifying the new 250m pixel based on the classification of the original 30m pixel, which occurs the most within that given 250m pixel. Therefore, areas with less development will classify out as more intact and areas with more development, less intact. This will be explained further in this section.

Data layers

Land cover datasets and rasterized major roads data were the inputs into this layer for Arizona and Sonora.

Table B-9. Application of land cover data layers for Intactness model.

Location	Dataset	Features	Intactness
Arizona	2016 USGS LANDFIRE https://landfire.gov/	Natural Land Cover, Grass, Shrubs, Forests, etc…	Intact/Not Impacted
		Disturbed/Introduced Natural Veg.	Intact/Not Impacted
		Agriculture	Not Intact/Impacted
		Urban/Ruderal Veg.	Not Intact/Impacted
		Urban/Impervious/Roads	Not Intact/Impacted
Sonora	2015 North American Land Change Monitoring System (NALCMS) http://www.cec.org/	Natural Land Cover, Grass, Shrubs, Forests, etc…	Intact/Not Impacted
		Tilled Agriculture	Not Intact/Impacted
		Managed Pastures	Not Intact/Impacted
		Urban/Impervious/Roads	Not Intact/Impacted

To assure major roads (in Arizona & Sonora) were captured, vector roads data were rasterized and added to the raster land cover data. The 30m resolution land cover data does not always capture all road features, even major roads. Surrounding land cover types with high spectral reflectance, or high canopy vegetation cover types can influence their spectral return, "washing out" or covering road features. Road data were gathered from the following sources;

Table B-10. Roads data used to complete Intactness model.

Location	Dataset	Features	Buffer
Arizona	U.S. Census Bureau, 2019 TIGER Data (https://www.census.gov/)	Interstates, U.S. Highways	90m
Sonora	2020 Instituto Nacional de Estadística y Geografía-INEGI (The National Institute of Statistics and Geography) (https://www.inegi.org.mx/default.html) ESRI, Inc. StreetMap and world datasets for ArcGIS 10.x	Federal & State Highways	90m

Minor and unpaved roads were not included for this intactness model, since there is little biological evidence that these features are an impedance (Rubke and O'Donnell 2018b, pp. 8-9). Large highways and roads were buffered to 90 meters then rasterized an added to the land cover data, assuring that at this stage of the model, large roads are spatially accounted for. The reclassified land cover layer (Table B-9) was then resampled to a 250 meter pixel size, the same as the suitable habitat probability model (Figure B-5). The Resampling Tool (ArcMap/Data Management/Raster/Raster Processing) was run with the Majority resampling method. This process selected the majority of the 30m and 90m pixels that fell within the new 250m pixel size, resulting in a representation of either strongly developed or impacted areas or areas more natural, less impacted areas. The model provided a depiction of where these more impacted edges interface with the suitable habitat model (Figure B-6).

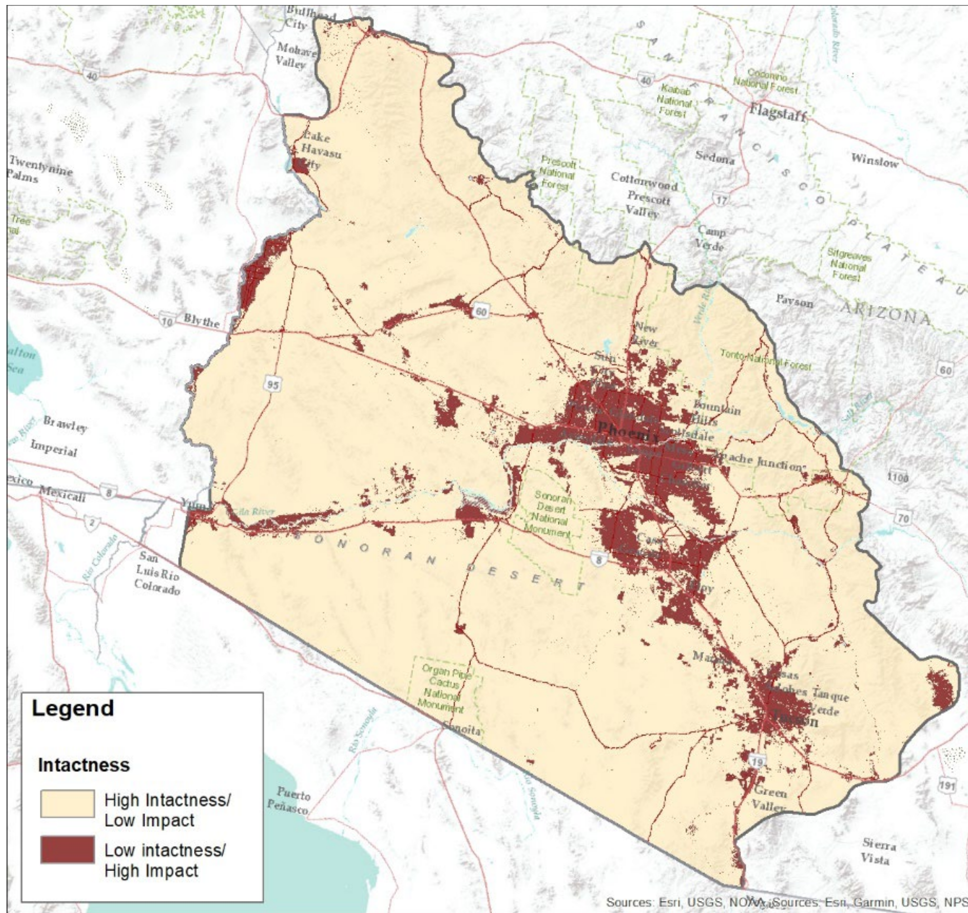


Figure B-5. Intactness model for Arizona portion of analysis area.

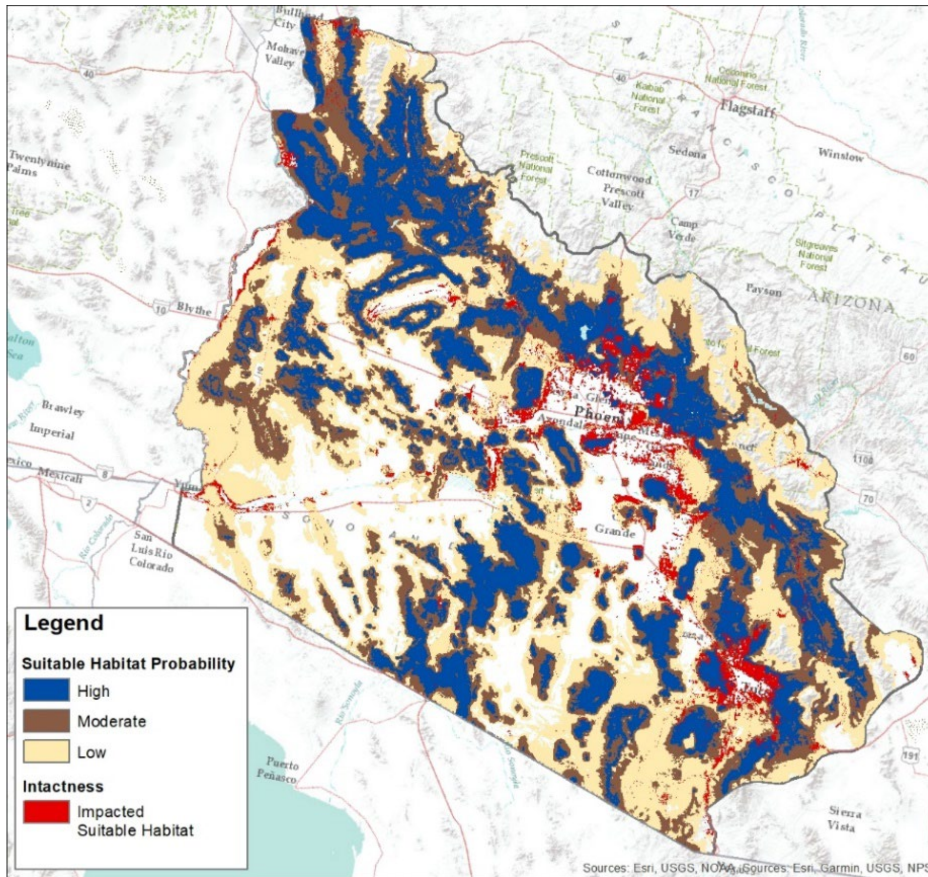


Figure B-6. Suitable habitat model affected by intactness model for Arizona.

Urban Influence on Sonoran desert tortoise Demographic Factors

To represent potential impacts to Sonoran desert tortoise and their habitat, a spatial buffer model was created to identify where human influence (from recreation and outdoor activities) may have an effect (Figure B-7). This model will expand beyond the intactness model to capture human activities that may negative affect tortoises, such as operation of off-road vehicles, all-terrain vehicles, and hiking/camping.

Table B-11. Buffer distances for Urban Influence effects.

Urban Area Type	Influence Buffer
Large Metro Areas (E. AZ), source; U.S. Census Bureau	20 km
Cities/Towns, greater than 10k population (W. AZ/Sonora), source; U.S. Census Bureau or extraction from land cover data.	10 km

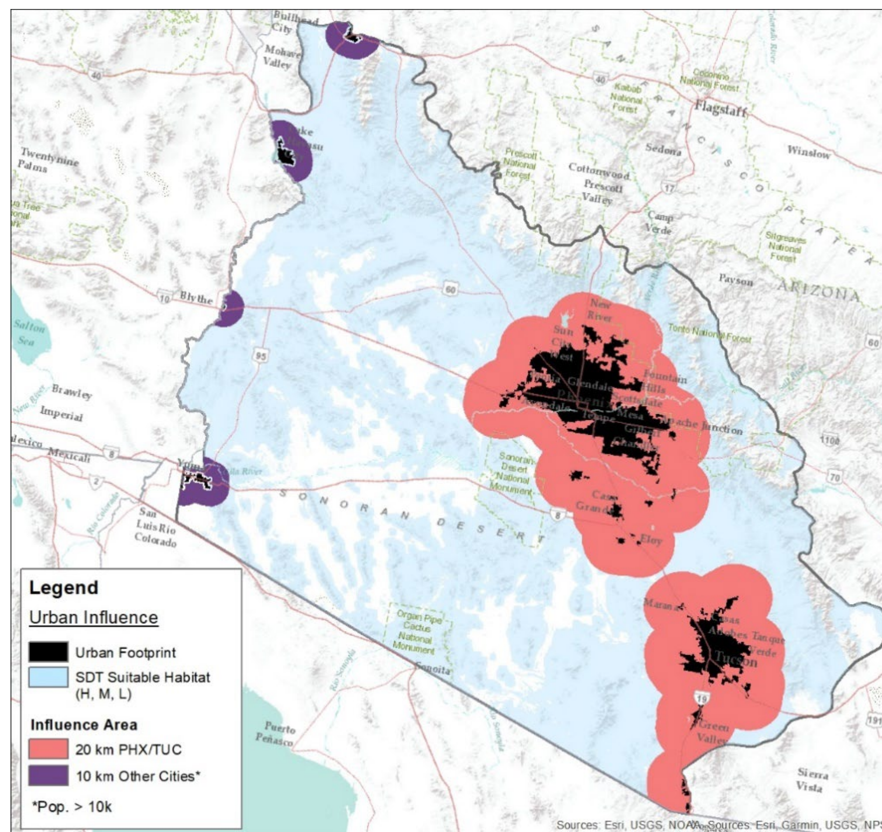


Figure B-7. Urban Influence buffers in Arizona.

Future Conditions: Long-Term Effects on Suitable Habitat Probability (Arizona)

Researchers from the University of Nevada-Reno and the USGS provided suitable habitat probability models for potential future conditions within the U.S. Analysis Area. The visualizations of these models, along with the Current Conditions Ensemble Model, are provided in Figures B-9-11. *Italicized information below provided by K. Nussear (University of Nevada-Reno), T. Esque (USGS), and C. Jones (AGFD).*

To evaluate the potential influences of future climate forecasts on the potential distribution for Sonoran desert tortoise we projected habitat predictions for two time periods (2040 and 2080) using two of the representative concentration pathways (RCPs; 4.5 and 8.5) produced under the IPCC (vanVuuren et al. 2011) which represent likely radiative forcing levels under different socioeconomic development scenarios. We used the NCAR CCSM-4 climate model for our habitat forecast, as this model is thought to be a good representation for the western United States (Gent et al., 2011). We downscaled precipitation and temperature forecasts to our 250m modeling grid using the delta method (Gleick 1986), which is a simplified downscaling where the future anomaly surfaces are interpolated to a modern climatology, which for our purposes was the PRISM historic data (Daly et al. 1994). Model forecasts were conducted using the BIOMOD_Projection function within biomod, which projects the selected models for each algorithm using a new raster dataset including the future climate variables. The selected models for each algorithm (described above) were projected for each individual algorithm, and weighted using the original TSS for each model to create average future projections for each algorithm, and these four models were then averaged to produce the ensemble model representing the future projection for each RCP and time period.

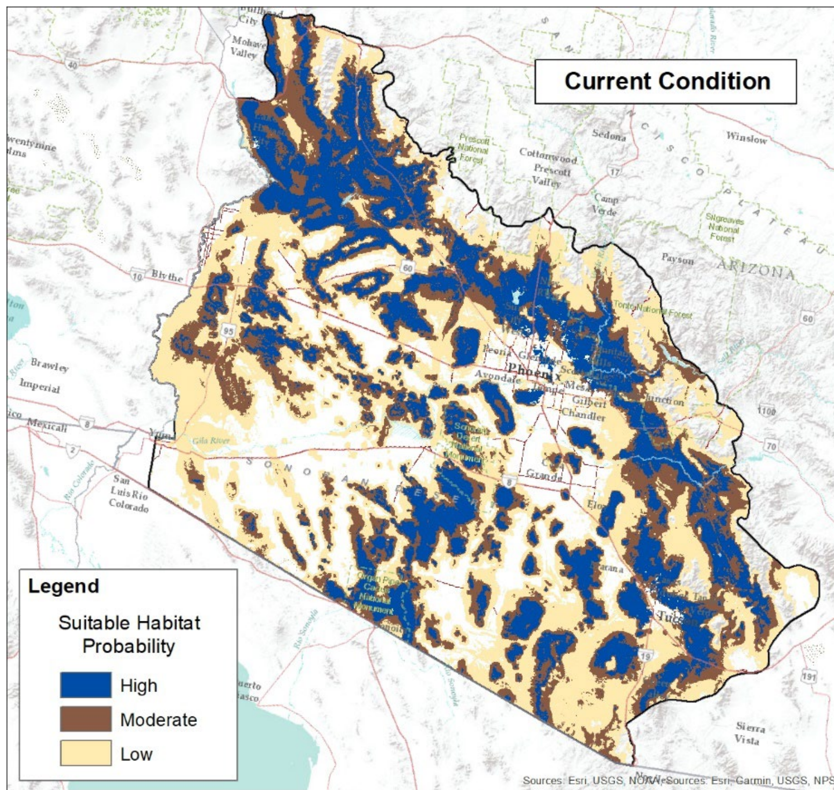


Figure B-9. Arizona Suitable Habitat Probability, Current Condition.

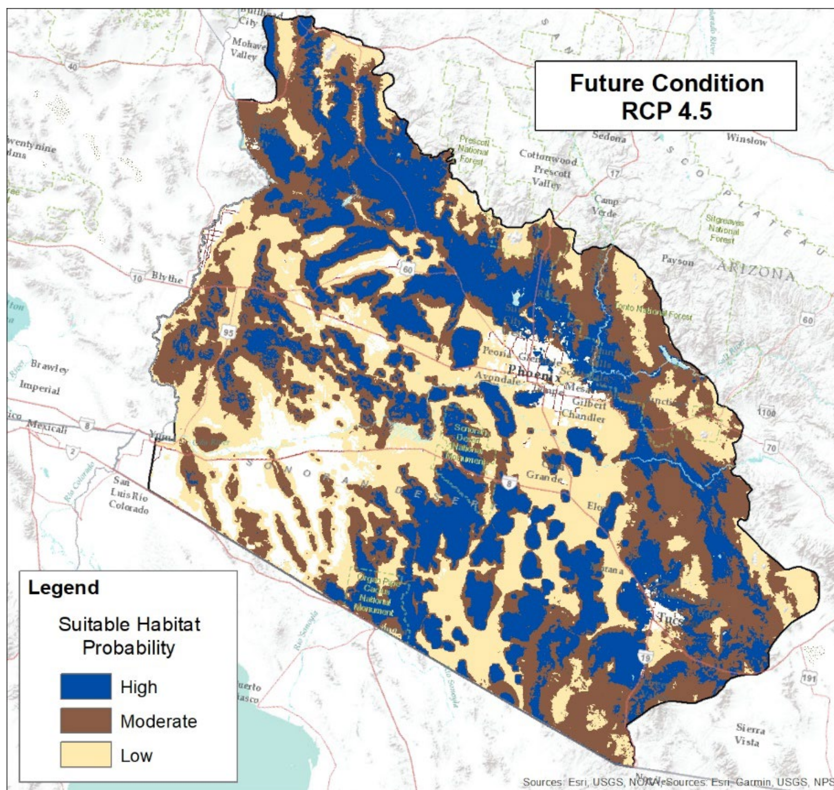


Figure B-10. Arizona. Suitable Habitat Probability, Future Condition RCP 4.5.

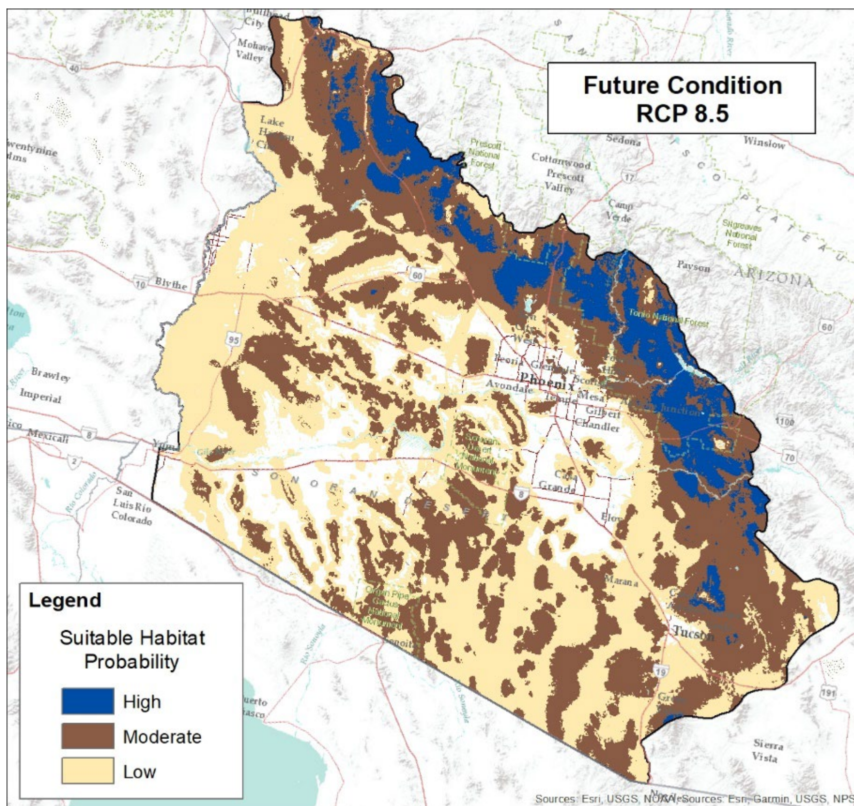


Figure B-11. Arizona. Suitable Habitat Probability, Future Condition RCP 8.5.

Future Conditions: Supporting Data Layers Created for the GIS Analysis (Arizona)

Several data layers were created to use with the suitable habitat data layers to look at human influences and urban expansion and their potential effects on Sonoran desert tortoise populations. These layers provided a spatial context to look at the effects of current and potential future human population growth for the Analysis Area.

Land ownership, Management and Protection Status

Land ownership and land management data were used to imply protection status for Sonoran desert tortoise and provide a spatial framework for examining future human growth potential. Several data layers used or referenced;

- **Conservation Biology Institute (CBI); Protected Areas Database, U.S., CBI Edition, v2.1** https://consbio.org/products/projects/pad-us-cbi-edition
- **World Database on Protected Areas (WDPA), Mexico.** https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA
- **Management Units for the Sustainable Use of Wildlife (2005), National Biodiversity Information System (Mexico)** http://www.conabio.gob.mx/informacion/gis/?vns=gis_root/region/biotic/umas05gw

For the Arizona portion, the land ownership data was used to give suitable habitat features an ownership designation (Figure B-12). Also, each ownership designation was given a management, or protection status descriptor, developed by USFWS biologists, to further describe the types, or levels, of protection

occurring for that specific feature. It was important to get a sense of not only areas there are considered protected by local, state or federal jurisdiction, but also to quantify areas where urban growth/development could occur in the long-term future.

<u>Arizona Ownership Designations:</u>
Federal Government: Owned by a Federal agency (NPS, USFS, BLM, etc.)
State Government: Owned by state of Arizona agency (parks, historic areas, trust lands etc.)
Local Governments: Owned by county or municipal governments (parks, open spaces, facilities, etc.)
Private: Owned by private citizens or entities.
Private Conservation: Owned by non-governmental conservation entities (TNC, etc.)
Tribal: Sovereign or trust Native American territories.
None: Ownership information not available.

<u>Arizona Protection Status:</u>
Managed: Land managed for wildlife habitat or low impact human activity (wilderness areas, wildlife management areas, preserves, some parks and monuments).
Multi-Use: Public land owned by public agencies (vast majority is Federal ownership), which allow more intrusive human activities (motorized vehicles, resource extraction, grazing, etc.) but provide some wildlife management benefits in addition to other uses. Also, includes Tribal/Native American lands.
Unprotected: Private lands with no indicated protection for wildlife or habitat.
Other: State Trust lands. Lands held by the state for the purpose of generating funds through leases, etc.
None: No protection status designated.

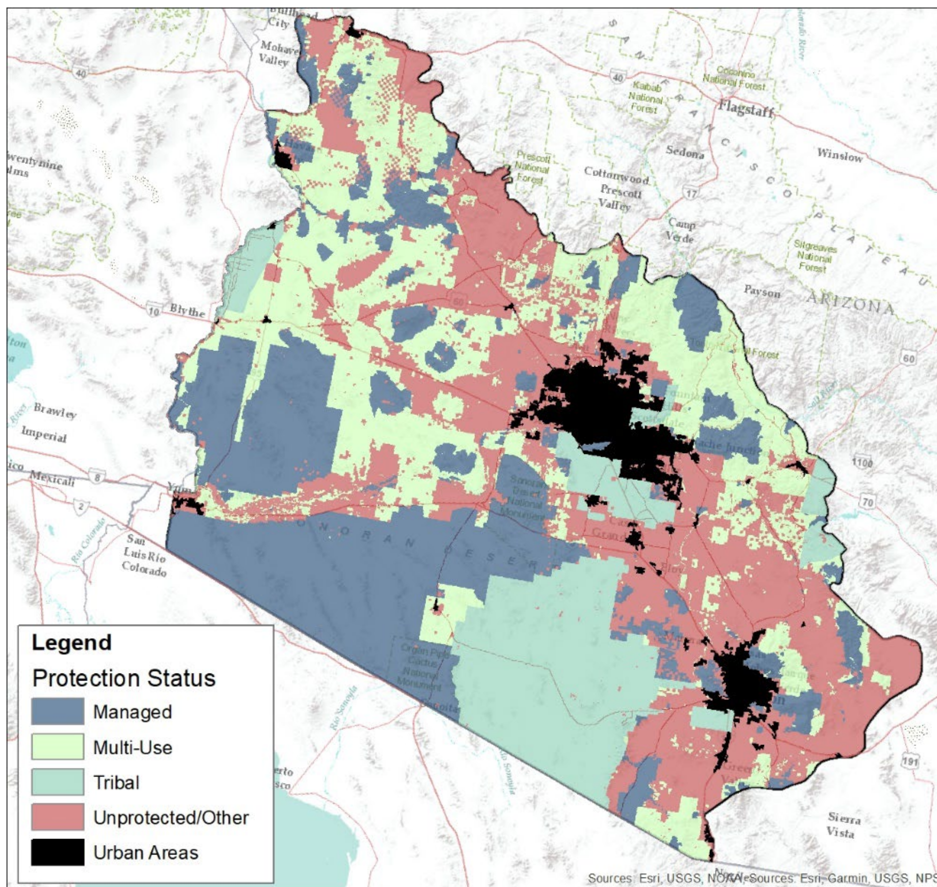


Figure B-12. Protection Status for Arizona portion of Analysis Area.

Assumptions applied to Protection Status for Sonoran desert tortoise Modeling, Current and Future

Areas designated as *Managed* were considered to have the highest protection status for Sonoran desert tortoise. *Multi-Use* areas were considered to have limited protection. For future condition projections, both of these areas were excluded from having any future human development/urban expansion potential. Areas designated as *Unprotected/Other/None* were considered to have little to no protection for Sonoran desert tortoise. These areas were identified as areas where future human development/urban expansion could potentially occur. As mentioned above, these areas spatially constrained the model when projecting future human development/urban expansion on the landscape (Table B-14).

Urban Growth/Expansion Potential: Ringed Buffer Layer

An urban footprint dataset was used to develop an "urban growth" model, by creating a ringed buffer system around urban areas with a human population of 10,000 or greater. Buffers were created using tools in in ArcMap (Analysis Tools/Proximity). This ringed buffer layer was then "unioned" with the suitable habitat data to calculate areas of Sonoran desert tortoise suitable habitat within each buffer distance. The different buffer distances relate to potential human urban expansion on Sonoran desert tortoise populations, with these effects lessening with greater distance (Figure B-13.). It should be noted that this potential future expansion potential can only occur in *Unprotected/Other/None* protection status areas, as described in the previous section. These areas represent areas where potential expansion could happen. Currently there is no way to project spatially, future urban footprints. More detailed explanations of these effects relate to Sonoran desert tortoise demographics and the resulting area calculations are in the main SSA report.

Table B-12. Urban influence buffer types and distances.

Urban Area Type	**Buffer Distances**	
	Low Impact Scenario	**High Impact Scenario**
Large Metro Areas (E. AZ), source; U.S. Census Bureau	5 km	20 km
Cities/Towns, greater than 10k population (W. AZ/Sonora), source; U.S. Census Bureau or extraction from land cover data.	1 km	5 km

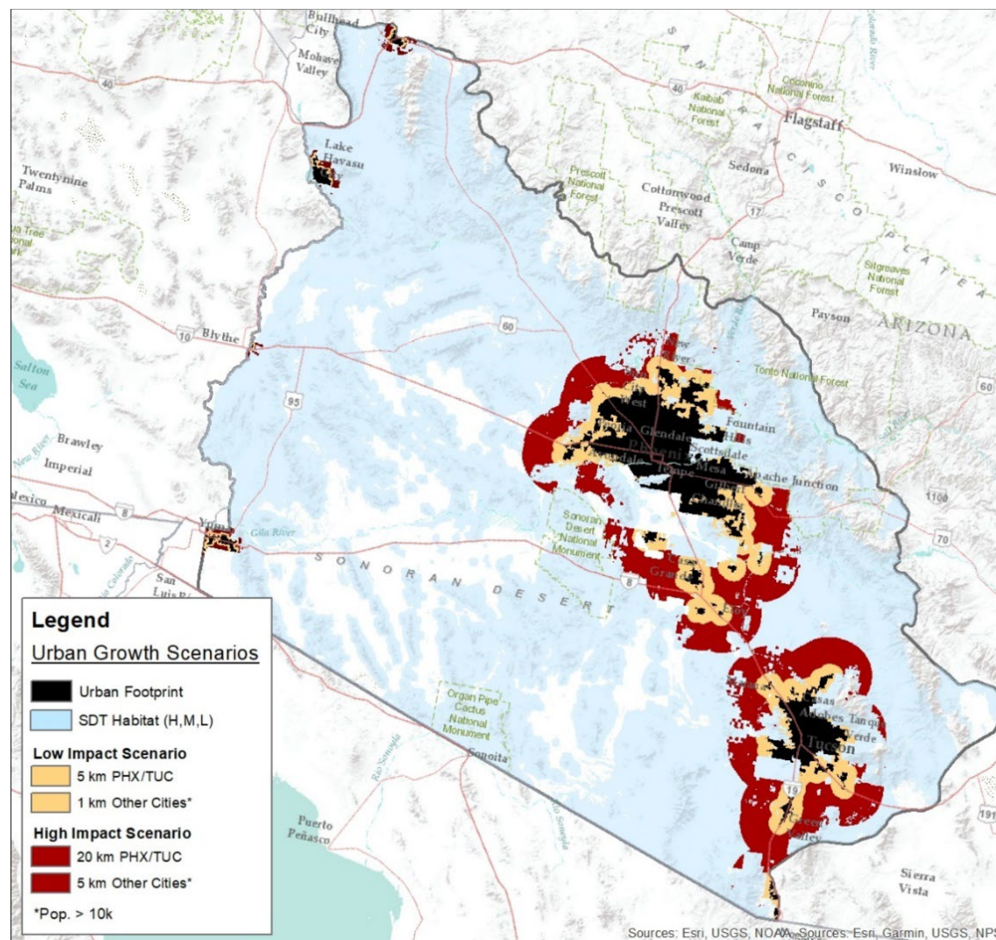


Figure B-13. Urban growth potential extent shown as low and high impact scenarios.

Future Conditions: Long-Term Effects on Suitable Habitat Probability (Sonora)

Since there were not equivalent data layers available for Sonora for use in the Ensemble Future Projection Models, they did not develop a model as was performed for Arizona. No GIS was performed to developed data layers to reflect potential changes in habitat under different climate change scenarios. To project the effects of climate change, we adjusted the proportion of habitat in Sonora in the three habitat classes based on the projections for Arizona (see Section 5.2.1).

For the Sonora portion of the analysis area, protection status was applied to the Sonoran desert tortoise suitable habitat data (Figure B-8) for general reference and information (Table B-15). The WDPA data had little information for developing a protection status category and coverage was limited within the Analysis Area, hence it was not used in any demographic analysis. The Management Unit for Sustainable Wildlife data, though covering more of the Analysis Area, again had little information on the actual level or type of protection for those areas. Suitable habitat within these areas can be calculated as needed. But the information was not used for any Sonoran desert tortoise demographic modeling or future projections for human development/urban expansion.

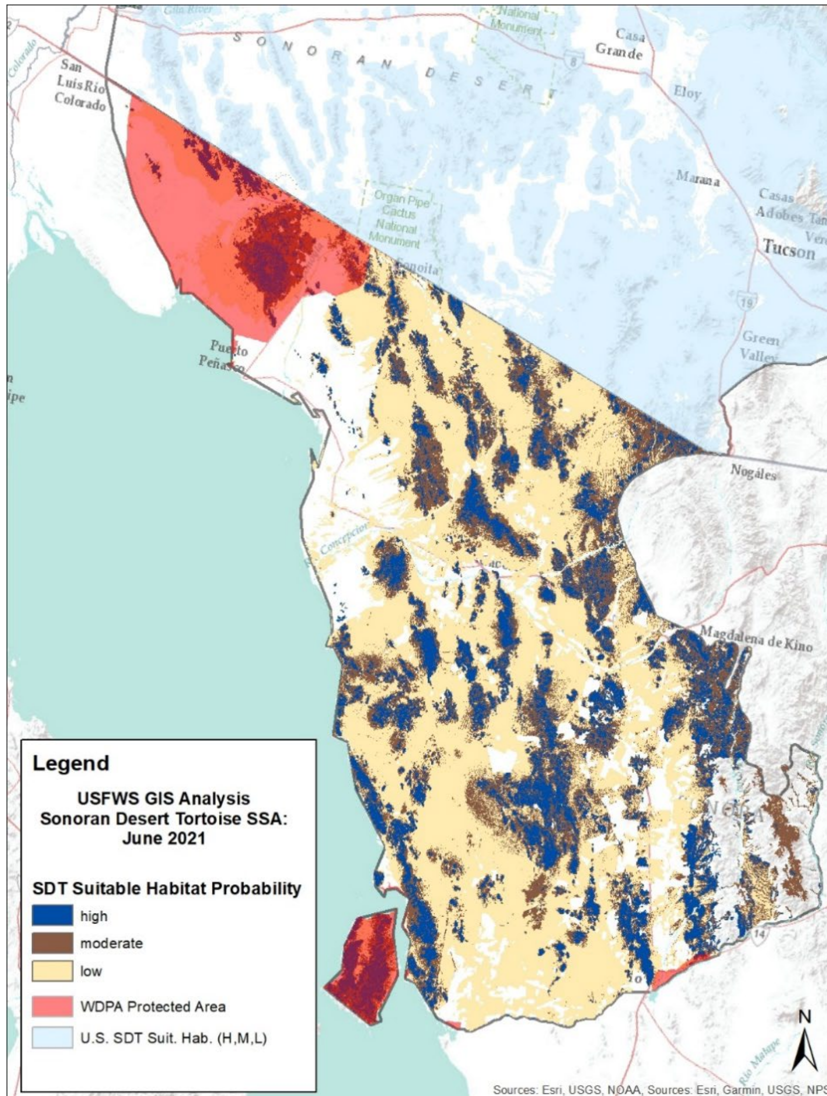


Figure B-8. Suitable habitat in Sonoroa, with protected areas.

Conclusion

This report is a summation of the GIS data analysis (data layer usage and geoprocessing techniques) devised to help provide a spatial understanding of the location and extent of potentially suitable habitat for Sonoran desert tortoise and to analyze how specific threats may affect these areas. The main SSA report provides a more detailed discussion on the actual results and summaries of the various threat analysis scenarios.

Literature Cited

References are provided in Appendix F of the Sonoran desert tortoise SSA Report.

Data Websites/References

AdaptWest; Current and projected climate data for North America (CMIP5 & CMIP6 scenarios): https://adaptwest.databasin.org/pages/adaptwest-climatena/

Arizona Game and Fish Department, Heritage Data Management System; Source for location monitoring plots; https://www.azgfd.com/wildlife/heritagefund/

Commission for Environmental Cooperation, North American Land Cover, 30m, 2015; http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2015-landsat-and-rapideye/

Conservation Biology Institute (CBI), U.S. Protected Areas Database (PAD-US CBI Edition, v2): Source for land ownership data, U.S. only; https://consbio.org/products/projects/pad-us-cbi-edition

Department of Interior, Bureau of Land Management, Rapid Ecological Assessment (REA) Sonoran Desert (SOD), 2010: Source for multiple threats datasets; https://landscape.blm.gov/geoportal/catalog/REAs/REAs.page

Instituto Nacional de Estadistica Y Geografia (INEGI): Source for landcover and roads data, Mexico; https://www.inegi.org.mx/default.html

ISRIC World Soils Information; Soils data for Mexico: https://files.isric.org/soilgrids/former/2017-03-10/data/TAXNWRB_250m_ll.tif

The Nature Conservancy: Digital representation of Brown and Lowe's "Biotic Communities of the Southwest" map (1979) developed by The Nature Conservancy in Arizona (2004). http://azconservation.org/downloads/biotic_communities_of_the_southwest_gis_data

U.S. Census Bureau, TIGER Products: Source for roads data layer; https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html

U.S. Geological Survey, LANDFIRE Existing Vegetation Type: Source for landcover data, U.S.; http://www.landfire.gov/

U.S. Geological Survey, National Elevation Dataset (via The National Map): Source for Elevation data, U.S. and Mexico; https://apps.nationalmap.gov/downloader/#/

World Database on Protected Areas (WDPA): Source for Protected Areas, Mexico; https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA

Appendix C: Cause & Effects Tables

Template for Cause and Effects Evaluation

THEME: ?			
[ESA Factor(s): ?]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
SOURCE(S)	*What is the ultimate source of the actions causing the stressor?*	See next page for confidences to apply at each step.	Literature Citations, with page numbers , for each step.
- Activity(ies)	*What is actually happening on the ground as a result of the action?*		
STRESSOR(S)	*What are the changes in evironmental conditions on the ground that may be affecting the species?*		
- Affected Resource(s)	*What are the resources that are needed by the species that are being affected by this stressor?*		
- Exposure of Stressor(s)	*Overlap in time and space. When and where does the stressor overlap with the resource need of the species (life history and habitat needs)?*		
- Immediacy of Stressor(s)	*What's the timing and frequency of the stressors? Are the stressors happening in the past, present, and/or future?*		
Changes in Resource(s)	*Specifically, how has(is) the resource changed(ing)?*		
Response to Stressors: - INDIVIDUALS	*What are the effects on individuals of the species to the stressor? (May be by life stage)*		
POPULATION & SPECIES RESPONSES	*[Following analysis will determine how do individual effects translate to population and species-level responses? And what is the magnitude of this stressor in terms of species viability?]*		
Effects of Stressors: - POPULATIONS [RESILIENCY]	*What are the effects on population characteristics (lower reproductive rates, reduced population growth rate, changes in distribution, etc)?*		
- SCOPE	*What is the geographic extent of the stressor relative to the range of the species/populations? In other words, this stressor effects what proportion of the rangewide populations?*		
Effects of Stressors: - SPECIES (Rangwide) [REDUNDANCY]	*What are the expected future changes to the number of populations and their distribution across the species' range?*		
Effects of Stressors: - SPECIES (Rangwide) [REPRESENTATION]	*What changes to the genetic or ecology diversity in the species might occur as a result of any lost populations?*		

This table of Confidence Terminology explains what we mean when we characterize our confidence levels in the cause and effects tables on the following pages.

Confidence Terminology	Explanation
Highly Confident	We are more than **90% sure** that this relationship or assumption accurately reflects the reality in the wild as supported by documented accounts or research and/or strongly consistent with accepted conservation biology principles.
Moderately Confident	We are **70 to 90% sure** that this relationship or assumption accurately reflects the reality in the wild as supported by some available information and/or consistent with accepted conservation biology principles.
Somewhat Confident	We are **50 to 70% sure** that this relationship or assumption accurately reflects the reality in the wild as supported by some available information and/or consistent with accepted conservation biology principles.
Low Confidence	We are less than **50% sure** that this relationship or assumption accurately reflects the reality in the wild, as there is little or no supporting available information and/or uncertainty consistency with accepted conservation biology principles. Indicates areas of high uncertainty.

THEME: Altered Native Plant Communities/Nonnative Vegetation			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
SOURCE(S)			
Activities	Nonnative grasses, primarily buffelgrass, red brome, and *Schismus* spp. (Mediterranean grass), of African and Mediterranean natural origin, have been invading desertscrub habitats, expanding their distribution within the range of the tortoise, limited only by each species' ecological parameters for survival and ongoing management actions. Historically, some of these plants were purposely introduced for soil stabilization and livestock forage in Arizona, while others were inadvertently introduced. In Mexico, land continues to be cleared for buffelgrass cultivation as livestock pasture. Any activity that results in soil disturbance potentially provides conditions for nonnative grass invasion, although they can invade undisturbed habitats, too. Vehicles, in particular, disperse seeds along roadways and trails. In Arizona, these plants are now considered noxious weeds in many areas, are no longer intentionally planted, and are actively managed against (remove and control introduction and spread) as agency resources allow (see Appendix A of "Sonoran Desert Tortoise Candidate Conservation Agreement"). Fire is an activity that results in disturbance and can result in invasion by nonnative species in burned areas (see discussion under Altered Fire Regime).	**Highly confident** that nonnative vegetation have become established at various densities and have continued to spread throughout the range of the tortoise over time. **Highly confident** of historical and current land activities that result(ed) in the establishment and spread of nonnative vegetation on the landscape.	Stevens and Falk 2009, p. 420; Bahre 1991, pp. 155-158; D'Antonio and Vitousek 1992, pp. 65, 75; Brooks 1999, p. 13; Brooks 2001, p. 4; Brooks and Pyke 2001, p. 3, 5; Brooks and Esque 2002, p. 337; Esque et al. 2002, p. 313; Van Devender 2002, p. 16; Brooks and Matchett 2006, p. 148; DeFalco 2007a, p. 1; Zouhar et al. 2008, p. 157; Abella 2010, p. 1249; AGFD 2010a, p. 13; Stritthholt et al. 2012, pp. 89-92; AIDTT 2015, Appendix A; Webb 2020, p. 22; Franklin and Molina-Freaner 2010, p. 1664; Walker and Pavlakovich-Kochi 2003, p. 14; Franklin et al. 2006, entire; Búrquez-Montijo et al. 2002, p. 133; Arriaga et al. 2004, p. 1505; Taylor et al. 2012, p. 4; Bean 2015; McDonald and McPherson 2013, p. 26; Salo 2005, pp. 168-170
STRESSOR(S)	Nonnative vegetation crowds out native plants through competition for space, water, and nutrients. Based on the ecological and climatic conditions present, nonnative plant species can completely replace native plants and shift the community composition, especially with multiple burns (see discussion under Altered Fire Regimes). As a result, the stressors include presence of nonnative species and reduction or elimination of native species.	**Highly Confident** of the potential for competitive pressure of nonnative vegetation on native plant species and variability over time and space based on ecological and climatic conditions present.	Stevens and Fehmi 2009, p. 383-384; Olsson *et al*. 2012a, entire; 2012b, pp. 10, 18-19; McDonald and McPherson 2011, pp. 1150, 1152; Franklin and Molina-Freaner 2010, p. 1664; Gray and Steidl 2015, p. 1982, Table 2; Webb 2020, p. 22; Brooks et al. 2016, p. 20, Bracamonte et al. 2017, p. 55
- Affected Resource(s)	Native forage and cover plant species used by tortoises are affected. Tortoises are chiefly herbivorous and forage on a wide variety of native herbs, grasses, woody plants, and succulents. Tortoises also use tree, shrub, subshrub, and cactus species as protective cover and for thermoregulation when active above ground during such activities as foraging, basking, and reproductive behaviors. Nonnative grasses are also used as forage by tortoises, ranging in nutritional potential depending on plant species and age class of tortoises using them. Of the nonnative plant species, only red brome, *Schismus*, and *Erodium cicutarium* (redstem filaree) are frequently eaten and considered relatively important nonnative species in their diet, although sharp seeds (particularly from red brome and cheatgrass) can get lodged between the tortoises' upper and lower jaw and become a source of infection. Navigation of tortoises through habitat invaded by buffelgrass may be negatively affected, especially for tortoises in the hatchling and juvenile size classes. Tortoises have been shown to avoid habitat with dense stands of nonnative grasses, particularly buffelgrass.	**Highly confident** that nonnative vegetation can negatively affect the quantity and distribution of native forage and cover plant species used by tortoises within their home range. **Moderately confident** that buffelgrass can negatively affect mobility of tortoises and can lead to avoidance of habitat patches where nonnative vegetation reaches high density.	Ogden 1993, pp. 1–8; Van Devender *et al.* 2002; pp. 175–176, 183; Brennan and Holycross 2006, p. 54; Oftedal 2007, p. 21; Ernst and Lovich 2009, p. 562; Meyer *et al.* 2010, pp. 28–29, 44–48, Gray 2012, pp. 18, 47-48; Esque *et al*. 2003, p. 107; DeFalco *et al*. 2006, p. 5; McLuckie *et al*. 2007, p. 8; Rieder *et al*. 2010, p. 2436; Medica and Eckert 2007, p. 447; Hazard *et al*. 2010, pp. 139–145; Nagy *et al*. 1998, pp. 260, 263; Webb 2020, p. 22; Brooks et al. 2016, p. 20, Bracamonte et al. 2017, p. 55
- Exposure of Stressor(s)	Tortoise exposure to effects from nonnative vegetation is generally broad over space and time as they generally occur in the specific habitats used by all life stages of tortoises. Management actions on the landscape can reduce the exposure of tortoises to the effects of the stressors.	**Moderately confident** in tortoise exposure to effects of nonnative vegetation.	D'Antonio and Vitousek 1992, p. 65; Bahre 1991, p.156-158; Stevens and Falk 2009, p. 420; Thomas and Guertin 2007, Appendices I and II; Gade 2015; Rogstad 2008, p. 9; Zylstra and Swann 2009, p. 16; USNPS 2014, pp. 7-8; Van Devender and Dimmitt 2006 pp. 3, 6, 10; Burquez-Montijo *et. al*. 2002, p. 138–139; AIDTT 2015, Appendix A

THEME: Altered Native Plant Communities/Nonnative Vegetation			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
- Immediacy of Stressor(s)	To varying degrees, nonnative vegetation is considered a stressor to tortoises in the past, present, and future.	**Highly confident** in the history of nonnative vegetation invasion and potential for continued invasion in the future.	D'Antonio and Vitousek 1992, p. 65; Bahre 1991, p.156-158; Stevens and Falk 2009, p. 420; Thomas and Guertin 2007, Appendices I and II; Rogstad 2008, p. 39; Tim Hughes, USBLM pers. comm., 2015; OPCNM 2011, p. 22; 2014, p. 36; Zylstra and Swann 2009, p. 16; Edwards and Leung 2009, p. 327; Bean 2015, entire; Gade 2015, entire; AIDTT 2015, Appendix A, Webb 2020, p. 22; Brooks et al. 2016, p. 20, Bracamonte et al. 2017, p. 55
Changes in Resource(s)	Nonnative vegetation can crowd out (compete with) native forage and cover plant species through competition for space, water, and nutrients affecting native plant species density and species composition within invaded areas. Competitive pressure varies by species involved, habitat setting, precipitation patterns and amounts, and other environmental and climatic conditions. In highly invaded habitat areas, less native plant cover, lower native plant diversity, lessened availability of high-PEP plant species important for regulating hydration levels in tortoises, lower regeneration of shelter plant species (shrubs and trees) are expected.	**Moderately confident** that in habitat areas affected by high-density nonnative vegetation invasions, negative effects to tortoise plant forage and cover species can be expected but largely contingent on environmental and climatic variability which changes over time and space. Confidence fluctuates over time and space from high (with conditions favoring nonnative plant species) to low (with conditions that favor native plant species).	Oftedal 2002, entire; Stevens and Fehmi 2009, p. 383-384; Olsson *et al*. 2012a, entire; 2012b, pp. 10, 18-19; McDonald and McPherson 2011, pp. 1150, 1152; Franklin and Molina-Freaner 2010, p. 1664; Gray and Steidl 2015, p. 1982, Table 2; Webb 2020, p. 22; Brooks et al. 2016, p. 20, Bracamonte et al. 2017, p. 55
Response to Stressors: - INDIVIDUALS	The response of individuals to these stressors will depend on timing and extent of annual rainfall. In high rainfall years, opportunities for hydration increase and the relative degree of nutrition in the tortoises forage base may not be as important which may lessen the effect on a tortoise's annual reproduction and survival in areas invaded by nonnative vegetation. During dry years, lower native plant diversity and density will exacerbate effects of nonnative vegetation (which tend to out-compete natives during periods of stress) by limiting the availability of high PEP plant species which affects a tortoises' ability to manage its water balance via physiological constraints. Nonnative annuals such as red brome and *Schismus* spp. have short-lived seed banks and may be reduced in density during dry years. Additionally, native perennial grasses are more likely to be resistant to invasion by red brome due to their extensive shallow root system, which outcompetes the shallow root system of red brome. Nonnative vegetation can reduce forage capacity of high-nutrition native plants in invaded areas; reduced forage quality and quantity can reduce fitness of individual tortoises at all life stages; and increased time and energy spent in foraging activities could increase predation risk. Lower fitness due to lower nutrition may reduce reproductive potential in individuals, survival and recruitment of juveniles, and survival of adults. The effect of nonnative grasses on tortoise nutrition is somewhat ameliorated by the fact that tortoises can and do forage to some extent on nonnative vegetation which could make up for losses in species composition and biomass of native species. Most of these nonnative forage species are a high source of energy and considered highly nutritious to adult tortoises. Nonnative vegetation, especially buffelgrass, may impede movement if grasses are at peak densities. Reduced canopy cover can increase body temperatures and reduce periods of surface activity, making individuals more susceptible to dehydration and predation.	**Highly confident** that effects to individuals described will occur in areas densely invaded by nonnative vegetation. **Somewhat confident** that effects to individuals described will occur in areas moderately invaded by nonnative vegetation. **Low confidence** that effects to individuals described will occur in areas sparsely invaded by nonnative vegetation.	Ogden 1993, pp. 1–8; Van Devender *et al*. 2002; pp. 175–176, 183; Oftedal 2007, p. 21; Ernst and Lovich 2009, p. 562; Meyer *et al*. 2010, pp. 28–29, 44–48, Gray 2012, pp. 18, 47; Gray and Steidl 2015, p. 1986; Esque *et al*. 2003, p. 107; DeFalco *et al*. 2006, p. 5; McLuckie *et al*. 2007, p. 8; Rieder *et al*. 2010, p. 2436; Medica and Eckert 2007, p. 447; Hazard *et al*. 2010, pp. 139–145; Nagy *et al*. 1998, pp. 260, 263; Olsson *et al*. 2012a, entire; Webb 2020, p. 22; Brooks et al. 2016, p. 20, Bracamonte et al. 2017, p. 55

THEME: Altered Native Plant Communities/Nonnative Vegetation			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
POPULATION & SPECIES RESPONSES			
Effects of Stressors: - POPULATIONS [RESILIENCY]	The literature has focused on effects of nonnative vegetation on individual tortoises; literature documenting population-level effects has thus far not been identified, even though nonnative vegetation has occurred within long-term monitoring plots for decades and in some cases, over a century. Theoretically, lower annual survival of juveniles and adults and lower reproductive output over time could reduce population sizes and lower overall population resiliency, but these population-level effects have not been identified through long-term monitoring, documented in the literature, or have otherwise not been identified in our review of existing literature. Population-level effects would only become discernable (via current research methods) over an extremely long period of time (decades to centuries) due to the life history and longevity of the species which is well-outside both the existing period of monitoring and our ability to predict such population-level effects in the foreseeable future. This stressor may increase the species' susceptibility to other stressors in areas heavily invaded by nonnative vegetation.	**Low confidence** in potential population-level effects because of a lack of research and observation from the sampling of long-term monitoring plots.	
- SCOPE	One or more species of nonnative vegetation occurs across most of the range of the species; becoming naturalized in some regions. Density of nonnative grasses likely varies considerably in time and space depending on ecological, environmental, and climatic variables. Some species, such as red brome in Arizona, has become naturalized in multiple terrain types on the landscape; both in Sonoran and Mojave desertscrub communities. Buffelgrass is constrained to Sonoran desertscrub; largely distributed in southern Arizona and northern Sonora where it occurs primarily along roadways, within washes, disturbed sites, with a scattered distribution of individual patches on steep, south-facing rocky slopes -apparently by wind-dispersed seeds. In addition to the land area subjected to the deliberate cultivation of buffelgrass in Sonora, estimates state that buffelgrass has naturally colonized two-thirds of the state. Cultivated buffelgrass pastures are most associated with the low valleys within the Plains of Sonora subdivision of Sonoran Desertscrub. While the Plains of Sonora is within the geographic core of the Sonoran desert tortoise's distribution in Mexico, the species is not expected to occur in the lower valleys that comprise most of the Plains of Sonora. Land managers in Arizona, particularly Federal agencies, have been implementing conservation measures to reduce the spread of nonnative grasses and restore native vegetation. Outside of federally-managed land, nonnative vegetation may or may not be managed. The effectiveness of these efforts depends in part on the agency resources that are available. Outside of designated conservation areas, management against nonnative vegetation is largely non-existent in Mexico.	**Moderately Confident** in the distribution of nonnatives **Moderately Confident** that management against nonnative grasses will continue into the future on Federal lands. **Low confidence** that nonnative grasses will be adequately managed on non-federal lands in the foreseeable future.	Strittholt *et al*. 2012, pp. 89-92; Thomas and Guertin 2007, Appendices I and II; Van Devender and Dimmitt 2006, entire; D'Antonio and Vitousek 1992, p. 65; Bahre 1991, p.156-158; Stevens and Falk 2009, p. 420; Stevens and Fehmi 2009 p. 379; Olsson *et al*. 2012a, p. 137; Búrquez-Montijo *et al*. 2002, p. 136, Figure 8.3; Rogstad 2008, p. 39; Tim Hughes, USBLM pers. comm., 2015; OPCNM 2011, p. 22; 2014, p. 36; Zylstra and Swann 2009, p. 16; Edwards and Leung 2009, p. 327; Bean 2015, entire; Gade 2015, entire; AIDTT 2015, Appendix A; Grissom 2015b, p. 3; Van Devender et al. 2009; p. 91

THEME: Altered Native Plant Communities/Nonnative Vegetation			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
- Scope (Conservation Efforts)	Conservation actions that include measures to reduce the likelihood of invasion of nonnative vegetation into new areas, slow the invasion process, or rehabilitate invaded areas can reduce the effects of nonnative vegetation on native vegetation. The Federal agencies that manage lands within the range of the SDT have management and implementation plans in place to address invasive species management. Below we summarize a few of these management efforts, but a complete list of actions that signatories to the CCA are taking to address this stressor can be found in Appendix A of the CCA. Buffelgrass control is the resource management priority at Saguaro National Park and Organ Pipe Cactus National Monument. Since 2007, the NPS has been treating between 160 and 650 acres per year with chemical and mechanical control. Herbicide treatments appear to be particularly promising for buffelgrass control. Most recently, Saguaro National Park has incorporated aerial herbicide delivery to control its spread in remote areas of the park and Organ Pipe Cactus National Monument has been extremely successful in controlling buffelgrass through follow-up treatments and a large volunteer effort. The BLM has treated 18 percent (475 acres) of buffelgrass-invaded habitat identified on their lands and is committed to continuing nonnative plant removal efforts, especially in SDT habitat. The USFS requires any seed mix used for re-vegetation be weed free and integrates measures into their multiple-use planning to minimize actions that could increase the spread of invasive species. The Coronado National Forest is committed to suppressing or eradicating buffelgrass on 1,000 to 1,500 acres of Sonoran Desert every year using herbicides and manual methods. The Tonto National Forest has also committed to working with partners to control or eradicate invasive plant species, especially buffelgrass, on their lands. Both the Department of Defense and FWS area also working with partners to remove and control the spread of nonnative plants on their lands and are committed to continuing these management efforts into the future. The Arizona Department of Transportation implements mitigation measures to prevent the establishment of nonnative grasses within rights-of-way and easements during periods of construction by using native seed mixes for reestablishment of disturbed areas and a state-wide herbicide treatment program for roadside areas. This action is important because roads (and other disturbed areas) can be a source of invasive species to SDT habitat and this action can ensure that these grasses never get a foot-hold.		AIDTT 2015, entire; McDonald and McPherson 2013, pp. 35-36
Effects of Stressors: **- SPECIES (Rangwide) [REDUNDANCY]**	The literature has focused on effects of nonnative grasses on individual tortoises; literature documenting population-level effects has thus far not been identified, even though these nonnative grasses have occurred within long-term monitoring plots for decades and in some cases, over a century. Theoretically, lower annual survival of juveniles and adults and lower reproductive output over time could reduce population sizes and lower overall population resiliency, but these population-level effects have not been identified through long-term monitoring, documented in the literature, or have otherwise not been identified in our review of existing literature. Population-level effects would only become discernable (via current research methods) over an extremely long period of time (decades to centuries) due to the life history and longevity of the species which is well-outside both the existing period of monitoring and our ability to predict such population-level effects in the foreseeable future. This stressor may increase the species' susceptibility to other stressors in areas heavily invaded by nonnative grasses.		

THEME: Altered Native Plant Communities/Nonnative Vegetation			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Effects of Stressors: - SPECIES (Rangwide) [REPRESENTATION]	The literature has focused on effects of nonnative vegetation on individual tortoises; literature documenting population-level effects has thus far not been identified, even though these nonnative vegetation have occurred within long-term monitoring plots for decades and in some cases, over a century. Theoretically, lower annual survival of juveniles and adults and lower reproductive output over time could reduce population sizes and lower overall population resiliency, but these population-level effects have not been identified through long-term monitoring, documented in the literature, or have otherwise not been identified in our review of existing literature. Population-level effects would only become discernable (via current research methods) over an extremely long period of time (decades to centuries) due to the life history and longevity of the species which is well-outside both the existing period of monitoring and our ability to predict such population-level effects in the foreseeable future. This stressor may increase the species' susceptibility to other stressors in areas heavily invaded by nonnative vegetation.		
Summary	Adequate time periods are well-outside of both the existing period of monitoring and our ability to predict such population-level effects in the future. We did not carry this stressor forward in our quantitative analyses.		

THEME: Altered Fire Regime			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
SOURCE(S)	Introduction and invasion of nonnative plants, which include *Pennisetum ciliare* (buffelgrass), *Bromus rubrens* (red brome), *Schismus* spp. (Mediterranean grass), *Brassica tournefortii* (Saharan (or Asian) mustard), genera *Centaurea* and *Cirsium* (thistles), and *Melinus repens* (natal grass). Buffelgrass, red brome, and Mediterranean grass are the nonnative plants most likely to affect the Sonoran desert tortoise and its habitat via this stressor. Nonnative grasses carry fire, and therefore can alter the ecosystem by increasing the frequency, duration, and magnitude of wildfires in a region that otherwise evolved in the absence of fire. Native forbs are capable of contributing to wildfires in desert ecosystems as well.	**Highly confident** that nonnative plants are widely considered to be the source of altered fire regimes in desertscrub communities; fire is uncommon in native desert ecosystems; and key cover species are not fire adapted	Bahre 1991, pp. 125, 155; D'Antonio and Vitousek 1992, pp. 65, 75; Brooks 1999, p. 13; Brooks 2001, p. 4; Brooks and Pyke 2001, p. 3, 5; Brooks and Esque 2002, p. 337; Esque *et al*. 2002, p. 313; Van Devender 2002, p. 16; Brooks and Matchett 2006, p. 148; DeFalco 2007a, p. 1; Zouhar *et al*. 2008, p. 157; Abella 2010, p. 1249; AGFD 2010a, p. 13, Brooks et al. 2016, p. 20; Esque et al. 2013, p. 224
- Activity(ies)	Wildfire in desert ecosystems can spread in entirely native, uninvaded desertscrub communities when two consecutive winters with above average precipitation create a substantial increase in annual plant production and source of fine fuels. However, in an ecological context, wildfire has a long return interval and was never an influential factor in Mojave or Sonoran desertscrub ecosystems because, while natural ignitions did occur, the amount and spatial orientation of fuels that could theoretically carry fire was not generally present due to the extent of bare ground between vegetated patches. In areas invaded by nonnative grasses, fine fuels tend to be more continuous and the amount of bare ground between vegetated patches has decreased resulting in increased fire potential. Nonnative grasses of concern are also fire-adapted, meaning that should fire occur repeatedly over time in the same area (rarely observed), negatively-affected native plant species may be quickly out-competed by positively-affected nonnative grasses, potentially resulting a grass/fire cycle and ultimately, type-conversion of habitat. Ignition sources include natural sources such as lightening (particularly during the late spring and arid fore-summer months when "dry" thunderstorms occur in the Sonoran Desert) and anthropogenic sources such as parking vehicles over dry vegetation, fireworks, discarded cigarettes, backcountry recreationists, and trash burning. Such human-caused wildfires in desertscrub are most common near urban developments, major roadways, and in areas where off-highway vehicle use is uncontrolled. Fires are set intentionally in Mexico to improve the vigor of buffelgrass fields.	**Highly confident** that nonnative grasses can change the fire regime of an area. **Moderately confident** that successive wildfires over the same area can result in a grass/fire cycle and eventual type-conversion of habitat. **Highly confident** in description of potential ignition sources.	D'Antonio and Vitousek 1992, p. 73; Esque 2007, p. 2; Brooks 1999, p. 13; Alford *et al*. 2004, entire; McLaughlin and Bowers 1982, p. 247; Esque et al. 2013, p. 224
STRESSOR(S)	Increased fire in desert ecosystems has the potential to increase the direct exposure of tortoises to fire as well as alter native vegetation communities. Nonnative grasses, particularly buffelgrass, can create wildfires with longer flame lengths, more rapid rates of spread, higher temperatures, and higher mortality of native flora. Such fires in desertscrub habitat can char the ground surface and affect the subsequent plant cover and species composition, potentially favoring nonnative grasses. The ecological effects of wildfire in dense, buffelgrass-invaded, Sonoran desertscrub have not been observed on a broad scale due to aggressive fire suppression policies and limited distribution in areas away from roads. However, effects are modeled to be potentially more severe based on the unique physical characteristics of buffelgrass which affect fire behavior, versus other common nonnative grasses. Should repeated burns occur in areas invaded by fire-adapted nonnative grasses, baseline conditions of the vegetation community could be altered in such a manner that severe changes in species composition could be expected (grass-fire cycle).	**Moderately confident** of the general effects of wildfire in desertscrub communities and anticipated effects on habitat affected by multiple burns.	Esque 2007, p. 2; Woodbury and Hardy 1948, p. 194; Brooks *et al*. 1999, p. 40; Brooks and Esque 2002, p. 335; Esque *et al*. 2003, p. 105; McLuckie *et al*. 2007, p. 7; Shryock *et al*. 2015, pp. 14–15, 20-21, 26, 36; 2015b, pp. 9-12; Abella 2010, p. 1270; McDonald and McPherson 2011, p. 1152; 2013, entire; Grissom 2015a, pp. 2-4
- Affected Resource(s)	The native vegetative community of the Sonoran desert tortoise is affected, specifically forage plants which provide necessary nourishment for reproduction and survival and cover plants which provide for thermoregulatory needs and aid in protection against predators while tortoises are surface active. The degree of effect on these resources can range from negligible to severe, influenced by a multitude of factors.	**Highly confident** that forage and cover plant species are the resources most affected by wildfire.	Averill-Murray *et al.* 2002a; Bury *et al*. 2002, p. 100; Lutz *et al*. 2005, p. 22; Grandmaison *et al*. 2010, p. 582; Shryock *et al*. 2015, pp. 14–15, 20-21, 26; 2015b, pp. 9-12

THEME: Altered Fire Regime			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
- Exposure of Stressor(s)	Wildfires in desertscrub that are naturally caused are most-likely to occur during late spring-early summer (May-June) when relative humidity is low and ambient temperatures are high; when "dry" thunderstorms with lightening strikes occur. Human-caused wildfire is likely to also occur during the spring (March - May) due to pleasant conditions for outdoor activities and conditions with low relative humidity and high(er) ambient temperatures. This period generally coincides with the period when reproductive female tortoises may be surface active from March through early May if suitable temperature conditions persist. However, documentation of wildfire-associated fatalities has been low. Wildfires caused by lightning strikes may also occur during the monsoon when tortoises of all age and size classes may be surface active, however higher relative humidity, moisture level of fuels, and ensuing precipitation generally prevent these fires from spreading naturally in a significant manner. In Mexico, cultivated buffelgrass pastures are repeatedly burned to increase vigor for livestock use. These pastures are most associated with the low valleys within the Plains of Sonora subdivision of Sonoran Desertscrub. While the Plains of Sonora is within the geographic core of Sonoran desert tortoise distribution in Mexico, the species is not expected to occur in the lower valleys as compared to bajada and hillside habitat and may not be directly affected by burning pastures.	**Moderately confident** about when human-caused and lightning-caused wildfires are most likely to occur. **Highly confident** that reproductive females tortoises are potentially disproportionately affected by spring and early summer wildfires as compared to other age- and size-classes of tortoises. **Low confidence** that induced fires in buffelgrass pasture in Mexico are having a significant effect on adjacent tortoise habitat due to limited data.	Averill-Murray *et al*. 2002a, p. 138; Brooks and Pyke 2001, p. 5; Esque *et al*. 2002, pp. 312-313, 321; Zouhar *et al*. 2008, pp. 155, 160; Rorabaugh 2010, p. 181; Alford *et al*. 2004, p. 452, Figure 1; Stritthholt *et al*. 2012, pp. 92-96; USBLM 2010, p. 9; Esque *et al*. 2003, pp. 106-107
- Immediacy of Stressor(s)	Wildfire in desertscrub is a recent phenomenon in an evolutionary context. Up until several decades ago, wildfires were only expected to occur in areas that received successive winter rains over a period of two to three years, leading to a build-up in native annuals as a fuel load. Over time and into the future, if the distribution and density of nonnative grass expand on the landscape, the frequency of ignitions and potentially the size of wildfires may increase (depending on location, terrain, and fuel load). Although occasional large fires could still happen, fire suppression policies are expected to minimize the severity and scope of wildfire in Arizona into the future.	**Moderately confident** in the scope and frequency of potential wildfires into the future.	Brooks and Pyke 2001, p. 5; Esque *et al.* 2002, p. 312; Zouhar *et al.* 2008, pp. 155, 160; Rorabaugh 2010, p. 181; Alford *et al*. 2004, p. 452, Figure 1; McLaughlin and Bowers 1982, p. 247; AIDTT 2015, Appendix A
Changes in Resource(s)	Forage Plants: The degree of effects can vary considerably over a burned area due to fire behavior and abiotic factors in some habitat types. For example, elevation, precipitation, aspect, slope, habitat heterogeneity, etc. affect a given burned area's recovery response in Arizona Upland Sonoran Desertscrub habitat invaded by red brome. Topographic heterogeneity within a burn perimeter can create patches of relatively unaffected habitat, creating a mosaic of different vegetation community conditions and leaving some forage potential for tortoises to exploit and continue to occupy that habitat. In addition, the bimodal precipitation pattern that is characteristic of the Sonoran Desert, tends to favor a more rapid recovery of vegetation, post-burn as compared to the Mojave Desert, for example. In Arizona Upland Sonoran Desertscrub invaded by red brome that has burned once, forage plant species have been shown to have greater overall abundance and plant cover within the first decade post-burn than in unburned reference sites. The rate of post-burn recovery of habitat is expected to be largely precipitation-driven, and may be accelerated during above-average precipitation years and restricted during years of drought. Although fire influences soil physical and chemical properties, soils may still remain intact after fire. Roots and seeds are not necessarily entirely removed by fire and these residual propagules may enhance plant reestablishment on fires. After disturbances such as fire that do not physically remove or heavily compact soils, perennial plant cover in these areas can rebound, in some instances, to levels similar to undisturbed areas within 40 years whereas species composition can take longer to recover in certain areas and environmental scenarios. Cover Plants: Plant types such as shrubs, cactus, and trees provide surface-active tortoises with protective cover to avoid potential predators as well as create a wide degree of thermoregulatory regimes over their home range to allow them to maintain preferred body temperatures and extend the period of time spent foraging, searching for mates, moving between known shelter sites, and other behaviors. Plants used as cover by tortoises have been found to be the most affected by wildfire and recover very slowly; however, some cacti in Arizona Upland Sonoran Desertscrub have been documented to show greater regeneration potential than shrubs or trees, particularly with higher annual precipitation. The number, location, or condition of subterranean shelter sites are not expected to be affected by wildfire and, thus, would continue to provide sufficient cover for tortoises.	**Somewhat confident** in the analysis pertaining to the effect of wildfire on plant forage species because of the large number of environmental and abiotic variables and habitat characteristics that collectively, positively or negatively influence both the degree of damage caused by fire and the recovery rate and condition of burned habitat. The effect of each fire is unique to the area burned and the variables of influence. **Highly confident** in the effect of wildfire on cover plants; universally supported in the nonnative grass/wildfire literature.	Esque 2007, p. 2; Woodbury and Hardy 1948, p. 194; Brooks *et al*. 1999, p. 40; Brooks and Esque 2002, p. 335; Esque *et al*. 2003, p. 105; McLuckie et al. 2007, p. 7; Shryock *et al*. 2015, pp. 14–15, 20-21, 26, 33,36; 2015b, pp. 9-12; Abella 2010, p. 1270-1273; McDonald and McPherson 2011, p. 1152; Grissom 2015a, pp. 2-4

THEME: Altered Fire Regime			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Response to Stressors: - INDIVIDUALS	Fire may kill a desert tortoise by incineration, elevating body temperature, poisoning from smoke inhalation, asphyxiation, and nutrient deficiencies in post-fire foraging. Survival rates of Sonoran desert tortoises are contingent upon several factors, including fire behavior, fire intensity, weather, soil type, substrate, vegetation, tortoise activity, and shelter depth. Season of wildfire will have varying effects to age classes and sexes of tortoises. Spring - early summer wildfires may affect reproductive females that are surface active and foraging to gain nutrients for subsequent egg development; however, we have limited data documenting fatalities associated with wildfires. Monsoon wildfires occur when all age classes are expected to be most active. Wildfires at any time could affect any age or sex tortoise that is occupying a shallow shelter. Multiple wildfires in the same area may exacerbate all effects; however, the specific, long-term effects of multiple fires on Sonoran Desert vegetation and tortoises are little understood. Forage and cover plant species used by tortoises may be affected differently. Forage plant species may be temporarily reduced in abundance or diversity, but may also rebound more quickly. A reduction of forage potential could lead to lower nutrition, lower growth rates, lower fecundity, and lower survivorship. Cover plant species are generally considered to be negatively affected for the long term. A reduction of cover plants can, depending on availability of other structural features, reduces the potential for tortoises to be surface active by altering their thermoregulatory abilities and increasing predation risk. Characteristics of the Sonoran Desert invaded by red brome such as heterogeneous topography (incised washes, boulder fields, cliff faces, etc.) and elevated precipitation, provide microsites that are favorable to recovery of numerous forbs, grasses, and subshrubs, particularly at higher elevations or on north-facing slopes, allowing post-fire recovery to occur at a much faster pace than typically observed in Mojave desertscrub (where much of the existing literature pertains). These factors likely enable adult tortoises to continue to use burned habitat, exploiting the increased availability of food plants and the thermal refugia afforded by heterogeneous topography. However, Sonoran desert tortoises in their small size classes have less mobility to explore the landscape, less access to food plants by their short stature, and less thermal inertia which may pose greater challenges in burned habitat which may make them more susceptible to effects of wildfire than adults. Post-fire monitoring of the 2020 Bush Fire in Sonoran desert tortoise habitat indicated several adult tortoises survived the fire and were in overall good health. Researchers established a control plot in unburned habitat nearby and, initial data regarding body index measures indicate that tortoises within the fire perimeter appeared to be in similar health than those tortoises monitored outside of the fire perimeter.	**Moderately confident** in assessment of effects to individual tortoises as effects from wildfire are highly variable and influenced by a wide array of environmental and abiotic factors.	Esque 2007, p. 2; Woodbury and Hardy 1948, p. 194; Brooks et al. 1999, p. 40; Brooks and Esque 2002, p. 335; Esque *et al*. 2003, p. 105-107; McLuckie *et al*. 2007, p. 7; Shryock *et al*. 2015, pp. 35-36, 39; 2015b, pp. 9-12; Jones 2021, entire
POPULATION & SPECIES RESPONSES			
Effects of Stressors: - POPULATIONS [RESILIENCY]	Literature documenting long-term population level effects to tortoises as a result of fire impacts does not exist. Theoretically, a low to moderate loss of individuals within a population biased towards reproductive females can be significant for a long-lived species with low reproductive capacity. The loss of reproductive females could cause declines in reproductive rates and population growth rates. Alternatively, that loss could be offset by subsequent years of increased recruitment. Nonetheless, research has not demonstrated population-level effects from wildfire. Post-fire monitoring of the 2020 Bush Fire in Sonoran desert tortoise habitat indicated several adult tortoises survived the fire and were in overall good health. Researchers established a control plot in unburned habitat nearby and, initial data regarding body index measures indicate that tortoises within the fire perimeter appeared to be in similar health than those tortoises monitored outside of the fire perimeter.	**Low confidence** that population level effects from wildfire are expected because of a lack of research and the amount of time required to detect potentially subtle trends in tortoise populations.	Esque *et al*. 2003, p. 107; Jones 2021, entire

THEME: Altered Fire Regime			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
- SCOPE	The acreage of desertscrub in Arizona that has burned historically is very small, in context of the range-wide distribution of the species. However, the area invaded by one or more of the most invasive, fire-prone, nonnative grasses is much larger. Ignition is required for a wildfire. Naturally-caused fires (e.g., lightning strikes) are influenced by summer temperature, elevation, winter precipitation, and distance to major rivers. Human-caused ignitions are the most common type of ignition historically and are likely to increase into the future based on human population growth predictions. Human caused fires are influenced by distance to highways, distance to urban areas, distance to major rivers, and winter precipitation. Ignition potential from human activity occurs year-round but does not necessarily result in an ensuing wildfire unless fuel loads, fuel moisture, and climatic conditions are favorable. The total number of ignitions on BLM land in Arizona from 1990-2008 was 854 (total area within fire perimeters were reported as 164,801 acres). Since the 1980s, within Sonoran desertscrub on the Tonto National Forest, the number of fires ranges from below 50 to over 200 per year. Over the last 30 years there have been 21,310 human-caused fires and 1,324 naturally-caused fires in Sonoran desertscrub within Arizona. It is important to note that, with all of these fires, we do not have data regarding the size of each fire and how much area within the burn perimeter actually burned. We assume, based on previous post-fire monitoring data that unburned islands of habitat occurred within these areas and the fires did not result in 100 percent loss of Sonoran Desert vegetation and that most of the fires reported were relatively small in size. Fires intentionally set in Mexico to improve the condition of buffelgrass pasture have the potential to affect adjacent tortoise populations but information is sparse in the literature and little research has been done on the effect of these fires on Sonoran desert tortoise habitat in Mexico. Additionally, many of these pastures occur in areas outside of tortoise habitat, as described above.	**Moderately confident** that future ignitions could increase in frequency in combination with a growing human population. **Moderately confident** that the area burned in Arizona should remain comparatively insignificant in a range-wide context **Low confidence** in our ability to accurately assess the potential risk of fire in Mexico to resident tortoises or their status in that county.	Strittholt *et al*. 2012, pp. 92-96; Alford *et al*. 2004 (entire); Esque *et al*. 2002, pp. 313, 321; USBLM 2010, p. 9
- Scope (Conservation Efforts)	Regardless of ignition frequency or location, wildfire in Sonoran desertscrub within Arizona is aggressively suppressed which has resulted in very few acres burned over time in comparison to the overall acreage on nonnative plant species within the range of the tortoise. Logistics, terrain, access, number of fires burning, and resources available all dictate the response to wildfire and affect the amount of habitat burned. Only in extremely rugged and remote terrain would a wildfire be expected to become significantly large, which has occurred in the past on an infrequent basis. We expect such suppression policies to continue into the future, limiting the spatial potential for wildfire to affect tortoise habitat in Arizona. Of the approximately 30,000 square miles of suitable tortoise habitat in Arizona, approximately 60% currently occurs within managed or multi-use government-owned properties.	**Moderately confident** that while potential ignition sources are many and varied, fire suppression policies in Arizona are expected to limit the area burned by wildfire.	AIDTT 2015, Appendix A
Effects of Stressors: - SPECIES (Rangwide) [REDUNDANCY]	One or more wildfires in desertscrub habitat that is invaded by nonnative grasses could begin to change the suitability of habitat for tortoises through the grass/fire cycle and slowly contribute to lowered survivorship and potentially population level effects if adult female tortoises are disproportionately affected. However, aggressive fire suppression policies in Arizona limit the potential for this scenario to occur. Fires intentionally set in Mexico to improve the condition of buffelgrass pasture have the potential to affect adjacent tortoise populations but most of these pastures occur outside of tortoise habitat (per above) and information is sparse in the literature and little research has been done on the effect of these fires on Sonoran desert tortoise habitat in Mexico.	**Moderately confident** that the area burned in Arizona should remain comparatively insignificant in a range-wide context and therefore will have an insignificant effect at the species level. **Low confidence** in our ability to accurately assess the potential risk of fire in Mexico to resident tortoise populations or their status in that country.	Esque *et al*. 2002, pp.313, 321

THEME: Altered Fire Regime			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Effects of Stressors: - SPECIES (Rangwide) [REPRESENTATION]	One or more wildfires in desertscrub habitat that is invaded by nonnative grasses could begin to change the suitability of habitat for tortoises through the grass/fire cycle and slowly contribute to lowered survivorship and potentially population level effects if adult female tortoises are disproportionately affected. However, aggressive fire suppression policies in Arizona limit the potential for this scenario to occur. Fires intentionally set in Mexico to improve the condition of buffelgrass pasture have the potential to affect adjacent tortoise populations but most of these pastures occur outside of tortoise habitat (per above) and information is sparse in the literature and little research has been done on the effect of these fires on Sonoran desert tortoise habitat in Mexico.	**Moderately confident** that the area burned in Arizona should remain comparatively insignificant in a range-wide context and therefore will have an insignificant effect at the species level. **Low confidence** in our ability to accurately assess the potential risk of fire in Mexico to resident tortoise populations or their status in that country.	Esque *et al*. 2002, pp.313, 321
Summary	The amount of suitable Sonoran desert tortoise habitat burned over the past several decades represents a small portion of the species overall range within Arizona. Within Sonora, we lacked detailed information on the potential extent and seveirty of this stressor. Thus, we did not carry this stressor forward within our quantitative analyses.		

THEME: Habitat Conversion			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
SOURCE(S)	Conversion of habitat from urban expansion and irrigated agriculture.	**Highly Confident** that urban growth and associated infrastructure will continue. **Low Confidence** that irrigated agricultural areas will expand.	SSDAN; 2000, entire; Gammage *et al*. 2011, p. 10; Pinal County Comprehensive Plan 2009, p. 109; Howland and Rorabaugh 2002, entire; Stoleson *et al*. 2005, pp. 54, 60; U.S. Census Bureau 2005, p. 1; USDA 2009, p. 7; Carter *et al*. 2021, entire
- Activity(ies)	Habitat is being graded and covered by pavement or converted to urban landscaping or (much less frequently) into irrigated, commercial agriculture.	**Highly Confident**	Gammage et al. 2008 entire, 2011 entire, USDA 2009, p. 7; Stoleson *et al*. 2005, pp. 54, 60
STRESSOR(S)	Complete removal of habitat including forage plants, cover plants, and shelter sites. Human activities related to conversion (e.g., clearing, construction).	**Highly Confident**	Howland and Rorabaugh 2002, pp. 335-336
- Affected Resource(s)	Vegetation used as forage and cover; shelter sites used for extended dormancy and nesting; uninterrupted open space to establish home ranges and facilitate short-, medium-, and long-distance dispersal movements. Generally urban development causes significant changes to habitat (usually removes it entirely) making regional and landscape movements challenging if not impossible. Generally, agricultural development, however, may still allow for these movements even though the habitat is no longer suitable for occupation of tortoises; depending on size and extent of agricultural area.	**Highly Confident**	Ogden 1993, pp. 1–8; Van Devender *et al*. 2002; pp. 175–176; Oftedal 2007, p. 21; Ernst and Lovich 2009, p. 562; Meyer et al. 2010, pp. 28–29, 44–48; Averill-Murray and Klug 2000, p. 69; Averill-Murray *et al*. 2002b, p. 126, Riedle 2015a; Burge 1979, p. 44; 1980, pp. 44–45; Barrett 1990, p. 205; Averill-Murray *et al*. 2002a, pp. 136–137, Grandmaison *et al*. 2010, p. 582
- Exposure of Stressor(s)	Commercial, residential, and agricultural development is mostly associated with valley bottoms and areas with limited slope. A lesser degree of residential development has occurred and is expected to continue within the upper bajadas and steeper slopes adjacent to development zones. Increased residential development has occurred within the lower bajadas and rolling hills above 1,300 feet elevation (e.g., large-scale communities such as Gold Canyon, Anthem, Dove Mountain) and is expected to continue into the future, adjacent to development zones. These building sites, if zoned for residential construction, are highly desirable as home-building sites for their view sheds. The Catalina Foothills and Oro Valley areas within greater Tucson are excellent examples of this type of development. Generally, Federally managed lands are protected from conversion to urban or industrial agriculture uses unless selected for disposal. Lands managed by the State Land Department and private lands may be developed at any time depending on market value and proximity to existing urban infrastructure. All life-history needs of the tortoise are negatively impacted by development where there is overlap with occupied habitat, although the degree of effects depends on the nature and density of the development.	**Highly Confident**	SSDAN; 2000, entire; Gammage *et al*. 2008 (entire), 2011, (entire); Pinal County Comprehensive Plan 2009, p. 109
- Immediacy of Stressor(s)	The Arizona economy has been and is expected to continue to be largely driven by the construction and development sectors. Loss of habitat has been occurring for decades and is expected to continue into the future as the human population continues to grow at changing rates over time. Regional, widespread megadrought or unfavorable economic conditions may ultimately limit development and population growth regionally. Land that is developed for commercial or residentail purposes is considered permanently lost as tortoise habitat. Land that is converted to commercial agriculture uses may ultimately be abandoned and return to a semi-natural state but is more likely to be converted into urban or residential uses if not used for agriculture. Similar trends pertaining to human population growth and urban development could be expected in Sonora, Mexico, perhaps at a slower pace and smaller scale. However, irrigated agricultural development in Sonora is not expected to be a significant stressor to Sonoran desert tortoise habitat in Mexico as most of the development occurs along large, flat river deltas which are not considered to be suitable for Sonoran desert tortoises.	**Highly confident that some development will continue within the range of the tortoise.** **Somewhat confident on growth predictions based on extenuating factors such as water supply and market forces.** **Moderately confident that urban growth will continue in Mexico within the range of the tortoise** **Low confidence on our ability to accurately predict growth and development potential in Sonora, Mexico.**	SSDAN; 2000, entire; Gammage *et al*. 2008 (entire), 2011 (entire); Pinal County Comprehensive Plan 2009, p. 109; Cook *et al*. 2015, p. 4; Stoleson *et al*. 2005, p. 54, 59-60; Rosen *et al*. 2014a, p. 23

THEME: Habitat Conversion			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Changes in Resource(s)	Habitat fully converted to urban development is no longer usable by tortoises. The amount of suitable habitat continues to be reduced over time. There is no expectation that land used for urban development will again become suitable for Sonoran desert tortoises. In Arizona, land that is converted to commercial agriculture uses may ultimately be abandoned and return to a semi-natural state but is more likely to be converted into urban or residential uses if not used for agriculture. Time required for recovery of habitat after abandonment of agricultural lands can be on the order of decades. The presence of nonnative species such as buffelgrass, cheatgrass, or red brome in disturbed Mojave or Sonoran desertscrub may further limit post-disturbance recovery. Other factors such as the amount of soil removed or the degree of soil compaction influence regeneration of habitat and are extremely variable.	**Highly confident** that areas developed for urban uses are lost entirely for tortoises into the future. **Low confidence** that land converted for commercial or irrigated agriculture will ever become suitable habitat for tortoises in the future.	Abella 2010, pp. 1270-1271, 1273; Brown and Minnich 1986, p. 411; Brooks 1999, p. 18
Response to Stressors: - INDIVIDUALS	Loss of forage plants, cover plants, and sheltering sites removes the ability for the species to adequately fulfill natural history needs and results in either immediate fatalities of individuals during construction or delayed fatalities from starvation, exposure, or predation should an individual survive the construction phase and/or be displaced from its home range.	**Highly confident** that a tortoise in harm's way from a construction or development project is unlikely to survive immediate, direct or delayed, indirect effects.	Howland and Rorabaugh 2002, pp. 335-336
POPULATION & SPECIES RESPONSES			
Effects of Stressors: - POPULATIONS [RESILIENCY]	Not all losses to Sonoran desert tortoise habitat have equal effects to tortoise populations. For example, the loss of primary (or "core") Sonoran desert tortoise habitat (within or adjacent to boulder-strewn bajadas) would have a disproportionately greater impact to a Sonoran desert tortoise population than a loss of similar size within the flat, creosote-bursage community found in valley floors or similar types of valley bottoms in Mexico (considered dispersal or "secondary" habitat). Both types of habitat are used by the Sonoran desert tortoise, but the latter is considered to have an exceptionally low density of tortoises; serving rather as a potential dispersal corridor during medium- to long-distance dispersal movements on rare occasion. While not as vital to the species as primary habitat (where home ranges are developed), dispersal habitat functions to an unknown degree in facilitating connectivity of populations over time; providing for exchange of genetic material among populations, and providing a potential source of individuals in the event of a localized, stochastic decline within a given population. The majority of habitat conversion within the range of the species has occurred and is expected to continue to occur within dispersal, or secondary, habitat and therefore has not directly resulted in the loss of any known tortoise populations. Indirect effects to populations from development adjacent to core, or primary, habitat could be occurring but require multiple decades, if not centuries, of monitoring to detect trends within populations. If the direct loss of habitat due to urban expansion is within high quality habitat areas and is large enough in area, population effects are likely to occur in the future.	**Moderately confident** that habitat conversion is not expected to affect the resiliency of tortoise populations range-wide.	Edwards *et al*. 2004, entire; Zylstra *et al*. 2013, entire

THEME: Habitat Conversion			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
- SCOPE	Within Arizona, future urban development is projected to be the most significant along the Sun Corridor Megapolitain area following I-19, I-10, and I-17, with additional development along I-40 near Kingman and along major state highways over the next 50 to 100 years. The I-11 corridor is planned to replace existing State Route 93, although the project appears to advance in a sporadic manner. If I-11 is completed, it would be conceivable that non-federal lands along its route would be developed over time. Landscape modeling has estimated that approximately 70% of Sonoran desert tortoise habitat has some level of development within 0.62 miles (1 km) and levels of development were highest near cities such as Phoenix and Tucson, Arizona. Currently, development in Arizona has replaced some historical tortoise habitat and projections (from preliminary GIS analysis) suggest as much as 10% of suitable tortoise habitat could be developed over the next 100 years. About 73% of currently suitable tortoise habitat in Arizona is likely not to be developed due to land ownership and management (government and tribal lands). Acres of agricultural development have been documented as decreasing over time and are not expected to significantly influence tortoise populations in the future in Arizona, unless a new type of crop significantly influences market forces and reverses this trend. In Sonora, Mexico, Hermosillo is the largest developed city that in the next several decades could expand north and east, potentially affecting tortoise populations. Small communities such as Sonoyta, Pitiquito, Benjamin Hill, Punta Chueca, Kino Bay, Moctezuma, and San Carlos could see expansion over time; however, we do not know what the growth of these areas wil be. Although in general, future development in Mexico is not currently seen as a significant stressor to tortoise populations over a significant area.	**Highly confident** that urban development has replaced some historical tortoise habitat in Arizona. **Somewhat confident** about the extent of future urban expansion. **Highly Confident** that urban development will not occur or will occur on a very small portion of Federal lands within the range of the tortoise. **Somewhat confident** about potential growth projections in Mexico.	SSDAN; 2000, entire; Gammage *et al*. 2011, p. 10; Pinal County Comprehensive Plan 2009, p. 109; Rosen *et al*. 2014a, pp. 22-23; USDA 2009, p. 7; Lehman 2021, entire; Carter et al. 2020, p. 175
Effects of Stressors: - SPECIES (Rangwide) [REDUNDANCY]	In the case of moderate to extreme projected growth and development scenarios, the number of tortoise populations could begin to decline. The rate of decline would be influenced by the scope and magnitude of the habitat conversion over time. This time scale may be on the order of decades to centuries. In addition to urbanization and agriculture, mining operations can result in habitat conversion for Sonoran desert tortoises. The Bagdad Mine, operated by Freeport-McMorRan Bagdad Inc (FBMI) has purchased approximately 16,810 acres of land (approximately 25 square miles) administered by the Arizona State Land Department. FBMI will use this area to expand their current operations, including adding to their existing tailings piles . At this time, we do not know how much of this 16,810 acres will be developed and how much will remain intact as viable habitat. We also do not know	**Low confidence**	Edwards *et al*. 2004, entire; Zylstra *et al*. 2013, entire, Phoenix New Times 2020, entire
Effects of Stressors: - SPECIES (Rangwide) [REPRESENTATION]	The effect of lost populations as a result of habitat conversion, in a range-wide context, depends on where populations are lost. Genetic connectivity and dispersal characteristics fit the isolation by distance model. Where habitat conversion interrupts connectivity between populations, the loss of fragmented populations may reduce genetic representation over time. These impacts, however, function at a time scale which far exceeds our ability to accurately predict such a range-wide impact.	**Low confidence** that representation of important genotypes among populations could decline as a result of habitat conversion.	Edwards *et al*. 2004, entire; Howland and Rorabaugh 2002, entire; Phoenix New Times 2020, entire
Summary	Habitat conversion influences the quantity and quality of suitable Sonoran desert tortoise habitat. We quantified the current scope of habitat conversion and urban influences and incorporated the effects of urban expansion and resulting urban influences within our quantitative assessments.		

THEME: Habitat Fragmentation			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
SOURCE(S)	Transportation infrastructure (roads, highways, interstates), canals, railroad tracks; international border pedestrian fences; other linear development that reduces or impedes movement of tortoises.	**Highly confident** that these linear developments can either completely preclude crossing of tortoises or reduce the percentage of tortoises that successfully cross.	Edwards *et al*. 2004, entire; Forman 2000, p. 33-34; Audsley 2010, p. 5; Sferra 2010, pers. comm.
- Activity(ies)	The ground surface is becoming altered in an expanding network of linear development to convey vehicular traffic (roads), railroad commerce (tracks), and water for domestic, industrial, and agricultural purposes (canals). Border security infrastructure construction and maintenance (fences).	**Highly Confident**	Forman 2000, p. 33-34
STRESSOR(S)	Tortoises move within and outside their home ranges for a variety of natural history functions including foraging for desired plant species in various areas, searching for mates; selecting, constructing, and seasonally rotating through shelter sites; and short-, medium-, and long-distance dispersal. Linear developments affect a tortoise's ability to freely move on the landscape and become a source of mortality within an area, depending on the type and scale of the linear development.	**Highly confident** that tortoises require the ability to move within and outside of their home ranges for a variety of life history functions. **Moderately confident** that linear development negatively affects an individual tortoises' ability to move in areas where linear development transects occupied home ranges.	Fahrig and Rytwinski 2009, p. 1; Boarman and Sazaki 2006, p. 99; Averill-Murray and Klug 2000, p. 69; Averill-Murray *et al*. 2002b, p. 126, Riedle 2015a; Ogden 1993, pp. 1–8; Van Devender *et al*. 2002; pp. 175–176; Oftedal 2007, p. 21; Ernst and Lovich 2009, p. 562; Meyer *et al*. 2010, pp. 28–29, 44–48; Lowery *et al*. 2011, p. 7, Grandmaison 2010, p. 5
- Affected Resource(s)	Navigable ground surface.	**Highly Confident**	Zylstra and Swann 2009, p. 10; Edwards *et al*. 2004, entire
- Exposure of Stressor(s)	Once a linear development such as a paved road (arterial, highway, interstate), canal, or railroad bed is constructed, the development is considered permanent. Exposure to this stressor occurs whenever a tortoise needs to move within or outside its home range where that movement is impeded or restricted by a form of linear development.	**Highly Confident**	Forman 2000, entire
- Immediacy of Stressor(s)	Current, ongoing, and increasing into the future. Over time, the density and scope of linear development has increased to keep pace with growing human population demands. Currently, some form of linear development occurs over most of the range of the species at various scales and densities. The forms of linear development we have identified are considered permanent and therefore are expected to cause effects as long as occupied tortoise habitat overlaps with the linear development.	**Highly Confident**	Forman 2000, entire; Edwards *et al*. 2004, entire
Changes in Resource(s)	In some areas, the ease of tortoise movement within and outside of home ranges has changed over time. Resident tortoises may or may not be able to successfully perform certain natural history functions depending on the location and type of linear development.	**Highly Confident**	Forman 2000, entire; Edwards *et al*. 2004, entire; Fahrig and Rytwinski 2009, p. 1; Boarman and Sazaki 2006, p. 99

THEME: Habitat Fragmentation			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Response to Stressors: **- INDIVIDUALS**	Individuals attempting to cross linear developments may be injured or killed by vehicular strikes, drowning, etc., or may simply be physically unable to cross the linear development. There are data documenting tortoise road fatality but not data documenting the frequency with which tortoises may cross a development successfully and unharmed; therefore, it is possible that some tortoises are successfully crossing these developments. The limited number of telemetry studies on tortoises showed they either did not cross any roads, made short-intermediate movements, or their signals were lost. Effects of linear development on individual tortoises are not equal. Regarding roads, highways, etc., we expect road width, road type (rugged, improved gravel, paved), speed limits, traffic volume, availability of washes traversing underneath roads, and quality of tortoise habitat being transected have the greatest effect on tortoise injury/mortality rates. Tortoises crossing roads that require slow(er) rates of speed have a higher likelihood of being noticed because drivers are more attentive. In these situations, the likelihood of collection or handling is greater. The larger the tortoise, the more likely it is to be seen. Tortoises crossing paved roads with higher speed limits may be less prone to being noticed and more prone to being injured or killed from a vehicle strike. Roads are an example of linear development that may allow an unknown percentage of tortoises to successfully cross whereas canals are largely considered impassible and may act as a sink to dispersing tortoises. Conservation measures such as tortoise fencing have been implemented along some forms of linear development. However, ongoing maintenance of these structures has not occurred and numerous breaches continue to exist. We are uncertain what effect these structures have had on limiting road fatality of neighboring tortoise populations. Other conservation measures such as implementation of reduced speed limits, education, and construction of tortoise-friendly culverts and underpasses, etc. are being considered for future development on many Federal lands. In addition there are efforts in place on Federal lands (*e.g*,. BLM, FWS, NPS) to restore connectivity between high value habitat where it has been modified.	**Highly confident** that some unknown number of tortoises are killed on the road, or by other forms of linear development, every year throughout their range and that various characteristics associated with specific linear developments influence permeability and injury/mortality rates within occupied habitat.	Boarman and Sazaki 2006, entire; Hoff and Marlow 2002, pp. 451-454; Boarman *et al*. 1997, p. 57; Forman and Alexander 1998, p. 213; Boarman 2002, pp. 54–55; Boarman and Sazaki 2006, p. 98; Dieringer 2010, p. 1; Grandmaison 2010, p. 5; Lowery *et al*. 2011, p. 7; USBLM 2007, p. 17; 2010b, p. 119; 2010a, pp. 31-32; 2012e, pp. 74-82; Gade 2015, entire; Leavitt and Hoffman 2014, entire; Grandmaison 2010, entire; Grandmaison and Frary 2012, entire; AIDTT 2015, Appendix A
POPULATION & SPECIES RESPONSES			
Effects of Stressors: **- POPULATIONS** **[RESILIENCY]**	While available data suggest that some rate of tortoise injury or fatality may be associated with linear development there are no data available which document population-level effects on population resiliency from this stressor. Theoretically, the resiliency of populations may be impacted if movements within a population or between populations are limited by linear developments. Effects could take many forms including reduced reproduction if juveniles are unable to disperse or adult males and females are unable to find each other; or reduced survival of individuals if access to ephemeral food sources is affected. However, no data are available that have connected effects of linear development to tortoises at the population level. Effects from linear development at the population level may be occurring but will not be measureable for many decades, if not centuries.	**Low confidence** that tortoise population resiliency is being negatively affected by linear development.	Boarman and Sazaki 1996, p. 1; Boarman *et al*. 1997, p. 57; Boarman 2002, pp. 54–55; Boarman and Sazaki 2006, p. 98; Dieringer 2010, p. 1; Saunders *et al*. 1991, pp. 23–24; Forman and Alexander 1998, entire; Seiler 2001, p. 3; Forman 2000, entire; Averill-Murray and Klug 2000, p. 68; Howland and Rorabaugh 2002, p. 335; Edwards *et al*. 2004, p. 496; van Riper 2014, pp. 13, 83–85; Friggins *et al*. 2012, p. 9, Figure 1-4; Notaro *et al*. 2012, p. 1378
- SCOPE	Linear development occurs within most portions of the species' range-wide distribution but varies significantly in effect to resident or nearby tortoise populations depending on the type of linear development and other characteristics. Most forms of major linear development (interstate highways, canals, railroad beds, etc.) occur on flat or gently sloping terrain, with some exceptions. In these situations, only moderate- to low-suitability habitat is affected. Some linear developments in tortoise habitat also have washes that can act as underpasses, allowing for permeability of some of these linear developments.	**Moderately confident** that linear development has occurred throughout most of the range of the species.	Strittholt *et al*. 2014, p. 159; Rosen *et al*. 2014a, pp. 20-21

THEME: Habitat Fragmentation			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Effects of Stressors: - SPECIES (Rangwide) [REDUNDANCY]	While available data suggest that some rate of tortoise injury or fatality may be associated with linear development there are no data available which document population-level effects on population redundancy from this stressor. Theoretically, if linear development severs connectivity between populations, redundancy could be affected through a reduction or elimination of population rescue (i.e., tortoises moving in from adjacent populations to repopulate an area that has been extirpated); however, as noted above, some of these linear developments are bisected by washes, which can help maintain connectivity. Population impacts may be occurring; however, no data are available that have connected effects of linear development to tortoises at the population level. Effects from linear development at the population level may be occurring but will not be measureable for many decades, if not centuries.	**Low confidence** that tortoise population redundancy is being negatively affected by linear development.	Spang *et al.* 1988, p. 9; Averill-Murray and Klug 2000, p. 68; Edwards *et al.* 2004, p. 486; Averill-Murray and Averill-Murray 2005, p. 71; Saunders *et al*. 1991, pp. 23–24; Forman and Alexander 1998, entire; Seiler 2001, p. 3; Forman 2000, entire; Howland and Rorabaugh 2002, p. 335; Edwards *et al*. 2004, p. 496
Effects of Stressors: - SPECIES (Rangwide) [REPRESENTATION]	Theoretically, if connectivity among populations is affected above a certain (unknown) threshhold, then genetic representation could be degraded over space and time. Special genetic evolutionary traits that may be particularly useful in the future, such as being adapted to naturally hyper-arid zones, may not be allowed to provide potential genetic safeguards to the species as a whole under future climatic conditions. For Sonoran desert tortoises, the concept of genetic isolation is primarily a factor of geographic distance. Research has found relatively high levels of polymorphism and heterozygosity and no evidence of recent loss of genetic diversity, i.e., no evidence of genetic bottlenecking that could result from the lack of mixing (gene exchange) among those Sonoran desert tortoise populations. However, the small sample size and number of alleles (genetic markers) used in the analysis might limit the ability to detect a bottleneck and long generation times, approximately 25 years, combined with relatively recent urban development makes it difficult to assess genetic effects of fragmentation on tortoise populations. Consequently, we would not be able to detect population-level effects from linear development on tortoise genetics for many decades if not centuries which is well-outside our ability to accurately predict.	**Low confidence** that tortoise population representation is being negatively affected by linear development.	Edwards *et al.* 2004, p. 486; Van Devender 2002, p. 16; Spang *et al*. 1988, p. 9; Averill-Murray and Klug 2000, p. 68; Edwards *et al*. 2004, p. 486; Averill-Murray and Averill-Murray 2005, p. 71; Saunders *et al*. 1991, pp. 23–24; Forman and Alexander 1998, entire; Seiler 2001, p. 3; Forman 2000, entire; Howland and Rorabaugh 2002, p. 335; Edwards *et al*. 2004, p. 496
Summary	While available data suggest that some rate of tortoise injury or fatality may be associated with linear development there are no data available which document population-level effects on population redundancy from this stressor.		

THEME: Human-Tortoise Interactions			
[ESA Factor(s): E]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
SOURCE(S)	Human population centers within the range of the tortoise; urban-wildland edge effects such as feral dogs; collection of wild tortoises as pets (Arizona and Mexico) and for food (Mexico) and release of captive tortoise; use of vehicles, OHVs, and ORVs in occupied tortoise habitat; general recreational activities (shooting, hiking, rock crawling, trail bike riding, rock climbing/bouldering, camping) in occupied tortoise habitat.	**Highly confident** that regional cities and towns are largely the source of people that inadvertently or purposefully interact with wild tortoises while involved with outdoor activities.	Sacco, pers. comm., 2007; Simmons, pers. comm., 2012; USBLM 2001, p. 1; Ouren *et al*. 2007, entire; AIDTT 2000, p. 10; Sullivan 2014, entire; Howland and Rorabaugh 2002, p. 340; Grandmaison and Frary 2012, pp. 264–265; Zylstra and Swann 2009, pp. 14-15; AGFD 2010a, pp. 9, 11-12; Jones 2008, p. 66; Hart *et al*. 1992, p. 120; Jones 2010, pers. comm.; AGFD 2014, p. 1; Berry 1986b, pp. 129-130; Zylstra *et al*. 2013, p.113; Averill-Murray and Swann 2002, p. 1; Bury *et al*. 2002, p. 102; Fritts and Jennings 1994, p. 52; Sullivan 2021, p.3
- Activity(ies)	Activities resulting in stressors to the tortoise are associated with human use or presence in tortoise habitats, including recreation, travel, collection, and feral dogs. Correlated with proximity to urban areas.	**Highly confident** that collectively, negative effects to tortoises occur from these activities. **Low confidence** that any single activity on a single occasion will result in an effect to tortoise(s).	Sacco, pers. comm., 2007; Simmons, pers. comm., 2012; USBLM 2001, p. 1; Ouren *et al*. 2007, entire; Kessler 2014; Willard 2014; AIDTT 2000, p. 10; Sullivan 2014, entire; Howland and Rorabaugh 2002, p. 340; Grandmaison and Frary 2012, pp. 264–265; Zylstra and Swann 2009, pp. 14-15; AGFD 2010a, pp. 9, 11-12; Jones 2008, p. 66; Hart *et al*. 1992, p. 120; Jones 2010, pers. comm.; AGFD 2014, p. 1; Berry 1986b, pp. 129-130; Zylstra *et al*. 2013, p.113; Sullivan 2021, p.3
STRESSOR(S)	Collection and disturbance. Above-normal rates of harassment (resulting in bladder voiding) and predation on individual tortoises within the urban-wildland interface, ~~or~~ within occupied habitat that is frequently visited by people from human population centers, or where vehicular access occurs. Tortoises are often documented as walking, resting, basking, and feeding on dirt roads and trails that occur within their home ranges which may increase the potential of tortoises being noticed (and therefore potentially handled or collected) or struck by a vehicle, and therefore may be especially susceptible to this form of stressor. Release of non-genetically pure, captive tortoises into wild populations can comprise genetic integrity of wild populations. Human-caused wildfire ignitions are frequently the result of human activities referenced above.	**Highly Confident** that tortoise injury or fatality occurs via stated mechanisms based on physical, genetic, or photographic evidence for each type of interaction. **Low confidence** on exactly how frequently these mechanisms act on individual tortoises or how many have been affected, or could be affected, over time.	Grandmaison *et al.* 2010, p. 587; Sullivan 2014; Sullivan *et al*. 2014, pp. 116–118; Boarman and Sazaki 1996, p. 1; 2006, p.98; Boarman *et al*. 1997, p. 57; Forman and Alexander 1998, p. 213; Boarman 2002, pp. 54–55; Dieringer 2010, p. 1; Bury et al. 2002, p. 103; Grandmaison and Frary 2012, pp. 264–265; Averill-Murray 2002a, pp. 430, 433–434; Hart *et al*. 1992, p. 120; AGFD 2010a, p. 9; Jones 2010, pers. comm.; AGFD 2014, p. 1; Averill-Murray and Swann 2002, p. 1; Edwards *et al*. 2010, p. 804; Zylstra 2008, p. 12; AGFD 2010a, p. 12; Berry 1986b, pp. 129-130; Zylstra *et al*. 2013, p.113; Sullivan 2021, p.3; Zylstra and Steidl 2021, entire; Zylstra 2021, entire
- Affected Resource(s)	Human interactions with tortoises are primarily direct effects on individual tortoises. Indirect effects of human land uses affect Sonoran desert tortoise habitat suitability, forage base, and vegetatve cover.		
- Exposure of Stressor(s)	Effects primarily occur when tortoises may be surface active; adult females in spring; either sex and all age classes during monsoon and during/after any precipitation at any time of year. Likelihood of exposure to these stressors is attenuated by the fact that tortoises may spend up to 98% of their time in their shelters. Exposure risk is likely to be highest during the spring (female tortoise activity) and in response to precipitation (all tortoises; winter and monsoon). Cool weather associated with precipitation is widely considered optimal for OHV use in the Sonoran Desert due to comfortable temperatures, softened soil, and dust-free conditions; tortoises are also surface active during these periods for rehydration purposes and may be more vulnerable to fatality associated with elevated OHV use within washes (particularly hatchlings and small juveniles that are likely to go unnoticed by riders). Sonoran desert tortoises have often been found walking, resting, basking, and feeding on dirt roads and trails that occur within their home ranges which increases the potential of tortoises being noticed by humans or struck by a vehicle. Adult tortoises are more visibly conspicuous than juveniles or hatchlings and may be disproportionately affected by these activities. Collection of wild tortoises and release of captive tortoises into wild populations may occur at any time and is most likely to occur in habitat adjacent or near to human population centers. In addition, effects from dogs primarily occur in proximity to human populations centers, but can also occur some distance from urban areas as a result of feral dogs. Exposure to human-caused wildfire effects are detailed in the "Altered Fire Regime" tab.	**Somewhat confident** in description of when certain sexes or age groups of tortoises are most likely to interact with humans. **Somewhat confident** in description of where tortoises are most likely to interact with humans.	Sullivan 2014, entire; 2021, entire; Grandmaison *et al*. 2010, p. 587; Sullivan *et al*. 2014, pp. 116–118; Nagy and Medica 1986, p. 79; AIDTT 2000, pp. 9-10
- Immediacy of Stressor(s)	Current and ongoing. Growing human populations over time have resulted in increasing demand for human access to wild areas including occupied Sonoran desert tortoise habitat. Some forms of recreation are increasing in frequency (OHV/ORV use, driving on roads, target shooting) while others may be stable or decrease in frequency over time (hiking, camping). Roads act as the primary avenue for human-tortoise interactions, and we consider all roads (other than primitive, two-track routes) to be permanent on the landscape.	**Highly confident** that over time, as human population grows and urban areas expand into the landscape, the incidence of human-tortoise interactions and the amount of tortoise habitat affected by urban-wildland interface effects will increase.	SSDAN; 2000, entire; Gammage *et al*. 2011, p. 10; Pinal County Comprehensive Plan 2009, p. 109; Howland and Rorabaugh 2002, entire
Changes in Resource(s)	N/A		

THEME: Human-Tortoise Interactions			
[ESA Factor(s): E]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Response to Stressors: - INDIVIDUALS	Injury, fatality (= collection), dehydration.	**Highly confident** that these effects to individual tortoises occur through associations with this stressor as documented in the literature. **Low confidence** that these effects occur in every instance, a majority of instances, some of the time, or infrequently. Frequency difficult to ascertain.	Grandmaison *et al.* 2010, p. 587; Sullivan 2014, entire; 2021, entire; Sullivan *et al*. 2014, pp. 116–118; Boarman and Sazaki 1996, p. 1; 2006, p.98; Boarman et al. 1997, p. 57; Forman and Alexander 1998, p. 213; Boarman 2002, pp. 54–55; Dieringer 2010, p. 1; Bury *et al*. 2002, p. 103; Grandmaison and Frary 2012, pp. 264–265; Averill-Murray 2002a, pp. 430, 433–434; Hart *et al*. 1992, p. 120; AGFD 2010a, pp. 9, 11-12; Jones 2008, p. 66; 2010, pers. comm.; AGFD 2014, p. 1; Averill-Murray and Swann 2002, p. 1; Edwards *et al*. 2010, p. 804; Berry 1986b, pp. 129-130
POPULATION & SPECIES RESPONSES			
Effects of Stressors: - POPULATIONS [RESILIENCY]	Population-level effects from these activities are expected to be most severe when they occur to adult tortoises because adult survivorship is thought to be a primary determinant of population status. Adult survivorship has been shown to improve with increasing distance from urbanized areas, specifically, that the odds of a Sonoran desert tortoise surviving one year increases 8 percent for each 10-km (6.2-mi) increase in distance from a city with a population greater than 10,000 people.	**Moderately Confident**	Howland and Rorabaugh 2002, pp. 339-342; Zylstra *et al*. 2013, p. 113-114; Zylstra and Steidl 2021, entire; Zylstra 2021, entire
- SCOPE	Access and visitation potential into occupied habitat is driven by proximity to urban areas. Wherever roads or trails provide access, these activities could occur. Visitation into occupied tortoise habitat and likelihood of predation from feral dogs are also strongly influenced by proximity to populated human areas. Along the international border with Mexico, road density and use has been growing rapidly for interdiction purposes. Preliminary GIS results: Of the approximately 30,000 square miles of suitable tortoise habitat in Arizona, approximately 24% currently occurs within 10 km of a city with a population of at least 10,000 people and within 20 km of the Phoenix and Tucson metropolotian areas. Sonoran desert tortoises are rarely viewed as a food source in Mexico, and there's little to no evidence that human consumption of tortoises remains a common practice.	**Moderately confident** in description of spatial relationship of stressor to tortoises. **Highly confident** in description of relative percentages of intactness of tortoise habitat.	Averill-Murray and Swann 2002, p. 1; Sayre and Knight 2010, p. 347; Sferra 2010, pers. comm.; USGAO 2009, entire; USBLM 2012d, p.58; 2012c, p. 111; 2013b, p. 80; 2007, p. 83, 85, 115; 2014, p. 1; USNPS 2006, entire; Rosen *et al*. 2014a, p. 20
- SCOPE (Conservation Efforts)	Several, existing conservation measures likely act to reduce effects of human-urban interactions with tortoises. For example, agencies have committed to enforcing regulations and policies that address the presence of feral dogs on their lands, restrict where dogs may be present, or prohibit dogs entirely. Other examples include regulations, policies, and training of staff which include identification of and enforcement against illegal release of captive tortoises. Travel management planning is being undertaken by several agencies. Through this process, illegal routes are either closed or made legal, and all routes (legal or not) are identified and mapped to better facilitate landscape-level management of OHV/ORV use. Additionally, many areas will have OHV access restricted to existing roads and routes. Off-road travel will not be allowed in many of these areas.		See Candidate Conservation Agreement (AIDTT 2015, entire)

THEME: Human-Tortoise Interactions			
[ESA Factor(s): E]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Effects of Stressors: - SPECIES (Rangwide) [REDUNDANCY]	It is unlikely that this stressor alone could affect population redundancy, except for the case where populations exist at low densities, are already threatened by persistent drought, or occur adjacent areas of very high human population densities and commensurate levels of outdoor recreation and visitation. In these examples, loss of adult tortoises may have a population level effect. Based on available information, no tortoise population has been extirpated by this stressor.	**Somewhat Confident** that isolated populations, if under drought stress, may be vulnerable to the effects of human-urban interactions where located near dense, human-populated areas. **High confidence** that this stressor does not uniformly affect tortoises across the geographic extent of their range. **Low Confidence** that this stressor has an appreciable effect on a range-wide scale as this stressor is much less significant in scope and magnitude in Mexico where approximately 40 percent of the species' range occurs.	Averill-Murray and Swann 2002, p. 7, Zylstra *et al* . 2013, p. 113, Zylstra 2008, p. 12; Zylstra and Swann 2009, pp. 14-15; AGFD 2010, pp. 11-12
Effects of Stressors: - SPECIES (Rangwide) [REPRESENTATION]	Low density populations in western and southwestern Arizona and in the Central Gulf Coast subdivsion of the Sonoran Desert in Mexico are generally not exposed to significant human interaction and we don't expect this stressor to significantly influence representation of the species across its range. This potential stressor does not act uniformly across the species range, rather, occurs in varying degrees over space and time, positively correlated with distance to human population centers and degree of access.	**Low confidence** that populations that occur in the most arid portions of the species' range possess unique attributes that make them more resistant to drought stress than populations in other areas of the species' range. **High confidence** that this stressor does not uniformly affect tortoises across the geographic extent of their range. **Low Confidence** that this stressor has an appreciable effect on a range-wide scale as this stressor is much less significant in scope and magnitude in Mexico where approximately 40 percent of the species' range occurs.	Averill-Murray and Swann 2002, p. 7, Zylstra *et al* . 2013, p. 113, Zylstra and Steidl 2021, entire; Zylstra 2008, p. 12; 2021, entire; Zylstra and Swann 2009, pp. 14-15; AGFD 2010a, pp. 11-12
Summary	Effects from human interactions with Sonoran desert tortoises have not resulted in the documented extirpation of any known populations. However, in the case where Sonoran desert tortoise populations exist at low densities, are already threatened by persistent drought, or occur adjacent to areas of very high human population densities with commensurate levels of outdoor recreation and visitation, loss of adults may have a subpopulation-level effect. We included the influences of urban areas in our current and future condition analysis of tortoise population projects		

THEME: Climate Change-Drought			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
SOURCE(S)	Global Climate Change	**Highly Confident** that drought will be more severe in Sonoran desert as a result of climate change over the next 50 to 100 years.	IPCC 2007, entire; 2014, entire; Gonzalez *et al*. 2018, entire
- Activity(ies)	Global climate change is caused by the increase in carbon emissions from numerous activities.		See IPCC publications
STRESSOR(S)	Long-term climate change may alter tortoise habitats through causing more extended droughts and decreased precipitation. Summaries of expected changes: (1) Warmer and fewer cold days and nights over most land areas, (2) warmer and more frequent hot days and nights over most land areas, (3) more frequent warm spells, heat waves, or both over most land areas, (4) changes in precipitation patterns favoring an increased frequency of heavy precipitation events (or proportion of total rainfall from heavy falls) over most areas, and (5) an increase in the area affected by droughts Predicted temperature trends for the Sonoran Ecoregion: (1) Widespread warming trends in winter and spring, (2) decreased frequency of freezing temperatures, (3) lengthening of the freeze-free season, and (4) increased minimum temperatures per winter year Predicted trends in precipitation: (1) Spring time drying, (2) increased precipitation, (3) summer and winter decline in precipitation in short-term (2015-2030), (4) long term (2045-2060) summer precipitation declines will be smaller compared to historic levels; (5) 9 to 12 percent decrease in annual precipitation. Other modeling found that annual precipitation levels in the southern Colorado River Basin could increase during the 2020s, but decrease through the 2050s, with continued decreases through the 2070s. Reduced/altered vegetation cover and reduced vegetation biomass. Reduced or altered abundance or availability of water for drinking. These effects are primarily precipitation-driven. Precipitation is likely the most important ecological variable driving tortoise population trends over time and existing models for precipitation can not reliably predict changes in magnitude, timing, or frequency of precipitation, especially regarding summer rain which is critical for tortoises because of its contribution to the plant community.	**Highly confident** that precipitation is the most important ecological variable affecting tortoise population trends over time. **Low confidence** that current models can accurately predict potential changes in monsoon precipitation due to climate change. **Moderately confident** that total annual precipitation within or throughout the range of the tortoise will be reduced due to climate change. Moderately confident - that total annual precipitation will decrease as a result of climate change. Over what timeframe? **Low confidence** about what predicted changes there may be to monsoon precipitation. Models strongly suggest less total precipitation but largely do not agree whether winter or summer rain cycles will be effected similarly.	IPCC 2007, p. 7; 2014, pp. 39-43; Cook *et al*. 2015, p. 4; Christensen *et al*. 2007, pp. 887-888; Weiss and Overpeck 2005, p. 2075; Notaro *et al*. 2012, pp. 1370, 1379–1380; Weltzin *et al*. 2003, p. 942; Seager *et al*. 2007, entire; Solomon *et al*. 2009, p. 1707; USBOR 2011, p. 56; Hereford *et al.* 2006, p. 25; McAuliffe and Hamerlynck 2010, p. 885; Strittholt *et al*., 2012, p. 11; Van Devender 2002, p. 10; Zylstra *et al*. 2013, pp. 113-114; Zylstra and Steidl 2021, entire; Gonzalez *et al*. 2018, entire
- Affected Resource(s)	Forage plants; water availability	**Highly confident** that climate change driven drought will affect the amount and diversity of forage plant species and affect the frequency and amount of precipitation which ultimately affects the overall availability of surface water for drinking by tortoises.	Averill-Murray *et al*. 2002a, pp. 140, 146; Ernst and Lovich 2009, p. 545; Martin and Van Devender 2002, p. 31

THEME: Climate Change-Drought			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
- Exposure of Stressor(s)	Climate models over the next 50 to 100 years generally agree that winter and spring precipitation may be influenced by climate change; model results regarding the influence of climate change on monsoon precipitation are less certain as monsoons are more difficult to model. Temperature changes occur year-round and may affect when and how long tortoises are surface active, depending on age class (smaller tortoises are more vulnerable to temperature effects). Tortoises of either sex or any age class come out to drink free-standing water in response to precipitation at any time of the year. Winter precipitation drives spring annual growth which is important for reproductive female tortoises to increase energy reserves for egg development; this relationship is less certain in Sonora where other Sonoran desertscrub subdivisions occur. Adult female tortoises may be disproportionately affected by changes in the quantity and quality of spring forage.	**Moderately confident** that climate change may decrease the amount of of winter and spring precipitation. **Low confidence** that monsoon precipitation will decrease due to climate change effects (models in disagreement). **Moderately confident** that changes in temperature associated with climate change will occur throughout the year. **Highly confident** that tortoises of either sex or any age class emerge to drink free-standing water as it becomes available at any time of the year. **Highly confident** that changes to winter precipitation will affect spring growth of annuals in Arizona and may disproportionately affect adult female tortoises which are largely the only sex and age class of tortoises know to be more regularly surface active during the spring. **Somewhat confident** that changes to winter precipitation will affect spring growth of annuals in Sonora and may disproportionately affect adult female tortoises which are largely the only sex and age class of tortoises know to be more regularly surface active during the spring.	IPCC 2007, p. 7; 2014, pp. 39-43; Cook *et al*. 2015, p. 4; Christensen *et al*. 2007, pp. 887-888; Weiss and Overpeck 2005, p. 2075; Notaro *et al*. 2012, pp. 1370, 1379–1380; Weltzin *et al*. 2003, p. 942; Strittholt *et al*. 2012, entire; Seager *et al*. 2007, entire; Solomon *et al*. 2009, p. 1707; USBOR 2011, p. 56; Shryock *et al*. 2015, p. 39; Sullivan *et al*. 2014, pp. 116–118; Averill-Murray and Klug 2000, p. 66; Bailey *et al*. 1995, p. 367; Esque *et al*. 2002, p. 324; Gonzalez *et al.* 2018, entire

THEME: Climate Change-Drought			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
- Immediacy of Stressor(s)	Climate change is occurring currently and is expected to continue into the future.	**Highly Confident**	IPCC 2007, p. 7; 2014, pp. 39-43; Cook *et al*. 2015, p. 4; Christensen *et al*. 2007, pp. 887-888; Weiss and Overpeck 2005, p. 2075; Notaro *et al*. 2012, pp. 1370, 1379–1380; Weltzin *et al*. 2003, p. 942; Gonzales *et al*. 2018, entire
Changes in Resource(s)	Decreasing annual precipitation (predicted declines in winter precipitation); summer rain less predictable (few storms of little rain or frequent storms of severe nature and significant flooding). Decreasing annual precipitation may affect the germination of annuals or regrowth of perennials. Decreased precipitation will reduce the frequency of access to free-standing water by tortoises for drinking.	**Moderately confident** that climate change may decrease the amount of winter and spring precipitation. **Low confidence** that monsoon precipitation will decrease due to climate change effects (models in disagreement). **Highly confident** that decreasing annual precipitation will reduce the frequency of when tortoises of either sex or any age class can emerge to drink free-standing water. **Moderately confident** that a decrease in annual precipitation will affect the forage base of tortoises.	IPCC 2007, p. 7; 2014, pp. 39-43; Cook *et al*. 2015, p. 4; Christensen *et al*. 2007, pp. 887-888; Weiss and Overpeck 2005, p. 2075; Notaro *et al*. 2012, pp. 1370, 1379–1380; Weltzin *et al*. 2003, p. 942; Sullivan *et al*. 2014, pp. 116–118; Oftedal 2002, p. 199; van Riper 2014, pp. 83-85; Gonzalez *et al.* 2018, entire

THEME: Climate Change-Drought			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Response to Stressors: - INDIVIDUALS	Desert tortoises evolved in arid conditions, and possess numerous physiological and behavioral adaptations to survive some degree of drought. Individuals may suffer from drought stress if precipitation does not occur at a high enough frequency to provide drinking opportunities. Timing and amount of precipitation affects the forage base positively or negatively depending on the photosynthetic pathway of plant species. Persistent drought, and subsequent changes in the tortoise forage base, can affect blood chemistry and water metabolism, reduce or eliminate the thymus and fat stores, and result in skeletal muscle and liver atrophy in desert tortoises. Prolonged drought conditions would force the tortoise to eat less-armored cacti and whatever nonwoody senescent material that have not disintegrated or been blown away. Prolonged drought coupled with low nutrition forage would mean lower growth rates, lower reproductive output, lower survivorship, and increased stress on bladder physiology. In years of low winter rainfall, winter annuals do not germinate which may affect the amount and diversity of forage species during the spring. However some species of small weedy annuals as well as herbaceous perennials do germinate offering some foraging opportunities. In years of high summer rainfall, characterized as highly localized events, a vast diversity of summer annuals and herbaceous perennials respond favorably offering good forage in areas that receive high precipitation. Rising average annual temperatures could affect sex-ratios during embryo development; biasing in favor of females. Minor increases in temperatures could have a beneficial effect on tortoise populations as a single male can fertilize numerous females.	**Highly confident** that tortoises evolved in arid conditions and possess numerous physiological and behavioral adaptations to survive some degree of drought. **Highly confident** that decreasing annual precipitation would reduce the number of opportunities tortoises have to drink free-standing water which may induce drought stress. **Moderately confident** on described physical effects of drought stress on individual tortoises; many variables involved. **Moderately confident** that the season, frequency, and amount of precipitation could be influenced by climate change and in turn, affect the forage base of tortoises both positively and negatively. **Somewhat confident** that predicted rises in air temperatures associated with climate change could have an effect on sex determination of tortoise embryos resulting in a sex bias within affected regions of their distribution.	Schmidt-Nelson and Bentley 1966, p. 911; Peterson 1996a, pp. 1325, 1831; Christopher 1999, p. 365; Duda *et al*. 1999, p. 1188; AIDTT 2000, p. 4; Berry *et al*. 2002, pp. 443–446; Dickinson *et al*. 2002, pp. 251–252; Oftedal 2002, pp. 199-200; Walther *et al*. 2002, pp. 393–394; Hereford *et al*. 2006, p. 25; Zylstra, *et al*. 2013, p.114; Zylstra and Steidl 2021, entire; Averill-Murray *et al*. 2002a, p. 146; Ernst and Lovich 2009, p. 545

THEME: Climate Change-Drought			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
POPULATION & SPECIES RESPONSES			
Effects of Stressors: - POPULATIONS [RESILIENCY]	Drought could result in demonstrable population declines over a short period of time. Even short-term variations in rainfall can have prolonged effects on a long-lived species because of impacts to reproduction, recruitment, and annual survival. In populations that have already experienced localized but prolonged drought adult Sonoran desert tortoise survival decreased 10-20 percent, and abundance of adults was reduced by ≥50 percent. Despite the declines, annual survival has since increased in these populations and the rate of change in population size was found to be greater than 1 indicating cumulative population growth over the range of the species in Arizona. Climate change scenarios project that drought severity and frequency will increase during 2035-2060, which is predicted to reduce adult annual survival by 3 percent during that time period, compared to the survival during 1987-2008. Tortoise mortality statistics from Mexico were positively correlated with temperature and negatively correlated with elevation and precipitation. There is concern that Sonoran desert tortoise adaptation processes will not be able to keep pace with the relatively fast-paced changes predicted as a result of climate change in the near- or mid-term. Considering the generation times of Sonoran desert tortoises and the observed rate of increase in global temperatures, the "evolutionary adaptation of tortoise physiology and behavior is a remote possibility." Tortoises in general have historically been found to be "weak dispersers" at large scales. In the case of Sonoran desert tortoises, steep transitions to northern, higher-elevation habitat may hamper the species' movement into these regions and resultant temperature regimes in these new areas may still be colder than what is physiologically-suitable, even under the effect of climate change. However, other responses of the Sonoran desert tortoise to climate change are possible such as (1) changing behavior in response to climatic stress or population declines, or (2) density-dependent factors allowing population persistence at lower abundance. With respect to the former, it is possible that increasing drought coupled with increasing temperatures may select for a behavioral shift in shelter site use in Sonoran desert tortoises, favoring the more humidity and temperature buffered earthen burrows over the less-buffered rock shelter sites. The most arid portions of the species current range include western and southwestern Arizona and in the Central Gulf Coast subdivision of Sonoran Desert in Mexico. Populations that currently occur in these most arid portions of the range are already at lowered densities and are considered to have added vulnerability to climate change-induced drought, could be significantly affected, and may become locally extirpated should multi-year drought conditions of sufficient magnitude become realized. Other populations to the east and northeast may be able to migrate to higher elevation habitat that may simultaneously by converting into desertscrub, to counter general trends of warming and drying. The ability (speed) of the species to evolve/migrate in keeping-up with predicted habitat shifts in response to climate change may significantly influence the viability of the species over time.	**Moderately confident** that drought associated with climate change could negatively affect adult survival rates within tortoise populations which is a fundamental driver in overall population resiliency over time, potentially leading to extirpation at the local population level should drought conditions persist for multiple years in the same area. **Low confidence** in predicting potential shifts in behavioral/evolutionary responses of tortoises to climate change. **Moderate confidence** that tortoise populations in the most arid portions of the species range may have higher vulnerability of local extirpation from drought-related climate change than populations that occur in less-arid portions of the range. **Somewhat confident** that tortoise populations along the eastern and northeastern portion of its range may be able to mitigate climate change effects by migrating up in elevation and latitude.	van Riper 2014, pp. 13, 83–85; Friggins *et al*. 2012, p. 9, Figure 1-4; Notaro *et al*. 2012, p. 1378; Weiss and Overpeck 2005, p. 2075; Galbraith and Price 2009, p. 80; Zylstra, *et al*. 2013, pp.113-114; Zylstra and Steidl 2021, entire; Skelly *et al*. 2007, pp. 1353–1355; Rosen *et al*. 2014a, pp. 37-38; 2014b, p. 56; 2014c, p. 88; USGS 2005, entire

THEME: Climate Change-Drought			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
- SCOPE	Range-wide exposure to effects of climate change with regional variability in magnitude over space and time.	**Highly Confident**	Seager *et al.* 2007, entire; Solomon et al. 2009, p. 1707; Overpeck and Udall 2010, p. 1642; Gonzalez *et al*. 2018, entire
Effects of Stressors: - SPECIES (Rangwide) [REDUNDANCY]	Increasing drought severity or extent could result in demonstrable population effects over the next 100 years and beyond. Climate change-driven drought increases could affect the persistence of some tortoise populations in the most arid portions of their range (western and southwestern Arizona and in the Central Coast subdivsion of the Sonoran Desert in Mexico) where connectivity is already challenged by expansive areas of very low habitat suitability which could affect species redundancy. Populations that can migrate to higher elevation habitats or more northerly latitudes may be able to remain viable under changing climate conditions. However, Sonoran desert tortoise survival rates are strongly influenced by severe droughts.	**Moderately confident** that drought associated with climate change could negatively affect adult survival rates within tortoise populations which is a fundamental driver in overall population viability over time, potentially leading to extirpation at the local population level and potential effects to species redundancy, should drought conditions persist for multiple years in the same area. **Moderate confidence** that tortoise populations in the most arid portions of the species range may have higher vulnerability of local extirpation from drought-related climate change than populations that occur in less-arid portions of the range. **Somewhat confident** that tortoise populations along the eastern and northeastern protion of its range may be able to mitigate climate change effects by migrating up in elevation and latitude.	van Riper 2014, pp. 13, 83–85; Friggins *et al*. 2012, p. 9, Figure 1-4; Notaro *et al*. 2012, p. 1378; Zylstra *et al*. 2013, p.114; Hatten et al. 2016, p. 17, Zystra and Steidl 2021, entire

THEME: Climate Change-Drought			
[ESA Factor(s): A]	**Analysis**	**Confidence / Uncertainty**	**Supporting Information**
Effects of Stressors: - SPECIES (Rangwide) [REPRESENTATION]	Increasing drought severity or extent could result in demonstrable population effects over the next 100 years and beyond. Increased regional drought severity could affect the persistence of some tortoise populations particularly in the most arid portions of their range where connectivity is already challenged by expansive areas of very low habitat suitability. Populations that can migrate to higher elevation habitats may be able to remain viable under changing climate conditions. The latter example of populations are expected to retain some level of genetic connectivity with each other depending on the effect of linear development at local-regional scales.	**Moderately confident** that drought associated with climate change could negatively affect adult survival rates within tortoise populations which is a fundamental driver in overall population viability over time, potentially leading to extirpation at the local population level and potential effects to species redundancy, should drought conditions persist for multiple years in the same area. **Moderate confidence** that tortoise populations in the most arid portions of the species range may have higher vulnerability of local extirpation from drought-related climate change than populations that occur in less-arid portions of the range. **Somewhat confident** that tortoise populations along the eastern and northeastern portion of its range may be able to mitigate climate change effects by migrating up in elevation and latitude.	Zylstra *et al*. 2013, pp.114-115; Zylstra and Steidl 2021, entire
Summary	Our analysis of the future condition of the Sonoran desert tortoise incorporated the potential effects of climate change by using projected habitat suitability estimates that incorporated climate changes in habitat variables and by assessing affects on increasing drought conditions on Sonoran desert tortoise survival rates		

Appendix D
Documentation of Conservation Activities Undertaken by Parties to the 2015 Sonoran Desert Tortoise CCA

Several actions described in the Candidate Conservation Agreement (CCA) have been implemented by the Parties since the CCA was signed in 2015. Key conservation actions are being tracked as they are implemented through the CCA.

Bureau of Land Management (BLM)

BLM is party to the CCA and administers public lands within the range of the Sonoran desert tortoise through 10 approved Resource Management Plans (RMP) for seven Field Offices and three National Monuments. Implementation of these RMPs in Sonoran desert tortoise habitat has resulted in consistent proactive conservation of Sonoran desert tortoise habitat and reduction of threats. These RMPs contain resource allocations, desired condition objectives and management actions that conserve the Sonoran desert tortoise and habitat on public lands. These planning decisions include, but are not limited to:

- Designation of Areas of Critical Environmental Concern, Wildlife Habitat Areas, Tortoise Habitat Categories and Areas Managed for Wilderness Characteristics which contain management prescriptions or use restrictions that conserve Sonoran desert tortoise habitat.
- Desired Plant Community, Desired Future Condition, and habitat connectivity objectives that address the habitat needs of the Sonoran desert tortoise.
- Management decisions to prioritize management of Sonoran desert tortoise habitat and implement conservation activities including, vehicle route closure and reclamation, invasive plant treatments and maintenance or restoration of habitat connectivity.
- Policy objectives to emphasize and give priority to management of Sonoran desert tortoise populations and habitat in the event of conflicting resource management objectives, while managing for no net loss in quantity and quality of Sonoran desert tortoise habitat to the extent practicable and using offsite mitigation (compensation) for unavoidable residual habitat loss.

Through BLM’s NEPA process for evaluating and permitting land and resource management activities, activities are evaluated for conformance with management objectives contained in relevant RMPs. In addition, standard operating procedures are described in the RMPs that direct BLM managers to:

- Inventory and evaluate all proposed activities on a case-by-case basis to determine potential impacts to the Sonoran desert tortoise and habitat.

- Avoid, minimize or mitigate impacts associated with all BLM authorized activities including mineral material sales, rights-of-way, recreational use, travel management, and livestock grazing through project design and modifications to allowable uses in order to achieve Sonoran desert tortoise management objectives.
- Mitigate impacts to Sonoran desert tortoise from locatable minerals activities to the extent allowable under 43 CFR Subpart 3809.
- Evaluate Sonoran desert tortoise habitat conditions relative to established objectives when considering livestock grazing permit renewal and adjust use to insure achievement or progress toward objectives.
- Implement full suppression of wildfire within Sonoran desert tortoise habitat and minimize impacts associated with fire suppression activities.
- Work with partners to control or eradicate invasive plant and wildlife species to achieve desired conditions.
- Educate the public land users on Sonoran desert tortoise conservation to increase compliance with regulations and minimize impacts from recreational activities.
- Monitor long term population trend range-wide and pursue alternative population monitoring methodologies to inform management.

A focus on long-term monitoring plots (LTMPs) has resulted in the BLM funding and completing surveys within 11 of the 17 of these plots. Those data have been made available for this SSA. Additionally, the BLM Kingman Field Office and AGFD Contract Branch are inventorying other areas for Sonoran desert tortoises. Thirty fires have occurred within the range of Sonoran desert tortoise habitat on BLM-managed lands across Arizona since 2015; however, not all of these fires were in Sonoran desert tortoise habitat. Based on reporting metrics, some of these fires occurred in Mohave desert tortoise habitat, but the metrics are not detailed enough to distinguish habitat differences. Sonoran desert tortoises continue to be a resource priority for all land management agencies when responding to wildfires and the following post-fire rehabilitation.

Loss of Sonoran desert tortoise habitat to large scale development has been limited on Federal lands. All actions seeking authorization to disturb Sonoran desert tortoise habitat on BLM-managed lands include conservation stipulations and best management practices to reduce the impacts to Sonoran desert tortoise habitat. Only one wind project was authorized on BLM-managed lands in since 2015; however, this wind project is in what we consider Mohave desert tortoise habitat north of Kingman, Arizona. No large-scale projects have been authorized on BLM-managed lands that have resulted in increased habitat fragmentation or conversion of Sonoran desert habitat.

Arizona State Agencies

Arizona Department of Transportation (ADOT) has worked with several land management agencies to implement control and eradication projects associated with reducing the presence and potential spreads of invasive weeds along ADOT Rights of Way (ROW) throughout the range of the Sonoran desert tortoise (ADOT 2021, entire). Additionally, ADOT has worked with partners, including AGFD, to design Sonoran desert tortoise-friendly road crossings for new roadway

projects. Five bridges and 36 culverts were designed and installed on the South Mountain Freeway project, which was completed in 2020 (ADOT 2021, pp. 6–8). ADOT also installed exclusion fencing to direct Sonoran desert tortoises and other wildlife to these bridges and culverts along the South Mountain Freeway project, as well as installing wildlife friendly cattleguards to aid in wildlife, including Sonoran desert tortoises, crossing busy intersections (ADOT 2021, pp. 12–14). In 2016, AGFD partnered with ADOT Environmental Planning Group, the Coalition for Sonoran Desert Protection, and Sky Island Alliance to evaluate the effectiveness of crossing structures installed along State Route 77 using integrated video and still camera surveillance. In addition, AGFD is affixed VHF transmitters and GPS loggers to monitor movements of Sonoran desert tortoise and activity centers in relation to State Route 77.

AGFD continues monitoring the LTMPs annually and also includes five vegetation transects per plot per year to monitor the habitat conditions for the Sonoran desert tortoise, as well as monitor for the presence of nonnative vegetation. AGFD continues to provide all projects within Sonoran desert tortoise habitat guidelines to survey for and handle them. No Sonoran desert tortoises were moved from within any project footprints, including development and roadway projects. Additionally, AGFD continues to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Military Installations

The Arizona Army National Guard (AZARNG) continues to work with AGFD to monitor Sonoran desert tortoise monitoring plots on all of their facilities. Monitoring included the presence of nonnative species, which leads to efforts to reduce harmful nonnative vegetation such as buffelgrass, starthistle, and Sahara mustard. AZARNG continues to implement best management practices into their activities that are designed to conserve and protect Sonoran desert tortoises and their habitat. These best management practices are detailed and carried out in accordance with AZARNG’s Integrated Natural Resource Management Plan (INRMP).

Luke Air Force Base and the Barry M Goldwater Range (BMGR) also continue to implement best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in accordance with their INRMPs into its activities. Sonoran desert tortoise is considered a conservation priority for these INRMPs. Additionally, the BMGR and Luke Air Force Base have implemented nonnative species control measures. Nonnative species prevention and control efforts between 2015–2020 have included mapping of buffelgrass (primarily along highway 85); herbicide treatment of multiple species (buffelgrass, fountain grass, Sahara mustard, and bitter cucumber gourd (*Citrullus colocynthis*)); involvement in a regional mapping effort using a smartphone app (GIS Cloud); involvement in the Sonoran Desert Cooperative Weed Management Area (CWMA) group; and development of a 2019 brochure "How to Identify and Report Invasive Weeds." The number of miles of road for BMGR East were calculated in 2018 to support the 2018 INRMP revision. From 2012 to 2018 the total miles of road within the BMGR East designated road system was reduced from 756 miles to 744 miles, including roads within Sonoran desert tortoise habitat.

Marine Corps Air Station Yuma (MCAS) also continues to implement best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in

accordance with its INRMP into MCAS activities. Sonoran desert tortoise is considered a conservation priority for this INRMP. Additionally, MCAS has partnered with neighboring National Park Service (NPS) offices to implement nonnative species control measures. Nonnative species prevention and control efforts between have included mapping of buffelgrass; herbicide treatment of multiple species, including buffelgrass and Sahara mustard. From 2012 to 2020 numerous redundant roads have been closed, including roads within Sonoran desert tortoise habitat. Additionally, MCAS continues to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Similar to the above military installations, the U.S. Army Yuma Proving Grounds (YPG) also continues to implement best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in accordance its INRMP into YPG activities. Sonoran desert tortoise is considered a conservation priority for this INRMP. Additionally, MCAS has partnered with neighboring USFWS and BLM offices to implement nonnative species control measures. Nonnative species prevention and control efforts between have included mapping of buffelgrass and herbicide treatment of buffelgrass on YPG ranges. From 2012 to 2020 numerous redundant roads have been closed, including roads within Sonoran desert tortoise habitat. Additionally, MCAS continues to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Other Federal Land Management Agencies

Kofa National Wildlife Refuge (KNWR) also continues to implement best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in accordance with its Resource Management Plan (RMP) into KNWR activities. Sonoran desert tortoise is considered a conservation priority for this RMP. KNWR has implemented nonnative species control measures. Nonnative species prevention and control efforts between have included mapping of buffelgrass, starthistle, and African daisy, as well as herbicide treatment for these species. From 2012 to 2020 numerous redundant roads have been closed, including roads within Sonoran desert tortoise habitat. Additionally, MCAS continues to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Coronado National Forest (CNF) continues to implement best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in accordance with its Land and Resource Management Plan (LRMP) into CNF activities. Sonoran desert tortoise is considered a Forest Service Sensitive Species and is, therefore, a conservation priority for this LRMP. CNF has implemented nonnative species control measures. Nonnative species prevention and control efforts between have included mapping of buffelgrass, as well as herbicide treatment for this species. CNF estimates that an average of 1,536 acres of buffelgrass was treated in Sonoran Desert habitat between 2015 and 2019 on two Ranger Districts. CNF is also assessing vehicle routes to determine which route to close or leave open, including routes within Sonoran desert tortoise habitat. Additionally, CNF continues to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Tonto National Forest (TNF) continues to implement best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in accordance with its Land and Resource Management Plan (LRMP) into TNF activities. Similar to the CNF, Sonoran desert tortoise is considered a Forest Service Sensitive Species and is, therefore, a conservation priority for this LRMP. TNF has implemented nonnative species control measures. Nonnative species prevention and control efforts between have included mapping of buffelgrass and fountain grass, as well as implementing herbicide treatment for this species. TNF inventoried, mapped, and removed buffelgrass and fountain grass from three locations on the Mesa Ranger District. Sites. TNF removed 406 acres at Jacob's Crosscut, 76 acres at Heiroglyphics/Lost Goldmine, and 31 acres at Wind Cave/Pass Mountain. Plants were manually removed and retreated over several years. TNF has improved an estimated 70,000 acres of terrestrial habitat through the installation of pipe rail and OHV staging areas throughout multiple highly used OHV areas (Wildcat, Four Peaks, Lower Sycamore, Sugarloaf, and Bulldog) since 2015. Approximately 223 miles of routes (<4,200 feet in elevation) have been selected to be decommissioned through the TNF Travel Management Planning process. TNF has mitigated 21 abandoned mining land features. Mitigations have included backfilling and tortoise-proof steel grates and gates. Additionally, CNF continues to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Bureau of Reclamation (Reclamation) contracted out a population study of Sonoran desert tortoise, along with a habitat assessment, at Lake Pleasant Regional Park. The study reported that "based on tortoise and sign detections and estimated tortoise abundance and density, the population of tortoises within the Park appears to be robust in areas where they are currently present, but tortoises may occupy less area within the Park than in 2003." The control or eradication of invasive plant species occurs along the 336-mile Central Arizona Project (CAP) Canal. The Central Arizona Water Conservation District (CAWCD) manages the CAP canal on behalf of Reclamation which includes responsibility for the annual control of invasive plant species. Annual management efforts are focused along the right-of-way of the CAP canal to primarily prevent interference with its operations. Reclamation's land manager at Lake Pleasant Regional Park, Maricopa County Parks and Recreation Department, is currently working on developing an Integrated Pest Management plan. In the meantime, Maricopa County Parks and Recreation Department periodically controls invasive, herbaceous weeds within the Park through spot treatments, applying a manual method. Unfortunately, no data are available regarding the acreage of these treatment areas. Reclamation also requires the implementation of best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in accordance with standard Reclamation policies for all Reclamation authorized activities. Additionally, Reclamation works with its partners and land managers to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Organ Pipe Cactus National Monument (OPCNM) continues to implement best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in accordance with its Resource Management Plan (RMP) into OPCNM activities. OPCNM reported approximately 3,300 acres of buffelgrass in 2019 and treated approximately eight acres of it. OPCNM continues to monitor off road vehicle (ORV) use across the park. This monitoring indicates a decrease in ORV tracks from 2017 to 2019. OPCNM staff continue to monitor

established plots and survey transects for Sonoran desert tortoise. Survey transects, occupancy plots, and casual observations suggest that tortoises occur throughout the monument in suitable habitat but local population viability is unknown. Like other CCA Parties above, OPCNM continues to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Saguaro National Park (SNP) continues to implement best management practices that are designed to conserve and protect Sonoran desert tortoises and their habitat in accordance with its Resource Management Plan (RMP) into SNP activities. SNP has aggressively treated areas affected by buffelgrass and other invasive grasses with a combination of methods including mechanical and chemical treatments by field crews and volunteers and aerial herbicide application with both boom and spot sprayer equipped helicopters. Treatment is partially dependent on the timing and intensity of monsoon rains, with field crews treating 40-60 acres of buffelgrass per year over the past five years. In the same period, an average of 400-500 acres were treated aerially each year with a peak of nearly 700 acres in 2018. Since establishment of the CCA, the SNP has mitigated 59 abandoned mining land features. Mitigations have included backfilling and tortoise-proof steel grates and gates. SNP is monitoring a variety of general environmental variables, including upland vegetation, with the NPS Sonoran Desert Inventory and Monitoring Network. SNP staff are seeking funds to conduct another round of monitoring of tortoises during 2021–2022, but have not yet been successful. The park cooperates with monitoring efforts by Pima County in adjacent Tucson Mountain Park. Additionally, SNP continues to implement a strong public outreach program aimed at educating the public regarding the need to protect and conserve Sonoran desert tortoise.

Local Activities

In addition to the CAA conservation activities described above, several communities in southeastern Arizona have developed Habitat Conservation Plans (HCPs). Among these are the Sonoran Desert Conservation Plan (Multi-Species Conservation Plan) developed by Pima County (Pima County 2010), the Town of Marana Habitat Conservation Plan, and the City of Tucson's Avra Valley and Southlands Habitat Conservation Plans. Each of these four HCP efforts identified the Sonoran desert tortoise as one of the covered species under their prospective plans. Since the initiation of these planning efforts, Pima County has completed their Multi-Species Conservation plan and was issued a USFWS permit in 2016. Implementation is ongoing and includes conservation measures for the Sonoran desert tortoise such as ongoing survey and monitoring and habitat acquisition and protection. These actions occur throughout Pima County-managed lands and significantly contribute to the conservation of the Sonoran desert tortoise. The City of Tucson has focused conservation planning for the Avra Valley and this HCP remains in progress and should be finalized soon. Progress on the Southlands HCP has been put on hold, as has the Town of Marana HCP. Currently, substantial habitat for Sonoran desert tortoise remains within the City of Tucson and Town of Marana jurisdictions and together with federally-managed natural preserves in adjacent areas such as Saguaro National Park and Ironwood National Monument, may present further opportunities for Sonoran desert tortoise conservation, should these municipalities offer cooperation on actions within their jurisdictions.

Appendix E
Stochastic Simulation Model Report for the Sonoran Desert Tortoise Species Status Assessment (SSA)

Summary

We updated the demographic population viability model developed by McGowan *et al*. (2017, entire) to represent Sonoran desert tortoise analysis units in Arizona, U.S. and Sonora, Mexico. The model was based on the best available demographic data and published analyses, and it included parametric uncertainty and environmental variation as sources of stochasticity in the projections. The model predicts the probability of quasi-extinction (i.e., the probability of abundance declining to less than a pre-determined abundance threshold) over 125 years under current habitat and plausible future conditions. For the purposes of this model and as part of the species status assessment, we are treating the species as two analysis units, one in Arizona, U.S., and one in Sonora, Mexico.

Life Cycle Model Structure

We built a female-only, stage-structured matrix model to reflect the Sonoran desert tortoise life cycle (Figure 3). The conceptual model of the tortoise's life cycle was elicited from taxa experts, based on published literature (Van Devender 2002, entire; Rostal *et al.* 2014, entire), and considering Mohave desert tortoise population models (Darst *et al*. 2013, entire). The life cycle diagram presents three main life stages (Adults, young juveniles (J_1) and older juveniles (J_2)). Young juveniles, once hatched, can survive each year and remain in the young juvenile age class for approximately 5 years. Little is known about the habits or survival rates of young juveniles because they are very hard to detect and study. However, this life stage, given its size (<40 mm), is likely the most susceptible to predation and other causes of mortality (McCoy *et al*. 2014, entire). Older juveniles remain in that age class for 10 or 12 years (until approximately the age of 15) and then transition into the breeding adult age class. Survival rates of newly hatched tortoises in their first year are very low. McCoy *et al*. (2014, entire) suggest that, for North American tortoises in general, first year survival is as low as 10%, and it increases about 1-2% annually thereafter, until the animals are in the subadult or older juvenile stage. Adult Sonoran desert tortoises have very high annual survival rates, with annual female survival rates (0.94-0.98) being slightly higher than males (0.93–0.97) (Zylstra and Steidl 2021, p. 6). Sonoran desert tortoises can live for many years as adults. Approximately 52% of females will breed in any given year and the females lay small clutches of approximately 5 eggs (~2.5 female eggs per female; Campbell *et al.* 2014, p. 2), but many nests fail before hatching (McCoy *et al.* 2014, entire).

In our simulation model we set mean annual survival ($\bar{S}^{A}$) to 0.96 (SD = 0.01), based on the results of Zylstra and Steidl (2021, p. 6). We created a probability of breeding parameter (P_b) with mean of 0.52 (SD = 0.06) and a fecundity or clutch size parameter with mean of 2.5 eggs per female (SD = 0.5; Campbell *et al.* 2014, p. 5). Zylstra and Steidl (2021, p. 6) estimated annual survival of older juveniles ($\bar{S}^{J2}$) to average 0.82 (SD = 0.03), but they had limited data for these parameter estimates. Young juvenile survival rates were largely unknown because of the difficulties in studying the early life stages. Experts agreed that generation time for Sonoran

desert tortoises is approximately 25 years. McGowan *et al*. (2017) used the *PopBio* package (Stubben and Milligan 2007, entire) in the program R v4.1.0 (R Core Development Team 2021) to test different values for the lesser known parameters ($\bar{S}^{J1}$, $\bar{T}^{12}$) to see what values led to the estimated generation time of approximately 25 years. The "generation.time" function calculates the expected average time between generations, defined as the average age at which a female produces her median offspring (Stubben and Milligan 2007, pp. 6–7). Using this approach, McGowan *et al*. (2017, p. 121) adjusted mean parameter values in the model and set mean young juvenile survival ($\bar{S}^{J1}$) at 0.01 (SD = 0.00012), and younger to older juvenile transition ($\bar{T}^{12}$) at 0.083 (SD = 0.00032). We used McGowan *et al*. (2017, p. 121) estimates for $\bar{S}^{J1}$ and $\bar{T}^{12}$ with the updated older juvenile and adult demographic parameters (Zylstra and 2021, p. 6). In our model the $\bar{S}^{J1}$ parameter is very low, but it includes nest survival (hatching probability) and the very low survival rates of the first few years of life (McCoy *et al*. 2014, entire). We set older juvenile survival and older juvenile to adult transition ($\bar{T}^{2A}$) to sum to the Zylstra and Steidl (2021, p. 6) annual survival estimate of 0.82. Mean older juvenile survival ($\bar{S}^{J2}$) was set to 0.75 and the transition rate to adulthood ($\bar{T}^{2A}$) was set to 0.07. With these parameters we constructed a projection matrix as follows:

$$\begin{bmatrix} N_{t+1}^{J1} \\ N_{t+1}^{J2} \\ N_{t+1}^{A} \end{bmatrix} = \begin{bmatrix} S_t^{J1} & 0 & (F_t * P_b) \\ T_t^{12} & S_t^{J2} & 0 \\ 0 & T_t^{2A} & S_t^{A} \end{bmatrix} * \begin{bmatrix} N_t^{J1} \\ N_t^{J2} \\ N_t^{A} \end{bmatrix}$$

Where:

N_t^{J1} = Young juvenile (J_1) abundance at time *t (or t+1)*
N_t^{J2} = Older juvenile (J_2) abundance at time *t (or t+1)*
N_t^{A} = Adult (*A*) abundance at time *t (or t+1)*
F_t = Fecundity at time *t*
P_b = Probability of breeding for adult females
S_t^{J1} = Young juvenile survival rate at time *t*
S_t^{J2} = Older juvenile survival rate at time *t*
S_t^{A} = Adult survival rate at time *t*
T_t^{12} = Young juvenile to older juvenile transition rate at time *t*
T_t^{2A} = Older juvenile to adult transition rate at time *t*

We incorporated the projection into a stochastic simulation model that replicated the population many times and projected the population a set number of years into the future. In the model survival rates, inter-size class transition rates, and proportion of females that breed were drawn from beta distribution derived from the mean and standard deviations described above, while fecundity rates were drawn from a log normal distribution. We used the methods described by McGowan *et al*. (2011, entire) to incorporate parametric uncertainty into the adult survival parameters since population growth is most sensitive to that parameter. This method is widely used within PVA models (McGowan *et al.* 2017, entire; Tucker *et al.* 2021, entire). This involves using the replication loop of the model to pick an average adult survival rate for the population that serves as the mean value for each year in that replicate of the population. Under this approach each replicate of the population projection has a different mean value of adult survival,

and those values are drawn from a beta distribution based on the empirically estimated mean and sampling variance. The model output mean population growth rate, abundance, and the proportion of replicates that went quasi-extinct. We used a quasi-extinction threshold of 2% of the starting population size for each replicate.

Density Estimation & Starting Population Sizes

Although estimates of Sonoran desert tortoise abundance exist at smaller spatial scales there is not a range-wide estimate for adult Sonoran desert tortoise to use as a starting population size in our model. We used information available at monitoring sites to estimate adult tortoise densities in differing habitat suitability areas and extrapolated those densities across the species' range to arrive at total population estimates in each analysis unit.

Survey Information

- We used information from the Arizona Game and Fish Department's (AGFD) and Bureau of Land Management's (BLM) long-term monitoring plots (LTMP). There are 17 LTMP sites that have been surveyed using capture-mark-recapture methods from 1987 to present (Dockens *et al.* 2011, entire; Woodman *et al.* 2009, entire; Hoffman *et al.* 2017, entire; Rubke *et al.*2017a, entire; Rubke *et al.* 2018a, entire; Rubke and O'Donnell 2019, entire; Rubke and O'Donnell 2020a, entire; Rubke and O'Donnell 2020b, entire; Rubke and O'Donnell 2021, entire). Each LTMP is surveyed multiple times during the summer monsoon season (August through October) when Sonoran desert tortoise are most active using standard survey techniques to search for juvenile and adult Sonoran desert tortoise (Zylstra *et al*. 2013, pp. 108–109). The monitoring data included Lincoln-Peterson abundance index estimates for all plots over the last 30 years. For more information on the specific techniques related to monitoring surveys or estimating Lincoln-Peterson abundance, please refer to the LTMP reports (Dockens *et al.* 2011, entire; Woodman *et al.* 2009, entire; Hoffman *et al.* 2017, entire; Rubke *et al.*2017a, entire; Rubke *et al.* 2018a, entire; Rubke and O'Donnell 2019, entire; Rubke and O'Donnell 2020a, entire; Rubke and O'Donnell 2020b, entire; Rubke and O'Donnell 2021, entire). In total, each of the 17 LTMP sites has been surveyed between 3 and 10 times (average of 6 surveys) with a mean survey frequency of 5 years and an average of 3.7 plots surveyed per year during the 34-year period of the study (Zylstra and Steidl 2021, p. 5).

Density Calculations

To estimate the density of adult Sonoran desert tortoise, we analyzed the data collected at the 17 LTMP sites. All 17 monitoring plots fell within areas that we categorized as high suitability habitat (Figure 15 and Appendix B), and there are Lincoln-Peterson abundance estimates for every survey during the monitoring period (1987–Present; Figure 16). We divided the abundance estimate for a given survey by plot area (in sq mi) to obtain an estimate of adult tortoise density at each site during a given survey year. Across the entire monitoring period, adult Sonoran desert tortoise density averaged 56 adult tortoises per sq mi (range 6–205 tortoise per sq mi). To derive an estimate of current Sonoran desert tortoise abundance and to minimize the influence of survey effort on density estimates, we subset the monitoring data to include only surveys conducted from 2000–Present that had greater than 35 person days of effort. This resulted in a total of 41

surveys at the 17 LTMP sites. Using these thresholds, average adult Sonoran desert tortoise density averaged 46 adult tortoises per sq mi (range: 6–155 tortoises per sq mi). With the subset of data that approximates the current condition of the Sonoran desert tortoise, we tested the fit of various probability distributions using the *fitdistrplus* package (Delignette-Muller and Dutang 2015, entire) for R v4.1.0 (R Core Team 2021). The distribution of density estimates was best described by a gamma distribution with a shape parameter of 1.48 and a rate parameter of 0.03.

Although the 2015 SSA used estimates from a study on the Ironwood Forest National Monument for low quality habitats (Averill-Murray and Averill-Murray 2005, p. 69), this survey area was largely within high suitability habitat based on the USGS model (Figure 15 and Appendix B). Further, many of the density estimates from that study fell within the range of estimates observed at the long-term monitoring plots. Thus, to ascertain adult Sonoran desert tortoise density estimates for the moderate and low suitability habitat classes, we took a two-pronged approach. First, we elicited a range of plausible density estimates from the tortoise biologists within the SSA team which included Brian Wooldridge (USFWS), Cristina Jones (AGFD), Elroy Masters (BLM), Jeff Servoss (USFWS), and Tom Jones (AGFD). The elicitation exercise used a modified Delphi Method and a 4-step elicitation process to estimate the lowest realistic density estimate, the highest realistic density estimate, the most likely realistic density estimate, and the confidence that the actual value falls within the lowest and highest estimate provided for both the moderate and low suitability habitats. Second, we used the range of elicited density estimates to derive a distribution of plausible adult Sonoran desert tortoise densities in the moderate and low suitability habitats. Given that the distribution of density estimates from the LTMP sites was best described by a gamma distribution, we assumed that the density estimates within the moderate and low suitability habitat classes also followed a gamma distribution. Using this approach, the experts suggest an average adult Sonoran desert tortoise density of 25 per sq mi (range: 5–35 tortoise per sq mi) in moderate suitability habitat and 6 tortoises per sq mi (range: 0–15 tortoises per sq mi) in low suitability habitat (Figure E-1). These estimates represent the average density of adult Sonoran desert tortoise across the range of the species. We then fit the gamma distributions to the elicited data such that the tortoise densities within the moderate distribution habitat were described with a gamma distribution with a shape parameter of 3.68 and a rate parameter of 0.13 and densities in the low suitability class were described by a gamma distribution with a shape parameter of 0.37 and a rate parameter of 0.05 (Figure E-1).

Starting Population Sizes

We estimated a range of starting population sizes for our two analysis areas, Arizona and Sonora, using our adult tortoise density distributions (see “Density Calculations” section above) and the amount of suitable Sonoran desert tortoise habitat by habitat class (see Appendix B). More specifically, we estimate our distribution of population sizes by taking 100,000 random draws of average adult tortoise density for each habitat suitability class. When drawing our density estimates, we imposed the following general constraints: 1) the density estimate for moderate and low suitability habitats cannot exceed the density estimate for the suitability classes of higher ranking; 2) the density estimate within a class cannot exceed the maximum observed value for high suitability habitats or the median of the highest plausible density elicited for moderate or low suitability habitats. We then multiplied the amount of habitat from each suitability class, in square miles, by its associated density estimate to arrive at an overall distribution of starting population sizes (Figure 18). We calculated estimated starting population size as follows:

$$N_0 = (D_H \times A_H) + (D_M \times A_M) + (D_L \times A_L) \qquad \text{(Eqn. 1)}$$

Where D was the density of adult tortoises in high suitability habitat areas (subscript H), moderate suitability habitat areas (subscript M) and low suitability habitat areas (subscript L), and A is the area of habitat (in square miles). This distribution of starting population sizes was used as an input into our simulation model.

Environmental Parameters

First, to model the effects of limiting habitat availability on the populations (for each of the two analysis units), we created a ceiling-type density-dependence function in the model, whereby if the population exceeded an established maximum population size, the proportion of females that breed declined to zero. Ceiling-type density-dependent functions are not usually realistic, e.g. all of the females in the population failing to breed in a single year is a severe effect, but ultimately it has the same effect as reducing the P_b parameter to 80% or 50% of normal rate. However, it impacts the population faster when all of them fail to breed. Ceiling-type density-dependent functions lack biological detail but are commonly used in population viability modeling when the functional form of density dependence in the population is unknown. In addition, they are useful for capturing effects of density dependence without speculating on the mathematical formulation of density on demographic rates (Lande 1993, entire; Middleton *et al.* 1995, entire). The maximum population size in a given simulation was determined by the amount (sq mi) of habitat in high, moderate, and low suitability classes multiplied by the maximum density for each of those classes. Using data from LTMP sites and the values elicited within our SSA team, we estimated maximum adult densities of 155 tortoises per sq mi in areas of high suitability habitat, 35 in moderate suitability habitat, and 15 in low suitability habitat. We estimated the maximum population size using Eqn. 1 and these maximum values.

Second, we included drought effect on survival of all adult and older juvenile age classes in our model and an effect of urban areas on survival of the adult age class. For the drought effect, we imposed an annual, linear decrease in the mean survival rate of adult and older juvenile tortoises according to the future scenario considered. Adult and older juvenile survival rates have a significant relationship with severe drought conditions (Zylstra and Steidl 2021, pp. 7–8). Specifically, a 1 unit increase in the averaged Palmer Drought Severity Index (PDSI) value corresponded to an approximately 62% increase (95% CI: 41–91%) in the odds of adult survival and a 45% increase (95% CI: 16–101%) (Zylstra, *pers. comm.*). PDSI values range from -4–4, with negative values indicating drier than normal conditions (i.e., drought) and positive values indicating wetter than normal conditions. Thus, if a scenario included an effect of drought, the average survival rate was reduced annually according to the projected change in severity of drought at the end of century. To account for the influence of urban areas, we determined the proportion of the population that fell within 20 km of cities within the Phoenix and Tucson Metropolitan areas and within 10 km of all other cities with a population greater than 10,000 people. For the proportion of the population that was influenced by urban areas in a specific year, we reduced the average survival rate for all age classes to approximate the results reported in Zysltra and Steidl (2021, entire). For the projection model, survival became the weighted average of the animals that were influenced and not influenced by urban areas, for example:

$$S_t^{A,u} = (P_{urban} \times S_t^A \times UE_t) + ((1 - P_{urban}) \times (S_t^A)) \quad \text{(Eqn. 2)}$$

Where P_{urban} is the proportion of the population exposed to urban influence areas, and $S_t^{A,u}$ is the survival rate of adults for the full population, given the proportion that was influenced by urban areas and drought. UE_t is the urban influence effect in a specific year which was modeled as a uniform random number between 0.98 and 1.0 (i.e., a 0% to 18% reduction in odds of survival (Zylstra 2021, *pers. comm.*)), to represent differing severity of urban influence from year to year.

Modelling Framework and Outputs

We used the model described above to run a set of four predetermined habitat, urban development, and climate-based scenarios (two each for Arizona and Sonora, see SSA report, Section 5.1 for an explanation of the scenarios). The model used a thousand replications to project population outcomes 125 years into the future under each scenario and tracked adult age class population size, population growth rate (rate of annual change) and whether the population fell below the quasi-extinction threshold in each year.

We also used an analysis similar to McGowan *et al.* (2014, entire) to build a triple loop simulation model that allowed us to simulate thousands of replicates with a wide variety of habitat, drought, and population size scenarios to examine the functional form of the relationship of those factors to extinction probability. In the outer most loop of the model we randomly selected 1,000 starting population sizes from our distribution of population size estimates described above. In the second loop the model replicated the population 1,000 times for each of the 1,000 sets of values passed forward from the outermost loop. In that second loop our model selected the mean values for the demographic parameters based on the statistical distributions described previously for each of the 1,000 replicates and those values were passed into the interior loop, also known as the annual loop. We projected the population 125 years into the future and tracked adult age class population size, population growth rate (rate of annual change) and whether the population fell below the quasi-extinction threshold in each year. For each of the 1,000 replicates in the secondary loop we reported the proportion of replicates that went quasi-extinct at 75, 100, and 125 years into the future, alongside the maximum abundance values, and the initial population size.

Modeling Results

Table E-1 and Table E-2 list the results of all the model runs with projected population growth rates, and mean tortoise abundance and quasi-extinction risk at 75, 100, and 125 years.

Current conditions

We ran a set of baseline conditions for Arizona, U.S. (Figure E-1 and Table E-1), and Sonora, Mexico (Figure E-2 and Table E-2), that capture current conditions given our uncertainty regarding population density and starting population size. The “Current Baseline” scenario represents no change in the current levels of stressor into the foreseeable future. In this scenario the population declined over time with mean population growth rate at 125 years were slightly negative ($\lambda \approx 0.990$) (Table E-1 and Table E-2). Probability of quasi-extinction for both Sonora and Arizona probability of quasi-extinction was 0.00% through 100 years with a 2% abundance threshold and less than 0.005 at 125 years (Table E-1 and Table E-2). In other words, there was

less than 0.5% probability of falling below 2% of the starting population 125 years into the future given no change in the level of threats and conditions currently experience by the tortoise. However, across the duration of the simulation under the "Current Baseline" scenario, median abundance declined by 18.3% in Arizona (Figure E-2 and Table E-1) and declined by 1.1% in Sonora (Figure E-3 and Table E-2).

Future conditions

The future scenario simulations added increased potential for drought (i.e., climate change effects) and urbanization as well as an annual habitat rate of change to mimic the effects of urbanization on habitat carrying capacity (see SSA report, Section 5.1 for more explanation of the future scenarios considered in the SSA). We ran two future scenarios each for Arizona (Figures E-4 and E-5) and for Sonora (Figures E-6 and E-7). The response of the simulations was varied (Table E-1 and Table E-2). The "Low Effects" scenario largely tracked our projection of the "Current Baseline" scenario for both analysis areas. The mean population growth rate at 125 years was 0.990 in Arizona (Table E-1) and 0.991 in Sonora (Table E-2) which corresponded to a slow decline in abundance through our 125-year simulation (Figures E-4 and E-6, respectively). Quasi-extinction probabilities were 0.00% at 100 years for both analysis areas and 0.40% and 0.20%, respectively, at 125 years (Tables E-1 and E-2). Across the duration of the simulation under the "Low Effects" scenario, median abundance declined by 18.5% in Arizona (Figure E-4 and Table E-1) and declined by 1.6% in Sonora (Figure E-6 and Table E-2). On the other hand, the "High Effects" scenario showed a decline in the median abundance and faster declines than both the "Current Baseline" and "Low Effects" future scenario. Mean population growth rate in Arizona was approximately 0.976, meaning, on average populations declined by approximately 2.4% annually, and was 0.977 in Sonora. Although the probability of quasi-extinction was still 0.00% at 75 years, it rose to 1.00% at 100 years and was 7.80% at 125 years (Table E-1). For Sonora, the probability of quasi-extinction was 0.00% at 75 years, 0.60% at 100 years, and 5.20% at 125 years (Table E-2). Across the duration of the simulation under the "High Effects" scenario, median abundance declined by 86.8% in Arizona (Figure E-5 and Table E-1) and declined by 82.6% in Sonora (Figure E-7 and Table E-2).

Table E-1. Results of the population simulation model for Arizona, U.S., under the "Current Baseline" and two future scenarios ("Low Effects" and "High Effects"), where N_0 is the median starting abundance of adult females; N_t is the median abundance (range)of adult females at time *t*; P_{Qet} is the median probability (range) of quasi-extinction at time *t*; and λ_{125} is the median population growth rate over 125 years; *% Change* is the percent change in abundance from initial values to 125 years.

Arizona, U.S.	*Initial Values*	*Results at 75 years*		*Results at 100 years*		*Results at 125 years*			
	N_0	N_{75}	P_{Qe75}	N_{100}	P_{Qe100}	N_{125}	P_{Qe125}	λ_{125}	% Change
Current **Baseline**	**282,679** *(54,045–796,435)*	**249,365** *(47,632–700,414)*	**0.00%** *(0.00–0.10%)*	**240,597** *(45,930–683,102)*	**0.00%** *(0.00–0.40%)*	**232,370** *(44,134–666,177)*	**0.40%** *(0.00–1.30%)*	0.989	-18.3%
Low Effects	**276,930** *(51,596–765,120)*	**242,807** *(45,903–670,127)*	**0.00%** (0.00–0.10%)	**233,109** *(43,894–651,161)*	**0.00%** *(0.00–0.40%)*	**225,604** *(42,831–633,273)*	**0.40%** *(0.00–1.30%)*	0.990	-18.5%
High Effects	**272,898** *(51,098–825,101)*	**123,817** *(24,012–371,681)*	**0.00%** *(0.00–0.30%)*	**72,057** *(14,164–214,663)*	**1.00%** *(0.20–2.10%)*	**35,972** *(7,139–107,355)*	**7.80%** *(5.20–10.80%)*	0.976	-86.8%

Table E-2. Results of the population simulation model for Sonora, Mexico, under the "Current Baseline" and two future scenarios ("Low Effects" and "High Effects"), where N_0 is the median starting abundance of adult females; N_t is the median abundance (range) of adult females at time *t*; P_{Qet} is the median probability (range) of quasi-extinction at time *t*; and λ_{125} is the median population growth rate over 125 years; *% Change* is the percent change in abundance from initial values to 125 years.

Sonora, Mexico	*Initial Values*	*Results at 75 years*		*Results at 100 years*		*Results at 125 years*			
	N_0	N_{75}	P_{Qe75}	N_{100}	P_{Qe100}	N_{125}	P_{Qe125}	λ_{125}	% Change
Current **Baseline**	**133,064** *(24,277–368,392)*	**131,519** *(24,195–368,773)*	**0.00%** *(0.00–0.10%)*	**132,141** *(24,809–372,804)*	**0.00%** *(0.00–0.30%)*	**133,554** *(24,893–377,116)*	**0.20%** *(0.00–0.90%)*	0.991	1.1%
Low Effects	**127,998** *(24,969–375,443)*	**127,390** *(25,851–378,682)*	**0.00%** *(0.00–0.10%)*	**128,692** *(25,808–388,552)*	**0.00%** *(0.00–0.30%)*	**130,159** *(25,965–391,983)*	**0.20%** *(0.00–0.90%)*	0.991	1.6%
High Effects	**129,182** *(24,357–376,839)*	**68,546** *(12,651–205,731)*	**0.00%** *(0.00–0.20%)*	**42,173** *(7,705–127,165)*	**0.60%** *(0.00–1.50%)*	**22,483** *(4,176–67,582)*	**5.30%** *(3.20–7.90%)*	0.977	-82.6%

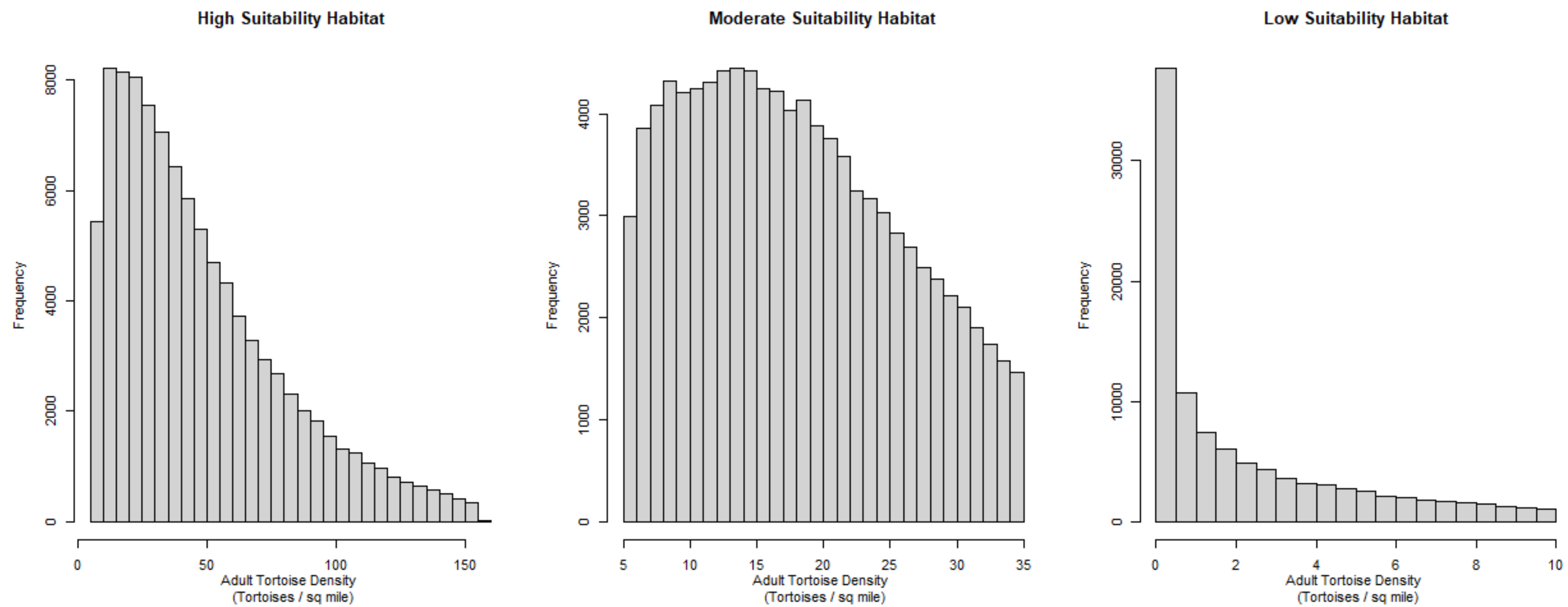


Figure E-1. Distribution of adult Sonoran desert tortoise density estimate (tortoises per sq mi) across the different habitat classes. Distributions were capped to the range of values observed (high suitability habitat classes) or the range of plausible densities elicited by tortoise biologists within the SSA team.

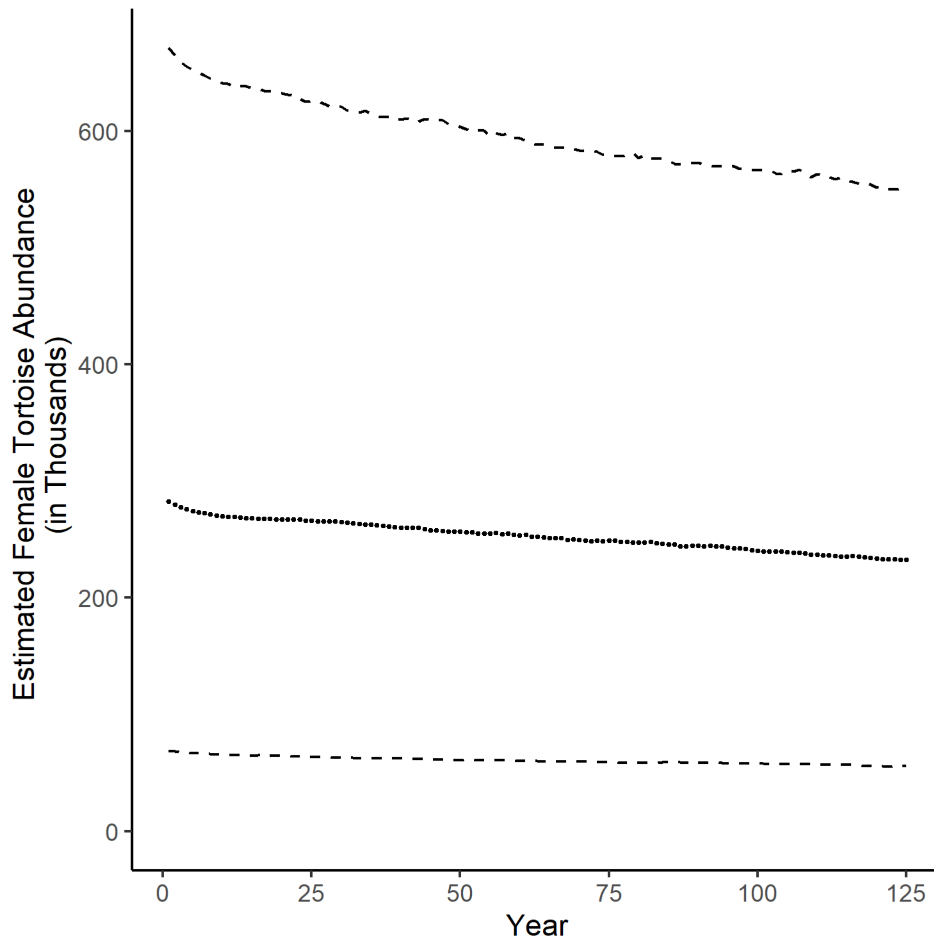


Figure E-2. Projected trend in female Sonoran desert tortoise abundance through time under the "Current Baseline" scenario for the Arizona analysis area. Black points represent median female abundance. Black dashed lines represent the 95% confidence interval on the median female abundance estimate across all simulations.

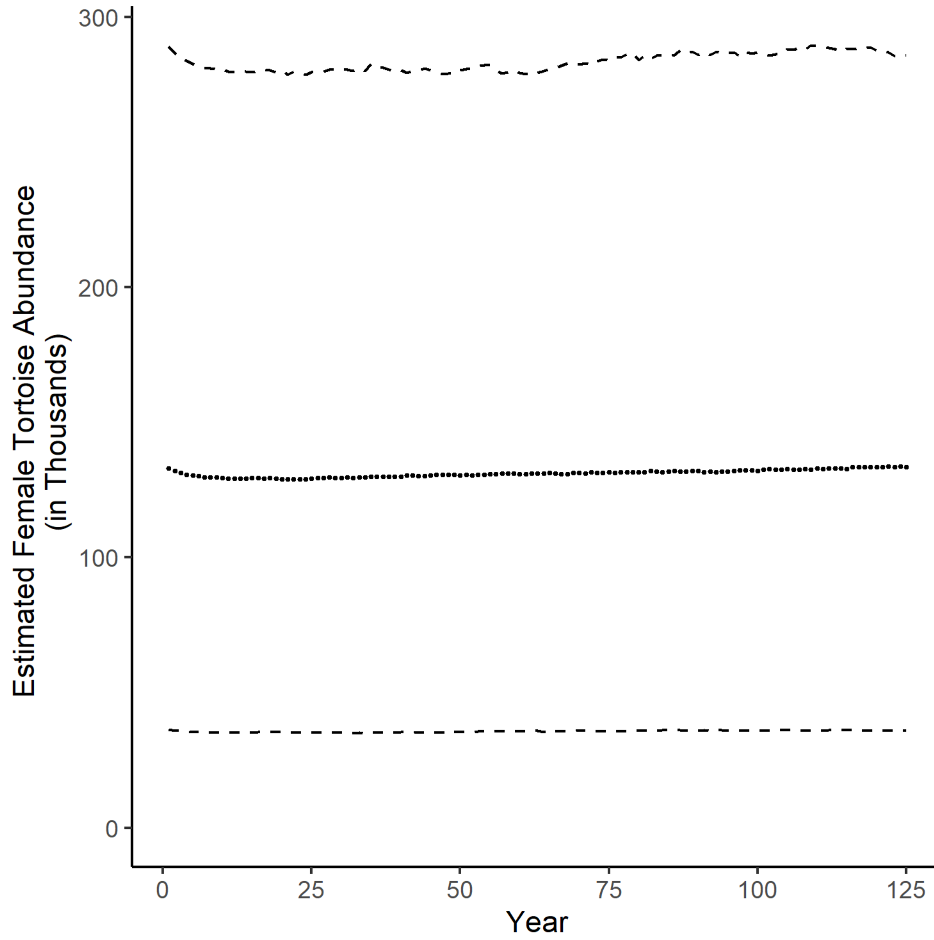


Figure E-3. Projected trend in female Sonoran desert tortoise abundance through time under the "Current Baseline" scenario for the Sonora analysis area. Black points represent median female abundance. Black dashed lines represent the 95% confidence interval on the median female abundance estimate across all simulations.

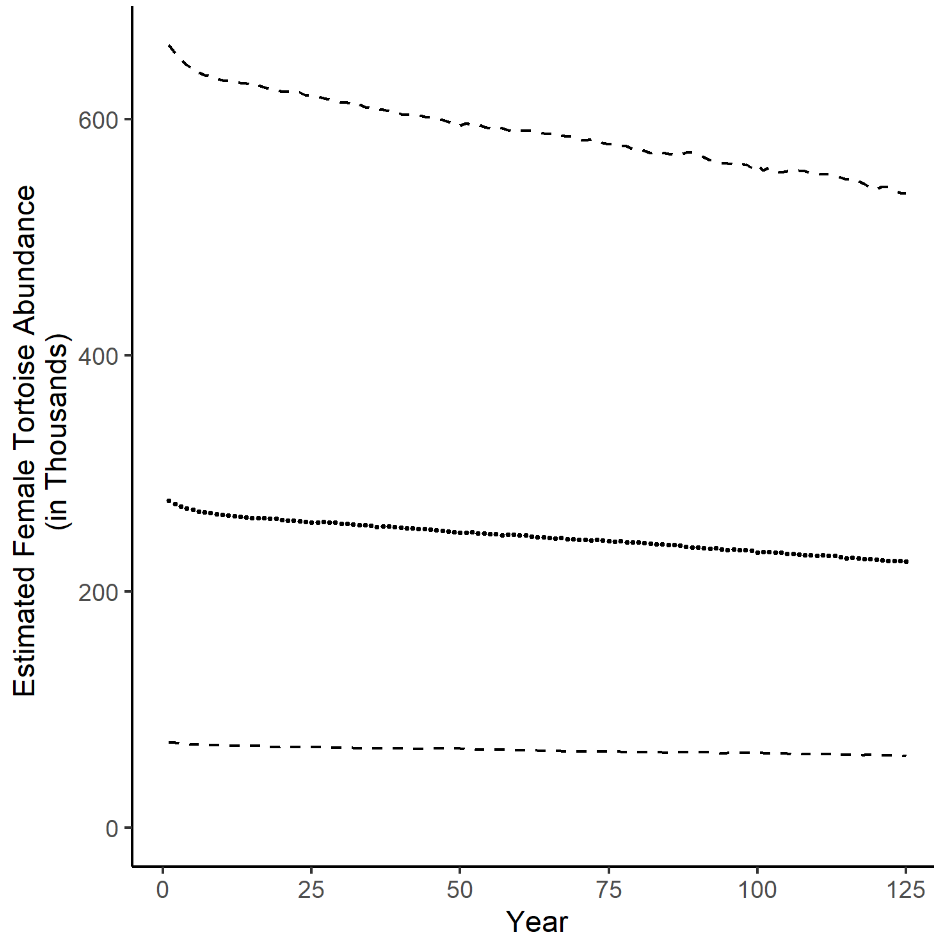


Figure E-4. Projected trend in female Sonoran desert tortoise abundance through time under the "Low Effects" future scenario for the Arizona analysis area. Black points represent median female abundance. Black dashed lines represent the 95% confidence interval on the median female abundance estimate across all simulations.

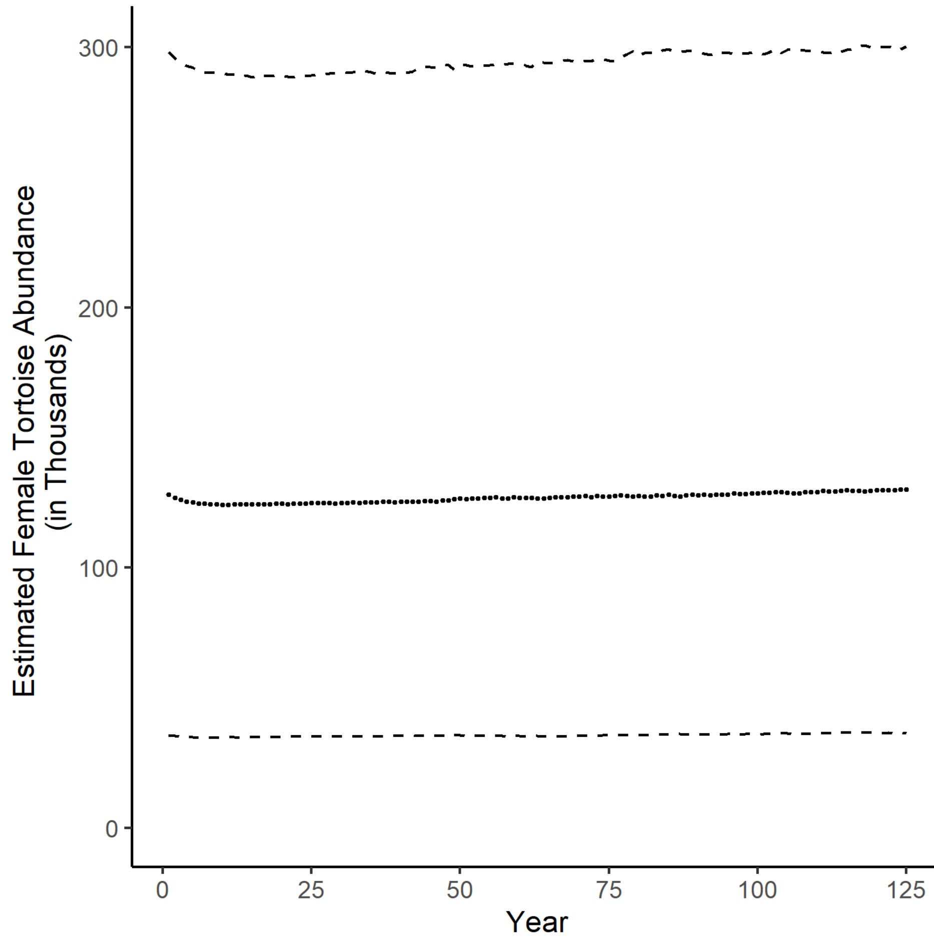


Figure E-5. Projected trend in female Sonoran desert tortoise abundance through time under the "Low Effects" future scenario for the Sonora analysis area. Black points represent median female abundance. Black dashed lines represent the 95% confidence interval on the median female abundance estimate across all simulations.

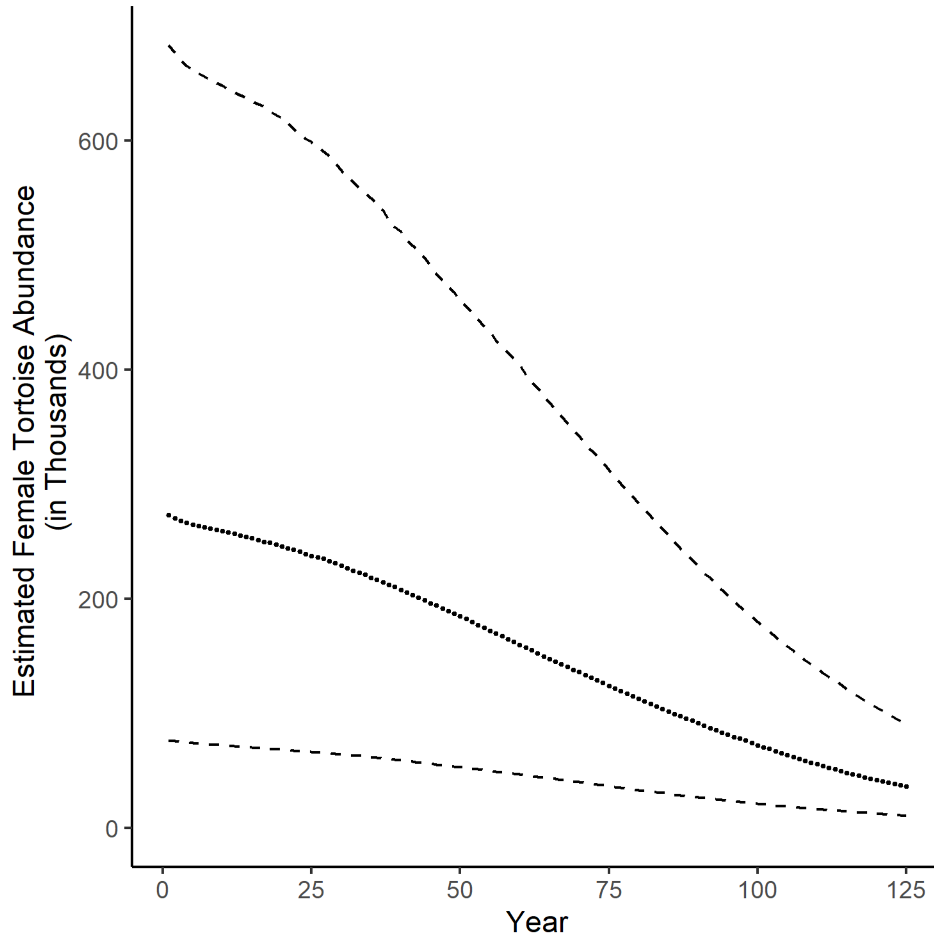


Figure E-6. Projected trend in female Sonoran desert tortoise abundance through time under the "High Effects" future scenario for the Arizona analysis area. Black points represent median female abundance. Black dashed lines represent the 95% confidence interval on the median female abundance estimate across all simulations.

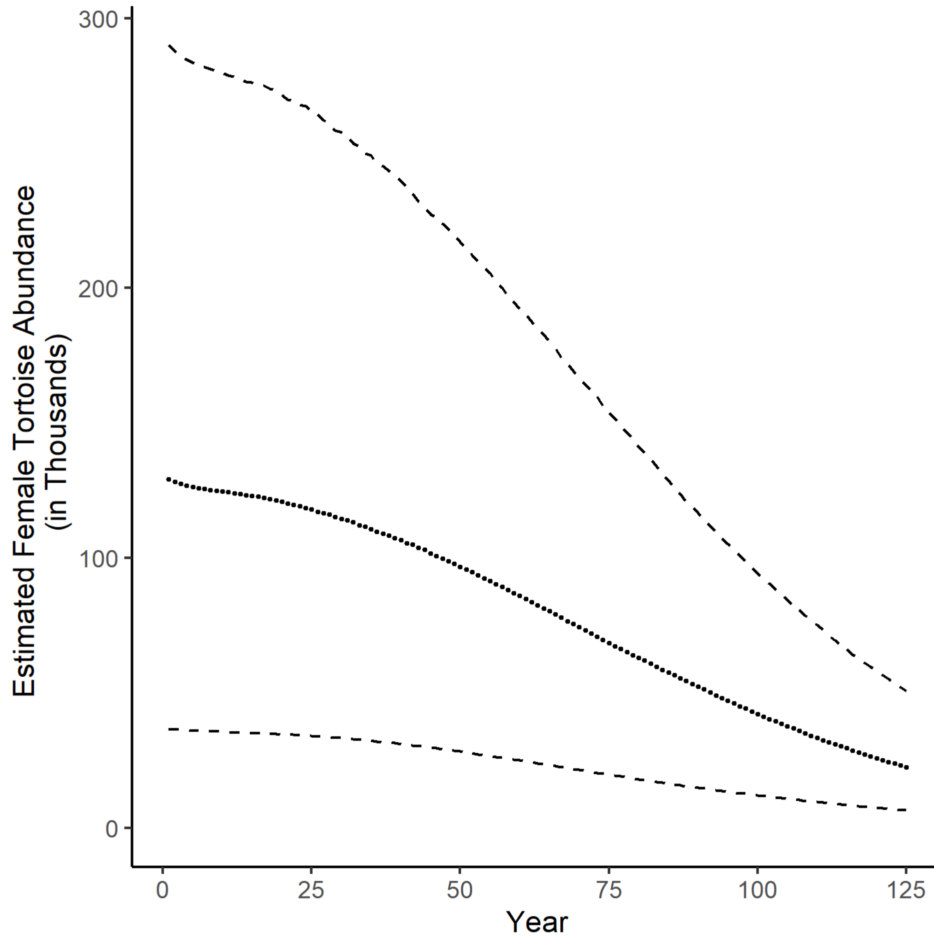


Figure E-7. Projected trend in female Sonoran desert tortoise abundance through time under the "High Effects" future scenario for the Sonora analysis area. Black points represent median female abundance. Black dashed lines represent the 95% confidence interval on the median female abundance estimate across all simulations

Appendix F
Literature Cited for the Sonoran Desert Tortoise SSA Report v2.1

Abella, S. R. 2010. Disturbance and plant succession in the Mojave and Sonoran desert of the American southwest. International Journal of Environmental Research and Public Health 7:1248–1284.

Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevis, B. Vilela, and R. P. Anderson. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545.

Alford, E. J., J. H. Brock, and Gottfried. 2004. Effects of fire on Sonoran Desert plant communities. Pp. 451-454 *in* G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. B. Edminister (eds) Connecting mountain islands and desert seas; biodiversity and management of the Madrean Archipeligo II and 5th conference on research and resource management in the southwestern deserts. U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Proceedings RMRS-P-36.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232.

Amarello, M., K. Setser, and M. Goode. 2004. *Masticophus flagellum* (Coachwhip). Diet. Herpetological Review 35(2):178.

Anderson, K. and K. H. Berry. 2019. *Gopherus agassizii* (Agassiz's desert tortoise). Predation. Herpetological Review 50(2):351.

Anderson, C. D., B. K. Epperson, M.-J. Fortin, R. Holderegger, P. M. A. James, M. S. Rosenberg, K. T. Scribner, and S. Spear. 2010. Considering spatial and temporal scale in landscape-genetic studies of gene flow. Molecular Ecology 19:3565–3575.

Araujo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22:42–47.

Arizona Game and Fish Department (AGFD). 2001. Heritage Data Management System Animal Abstract: Desert Tortoise (*Gopherus agassizii*). Revised 2001-03-28. 11 pp.

Arizona Game and Fish Department (AGFD). 2010. Public submission in response to the Fish and Wildlife Service's notice of petition finding and initiation of status review: "Endangered and Threatened Wildlife and Plants; 90-Day Finding on a Petition To List the Sonoran Population of Desert Tortoise (*Gopherus agassizii*) as a Distinct Population Segment (DPS) With Critical Habitat" (Docket No. FWS-R2-ES-2009-0032). 20 pp.

Arizona Game and Fish Department (AGFD). 2012b. Assessment of desert tortoise movement, permeability, and habitat along the proposed State Route 95 realignment. Final Report #650 prepared for the Arizona Department of Transportation in cooperation with the U.S. Department of Transportation Federal Highway Administration. 152 pp.

Arizona Game and Fish Department (AGFD). 2014. Reward increases again for information to solve illegal desert tortoise shooting. Press release dated November 10, 2014. Available at: http://azgfd.net/artman/publish/NewsMedia/Reward-increases-again-for-information-to-solve-illegal-desert-tortoise-shooting.shtml. Last accessed: November 10, 2014.

Arizona Interagency Desert Tortoise Team (AIDTT). 2000. Averill-Murray, R.C., ed. Status of the Sonoran population of the desert tortoise in Arizona: an update. Arizona Interagency Desert Tortoise Team and Arizona Game and Fish Department, Phoenix. 48 pp.

Arizona Interagency Desert Tortoise Team (AIDTT). 2015. Candidate conservation agreement for the Sonoran desert tortoise (*Gopherus morafkai*) in Arizona. May 27, 2015. 138 pp.

Arizona-Sonora Desert Museum (ASDM). 2021. Sonoran Desert Cooperative Weed Management Area: Sahara mustard (*Brassica tournefortii*). Available at https://sdcwma.org/species/saharamustard.php. Accessed on July 1, 2021.

Arriaga, L., A. E. Castellanos, E. Moreno, and J. Alarcón. 2004. Potential ecological distribution of alien invasive species and risk assessment: a case study of buffelgrass in arid regions of Mexico. Conservation Biology 18(6):1504–1514.

Aslan, C. E., A. Schaefer, and D. E. Swann. 2003. *Gopherus agassizii*. (Desert Tortoise). Elevational Range. Herpetological Review 34(1):57.

Audsley, L. 2010. The truth about Arizona's border fence. Arizona Wildlife Views 52(3):5-8.

Averill-Murray, R. C. 2002a. Effects on survival of desert tortoises (*Gopherus agassizii*) urinating during handling. Chelonian Conservation and Biology 4(2):430–435.

Averill-Murray, R. C. 2002b. Reproduction of *Gopherus agassizii* in the Sonoran desert, Arizona. Chelonian Conservation and Biology 4(2):295–301.

Averill-Murray, R. C, and A. Averill-Murray. 2005. Regional-scale estimation of density and habitat use of the desert tortoise (*Gopherus agassizii*) in Arizona. Journal of Herpetology 39(1):65–72.

Averill-Murray, R. C., and C. M. Klug. 2000. Monitoring and ecology of Sonoran desert tortoises in Arizona. Nongame and Endangered Wildlife Program Technical Report 161. Arizona Game and Fish Department, Phoenix, Arizona. 115 pp.

Averill-Murray R. C. and D. E. Swann. 2002. Impacts of urbanization on desert tortoises at Saguaro National Park: tortoise density along the southern park boundary. Nongame and Endangered Wildlife Program Technical Report 199. Arizona Game and Fish Department, Phoenix, Arizona. 14 pp.

Averill-Murray, R. C., B. E. Martin, S. J. Bailey, and E. B. Wirt. 2002a. Activity and behavior of the Sonoran desert tortoise in Arizona. pp. 135–158 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Averill-Murray, R. C., A. P. Woodman, and J. M. Howland. 2002b. Population ecology of the Sonoran desert tortoise in Arizona. pp. 109-134 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Averill-Murray, R. C., T. E. Christopher, and B. T. Henen. 2018. Reproductive ecology and life history of female Sonoran desert tortoises (*Gopherus morakai*). Herpetological Monographs 32(2018):32–50.

Averill-Murray, R. C., C. H. Fleming, and J. D. Riedle. 2020. Reptile home ranges revisited: a case study of space use of Sonoran desert tortoises (*Gopherus morafkai*). Herpetological Conservation and Biology 15(2):253–271.

Avery, H. W. and A. G. Neibergs. 1997. Effects of cattle grazing on the desert tortoise, *Gopherus agassizii*: nutritional and behavioral interactions. Proceedings: Conservation, Restoration and Management of Tortoises and Turtles – An International Conference, pp. 13–20.

Babb, R.D., T.C. Brennan, D.D. Kandiyeli, C.M. Akins and T.R. Jones. 2013. *Gopherus morafkai* (Sonoran Desert Tortoise) Geographic Distribution. Herpetological Review 44:623.

Bagne, K. E. and D. M. Finch. 2012. Vulnerability of species to climate change in the Southwest: threatened, endangered, and at-risk species at the Barry M. Goldwater Range, Arizona. Gen. Tech. Rep. RMRS-GTR-284. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 139 pp.

Bahre, C. J. 1991. A legacy of change: historic human impact on vegetation in the Arizona borderlands. University of Arizona Press. Tucson, Arizona. 231 pp.

Bailey, S. J., C. R. Schwalbe, and C. H. Lowe. 1995. Hibernaculum use by a population of desert tortoises (*Gopherus agassizii*) in the Sonoran Desert. Journal of Herpetology 29(3):361-369.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3: 327-338.

Barrett, S. L. 1990. Home range and habitat of the desert tortoise (*Xerobates agassizii*) in the Picacho Mountains of Arizona. Herpetologica 46(2):202–206.

Barrett, S. L. and J. A. Humphrey. 1986. Agonistic interactions between *Gopherus agassizii* (Testudinidae) and *Heloderma suspectum* (Helodermatidae). The Southwestern Naturalist 31(2):261–263.

Bean, T. 2015. Email response to U. S. Fish and Wildlife Service questionnaire regarding the conservation and status of the Sonoran desert tortoise. Received January 6, 2015.

Berry, K. H. 1986a. Desert tortoise (*Gopherus agassizii*) relocation: implications of social behavior and movements. Herpetologica 42(1):113–125.

Berry, K. H. 1986b. Incidence of gunshot deaths in desert tortoise populations in California. Wildlife Society Bulletin 14(2): 127-132.

Berry, K. H., E. K. Spangenberg, B. L. Homer, and E. R. Jacobson. 2002. Deaths of desert tortoises following periods of drought and research manipulation. Chelonian Conservation and Biology 4(2):436-448.

Boarman, W. I. 2002. Threats to desert tortoise populations: a critical review of the literature. U.S. Geological Survey, Western Ecological Research Center. San Diego, California. 91 pp.

Boarman, W. I. and M. Sazaki. 1996. Highway mortality of desert tortoises and small vertebrates: success of barrier fences and culverts. Unpublished manuscript. 6 pp.

Boarman, W. I. and M. Sazaki. 2006. A highway's road-effect zone for desert tortoises (*Gopherus agassizii*). Journal of Arid Environments 65:94–101.

Boarman, W. I., M. Sazaki, and B. Jennings. 1997. The effect of roads, barrier fences, and culverts on desert tortoise populations in California, USA. Proceedings: Conservation, Restoration and Management of Turtles and Tortoises – An International Conference. pp. 54–58.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Bracamonte, J, C. Tinoco-Ojanguren, M. E. Sanchez Coronado, and F. Molina-Freaner. 2017. Germination requirements and the influence of buffelgrass invasion on a population of *Mammillaria grahamii* in the Sonoran Desert. Journal of Arid Environments 137(2017):50–59.

Bradford, J. B., D. R. Schlaepfer, W. K. Lauenroth, and K. A. Palmquist. 2019. Robust ecological drought projections for drylands in the 21st century. Global Change Biology 26:3906-3919.

Bradley, B., C. A. Curtis, and J. Chambers. 2016. *Bromus* response to climate and projected changes with climate change. Chapter 9 *In*: J. M. Germino, M. J., J. C. Chambers, and C. S. Brown (Eds.). 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western US: Causes, consequences, and management implications. Springer International Publishing. Switzerland. 475 pp.

Brennan, T. C. and A. T. Holycross. 2006. A field guide to amphibians and reptiles in Arizona. Arizona Game and Fish Department, Phoenix. 150 pp.

Brooks, M. L. 1999. Alien annual grasses and fire in the Mojave Desert. Madrono 46(1):13–19.

Brooks, M. L. 2001. Fire and invasive plants in the wildlands of California. Noxious Times (Spring):4–5.

Brooks, M. L., and T.C. Esque. 2002. Alien annual plants and wildfire in desert tortoise habitat: status, ecological effects, and management. Chelonian Conservation and Biology 4:330–340.

Brooks, M. L. and J. R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. Journal of Arid Environments 67:148–164.

Brooks, M. L., and D. A. Pyke. 2001. Invasive plants and fire in the deserts of North America. Pages 1–14 *in* K. E. M. Galley and T. P. Wilson (eds.). Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

Brooks, M. L., T. C. Esque, and C. R. Schwalbe. 1999. Effects of exotic grasses via wildfire on desert tortoises and their habitat. Desert Tortoise Council Symposium. St. George, Utah.

Brooks, M. L., C. S. Brown, J. C. Chambers, C. M. D'Antonio, J. E. Keeley, and J. Belnap. 2016. Exotic annual *Bromus* invasions: comparisons amoung species and ecoregions in the western United States. Chapter 2 *In*: J. M. Germino, M. J., J. C. Chambers, and C. S. Brown (Eds.). 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western US: Causes, consequences, and management implications. Springer International Publishing. Switzerland. 475 pp.

Brown, D.E. (ed). 1994. Biotic communities of the southwestern United States and Northwestern Mexico. University of Utah Press. Salt Lake City, UT. 315 pp. plus Appendices.

Burge, B. 1979. A survey of the present distribution of the desert tortoise, *Gopherus agassizii*, in Arizona. Pages 27-74 *in* E. St. Amant (ed). Proceedings of the 1979 Symposium of the Desert Tortoise Council, Long Beach, California.

Búrquez-Montijo, A., M. E. Miller, and A. Martínez-Yrízar. 2002. Mexican grasslands, thornscrub, and the transformation of the Sonoran Desert by invasive exotic buffelgrass (*Pennisetum ciliare*). pp. 126–146 *in* Tellman, B. (ed.) 2002. Invasive Exotic Species in the Sonoran Region. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Bury, R. B., D. J. Germano, T. R. Van Devender, and B. E. Martin. 2002. The desert tortoise in Mexico: distribution, ecology, and conservation. pp. 86–108 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Bury, R. B., and R. A. Luckenbach. 2002. Comparison of Desert Tortoise (*Gopherus agassizii*) Populations in an Unused and Off-Road Vehicle Area in the Mojave Desert. Chelonian Conservation and Biology 4(2):457–463.

Campbell, S. P., R. J. Steidl, and E. R. Zylstra. 2014. Spatial variation in demography and population viability of Sonoran desert tortoises. Final report to Arizona Game and Fish Department. Prepared by the School of Natural Resources and the Environment, Univerity of Arizona, Tucson, Arizona. 40 pp.

Campbell, S. P., R. J. Steidl, and E. R. Zylstra. 2015. Recruitment of desert tortoises (*Gopherus agassizii* and *G. morafkai*): a synthesis of reproduction and first-year survival. Herpetological Conservation and Biology 10(2):583–591.

Campbell, S. P., E. R. Zylstra, C. R. Darst, R. C. Averill-Murray, and R. J. Steidl. 2018. A spatially explicit model to characterize population viability. Ecological Applications 28(8):2055–2065.

Carter, S. K., K. E. Nussear, T. C. Esque, I. I. F. Leinwand, E. Masters, R. D. Inman, N. B. Carr, and L. J. Allison. 2020. Quantifying development to inform management of Mojave and Sonoran desert tortoise habitat in the American southwest. Endangered Species Research 42:167-184. Available at: https://doi.org/10.3354/esr01045.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C. G. Menéndez, J. Räisänen, A. Rinke, A. Sarr and P. Whetton. 2007. Regional climate projections. pp. 847-940 *In* Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Christopher, M. M. 1999. Physical and biochemical abnormalities associated with prolonged entrapment in a desert tortoise. Journal of Wildlife Diseases 35(2):361–366.

Cook, B. I., T. R. Ault. And J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American southwest and central plains. Science Advances Vol. 1 No. 1e1400082. Accessed February 13, 2015: http://advances.sciencemag.org/content/advances/1/1/e1400082.full.pdf

Cooper, J. G. 1863. *Xerobates agassizii* – Agassiz Land Tortoise. Proceedings of the California Academy of Natural Sciences 1858-1862. Towne and Bacon; Excelsior Steam Printing Office. San Francisco, California.

Crother, B. I., R. M. Bonett, J. Boundy, F. T. Burbrink, K. de Queiroz, D. R. Frost, R. Highton, J. B. Iverson,.E. L. Jockusch, F. Kraus, K. L. Krysko, A. D. Leaché,.E. Moriarty Lemmon, R. W. McDiarmid, J. R. Mendelson III, P. A. Meylan, T. W. Reeder, S. Ruane, Michael E. Seidel. 2017. Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. Eighth Edition. Society for the Study of Amphibians and Reptiles Herpetological Circular No. 43. 104 pp.

Curtin, A. J., G. R. Zug, and J. R. Spotila. 2009. Longevity and growth strategies of the desert tortoise (*Gopherus agassizii*) in two American deserts. Journal of Arid Environments 73(4-5):463–471.

Dahlby, A. 2021. Email correspondence dated January 19, 2021, in response to December 2, 2021, public information request from the U.S. Fish and Wildlife Service regarding the Sonoran desert tortoise. 6 pp.

D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Darst C.R., P.J. Murphy, N.W. Strout, S.P. Campbell, K.J. Field, L. Allison, and R.C. Averill-Murray. 2013. A strategy for prioritizing threats and recovery actions for at-risk species. Environmental Management 51:786-800.

DeFalco, L. A. 2007a. Competitive interactions between a non-native annual grass and Mojave Desert perennials. Publication Brief for Resource Managers. U.S. Geological Survey, Western Ecological Research Center. 2 pp.

DeFalco, L. A., T. C. Esque, K. E. Nussear, S. J. Scoles, M. A. Walden, and K. K. Drake. 2006. Monitoring the effectiveness of seeding burned critical habitat for the desert tortoise. U.S. Geological Survey, Western Ecological Research Center. 27 pp.

Delignette-Muller, M. L., and C. Dutang. 2015. fitdistrplus: An R package for Fitting Distributions. Journal of Statistical Software, 64(4):1–34.

de Vos, J.C., Jr., R. Miller, S.L. Walchuk, W.D. Ough, and D.E. Taylor. 1983. Biological resource inventory Tucson Division--Phase B Central Arizona Project. Arizona Game and Fish Dept. Report to U.S. Bureau of Reclamation, Boulder City, NV. Contract No. 1-07-32-V0151. 470pp.

Dickinson, V. M., J. L. Jarchow, M. H. Trueblood, and J. deVos. 2002. Are free-ranging desert tortoises healthy? pp. 242–264 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Dieringer, S. 2010. Public submission in response to the Fish and Wildlife Service's notice of petition finding and initiation of status review: "Endangered and Threatened Wildlife and Plants; 90-Day Finding on a Petition To List the Sonoran Population of Desert Tortoise (*Gopherus agassizii*) as a Distinct Population Segment (DPS) With Critical Habitat" (Docket No. FWS-R2-ES-2009-0032). 1 p.

Dimmitt, M. A. and T. R. Van Devender. 2009. Sahara mustard (*Brassica tournafortii*): a serious new threat to low desert ecosystems in the southwestern United States and northwestern Mexico pp. 241-250 *in* Van Devender, T. R., F. J. Espinosa-Garcia, B. L. Haper-Lore, and T. Hubbard (eds). 2009. Invasive plants on the move: controlling them in North America. Based on presentations from Weeds Across Borders 2006 Conference. Arizona-Sonora Desert Museum, Tucson, Arizona. 422 pp.

Di Cola, V., O. Broennimann, B. Petitpierre, F. T. Breiner, M. d'Amen, C. Randin, ... and A. Guisan. 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40:774-787.

DiTomaso, J. M., G. B. Kyser, and M. S. Hastings. 1999. Prescribed burning for control of yellow thistle (*Centaurea solstitialis*) and enhanced native plant diversity. Weed Science 47(2):233–242.

Dockens, P.E.T., T.C. Ashbeck, and S. Hale. 2011. Desert Tortoise Surveys at the Buck Mountains Long-term Monitoring Plot, Mohave County, Arizona, 2010. EcoPlan Associates, Inc., Mesa, Arizona. Report to the Arizona Game and Fish Department. 61 pp.

Dolby, G. A., T. H. Webster, D. DeNardo, T. Edwards, H. Byrne, K. Kusumi, and M. A. Wilson. 2021. Characterizing the Sonoran desert tortoise through genomic analyses of hybrids and speciation. #I17001, Unpublished report to the Arizona Game and Fish Department, Phoenix, Arizona. 27 pp.

Drake, K. K., L. Bowen, K. E. Nussear, T.C. Esque, A.J. Berger, N. A. Custer, S. C. Waters, J. D. Johnson, A. K. Miles, and R. L. Lewinshon. 2016. Negative impacts of invasive plants on conservation of sensitive desert wildlife. Ecosphere 7(10): e015131. 1-20.

Duda, J. J., A. J. Krzysik, and J. E. Freilich. 1999. Effects of drought on desert tortoise movement and activity. Journal of Wildlife Management 63(4):1181–1192.

Edwards, T. 2003. Desert tortoise conservation genetics. Masters Thesis submitted to the School of Renewable Natural Resources, University of Arizona. Tucson, Arizona. 88 pp.

Edwards, T. 2015. A biogeographic perspective of speciation among desert tortoises in the genus *Gopherus*. Dissertation. The University of Arizona, ProQuest, UMI Dissertations Publishing, 2015. 3702126. 167 pp. http://gradworks.umi.com/37/02/3702126.html

Edwards, P.K. and B. Leung. 2009. Re-evaluating eradication of nuisance species: invasion of the tunicate, *Ciona intestinalis*. Frontiers in Ecology and Environment 7:326–332.

Edwards, T., C. R. Schwalbe, D. E. Swann, and C. S. Goldberg. 2004. Implications of anthropogenic landscape change on inter-population movements of the desert tortoise (*Gopherus agassizii*). Conservation Genetics 5:485–499.

Edwards, T., C. J. Jarchow, C. A. Jones and K. E. Bonine. 2010. Tracing genetic lineages of captive desert tortoises in Arizona. Journal of Wildlife Management 74(4):801–807.

Edwards, T., K. H. Berry, R. D. Inman, T. C. Esque, K. E., Nussear, C. A. Jones, and M. Culver. 2015. Testing taxon tenacity of tortoises: evidence for a geographical-selection gradient at a secondary contact zone. Ecology and Evolution 5(10):2095-2114. DOI: 10.1002/ece3.1500

Edwards, T., A. E. Karl, M. Vaughn, P. C. Rosen, C. M. Torres, R. W. Murphy. 2016. The desert tortoise trichotomy: Mexico hosts a third, new sister-species of tortoise in the *Gopherus morafkai–G. agassizii* group. ZooKeys 562: 131– 158. doi: 10.3897/zookeys.562.6124

Emblidge, P. G., K. E. Nussear, T. C. Esque, C. M. Aiello, and A. D. Walde. 2015. Severe mortality of a population of threatened Agassiz's desert tortoises: the American badger as a potential predator. Endangered Species Research 28:109–116.

Ennen, J. R., J. E. Lovich, R. C. Averill-Murray, C. B. Yackulic, M. Agha, C. Loughran, L. Tennant, B. Sinervo. 2017. The evolution of different maternal investment strategies in two closely related desert vertebrates. Ecology and Evolution 2017:1-13. DOI: 10.1002/ece3.2838

Ernst, C. H. and J. E. Lovich. 2009. Turtles of the United States and Canada. Second Edition. The Johns Hopkins University Press. Baltimore, Maryland. 840 pp.

Esque, T. 2007. Bufflegrass fuel loads in Saguaro National Park, Arizona, increase fire danger and threaten native species. Park Science. 6 pp.

Esque, T. C. and E. L. Peters. 1994. Ingestion of bones, stones, and soil by desert tortoises. pp. 105-111. *in* Fish and Wildlife Research 13. U.S. Department of the Interior, National Biological Survey. 212 pp.

Esque, T. C., A. Burquez, C. R. Schwalbe, T. R. Van Devender, P. J. Anning, and M. J. Nijhuis. 2002. Fire ecology of the Sonoran desert tortoise. pp. 312-333 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Esque, T. C., C. R. Schwalbe, L. A. DeFalco, R. B. Duncan, and T. J. Hughes. 2003. Effects of desert wildfires on desert tortoise (*Gopherus agassizii*) and other small vertebrates. The Southwestern Naturalist 48(1):103–111.

Esque, T. C., R. H. Webb, C. S. A. Wallace, C. van Riper III, C. McCreedy, and L. Smythe. 2013. Desert fires fueled by native annual forbs: effects of fire on communities of plants and birds in the lower Sonoran Desert of Arizona. Southwestern Association of Naturalists. Available: https://www.jstor.org/stable/24643662.

Esque, T. C., K. K. Drake, and K. E. Nussear. 2013. Water and food acquisition and their consequences for life history and metabolism of North American tortoises: chapter 10. pp. 85-95 *in* Rostal, D. C., E. D. McCoy, and H. R. Mushinsky (ed.). 2014. Biology and Conservation of North American Tortoises. John Hopkins University Press. Baltimore, MD.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14: 21. Available at: http://www.ecologyandsociety.org/vol14/iss1/art21/

Forman, R. T. T. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14(1):31–35.

Forman, R. T. T. and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Fourcade, Y., J. O. Engler, D. Rodder, J. Secondi. 2014. Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. PLoS ONE 9: e97122.

Franklin, K. and F. Molina-Freaner. 2010. Consequences of buffelgrass pasture development for primary productivity, perennial plant richness, and vegetation structure in the drylands of Sonora, Mexico. Conservation Biology 24(6):1664–1673.

Franklin, K., K. Lyons, P. L. Nagler, D. Lampkin, E. P. Glenn, F. Molina-Freaner, T. Markow, and A. R. Huete. 2006. Buffelgrass (*Pennisetum cilare*) land conversion and productivity in the plains of Sonora, Mexico. Biological Conservation 127:62–71.

Friggins, M. M., M. V. Warwell, J. C. Chambers, and S. G. Kitchen. 2012. Modeling and predicting vegetation response of western USA grasslands, shrublands, and deserts to climate change. Finch, Deborah M., ed. 2012. Climate change in grasslands, shrublands, and deserts of the interior American West: a review and needs assessment. Gen. Tech. Rep. RMRS-GTR-285. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 139 pp.

Fritts, T. H. and R. D. Jennings. 1994. Distribution, status, and habitat use of the desert tortoise in Mexico. pp. 49–56 *in* Fish and Wildlife Research 13. U.S. Department of the Interior, National Biological Survey. 212 pp.

Gade, K. 2015. Email response to U. S. Fish and Wildlife Service questionnaire regarding the conservation and status of the Sonoran desert tortoise. Received January 15, 2015.

Galbraith, H. and J. Price. 2009. A Framework for Categorizing the Relative Vulnerability of Threatened and Endangered Species to Climate Change. Prepared for the Global Change Research Program, National Center for Environmental Assessment, Office of Research and Development, U.S. Environmental Protection Agency. Washington, D.C. 121 pp.

Gammage, G., Jr., J. S. Hall, R. E. Lang, R. Melnick, and N. Welch. 2008. Megapolitan, Arizona's sun corridor. Morrison Institute for Public Policy, Arizona State University, Phoenix, Arizona. 51 pp.

Gammage, G. Jr., M. Stigler, S. Clark-Johnson, D. Daugherty, and W. Hart. 2011. Watering the sun corridor: managing choices in Arizona's megapolitain corridor. Morrison Institute for Public Policy, Arizona State University. 40 pp. Available at: http://morrisoninstitute.asu.edu/sites/default/files/content/products/SustPhx_WaterSunCorr.pdf. Last accessed: December 7, 2014.

GDAL/ORG contributors. 2021. GDAL/OGR Geospatial Data Abstraction software Library. Open Source Geospatial Foundation. URL https://gdal.org.

Germano, D. J., F. H. Pough, D. J. Morafka, E. M. Smith, and M. J. Demlong. Growth of desert tortoises. pp. 265-288 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Germino, M. J., J. Belnap, J. M. Stark, E. B. Allen, and B. M. Rau. 2016. Ecosystem impacts of exotic annual invaders in the genus *Bromus*. Chapter 3 *In*: J. M. Germino, M. J., J. C. Chambers, and C. S. Brown (Eds.). 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western US: Causes, consequences, and management implications. Springer International Publishing. Switzerland. 475 pp.

Gonzalez, P., G.M. Garfin, D.D. Breshears, K.M. Brooks, H.E. Brown, E.H. Elias, A. Gunasekara, N. Huntly, J.K. Maldonado, N.J. Mantua, H.G. Margolis, S. McAfee, B.R. Middleton, and B.H. Udall, 2018: Southwest. In Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II [Reidmiller, D.R., C.W. Avery, D.R. Easterling, K.E. Kunkel, K.L.M. Lewis, T.K. Maycock, and B.C. Stewart (eds.)]. U.S. Global Change Research Program, Washington, DC, USA, pp. 1101–1184. https://doi.org/10.7930/NCA4.2018.CH25.

Grandmaison, D. D. 2010. Progress report: assessment of desert tortoise movement, permeability, and predictive habitat modeling along the proposed Arizona State Route 95 alignment. Unpublished report. Arizona Game and Fish Department, Research Branch. 12 pp.

Grandmaison, D. and V. J. Frary. 2012. Estimating the probability of illegal desert tortoise collection in the Sonoran desert. The Journal of Wildlife Management 76(2):262–268.

Grandmaison, D. D., M. F. Ingraldi, and F. R. Peck. 2010. Desert tortoise micro-habitat selection on the Florence Military Reservation, south-central Arizona. Journal of Herpetology 44(4):581–590.

Gray, K. M. 2012. Effects of buffelgrass invasion on Sonoran desert tortoises. Thesis submitted to the School of Natural Resources and the Environment, University of Arizona, in partial fulfillment of the requirements for the degree of Master of Science. 60 pp.

Gray, K. M. and R. J. Steidl. 2015. A plant invasion affects condition but not density or population structure of a vulnerable reptile. Biological Invasions 17:1979–1988.

Grissom, P. 2015a. Email response to U. S. Fish and Wildlife Service questionnaire regarding the conservation and status of the Sonoran desert tortoise. Received January 7, 2015.

Grissom, P. 2015b. Peer reviewer comments on draft Sonoran desert tortoise species status report. Received July 14, 2015.

Hart, S., P. Woodman, S. Bailey, S. Boland, P. Frank, G. Goodlett, D. Silverman, D. Taylor, M. Walker, and P. Wood. 1992. Desert tortoise population studies at seven sites and a mortality survey at one site in the Sonoran Desert, Arizona. Report submitted to the Arizona Game and Fish Department and the U.S. Bureau of Land Management. Contract Numbers G10075-A and N651-C1-3066. 137 pp.

Hatten, J. R., J. T. Giermakowski, J. A. Holmes, E. M. Nowak, M. J. Johnson, K. E. Ironside, C. van Riper III, M. Peters, C. Truettner, and K. L. Cole. 2016. Identifying bird and reptile vulnerabilities to climate change in the Southwestern United States: U.S. Geological Survey Open-File Report 2016-1085. Available: http://dx.doi.org/10.3133/ofr20161085.

Hazard, L. C., D. R. Shemanski, and K. A. Nagy. 2010. Nutritional quality of natural foods of juvenile and adult desert tortoises (*Gopherus agassizii*): calcium, phosphorus, and magnesium digestibility. Journal of Herpetology 44(1):135–147.

High Country News. 2021. Rapid growth in Arizona's suburbs bets against an uncertain water supply. Published June 1, 2021. Available at: https://www.hcn.org/issues/53.6/south-water-rapid-growth-in-arizonas-suburbs-bets-against-an-uncertain-water-supply. Accessed August 25, 2021.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199:142–152.

Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998(2):367–375.

Hereford, R., R. H. Webb, and C. I. Longpre. 2006. Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893–2001. Journal of Arid Environments 67:13–34.

Hoff, K. and R. M. Marlow. 2002. Impacts of vehicle road traffic on desert tortoise populations with consideration of conservation of tortoise habitat in southern Nevada. Chelonian Conservation and Biology 4(2):449–456.

Hoffman, H. A., C. A. Rubke, K. O. Sullivan, and D. J. Leavitt. 2017. Sonoran Desert Tortoise Population Surveys at Two Long-term Monitoring Plots in Arizona, 2015: Tortilla Mountains and Maricopa Mountains. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 50 pp.

Howland, J. M. and J. C. Rorabaugh. 2002. Conservation and protection of the desert tortoise in Arizona. pp. 334-354 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Hughes, T. 2015. Email communication from Tim Hughes, Threatened and Endangered Species Specialist, U.S. Bureau of Land Management. Received February 3, 2015.

Inman, R.D., K. E. Nussear, T. C. Esque, A. G. Vandergast, S. A. Hathaway, D. A. Wood, K. R. Barr, and R. N. Fisher. 2014. Mapping habitat for multiple species in the desert southwest: U.S. Geological Survey Open-File Report 2014- 1134. 92 pp. Available at: http://dx.doi.org/10.3133/ofr20141134.

Inman, R., A. S. Fotheringham, J. Franklin, T. Esque, T. Edwards, and K. Nussear. 2019. Local niche differences predict genotype associations in sister taxa of desert tortoise. Diversity and Distribution 2019(00):1-16. Available: https://doi.org/10.1111/ddi.12927

Intergovernmental Panel on Climate Change (IPCC). 2007. Climate change 2007: the physical science basis - summary for policymakers. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. 21 pp. Available at: https://www.ipcc.ch/report/ar4/wg1/

Intergovernmental Panel on Climate Change (IPCC). 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.https://www.ipcc.ch/report/ar5/syr/

Janzen, F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. Proceedings of the National Academy of Sciences 91(16):7847–7490.

Jarnevich, C. S., N. E. Young, C. C. Thomas, P. Grissom, D. Backer, and L. Frid. 2020. Assessing ecological uncertainty and simulation model sensitivity to evaluate and invasive plant species' potential impacts to the landscape. Scientific Reports 10:19069. Available at: https://doi.org/10.1038/s41598-020-75325-w

Jones, C. A. 2008. *Mycoplasma agassizii* in the Sonoran population of the desert tortoise in Arizona. Master of Science Thesis. University of Arizona. 126 pp.

Jones, C. A. 2010. E-mail correspondence from Cristina Jones, Turtles Project Coordinator, Arizona Game and Fish Department, regarding the incidence of potential gunshot deaths of Sonoran desert tortoises in the vicinity of Sugarloaf Mountain on the Cave Creek Ranger District of the Tonto National Forest in Arizona. (April 13, 2010).

Jones, C. A. 2021. Email correspondence dated May 5, 2021, from Cristina Jones (Turtles Project Coordinator, Arizona Game and Fish Department) regarding preliminary results from post-fire monitoring within and adjacent to the perimeter of the 2020 Bush Fire. Received at 1051 hrs.

Jones, T. R. and C. Rubke. 2021. Email correspondence dated August 27, 2021, from Thomas R. Jones (State Herpetologist, Arizona Game and Fish Department) and Chad Rubke (Desert Tortoise Biologist, Arizona Game and Fish Department) providing a summary of the Sonoran desert tortoises Long-term Monitoring Plots. Received at 1516 hrs.

Jurand, B. S., S. R. Abella, and A. A. Suazo. 2013. Soil seed bank longevity of the exotic annula grass *Bromus rubens* in the Mojave Desert, USA. Journal of Arid Environments 94:68–75.

Kessler, K. 2014. Email response to U. S. Fish and Wildlife Service questionnaire regarding the conservation and status of the Sonoran desert tortoise. Received December 10, 2014.

Kimble, S. J. A., O. E. Rhodes Jr., and R. N. Williams. 2014. Unexpectedly Low Rangewide Population Genetic Structure of the Imperiled Eastern Box Turtle *Terrapene c. Carolina*. PLoSOne 9: e92274.

Lamb, T. and A. M. McLuckie. 2002. Genetic differences among geographic races of the desert tortoise. pp. 67-85 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Lamb, T., J. C. Avise, and J. W. Gibbons. 1989. Phylogeographic patterns in mitochondrial DNA of the desert tortoise (*Xerobates agassizii*), and evolutionary relationships among the North American gopher tortoises. Evolution 43(1):76–87.

Lamberski, N. 2013. Body condition scores for desert tortoises. Unpublished technical guidance from the San Diego Zoo Safari Park; Escondido, CA. 3 pp.

Lambert, A. M., C. M. D'Antonio, and T. L. Dudley. 2010. Invasive species and fire in California ecosystems. Fremontia 38:2/38:3:29–36.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist. 142:911–927.

Latch E. K., W. I. Boarman, A. Walde, and R. C. Fleischer. 2011. Fine-scale analysis reveals cryptic landscape genetic structure in desert tortoises. PLoS ONE 6:e27794.

Leavitt, D. J. and H. A. Hoffman. 2014. Assessing the efficacy of the desert tortoise fencing and crossing structures between mile posts 204-206 of State Route 87. Final report submitted to the Arizona Department of Transportation. 15 pp.

Leavitt, D. J., C. A. Rubke, and H. A. Hoffman. 2016. A spatially explicit model of functional connectivity for Sonoran desert tortoises (*Gopherus morafkai*) on the Arizona Army National Guard Florence Military Reservation. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 26 pp.

Leavitt, D. J., C. A. Rubke, and W. L. Crumbo. 2017. INRMP Required species monitoring: Sonoran desert tortoise (*Gopherus morafkai*) radio-telemetry on the National Guard Florence Military Reservation. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 29 pp.

Lehman, R. 2021. Email correspondence from Robert Lehman (Biologist, Arizona Ecological Services Office, U.S. Fish and Wildlife Service) regarding proposed development of the Interstate 11 corridor through Arizona. Received June 6, 2021; 1632 hrs.

Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. R News vol. 2/3:18–23.

Lovich, J. E., R. C. Averill-Murray, M. Agha, J. R. Ennen, and M. Austin. 2017. Variation in annual clutch phenology of Sonoran desert tortoises (*Gopherus morafkai*) in central Arizona. Herpetologica 73(4):313–322.

Lowery, S. F., S. T. Blackman, and D. D. Grandmaison. 2011. Tangerine Road and La Cholla Boulevard mortality hotspot evaluation. Technical report prepared for the Town of Oro Valley Public Works Operations Division and the Town of Marana Environmental Engineering Division, Pima County, Arizona. Arizona Game and Fish Department. 42 pp.

Lutz, C. L., J. D. Riedle, and R. C. Averill-Murray. 2005. Desert tortoise habitat use and home range size on the Florence Military Reservation: final report. Nongame and Endangered Wildlife Program Technical Report 242. Arizona Game and Fish Department, Phoenix, Arizona. 47 pp.

Marlow, R. W. and K. Tollestrup. 1982. Mining and exploration of natural mineral deposits by the desert tortoise (*Gopherus agassizii*). Animal Behavior 30:475-478.

Martin, B. E. and T. R. Van Devender. 2002. Seasonal diet changes in *Gopherus agassizii* (desert tortoise) in desert grassland of southern Arizona and its behavioral implications. Herpetological Natural History 9(1):31–42.

McAuliffe, J.R. and E.P. Hamerlynck. 2010. Perennial plant mortality in the Sonoran and Mojave deserts in response to severe, multi-year drought. Journal of Arid Environments 74:885-896.

McCoy E.D., Aguirre G., Katzmeir R.T., and Tracy, C.R. 2014. Demography of North American Tortoises in Rostal D.C., McCoy E.D., Mushinsky H.R. (eds.), Biology and Conservation of North American Tortoises. Johns Hopkins University Press, Baltimore, MD, USA.

McDonald, C. J. and G. R. McPherson. 2011. Fire behavior characteristics of buffelgrass-fueled fires and native plant community composition in invaded patches. Journal of Arid Environments 75(2011):1147–1154.

McDonald, C. J. and G. R. McPherson. 2013. Creating hotter fires in the Sonoran Desert: buffelgrass produces copious fuels and high fire temperatures. Fire Ecology 9(2):26–39.

McDougall, C. A., A. B. Welsh, T. Gosselin, W. G. Anderson, and P. A. Nelson. 2017. Rethinking the influence of hydroelectric development on gene flow in a long-lived fish, the Lake Sturgeon *Acipenser fulvescens*. PLoSOne 12:e0174269.

McGowan, C. P., M. C. Runge, and M. A. Larson. 2011. Incorporating parametric uncertainty into population viability analysis models. Biological Conservation, 144(5), 1400-1408.

McGowan, C. P., D. H. Catlin, T. Shaffer, C. L. Gratto-Trevor, and C. Aron. 2014. Establishing endangered species recovery criteria using predictive simulation modeling. Biological Conservation 177:220–229.

McGowan, C. P., N. Allan, J. Servoss, S. Headwall, and B. Wooldridge. 2017. Incorporating population viability models into species status assessment and listing decisions under the U.S. Endangered Species Act. Global Ecology and Conservation 12:191–130.

McLaughlin, S. P. and J. E. Bowers. 1982. Effects of wildfire on a Sonoran Desert plant community. Ecology 63(1):246–248.

McLuckie, A. M., T. Lamb, C. R. Schwalbe, R. D. McCord. 1999. Genetic and Morphometric Assessment of an Unusual Tortoise (*Gopherus agassizii*) Population in the Black Mountains of Arizona. Journal of Herpetology 33(1):36–44.

McLuckie, A. M., M. R. M. Bennion, and R. A. Fridell. 2007. Tortoise mortality within the Red Cliffs Desert Reserve following the 2005 wildfires. Report to the Utah Division of Wildlife Resources. Publication No. 07-05. 30 pp.

Medica, P. A. and S. E. Eckert. 2007. *Gopherus agassizii* (desert tortoise): food/mechanical injury. Herpetological Review 38(4):446–448.

Meir, E., and W. F. Fagan. 1999. Will observation error and biases ruin the use of simple extinction models? Conservation Biology 14:148–154.

Meyer, W. W., P. R. Ogden, K. E. Cline, E. Lamar Smith, G. B. Ruyle, F. K. Meyer, and J. A. Cordrey. 2010. An eighteen year study of population dynamics, diet and health of the Sonoran desert tortoise (*Gopherus agassizii*) in the San Pedro Valley of southern Arizona. Unpublished report submitted to the U.S. Fish and Wildlife Service. 54 pp.

Middleton, D. A. J., A. R. Veitch, and R. M. Nisbet. 1995.The effect of an upper limit to population size on persistence time. Theoretical Population Biology 48:277–305.

Molina-Padilla, G. and T. R. Van Devender. 2019. *Gopherus morafkai* (Morafka's desert tortoise). Geographic Distribution. Herpetological Review 50(4):744–745.

Murphy, R. W., K. H. Berry, T. Edwards, A. E. Leviton, A. Lathrop, and J. D. Riedle. 2011. The dazed and confused identity of Agassiz's land tortoise, *Gopherus agassizii* (Testudines, Testudinidae) with the description of a new species, and its consequences for conservation. ZooKeys 113:39-71. doi: 10.3897/zookeys.113.1353.

Murray, I. 2021. Partner review submittal regarding the draft species status assessment report for the Sonoran desert tortoise. Submitted to the US Fish and Wildlife Service on August 16, 2021.

Nagy, K. A., B. T. Henen, and D. B. Vyas. 1998. Nutritional quality of native and introduced food plants of wild desert tortoises. Journal of Herpetology 32(2):260–267.

Nagy, K. A., M. W. Tuma, and L. S. Hillard. 2011. Shell hardness measurement in juvenile desert tortoises, *Gopherus agassizii*. Herpetological Review 42(2):191-195.

National Oceanic and Atmospheric Administration (NOAA). 2021a. Drought information statement: Phoenix, AZ Weather Forecast Office (1:45 pm MST; May 23, 2021). National Weather Service. Phoenix, AZ. Available at: https://www.drought.gov/drought-information-statements.

National Oceanic and Atmospheric Administration (NOAA). 2021b. Drought information statement: Tucson, AZ Weather Forecast Office (6:10 pm MST; May 28, 2021). National Weather Service. Phoenix, AZ. Available at: https://www.drought.gov/drought-information-statements.

Notaro, M., A. Mauss, and J. W. Williams. 2012. Projected vegetation changes for the American Southwest: combined dynamic modeling and bioclimactic-envelope approach. Ecological Applications. 22(4):1365–1388.

Nussear, K. E., and T. D. Tuberville. 2014. Habitat characteristics of North American tortoises: chapter 9. pp. 77-84 *in* Rostal, D. C., E. D. McCoy, and H. R. Mushinsky (ed.). 2014. Biology and Conservation of North American Tortoises. John Hopkins University Press. Baltimore, MD.

Oftedal, O. T. 2002. Nutritional ecology of the desert tortoise in the Mohave and Sonoran deserts. pp. 194–241 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Oftedal, O. T. 2007. Nutritional ecology of the Sonoran desert tortoise. Final Report to the Arizona Game and Fish Department. Heritage Grant I04004. 83 pp.

Ogden, P. R. 1993. Diets of desert tortoise (*Xerobates agassizii*) along the San Pedro watershed in Arizona. Symposium of Vegetation Management of Hot Desert Rangeland Ecosystems. July 28-30, 1993. Phoenix, Arizona. 8 pp.

Olsson, A. D., J. L. Betancourt, M. A. Crimmins, and S. E. Marsh. 2012a. Constancy of local spread rates for buffelgrass (*Pennisetum ciliare* L.) in the Arizona Upland of the Sonoran Desert. Journal of Arid Environments 87:136–143.

Olsson, A. D., J. Betancourt, M. P. McClaran, and S. E. Marsh. 2012b. Sonoran Desert ecosystem transformation by a C_4 grass without the grass/fire cycle. Diversity and Distributions 18:10–21.

Organ Pipe Cactus National Monument (OPCNM). 2011. Organ Pipe Cactus National Monument: Superintendent's 2010 report on natural resource vital signs. National Park Service, Ajo, Arizona. 27 pp.

Ortenburger, A. I. and R. D. Ortenburger. 1927. Field observations on some amphibians and reptiles of Pima County, Arizona. Proceedings of the Oklahoma Academy of Sciences. 6:101–121.

Ouren, D. H., C. Haas, C. P. Melcher, S. C. Stewart, P. D. Ponds, N. R. Sexton, L. Burris, T. Fancher, and Z. H. Bowen. 2007. Environmental effects of off-highway vehicles on Bureau of Land Management lands: a literature synthesis, annotated bibliographies, extensive bibliographies, and internet resources: U. S. Geological Survey, Open-File Report 2007-1353, 225 pp.

Owens, A. K., C. A. Jones, and A. K. Bartoli. 2019. *Gopherus morafkai* (Sonoran desert tortoise). Minimum size at reproduction. Natural History Notes. Herpetological Review 50(4):772.

Palmer, K. S., D. C. Rostal, J. S. Grumbles, and M. Mulvey. 1998. Long-term sperm storage in the desert tortoise (*Gopherus agassizii*). Copeia 1998(3):702–705.

Pascale, S., W. R. Boos, S. Bordoni, T. L. Delworth, S. B. Kapnick, H. Murakami, G. A. Vecchi, and W. Zhang. 2017. Weakening of the North American monsoon with global warming. Nature Climate Change 7:806-813.

Pascale, S., S. B. Kapnick, S. Bordoni, and T. L. Delworth. 2018. The influence of CO_2 forcing on North American moisture surges. Journal of Climate 31:7949-7968.

Peters, M. P. and L. R. Iverson. 2016. Projected drought for the conterminous United States in the 21st century. Chapter 2 of "Effects of Drought on Forests and Rangelands in the United States. Publication of the U.S. Forest Service. Available at: https://www.fs.fed.us/research/publications/gtr/gtr_wo98/gtr_wo98_chapter2.pdf. Accessed: August 30, 2021.

Phoenix New Times. 2021. Arizona quietly sells 16,810 acres to Freeport-McMoRan for mining waste. Article printed on January 31, 2021. Available at: https://www.phoenixnewtimes.com/news/arizona-sells-land-to-freeport-mcmoran-for-mining-waste-in-bagdad-11433682. Accessed: June 24, 2021.

Pike, D. A., J. C. Chambers, J. L. Beck, M. L. Brooks, and B. A. Mealor. 2016. Land uses, fire, and invasion: exotic annual *Bromus* and human dimensions. Chapter 11 *In*: J. M. Germino, M. J., J. C. Chambers, and C. S. Brown (Eds.). 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western US: Causes, consequences, and management implications. Springer International Publishing. Switzerland. 475 pp.

Pinal County Comprehensive Plan. 2009. We create our future: Pinal County Comprehensive Plan. February, 2009, public hearing draft. 320 pp. + Appendices.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Ranching and Sonoran Desert Tortoise Working Group. Draft. 2015. Best management practices for ranching in Sonoran desert tortoise *(Gopherus morafkai)* habitat in Arizona. 40 pp. plus appendices.

Rieder, J. P., T. A. S. Newbold, and S. M. Ostoja. 2010. Structural changes in vegetation coincident with annual grass invasion negatively impacts sprint velocity of small vertebrates. Biological Invasions 12:2429–2439.

Rogstad, A. 2008. Southern Arizona buffelgrass strategic plan. Buffelgrass Working Group. Available at: http://www.buffelgrass.org/sites/default/files/bgstrategicplancomplete.pdf. Last accessed: December 7, 2014.

Rorabaugh, J. C. 2008. An introduction to the herpetofauna of mainland Sonora, México, with comments on conservation and management. Journal of the Arizona-Nevada Academy of Science 40(1):20–62.

Rorabaugh, J. C. 2010. Conservation of amphibians and reptiles in northwestern Sonora and southwestern Arizona. Pp. 181-204 *in* W. Halvorson, C. Schwalbe, and C. van Riper III (eds.) Southwestern Desert Resources. University of Arizona Press. Tucson, Arizona.

Rosen, P. C., M. L. Vaughn, C. Meléndez Torres, and A. E. Karl. 2014a. Distribution and conservation status of desert tortoises in northwestern Mexico. pp. 10-47 *in* Rosen, P. C. (ed.). 2014. Conservation status, ecology, and distribution of desert tortoises in Mexico: the Mexico tortoise project, 2001-2013. Final report to the U.S. Fish and Wildlife Service, Arizona Ecological Services Office. Scientific Support Program Grant No. GX11BD30EH81500. 161 pp.

Rosen, P. C., M. L. Vaughn, C. Meléndez Torres, and A. E. Karl. 2014b. Geographic patterns of mortality observed in desert tortoises in northwestern Mexico, 2001-2013. pp. 48-60 *in* Rosen, P. C. (ed.). 2014. Conservation status, ecology, and distribution of desert tortoises in Mexico: the Mexico tortoise project, 2001-2013. Final report to the U.S. Fish and Wildlife Service, Arizona Ecological Services Office. Scientific Support Program Grant No. GX11BD30EH81500. 161 pp.

Rosen, P. C., P. A. Holm, and E. B. Wirt. 2014c. Post-drought population resurvey of desert tortoises (*Gopherus morafkai*) in southwestern Arizona. pp. 70-95 *in* Rosen, P. C. (ed.). 2014. Conservation status, ecology, and distribution of desert tortoises in Mexico: the Mexico tortoise project, 2001-2013. Final report to the U.S. Fish and Wildlife Service, Arizona Ecological Services Office. Scientific Support Program Grant No. GX11BD30EH81500. 161 pp.

Rostal, D. C., E. D. McCoy, and H. R. Mushinsky (ed.). 2014. Biology and Conservation of North American Tortoises. John Hopkins University Press. Baltimore, MD.

Rubke, C. A., W. L. Crumbo, and D. J. Leavitt. 2017. Sonoran Desert Tortoise Population Surveys at Two Long-term Monitoring Plots in Arizona, 2016: Harquahala Mountains and Hualapai Foothills. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 51 pp.

Rubke, C. A. and D. J. Leavitt. 2017b. Radio-telemetry monitoring of Sonoran desert tortoises (*Gopherus morafkai*) along the proposed right-of-way for State Route 202L South Mountain Freeway. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 22 pp.

Rubke, C. A., W. L. Crumbo, and D. J. Leavitt. 2018. Sonoran Desert Tortoise Population Surveys at Three Long-term Monitoring Plots in Arizona, 2017: Bonanza Wash, Four Peaks, and Harcuvar Mountains. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 69 pp.

Rubke, C. A. and R. P. O'Donnell. 2018b. Radio-telemetry monitoring of Sonoran desert tortoises (*Gopherus morafkai*) on the Arizona Army National Guard Florence Military Reservation. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 31 pp.

Rubke, C. A., and R. P. O'Donnell. 2019a. Sonoran Desert Tortoise Population Surveys at Three Long-term Monitoring Plots in Arizona, 2018: Arrastra Mountains, East Bajada, and Little Shipp Wash. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 78 pp.

Rubke, C. A., and R. P. O'Donnell. 2019b. Radio-telemetry monitoring of Sonoran desert tortoises (*Gopherus morafkai*) on the Arizona Army National Guard Florence Military Reservation: 2019 report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 34 pp.

Rubke, C. A., and R. P. O'Donnell. 2020a. Sonoran Desert Tortoise Population Survey at the Eagletail Mountains Long-term Monitoring Plot 2019. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 32 pp.

Rubke, C. A. and R. P. O'Donnell. 2020b. Sonoran desert tortoise monitoring: Barry M. Goldwater Range-East – long-term monitoring plot. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 47 pp.

Rubke, C. A., and R. P. O'Donnell. 2020c. Radio-telemetry monitoring of Sonoran desert tortoises (*Gopherus morafkai*) on the Arizona Army National Guard Florence Military Reservation: 2020 report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 31 pp.

Rubke, C. A., and R. P. O'Donnell. 2021a. Sonoran Desert Tortoise Population Surveys at Four Long-term Monitoring Plots in Arizona, 2020: Granite Hills, Harcuvar Mountains, New Water Mountains, and San Pedro Valley. Final Report. Arizona Game and Fish Department, Phoenix, Arizona, USA. 79 pp.

Rubke, C. A., and R. P. O'Donnell. 2021b. Wintertime radio-telemetry monitoring of Sonoran desert tortoises (*Gopherus morafkai*) on the Arizona Army National Guard Florence Military Reservation. Arizona Game and Fish Department, Phoenix, Arizona, USA. 27 pp.

Sacco, J. 2007. Telephone interview with Mr. Joe Sacco, OHV Coordinator, Arizona Game and Fish Department (July 5, 2007).

Salo, L. F. 2005. Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible modes for early introductions, subsequent spread. Biological Invasions 7:165–180.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5(1):18–32.

Sayre, N. F. and R. L. Knight. 2010. Potential effects of United States-Mexico Border hardening on ecological and human communities in the Malpai Borderlands. Conservation Biology 24(1):345–348.

Schmidt-Nielsen, K. and P. J. Bentley. 1966. Desert tortoise *Gopherus agassizii*: cutaneous water loss. Science 154(3751):911.

Seager, R., T. Mingfang, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. Huang, N. Harnik, A. Leetmaa, N. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316(5828):1181–1184.

Secretaria de Desarrollo Social (SEDESOL). 2010. NORMA Oficial Mexicana NOM-059-ECOL-2001, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. 77 pp.

Seiler, A. 2001. Ecological effects of roads: a review. Swedish University of Agricultural Sciences. 40 pp.

Sferra, S. 2010. Interview with Susan Sferra, Wildlife Biologist, Arizona Ecological Services Office, U.S. Fish and Wildlife Service (assigned to International Border issues). Subject of interview: environmental effects of enforcement activities and construction of barrier devices along the Arizona-Mexico International Border (July 2, 2010).

Sheffield, J., E.F. Wood, and M.L. Roderick. 2012. Little change in global drought over the past 60 years. Nature 491:435-440.

Shryock, D.F., T. C. Esque, and F. C. Chen. 2015a. A 30-year chronosequence of burned areas in Arizona—Effects of wildfires on vegetation in Sonoran Desert Tortoise (*Gopherus morafkai*) habitats: U.S. Geological Survey Open-File Report 2015-1060. 71 pp.

Shyrock, D. F., T. C. Esque, and F. C. Chen. 2015b. Topography and climate are more important drivers of long-term, post-fire vegetation assembly than time-since-fire in the Sonoran Desert, US. Journal of Vegetative Science. Available: https://doi.org/10.1111/jvs.12324.

Simmons, J. 2012. E-mail communication between Marit Alanen, Fish and Widllife Biologist, U.S. Fish and Wildlife Service and Jimmy Simmons, OHV Program Manager, Arizona Game and Fish Department. March 16, 2012 (1105 hrs).

Skelly, D. K., L. N. Joseph, H. P. Possingham, L. K. Freidenburg, T. J. Farrugia, M. T. Kinnison, and A. P. Hendry. 2007. Evolutionary responses to climate change. Conservation Biology 21(5):1353–1355.

Smith, D.R., N.L. Allan, C.P. McGowan, J.A. Szymanski, S.R. Oetker, and H.M. Bell. 2018. Development of a species status assessment process for decisions under the U.S. Endangered Species Act. Journal of Fish and Wildlife Management 9:302–320.

Social Science Data Analysis Network (SSDAN). 2000. Census 2000. Available at www.CensusScope.org

Sokol, O. M. 1971. Lithophagy and geophagy in reptiles. Journal of Herpetology 5(1-2):69-71.

Solomon, S., G. K. Plattner, R. Knutti, and P. Friedlingstein. 2009. Irreversible climate change due to carbon dioxide emissions. Proceedings of the National Academy of Sciences 106(6):1704–1709.

Spang, E. F., G. W. Lamb, F. Rowley, W. H. Radtkey, R. R. Olendorff, E. A. Dahlem, and S. Slone. 1988. Desert tortoise habitat management on the public lands: a rangewide plan. U. S. Bureau of Land Management. 31 pp.

Starfield, A.M. 1997. A pragmatic approach to modeling for wildlife management. The Journal of Wildlife Management 61:261–270.

Stevens, J. M. and J. S. Fehmi. 2009. Competitive effect of two nonnative grasses on a native grass in southern Arizona. Invasive Plant Science and Management 2:379–385.

Stevens, J. and D. A. Falk. 2009. Can buffelgrass invasions be controlled in the American Southwest? Using invasion ecology theory to understand buffelgrass success and develop comprehensive restoration and management. Ecological Restoration 24(7):417–427.

Stitt, E. and C. Davis. 2003. *Gopherus agassizii* (desert tortoise) caliche mining. Herpetological Review 34(1):57.

Strittholt, J.R., S.A. Bryce, B.C. Ward, and D.M. Bachelet. 2012. Sonoran Desert rapid ecoregional assessment report. Prepared for the U.S. Department of the Interior, Bureau of Land Management, Denver, Colorado. 222 pp. + appendices.

Stubben, C.J. and Milligan, B.G. 2007. Estimating and Analyzing Demographic Models Using the popbio Package in R. Journal of Statistical Software 22:11.

Sullivan, B. 2014. Email response to U. S. Fish and Wildlife Service questionnaire regarding the conservation and status of the Sonoran desert tortoise. Received December 30, 2014.

Sullivan, B. K. 2021. Correspondence dated January 4, 2021, in response to December 2, 2021, public information request from the U.S. Fish and Wildlife Service regarding the Sonoran desert tortoise. 6 pp.

Sullivan, B. K. and T. M. Cahill. 2019. Seasonal timing of consumption of calcium-rich caliche in the Sonoran desert tortoise (*Gopherus morafkai*) in central Arizona. Chelonian Conservation and Biology 18(1):98–101.

Sullivan, B.K. and E. A. Sullivan. 2015. Winter basking by hatchling Sonoran desert tortoises, *Gopherus morafkai*. Sonoran Herpetologist, 28(1):10–11.

Sullivan, B. K. and E. Sullivan. 2016. *Gopherus morafkai* (Sonoran desert tortoise). Drinking behavior. Natural History Notes. Herpetological Review 47(1):123–124.

Sullivan, B.K. and E. A. Sullivan. 2018. Late spring mining of minerals by female Sonoran Desert Tortoises, *Gopherus morafkai*. Sonoran Herpetologist, 31(3):56-57.

Sullivan, B. K., R. Averill-Murray, K. O. Sullivan, J. R. Sullivan, E. A. Sullivan, and J. D. Riedle. 2014. Winter activity of the Sonoran desert tortoise (*Gopherus morafkai*) in central Arizona. Chelonian Conservation and Biology 13(1):114–119.

Sullivan, B. K., A. K. Owens, K. O. Sullivan, and E. A. Sullivan. 2016. Spatial ecology of Sonoran desert tortoises (*Gopherus morafkai*): I. Fidelity in home range, refuge use and foraging behavior. Journal of Herpetology 50:509–519.

Suzart de Albuquerque, F., M. A. Marcías-Rodríquez, A. Búrquez, and Y. Astudillo-Scalia. 2019. Climate change and the potential expansion of buffelgrass (*Cenchrus ciliaris* L., Poaceae) in biotic communities of southwest United States and northern Mexico. Biological Invasions 21:3335-3347.

Switalski, A. 2018. Off-highway vehicle recreation in drylands: A literature review and recommendations for best management practices. Journal of Outdoor Recreation and Tourism. Available: https://doi.org/10.1016/j.jort.2018.01.001.

Taylor, K., T. Brummer, M. L. Taper, A. Wing, and L. J. Rew. 2012. Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Diversity and Distributions 2012:1–10.

Thomas, K. A. and P. Guertin. 2007. Southwest exotic mapping program 2007: occurrence summary and maps of select invasive, non-native plants in Arizona. U.S. Geological Survey, Southwest Biological Science Center, Sonoran Desert Research Station and University of Arizona, School of Natural Resources. 85 pp.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araujo. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32:369–373.

Tohono O'odham Nation. 2021. Correspondence dated March 29, 2021, in response to December 2, 2021, public information request from the U.S. Fish and Wildlife Service regarding the Sonoran desert tortoise. 3 pp.

Tucker, A. M., C. P. McGowan, E. S. Mulero Oliveras, N. F. Angeli, and J. P. Zegarra. 2021. A demographic projection model to support conservation decision making for an endangered snake with limited monitoring data. Animal Conservation 24:291–301.

U.S. Bureau of Land Management (USBLM). 2001. National management strategy for motorized off-highway vehicle use on public lands. 54 pp.

U.S. Bureau of Land Management (USBLM). 2007. Record of decision and Lake Havasu Field Office approved resource management plan. 492 pp.

U.S. Bureau of Land Management (USBLM). 2010. Public submission in response to the Fish and Wildlife Service's notice of petition finding and initiation of status review: "Endangered and Threatened Wildlife and Plants; 90-Day Finding on a Petition To List the Sonoran Population of Desert Tortoise (*Gopherus agassizii*) as a Distinct Population Segment (DPS) With Critical Habitat" (Docket No. FWS-R2-ES-2009-0032). 20 pp.

U.S. Bureau of Land Management (BLM). 2010a. Record of decision for the approved resource management plan. Bradshaw-Harquahala. 242 pp.

U.S. Bureau of Land Management (BLM). 2010b. Record of decision for the approved resource management plan. Yuma Field Office. 408 pp.

U.S. Bureau of Land Management (BLM). 2012d. Approved resource management plan amendments/record of decision (ROD) for solar energy development in six southwestern states. 197 pp.

U.S. Bureau of Land Management (BLM). 2012e. Lower Sonoran record of decision and approved resource management plan. 182 pp.

U.S. Bureau of Land Management (BLM). 2013a. Abandoned Mines: A New Legacy. 36 pp.

U.S. Bureau of Land Management (BLM). 2013b. Ironwood Forest National Monument record of decision and approved resource management plan. 116 pp.

U.S. Bureau of Land Management (BLM). 2014. 2020 travel and transportation management vision. 27 pp.

U.S. Bureau of Reclamation (USBOR). 2011. West-side climate risk assessments: bias-corrected and spatially downscaled surface water projections. Technical Memorandum No. 86-68210-2011-01. 138 pp.

U.S. Fish and Wildlife Service (USFWS). 2015. Species status assessment for the Sonoran desert tortoise. Version 1.0, September 2015. U.S. Fish and Wildlife Service, Southwest Region, Albuquerque, NM. 95 pp. plus appendices.

U.S. Fish and Wildlife Service (USFWS). 2016. USFWS Species Status Assessment Framework: an integrated analytical framework for conservation. Version 3.4 dated August 2016. 21 pp.

U.S. Geological Survey (USGS). 2005. Map of average annual precipitation for Arizona. Available at: http://nationalmap.gov/small_scale/printable/images/pdf/precip/pageprecip_az3.pdf. Accessed: 05-11-2015.

U.S. Government Accountability Office (USGAO). 2009. Enhanced Planning Could Assist Agencies in Managing Increased Use of Off-Highway Vehicles. Report to the Subcommittee on National Parks, Forests and Public Lands, Committee on Natural Resources, House of Representatives. 60 pp.

U.S. National Park Service (NPS). 2006. Management policies. 180 pp.

U.S. National Park Service (NPS). 2014. Restoration management plan environmental assessment. Saguaro National Park. Tucson, Arizona. 201 pp.

Van Devender, T. R. 2002. Natural history of the Sonoran tortoise in Arizona: life in a rock pile. pp. 3–28 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Van Devender, T. R., R. C. Averill-Murray, T. C. Esque, P. A. Holm, V. M. Dickinson, C. R. Schwalbe, E. B. Wirt, and S. L .Barrett. 2002. Grasses, mallows, desert vine, and more. pp. 160–193 *in* Van Devender, T. R (ed.). 2002. The Sonoran Desert Tortoise: Natural History, Biology, and

Conservation. The University of Arizona Press and the Arizona-Sonora Desert Museum. Tucson, Arizona.

Van Devender, T. R. and M. Dimmitt. 2006. Final report on "conservation of Arizona Upland Sonoran Desert habitat. Status and threats of buffelgrass (*Pennisetum ciliare*) in Arizona and Sonora. Project No. 2004-0013-003. Arizona-Sonora Desert Museum. Tucson, Arizona. 28 pp.

Van Devender, T. R., R. S. Felger, A. L. Reina-Guerrero, and J. J. Sanchez-Escalante. 2009. Sonora: non-native plants and invasive plants pp. 85-124 *in* Van Devender, T. R., F. J. Espinosa-Garcia, B. L. Haper-Lore, and T. Hubbard (eds). 2009. Invasive plants on the move: controlling them in North America. Based on presentations from Weeds Across Borders 2006 Conference. Arizona-Sonora Desert Museum, Tucson, Arizona. 422 pp.

Van Riper III, C., J. R. Hatten, J. T. Giermakowski, D. Mattson, J. A. Holmes, M. J. Johnson, E. M. Nowak, K. Ironside, M. Peters, P. Heinrich, K. L. Cole, C. Truettner, and C. R. Schwalbe. 2014. Projecting climate effects on birds and reptiles of the southwestern United States. U.S. Geological Survey Open-File Report 2014–1050. 100 pp. Available at: http://dx.doi.org/10.3133/ofr20141050. Last accessed: December 5, 2014.

Vaughan, S. L. 1984. Home range and habitat use of the desert tortoise (*Gopherus agassizii*) in the Picacho Mountains, Pinal County, Arizona. Thesis presented in partial fulfillment of the requirements for the degree of Master of Science. Arizona State University. Tempe, Arizona. 124 pp.

Walde, A. D., M. L. Harless, D. K. Delaney, and L. L. Pater. 2007b. Osteophagy by the desert tortoise (*Gopherus agassizii*). The Southwestern Naturalist 52(1):147–149.

Walker, M. P. and V. Pavlakovich-Kochi. 2003. The State of the Arizona-Sonora Border Region: Shared Pollution, Shared Solutions. Unpublished paper. 35 pp. Available at: http://www.scerp.org/bi/BIV/AZSon.pdf

Walther, G. R, E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Waples, R.S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. Journal of Heredity 89:438–450.

Watling, J. I., L. A. Brandt, D. N. Bucklin, I. Fujisaki, F. J. Mazzotti, S. S. Romanach, and C. Speroterra. 2015. Performance metrics and variance partitioning reveal sources of uncertainty in species distribution models. Ecological Modelling 309:48–59.

Webb, A. D. 2020. Pima County ecological monitoring program's monitoring protocol for tracking invasive plant occurrences. Ecological Monitoring Program, Pima County Multi-species Conservation Plan. Report to the U.S. Fish and Wildlife Service, Tucson, Arizona. 68 pp.

Weiss, J. L. and J. T. Overpeck. 2005. Is the Sonoran Desert losing its cool? Global Change Biology 11:2065–2077.

Weltzin, J. F. M. E. Loik, S. Schwinning, D. G. Williams, P. A. Fay, B. M. Haddad, J. Harte, T. E. Huxman, A. K. Knapp, G. Lin, W. T. Pockman, M. R. Shaw, E. E. Small, M. D. Smith, S. D. Smith, D. T. Tissue, and J. C. Zak. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53(10):941–952.

Willard, T. E. 2014. Email response to U. S. Fish and Wildlife Service questionnaire regarding the conservation and status of the Sonoran desert tortoise. Received December 15, 2014.

Woodbury, A. M. and R. Hardy. 1948. Studies of the desert tortoise (*Gopherus agassizii*). Ecological Monographs 18(2):145–200.

Woodman, P., T. Poole, and J. Smith. 2009. Desert Tortoise Population Survey at Three Plots in Arizona, Fall, 2008. Kiva Biological Consulting Co., Inyokern, CA. Report the Arizona Game and Fish Department. 97 pp.

Zouhar, K., J. K. Kapler, S. Sutherland, and M. Brooks. 2008. Wildland fire in ecosystems: fire and nonnative invasive plants. Gen. Tech. Rep. RMRS-GTR-42-vol. 6. Ogden, Utah. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 355 pp.

Zylstra, E. R. 2008. Effects of free-roaming dogs on desert tortoise populations in Saguaro National Park. School of Natural Resources, University of Arizona, Tucson, Arizona. Report to Saguaro National Park. 26 pp.

Zylstra, E. R. 2021. Email correspondence dated June 18, 2021, from Erin Zylstra (Postdoctoral Research Associate, Department of Integrative Biology, Michigan State University) regarding demography modeling of Sonoran desert tortoises. Received at 0921 hrs.

Zylstra, E. R. and R. J. Steidl. 2008. Habitat use by Sonoran Desert tortoises. Journal of Wildlife Management 73(5):747–754.

Zylstra, E. R. and R. J. Steidl. 2009. Designing a framework for monitoring Sonoran desert tortoises (*Gopherus agassizii*) in Arizona. School of Natural Resources, University of Arizona, Tucson, Arizona. Report to Arizona Game and Fish Department. 66 pp.

Zylstra, E. R. and D. E. Swann. 2009. A history of tortoise research at Saguaro National Park. Natural Resource Report NPS/SODN/NRR – 2009/100. National Park Service, Fort Collins, Colorado. 50 pp.

Zylstra E. R. and R. J. Steidl. 2021. Demography of Sonoran desert tortoises in Arizona, 1987-2020. Unpublished report submitted to the Arizona Game and Fish Department. Phoenix, AZ. 22 pp.

Zylstra, E. R., R. J. Steidl, C. A. Jones, and R. C. Averill-Murray. 2013. Spatial and temporal variation in survival of a rare reptile: a 22-year study of Sonoran desert tortoises. Oecologia 173:107–116.