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# Population Viability Analysis for Two Species of Imperiled Freshwater Turtles

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Abstract. – **In the first range-wide population viability model for the northwestern and southwestern pond turtles (*Actinemys marmorata* and *Actinemys pallida,* respectively), a stage-based population projection matrix was assembled with 3 life stages: hatchling, juvenile, and adult. Vital rates were defined using biologically appropriate statistical distributions, with additional parametric uncertainty included for the adult survival parameter. A triple-loop stochastic simulation model was built around a population viability analysis to project pond turtle populations into the future. Initial abundance was calculated using available historical presence data and remotely sensed landscape condition metrics. A negative binomial regression was used to predict the relationship between abundance, habitat area, and human modification. Populations of pond turtles are dominated by adult individuals, so we applied a nonstable stage distribution to initial abundance values. Initial abundances of analysis units were variable across the species' ranges, but all populations declined precipitously in the population projections. By the end of the century, the mean range-wide probability of extinction was 44.3% for the northwestern species and 57.8% for the southwestern species. Consistent with other long-lived chelonian species, population growth rate was most sensitive to adult survival, indicating that where possible, conservation efforts focusing on increasing or maintaining adult survival would benefit the species. Elasticity analysis indicated a bet-hedging life history strategy where long-term reproductive output is maximized through longevity, small clutches, and frequent reproductive bouts in the face of highly variable juvenile survival. The population dynamics presented here indicate that efforts to bolster adult survival would be most beneficial in terms of long-term population viability, which can inform targeted research and management. The feasibility of such efforts is an important consideration in conservation management for these long-lived species.**

Key Words. – **population viability analysis; stochastic simulation; population model; extinction risk; turtle; chelonian**

A valuable tool in conservation, population viability analysis (PVA), is used to understand population dynamics, assess overall status, and identify potential threats to species or populations (Bessinger and McCollough 2002; Morris and Doak 2002; Lacy 2019). In the face of multifaceted resource limitations in conservation (Brooks et al. 2006), the information provided by PVA can inform directed management and research (e.g., Crouse et al. 1987; Davis 2022; McGowan et al. 2017). For at-risk species, elasticity results can prove particularly useful for prioritization or optimization efforts by identifying the life stage(s) that are most influential on population growth rate (Caswell 2006; Naujokaitis-Lewis et al. 2009). In addition to outputs, the flexibility of data requirements for PVA makes it a widely applicable tool, as researchers can tailor it to incorporate specific types of uncertainties present for a given population or species (Akçakaya and Sjögren-Gulve 2000; Bakker et al. 2009; McGowan, et al. 2011a; Lacy 2019).

Parametric uncertainty is common to wildlife data and results from sampling variation, observer error, sampling error, and/or biased methods. Well-designed and coordinated data collection efforts can ideally reduce parametric uncertainty, but factors such as species range, study objective(s) and scale, generation time, and logistical challenges, among others, limit such efforts (Goodman 2002; Calder et al. 2003; McGowan et al. 2011a). Custom-built models can be constructed in numerous ways to account for specific levels of parametric and other uncertainties (e.g., Naujokaitis-Lewis et al. 2009; McGowan et al. 2011a; Davis 2022; Omeyer et al. 2022), whereas generic programs such as VORTEX do not have such capacity, although their ease of use makes them a popular choice (Chaudhary and Oli 2020). A comprehensive review of PVAs for birds and mammals found that model quality was overall lower for analyses built using generic programs (Chaudhary and Oli 2020); however, decision context (i.e., model purpose, time constraints) was not part of their meta-analysis, although this is an important consideration when judging quality (Lawson et al. 2021). Considering the tradeoffs of each method in the context of the research question or objectives is a vital step when planning a PVA.

The northwestern and southwestern pond turtles, (*Actinemys marmorata* and *Actinemys pallida*, respectively) are 2 species of imperiled freshwater turtle for which there are multiple types of uncertainty. They are threatened by drought, disease, invasive species (i.e., American bullfrogs [*Lithobates catesbeianus*]), land alteration, and roads, among other factors (i.e., Nicholson et al. 2020; Manzo et al. 2021; Cummings et al. 2022). Northwestern pond turtles are listed as Endangered within the state of Washington, where populations are largely reliant on head-starting (Pramuk et al. 2012; Hallock et al. 2017). Once considered to be a single species, the western pond turtle (*Actinemys marmorata*), the 2 species were only recently separated based on genetic analysis (Spinks et al. 2014), so there is limited information regarding the differences in life history between the two. The northwestern and southwestern pond turtle are endemic to Washington, Oregon, California, Nevada, and Baja, México (Fig. 1). Extrapolating results from location-specific studies can be problematic for these species because of the diversity of ecological conditions and threats across their wide latitudinal range. For example, turtles in Washington are likely exposed to different conditions than those in southern California. Additionally, the long life span (50+ yrs in the wild; Bury et al. 2012, 2019) and difficulties associated with finding young turtles creates uncertainty about presence, survival, and other demographic traits. Two existing PVAs for the species were performed on small populations using program VORTEX (Pramuk et al. 2012; Manzo et al. 2021). Pramuk et al. (2012) reported efforts by Washington Department of Fish and Wildlife to model their state-listed northwestern pond turtle populations to determine the efficiency of their ongoing head-starting efforts. Manzo et al. (2021) modeled a small, theoretical "general population" of pond turtles using 2 different estimates of adult survival from Germano (2016) and Holland (1994) and found that extinction probabilities varied significantly depending on which estimate was used, highlighting the need for additional incorporation of uncertainty into modeling efforts.

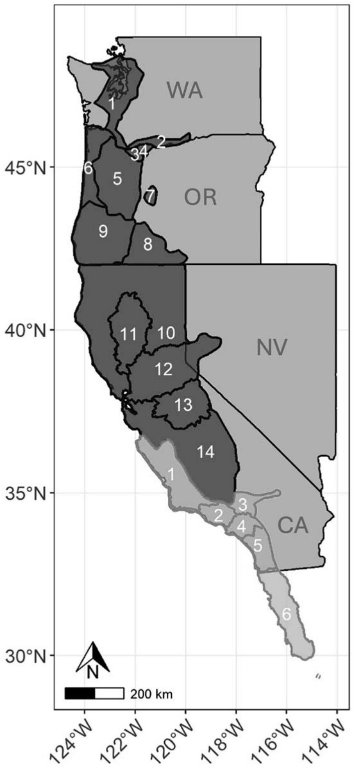

**Figure 1.** Range map for the northwestern pond turtle (*Actinemys marmorata*; blue) and southwestern pond turtle (*Actinemys pallida*; red) in the western United States (Washington [WA], Oregon [OR], Nevada [NV], and California [CA]) and México. Each range is subdivided into unique analysis units (AU), which are labeled in white numbers.

Here we present a custom-built triple-loop stochastic simulation model with a stage-based PVA at its core for the northwestern and southwestern pond turtles. These efforts build upon previous PVAs for the species by broadening to the entire range of each species, explicitly incorporating parametric uncertainty, and implementing an initial nonstable stage distribution. Using elasticity analysis, we identify the life history parameters most influential on population growth. To our knowledge, there are no existing species-level PVAs for either pond turtle species; a knowledge gap that this paper fills. Results of range-wide population dynamics presented here can help both range-wide and location-specific management for conservation of these species. We also present results at a smaller, secondary spatial scale to provide additional information on local population trends (Fig. 1). We provide the code for our simulation model in a public US Geological Survey software release (Gregory and McGowan 2023) with the hope that the triple loop structure with parametric

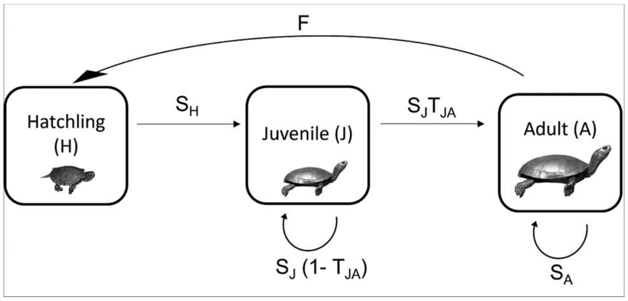

**Figure 2.** Stage-based life history diagram for both western pond turtle (WPT) species (*Actinemys marmorata* and *Actinemys pallida*), representing 3 life history stages: hatchling (H), juvenile (J), and adult (A). Arrows represent moving from one stage to another, or remaining in a stage, by the next time step (t + 1). $S_H$ is hatchling survival; $S_J$ is juvenile survival; $S_A$ is adult survival; $T_{JA}$ is juvenile to adult transition probability; and $S_J$ $(1 - T_{JA})$ is the probability that a juvenile survives and does not transition to the adult life stage, remaining a juvenile.

uncertainty can be applied to other species with multiple types of uncertainty.

## METHODS

*Model Structure.* — A stage-based life history diagram was elicited from taxa experts and a review of published literature (Fig. 2). Here, we refer to both species together as western pond turtle (WPT) or WPT species, but when specifically referring to the northwestern or southwestern species, we refer to them as NWPT and SWPT, respectively. Life history was described and modeled in stages, rather than age classes, because of the lack of information on age-specific demographic rates and effects of threats to the species. We parametrized 3 stage classes: hatchling, juvenile, and adult in a single-sex (female-only), postbreeding census (Fig. 2). Hatchlings were defined as small individuals ages 0–1 yrs. Juveniles were nonreproducing individuals with a carapace length $< 120$ mm, aged 1–7 yrs old. Adult turtles were characterized by carapace length $> 120$ mm and presumed sexual maturity (Bury et al. 2010), although evidence exists that turtles smaller than 120 mm and 15+ yrs old in southern California can be reproductive (Fisher, unpubl. data, 2019).

A population projection matrix (A, Eq. 1) was developed based on the life history diagram (Fig. 2; Caswell 2006). $S_H$, $S_J$, and $S_A$ represent hatchling, juvenile, and adult survival, respectively. F is defined as fertility of an individual (Eqs. 1 and 3), and $T_J$ is the probability of transitioning from the juvenile life stage to the adult life stage. The components and values of these demographic parameters are described in detail below (see "Demographic Rates"; Tables 1 and 2). To project populations through time, the population projection matrix was multiplied by a population size vector (Eq. 2) to calculate the size vector in the next time step.

$$A = \begin{bmatrix} 0 & 0 & F \\ SH & SJ\,(1 - TJ) & 0 \\ 0 & SJTJ & SA \end{bmatrix} \qquad [1]$$

$$\begin{bmatrix} N^H_{t+1} \\ N^J_{t+1} \\ N^A_{t+1} \end{bmatrix} = A \times \begin{bmatrix} N^H_t \\ N^J_t \\ N^A_t \end{bmatrix} \qquad [2]$$

With the population projection matrix (Eq. 1) at its core, a triple-loop stochastic simulation model was used to predict the species abundance to 2100 (inner loop, Eq. 2), with 1000 replicates for each species (middle loop), for each unique analysis unit (AU; outer loop). AUs were determined by the US Fish and Wildlife Service (USFWS) on a combination of factors such as unique genetic populations and management units (USFWS 2023). The AUs in Washington (1 and 2) were not included in this analysis because populations are conservation-dependent and sustained by a head-starting and reintroduction program. Thus, the population dynamics do not match our model for the rest of the range and therefore the Washington AUs were not included in this projection modeling effort. Later on, we discuss the results of the existing PVA for the Washington populations (USFWS 2023) alongside our own. The triple-loop structure allows for incorporation of spatially explicit population parameters (i.e., initial abundance), and uncertainty in demographic rates (McGowan et al. 2011a; McGowan et al. 2017). The R package "popbio" (Stubben and Milligan 2007) was used to perform an

**Table 1.** Description of stage-based survival and transition probability distributions for the northwestern pond turtle (NWPT; *Actinemys marmorata*) and southwestern pond turtle (SWPT; *Actinemys pallida*). Distribution of values indicates the distribution from which each parameter value was drawn for each time step in the model. To include parametric uncertainty for the survival parameters, the drawn value served as the mean value in a beta distribution with a coefficient of variation of 0.1 for hatchling and juvenile survival and 0.01 for adult survival.

| Parameter | Species | Distribution of values | Source(s) |
|---|---|---|---|
| Hatchling survival ($S_H$) | NWPT, SWPT | Uniform (min = 0.1, max = 0.15) | Holland 1994 |
| Juvenile survival ($S_J$) | NWPT, SWPT | Uniform (min = 0.731, max = 0.838) | Germano 2016 |
| Adult survival ($S_A$) | NWPT, SWPT | Uniform (min = 0.731, max = 0.99) | Germano 2016; Manzo et al. 2021; Holland 1994 |
| Juvenile to adult transition probability ($T_{JA}$) | NWPT, SWPT | 1/6 = 1/(max − min juvenile age) | Standard method, see McGowan et al 2017 |

**Table 2.** Description of distribution of parameters used to calculate fertility (F) for the northwestern pond turtle (NWPT; *Actinemys marmorata*) and southwestern pond turtle (SWPT; *Actinemys pallida*). Distribution of values indicates the distribution from which each parameter value was drawn for each time step in the model.

| Parameter | Species | Distribution of values | Source(s) |
|---|---|---|---|
| Fecundity (Fec) | NWPT | Normal (mean = 6.24, SD = 2.07) | Germano and Rathbun 2008; Germano 2016; Germano et al. 2022 |
| Fecundity (Fec) | SWPT | Normal (mean = 4, SD = 1) | Lovich and Meyer 2002 |
| Nest survival (NS) | NWPT, SWPT | Uniform (min = 0.09, max = 0.78) | Holte 1988; Holland 1994; Rosenberg 2013 |
| Hatching success (HS) | NWPT, SWPT | Normal (mean = 0.72, SD = 0.2) | Holland 1994; Rosenberg 2013 |
| Proportion breeding (PB) | NWPT | Uniform (min = 0, max = 0.9) | Ashton et al. 2015; Germano 2016 |
| Proportion breeding (PB) | SWPT | Uniform (min = 0.125, max = 0.53) | Lovich and Meyer 2002; Belli 2015 |
| Probability of double clutching | NWPT | Uniform (min = 0.05, max = 0.1) | Germano and Rathbun 2008; Germano 2016 |
| Probability of double clutching | SWPT | Beta 4 (a = 2, b = 1, min = 0.04, max = 0.5) | Goodman 1997; Lovich and Meyer 2002; Scott et al. 2008; Belli 2015 |
| Hatchling sex ratio (HSR) | NWPT, SWPT | Uniform (min = 0.325, max = 0.69) | Gordon 2009; Dallara 2011; Christie and Geist 2017; Nicholson et al. 2020 |

elasticity analysis at each time step to determine the influence of life history parameters on population growth rate. Quasi-extinction thresholds are common for PVAs to account for demographic stochasticity and reflect the fact that a population may be in an extinction vortex and doomed to extinction (i.e., not enough individuals to reproduce) when population size is nonzero (Gerber and González-Suárez 2010; McGowan et al. 2014). The quasi-extinction threshold was defined as 5% of the initial abundance (Carroll et al. 2019), which species experts deemed appropriate. We chose to use a proportional threshold instead of a numeric one because of the uncertainty associated with initial abundances. Hereafter, the term extinction is used in place of quasi-extinction.

*Demographic Rates.* — Estimates of demographic parameters were sourced from the best available information in the form of published literature and data provided to the USFWS by researchers and state and federal agencies. Appropriate statistical distributions were selected for each demographic parameter based on possible values and the patterns of parameter values reported in the literature (Tables 1 and 2). For some parameters, there was no species-specific information, so we assumed the values and distributions to be the same for both species. For each time step and replicate in the model, a value was drawn randomly from these distributions to account for uncertainty and mimic annual variability.

Survival for all age classes was modeled using the same distribution for both species. Holland (1994) estimated hatchling survival to be 0.1–0.15 (Table 1), and in the absence of likelihood of values within that range, we modeled hatchling survival using a uniform distribution. A uniform distribution was also used to represent juvenile survival, with upper and lower limits drawn from Germano (2016). Available estimates of adult survival were dominated by values close to 1.0 in the WPT literature (Table 1; Holland 1994; Manzo et al. 2021). However, Germano (2016) estimated adult survival to be as low as 0.731. We used a 4-parameter beta distribution to represent the skewedness of adult survival data such that lower values around the Germano (2016) estimate were possible, but less likely. Parametric uncertainty was included for all the survival parameters due to inconsistency of values within the literature (McGowan et al. 2011a). The values drawn from the distributions in Table 1 were used as mean values, with a coefficient of variation of 0.1 for hatchling and juvenile survival, and 0.01 for adult survival, to calculate alpha and beta parameters. A lower coefficient of variation was used for adult survival because mean values were close to 1.0, and any higher coefficient of variation would have resulted in an estimate over 1.0, violating the requirements of a beta distribution and prohibiting proper function of the model. The generated alpha and beta parameters from the parametric uncertainty portion of the simulation were used in a beta distribution within the innermost loop of the simulation to generate values of survival for each stage class in each year.

Juveniles mature to the adult life stage after approximately 7 yrs, so we defined the probability of transitioning from juvenile to adult as 1/6 such that after 6 yrs in the juvenile stage, juveniles will, on average, have transitioned to the adult stage. This is similar to a method used by Sweka et al. (2007), McGowan et al. (2011b, 2017), and others in demographic population viability models where the interstage transitions rates were not estimated from empirical data. We acknowledge that Kendall et al. (2019) suggested an alternative method for calculating transition probabilities, but WPT populations likely do not meet the stable age and asymptotic growth assumption of that approach, so we used the simpler method with fewer assumptions and tested model sensitivity to the parameter.

In WPT life history, fertility (F) represents the number of female offspring that one adult female contributes to the hatchling population in a single year. Fertility was defined as the product of multiple components of recruitment and reproduction (Eq. 3; Table 2)

$$F = \left(Fec \times NS \times HS \times PB + p(double\ clutch) \times Fec \times NS \times HS \times PB\right) \times HSR \times S_A \quad [3]$$

where fecundity (Fec) is the number of eggs laid per female (Lovich and Meyer 2002; Germano 2016). Nest survival (NS) is the probability that a nest is not predated or destroyed in any way during the incubation process. Hatching success (HS) is the probability that eggs hatch successfully within a surviving nest. Proportion breeding (PB) is the proportion of females that are breeding in a given year. The probability of double clutching (p[double clutch]) is the chance that an individual lays 2 clutches of eggs within a single year. This is a female-only model, therefore total fertility was then multiplied by a hatchling sex ratio (HSR) to calculate the number of female hatchlings in a given year. Lastly, because this is a postbreeding census (Kendall et al. 2019), we included adult survival in the fertility term by multiplying everything by an adult survival value drawn from the previously described distribution. The distributions for values of each parameter in Equation 3 can be found in Table 2, along with relevant sources.

*Determining Initial Abundance.*— To determine the initial abundance of each AU, a stepwise process was performed to incorporate best available presence data, available habitat information, and a human landscape modification metric (Fig. 3). We used the hydrologic unit code 12 (HUC12; Jones et al. 2022) as the base spatial scale for estimating initial population size. HUC12 was agreed upon by experts as the smallest spatial scale for demographic and habitat processes affecting the turtles, allowing for more specific estimates of initial population size. Once abundance was estimated for each HUC12 unit, abundances were summed across an AU to calculate initial population size for each AU.

First, we calculated a probability of current occupancy for each HUC12 using historical observational data of the WPT species. The historical observational dataset was composed of a variety of data (i.e., mark–recapture, diet studies, occupancy surveys) provided to the USFWS by species experts and state and federal agencies, among others, in a formal data solicitation request by the USFWS. We determined the number of years since the most recent observation in each HUC12, which was then used in a Bernoulli trial-based model where occupancy (0 or 1; present or not present) was determined by a probability of persistence (Eq.4). Probability of persistence was calculated by raising adult survival to the power of the number of years since turtles had been observed in the HUC12 (Eq. 4). This function would be equivalent to the probability that at least 1 adult observed at some time in the past was still present in 2022 (starting year of the model). Adult survival rate was drawn from the previously described distribution (Table 1). While there are likely issues of detection, we included many replicates and uncertainty in the adult survival (SA) estimates to account for this, and the dataset represents the best available information for the species,

$$occupancy = Bernoulli\left(SA^{\#\,years\ since\ observed}\right) \quad [4]$$

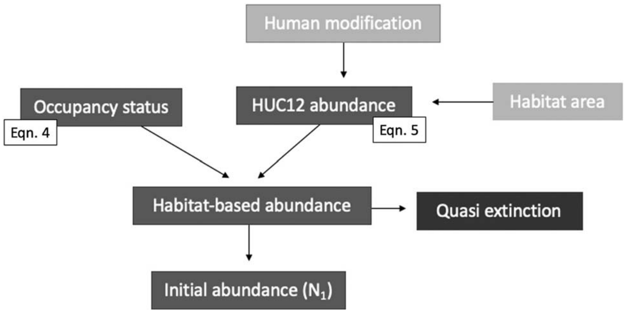

**Figure 3.** Conceptual diagram of method for calculating initial abundance for each analysis unit (AU) for both western pond turtle (WPT) species (*Actinemys marmorata* and *Actinemys pallida*). HUC12 represents hydrologic unit code 12, a spatial subunit of analysis for calculating initial abundance (see "Methods, Model Structure").

To determine the abundance of turtles in each HUC12, we used a negative binomial generalized linear regression model with HUC12-specific habitat area and human modification (H) as potential explanatory variables. Robust population estimates are largely not available for the WPT, so we transformed unique capture data (Manzo et al. 2021) using detection probability estimates from Fulton et al. (2022) with additional uncertainty. Approximate abundances were calculated by dividing capture estimates by a detection probability randomly drawn from a uniform distribution with a lower bound of 0.09 and an upper bound of 0.17 (Fulton et al. 2022). Using the location information from Manzo et al. (2021), we determined the HUC12-specific habitat area and H values for each corresponding abundance estimate. H combines numerous remotely sensed datasets into a single metric (Theobald et al. 2020), including a number of factors that affect life history, namely roads, which pose a female-biased road mortality risk (Steen et al. 2006; Nicholson et al. 2020; Keevil et al. 2023), among others such as urban build-up, agricultural development, and human intrusions (a calculated measure of human use on a landscape; see Theobald et al. 2020 for more details). We hypothesized that H has a negative effect on HUC12 abundance, based on the likelihood that increasing levels of H in the landscape surrounding a water body and riparian habitat leads to fewer suitable nesting sites (Legler 1954; Burke and Gibbons 1995), increased mesopredator populations to consume nests and juvenile turtles (Wang et al. 2015), increased invasive species pressure (Lambert et al. 2019; Nicholson et al. 2020; Fulton et al. 2022), increased probability of adult mortality while crossing roads to find nest sites (Gibbs and Shriver 2002), and less available overwintering habitat (Davis 1998). We classified habitat area as riparian, delineated by the National Riparian Areas Base Map from the US Forest Service (Abood and Wieczorek 2022), which we predicted would have a positive relationship with turtle abundance in a HUC12 unit (hereafter, HUC12 abundance).

The results of the negative binomial regression analysis revealed that as expected, HUC12 abundance increases as habitat area increases and as H decreases, (Eq. 5; Supplemental Table S1; Supplemental Fig. S1; all supplemental material is available at http://dx.doi.org/10.2744/CCB-1593.1.s1). Comparatively, H was more influential over HUC12 abundance than habitat area. We then used the negative binomial relationship (Eq. 5) to determine the HUC12 abundances for all sites with historical WPT observational data. The habitat area and H information was extracted for each observation and inputted into Eq. 5 with relevant uncertainty around the intercept and beta coefficient terms from the regression results. The HUC12 abundance values were then multiplied by the current occupancy status and adult sex ratio (ASR) to determine the abundance of each HUC12. For each calculation, ASR was sampled from a normal distribution with a mean of 0.4 (Nicholson et al. 2020) and a 10% coefficient of variation, in the absence of standard deviation information.

$$HUC12\ abundance = 5.421 + 7.062 \times 10^{-6}(habitat\ area) - 1.386(H) \quad [5]$$

In the absence of stage distribution information, stable stage distribution is often used to initialize a PVA; however, in the case of WPT, populations are largely dominated by adults, with most estimates of proportions of adults: nonadult between 0.75–1.0, with some values as low as 0.55 (Holland 1994; Germano and Bury 2001; Lovich and Meyer 2002; Spinks et al. 2003; Germano and Rathbun 2008; Bury et al. 2010; Sloan 2012; Belli 2015). To capture this skewed stage-class distribution, we used a 4-parameter beta distribution with a minimum of 0.55. For each replicate in the model, a value of proportion of adults was drawn from this distribution, which was then subtracted from 1 to calculate the combined remaining proportion of hatchlings and juveniles. There was no information available on the relative proportions of hatchlings to juveniles, so we assumed a stable stage distribution between these 2 stages. We calculated the mean and variance of proportion of hatchlings to proportion of juveniles when all 3 stages (hatchlings, juveniles, adults) are in a stable stage distribution for 100 replicates. To account for parametric uncertainty, we drew values of hatchling to juvenile proportions from a beta distribution with parameters calculated from the ratio mean and variation values. The drawn values were then multiplied by the remaining nonadult proportion and HUC12 abundance to calculate the initial hatchling and juvenile abundances.

## RESULTS

*Initial Abundance.* — The mean initial abundance for each AU of the NWPT ranged from 273 to 22,577 individuals, for a range-wide total of 102,234 turtles. Generally, abundance increased with size of the AU, with larger AUs (8–10) having the highest estimated initial abundances. Smaller AUs (3, 4, 7) had the lowest abundance values (Fig. 4). The same pattern of abundance increasing with AU size was observed for the SWPT as the largest AU (1) had the greatest abundance (Fig. 4). Despite being of similar size to AUs 4 and 5, AU 3 had a lower abundance because it includes part of the Mojave Desert where isolated, relict populations of both species are located (Lovich and Meyer 2002; Lovich et al. 2021). Mean initial abundance of the SWPT AUs ranged from 787 to 15,584 individuals, with a range-wide mean initial abundance of 27,955 turtles. As expected, high standard deviations for both species demonstrate uncertainty in initial abundance for the WPT species.

*Future Projections.* — All populations of the NWPT were predicted to decline precipitously in the future, regardless of the initial abundance (Fig. 4). By the end of the century, there were no more than 4000 NWPT in any given AU. Population growth rate ($\lambda$) had little variation and was below 1 for the duration of the simulation, indicating negative population growth, consistent with the abundance results. Across all AUs, $\lambda$ was approximately 0.97–0.98 throughout the simulation, with standard errors less than 0.003. In other words, populations declined by approximately 2%–3% each year. Probability of extinction was very low for the first 20 yrs of the simulation, after which it began to increase steadily to the year 2100 (Fig. 4). In 2100, probability of extinction ranged from 0.407 (AU 4) to 0.476 (AU 9) across all AUs, for an average of 0.443 (Fig. 4). There was little variation in mean extinction probability between AUs for the NWPT.

Trends of declining abundance and negative population growth were also observed for the SWPT. Abundance declined precipitously across all AUs, with abundance in 2100 ranging from 18 to 442 individuals (Fig. 4). Population growth rate $\lambda$ was also consistently below 1 throughout the simulation, with a mean value of 0.97 in 2100. Probability of extinction in 2100 of the SWPT was higher than that of the NWPT (Fig. 4). Mean extinction probability in 2100 was 0.578 for the SWPT across all AUs, with a range of 0.546 (AU 5) to 0.593 (AU 1). Additional summary statistics are provided in Supplemental Table S2.

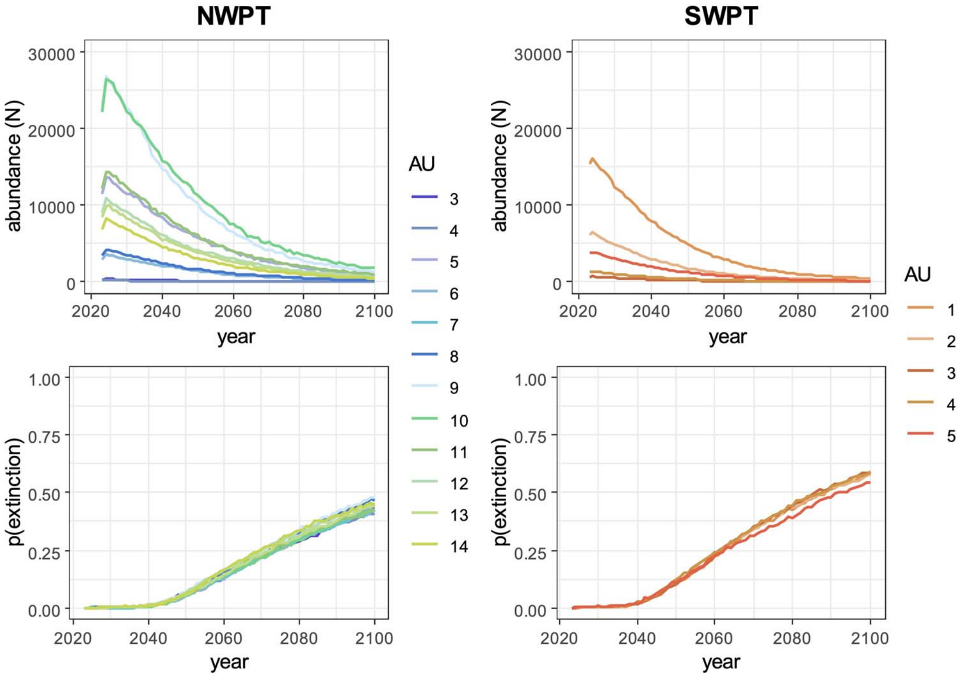

**Figure 4.** Projected median abundance (N, top row) and mean probability of extinction (p[extinction], bottom row) for the NWPT (northwestern pond turtle, *Actinemys marmorata*: left column) and the SWPT (southwestern pond turtle, *Actinemys pallida*; right column). See Figure 1 for locations of analysis units (AU). AUs 1 and 2 were not modeled due to conservation status of populations in those regions (see "Methods").

*Elasticity.* — Elasticity was highest for the adult survival parameter for both species (Fig. 5). Fertility, hatching survival, and the probability of surviving and transitioning to adulthood had very low elasticity values and thus did not have much influence over population growth rate. Elasticity of adult survival was slightly higher for the SWPT vs. the NWPT. Correspondingly, the elasticity probability of surviving and remaining a juvenile was slightly higher for the NWPT. The elasticities of adult survival and probability of surviving and remaining a juvenile were highly skewed in opposite directions and were directly related to the value of adult survival (Fig. 6). As the value of adult survival increased, the elasticity of adult survival increased and the probability of surviving and remaining a juvenile decreased. In other words, greater adult survival means greater influence of adult survival on population growth rate.

## DISCUSSION

Using a triple-loop stochastic simulation model with a PVA, we projected WPT population abundance, growth rate, and extinction risk into the future. Demographic rates were included as probabilistic distributions whose shape was informed by the literature. Information on survival was highly uncertain, so we included additional parametric uncertainty to best capture the variation in available values. To initialize the model, we developed a novel method for estimating WPT abundance of specific population units (AUs) by combining available historical observational data, survival estimates, and habitat area and condition information. Despite variation of initial abundance values for each AU, there was little spatial variation in population dynamics. The NWPT and SWPT declined throughout the simulation, with mean range-wide probabilities of extinction in 2100 of 44.3% and 57.8%, respectively. Elasticity analysis revealed that population growth rate was most sensitive to adult survival for both species, confirming the necessity of including adequate parametric uncertainty for this parameter and emphasizing the importance of protecting adult individuals.

Consistent with existing PVAs for the species (Pramuk et al. 2012; Manzo et al. 2021), results presented here demonstrate an increasing extinction risk for into the future. Manzo et al. (2021) found that results were dependent on the values of adult mortality (inversely, adult survival), which was observed here in the sensitivity of population growth rate to adult survival (Fig. 5 and 6). Interestingly, Manzo et al. (2021) stated that adult survival would need to be 0.57 (0.43 adult mortality) for extinction probability of their generic population to be 0.5 or greater, but here we found that adult survival values of 0.731 or higher led to such an extinction probability. The pattern of increased extinction risk when adding parametric uncertainty to the population model follows the results of McGowan et al. (2011a). In their models of Washington NWPT populations, Pramuk et al. (2012) also reported high sensitivity of population growth rate to adult survival, with some sensitivity to subadult survival for their NWPT populations. They predicted severe declines in their populations into the future in the absence of head-starting efforts (Pramuk et al. 2012).

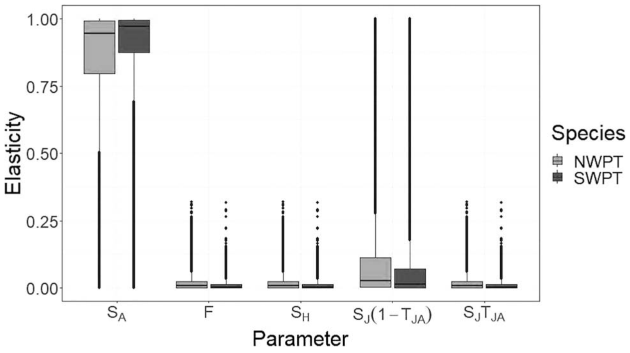

**Figure 5.** Boxplots of elasticity values of demographic parameters between the northwestern pond turtle (NWPT; *Actinemys marmorata*) and the southwestern pond turtle (SWPT; *Actinemys pallida*). All elasticity values in each year of the simulation are included here (over 7,410,000 values). Box plots depict the minimum, first quartile, median, third quartile, and maximum, with outliers depicted as single points. F is fertility; $S_H$ is hatchling survival; $S_J$ is juvenile survival; $S_A$ is adult survival; $T_{JA}$ is juvenile to adult transition probability; and $S_J\ (1 - T_{JA})$ the probability that a juvenile survives and does not transition to the adult life stage, remaining a juvenile.

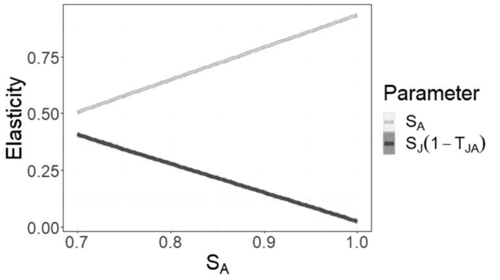

**Figure 6.** Trendlines of elasticity values of adult survival (red) and the probability of surviving and remaining a juvenile (blue) as adult survival increases for both western pond turtle (WPT) species (*Actinemys marmorata* and *Actinemys pallida*). $S_A$ represents the probability of adult survival, and $S_J\ (1 - T_{JA})$ represents the probability of surviving and remaining a juvenile (Table 1). As the value of $S_A$ increases, the elasticity of $S_A$ increases and that of $S_J\ (1 - T_{JA})$ decreases. In biological terms, as adult survival increases, it increasingly becomes the most influential parameter for population viability which is consistent with a bet-hedging life history strategy.

Drawing direct comparisons between results presented here and that of the existing WPT PVAs is tenuous because of the differences in analysis scale, population structure, and treatment of uncertainty. Here, we analyzed populations at both the range-wide scale and for unique AUs, whereas previous efforts evaluated a "general" WPT population (Manzo et al. 2021) or head-started populations (Pramuk et al. 2012). We custom-built our model in program R using a stage-structured population (Fig. 2), whereas previous efforts used program VORTEX using an age-based, individual-based model. In the absence of age-specific demographic rates, the age-structure in VORTEX requires some extrapolation of WPT demographic rates in the Manzo et al. (2021) analysis, without the ability to include parametric uncertainty. Further, individual-based models in VORTEX are difficult and potentially inappropriate to implement for wide-ranging populations (Morris and Doak 2002). Stage-structured models are commonly used when life stage, not age, is more descriptive of survival and reproduction, or when age-specific information is not available (Caswell 2006). For the WPT, there is little age-based demographic information because of difficulties associated with aging adult turtles (annual scutes are unidentifiable after approximately 16 yrs; Bury and Germano 1998; Wilson et al., 2003; Germano 2016) and the challenges of monitoring a long-lived species throughout their lifespan. With these challenges in mind, annual estimates of survival for the juvenile life stage specifically could be valuable as there is potentially a gradient of increasing survivorship across the stage (Germano 2016; Kameda et al. 2023). Additionally, since WPTs occupy a diversity of habitats, it is questionable to expand results from a specific location to the entire range, variation which we attempted to capture in the parametric uncertainty aspect of this work. Spatially representative estimates of life history parameters of AU would make this model more spatially explicit, likely improving accuracy of the results.

Elasticity is a valuable tool within a PVA that can provide information on the most vital life stages to population growth rate (Benton and Grant 1999). For long-lived chelonians (turtles and tortoises), sensitivity of population growth rate to adult or reproductive life stages is common (Figs. 5 and 6; Crouse et al. 1987; Cunnington and Brooks 1996; Enneson and Litzgus 2008; Páez et al. 2015; Lawson 2021; Folt et al. 2021). Bet-hedging theory states that to maximize long-term reproductive output when juvenile survival is unpredictable, selection favors longevity, and smaller and more frequent reproductive efforts (Cunnington and Brooks 1996; Lovich et al. 2015). Comparison of elasticities between WPT species are consistent with bet-hedging theory (Fig. 6). The SWPT lays fewer eggs per brood on average but has a higher probability of double clutching within a single year than the NWPT (Table 2), resulting in a higher adult survival elasticity value (Fig. 6), thus demonstrating a greater degree of bet-hedging. Further study into the differences of survival rates between the NWPT and SWPT would be interesting to explore relative to the divergence of life history strategies between these closely related species.

While adult survival has been shown to highly influence population growth for the WPT and other chelonian species (i.e., Enneson and Litzgus 2008; Mogollones et al. 2010; Zimmer-Shaffer et al. 2014; Folt et al. 2021), active management of the WPT species has often involved younger life stages. Head-starting of hatchlings, removal of invasive predators of hatchlings and juveniles, and nest-predator exclusions are examples of management strategies to protect subadult WPTs (i.e., Holte 1988; Pramuk et al. 2012). At first, it might seem contradictory to manage for life stages that are not as influential on population growth rate (i.e., Frazer 1992) when trying to reverse population declines, but in reality, managers are faced with issues of partial controllability. Partial controllability is the inability to accurately carry out management actions to reach a desired outcome or effect on a system because of incomplete control of management implementation (Martin et al. 2009). When adult survival has less interannual variation compared to other demographic rates, as is the case of the WPT, it is possible that intense management efforts would only result in an incremental increase (Enneson and Litzgus 2008; Warret Rodrigues et al. 2021). Additionally, efforts to increase adult survival can be limited by logistics such as the duration and cost of long-term management. It can be reasonable to focus efforts on more practical, immediate management of younger age classes, but it is also important to consider the contribution of current efforts to long-term species viability. In the case of the WPT, primary threats to adult survival are factors that are very difficult to control and directly manage, such as road mortality of nesting females and climate change (Nicholson et al. 2020; Manzo et al. 2021), so management actions to increase recruitment or younger life stages may be warranted (Enneson and Litzgus 2008).

The model presented here is the first range-wide analysis for the WPT, building on the work of previous PVAs at smaller spatial scales. Altogether, the key advances of this work for the WPT include methods for determining initial abundance, a nonstable initial stage distribution, parameters defined using probability distributions, and the inclusion of parametric uncertainty. The population dynamics presented here can be used to inform targeted research and management. Here, values of initial abundance and survival rates have high levels of uncertainty, and future efforts to improve the knowledge of these parameters would strengthen model results and conclusions. Lastly, this predictive model does not include future projections of threats to the species and thus results may underestimate extinction risk; however, there is still notable extinction probability by the end of the century. Incorporating the magnitude of current and future threats into this stochastic simulation model could improve the overall assessment of future extinction risk for both WPT species. More broadly, the methods presented here, particularly the model's parametric uncertainty structure, can be applied to other long-lived chelonian species for which there are multiple sources of uncertainty.

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