DEMOGRAPHIC MODELING OF CONSERVATION STRATEGIES FOR THE YOSEMITE TOAD (*ANAXYRUS CANORUS)*

By

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ABSTRACT

DEMOGRAPHIC MODELING OF CONSERVATION STRATEGIES FOR THE YOSEMITE TOAD (*ANAXYRUS CANORUS*)

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The Yosemite toad (*Anaxyrus canorus*) is an anuran species endemic to the Sierra Nevada in California that, like many amphibians globally, has suffered population declines. The documented decline in *A. canorus* populations across their historic range highlights the need for an effective management strategy to protect the species from future extirpation. For this study, I estimated survival rates of *A. canorus* using a Cormack-Jolly-Seber model populated with data from a demographic study. I then used a female-only post-birth pulse stochastic Lefkovitch matrix model using vital rates I estimated and from the literature to simulate the effect of different management scenarios and to optimize a supplementation or reintroduction management plan. Without any management action, small populations of *A. canorus* populations have ≥50% risk of quasi-extinction over the next 13 years. The implementation of effective management strategies is critical to prevent further extinction of existing small populations. My results suggest that the effectiveness of a supplementation or a reintroduction management plan is dependent on the initial population size of the receiving population, life stage at release and number of individuals released into a wild population. I found that supplementing small toad populations with female adults is the most effective supplementation strategy to increase the stochastic growth rate and minimize the risk of quasi-extinction. This thesis suggests that modeling *A. canorus* population dynamics and trends of extant populations can help inform conservation strategies.

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INTRODUCTION

Since the 1990s, numerous amphibian populations have experienced widespread declines and at least one-third of all amphibian species worldwide are threatened with extinction (Stuart et al., 2004; Wake & Vredenburg, 2008; Ripple et al., 2017). There are several likely causes of such rapid and widespread population declines including habitat alteration, disease, invasive species and climate change (USFWS, 2002; Brown et al., 2015; Grant et al., 2016).

Supplementation (adding individuals to existing populations) or reintroduction (re-establishing a population within the species' historical range) has been used as an effective conservation strategy to prevent extirpation or extinction of sensitive amphibian species (Zippel & Mendelson, 2008; Forstner et al., 2013; Polasik et al., 2016). While supplementation or reintroduction may not directly address habitat limitations or other stressors causing the decline of the species, these strategies can provide insight on basic population dynamics. Developing a basic understanding of the population dynamics of a species can help inform managers on the level of effort that is necessary to reduce extinction probability and provide data to compare population dynamics before and after a management plan is implemented (Morris & Doak, 2002; Scott et al. 2005; Kissel et al., 2014). Comparing the population dynamics pre- and post-implementation of a management plan will provide a baseline to help define what makes a project successful and allow for an adaptive approach to help ensure that desired outcomes are achieved. Additionally, if monitored and quantified, such conservation strategies can increase the understanding of key threats leading to population declines (Fischer & Lindenmayer, 2000; Zippel & Mendelson, 2008).

Even seemingly pristine, protected habitats are not immune to amphibian population decline or the loss of amphibian biodiversity. For example, amphibian populations have declined in areas with strict conservation measures, such as Yosemite National Park in the USA and the Monteverde Cloud Forest Preserve in Costa Rica (Sherman & Morton, 1993; Drost & Fellers, 1994; Pounds et al., 2015). The Yosemite toad (*Anaxyrus canorus*) is an anuran species endemic to the Sierra Nevada mountain range in California that has suffered severe population declines even though its historic range is largely within protected environments (Sherman & Morton, 1993; Brown et al., 2015). Due to the documented decline in occupancy within the historic range of the toad, the U.S. Fish and Wildlife Service listed *A. canorus* as a threatened species under the Endangered Species Act in 2014 (US Fish & Wildlife Service, 2014). Over the past decade, the decline of *A. canorus* has prompted investigations into potential causes as well as management solutions that can protect the species from future extinction. The National Park Service and the US Forest Service have conducted extensive surveys for *A. canorus* and have determined areas where toad populations exist, as well as areas where toads are thought to be extirpated (Brown et al., 2013; Berlow et al., 2013). However, no single cause has been identified as a leading contributor to decline, limiting the ability of managers to implement conservation strategies (Brown et al., 2015).

The known historic distribution of *A. canorus* and a well-documented decline in population numbers makes the toad a good candidate for a potential supplementation or reintroduction management plan (Brown et al., 2013; Brown, 2015). The general objective of this study was to investigate how to design and implement a strategy to maximize the chances of successful supplementation or reintroduction (i.e., the number and what life stages of individuals are needed to sustain a viable *A. canorus* population). To address this, I created a stage-based matrix projection model using estimates of fecundity, life stage transformation and survival rates (Caswell, 2001). While the results of this thesis can help inform management in implementing a supplementation or reintroduction program, I mainly address supplementation as a management plan in the analysis in this thesis.

Matrix-based population models are commonly used to inform management decisions, offering insight into effective actions to protect species of conservation concern (Caswell, 2001; Morris & Doak, 2002). Matrix population models can be used to infer a population's projected growth rate, risk of extinction over a specified period of time, stable stage distribution (SSD), and the impact that each life stage has on population dynamics (Caswell, 2001). Matrix projection models have been used to provide guidance in designing and implementing supplementation management plans for captive breeding, reintroduction and translocation programs (Tenhumberg et al., 2004; Canessa et al., 2014; Kissel et al, 2014; Gerber et al., 2017) and monitoring supplemented populations to assess the effectiveness of management actions (Muths & Dreitz, 2008).

My work modeling the population dynamics of *A. canorus* contributes information on the key ecological attributes or vital rates of healthy *A. canorus* populations and provides a roadmap for management action. Specifically, I address three main objectives: 1) determine which vital rates have the greatest effect on population growth of *A. canorus* using a stochastic population growth model; 2) identify areas or breeding populations for which supplementation could result in an increase in population viability and reduce extinction risk ≤50% over 13 years (three generations)[1] ; and 3) identify the quantity of individuals at each life stage that is necessary to maintain a viable *A. canorus* population.

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[1] The criteria for down-listing a species form critically endangered to endangered under the International Union for Conservation of Nature (IUCN, 2018).

MATERIALS AND METHODS

Study Species

Yosemite Toad (*Anaxyrus canorus*)

Anaxyrus canorus is part of the family *Bufonidae*, a group estimated to face the greatest risk of extinction of anuran species worldwide (Stuart et al., 2004). The historic range of the *A. canorus* extends from Ebbetts Pass in the north to the southern extent of the Kings River in Fresno County (Figure 1). *Anaxyrus canorus* has experienced significant declines in both abundance as well as distribution. In the mid-1990s, the species was estimated to be extirpated from roughly 50% of their historic range (Sherman & Morton, 1993; Drost & Fellers, 1994; Jennings, 1996; Brown & Olsen, 2013; Thompson et al., 2016). More recent studies have determined that *A. canorus* still inhabit 84% of recent sites (1990-2001), but have disappeared from >80% of historic (prior to 1990) localities (Brown, 2015).

Anaxyrus canorus inhabitants both aquatic and terrestrial high elevation habitat (1,950-3,444 m), using upland habitat, meadows and springs to forage and for refuge. In the springtime, following seasonal snowmelt, toads congregate and breed in stagnant shallow pools, often associated with wet meadows (Figure 2, Figure 3). *Anaxyrus canorus* breeds for 1-2 weeks in the spring, and then disperses to upland habitat. Females lay strands of 1,500-2,000 eggs in shallow bodies of water. Eggs will hatch in 6-8 days and tadpoles will typically metamorphose in 6-8 weeks (Sherman & Morton, 1993; Drost

& Fellers, 1994; Brown, 2015). Male toads become reproductive between 3-5 years of age, and females become reproductive between 4-6 years of age (Sherman, 1980; Sherman & Morton 1993; Brown et al., 2015). *Anaxyrus canorus* rely on flooded meadows, ephemeral pools or shallow ponds to breed (Figure 2, Figure 3). The shallow bodies of water used for *A. canorus* breeding sites can undergo significant fluctuations in temperature and can dry up quickly if there is not enough snow melt or spring recharge. If a site dries up before the toad goes through metamorphosis, early life stages can experience high mortality rates (Sherman, 1980; Sherman & Morton, 1993; Brown et al., 2015).

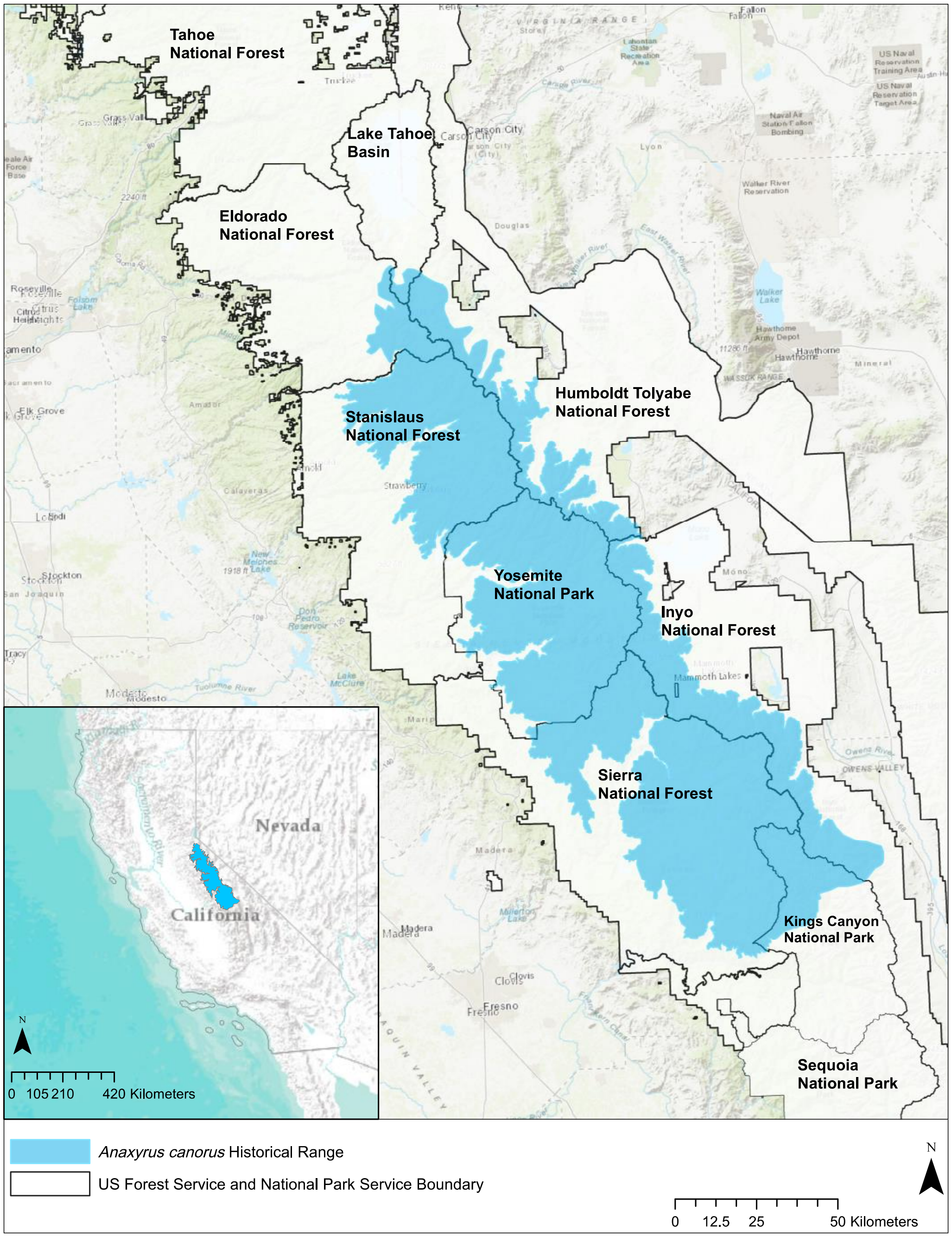

Figure 1. Map of *Anaxyrus canorus* historical range on National Forest and National Park land. The USFS CMR study occurred in 19 meadow sites in the Sierra National Forest, the Stanislaus National Forest and in Yosemite National Park. The specific site locations are not shown on the map. Map was generated using a GIS layer of the *A. canorus* historical range (USFS, 2016), National Forest Boundary layer (USFS, 2022) and National Park Service Layer (NPS, 2022).

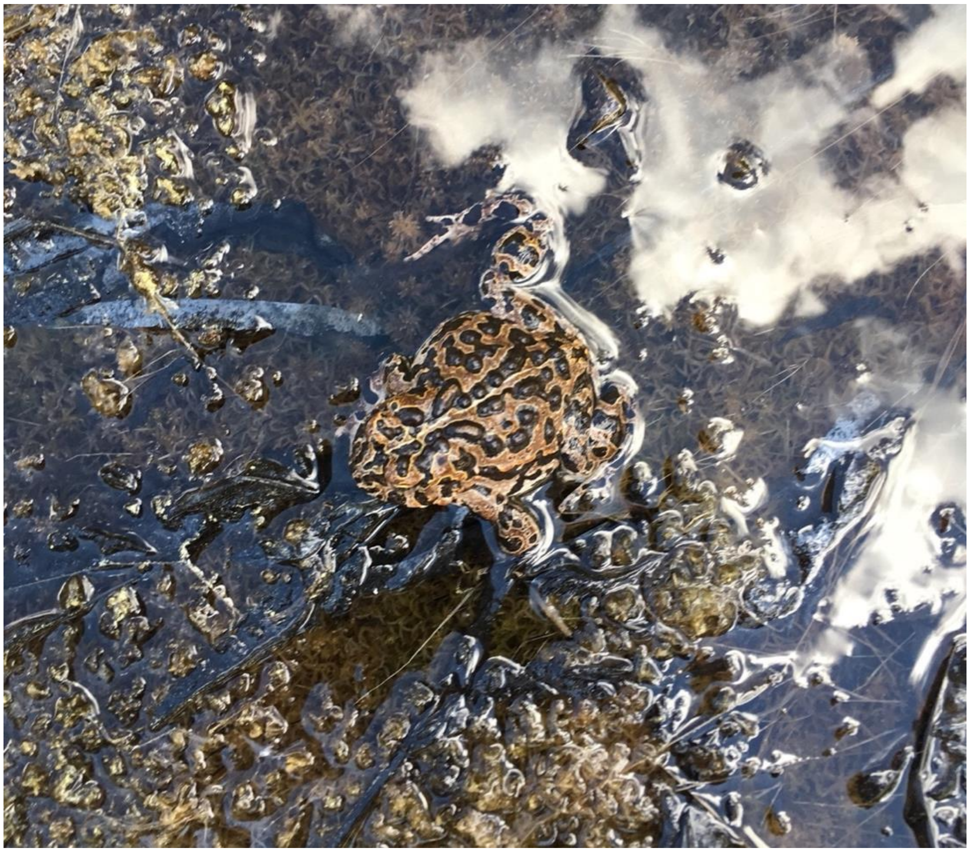

Figure 2. Adult Female *Anaxyrus canorus* in a shallow pool of water at meadow site photographed in summer, 2019 in Yosemite National Park, California. Photo: Corrina Kamoroff

Figure 3. Pair of *Anaxyrus canorus* in a shallow pool of water at meadow site photographed in summer, 2019 in Yosemite National Park, California. A male *A. canorus* is shown on top of a female toad in amplexus. Photo: Corrina Kamoroff

STUDY SITE

Anaxyrus canorus demographic survey data was collected between 2005 and 2010 and generously made available for this study by the U.S Forest Service (USFS). The study was conducted in the Sierra National Forest, the Stanislaus National Forest, and in Yosemite National Park (Figure 1). Capture-Mark-Recapture (CMR), occupancy, and life history data on *A. canorus* was collected from 19 meadows including seven meadow sites in the Stanislaus National Forest, ten meadow sites in the Sierra National Forest, and two meadow sites in the Yosemite National Park. Each meadow site varied in elevation and size and all sites were located within the current range of *A. canorus* (Figure 1). The size of each meadow site ranged from 0.8 to 8.54 ha in size (mean = 3.3). The elevation of the study sites ranged from 2,122 m to 2,679 m in elevation (mean = 2414) in the Sierra Nevada mountain range (Lind et al., 2010).

FIELD SURVEYS AND DATA COLLECTION

The USFS *A. canorus* study surveyed 19 meadow sites for at least two consecutive years over the six-year study (between 2005 and 2010). Survey effort varied by site and year. When possible, they surveyed each site three times (May-October) each year, once in late spring to survey for adult toads and egg masses, once in mid-summer to survey for tadpoles and once in late summer to survey for metamorphosed individuals. Each year, the timing of the surveys varied to compensate for site location, elevation, snowpack and other logistical factors for each meadow site. Each site was surveyed to determine occupancy of *A. canorus*, and a CMR effort was conducted. To determine presence or absence of *A. canorus,* the USFS conducted a Visual Encounter Survey (VES) at each meadow site. During the VES, surveyors walked transects across each meadow site, concentrating more survey effort (measured by amount of time spent) in areas that were considered good habitat for the species (i.e., shallow pools of water or wet areas). During late spring and summer surveys, a more intense survey effort was conducted in areas that were determined to have breeding activity during early spring surveys. All individual toads that went through metamorphosis were weighed, measured and documented. All captured adult toads were scanned for Passive Integrated Transponder (PIT) tags to determine if they were new or recaptured individuals. New adult *A. canorus* (with snout vent length ≥ 50 mm), not actively in amplexus, were surgically implanted with a uniquely numbered PIT tag (Lind et al., 2010). Sex was determined by visually inspecting each adult *A. canorus. Anaxyrus canorus* are sexually dimorphic: males tend to exhibit olive green to yellow green coloration while females tend to exhibit brown or grey coloration with larger dark spots (Figure 2, Figure 3). Encounter histories of individually-marked animals were created from initial captures and recaptures on an annualized basis (Lind et al., 2010).

ANALYTICAL METHODS

Cormack-Jolly-Seber Model

I estimated the annual survival and recapture probability of *A. canorus* using a hierarchical Cormack-Jolly-Seber (CJS) model. I completed separate analyses to estimate annual survival probabilities of males and females for 19 meadow sites using the USFS demographic dataset collected between 2005 and 2010. I estimated survival using data from marked and recaptured adult individuals from survey encounters in successive years, using annualized encounter histories. The USFS did not PIT tag individuals with SNV <50 mm in length. As a result, I did not use the dataset to estimate survival parameters for early life stages of *A. canorus*. Instead, I used survival estimates from scientific literature for eggs, tadpoles, metamorphs and juvenile life stages of *A. canorus* and from the boreal toad (*Anaxyrus boreas*) when the mean vital rate were not available for *A. canorus* (Mullally, 1953; Sherman, 1980; Sherman & Morton, 1993; Brown, 2015; Lindaur, 2019; Crockett et al., 2021).

In the CJS model, I included a random effect of study site on apparent survival (φ) and recapture probability (ρ), which describes the variation in mean logit-scale parameters among sites as a normally-distributed random variable (Cormack, 1964; Jolly, 1965; Seber, 1965). The model parameters were estimated using a Bayesian framework where the posterior probability distribution of model parameters was approximated using Markov chain Monte Carlo (MCMC) methods. I choose to work with a Bayesian framework as it allowed for the estimation of parameters of the CJS model using a relatively small dataset (the dataset only contained 265 captured adult individuals, across 19 sites) over a relatively short period of time (six years) using an uneven sampling effort between sites (Kéry & Schaub, 2011; Kéry & Royle, 2020). The CJS model assumes an open population where births, deaths, emigration and immigration are possible. In the CJS model, permanent emigration and mortality are not distinguishable within the population, thus I refer to the estimated survival probabilities as apparent survival (Kéry & Schaub, 2011). Random effects for site were specified in the model to account for variation in survival and recapture estimates due to meadow site. All CJS modeling was completed using JAGS (v4.3.0) and run in Program R (v3.6.3;R Development Core Team, 2020) using package R2jags (v0.7-1; Su and Yajima, 2012). I determined model convergence by examining $\hat{R}$ values (Brooks & Gelman, 1998; Kéry & Schuab, 2011) and visually inspecting trace plots of chains (Kéry & Schaub, 2011). The CJS model was run using three chains, each with 100,000 iterations with the first 5,000 iterations discarded (burn-in), each chain was thinned by five, and 19,000 iterations were saved (Appendix A). To estimate apparent survival and detection probability, I used *A. canorus* capture history for PIT tagged individuals that were classified as adults (SNV ≥50mm). Goodness-of-fit was assessed using a posterior predictive check based on the Bayesian p-value (Meng, 1994; Rubin, 1996). The Bayesian p-value represents the proportion of times the simulated data has a discrepancy measure more or less extreme than the actual data set. A Bayesian p-value close to 0.5 suggests that the model is a good fit and extreme values close to 0 or 1 suggests that the model is not a good fit for the dataset (Meng, 1994; Rubin, 1996; Kéry & Schaub, 2011).

Stochastic Matrix Projection Model

I used scientific literature values as well as survival estimates obtained from this study to parametrize a female-only post-birth pulse stochastic Lefkovitch matrix model (Table 1) (Lefkovitch, 1965; Caswell, 2001). Since the life stages (including egg mass, tadpole, metamorph, juvenile and adult) of *A. canorus* are unequal in time duration, I combined the survival estimates of early age classes (egg mass, tadpole and metamorph) into a single life stage that is one year in length to represent the species' first year of life. I refer to the second stage class as the young of the previous year (YOPY), and the vital rate product (egg mass, tadpole, and metamorph) as young of the year (YOY) vital rates. I created a stage-based matrix model with five life stages for *A. canorus:* Eggs (because the matrix model is a post-birth pulse), YOPY, third-year juveniles, fourth-year juveniles, and adults (≥ 4 years old) (Figure 4). I then used vital rate estimates obtained from the CJS model and the literature to populate the matrix (**Error! Reference source not found.**). Because of the low capture and recapture rates and low detection probability of adult female *A. canorus*, estimates for adult female survival may not be reliable. As a result, I used male survival rate as a proxy for female survival, which explicitly assumes male and female survival are equal. It has been documented that *A. boreas,* a species closely related to *A. canorus*, have adult male and female estimated survival rates (0.78 and 0.87 respectively) that are similar enough to each other to infer accurate ecological conclusions when using male survival as a proxy for female survival (Piliod et al., 2010; Biek et al., 2002). It should be noted that the male survival estimate for *A. boreas* is 9% lower than the estimated survival rate for females. If the same is true for *A. canorus,* using males as a proxy for females may result in slightly conservative estimates of risk of quasi-extinction and population growth. However, because the male and female estimated vital rates are relatively high and similar to one another, using males as a proxy for females is not expected to significantly change the conclusions drawn from the matrix population model used for this study. A description and justification of how vital rate estimates were derived can be found in Appendix D and in the Discussion of this thesis. The annual fecundity was calculated as the estimated number of eggs divided by two. This was done assuming a 1:1 sex ratio multiplied by the probability of females laying eggs each year. An unequal sex ratio could bias the population growth rate estimates (Sherman & Morton, 1993; Drost & Fellers, 1994; Brown et al., 2012).

Table 1. Summary of *Anaxyrus canorus* vital rates and sources that were used to populate the stochastic matrix projection model. The table includes the mean vital rate value, the variance[2] and the data source.

Vital Rate	**Mean**	**Min**	**Max**	**Variance**	**SD**	**Source**
Young of the Year Survival	0.020	0.0	0.30	0.0056	0.075	Crockett et al., 2021
2nd year juvenile Survival	0.348	0.18	0.4	0.003	0.055	Sherman, 1980; Clarke, 1997; Kelleher & Tester. 1969
3rd year juvenile Survival	0.348	0.18	0.4	0.003	0.055	Sherman, 1980; Clarke, 1997; Kelleher & Tester, 1969
Adult Survival	0.67	-	-	0.0053	0.0728	USFS Data/This project
Probability of laying	0.5	0.0	1.0	0.0625	0.25	Brown, 2015
Fecundity (females)	875	750	1000	3906.25	62.5	Mullally, 1953; Karlstorm, 1962; Sherman, 1980

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[2] The available data from the literature (for YOY, YOYP and juvenile life stages) did not allow me to distinguish between the process and sampling variance for the vital rates for earlier life stages.

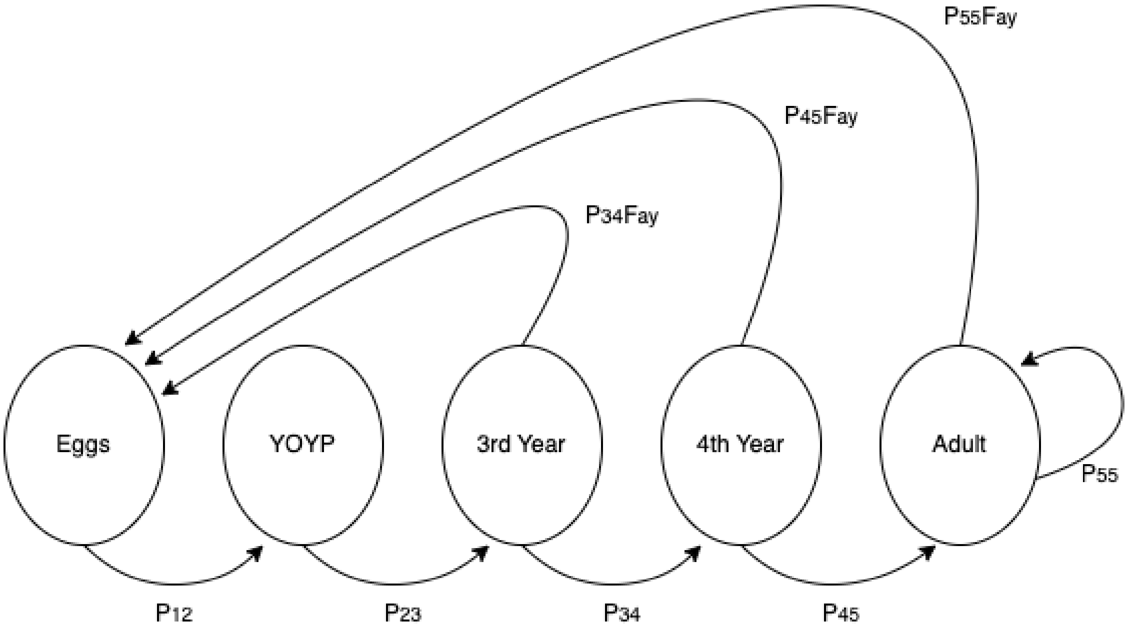

Figure 4. Life history diagram for *Anaxyrus canorus* with a post-birth pulse stage-structured life history. The circles represent the five stage classes: Eggs, young of the previous year (YOPY), 3nd year and 4th year, and adults (>4 years old). Each stage class is linked (bottom arrows) by the probability (P_{ij}) of surviving and transitioning from one stage to next or surviving and remaining in the same life stage. The upper curved arrows represented the fecundity (F_{ij}) of the toad and link adults to Eggs. In a post-birth pulse stage-structured model, the life stages represent the life stage immediately after the annual birth pulse of a population occurs.

$$\boldsymbol{L}=\begin{bmatrix} 0 & 0 & 0 & P_{54}*(F_5*0.5) & P_{55}*(F_5*0.5) \\ P_{12} & 0 & 0 & 0 & 0 \\ 0 & P_{23} & 0 & 0 & 0 \\ 0 & 0 & P_{34} & 0 & 0 \\ 0 & 0 & 0 & P_{54} & P_{55} \end{bmatrix}$$

Figure 5. Female only, post-birth pulse Lefkovitch matrix (L) modeling the life stages of *Anaxyrus canorus*. The probability of transitioning from one stage to next or remaining in the same stage is represented by “P”. The fecundity is represented by “F”. P_{ij} is the probability that an individual in stage i transitions to class j and survives. F_i is the fertility for stage i. Each value was obtained from data collected by the USFS and from literature values, as described in Appendix D.

For the matrix model, I projected the population at a time interval (t) of one year using the equation:

$$\mathrm{N(t+1) = L*N(t)}$$

where $\mathrm{N(t)}$ is a five-element population size vector at time t, and L is a five by five projection matrix. I simulated the effect that supplementation scenarios would have on population growth and quasi-extinction probability (the threshold that a population will likely experience extinction, even if there are still individuals in the population) by manipulating the starting population vector. A quasi-extinction threshold of 450 (including all female age classes at SSD) was used in the analysis. A population may be a considered a good candidate for supplementation if the population has a quasi-extinction risk >50% over 10 years or three generations (13 years), which is the criteria to down-list a species from Critically Endangered to Endangered under the International Union for Conservation of Nature (IUCN) (IUCN, 2018). I modeled the extinction probability and stochastic growth rate for a population with a given number of adult females at SSD for the mean matrix.

To determine what populations of *A. canorus* warrant some level of supplementation effort to protect the species from extinction as well as what populations may be considered donor site for translocation efforts, I ran the projection model with an increasing population size at SSD to determine what population size decreased the risk of quasi-extinction ≤50% and ≤20%. The model was run simulating the supplementation of a wild population to stage class 1 with eggs, 2nd year juveniles, 3rd year juveniles and adults. Simulations with an initial population size starting with one and three breeding females (median adult female population size from the USFS dataset) were run to determine what level of effort (how many individuals of each life stage) would be needed to decrease the risk of quasi-extinction. SSD for *A. canorus* was determined from the mean matrix using the right eigenvector in the R package Popbio (v2.7; Stubben and Milligan, 2007). I calculated generation time using the function generation.time from R package Popbio (v2.7; Stubben and Milligan, 2007). Stochasticity was included in the model by incorporating process variance estimates around the estimated mean values for each vital rate (Table 1) (Morris and Doak, 2002). The matrix model was populated for projection interval using survival and fecundity vital rates sampled from beta and lognormal distributions, respectively. The stochastic matrix projection was repeated in 1,000 independent simulations, for each scenario, over a 13-year projection interval (~3 generations). Matrix models and model evaluation were run in Program R (v3.6.2; R Development Core Team, 2020) using the function vitalism from package Popbio (v2.7; Stubben and Milligan, 2007). Code for the matrix projection models is shown in Appendix B. To calculate the efficacy of each supplementation scenarios, I calculated the change in probability of extinction and change in stochastic growth rate compared to an un-supplemented wild *A. canorus* population.

RESULTS

Cormack-Jolly-Seber Model

From 2005 to 2010 the U.S Forest Service surveyed 19 meadows sites within the range of the *A. canorus* on National Forest and National Park ownership. A total of 266 adult *A. canorus* were marked with a unique PIT tag. Of the total captured adults, 185 (69%) were male and 81 (30%) were female. During the study, marked adult males and females were captured an average of 1.34 and 1.07 times, respectively. The total number of male and female *A. canorus* that were captured, released and recaptured on subsequent occasions are summarized in tables below (Table 2, Table 3, Table 4). Survival and detection probabilities varied by sex. The CJS model estimated adult male *A. canorus* survival probability to be 0.665 (sampling variance of 0.096, 95% CI: 0.472-0.863) and detection probability to be 0.287 (sampling variance of 0.071, 95% CI: 0.164-0.443). The CJS model estimated female adult *A. canorus* survival probability to be 0.757 (sampling variance of 0.182, 95% CI: 0.331-0.992) and detection probability to be 0.070 (sampling variance of 0.49, 95% CI: 0.16-0.196). The random effect of site on adult male survival probability is described by the process (spatial) variance of 0.878 (sampling variance of 0.594, 95% CI: 0.058-2.398). The random effect of site on adult male detection probability is described by the process (spatial) variance of 0.591 (sampling variance of 0.470, 95% CI: 0.027-1.798). The random effect of site on adult female survival probability is described by the process (spatial) variance of 1.352 (sampling variance of

0.847, 95% CI: 0.070-2.892). The random effect of site on adult female detection probability is described by the process (spatial) variance of 0.777 (sampling variance of 0.847, 95% CI: 0.070-2.892). Adult male survival probability estimates by site ranged from 0.532 to 0.804 and adult male detection probability estimates ranged from 0.238 to 0.407. Adult female survival probability estimates by site ranged from 0.666 to 0.840 and adult female detection probability estimates ranged from 0.052 to 0.108. $\hat{R}$ values of 1.0001 suggest that convergence occurred for both the female and male CJS models.

Table 2. Table tabulating the number of adult male *Anaxyrus canorus* that were captured, released and recaptured on subsequent occasions during the USFS demographic study. Columns of the table are populated with release and recapture occasions

Release Occasion	**Recapture Occasion**	**# Adult Males Recaptured and Released**
1	2	1
1	3	1
1	4	0
1	5	0
1	6	0
2	3	12
2	4	9
2	5	2
2	6	2
3	4	17
3	5	4
3	6	1
4	5	7
4	6	7
5	6	5

Table 3. Table tabulating the number of adult female *Anaxyrus canorus* that were captured, released and recaptured on subsequent occasions during the USFS demographic study. Columns of the table are populated with release and recapture occasions.

Release Occasion	**Recapture Occasion**	**# Adult Females Recaptured and Released**
1	2	0
1	3	0
1	4	0
1	5	0
1	6	0
2	3	0
2	4	0
2	5	1
2	6	0
3	4	1
3	5	1
3	6	1
4	5	0
4	6	2
5	6	0

Table 4. Table tabulating the number of adult male and female *Anaxyrus canorus* that were never recaptured after the initial capture during the USFS demographic study.

Release Occasion	**# Adult males ever recaptured**	**# Adult females never recaptured**
1	2	1
2	42	15
3	43	14
4	48	26
5	28	13

Matrix Projection Model

Without supplementation, an initial *A. canorus* wild population at SSD with one to three adult females has a stochastic growth rate between 0.993 to 0.996, which is equivalent to 0.7% to 0.4% annual rate of decrease in population size (Table 5) Wild populations of *A. canorus* at SSD with ≤ three and ≤ 13 adult females have a ≥50% and ≥20% 13-year risk of quasi-extinction, respectively (Figure 6). Without supplementation, a wild A. canorus population has a deterministic growth rate of 1.297 (Table 5). Eleven (57%) of the 19 breeding sites from the USFS dataset have an estimated adult female population of ≤ three and as a result have a projected ≥50% risk of quasi-extinction (Figure 6).

Scenarios supplementing wild populations with an initial population size that is at SSD with one (Figure 7) and with three (Figure 8) adult females suggest that adding adult females to a wild population will take the least amount of effort (fewest number of individuals) to significantly minimize the risk of quasi-extinction over 13-years (three generations). Supplementing a wild population with 3-year-olds appears to be the second most effective method followed by supplementing a population with 2-year-olds and then YOY (eggs) (Figure 7, Figure 8, Table 6**Error! Reference source not found.**).

Table 5. The deterministic growth rate, stochastic growth rate, lower and upper confidence intervals, and the 13-year quasi-extinction potential for *Anaxyrus canorus* for three scenarios. The three scenarios represent running the model with an initial population of one adult female (smallest population), three adult females (median population), and 17 adult females (large population). Each scenario was run with the population size starting at Stable Stage Distribution with a female population size of 1, 13, or 17.

Female Adult Population Size	**Deterministic Population Growth Rate**	**Stochastic Population Growth Rate**	**LC**	**UC**	**13-yer Quasi-Extinction**
1	1.297	0.993	0.6931425	1.4285580	84%
3	1.297	0.996	0.688251	1.439100	56%
17	1.297	1.001	0.701781	1.428686	15%

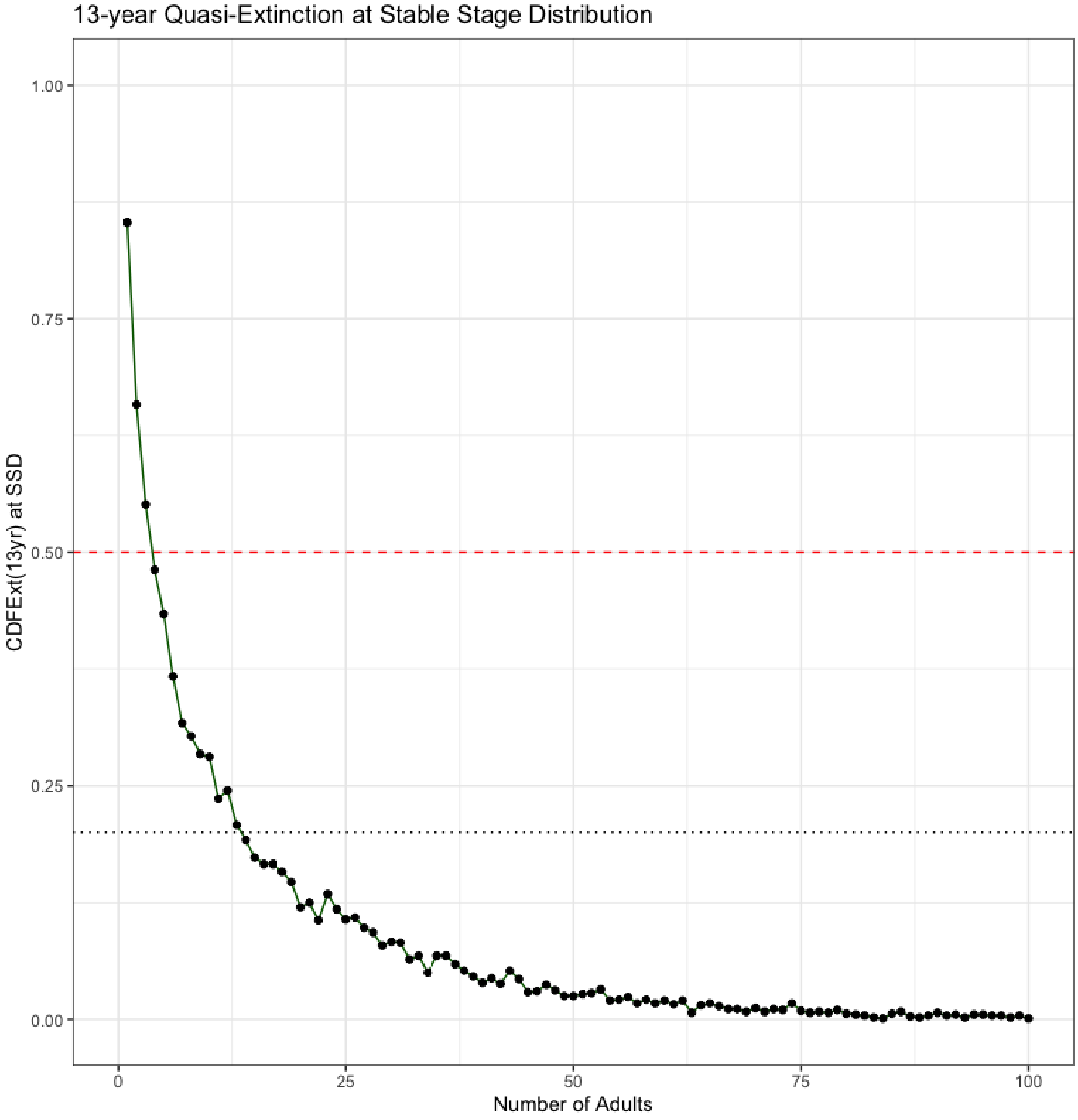

Figure 6. 13-year quasi-extinction probability with increasing female population size starting at Stable Stage Distribution (SSD) with one adult breeding female. The X axis represents increasing starting population size of one to 100 adult female *Anaxyrus canorus*. The red dashed line represents 50% risk of quasi-extinction, the black dotted line represents the 20% risk of quasi-extinction.

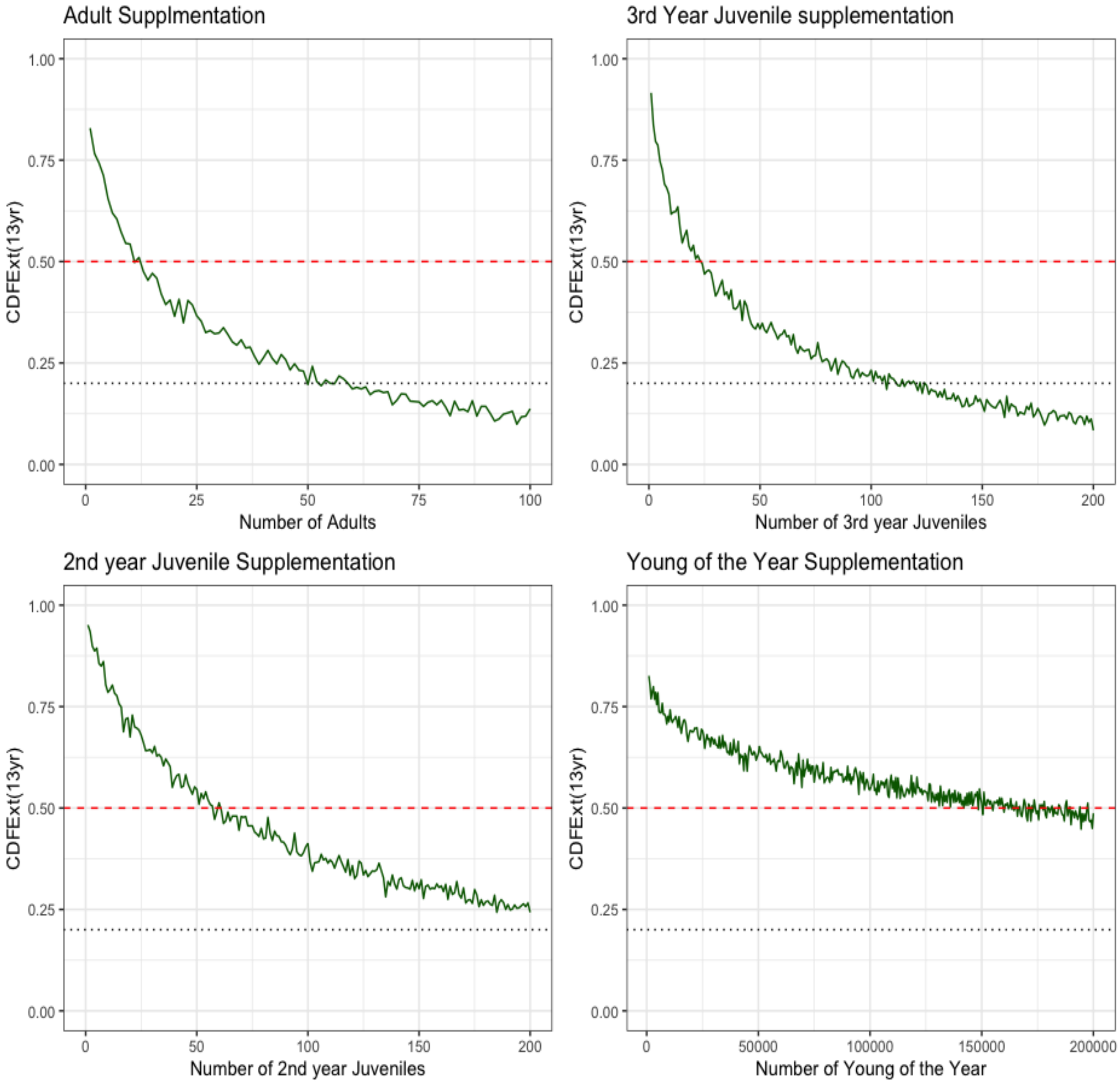

Figure 7. Quasi-extinction risk of a population starting with one adult female *Anaxyrus canorus*. The graphs represent supplementation scenarios adding adults (top left), 2nd year juveniles (top right), 3rd year Juveniles (bottom left), and young of the year (bottom right). The red dashed line represents 50% quasi-extinction risk, the black dotted line represents the 20% quasi-extinction risk

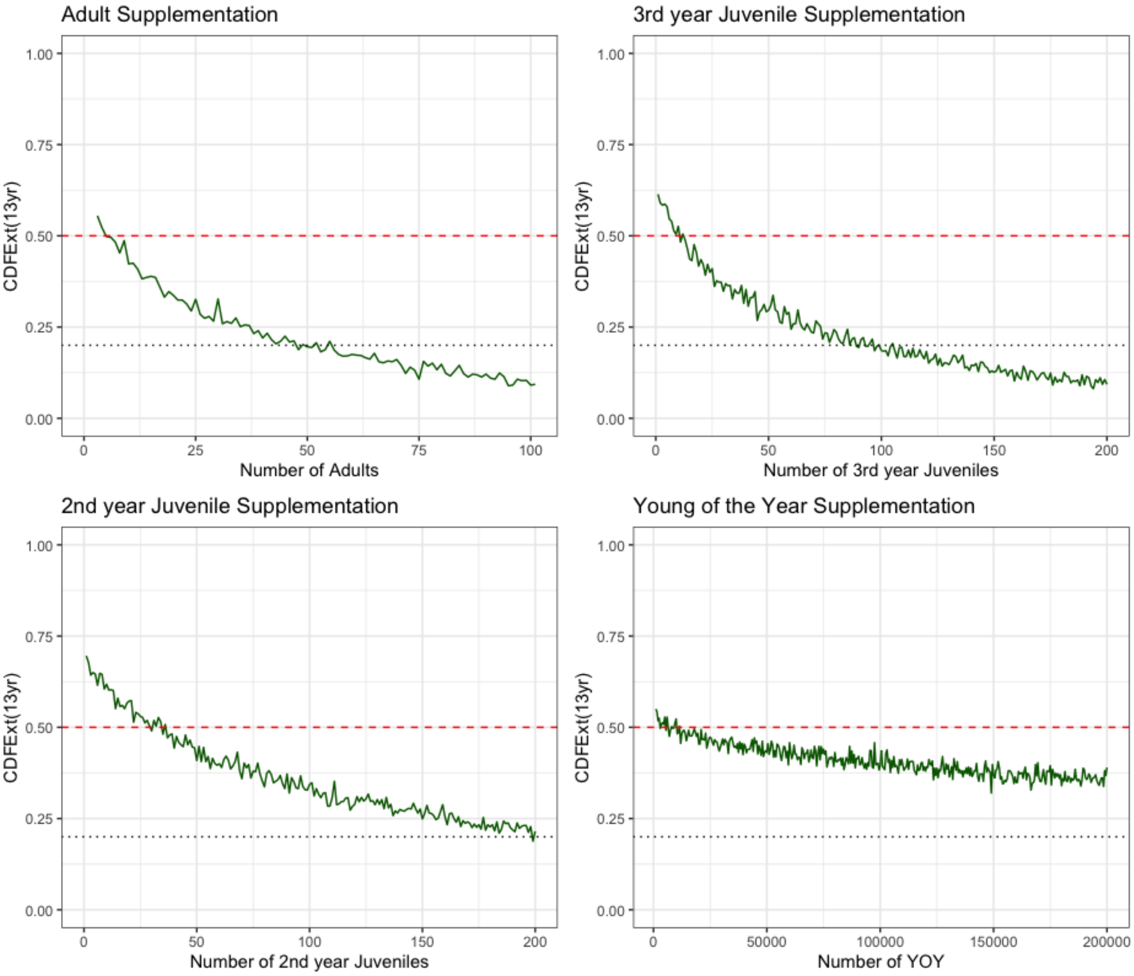

Figure 8. Quasi-extinction risk of a population starting with 3 adult female *Anaxyrus canoru*s. The graphs represent supplementation scenarios adding adults (top left), 2nd year juveniles (top right), 3rd year juveniles (bottom left), and young of the year (bottom right). The red dashed line represents 50% population quasi-extinction risk, the black dotted line represents 20% population quasi-extinction risk.

Table 6. Supplementation effort required for four different life stages of *Anaxyrus canorus* to decrease the quasi-extinction probability to be <20% and <50% for supplementation scenarios with a female population at Stable Stage Distribution.

Adult Population Size	**Quasi-extinction Risk**	**# YOY**	**# 2nd yr. Juvenile**	**# 3rd yr. Juvenile**	**# Adult**
1	**<50%**	~180,000	~58	~24	~11
1	**<20%**	>200,000	>200	~66	~36
3	**<50%**	~6,500	~37	~13	~5
3	**<20%**	>200,000	~110	~45	~26

DISCUSSION

The results of my modeling of *A. canorus* populations suggest that small populations are highly susceptible to local extirpation over short time horizons. Small toad populations (≤3 female adult individuals) have a 0.7% to 0.4% annual rate of decrease in population size and a 56%-84% risk of quasi-extinction over a 13-year period, which meet the IUCN criteria for being Critically Endangered (IUCN, 2018; Figure 6). These somewhat pessimistic results were obtained despite not incorporating demographic or genetic stochasticity in to my population viability analyses, which would only increase the risk of local quasi-extinction. The median population size (containing three female adults) in the USFS demographic study highlights the need for effective management strategies to be implemented, as no action may lead to future extirpation of existing populations. Eleven (57%) of the 19 breeding sites from the USFS dataset have an estimated adult female population of ≤ three and as a result have a projected ≥50% risk of quasi-extinction (Table 6, Figure 6).

Based on the simulations, supplementation can reduce the risk quasi-extinction for small wild populations of *A. canorus* to have a <20% risk of quasi-extinction over a 13-year period (Table 6, Figure 7, Figure 8). The effectiveness of a supplementation management plan is dependent on the initial population size of the receiving population, life stage of the reintroduced individuals, and the number of individuals released (Table 6, Figure 6, Figure 7, Figure 8). I found that supplementing small toad populations with female adults is the most effective supplementation strategy to increase the stochastic growth rate and minimize the risk of quasi-extinction for *A. canorus* populations (Table 6). For example, supplementing a small population (≤3 female adults) with five female adults can decrease the risk of quasi-extinction to be <50%. In contrast, supplementation is less effective with younger life stages; it would take the addition of 13 or 37 three- and two-year-old females respectively to decrease the quasi-extinction risk <50%. Similarly, adding >100,000 eggs (to the first element of the matrix) to a small wild population does not significantly minimize the risk of quasi-extinction or increase the population growth rate (Table 6, Figure 7, Figure 8).

I also analyzed thresholds for wild populations to be considered as a donor population for translocation efforts. To be designated as a donor site for translocation efforts, a population should be relatively large with a growth rate >1.0 (Semlitsch, 2002). A wild population with ≥13 adult females has a risk of quasi-extinction that is <20% with a stochastic growth rate of 0.99 (95%CI 0.690-1.433) and as a result may be considered as a donor site (Figure 6; Semlitsch, 2002). Other factors such as site location, disease, genetics and habitat should also be considered when implementing a translocation effort as part of a management plan (Bloxam & Tonge, 1995; Semlitsch, 2002). Alternatively, because adding even large numbers of YOY to a population appears to have a negligible impact on decreasing the risk of quasi-extinction, captive rearing YOY into four-year old females may be an effective management strategy without putting undue pressure on a source population. Captive rearing programs have successfully established self-sustaining wild toad populations such as the Wyoming Toad (*Anaxyruss baxteri*), Houdson toad (*Anaxyrus houstonensis*) (Griffiths & Pavajeau, 2008; Forstner et al., 2013; Polasik et al., 2016). Captive breeding may also be a feasible option for *A. canorus* conservation efforts.

Vital Rates

The results and conclusions of this thesis depend on the parameters used and the assumptions made while modeling different scenarios for *A. canorus*. Some of the vital rates used in this thesis contain a high level of uncertainty because survival estimates for YOY were not available. As a result, YOY vital rates from *A. boreas* from the scientific literature were used to populate the model. Additionally, the available data from the literature (for YOY and juvenile life stages) did not allow me to distinguish between process and sampling variance for the vital rates for earlier life stages. Stochastic processes have been shown to increase the risk of extinction and decrease population growth (Lande, 1993). My study also suggests that increased process variance, representing stochasticity, decreases the population growth rate and increases the risk of quasi-extinction. Not separating the process and sampling variance may provide an over-estimation of process variance in the model and result in conservative estimates of quasi-extinction risk and stochastic growth rates (Gould & Nichols, 1998; Mills & Lindberg, 2000).

Additionally, due to limited data on adult females, male vital rates were used as proxy for females. Adult male vital rate estimates derived from the CJS model for this thesis are comparable to previous efforts to estimate vital rate parameters for *A. canorus.* For example, Brown et al. (2012), using a Pollock's robust design model, estimated φ of adult *A. canorus* males to be between 0.49 and 0.79. The mean survival probability estimate derived from the CJS model for this thesis (φ=0.670; Table 1) is within the range of the mean survival values estimated by Brown et. al. (2012). I used the estimated adult male survival derived from the CJS model for this thesis as a proxy for female adult survival to populate the matrix projection model. Adult female *A. canorus* often skip breeding seasons and spend a limited period of time at breeding sites. As a result, adult females can be difficult to reliably locate for a Mark-Capture-Recapture effort to study their population dynamics (Sherman, 1980; Morton, 1982; Martin, 2008). Likely due to the challenges associated with studying adult females, the USFS dataset that was used for a portion of this research had a small sample size (n=81) and low recapture rate (n=9) to estimate vital rate parameters for female *A. canorus,* limiting inference. If the actual survival rates used for male and females are substantially different from one another, the conclusions based on the analysis of the matrix projection model may be inaccurate.

CONCLUSIONS AND FUTURE RESEARCH

To my knowledge, this is the first study to model supplementation strategies and investigate how different vital rates influence population dynamics for *A. canorus*. Comparable to the conclusions of my study, prior studies using matrix population models to investigate the population dynamics of *A. boreas*, the Northern red-legged frog (*Rana aurora*), and the Oregon spotted frog (*Rana pretiosa*) suggest that post-metamorphic life stages have a greater influence on a population's dynamics than early life stages of the species (Beik et al., 2002; Vonesh & De la Cruz, 2002; Kissel et al., 2014). However, dissimilar to the results of my study, Kissel et al. (2014) has shown that with enough effort, adding early life stages of *R. pretiosa* to a wild population can significantly decrease the risk of quasi-extinction for a population.

Recent work by Muths et al. has shown that the prevalence of disease can alter the populations dynamics of *A. boreas.* With the absence of disease, a long-lived species such as *A. canoru*s and *A. borea*s is likely to have at least one reproductive year productive enough help a population persist. However, if an amphibian population is impacted by disease, adults may become short-lived, making populations rely on recruitment of younger life stages. Therefore, younger life stages of the species may have a greater influence on population dynamics than reproductive adults (Muths et al. 2011). My thesis suggests that supplementing small toad populations with female adults is the most effective supplementation strategy for *A. canorus* populations. However, the research by Muths et al. highlights the need to consider how disease, or other factors that may cause the species to be short lived, will alter the population dynamics of a species such as *A. canorus.*

While this study offers insight into how to bolster wild *A. canorus* populations, additional intensive studies on the population dynamics and vital rates of the *A. canorus* (especially YOY and juvenile life stages) may bolster confidence in conclusions of the model output used in this study. Long-term monitoring should also be implemented to determine if a management plan is successful to help ensure that desired outcomes are achieved and that resources are effectively being used to prioritize important management actions.

The results of my study suggest that supplementation may be a critical management tool in minimizing quasi-extinction risk of declining amphibian species. While supplementation alone may not address the direct causes of decline for a species, this work suggests that it can minimize the risk of extinction and buffer populations from stochastic events such as extreme weather or disease while the direct cause of decline of the species is further studied. Additionally, when population demographics and vital rates are known for other species, the models can easily be adapted to assist in making future management decisions for other endangered species.

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APPENDICES

Appendix A: R code for the parameterization of the Cormack-Jolly-Seber (CJS) model, modified from Kéry and Schaub (2012). The code for the CJS model was run to apparent survival and recapture probability of adult *Anaxyrus canorus.* Data used in the model was from the USFS dataset shared for this project. The Cormack-Jolly-Seber model was specified in the JAGS dialect of BUGS.

```
#multisite CJS jags code adapted from Kéry and Schaub
(2012).

str(ch <- array(NA, dim = c(max(nind), nyear, nsite)))

for(s in 1:nsite){
    site <- CHmatrix[as.numeric(as.factor(sitevec))== s, ]
  ch[1:nind[s],1:6,s] <-site
}


#f
str(f <- matrix(NA, nrow=max(nind), ncol=nsite))

for(s in 1:nsite) {
  get.first <- function(x) { min(which(x!=0)) }
  f.s <- apply(ch[,,s],1,get.first) #vector for site s
  f[,s] <- f.s
}


str(bdata <- list(y = ch, f = f, n.ind = nind,
                  n.occ = 6, nsite = nsite))

cat(file = "cjs3.txt","
model {

for(s in 1:nsite){
  phi[s] <- ilogit(lphi[s])
  lphi[s] ~ dnorm(mu.lphi, tau.lphi)
  p[s] <- ilogit(lp[s])
  lp[s] ~ dnorm(mu.lp, tau.lp)
}
```

```
# (hyper-)priors for the hyperparameters that
# characterize the community

mu.lphi <- logit(mean.phi) # Hyperpriors for survival
hyperparams
mean.phi ~ dunif(0,1) # mean hyperparam.(community average)
tau.lphi <- pow(sigma.lphi, -2)
sigma.lphi ~ dunif(0, 3) # sd hyperparam.(community
heterogeneity)
mu.lp <- logit(mean.p) # Hyperpriors for recapture
hyperparams
mean.p ~ dunif(0,1) # mean hyperparam.
tau.lp <- pow(sigma.lp, -2)
sigma.lp ~ dunif(0, 3) # sd hyperparam.

# 'Likelihood'

for(s in 1:nsite){ # Loop over sites
  for(i in 1:n.ind[s]){ # Loop over individuals
    # Define latent state at first capture
      z[i,f[i,s], s] <- 1
        for(t in (f[i,s]+1):n.occ){ # Loop over occasions
          # State process: the latent alive/dead state
            z[i,t,s] ~ dbern(z[i,t-1,s] * phi[s])# phi
indexed by species now
          # Obs. process: relates true state to observed
state, y = ch
          y[i,t,s] ~ dbern(z[i,t,s] * p[s]) # p also
indexed by species
        }
  }
}
}
")

# Initial values
zst <- ch

zst
for(s in 1:nsite){
  zst[,,s] <- zinit(ch[,,s])
}
```

```
inits <- function(){list(z = zst, mean.phi = runif(1),
sigma.lphi = runif(1),
                         mean.p = runif(1), sigma.lp =
runif(1))}

# Parameters monitored, could add z here
params<- c("mean.phi", "mu.lphi", "sigma.lphi", "mean.p",
"mu.lp",
           "sigma.lp", "phi", "p")
# MCMC settings
na <- 1000 ; ni <- 100000 ; nt <- 5 ; nb <- 5000 ; nc <- 3
# Call JAGS (ART 12 min), check convergence and summarize
posteriors
out3 <- jags(bdata, inits, params, "cjs3.txt", n.chains =
nc,
             n.thin = nt, n.iter = ni, n.burnin = nb)
par(mfrow = c(3,3)) ; traceplot(out3)
```

Appendix B: R code for the parameterization of the Matrix Project Population model, Matrix models and model evaluation were run in Program R (v3.6.2; R Development Core Team, 2020) using the function vitalism from package Popbio (v2.7; Stubben and Milligan, 2007).

```
#vital rates for A. canorus
vrs    <- c(0.020,  #YOY annual survival
            0.3480, #2nd year Juvenile annual survival
            0.3480, #3rd year Juvenile annual survival
            0.668,  #Adult survival
            875)    #Reproductive success

makemx <- function(vrs)
     {matrix(c(0,0,(vrs[5]*0.5)*vrs[3],(vrs[5]*0.5)*vrs[4],
                                  vrs[1],0,0,0,
                                  0,vrs[2],0,0,
                                  0,0,vrs
     [3],vrs[4]),nrow=4, ncol=4, byrow=TRUE)}

BUCA <- makemx(vrs)

##projection ANNUAL VARIANCE of each vital rate

vrvar  <- c(0.0056,  #YOY survival
            0.003, #2nd year Juvenile survival
            0.003, #3rd year Juvenile survival
            0.0053,   #adult survival
            3906.25) #reproductive success

corrout <- diag(0,5)
corrin <- diag(5)

#code for lnorms in vitalsim
lnorms <- function(n, mean = 2, var = 1) {
  if(length(n)>1) {
    nmeans <- log(mean) - 0.5 * log(var/mean^2 + 1)
    nvars <- log(var/mean^2 + 1)
    normals <- rnorm(n) * sqrt(nvars) + nmeans
    lns <- exp(normals)
    lns } else {
      n <- 1
      nmeans <- log(mean) - 0.5 * log(var/mean^2 + 1)
      nvars <- log(var/mean^2 + 1)
      normals <- rnorm(n) * sqrt(nvars) + nmeans
```

```
      lns <- exp(normals)
      lns }
}

trace(popbio::lnorms, edit=TRUE)

#Small population with 1 female adult
WildpopulationSmall<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                              vrtypes=c(rep(1,4),
     rep(3,1)), n0=c(440,7,2,1), Ne=450, yrspan=20,
                              tmax=13, runs=1000)

#median population with 3 female adults
WildpopulationMedian<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                               vrtypes=c(rep(1,4),
     rep(3,1)), n0=c(1320,21,6,3), Ne=450, yrspan=20,
                               tmax=13, runs=1000)

#large population with 17 female adults
WildpopulationLarge<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                              vrtypes=c(rep(1,4),
     rep(3,1)), n0=c(7480,119,34,17), Ne=450, yrspan=20,
                              tmax=13, runs=1000)

#Increasing population size at SSD
x_int<-seq(1,40,1)
outputADULT<-list()
for(i in seq_along(x_int)) {
  outputADULT[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                             vrtypes=c(rep(1,4), rep(3,1)),
     n0=c((440*x_int[i]),(7*x_int[i]), (2*x_int[i]),
     x_int[i]),
                             Ne=450, yrspan=20, tmax=13,
     runs=1000)
}

#Supplementing with YOY, population starting at 5 female
     adults
y_int<-seq(1000, 20000, 500)
YOY5AF<-list()
```

```
for(i in seq_along(y_int)) {
  YOY5AF[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                       vrtypes=c(rep(1,4), rep(3,1)),
     n0=c(y_int[i],35,10,5),
                       Ne=450, yrspan=20,
                       tmax=13, runs=1000)
}

#Supplementing with 2nd year juveniles, population starting
     at 5 females
y_int<-seq(1,100,1)
JUV5AF2<-list()
for(i in seq_along(y_int)) {
  JUV5AF2[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                        vrtypes=c(rep(1,4), rep(3,1)),
     n0=c(2200,y_int[i],10,5),
                        Ne=450, yrspan=20,
                        tmax=13, runs=1000)
}

#Supplementing with 3rd year juveniles, population starting
     at 5 female
y_int<-seq(1,100,1)
JUV5AF3<-list()
for(i in seq_along(y_int)) {
  JUV5AF3[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                        vrtypes=c(rep(1,4), rep(3,1)),
     n0=c(2200,35,y_int[i],5),
                        Ne=450, yrspan=20,
                        tmax=13, runs=1000)
}
#Supplementing with adults population starting at 5 females
     (SSD)
y_int<-seq(1,50,1)
Adultsup5<-list()
for(i in seq_along(y_int)) {
  Adultsup5[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                          vrtypes=c(rep(1,4), rep(3,1)),
     n0=c(2200,35,35,y_int[i]),
                          Ne=450, yrspan=20,
```

```
                           tmax=13, runs=1000)
}



}
#Supplementing with YOY, population starting at 1 female
y_int<-seq(1000, 20000, 500)
YOY1AF<-list()
for(i in seq_along(y_int)) {
  YOY1AF[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                        vrtypes=c(rep(1,4), rep(3,1)),
     n0=c(y_int[i],7,2,1),
                        Ne=450, yrspan=20,
                        tmax=13, runs=1000)
}

#Supplementing with 2nd year juveniles, population starting
     at 1 female
y_int<-seq(1,100,1) #Initial Adult population size starting
     at stable stage distribution
JUV1AF2<-list()
for(i in seq_along(y_int)) {
  JUV1AF2[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                        vrtypes=c(rep(1,4), rep(3,1)),
     n0=c(440,y_int[i],2,1),
                         Ne=450, yrspan=20,
                         tmax=13, runs=1000)
}

#Supplementing with 3rd year juveniles, population starting
     at 1 female
y_int<-seq(1,100,1)
JUV1AF3<-list()
for(i in seq_along(y_int)) {
  JUV1AF3[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                         vrtypes=c(rep(1,4), rep(3,1)),
     n0=c(440,7,y_int[i],1),
                         Ne=450, yrspan=20,
                         tmax=13, runs=1000)
}
```

```
#Supplementing with 50, population starting at 1 females

y_int<-seq(1,50,1) #Initial Adult population size starting
     at stable stage distribution
Adultsup1<-list()
for(i in seq_along(y_int)) {
  Adultsup1[[i]]<-vitalsim(vrs, vrvar, corrin, corrout,
     makemx,
                         vrtypes=c(rep(1,4), rep(3,1)),
     n0=c(440,7,2,y_int[i]),
                         Ne=450, yrspan=20,
                         tmax=13, runs=1000)
}
```

Appendix C: Number of New (N) and Recaptured (R) *Anaxyrus canorus* captured by site between 2005 and 2010 during the US Forest Service demographic study.

Site	**New Female (N)**	**Recapture Female (R)**	**New Male (N)**	**Recapture Male (R)**
BB	3	0	23	15
BP	0	0	9	7
BT	2	1	1	1
CM	4	0	5	3
CS	17	3	23	8
CT	1	0	3	0
EX	4	0	16	2
FP	4	1	16	14
HL	2	1	10	6
HM	11	2	14	9
MA	11	0	21	3
MM	4	0	7	1
MT	3	0	3	0
RT	3	0	7	7
SN	2	1	5	1
ST	2	0	9	1
TM	1	0	2	0
TP	4	0	2	0
WC	3	0	9	2
Total	**81**	**9**	**185**	**80**

Appendix D: Comprehensive description of how vital rates for *Anaxyrus canorus* used in the matrix projection model were determined.

Young of The Year Survival

No known quantitative estimates of *A. canorus* metamorph survival are currently available in the scientific literature. The mean value estimates used in this analysis are based on values provided by Crockett et al. (2021) for the Boreal toad (*Anaxyrus boreas*). YOY survival was calculated by combining embryo survival, larval survival and metamorph survival into the first year of life (YOY) for *A. canorus* (Equation 1). From embryo through metamorphosis Crockett et al. (2021) estimated *A. boreas* to have a survival rate to have a low value of 0.0 and a high of 0.06. I used the mid-point value between 0.0 and 0.06 as the mean value (0.02) for YOY survival. The standard deviation is based on one quarter of the difference between the high and the low values of the vital rate (Hozo et al. 2005).

Equation 1.

(Embryo Survival) x (Larval Survival) x (Metamorph Survival) = YOY Survival

2nd and 3rd Year Survival

Mean estimates for juvenile survival was recorded as 0.348 by Kagarise Sherman (1980). There is limited data available for 2nd and 3rd year survival estimates for *A. canorus*. Clark (1977) estimated the survival rate of juveniles of the Woodhouse toad (*Anaxyous woodhousii)* to be 0.18. Kelleher (1969) estimated the juvenile Manitoba toad (*Anaxyrus hemiophrys*) to have survival rate between 0.29 to 0.40. I used the survival estimates of 0.18 from Clark (1977) as the low value for survival estimates and a high value of 0.40 from Kelleher (1969). The standard deviation is based on one quarter of the difference between the high and the low values of the vital rate (Hozo et al., 2005).

Adult Survival

A mean survival estimate of 0.67 with a variance of 0.0053 is based on the mean annual survival estimates of males in the USFS dataset that I analyzed for this project. Males were used as a proxy for females since the female recapture rate was low.

Probability of laying

Studies on A. *canorus* estimated that females skip breeding years and lay eggs every other year (Sherman, 1980; Brown, 2015). Thus, the probability of females depositing egg masses is assumed to be 0.5.

Fecundity

Fecundity is the average number of female eggs produced per female. Clutch size estimation is half of the mean clutch size (1,750) to represent female eggs, assuming a 1:1 sex ratio of *A. canorus* (Sherman & Morton, 1993; Drost & Fellers, 1994; Brown, 2015).

Variance

If the variance was not reported for individual studies, then one quarter of the range between the high and the low reported means was used as the standard deviation (Hozo et al., 2005). This is based on the assumption that the range approximates a 95% confidence interval with two standard deviations above and below the mean (Hozo et al., 2005). Since the variance was not reported in the literature for younger life stages, I was not able to distinguish between the process (temporal) and sampling variance.

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