Articles

Conservation of Northwestern and Southwestern Pond Turtles: Threats, Population Size Estimates, and Population Viability Analysis

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Abstract

Accurate status assessments of long-lived, widely distributed taxa depend on the availability of long-term monitoring data from multiple populations. However, monitoring populations across large temporal and spatial scales is often beyond the scope of any one researcher or research group. Consequently, wildlife managers may be tasked with utilizing limited information from different sources to detect range-wide evidence of population declines and their causes. When assessments need to be made under such constraints, the research and management communities must determine how to extrapolate from variable population data to species-level inferences. Here, using three different approaches, we integrate and analyze data from the peer-reviewed literature and government agency reports to inform conservation for northwestern pond turtles (NPT) *Actinemys marmorata* and southwestern pond turtles (SPT) *Actinemys pallida*. Both NPT and SPT are long-lived freshwater turtles distributed along the west coast of the United States and Mexico. Conservation concerns exist for both species; however, SPT may face more severe threats and are thought to exist at lower densities throughout their range than NPT. For each species, we ranked the impacts of 13 potential threats, estimated population sizes, and modeled population viability with and without long-term droughts. Our results suggest that predation of hatchlings by invasive predators, such as American bullfrogs *Lithobates catesbeianus* and Largemouth Bass *Micropterus salmoides*, is a high-ranking threat for NPT and SPT. Southwestern pond turtles may also face more severe impacts associated with natural disasters (droughts, wildfires, and floods) than do NPT. Population size estimates from trapping surveys indicate that SPT have smaller population sizes on average than do NPT ($P = 0.0003$), suggesting they may be at greater risk of local extirpation. Population viability analysis models revealed that long-term droughts are a key environmental parameter; as the frequency of severe droughts increases with climate change, the likelihood of population recovery decreases, especially when census sizes are low. Given current population trends and vulnerability to natural disasters throughout their range, we suggest that conservation and recovery actions first focus on SPT to prevent further population declines.

Keywords: *Actinemys marmorata*; *Actinemys pallida*; western United States; drought; predation

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Introduction

Assessing the conservation status of long-lived, widely distributed taxa is challenging (Wheeler et al. 2003; Wallace et al. 2011). Long-lived species exhibit delayed population responses to changes in the environment, and as a consequence, accurate status assessments depend on data collected over a long period (Congdon et al. 1993, 1994; Wheeler et al. 2003; Germano 2016; Hallock et al. 2017). Given their long life span, the persistence of adults can mask the actual viability of a population and suggest healthy populations even when there is little or no recruitment (Hays et al. 1999). Furthermore, to reach meaningful conclusions about the conservation status of any species, including long-lived ones, long-term monitoring data from multiple populations are required to determine whether changes in population sizes and their causes are regional or restricted to local populations (Germano and Bury 2001; Wheeler et al. 2003; Brown et al. 2015; Hallock et al. 2017). Unfortunately, such detailed information is often lacking for long-lived species because it is generally beyond the scope of any one researcher or research group to investigate the long-term variation in status and trends of several populations.

Even for taxa that are known to be declining, protection and recovery under the U.S. Endangered Species Act (ESA 1973, as amended) requires substantial, range-wide evidence to determine whether listing is warranted. For long-lived, widespread species, wildlife managers may utilize limited information from multiple sources to stitch together range-wide evidence of population declines and their causes. If assessments need to be made under such constraints, both the research and management communities must confront the difficult problem of extrapolating from variable population data to make species-level inferences. Here, using three different methods, we develop a strategy to inform conservation decision-making for northwestern pond turtles (NPT) *Actinemys marmorata* and southwestern pond turtles (SPT) *Actinemys pallida*.

Until recently, NPT and SPT were considered a single polytypic species and were collectively referred to as the western pond turtle, *A. marmorata*. In 2014, the taxonomy of western pond turtles was revised to recognize two distinct species: NPT and SPT (Spinks et al. 2014). Both NPT and SPT are long-lived (adults may live >40 y in the wild) and widely distributed in the western United States and Mexico (Bury and Germano 2008). Northwestern pond turtles are distributed from Washington State south and inland through California’s San Joaquin Valley, including outlying populations in Nevada (Spinks et al. 2014; Thomson et al. 2016; Bury 2017). Southwestern pond turtles are distributed from south of San Francisco Bay along the central California coast to roughly 100 km south of El Rosario, Baja California, Mexico (Spinks et al. 2014; Valdez-Villavicencio et al. 2016). Hereafter, when we refer to western pond turtles (WPT), we are referring to both NPT and SPT.

Western pond turtles are declining across their range and have been granted some level of recognition in the four U.S. states where they occur. Currently, WPT are listed as endangered in the state of Washington (WDFW 1993), “sensitive/critical” in Oregon (ODFW 2021), a “Species of Conservation Priority” in Nevada (NDOW 2012), and a “Species of Special Concern” in California (Thomson et al. 2016). They are not protected in their limited range in Mexico (Macip-Ríos et al. 2015). Local population declines have been attributed to habitat loss and fragmentation, reduced water availability, competition and/or predation from invasive species (particularly American bullfrogs *Lithobates catesbeianus*, and possibly red-earred sliders *Trachemys scripta elegans*), male-biased population structure resulting from road mortality of nesting females, and other threats (Holland 1994; Reese and Welsh 1998; Madden-Smith et al. 2005; Bury and Germano 2008; Thomson et al. 2016; Lambert et al. 2019; Nicholson et al. 2020).

In 1992, Dan Holland, Mark Jennings, and Marc Hayes submitted a petition to the U.S. Fish and Wildlife Service to list WPT as threatened or endangered pursuant to the U.S. Endangered Species Act (ESA 1973). Listing under the Endangered Species Act (ESA 1973) was not warranted, in part because information regarding the long-term impacts of threats and species status was considered to be largely anecdotal (USFWS 1993). However, WPT remained a species of conservation concern. In 2012, the Center for Biological Diversity petitioned the U.S. Fish and Wildlife Service to list WPT, then recognized as a single species, as threatened or endangered under the Endangered Species Act (ESA 1973), as part of a petition covering 53 species of reptiles and amphibians throughout the United States. In 2014, the Center for Biological Diversity notified the U.S. Fish and Wildlife Service of research that identified WPT as two distinct species (Spinks et al. 2014) to reaffirm conservation concerns for NPT and SPT. The U.S. Fish and Wildlife Service announced in 2015 that protection under the Endangered Species Act (ESA 1973) may be warranted for WPT, and the listing status is currently
under review (USFWS 2015). The recognition of two species rather than one established a new baseline for separate assessments and conservation actions because each species may experience different levels of decline. However, most of the literature and data on site-specific threats and geographical patterns of population declines predate the recognition of NPT and SPT as two distinct species. As a result, the information regarding potential threats and population declines, which are scattered across the published and unpublished literature, have not been collated and analyzed separately for either species.

In this study, we collate and analyze data from the peer-reviewed literature, government agency reports, and unpublished field notes for NPT and SPT separately, disentangling much of the earlier literature. We aggregate this disparate data to examine potential threats, estimate population size, and explore population viability for each species to the extent possible. We demonstrate how the integration and analysis of data from multiple sources can guide our analysis of conservation standing for NPT and SPT. We first describe the criteria and process used to rank the impacts of 13 potential threats to each species. Ranking threats provides managers with a transparent way to prioritize conservation actions. This approach can also reveal trends among high-ranking threats and highlights additional research needs for listing or delisting actions. We then analyze data from trapping and hand-capture surveys conducted sporadically from 1993 to 2019, many of which are currently unpublished, to estimate population sizes using the average number of unique individuals captured annually at many sites across the range of each species. To complement our threat and population size analyses, we also developed a population viability analysis (PVA) model to project population viability over the next century, focusing on juvenile and adult mortality rates as demographic parameters, and drought (a high-impact threat) as a recurring catastrophe. Although we utilize these methods to make inferences for NPT and SPT, we believe that similar methods can be applied broadly to other long-lived, widespread species of conservation concern.

Methods

Threat categories

| Threat categories | Scoring |
|-------------------|---------|
| Competition with nonnative species | 5 |
| Contaminants | 4 |
| Dams | 3 |
| Drought | 3 |
| Flood | 2 |
| Harvesting | 1 |
| Land alteration | 1 |
| Natural predators | 4 |
| Pathogens | 5 |
| Predation (American bullfrogs and Largemouth Bass) | 3 |
| Rising temperatures | 2 |
| Roadways | 1 |
| Wildfire | 4 |

We assigned a numerical score to each threat category using the scoring provided by each species within California. We extracted information from 28 individual sources for NPT and 16 for SPT; several of these sources contained information for more than one population of one or both species.

Threats and observations. We collated a list of 13 threat categories that were mentioned in the literature as potentially detrimental to populations of WPT (Table 1). A detailed review of each threat category is provided in Text S1 (Supplemental Material). For each species, we documented observations under each threat category, where we defined an observation as an author’s statement of how a potential threat was affecting a population. Populations were not always identified at the same scale; some were restricted to a pond and others were assessed at a larger scale (i.e., multiple ponds, a stretch of river, etc.), and we followed the conventions provided by each author. If more than one source reported on the same population under a threat category and provided a similar interpretation of the same threat, we only counted it once. For example, if one author studied a stretch of river and another author studied a larger area that includes that stretch, and they both made the same assessment of a threat, we treated their findings as a single observation. However, the vast majority of observations were nonoverlapping.

A single source (a paper) could report an observation for more than one population under a threat category (for example, if more than one site was affected by pathogens), or multiple observations across threat categories (for example, if a site was affected by drought and wildfire). In some cases, the authors discussed potential range-wide threats to the species but did not provide an interpretation of how a threat affected individual populations. We excluded these discussions from our analysis.

Scoring. We assigned a numerical score to each observation under a threat category using the scoring...
Table 2. Scoring system used to rank the impacts of 13 potential threats on northwestern pond turtles *Actinemys marmorata* and southwestern pond turtles *Actinemys pallida*. For each threat category, we documented observations for each species, where an observation was described as an author’s statement of how a potential threat impacts a study population. This information was derived from peer-reviewed literature, as well as published and unpublished reports from the western United States (1992–2021). We assigned a numerical score to each observation based on the threat’s impact on a population. Scores for each observation are provided in Table S1 (Supplemental Material).

| Score | Threat impact                     |
|-------|-----------------------------------|
| 0     | No observed or known effect on population health or population size |
| 1     | Negative effect on population health or decrease in population size |
| 2     | Extirpation                        |

system in Table 2. All scores are available in Table S1 (Supplemental Material). For each threat category, we calculated the “sum score” and the “mean score.” We calculated the “sum score” by adding the scores under a threat category. For example, if there were two observations under the threat category for wildfire and they each received a score of 1, then the “sum score” for wildfire would be 2. We calculated the “mean score” by taking the average of the scores under a threat category. Using the previous example, the “mean score” for wildfire would be 1. We calculated both scores separately for each threat for NPT and SPT. The “sum score” accounts for the number of times a threat has been evaluated (number of observations) and the impact of that threat when it was observed. For example, we expect a threat category with a high “sum score” to result in many population declines and extirpations. The “mean score” represents the average impact we expect a threat to have on a population when it does occur. Although both scores are useful, we used the “sum score” to represent the overall rank of each threat category because it accounts for the number of observations and their associated impacts. In cases where threats had identical “sum scores,” we used the “mean score” to break the tie. We ran a Spearman’s correlation to determine the relationship between the “sum score” and the “mean score” within and between species.

**Population size estimates**

To visualize where NPT and SPT are maintaining healthy population sizes, we compiled rough estimates of census population sizes by calculating the average number of unique individuals captured annually at 50 populations for NPT and 81 populations for SPT. These data were obtained from peer-reviewed literature, reports produced by government agencies, and unpublished data sets contributed by field researchers (Table S2, Supplemental Material). We define a population as the group of individuals being sampled at a site, as determined by field researchers who collected the data. Not all of our included studies state that they are a census of the population or a credible population estimate, but we assume that field efforts maximized the capture of as many WPT as possible at each site. Western pond turtles were captured in traps, by hand, or through a combination of the two, and were marked to identify unique captures. We did not use data from visual surveys of basking turtles (e.g., Thomson et al. 2010) because they may recount the same individuals. Annual captures for most sites were based on at least several “trap-days,” defined as the number of traps multiplied by the number of days that traps were deployed, as well as several “person-hours,” defined as the number of people multiplied by the number of hours each searched for WPT. We excluded estimates of population size using mark-recapture efforts because such estimates were not available for most sites, and only recorded data from sites that are known to contain (or did contain) WPT. We mapped the location of each population using global positioning system coordinates. On a few occasions, populations from sites that lacked coordinates and could not be identified by name were excluded from our analysis, although this was rare. If more than one researcher collected data from the same population, we used the most recent data set.

These data represent most of the trapping and hand-capture surveys for WPT conducted over the past 27 y (1993–2019). For each site, we calculated the average number of unique individuals captured annually (Table S3, Supplemental Material). We used the most recent 7 y of data for sites that contain NPT, because 7 y coincides with the earliest observed age of sexual maturity for NPT (Bury and Germano 2008). We used the most recent 4 y of data for sites that contain SPT, because 4 y coincides with the earliest observed age of sexual maturity for SPT (Bury and Germano 2008). We binned the annual captures from each site into categories of <1, 1–50, 51–100, and >100 individuals. We considered using a standardized metric based on capture effort but decided that the variability in field techniques was such that standardization was essentially impossible. Rather, we assume that field surveys were optimized to capture as many WPT as possible given site conditions, and so were at least broadly comparable. We used two-tailed t-tests on the mean differences in population counts between NPT and SPT for each count category (alpha = 0.05), and a chi-square test to determine whether the distribution of population size estimates differed between NPT and SPT.

**Population viability analysis**

*Population viability analysis software.* We used Vortex 10 (Lacy and Pollak 2018) to model the future demographic trends and viability of a general population of WPT. Vortex employs an individual-based approach to model population dynamics as sequential events that
occur according to defined probabilities, including their stochastic variances. To parameterize our PVA model, we extracted demographic estimates of age-specific vital statistics for WPT from the primary literature. We designed a single PVA model for WPT because our literature review indicated that NPT and SPT do not substantially differ for most life-history variables that are used to parameterize the model, including birth, death, and maturation rates. Also, no single study estimated all the vital rates necessary to parameterize the model, and a few variables (particularly first-year survival) differed considerably between published reports. For variables with only a single estimate, or where multiple estimates were roughly consistent across studies, model parameterization was straightforward. For those that varied, we explored a range of values to better understand the sensitivity of the PVA model to that variation. We then used our PVA model to further explore the effects of changes in the frequency of catastrophic droughts based on current and future climate scenarios.

**Demographic parameters.** In 2012, Pramuk et al. (2013) conducted a PVA for NPT in Washington, USA. The most appropriate baseline demographic parameters for these populations were selected using data from field observations in Washington, which included the number of individuals removed or added to populations through an extensive head-starting program (Pramuk et al. 2013). Populations in Washington are reliant on head-started NPT, so we did not use these values to parameterize our PVA model. Generally, the longest-term and most reliable demographic parameters for our baseline population model were derived from Germano (2016). This long-term study, conducted from 1995 to 2006 at Goose Lake in Kern County, California, is near the southern-most, hottest, and driest extent of the range of NPT in the southern San Joaquin Valley (Table 3). Importantly, this study provides annual mortality rates observed among age classes, which most studies lack. The other available demographic study is summarized in an unpublished, but widely cited report (Holland 1994). That study, which included information from both NPT and SPT, reported survivorship estimates based on preliminary analyses of long-term mark and recapture data collected from 1) 1980–1991 from several sites on the central coast of California (Pico Creek, Little Pico Creek, Arroyo Laguna, Arroyo Tortuga, Arroyo de la Cruz); 2) 1985–1991 from other populations in California, Oregon, and Washington; and 3) some additional Oregon sites through 1993 (Holland, personal communication).

Germano (2016) and Holland (1994) both reported relatively low adult mortality rates. However, mortality rates reported among young age classes differed dramatically. Germano (2016) reported annual mortality rates of up to 26.9% for juveniles of <80-mm carapace length, while Holland (1994) found an average hatching success of 70% (thus, 30% mortality), but annual mortality rates of up to 90% for juveniles of <120-mm carapace length (Table 4). Given the considerable differences in juvenile mortality in these two studies, we modeled two scenarios in our PVA. We used the baseline values for all parameters in Table 3 except “mortality rates” and ran the model using 1) Germano’s (2016) mortality rates for juveniles and adults and 2) Holland’s (1994) mortality rates for juveniles and adults. We also explored additional scenarios with varying levels of first-year mortality. We used the baseline values for all parameters except “mortality from age 0 to 1” (Table 3) and varied this parameter using estimates from Germano (2016) and Holland (1994) to determine how first-year mortality affects the probability of extinction ($P_e$). In a separate set of analyses, we modeled scenarios with varying levels of adult female mortality, because it has often been assumed to be an important vital rate for long-lived turtle population persistence (Heppell 1998). Using the baseline values for all parameters except “annual mortality of females after age 7” (Table 3), we varied this parameter using estimates from Germano (2016) and Holland (1994) to determine how adult female mortality impacts $P_e$.

**Catastrophe parameters.** We explored the impacts of catastrophic droughts using the Germano-based vital statistics in Table 3 because they returned generally stable population estimates. Long-term droughts that last a minimum of 4 y have been known to cause major declines in populations of WPT (Purcell et al. 2017), and in some cases extirpation (Holland 1992; Lovich et al. 2017). To determine the impact of current and future long-term droughts on population viability, we parameterized droughts as a catastrophe in Vortex and modeled the future viability of a baseline population at Goose Lake because it was modeled to be healthy under normal, nondrought conditions (Germano 2016; Table 3). Vortex models any catastrophic event as a special case with three parameters: frequency, severity with respect to reproduction, and severity with respect to survival. Although catastrophes tend to have a major influence on $P_e$, these effects are often difficult to estimate (Reed et al. 2003). To quantify the frequency and the severity of catastrophic droughts, we followed Holland (1992) and assumed that most of the impacts associated with catastrophic droughts accrue over time and that the fourth and fifth year of a hydrological drought (defined as a continuous period of below-average runoff) represent the years with the highest impacts. We parameterized the frequency of catastrophic droughts by counting the number of hydrological droughts in California that lasted a minimum of 4 y in the past century. Although California does not have a state statutory process for defining or declaring drought, the California Department of Water Resources identified the state’s most significant droughts in the observed record based on their impacts on statewide runoff and reservoir storage, or their duration (CDWR 2015). We counted three such events: 1929–1934, 1987–1992, and 2012–2015 (CDWR 2015). Accordingly, we used a baseline drought frequency of 3%, or 3 droughts/100 y. In Vortex,
Table 3. Parameter values used to model future demographic trends and population viability of northwestern pond turtles (NPT) *Actinemys marmorata* and southwestern pond turtles (SPT) *Actinemys pallida* with Vortex 10 (Lacy and Pollack 2018). We implemented a single population viability analysis model for both species, given that NPT and SPT do not differ drastically in most of the life-history variables that we used to parameterize the model. These demographic parameters were obtained from studies conducted between 1980 and 2006 in the western United States and were used to represent a generalized population of NPT or SPT. The parameters under “Catastrophes” were used to explore the impacts of long-term droughts on NPT and SPT. “SD” is standard deviation.

| Parameter | Value |
|-----------|-------|
| **Scenario settings** | |
| Number of iterations | 100 |
| Number of years | 100 |
| Duration of each year in days | 365 |
| Run as a population-based model? | Yes |
| Extinction definition | Only 1 sex remains |
| Number of populations | 1 |
| Order of events in a Vortex year | Default |
| **Species description** | |
| Inbreeding depression | No |
| Environmental variation correlation between reproduction and survival | 1 |
| **Reproductive system** | |
| Reproductive System | Polygynous |
| Age of first offspring females | 7 (Bury and Germano 2008) |
| Age of first offspring males | 7 (Bury and Germano 2008) |
| Maximum age of reproduction | 45 (Holland 1994) |
| Maximum # broods/year | 3 (Bury et al. 2012) |
| Maximum # progeny/brood | 11 (Germano 2016) |
| Sex ratio at birth in % males | 50 |
| Density dependent? | No |
| **Reproductive rates** | |
| % Adult females breeding | 62.4 (Germano 2016) |
| Environmental variation (SD) in % Breeding | 10 |
| Distribution of broods each year | 1 (94%); 2 (5%); 3 (1%); (Germano 2016) |
| # Offspring/female/brood (normal distribution) | 7 (Germano 2016) |
| SD | 1.6 (Germano 2016) |
| **Mortality rates** | |
| Mortality of females as % | |
| Mortality from 0 to 1 | 49 (Germano 2016; Holland 1994) |
| SD | 10 |
| Mortality from 1 to 2 | 21.5 |
| SD | 3 |
| Mortality from 2 to 3 | 16.2 (Germano 2016) |
| SD | 3 |
| Mortality from 3 to 4 | 18.3 |
| SD | 3 |
| Mortality from 4 to 5 | 20.5 |
| SD | 3 |
| Mortality from 5 to 6 | 22.6 |
| SD | 3 |
| Mortality from 6 to 7 | 24.8 |
| SD | 3 |
| Annual mortality after age 7 | 26.9 (Germano 2016) |
| SD | 3 |
| Mortality of males as % | |
| Mortality from 0 to 1 | 49 (Holland 1994; Germano 2016) |
| SD | 10 |
| Mortality from 1 to 2 | 21.5 |
| SD | 3 |
| Mortality from 2 to 3 | 16.2 (Germano 2016) |
| SD | 3 |
| Mortality from 3 to 4 | 16.7 |
| SD | 3 |
| Mortality from 4 to 5 | 17.2 |
| SD | 3 |
| Mortality from 5 to 6 | 17.7 |
| SD | 3 |
Table 3. Continued.

| Parameter                              | Value               |
|----------------------------------------|---------------------|
| Mortality from 6 to 7                  | 18.2\(^1\)          |
| SD                                     | 3                   |
| Annual mortality after age 7           | 18.7 (Germano 2016) |
| SD                                     | 3                   |
| **Catastrophes**                       |                     |
| **Drought**                            |                     |
| Frequency %                            | 3 (CDWR 2015)\(^2\) |
| Reproduction                           | 0.32 (Holland 1994) |
| Survival                               | 0.40 (Holland 1992) |
| **Mate monopolization**                |                     |
| % Males in breeding pool               | 100                 |
| Specified age distribution?            | Yes                 |
| Initial population size                | 653 (Germano 2016)\(^3\) |
| **Carrying capacity**                 |                     |
| K                                      | 1,300\(^4\)         |
| SD in K due to environmental variation | 0                   |

\(^1\) Age 7 is the approximate median age of first reproduction observed among females and males throughout the combined range of NPT and SPT (Bury and Germano 2008).

\(^2\) Assumption that NPT and SPT can reproduce until death (Holland 1994).

\(^3\) The initial sex ratio is assumed to be 1:1 given no current evidence to the contrary.

\(^4\) The mean percentage of adult females breeding is approximately 62.4%, calculated using the percent females gravid from May, June, and July (Germano 2016).

\(^5\) The proportion of double broods was calculated from 6 double clutches out of 113 total clutches (5%). Triple clutches were set at 1% because they are possible but highly unlikely.

\(^6\) SD was calculated from the standard error (SE) of 0.15 provided by Germano (2016), using the equation SE = [SD/sqrt (m)]. Thus, 0.15 = [SD/sqrt (113)].

\(^7\) The mortality rate from age 0 to 1 was calculated using an average 70% hatching success (Holland 1994) and a mortality rate of 26.9% for juveniles of <80 mm carapace length (Germano 2016). The overall survival rate is thus 0.70 × 0.731 = 0.51. The mortality rate equals 1 – 0.51 = 0.49 × 100 = 49%.

\(^8\) Average mortality rate for juveniles of <80 mm carapace length and 80–119 mm (Germano 2016).

\(^9\) Assumption that the mortality schedule from age 3 to 6 increases gradually before stabilizing at the respective adult mortality rates estimated by Germano (2016).

\(^1\) There was a total of 3 droughts that lasted a minimum of 4 y in the past 100 y, as defined by the California Department of Water Resources (i.e., 1929–1934, 1987–1992, 2012–2015).

\(^2\) During the 1987–1992 drought, <20% of potentially reproductive females were gravid (Holland 1994). We assume that 62.4% of adult females are gravid in a noncatastrophic year (Germano 2016). The severity factor with respect to reproduction is given by (20%)/(62.4%) = 0.32.

\(^3\) Population declines during the 1987–1992 drought revealed an average decrease of 69% (or a survival rate of 31%; Holland 1992). The average adult survival rate during a noncatastrophic year at Goose Lake was 77.2% (Germano 2016). The severity factor with respect to survival is thus given by (31%)/(77.2%) = 0.40.

\(^4\) The initial population size used in Vortex was slightly higher than the population size Germano (2016) estimates because Vortex requires a breakdown of the population by year classes. Our closest estimates using a specified age distribution resulted in a slightly larger population size estimate.

\(^5\) We assumed carrying capacity to be twice the initial population size because there is no indication that the population was at carrying capacity.

This means that in each 100-y simulation model, there are on average three temporally uncorrelated droughts (Table 3). We parameterized the impact on reproduction and survival by determining fecundity and survival rates during drought years. During the 1987–1992 drought, Holland (1994) studied populations in central and southern California and found that in several instances <20% of the females of potential reproductive size were gravid during the oviposition season. Furthermore, several sites throughout California experienced an average cumulative population decline of 69% over the first 5 y of the drought (Holland 1992). In Vortex, fecundity and survival rates for years in which drought occurs were obtained by multiplying the rates in a “normal,” noncatastrophe year by a severity factor ranging from 0.0 to 1.0 to reduce them to levels observed by Holland (1992, 1994; Table 3).

Although our baseline drought frequency for the previous century is 3%, we expect drought frequency to increase throughout the 21st century in California, as less precipitation is expected to occur (Dong et al. 2019). We explored a series of scenarios with varying levels of drought frequency. Using the baseline values for all other parameters (Table 3), we increased the “drought frequency %” parameter by increments of 1% to investigate the combined impact of increasing drought frequency on P\(_{\text{e}}\). In the model, the year a catastrophe occurs is considered the fourth year of a drought. The onset of a catastrophe is stochastic in Vortex. Therefore, as drought frequency increased, there was a greater chance that catastrophes occurred within a few years of...
Table 4. Mortality rates for northwestern pond turtles Actinemys marmorata and southwestern pond turtles Actinemys pallida as reported by Germano (2016) and Holland (1994). We designed a single population viability analysis model for both species, which required age-specific mortality rates. Germano (2016) and Holland (1994) both reported relatively low adult mortality rates; however, mortality rates reported among young age classes (<120 mm carapace length) differed dramatically between the two studies. These studies were conducted in the western United States.

| Carapace length (mm) | Carapace length (mm) | Mortality rate (%) | Mortality rate (%) |
|----------------------|----------------------|-------------------|-------------------|
| Germano (2016)       | Holland (1994)       |                   |                   |
| <80                  | <120                 | 26.9              | 85–90             |
| 80–119               | 85–90                | 16.2              | 3–5               |
| >120 Male; Female    | >120                 | 18.7; 26.9        |                   |

* Holland (1994) mentions a separate 30% hatching mortality rate that is not accounted for in the mortality rate for juveniles of <120 mm carapace length.

each other. Although we are only modeling 4-y droughts, we modeled these overlapping droughts as a drought that lasts longer than 4 y. For example, if drought number 1 occurs in year 5 and drought number 2 occurs in year 6, then survival and reproduction will decrease in year 5 and then again in year 6, according to the severity factor inputs for catastrophes in Table 3. These impacts build on each other, and consecutive catastrophes led to bigger drops in population size because the population does not have adequate time to recover from the first catastrophe. We would expect droughts that last longer than 4 y to have a similar effect.

Finally, we explored the interaction of first-year mortality and drought frequency across a reasonable range of parameter values. We used baseline values for all parameters except “mortality from 0 to 1 and drought frequency %” (Table 3) and increased the first-year mortality rate by increments of 1% under three different drought frequency (n) scenarios: n = 0%, n = 3%, and n = 6% to determine the joint impact of first-year mortality and increasing drought frequency on P∞.

Results

Threat analysis

Threat-related observations, regardless of impact, were documented more frequently throughout the range of NPT (n = 72) than that of SPT (n = 48; Table 5a, 5b). There was not a significant correlation between the “sum score” and the “mean score” within each species’ threat analysis (Table S4, Supplemental Material). However, there was a positive correlation (r = 0.680, P = 0.044; Table S4, Supplemental Material) between the “mean score” in the threat analysis for NPT and the “mean score” in the threat analysis for SPT. This suggests that the shared threats between the two species affected populations in similar, but not identical, ways (e.g., drought and land alteration had a higher “mean score” among populations of both species than roadways).

The top three documented threats for NPT in declining order of importance were predation by invasive predators, pathogens, and land alteration (Table 5a). For SPT, the top three threats were drought, predation by invasive predators, and flood (Table 5b). Predation by invasive species emerged as a top threat for NPT and SPT, with presumably the strongest effects on hatchlings and juveniles (Hallock et al. 2017).

Of the 13 threat categories assessed for SPT, drought had the highest “sum score” (17), the third-highest mean score (1.06), and the highest number of observa-
Table 5b. Results of the threat analysis for southwestern pond turtles Actinemys pallida. Under each threat category, we documented observations for the species, where an observation was defined as an author’s statement of how a potential threat is affecting a population. This information was derived from peer-reviewed literature, as well as published and unpublished reports from the western United States (1992–2021). Observations were assigned a numerical score of 0, 1, or 2 (see Table 2). The “sum score” was calculated by adding the scores in a threat category, while the “mean score” was calculated by taking the average of the scores in a threat category. “N/A” indicates that there were no observations for a threat category. The 13 threat categories were ranked using the “sum score,” and ties were resolved using the “mean score.”

| Threat                                | Rank | Sum score | Mean score | No. of observations |
|---------------------------------------|------|-----------|------------|---------------------|
| Drought                               | 1    | 17        | 1.06       | 16                  |
| Predation (bullfrogs and Largemouth Bass) | 2    | 6         | 1.00       | 6                   |
| Flood                                 | 3    | 5         | 0.56       | 9                   |
| Land alteration                       | 4    | 4         | 1.33       | 3                   |
| Wildfire                              | 5    | 3         | 1.50       | 2                   |
| Natural predators                     | 6    | 3         | 1.00       | 3                   |
| Roadways                              | 7    | 3         | 0.75       | 4                   |
| Harvesting                            | 8    | 1         | 1.00       | 1                   |
| Dams                                  | 9    | 0         | 0.00       | 1                   |
| Pathogens                             | 9    | 0         | 0.00       | 1                   |
| Competition with nonnative species    | N/A  | N/A       | N/A        | 0                   |
| Rising temperatures                   | N/A  | N/A       | N/A        | 0                   |
| Contaminants                          | N/A  | N/A       | N/A        | 0                   |
| Total                                 |      |           |            | 48                  |

Among the top five threats to SPT, most of their impacts are associated with, and potentially driven by, climate change (i.e., drought, floods, and wildfires). This is not the case for NPT, where only drought (ranking fourth in importance) was climate-change-related. This may indicate differences in the importance of future climate change to each species, or differences in researcher focus within the distributional range of each species (Text S1, Supplemental Material).

Local extirpations are of particular concern from a conservation perspective. Our review indicates that local extirpations of NPT were associated with land alteration and droughts (Figure 1a). For SPT, local extirpations primarily occurred in populations affected by droughts, while floods, land alteration, and wildfires were associated with a much smaller number of observed extirpations (Figure 1b). Droughts that lasted ≥4 y often resulted in local extinction for both species. For example, the 1987–1992 drought, as described by Holland (1992), had major effects on populations of WPT in southern and central California. Overall, impacts associated with the desiccation of aquatic habitat include increased fragmentation, increased vulnerability to predators, reduced water quality, and depletion of food sources leading to starvation (Holland 1992; Leidy et al. 2016; Lovich et al. 2017; Purcell et al. 2017). Droughts had consistently negative and pervasive effects for both NPT and SPT; therefore, we further explored the impacts of increases in drought frequency based on climate models for the 21st century (see Population Viability Analysis).

Population size estimates
Trapping and hand-capture surveys conducted intermittently at 131 sites from 1993 to 2019 were used to visualize and estimate counts for NPT and SPT (Figure 2; Table S3, Supplemental Material). Substantial head-starting efforts in Washington coincided with high population estimates (Hallock et al. 2017); however, these populations are not shown in Figure 2 because the data did not fit our criteria (see Methods). Large population size estimates tend to occur along the Trinity River in Trinity County, California, parts of California’s Central Valley, and sparsely along the central and southern California coast. Sites with low mean annual captures (<1) occurred in San Diego County, Kern County, northern Los Angeles County, and San Bernardino County along the Mojave River. Southeastern pond turtles were dominated by smaller populations than were NPT (Figure 2; Table 6), and a chi-square test confirmed that the distribution of populations in each population size category in Table 6 differed between the two species ($P_0 = 0.026$). Most populations of both species contained 1–50 individuals, and within this size class, SPT had significantly lower population size estimates than did NPT (t-test, $P = 0.0003$; Table 6).

Population viability analysis
Determining baseline vital statistics. Overall, Germano’s (2016) and Holland’s (1994) respective mortality schedules lead to different conclusions for the probability of population persistence (Figure 3a). When using Germano’s (2016) values in the PVA model, the probability of extinction ($P_e$) is 0.00 (0 out of 100 simulations go extinct within 100 y). By contrast, when using Holland’s (1994)
values in the PVA model, $P_e$ is 1.00 (all 100 simulations go extinct within 100 y). Given this, we used the PVA model to further explore the importance of two seemingly critical parameter values for which Germano (2016) and Holland (1994) differed: first-year mortality and adult female mortality.

When using the first-year mortality rate of 91% (includes hatching mortality) from Holland (1994), $P_e$ is 1.00 (Figure 3b). In contrast, when using the lower observed first-year mortality rate of 49% (includes hatching mortality; Germano 2016), $P_e$ is 0.00 (Figure 3b). Sensitivity analyses showed that this difference in first-year mortality is an important determinant of population viability over time (Figure 3b). In contrast, differences in adult female mortality rates between the two studies did not change model outcomes, and both the Germano (26.9% annual adult female mortality) and Holland (4% annual adult female mortality) estimates led to stable populations with $P_e = 0.00$ (Figure 3c). Sensitivity analyses revealed that $P_e$ began to rise when adult female mortality rates exceeded 35%/y, and $P_e$ increased sharply to near 1.00 at about 50% adult female mortality per year (Figure 3c). Given these results, we used Germano's (2016) mortality schedule to further investigate catastrophic population threats because it allowed us to infer the impacts associated with droughts in an otherwise viable population, which was not possible using the vital statistics reported in Holland (1994).

**Catastrophic droughts and population viability.** To model the effect of catastrophic droughts on the population viability of WPT, we used baseline values for all parameters in Table 3 to determine $P_e$. The empirical baseline drought frequency is 3% (see Methods; Table 3). Without catastrophic droughts, $P_e$ was 0.00; however, with 3 catastrophic droughts per century, $P_e$ increased to 0.15 (Figure 4). As drought frequency increased, $P_e$ reached 0.50 between 4% and 5% (Figure 4). The probability of extinction reached 1.00 at a drought frequency of 14% (Figure 4).

Droughts are expected to increase in frequency with climate change (Diffenbaugh et al. 2015), while simultaneously, juvenile mortality may increase as a result of the introductions and persistence of invasive predators (i.e., bullfrogs or centrarchid fishes). We explored varying first-year mortality rates under three different drought frequency ($n$) scenarios: $n = 0$, $n = 3$, and $n = 6$. Without catastrophic droughts ($n = 0$), $P_e$ did not reach 0.50 until a first-year mortality rate of 71% (Figure 5). At the current baseline drought frequency ($n = 3$), $P_e$ reached 0.50 at approximately 60% first-year mortality. However, when drought frequency doubled ($n = 6$), $P_e$ reached 0.50 at a first-year mortality rate of only 44%.

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**Figure 1.** Breakdown of threat impact scores for observations under each threat category for (a) northwestern pond turtles (NPT) *Actinemys marmorata* and (b) southwestern pond turtles (SPT) *Actinemys pallida*. Under each threat category, we show the number of observations for each species, where an observation was defined as an author's statement of how a potential threat is affecting a population. This information was derived from peer-reviewed literature, as well as published and unpublished reports from the western United States (1992–2021). Observations were assigned a numerical score of 0, 1, or 2 (see Table 2). “N/A” indicates the absence of empirical observations of a threat impact on a population.
Figure 2. Population size estimates for northwestern pond turtles *Actinemys marmorata* and southwestern pond turtles *Actinemys pallida* based on the average number of unique individuals captured annually per site (Table S3, Supplemental Material). Trapping and hand-capture surveys were conducted intermittently at 131 sites in the western United States and Mexico from 1993 to 2019 for northwestern pond turtles (50 sites) and southwestern pond turtles (81 sites). Records were obtained from field data sets, unpublished and published reports, and peer-reviewed literature (Table S2, Supplemental Material). Range maps were obtained from the USGS (2018) for Washington and Oregon, Thomson et al. (2016) for California, and the Amphibian and Reptile Atlas of Peninsular California (2014) for Baja California, Mexico. We binned the results into four range categories: <1, 1–50, 51–100, and >100 individuals.

Table 6. Descriptive statistics for the average number of unique individuals captured annually within each population size estimate category. To determine where northwestern pond turtles *Actinemys marmorata* and southwestern pond turtles *Actinemys pallida* are maintaining large population sizes, we compiled rough estimates of census population sizes by calculating the average number of unique individuals captured annually among different populations (Table S3, Supplemental Material). Trapping and hand-capture surveys were conducted intermittently from 1993 to 2019 in the western United States and Mexico. We binned the results into four range categories: <1, 1–50, 51–100, and >100 individuals.
Despite having relatively large, essentially nonoverlapping distributions, our analyses indicate that NPT and SPT often face similar threats. This may be expected, given that these sister taxa were considered a single species until 2014, and that both taxa have similar ecological and habitat requirements. The top three threats to NPT in order of decreasing impact were predation by nonnative bullfrogs and Largemouth Bass Micropterus salmoides, pathogens, and land alteration (Table 5a), while for SPT the top three threats were drought, predation by nonnative bullfrogs and Bass, and floods (Table 5b). Our literature survey also indicates that SPT may be more vulnerable to natural disasters that will intensify with climate change (i.e., droughts, wildfires, and floods), an effect likely compounded by generally smaller population sizes for this species (Figure 2). Droughts directly affect both survival and reproduction, representing a significant threat to both species as confirmed with our PVA model.

Although NPT and SPT often face similar threats, conservation strategies for each species may need to prioritize mitigating these threats differently. For exam-
The greater number of drought-related impacts among populations of SPT (Table 5b) suggests that it is a more severe threat for SPT than for NPT. According to Dong et al. (2019), the strength of drought and the sensitivity of vegetation to drought are greater in southern California, a region that encompasses most of the range of SPT, but only the southernmost portion of the range of NPT. During the 2012–2016 drought, the greatest drought-related normalized difference vegetation index (greenness) declines occurred in southern California’s coastal regions and along low-lying areas of the San Joaquin Valley and foothills, indicating severe effects of water stress, while parts of northern California did not appear to be as severely affected (Dong et al. 2019). This suggests that increasing drought frequency will most negatively affect SPT and southern San Joaquin Valley parts of the range of NPT.

A single proximate event, such as drought, may lead to population declines through multiple interrelated effects. For example, drought conditions also create favorable conditions for wildfires, another high-impact threat for SPT (Table 5b). The catastrophic impacts of wildfire include inputs of ash into aquatic habitats, reduction in vegetation and leaf litter (important terrestrial habitat for overwintering), and direct mortality of WPT (Lovich et al. 2017). Between 1970 and 2003, forest wildfire activity in the western United States (from Washington south through California) increased suddenly in the mid-1980s, with greater large-wildfire frequency, longer wildfire durations, and longer wildfire seasons (Westerling et al. 2006). Climate change projections throughout California’s chaparral ecosystems suggest increased fire activity including an extended fire season and a greater frequency of large fires (Molinari et al. 2018). Large and severe fires associated with warm, dry conditions are also expected to increase in frequency with climate change in Washington and Oregon, the northernmost range of NPT (Halofsky et al. 2020). Although the impacts of wildfires on NPT have not been well-documented (Text S1, Supplemental Material), wildfires occur throughout their range and likely have similar impacts to those documented for SPT (Lovich et al. 2017). Notably, the 2020 wildfire season was particularly severe across much of the northern California range of NPT (Higuera and Abatzoglou 2020).

Flood represents another type of natural disaster expected to increase under climate change. Floods impact SPT in two primary ways: flushing of individuals from their aquatic and terrestrial habitat and inundation of nesting sites (Rathbun et al. 1992; Nerhus 2016). Recent flood events have been implicated in the extirpation or extreme reduction of isolated SPT populations along the Mojave River in San Bernardino County, California (Figure 2; Lovich et al. 2021). Although evidence suggests that NPT and SPT are adapted to current regimes throughout most of their range (Rathbun et al. 2002) and can therefore persist under historical conditions, regime shifts associated with climate change are expected to increase the frequency and severity of major flood events throughout the majority of the range of WPT (Swain et al. 2018).

An important, but poorly studied threat for both species is rising temperatures associated with climate change. The limited available evidence suggests that increases in incubation temperature could result in skewed sex ratios and decreased hatching success (Christie and Geist 2017). These impacts may be particularly problematic for populations near their thermal limits. Although difficult to manage, the vulnerability of native biodiversity to climate change is worth assessing when planning for the future management of each species. Given the difficulty of observing changes like hatching sex ratio, our baseline PVA model provides a resource for managers to model and predict the population-level severity of these life-history changes.

Ultimately, drought emerged as the most important of the 13 potential threats. It received the highest “mean score” for NPT (Table 5a) and was ranked as the number one threat to SPT (Table 5b). Drought severity and frequency are expected to increase as a result of climate change (Diffenbaugh et al. 2015), so we further explored the effects of catastrophic droughts on WPT with our PVA model. The model indicates that WPT will suffer large population declines from major droughts that last a minimum of 4 y. If the frequency or length of 100-y droughts increases, as expected under most climate change scenarios, our PVA model predicts even greater population declines or local extirpations (Figure 4), emphasizing the importance of considering the impacts of catastrophic droughts in the long-term management of WPT. It is important to keep in mind that our PVA results are based on mortality schedules from what are believed to be very healthy populations, and that
Accordingly, our PVA model is a best-case scenario for the dangers of drought-induced population decline. If less optimistic mortality schedules are used, this would further increase the importance of variation between different populations, as illustrated in Figure 3a, emphasizes the need for additional data on population mortality schedules. It may be that geographic variation in mortality schedules is a reality among different populations of WPT, resulting in extirpations for some and persistence for others. Alternatively, the few studies that have collected these data may simply have large confidence intervals, and true mortality schedules may fall between these estimates. Although difficult and time-consuming, ecological studies that quantify such variability are valuable for the successful management of widespread, long-lived species like WPT. In the meantime, decision-makers can proceed based on the best available scientific evidence as summarized here.

Impacts associated with drought are pervasive and work synergistically to increase mortality (Holland 1992; Leidy et al. 2016; Purcell et al. 2017). Our PVA results demonstrate that when populations are small and recruitment is low, drought becomes especially important and can influence the fate of a population. Western pond turtles require access to aquatic habitat for survival; therefore, drought resilience is an important habitat parameter, especially for SPT and more southerly populations of NPT like Goose Lake. Assuming the trapping data for NPT and SPT are reasonably unbiased, SPT appear to exist in lower population numbers than NPT (Table 6), suggesting that SPT are more vulnerable to stochastic droughts and other catastrophic causes of population decline, with a resulting greater likelihood of local extirpation. However, scaling our findings up to species-level extinction risk requires additional analysis. In particular, we cannot address the possibility of population rescue via colonization from adjacent, more robust populations, should they exist on particular landscapes. Situations where metapopulation dynamics may facilitate such demographic rescue can be incorporated into our PVA model and would be an appropriate extension when inferring a timeline for, or likelihood of, metapopulation or species-level extinction.

Given that they have significantly smaller population size estimates and have increased vulnerability to natural disasters, we suggest that the most immediate need for conservation and protection is for SPT to prevent further declines. Although it may be difficult to manage impacts associated with natural disasters, conservation strategies can focus on increasing population resilience to catastrophes by managing other threats to maintain larger population numbers and promote recruitment. Given the faster reproductive development of SPT compared with NPT (Germano and Bury 2001), fairly rapid recruitment and population increases may be possible if threats are abated in the range of SPT. Invasive predator control and management of both aquatic and terrestrial habitat to reduce the impacts of droughts or floods are important, implementable solutions, and at least two sources have suggested that bullfrog removal can lead to rapid increases in juvenile survival (Brown et al. 2015; Hallock et al. 2017).

Supplemental Material

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Text S1. A detailed review of 13 potential threats for northwestern pond turtles (NPT) Actinemys marmorata and southwestern pond turtles (SPT) Actinemys pallida. For each threat, we provide a general description, followed by more species-focused discussions for each taxon based on available studies from the peer-reviewed literature, plus published and unpublished reports from the western United States (1992–2021).

Available: https://doi.org/10.3996/JFWM-20-094.S1 (56 KB DOCX)

Table S1. Threat observations used to analyze 13 potential threats for northwestern pond turtles (NPT) Actinemys marmorata and southwestern pond turtles (SPT) Actinemys pallida based on the peer-reviewed literature, plus published and unpublished reports from the western United States (1992–2021). We assigned a numerical score to each observation based on the threat’s impact (see Table 2).

Available: https://doi.org/10.3996/JFWM-20-094.S2 (103 KB XLSX)

Table S2. Number of unique northwestern pond turtles (NPT) Actinemys marmorata and southwestern pond turtles (SPT) Actinemys pallida captured and marked annually per site in the western United States and Mexico (1993–2019). These data were obtained from peer-reviewed literature, published and unpublished reports, and unpublished data sets contributed by field researchers as listed at the end of this table.

Available: https://doi.org/10.3996/JFWM-20-094.S3 (32 KB XLSX)

Table S3. Average number of unique northwestern pond turtles (NPT) Actinemys marmorata and southwestern pond turtles (SPT) Actinemys pallida captured and marked annually per site in the western United States and Mexico (1993–2019). These values were calculated using data obtained from peer-reviewed literature,
published and unpublished reports, and unpublished data sets contributed by field researchers as listed at the end of this table.

Available: https://doi.org/10.3996/JFWM-20-094.S4 (26 KB XLSX)

**Table S4.** Results of Spearman correlation between the “sum score” and “mean score” (Table 5a, 5b) for northwestern pond turtles (NPT) *Actinemys marmorata* and southwestern pond turtles (SPT) *Actinemys pallida*. The “sum score” and “mean score” were obtained from the threat analysis for NPT and SPT based on available studies from the peer-reviewed literature, plus published and unpublished reports from the western United States (1992–2021). Cell values are Spearman’s rho (correlation coefficient), followed by its significance *P*-value (two-tailed).

Available: https://doi.org/10.3996/JFWM-20-094.S5 (15 KB DOCX)

**Reference S1.** Holland DC. 1992. A synopsis of the ecology and status of the western pond turtle (*Clemmys marmorata*) in 1991. Report to the U.S. Fish and Wildlife Service National Ecology Research Center, San Simeon, California. Available: https://doi.org/10.3996/JFWM-20-094.S6 (8.7 MB PDF)

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