



Original Research Article

Incorporating population viability models into species status assessment and listing decisions under the U.S. Endangered Species Act



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ARTICLE INFO

Article history:

Received 20 March 2017

Received in revised form 27 September 2017

Accepted 27 September 2017

Keywords:

Climate effects on viability
Endangered species listing decisions
Parametric uncertainty
Sensitivity analysis
Sonora desert tortoise

ABSTRACT

Assessment of a species' status is a key part of management decision making for endangered and threatened species under the U.S. Endangered Species Act. Predicting the future state of the species is an essential part of species status assessment, and projection models can play an important role in developing predictions. We built a stochastic simulation model that incorporated parametric and environmental uncertainty to predict the probable future status of the Sonoran desert tortoise in the southwestern United States and North Central Mexico. Sonoran desert tortoise was a Candidate species for listing under the Endangered Species Act, and decision makers wanted to use model predictions in their decision making process. The model accounted for future habitat loss and possible effects of climate change induced droughts to predict future population growth rates, abundances, and quasi-extinction probabilities. Our model predicts that the population will likely decline over the next few decades, but there is very low probability of quasi-extinction less than 75 years into the future. Increases in drought frequency and intensity may increase extinction risk for the species. Our model helped decision makers predict and characterize uncertainty about the future status of the species in their listing decision. We incorporated complex ecological processes (e.g., climate change effects on tortoises) in transparent and explicit ways tailored to support decision making processes related to endangered species.

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Assessment of a species' biological status is a key part of U.S. Endangered Species Act decision-making by the U.S. Fish and Wildlife Service (Doremus, 1997; Regan et al., 2012; Smith et al., in review). Historically, status assessments have included current abundance estimation, recent population trends, and an accounting of past and on-going factors affecting the species (Waples et al., 2013). However, predictive modeling can play a crucial role in management decisions for protected species by incorporating qualitative information into explicit quantitative risk assessments (Smith et al., in review, McGowan and Ryan, 2009; McGowan and Ryan, 2010). Model-based predictions can project future population size and growth, present the

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uncertainty in those predictions, and assess the effectiveness of management actions on future population status (Morris and Doak, 2002). Explicit predictions about future outcomes, and the uncertainty associated with those predictions, allow decision makers to understand and base their decisions on the likely future status of, and risks to, a species.

Population viability models have a long history of use in assessment of species at risk of endangerment or extinction and in assessing the relative importance of demographic parameters for species viability (e.g., Boyce, 1992; Morris and Doak, 2002). More recently researchers and managers are applying population viability-type models to support specific decision contexts for species conservation (e.g., McGowan and Ryan, 2009; New et al., 2012; Converse et al., 2013; Doak et al., 2015; Wolf et al., 2015; Robinson et al., 2016). Models tailored to specific decision contexts may not allow for broad advances in population ecology theory, but they can support management decisions by evaluating uncertainties and stochastic elements that often impede decision making. One key feature to making models especially useful in decision contexts is to work directly with decision-makers to establish desired model outputs and formats to aid in decision making (Smith et al., in review).

Decisions on whether or not to list species as endangered (i.e., in danger of extinction) or threatened (i.e., likely to become endangered in the future) under the Endangered Species Act could benefit from explicit models that characterize uncertainty in predictions. Deciding to list or not list a species comes with the risk of providing a species protection that is not needed, or not providing protection to a species that might require protection to avoid extinction. The risk assessments that support these important decisions could be greatly enhanced in some cases by explicit extinction probability predictions, and the predicted range of future population status (e.g., estimated median future abundance and the 2.5 and 97.5 percentiles on future abundance). Explicit presentation of these uncertainties allows decision makers to understand the most likely future state of a population and species, and also provide an estimate of the probability that the future state of the population is lower or higher than the most likely prediction. If done effectively, a decision-maker can visualize and understand what the distribution of future population status is and use that information to determine whether protection is warranted. Tailored models can incorporate the best available demographic data, specific threats, and management benefits experienced by populations to project demographic and environmental stochasticity along with parametric uncertainty. Models specifically tailored to a decision context allow for developing scenarios that evaluate ongoing and future influences on populations and species with greater specificity than a sensitivity analysis in a traditional population viability analysis (e.g., Morris and Doak, 2002).

We built a demographic population viability model to represent Sonoran desert tortoise (*Gopherus morafkai*, hereafter SDT) populations in Arizona, U.S.A. and Sonora, Mexico. The model was based on the best available demographic data and published analyses, and it included parametric and environmental variation as sources of uncertainty in the projections (McGowan et al., 2011). The model predicts the probability of quasi-extinction (i.e., the probability of abundance declining to less than a pre-determined abundance threshold) at each time step under current habitat and environmental conditions and possible future scenarios of changing habitat and environmental conditions. Our work focused on predicting future extinction risk because the decision-makers in the U.S. Fish and Wildlife Service desired some assessment of future extinction probability and because the Endangered Species Act listing requirements are focused on imminent extinction probability. We also incorporated a framework to evaluate a wide array of future possible conditions and estimate the relationship between those varied future conditions and quasi-extinction probability through regression analysis of the model output. For the purposes of this modeling exercise and as part of the species status assessment, hereafter SSA, we are treating the species as two large populations, one in Arizona, U.S. and one in Sonora, Mexico (U.S. Fish and Wildlife Service, 2015). The Service decided to subdivide the species into two populations because of differing management practices, grazing practices, invasive grass communities and other issues in Arizona vs. Sonora. We anticipated that, though the species are genetically and ecologically indistinct, future scenarios would be different for these two portions of the range. The model was a key part of the SSA that was conducted in order to inform whether or not to list the SDT as a threatened or endangered species under the Endangered Species Act (U.S. Fish and Wildlife Service, 2015).

1. Methods

1.1. Model development

We built a female-only, stage-structured matrix model to reflect the SDT life cycle (Fig. 1). The conceptual model of the SDT's life cycle was elicited from taxon experts, based on published literature (Van Devender, 2002; Rostal et al., 2014), and Mojave desert tortoise (*Gopherus agassizii*) population models (Darst et al., 2013). The life cycle diagram presents three main life stages (Adults (A), small juveniles (J_1) and large juveniles (J_2)). Small juveniles, once hatched, can survive each year and remain in the J_1 age class for approximately 5 years (McCoy et al., 2014). Little is known about the habits or survival rates of J_1 because they are difficult to detect in the wild and, therefore, have received little study. However, given its size (<40 mm), J_1 is expected to be the life stage most susceptible to predation and other causes of mortality (McCoy et al., 2014), and survival rates of newly hatched tortoises in their first year are presumed to be very low. McCoy et al. (2014), 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 large juvenile stage. Larger juveniles have approximately 0.77 annual survival and remain in J_2 for 10 or 12 years (until approximately the age of 15) and then transition into the breeding adult age class. Adults have very high survival rates, 0.93–0.98 annually (Zylstra et al., 2013), and, given these high survival rates, live for many years as adults. Approximately 52% of females will breed in any given year, and females lay small clutches of approximately 5 eggs with

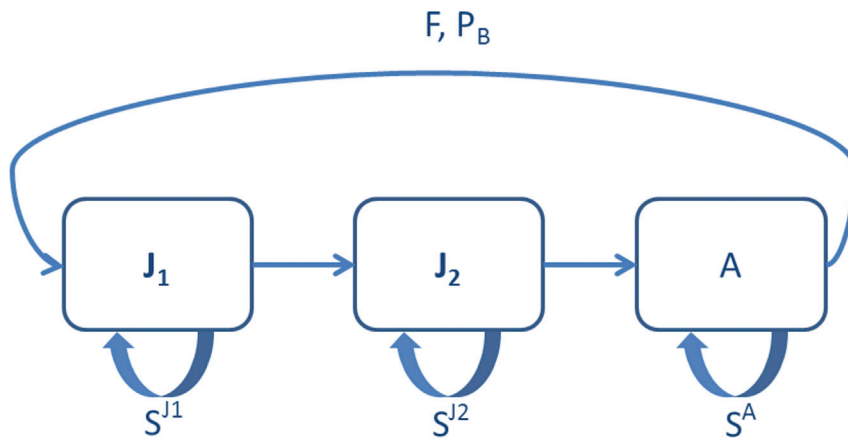


Fig. 1. Life cycle diagram of SDT. Adults (A) produce hatchlings (J_1) (via fecundity (F) and breeding probability (P_b) parameters) and which can survive (S^{J1}) and after approximately 5 years become older juveniles (J_2) which can survive (S^{J2}) and after an additional 10–12 become adults.

approximately equal sex ratios (~2.5 female eggs per female; Campbell et al., 2014), but many nests most likely fail before hatching, as is the case with other species of North American tortoises (McCoy et al., 2014).

In our simulation model, we set mean annual adult survival (\bar{S}^A) to 0.95 (SD = 0.009), based on the results of Zylstra et al. (2013). We created a probability of annual breeding parameter (P_b) with mean of 0.52 (SD = 0.06) and a fecundity (F) or clutch size parameter with mean of 2.5 eggs per female (SD = 0.5; Campbell et al., 2014). Zylstra et al. (2013) estimated annual survival of large juveniles (\bar{S}^J) to average 0.77 (SD = 0.032), but they had limited data informing these parameter estimates. Small juvenile survival rates were largely unknown because of the difficulties in studying the early life stages. Experts agreed that generation time for SDT is approximately 25 years. We used the ‘PopBio’ package (Stubben and Milligan, 2007) in program R (R core development team, 2013), using the well-studied adult survival and fecundity rates, to test different values for the lesser known parameters (small juvenile survival, \bar{S}^{J1} ; small to large juvenile transition, \bar{T}^{12} ; large juvenile to adult transition, \bar{T}^{2A}). Our goal was to see what values for those unknown parameters led to the estimated 25-year generation time. The “generation.time” function calculates the expected average time between generations, defined as the average age at which a female produces her median off spring (Morris and Doak, 2002; Stubben and Milligan, 2007) for an input projection matrix. We calculated the expected generation time for a variety of matrices, varying the unknown parameters (i.e., \bar{S}^{J1} , \bar{T}^{12}) and selected values for those parameters that returned a generation time of 25 years. With this “trial and error” type approach we adjusted mean parameter values in the model and settled on mean annual small juvenile survival (\bar{S}^{J1}) of 0.006 (SD = 0.00012) and small to large juvenile transition (\bar{T}^{12}) of 0.083 (SD = 0.00032). In our model, the \bar{S}^{J1} parameter is very low, but it combines nest survival (hatching probability, see above) with the very low survival rates of the first few years of life (McCoy et al., 2014). Though uncertain and low, these early life stage parameters values are consistent with the life history strategy of other long-lived turtles (e.g., logger head sea turtles, Crouse et al., 1987). We set large juvenile survival and large juvenile to adult transition (\bar{T}^{2A}) to sum to the Zylstra et al. (2013) annual survival estimate of 0.77. Mean large juvenile annual survival (\bar{S}^{J2}) was set to 0.67, and the transition rate to adulthood (\bar{T}^{2A}) was set to 0.1, since the individuals stay in this stage for approximately 10 years, we assume that on average 10% transition annually. This assumption technically allows some individuals to transition to the breeding adult stage before reaching the typical age, however this is standard consequence of using a stage-based matrix model instead of an age-based model (Caswell, 2001). With these parameters, we constructed a projection matrix as follows:

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

We incorporated the projection into a stochastic simulation model that replicated the population 1000 times and projected the population 200 years into the future (i.e., approximately 8 generations). In the model survival rates (S_t^{J1} , S_t^{J2} , S_t^A), inter-size class transition rates (T_t^{12} , T_t^{2A}), and proportion of females that breed (P_b) were drawn from beta distributions derived from the mean and standard deviations described above, while fecundity rates (F_t) were drawn from a log-normal distribution. In addition to modeling temporal stochasticity using the standard deviation estimates and statistical

distribution draws described above, we used the methods described by McGowan et al. (2011) to incorporate parametric uncertainty into the adult survival. Published estimates of parameter variance did not partition variance into sampling and process variance (e.g. Gould and Nichols, 1998) and therefore parametric uncertainty levels for any of the parameters are unknown. The approach presented by McGowan et al. (2011) 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 (Fig. 1). 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 parameter mean and variance due to parametric uncertainty (McGowan et al., 2011). The parametric uncertainty modeling allows us to automate alternative parameterizations of the model to account for the fact that parameter estimates are uncertain because of small sample sizes with limited spatial coverage from the empirical mark-recapture and demographic studies (Meir and Fagan, 2000). The other standard deviations and variance parameters reported above were used in the model as temporal variability to mimic environmental stochasticity (McGowan et al., 2011).

The model predicted mean population growth rate, abundance (female adults), and the proportion of replicates that went quasi-extinct on an annual basis. We used two different thresholds for quasi-extinction, 2% and 4% of the estimated maximum possible population size (~7000 and 12,000 adult females in Arizona, respectively, and ~4000 and 8000 adult females in Sonora, respectively), to allow decision makers to see the implications of choosing a quasi-extinction threshold. Each year in the simulation, the program tallied the number of replicates that were below the quasi-extinction threshold independently of the previous or subsequent years. Our measure of quasi-extinction is therefore an annual snapshot of the proportion of population replicates that had declined to very low abundance. These two thresholds represented massive declines from current estimated abundances but these quasi-extinction levels would also represent densities of 0.6 and 1.2 total adult tortoises per km² under the low or high thresholds. Experts believed that these densities were probably below densities at which tortoises would be able to successfully find mates for sustaining reproduction. If SDT actually decline to these low abundances, it is more probable that they persist in small numbers of populations restricted to the highest quality habitats potentially subject to Allee effects and other negative effects of small, isolated populations. However, genetic analyses indicate that currently there is gene flow across the range of the species, despite what appears to be patchy distribution at large spatial scales (Averill-Murray et al., 2002). Our quasi-extinction thresholds reflect small population sizes near extirpation or extinction because the ESA is focused on protecting species that have some elevated risk of extinction. The threshold is, therefore, set at a very low population size, near extinction, in order to present the decision makers with the desired metrics about the population and its future status.

1.2. Conceptual model of SDT ecology and stressors

We organized a workshop of tortoise experts (see acknowledgements section for a list of the participating experts) where we elicited a conceptual model of SDT ecology seeking to identify ecological stressors to individuals and the populations. We used the basic concepts of conceptual modeling as a guide for developing the diagrams to represent SDT ecology and threats (Davies et al., 2006). The workshop participants used available scientific literature and experience to formulate opinions regarding ecology and potential environmental stressors to explore and evaluate.

At the meeting we discussed many potential population stressors, including invasive grasses, urbanization, recreational disturbance, released tortoise pets, road mortality, and many others. Experts identified climate change-induced drought as a potential major factor in SDT population viability. Some researchers have concluded recently that Sonoran Desert scrub habitat might expand under some climate change scenarios, thus benefitting SDT provided the species is able to move into expanding habitat at a rate commensurate with changes to its existing habitat (Van Riper et al., 2014). However, other researchers expect climate change to negatively impact tortoises (Zylstra et al., 2013) primarily through increasing severity and magnitude of drought (Seager et al., 2007; IPCC, 2014; Cook et al., 2015). To a lesser extent warming temperatures could affect sex ratios at the population level as atmospheric temperatures can affect nest temperatures that determine the sex of developing eggs (Janzen, 1994). Climate change could also affect quality of plants for SDT foraging by altered timing or intensity of seasonal monsoon rains that, in turn, could affect the annual probability of breeding, clutch size, and life-stage transitions (via juvenile growth rates). Climate change, via drought frequency and magnitude, might also affect survival rates of juvenile and adult tortoise, as Zylstra et al. (2013) reported a 0.1 to 0.15 decline in annual survival probability for marked tortoise during periods of drought, though overall estimated population growth rates were stable during that 22-year study, despite droughts.

The process of developing a conceptual model versus simply identifying important factors with experts allowed their input to aid model development. The experts identified a number of other concerns (e.g., such as invasive grasses, urbanization, human recreation) to explore with respect to SDT population viability, many of which are highly uncertain or lack data to formalize a functional relationship beyond conceptual linkages. Through that process, however, we identified two key factors with high potential to affect tortoise populations in the future: habitat availability and drought. Many of the stressors (nonnative grasses, wildfire, and various effects from urbanization) identified in the literature and in the conceptual modeling workshop affect SDT populations via changes in habitat quantity and quality, and climate change-induced drought could be accounted for in changes to annual survival of SDT. We incorporated these two primary factors into our simulation model and explored the effects of each on population viability.

1.3. Environmental parameters

To model the effects of limiting habitat quantity and quality on the population, we created a ceiling-type density-dependence function in the model (e.g., [Morris and Doak, 2002](#)), whereby if the population exceeded an established maximum population size ceiling (used interchangeable with carrying capacity hereafter), the proportion of females that breed (P_b) declined to zero. Ceiling-type density-dependent functions are simple and not ecologically realistic in simulating that all of the females in the population fail to breed in a single year once the carrying capacity is reached. However, reducing the P_b parameter to zero has the same effect as reducing P_b parameter to 80% or 50% of normal but reducing to zero affects the population faster. Thus, the population is more quickly restored to the carrying capacity when the population exceeds the ceiling threshold. Ceiling-type density-dependent functions lack biological detail but are standard in population viability modeling when the functional form of density-dependence in the population is unknown (e.g., [Morris and Doak, 2002](#); [McGowan and Ryan, 2009](#)). In addition, they are useful for capturing effects of density-dependence without speculating on the exact mechanism or mathematical formulation of density on demographic rates ([Lande, 1993](#); [Middleton et al., 1995](#); [Morris and Doak, 2002](#)). The maximum population size (i.e., the carrying capacity) in a given simulation was determined by the amount of habitat (km^2) in a given quality multiplied by the average expected density of adult female SDT for each of those habitat qualities. A separate geospatial analysis estimated availability of predicted potential SDT habitat and ranked the habitat conditions across the species range as high, medium, and low condition ([U.S. Fish and Wildlife Service, 2015](#)) based on land cover, vegetation type, slope, and elevation because these features are useful predictors of potential SDT habitat ([Zylstra and Steidl, 2008](#)). We further categorized potential habitat quality into primary, secondary, and tertiary suitability based on land management, proximity to urban areas, presence of invasive vegetation, and potential fire risk ([USFWS, 2015](#); [Smith et al., in review](#)). Using data from long-term monitoring plots ([Zylstra and Steidl, 2009](#)), we estimated densities of 17.1 per km^2 in areas of primary habitat, 9.4 per km^2 in secondary habitat, and 2.0 per km^2 in tertiary habitat ([U.S. Fish and Wildlife Service, 2015](#)). The model calculated maximum population size as follows:

$$Pop_{max} = (D_p \times A_p) + (D_s \times A_s) + (D_t \times A_t)$$

where D was the density in primary (subscript p), secondary (subscript s), and tertiary (subscript t) habitat where A is the area of habitat (in square kilometers).

We conducted two primary sets of simulations with this habitat-derived ceiling-type density-dependent function. First, we set specific habitat quality amounts derived from GIS analyses and simulated population changes under specific habitat scenarios. Within a simulation, we allowed the ceiling threshold to be reduced annually, to represent habitat loss or degradation over time. Secondly, we established a maximum habitat area drawn from a uniform random distribution ranging from 120% to 20% of current total habitat. We randomly assigned habitat into the three quality classes by multiplying the total by three randomly generated proportions that summed to 1.0. With this approach we could explore the effect of a wide variety of differing amounts of habitat and population ceilings on the probability of extinction through regression based sensitivity analyses (described in detail below).

We included a drought effect on survival of all age classes in our model. We drew a random value of the proportion of the population exposed to drought in any specific year from a beta distribution derived from historic drought data using the annual proportion of Arizona counties within the SDT range exposed to moderate to severe drought from 1900 to 2000 (Western Regional Climate Center, Reno, NV, West Wide Drought Tracker, <http://www.wrcc.dri.edu/wwdt/time/>; accessed 5/7/2015). We downloaded the 12-month average Palmer Drought Severity Index (PDSI) beginning in January and ending in December of each year from 1901 through 2000 for each of seven counties within all or a portion of the range of the SDT in Arizona. For each year, we determined whether each county had been in at least moderate drought, i.e., the PDSI was less than -1.99 for the 12 months ending in December. We divided the spatial area of the drought counties by the total area of the seven counties in the SDT range to approximate the annual average proportion of the SDT range that experienced moderate or higher drought. Annual survival for adults and juveniles exposed to drought was reduced to approximate the results reported in [Zylstra et al., \(2013\)](#). For the projection simulation model, survival became the weighted average of the animals exposed and not exposed to drought, for example for adult survival:

$$S_t^{A,d} = (P_{drought} \times S_t^A \times DE_t) + ((1 - P_{drought}) \times S_t^A)$$

where $P_{drought}$ is the proportion of the population exposed to drought and $S_t^{A,d}$ is the survival rate of adults for the full population, given the proportion that was exposed to drought. DE_t is the drought effect in a specific year which was modeled as a uniform random number between 0.8 and 0.99 (i.e., a 1%–20% reduction in survival due to the drought) to represent differing drought severity from year-to-year. Some droughts have low severity and do not affect survival much while others, especially multi-year droughts, can have greater effects on survival ([Zylstra et al., 2013](#)). With this framework, we can model a wide array of droughts of different magnitudes and spatial extents to account for possible impacts of climate change related to drought, and thus we examined the effect of intensity and magnitude of drought on extinction probability.

1.4. Model outputs

We used the model described above to run a set of 18 predetermined habitat, population, and climate-based scenarios (9 each for Arizona, U.S., and Sonora, Mexico, [USFWS, 2015](#)). The simulated scenarios combined different future habitat states and loss rates with different climate change intensities to represent a range of possible future ecological conditions for the SDT populations. For these scenarios, we set the initial population at carrying capacity for each region. We have no current data on actual population abundance, so we used available habitat as a proxy and assumed the habitat was saturated. We also tested the importance of differing starting populations using a regression sensitivity analysis described below. The model used 1000 replications to project annual population outcomes 200 years into the future under each scenario and tracked adult age class, population size, population growth rate (rate of annual change) and to project whether the population fell below the predetermined quasi-extinction threshold in each year.

1.5. Extinction sensitivity to drought and habitat loss

We used an analysis similar to [McGowan et al. \(2014\)](#) 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 between those factors to quasi-extinction probability ([Fig. 2](#)). For this analysis, we used 12,000 individuals as our quasi-extinction threshold. In the outermost loop of the model, we selected 1000 maximum total habitat areas and the mean proportions in each habitat quality category. The minimum possible values for total habitat was 20% of the current amount and the maximum was set at 120% of the current amount, derived from the separate GIS analysis of available habitat in Arizona and Sonora ([U.S. Fish and Wildlife Service, 2015](#)). We also selected 1000 values for increasing the mean of the proportion of the population exposed to droughts from a uniform distribution between 0.1 and 2.0 (representing between a 10% and 200% increase in the mean, i.e. mean population exposed to drought between 0.11 and 0.3 proportion of population). We multiplied this uniform random value by the empirically derived mean proportion of SDT exposed to drought value as the mean P_{drought} each year in that replicate of the simulation. Furthermore, we randomly selected 1000 random starting population sizes between 75,000 and 500,000 females. In the second loop ([Fig. 2](#)), the model replicated the population 1000 times for each of the 1000 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 1000 replicates, and those values were passed into the interior loop, also known as the annual loop ([Fig. 2](#)). The analysis projected the population 200 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 1000 replicates in the secondary loop, we saved the proportion of replicates that went quasi-extinct at 25 years, 50 years, 100 years, and 200 years into the future, alongside the maximum abundance values, the initial population size, and the mean proportion affected by drought for that set of replicates.

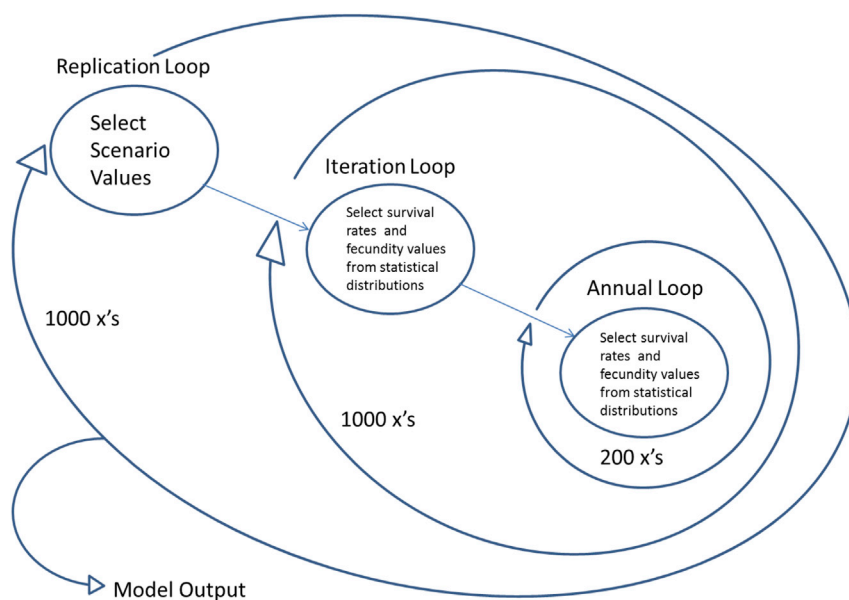


Fig. 2. Demonstration of the triple loop structure used in the SDT simulation model to generate 1000 probabilities of extinction with 1000 initial population sizes, habitat inputs and proportion of the population exposed to drought.

At the end of that simulation, we had 1000 measures of extinction probability at 25, 50, 100, and 200 years coupled with maximum abundance, initial abundance, and proportion exposed to drought. We used those results as data to assess binomial regression models of extinction probability with maximum abundance, initial abundance, and proportion exposed to drought as covariates in the regression models using a logit link function. Using AIC model selection criteria (Burnham and Anderson, 2004), we evaluated and compared multiple models of quasi-extinction. Models had one, two, or three covariates of mean drought, starting population size, and/or maximum population size. The regression parameters in those models show the relative probable effect of each covariate on the probability of quasi-extinction and whether the covariate has a positive or negative association with probability of quasi-extinction. With the regression parameters, we can also predict the probability of quasi-extinction for specified sets of covariate values. We used the regression parameters to generate tables of expected quasi-extinction probabilities under varying conditions.

2. Results

2.1. Continuation of current conditions

We used the simulation model to evaluate a set of baseline conditions and four future scenarios each for Arizona, U.S. (Table 1) and Sonora, MX (Table 2), which assume the continuation of current habitat and drought conditions given our uncertainty regarding population density and starting population size. The 'baseline' scenario represents the best possible case for SDT with no climate change-related effects on drought and all habitats in the best possible condition. The other four continuation of current condition scenarios in Arizona and Sonora project current conditions into the future (Table 1). In all scenarios the population declined over time with mean population growth rates slightly negative ($\lambda \approx 0.996$). Probability of quasi-extinction varied among scenarios because we used two different quasi-extinction thresholds (2% and 4% of maximum population size) to allow decision-makers to see the consequences of picking a quasi-extinction threshold. Under all continuation of current conditions scenarios for Arizona and Sonora, probability of quasi-extinction was ~ 0.00 at 50 years and <0.01 at 100 years was for scenarios with a 2% abundance quasi-extinction threshold and approximately 0.05 for all scenarios using the 4% abundance quasi-extinction threshold. In other words, there was less than a 0.01 probability of falling below 2% of the initial population and approximately 0.05 probability of falling below 4% of the initial population size 100 years into the future.

We note that results from all scenarios (continuation of current conditions and projected future conditions; see below) median abundance exhibited steep declines in the first few years, but those declines are a mathematical artifact of setting the initial population size equal to the population ceiling in the simulations. When the population starts at the carrying capacity, the median abundance will initially decline because a large proportion of the 1000 replicates will decline and those that do not decline cannot exceed the maximum population ceiling, therefore, the median representing the "middle trajectory" will decrease. These results do not mean that we expect to see immediate rapid decline in the population before growth rates stabilize after 10 or so years unless the population is at carrying capacity.

Table 1

Predicted population growth rates, change in median female abundances, and the probabilities of quasi-extinction (model outputs) for the baseline, four continuation of current conditions scenarios ("Scenarios 1–4"), and four projected future conditions scenarios ("Scenarios 5–8") in Arizona, U.S. at 50 and 100 years into the future. The scenarios had varying droughts, maximum population sizes (Max Pop), habitat loss rates, initial population sizes (Initial Pop), and quasi-extinction thresholds (Qe threshold).

Scenario inputs						Scenario outputs				
	Drought	Max Pop	Habitat loss rate	Initial Pop	Qe Threshold	Population growth rate	Median population change, 50 years	Qe 50 yrs	Median population change, 100 years	Qe 100 yrs
Baseline	Historic Drought	320,000	0	320,000	7000	0.997	6433	0.000	−3294	0.000
Scenario 1	Historic Drought 10%	290,000	0	290,000	7000	0.996	−12,507	0.000	−33,684	0.001
Scenario 2	Historic Drought 10%	140,000	0	140,000	12,000	0.996	−1880	0.000	−5887	0.031
Scenario 3	Historic Drought 10%	240,000	0	240,000	7000	0.995	−5726	0.000	−10,987	0.002
Scenario 4	Historic Drought 10%	120,000	0	120,000	12,000	0.995	−789	0.000	−6076	0.031
Scenario 5	Historic Drought 15%	290,000	9%	290,000	7000	0.996	−7955	0.000	−26783	0.000
Scenario 6	Historic Drought 15%	140,000	9%	140,000	12,000	0.996	−2575	0.000	−13767	0.030
Scenario 7	Historic Drought 25%	240,000	9%	240,000	7000	0.995	−14323	0.000	−42031	0.001
Scenario 8	Historic Drought 25%	120,000	9%	120,000	12,000	0.995	−11247	0.000	−28780	0.047

Table 2

Predicted population growth rates, change in median female abundances, and the probabilities of quasi-extinction (model outputs) for the baseline, four continuation of current conditions scenarios (“Scenarios 1–4”), and four projected future conditions scenarios (“Scenarios 5–8”) in Sonora, Mexico, at 50 and 100 years into the future. The scenarios had varying drought, maximum population size (Max Pop), habitat loss rates, initial population sizes (Initial Pop), and quasi-extinction thresholds (Qe threshold).

Scenario inputs					Scenario outputs					
	Drought	Max Pop	Habitat loss rate	Initial Pop	Qe Threshold	Population growth rate	Median population change, 50 years	Qe 50 yrs	Median population change, 100 years	Qe 100 yrs
Base line	Historic Drought	320,000	0	320,000	4000	0.997	5601	0.000	−523	0.004
Scenario 1	Historic Drought 10%	290,000	0	290,000	4000	0.997	338	0.000	−3571	0.005
Scenario 2	Historic Drought 10%	140,000	0	140,000	8000	0.997	891	0.000	−2060	0.028
Scenario 3	Historic Drought 10%	240,000	0	240,000	4000	0.997	−3198	0.000	−8147	0.001
Scenario 4	Historic Drought 10%	120,000	0	120,000	8000	0.996	−3621	0.000	−8823	0.044
Scenario 5	Historic Drought 15%	290,000	9%	290,000	4000	0.996	−5573	0.000	−17538	0.002
Scenario 6	Historic Drought 15%	140,000	9%	140,000	8000	0.996	−2749	0.000	−8941	0.059
Scenario 7	Historic Drought 25%	240,000	9%	240,000	4000	0.995	−7692	0.000	−16796	0.004
Scenario 8	Historic Drought 25%	120,000	9%	120,000	8000	0.995	−5653	0.002	−11769	0.086

2.2. Projected future conditions

The projected future scenario simulations increased the potential for drought (i.e., climate change effects) and annual habitat loss and degradation rates to mimic the effects of urbanization, wildfire, and exotic vegetation encroachment on habitat carrying capacity (U.S. Fish and Wildlife Service, 2015). We ran four future scenarios each for Arizona (Table 1) and for Sonora (Table 2). The simulations showed a decline in the median abundance and faster declines than the continuation of current conditions scenarios. Mean population growth in Arizona was approximately 0.99, meaning, on average populations declined by approximately 0.8% annually, and was 0.99 in Sonora. Quasi-extinction probabilities were higher than the “current conditions” scenarios, but were still dependent on whether 2% or 4% of the initial population was used as the quasi-extinction threshold. For the Arizona population, under the worst climate change and habitat loss scenario we simulated (Table 1, scenario 8), the probability of quasi-extinction was 0.00 at 50 years and 0.07 at 100 years. The worst-case scenario for Sonora (Table 2) had a probability of quasi-extinction of 0.00 at 50 years and 0.09 at 100 years.

2.3. Full simulation and regression modeling results

A regression model with maximum population size (*MaxPop*), initial female abundance (*NAI*), and mean drought exposure (*MDR*) as the independent variables and quasi-extinction probability as the dependent variable was the best model to explain variation in quasi-extinction probability at 100 years and 200 years. At 50 years, the regression model explained less of the variation in quasi-extinction probability but that is most likely because a smaller proportion of the population trajectories fell below the quasi-extinction threshold; at 25 years none of the simulated populations surpassed the quasi-extinction threshold so no regression model converged on beta parameter estimates. We tested regression models with drought as the only covariate, and, while these models performed well, the AIC model selection analysis indicated that adding initial abundance and maximum population size improved model fit. Differing levels of *MaxPop* relate to differing amounts of available habitat. The regression equation for 200 years was:

$$P_{Qe200} = -3.019 + (14.13 \times MDR) - (1.588e^{-6} \times NAI) - (1.145e^{-6} \times MaxPop).$$

The regression parameters indicate that drought has a relatively large and positive effect on quasi-extinction probability and initial population size and maximum population size have a smaller but significantly negative effects on quasi-extinction ($p < 0.01$ for both covariates). The regression equation for 100 years was:

$$P_{Qe100} = -5.602 + (18.42 \times MDR) - (5.363e^{-6} \times NAI) - (1.797e^{-6} \times MaxPop).$$

The regression equation for 50 years was:

$$P_{Qe50} = -10.68 + (2.894 \times MDR) - (3.429e^{-5} \times NAI) - (2.155e^{-6} \times MaxPop).$$

Generally, as the time of the simulation shortened, the strong positive effect of drought on quasi-extinction probability remained and the weaker, but significant, effect of NAI and *MaxPop* also remained.

With the regression parameter estimates (intercept and slope terms), we constructed tables demonstrating the changing expected probability of quasi-extinction under varying drought and initial abundance conditions, along with habitat-limited maximum population size (e.g., [Tables 3 and 4](#)). The tables enable us to visualize more effectively the relationship between these variables. We can also use the regression equation to calculate the expected quasi-extinction probability for any combination of values for the independent variables. Under this analysis, at 50 years, for example, there is very low probability of quasi-extinction (falling below fewer than 8000 females in Arizona) regardless of starting population size or drought magnitude. As another example, at 100 years quasi-extinction probability gets as high as 0.35 when, on average, 30% of the population is exposed to drought annually and there are only 100,000 females in the population initially. Whereas with, on average, 15% of the population exposed to drought and an initial abundance of 150,000 females, predicted quasi-extinction probability at 100 years was 0.025. These tables essentially allow us to evaluate additional future scenarios simultaneously within the range of possible future variation.

3. Discussion

Our model predicts steady, gradual decline in SDT population size over time and near zero quasi-extinction probabilities in the next 50–75 years (2–3 tortoise generations). Low extinction risk in this timeframe is not unexpected due, in part, to long life spans (i.e., high annual survival rates) of adult tortoises. With mean annual adult survival rates at 0.95, there is approximately a 0.36 probability that an adult SDT alive today will still be alive 20 years in the future and a 0.21 probability that they will be alive in 30 years. The high capacity for longevity in the SDT population likely insulates the species from high short-term extinction risk. However, population modeling analyses for the Mojave Desert Tortoise, which has a similarly long life span under natural conditions, predicted steep and swift declines in population abundance and high extinction risk in a matter of a few decades even with management intervention ([Doak et al., 1994](#); [Reed et al., 2009](#)).

Predicted habitat loss and habitat degradation rates had a small overall effect on projected future abundance and on estimated quasi-extinction probability in our simulations. Over the range of habitat availability and habitat loss rates that we simulated, habitat was a secondary limiting factor to SDT population viability as compared to drought effects on survival and viability. That could be because of the way we structured density dependence in the model as a ceiling-type density-dependent function. The ceiling-type density-dependent function assumes no change in demographics until the population reaches the population ceiling, which could result in over-estimating population growth rate and underestimating extinction risk. However, assuming any functional form for density dependence will affect population behavior in the model and could also bias estimates of population growth higher or lower depending on the function the model assumes. Therefore, we chose a simple ceiling function that makes minimal assumptions about population dynamics. With a more sophisticated model of density effects on demographics, the model output may have been more sensitive to habitat loss. However, we did not have sufficient data to develop a more ecologically sophisticated model, and it is unclear if a more sophisticated analysis would have added more value to the decision-making process. On the other hand, given the severe ceiling threshold function (i.e., if the ceiling is exceeded $P_b = 0.0$), we would have expected a more sensitive response to habitat loss if it was a major limiting factor. In our case, habitat loss probably had a small effect on quasi-extinction probability because of the spatial scale at which we modeled the populations. Each modeled population had thousands of square kilometers of habitat available remaining at the end of the model scenarios, even after decades of simulated habitat loss. This is consistent with the expected future habitat conditions across the landscape for SDT as much of the U.S. range is under public ownership and management and is, therefore, unlikely to become urbanized ([U.S. Fish and Wildlife Service, 2015](#)). If we had modeled more, spatially limited sub-populations, loss of habitat may have been sufficient to put some sub-populations at higher risk of extirpation. The specific scenario simulations are helpful because they present our best estimates of plausible future environmental conditions.

Table 3

Quasi-extinction probability (i.e., the probability of falling below 8000 females) at 100 years, given 350,000 females as the maximum population size and varying values for initial female abundance and mean drought exposure.

100 years	Max pop = 350,000 females						
	Starting population size						
	100,000	150,000	200,000	250,000	300,000	350,000	400,000
Magnitude of drought							
0.10	0.013	0.010	0.008	0.006	0.005	0.004	0.003
0.15	0.033	0.025	0.019	0.015	0.011	0.009	0.007
0.20	0.078	0.061	0.047	0.037	0.028	0.022	0.017
0.25	0.176	0.141	0.111	0.087	0.068	0.053	0.041
0.30	0.349	0.291	0.239	0.194	0.155	0.123	0.097

Table 4

Quasi-extinction probability (i.e., the probability of falling below 8000 females) at 50 years, given 350,000 females as the maximum population size and varying values for initial female abundance and mean drought exposure.

50 years	Max pop = 350,000 females							
	Starting population size							
	Magnitude of drought	100,000	150,000	200,000	250,000	300,000	350,000	400,000
0.10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.20	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.25	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.30	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000

It is important for decision-makers, biologists, and modelers to recognize that not all details of a system need to be incorporated into a model of that system in order for the model to be useful for informing decisions (Starfield, 1997; Nicolson et al., 2002; McGowan and Ryan, 2010). Climate change-induced drought showed strong potential to greatly increase quasi-extinction risk beyond 100 years (Table 3). This result is not surprising since typically long-lived species' population growth is most sensitive to the adult survival parameter in a Leslie matrix analysis, and climate-driven drought negatively impacted survival through simulated drought magnitude and intensity. Though we did not model climate and weather systems directly in our model, the approach we used captured the essential aspect of climate change effects on the SDT, as indicated by taxa experts at our workshop and in the literature (Zylstra et al., 2013). Given the simplicity of our climate change functions in this model, it may be valuable in future analyses to explore additional formulations of climate change and other climate change scenarios. However, the regression analysis of simulated data provided a powerful tool to estimate the probable effect of climate change-driven drought on quasi-extinction probability up to 200% more intense and frequent than historical rates over the past century.

The regression analyses allowed us to explore a wide variety of scenarios in simulations without the time-consuming effort to design and test each of those scenarios. This analysis is akin to a sensitivity analysis (Wisdom and Mills, 1997; Boyce, 1992; Morris and Doak, 2002) and could be expanded to conduct a global sensitivity analysis. We did not execute a global sensitivity analysis because the results had no bearing on the listing decision at hand. The regression analysis provided an efficient way to summarize the results of those numerous scenarios to communicate with the decision makers. McGowan et al. (2014) used this approach to identify the conditions under which risk was acceptably low in order to identify recovery criteria for a threatened population of piping plovers (*Chardrius melodus*). Similarly, these relationships can be used for evaluating questions such as, 'how severe would climate change effects have to be to increase the risk of quasi-extinction to an unacceptable level over a given future time period'. Furthermore, the regression analyses and tables of predicted outcomes (Tables 3 and 4) allow for an analysis of a much wider array of possible future system states (population status, climate change intensity, etc.) and could be an important contributor to inform agency decisions. We could improve the presentation of uncertainty in the regression analysis results by generating tables that use the upper and lower bound of the 95% confidence intervals of the regression parameter estimates, thereby showing the full range of expected effects of the important variables on quasi-extinction probability.

The output of our model was used as one key piece of the analysis for the SSA of the SDT. The assessment informed agency decision-makers during their determination of whether the biological status of the SDT met the definition of an endangered or threatened species under the U.S. Endangered Species Act. An endangered species is defined as one that is in danger of extinction throughout all or a significant portion of its range. A threatened species is one that is likely to become endangered in the future throughout all or a significant portion of its range. Choosing the 75 year prediction horizon for this decision was a policy-guided choice by the FWS decision-makers. We provided the opportunity to consider risks up to 200 years into the future, however, decision-makers felt there was too much uncertainty in considering futures beyond about 75 years.

There are numerous potential approaches for modeling populations and systems to predict future species' status in ways that would inform ESA listing decisions (e.g., agent-based modeling or stochastic dynamic models). We do not argue that our model is the only appropriate approach for informing SDT listing or management, only that our model and projection framework were useful in supporting the decisions at hand. While our model complexity was useful for evaluating future scenarios and predicting tortoise population states in the future, this level of model complexity is not required to support and inform all endangered species decision making. We had useful data available and reliable experts to help with model development, but in many endangered species decision contexts such data are not available. However, the steps of conceptual modeling and scenario evaluation are still possible and useful in all species assessments to inform policy decisions (Smith et al., in review).

We recognize that the model and its output cannot answer the question of whether the SDT should be afforded protection under the Endangered Species Act. There are additional policy issues for decision makers to consider in addition to the results of this or any ecological risk model. For example, what time frame should be considered? What level of extinction risk or future population decline is tolerable over that time frame? No quantitative risk analysis can answer these questions; however, using a model, such as we have here, can give the decision-maker explicit predictions about future population states, extinction probability estimates, and the uncertainty surrounding those predictions upon which to base the policy

decision. The decision-makers in this instance determined that the levels of risks facing the SDT did not warrant protection as an endangered species. Decision-makers further decided to use a 75-year maximum prediction horizon as the prediction period for this analysis and subsequently determined that the predicted abundance was high enough and quasi-extinction risk was low enough over that time frame, that listing as a threatened species was also not warranted at this time (U.S. Federal Register, 2015). Our modeling played a key role in providing the information that decision makers used to make their decision.

Acknowledgements

We appreciate the assistance we received from many experts in conducting the SDT Species Status Assessment, including R. Averill-Murray, T. Edwards, T. Esque, C. Jones, T. Jones, S. Abella, P. Grissom, T. Hughes, E. Masters, R. Steidl, and E. Zylstra. We also recognize the excellent assistance of other biologists in the Fish and Wildlife Service on this assessment, including K. Boyer, J. Dick, M. Dick, M. Martinez, S. Quamme, and S. Richardson. We thank the U.S. Geological Survey, the U.S. Fish and Wildlife Service, and Auburn University for financial and logistical support of this work (USGS-G15AC00038). We also thank D.R. Smith, N. Angeli, two anonymous reviewers and the editorial staff at the journal for reviewing and helping to improve this paper. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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