



# A discrete stage-structured model of California newt population dynamics during a period of drought



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## ABSTRACT

We introduce a mathematical model for studying the population dynamics under drought of the **California newt** (*Taricha torosa*), a **species of special concern** in the state of California. Since 2012, California has experienced a **record-setting drought**, and multiple studies predict drought conditions currently underway will persist and even increase in severity. Recent declines and **local extinctions of California newt populations** in Santa Monica Mountain streams motivate our study of the impact of drought on newt population sizes. Although newts are terrestrial salamanders, they migrate to streams each spring to breed and lay eggs. Since egg and larval stages occur in water, a precipitation deficit due to drought conditions reduces the space for newt egg-laying and the necessary habitat for larval development. To mathematically forecast newt population dynamics, we develop a nonlinear system of discrete equations that includes demographic parameters such as survival rates for newt life stages and egg production, which depend on habitat availability and rainfall. We estimate these demographic parameters using 15 years of stream survey data collected from Cold Creek in Los Angeles County, California, and our model captures the observed decline of the parameterized Cold Creek newt population. Based upon data analysis, we predict how the number of available newt egg-laying sites varies with annual precipitation. Our model allows us to make predictions about how the length and severity of drought can affect the likelihood of persistence and the time to critical endangerment of a local newt population. **We predict that sustained severe drought will critically endanger the newt population but that the newt population can rebound if a drought is sufficiently short.**

## 1. Introduction

Amphibian populations are declining worldwide due to multiple pressures including climate change, habitat destruction, and invasive species (Kats and Ferrer, 2003; Blaustein et al., 2011). From 1967 to 1997, amphibian populations in North America declined at a rate of 2% annually (Houlahan et al., 2000). A more recent study by Adams et al. (2013) suggests a more severe rate of decline, estimating that the occupancy of amphibian populations is decreasing by 3.7% annually. In addition to amphibian fauna in North America, global amphibian species continue to be threatened with nearly 168 species believed to have gone extinct and at least 43% of species experiencing population declines within the last two decades (AmphibiaWeb, 2016).

Since 2012, California has experienced a record-setting drought characterized by elevated temperatures and a substantial moisture deficit (Griffin and Anchukaitis, 2014). Factors that account for an increased probability of co-occurring warm-dry conditions include low precipitation, warmer temperatures, and an increased evaporative demand. From 1946 to 2015, the average annual precipitation recorded at Los Angeles Airport was 30 cm, but the average over our period of study, 2000–2015, decreased to 26 cm (WRCC, 2015). Multiple recent studies predict an increased risk for longer, more severe drought, which has severe effects on naturally occurring ecosystems (Cook et al., 2015; Diffenbaugh et al., 2015; Underwood, 2015). Although there are many factors that have led to amphibian population declines, Grant et al. (2016) concluded that low precipita-

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tion levels are a primary contributor. We will explore how the historically severe drought currently underway in California impacts newt populations that require stream permanence for breeding.

The California newt (*Taricha torosa*), a species of special concern in the state of California, inhabits streams in the Santa Monica Mountains (SMM) that are experiencing ongoing drought. Although newts are terrestrial salamanders, each spring they migrate to streams to breed and lay eggs. A precipitation deficit due to drought conditions reduces the available space for newt egg-laying and the necessary habitat for larval development. Severe drought conditions as well as predation by invasive predators have contributed to observed newt population declines in SMM streams (Gamradt and Kats, 1996). The California newt is ecologically important in part because newts connect aquatic and terrestrial habitats through their annual migration from land burrows to streams for breeding (Davic and Hartwell, 2004). As a secondary consumer, the California newt regulates species diversity in the stream ecosystem (Davic and Hartwell, 2004). Thus, amphibian population declines can indicate changes in ecosystem health in response to climate factors such as drought (Gamradt and Kats, 1996).

Mathematical modeling can help to determine the impact of California's extreme drought on newt populations as well as make predictions about long-term recovery versus extinction following drought. In this paper we develop a set of nonlinear difference equations that describe a population of newts as they persist and transition through three key life stages: egg, juvenile, and reproductively mature adult. In our model, we account for the impact of the drought by incorporating how annual precipitation affects the proportion of newts that lay eggs each year. Our model forecasts newt population dynamics in future years given a variety of precipitation levels and regimes. Our model is used to make predictions about how the length and severity of drought can affect the likelihood and time to critical endangerment of a local newt population. In particular, we predict that the newt population can persist for short periods of drought but will reach a critically low population size if the drought is too prolonged or too severe.

Systems of discrete equations have a long history in the mathematical investigation of ecosystem dynamics. Leslie (1945) and Lewis (1942) independently developed and utilized age-structured matrix models, and Lefkovich (1965) introduced the idea of stage-based modeling in ecology. Matrix models have been applied widely to ecological systems (Hughes, 1984; Piñero et al., 1984; Doak et al., 1994; Brewster-Geisz and Miller, 2000). Vonesh and Cruz (2002) developed matrix models for frog and salamander species that incorporate the amphibian life cycle and density dependence in the larval stage. We adapt our model from Crouse et al. (1987), who developed matrix models involving loggerhead sea turtles. Their models include multiple life stages and derive the probabilities of persistence and transition based on the duration of those stages. Similar stage-based models have been explored in detail by Caswell (2001).

## 2. Methods

### 2.1. Newt life cycle

To develop a mathematical model, we consider the stages of the *T. torosa* life cycle as shown in Fig. 1. During the rainy winter months in Southern California, adult newts migrate from terrestrial burrows to streams to breed. In the spring, female newts lay 2–3 egg masses with 15–30 embryos each and then return to their burrows where they live underground until the next breeding season (Brame, 1968; Kats et al., 2013; Ritter, 1897). In late spring, egg masses hatch and carnivorous larvae develop, grow, and begin metamorphosis into juveniles at the end of summer (Gamradt and Kats, 1996). The egg and larval stages occur in water, which makes them particularly sensitive to drought (Gamradt and Kats, 1996). Juveniles inhabit terrestrial burrows until they mature to become reproductively active adults after 6 years

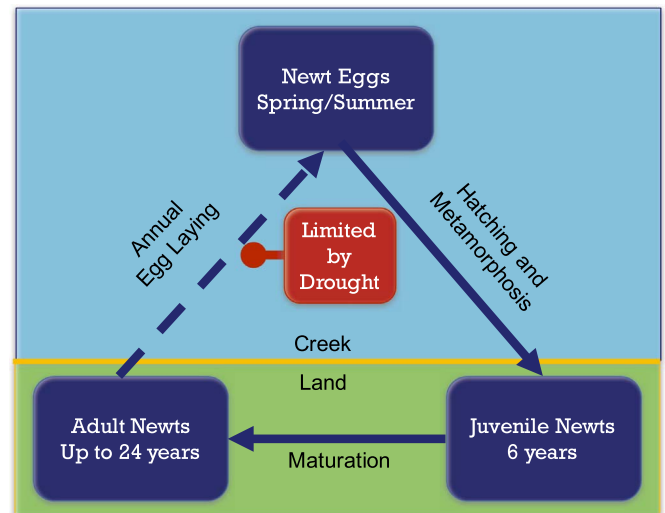


Fig. 1. The life cycle of the California newt, *Taricha torosa*.

(Twitty, 1961). Newts can live up to approximately 30 years and can reproduce most years of their adult lives (Twitty, 1966). The adult newts and egg masses avoid native predators by excreting tetrodotoxin (TTX), a potent neurotoxin. However, the newt larvae are not protected by TTX and thus are more susceptible to predation (Bucciarelli et al., 2014).

### 2.2. Discrete population model

We construct a discrete model of *T. torosa* life stages that accounts for the impact of California's extreme drought by incorporating a data-driven newt egg-laying term that is dependent upon variable annual precipitation. The stage-structured model of newt maturation and survivorship tracks egg,  $E_t$ , juvenile,  $J_t$ , and adult,  $A_t$ , newt life stages on an annual time scale. Since field observations of adult newts and their eggs both occur in late spring, the number of eggs produced depends upon the current number of adults. Our model assumes that eggs laid in year  $t$  hatch into larvae and undergo metamorphosis into juveniles by year  $t + 1$  with probability  $T_J$ . That is, we consider eggs and larvae as one life stage that produces the next year's new juveniles. Eggs that do not survive through metamorphosis are no longer tracked in the model. Juveniles persist with probability  $P_J$  and mature into reproductive adults with probability  $T_A$ . Adults persist with probability  $P_A$  and lay eggs at a nonlinear rate that depends on space availability as determined by variable rainfall. The persistence and transition probabilities depend upon the annual survivorship of juvenile and adult newts. Our system of difference equations for these populations is given by

$$E_{t+1} = \frac{\frac{1}{2} \alpha A_{t+1}}{1 + \frac{A_{t+1}}{2\beta(r)}} \quad (1a)$$

$$J_{t+1} = T_J E_t + P_J J_t \quad (1b)$$

$$A_{t+1} = T_A J_t + P_A A_t. \quad (1c)$$

The terms that describe egg production as well as probabilities of juvenile persistence and transition to adulthood are derived below.

### 2.3. Egg production model

We derive the equation for the number of new eggs laid in year  $t + 1$  using a Michaelis–Menten enzyme kinetics metaphor that takes into account competition between newts for open stream sites. We consider

the interaction between egg-laying newts and their stream habitat as a reaction, (2), where an adult female newt,  $A_L$ , binds reversibly to a stream habitat,  $H$ , to form a newt-stream complex,  $C$ , which then reacts irreversibly to generate a product of  $\alpha$  eggs per female. Once a female newt lays eggs, that newt is not capable of laying more eggs for another year and leaves the stream as a sterile adult newt,  $A_S$ . That stream habitat is then immediately available for other newts to lay eggs. This gives the reaction



where  $k_1$  is the rate that adult female newts enter a stream habitat,  $k_{-1}$  is the rate at which female newts leave a stream habitat without having laid eggs, and  $k_2$  is the rate at which eggs are laid and the subsequently sterile newt leaves the stream. Since a newt lays only once per year,  $k_2 = 1/\text{yr}$ .

For the purpose of our derivation, we write differential equations to characterize this reaction and nondimensionalize using  $\tau = k_{-1}t$  and  $\epsilon = k_{-1}/k_1 \ll 1$ . Here, we assume that if a newt is able to enter the stream and find space to lay eggs, it will rarely leave without laying; thus, the forward reaction is favored and  $k_1 \gg k_{-1}$ . Using standard quasi-steady state analysis (e.g. Murray, 2002), we obtain a Michaelis–Menten term for the newt-stream complex, which we substitute into the reaction's differential equation for eggs. We discretize this, assume a time step of 1 year, and enforce that no eggs carry over from a previous year. Since only female newts lay eggs and given that newt populations have roughly 1:1 sex ratios (Marshall et al., 1990), we set  $A_L = A_{t+1}/2$ . This yields the equation

$$E_{t+1} = \frac{H_0 \alpha \frac{A_{t+1}}{2\beta(r)}}{1 + \frac{A_{t+1}}{2\beta(r)}} \quad (3)$$

where  $\beta(r) = k_1/(k_{-1} + k_2)$  and  $H_0 = H + C$  is a measure of stream space. The term  $\beta(r)$  represents the number of adult female newts at which the stream habitat allows for half of the females to lay eggs. We incorporate drought conditions by allowing  $\beta(r)$  to fluctuate with variable rainfall levels,  $r$ . We set  $H_0$  to be  $\beta(r)$  because both terms measure stream space and would vary with rainfall. Thus, the egg production term used in our model is (1a).

## 2.4. Juvenile and adult population models

We model the number of new juveniles and adults at time  $t + 1$  by

$$J_{t+1} = T_J E_t + P_J J_t, \\ A_{t+1} = T_A J_t + P_A A_t,$$

where eggs transition to juveniles with probability  $T_J$  and juveniles annually persist with probability  $P_J$ . Similarly, juvenile newts mature into reproductive adults with probability  $T_A$ , and adults persist yearly with probability  $P_A$ . Unlike egg production, which renews each year, newts remain in the juvenile stage for multiple years. Thus, a proportion of juveniles remain as juveniles and a proportion of juveniles transition into adults. To account for the six-year duration of the juvenile stage, we adapt a stage-based model for sea turtle populations from Crouse et al. (1987). We assume that all juveniles, regardless of their age, are subject to the same probability of annual survivorship,  $\sigma$ . Juveniles that do not survive to the next year are no longer tracked in the model. At a given time step  $t$ , there are juveniles  $J_t^1, J_t^2, \dots, J_t^6$  who have been in the juvenile stage for one to six years. Thus, eggs transition to juveniles and then to adults as follows with the associated probabilities

$$E_t \xrightarrow{T_J} J_t^1 \xrightarrow{\sigma} J_t^2 \xrightarrow{\sigma} J_t^3 \xrightarrow{\sigma} J_t^4 \xrightarrow{\sigma} J_t^5 \xrightarrow{\sigma} J_t^6 \xrightarrow{\sigma} A_t.$$

Assuming that the number of new newts that enter the juvenile stage

each year is roughly constant, the number of juveniles that persist for  $i$  years is  $J_t^i = \sigma^{i-1} J_t^1$ . Here we assume that the juveniles in their first five years will persist in the juvenile stage with the same annual survivorship,  $\sigma$ . The newts in their sixth and final year of the juvenile stage transition to the adult stage with annual survivorship  $\sigma$ . Therefore, the total population of juveniles is given by

$$J_t = \overbrace{J_t^1 + J_t^2 + J_t^3 + J_t^4 + J_t^5}^{\text{persist}} + \overbrace{J_t^6}^{\text{transition}} \\ = J_t^1 (1 + \sigma + \sigma^2 + \sigma^3 + \sigma^4) + J_t^1 (\sigma^5)$$

Then the proportion of juveniles that survive and persist as juveniles is given by

$$P_J = \left( \frac{1 + \sigma + \sigma^2 + \sigma^3 + \sigma^4}{1 + \sigma + \sigma^2 + \sigma^3 + \sigma^4 + \sigma^5} \right) \sigma.$$

Note that the numerator and denominator are geometric sums that can be rewritten as

$$\left( \frac{1 - \sigma^5}{1 - \sigma} \right) \quad \text{and} \quad \left( \frac{1 - \sigma^6}{1 - \sigma} \right)$$

respectively. Thus, the proportion of juveniles that survive and persist can be rewritten as

$$P_J = \left( \frac{1 - \sigma^5}{1 - \sigma^6} \right) \sigma. \quad (4)$$

Similarly, the proportion of juveniles that transition to adulthood is given by

$$T_A = \left( \frac{\sigma^5}{1 + \sigma + \sigma^2 + \sigma^3 + \sigma^4 + \sigma^5} \right) \sigma = \left( \frac{1 - \sigma}{1 - \sigma^6} \right) \sigma^6. \quad (5)$$

To enforce a maximum newt lifespan of 30 years, we set the duration of the adult stage to 23 years. Using a similar argument to the derivation of (4), the persistence of adults is given by

$$P_A = \left( \frac{1 - \sigma^{22}}{1 - \sigma^{23}} \right) \sigma. \quad (6)$$

## 2.5. Data and parameterization

We biologically ground the model with annual surveys of SMM streams that are described in Kats et al. (2013). These surveys document severe declines and some extinctions of local newt populations in various SMM streams. Several of these streams have been invaded by non-native red swamp crayfish, *Procambarus clarkii*, that have affected the local ecosystem. In Malibu Creek, invasive crayfish have eradicated the local newt population. Due to high stream gradients and flooding events, newt populations in Trancas Creek and Las Virgenes Creek have persisted despite invasive crayfish predation, but observations of newts have sharply declined. Cold Creek remains pristine, where *T. torosa* populations inhabit the stream in the absence of invasive crayfish populations. We focus on annual surveys of a 400 m stretch of upper Cold Creek from 2000 to 2015. Our data from this stretch of Cold Creek captures the entire newt population since newts primarily lay in this portion of the stream and do not migrate between streams. The stream surveys include both habitat and species observations. Pools, riffles, runs, and dry stretches comprise each stream, and the length, width, and depth of each are recorded. The surveys record observations of various species that inhabit the streams including *T. torosa* adults, juveniles, larvae, and egg masses. There are no observations of invasive crayfish in the stream surveys for Cold Creek. We also obtained estimates for the adult newt population at Cold Creek extrapolated from mark-recapture data of the observed reproductive adults in Cold Creek (Bucciarelli et al., unpublished). This

**Table 1**

Parameters for the newt population model (1). When the value of  $\sigma$  is varied, the values of  $P_j(\sigma)$ ,  $T_A(\sigma)$ , and  $P_A(\sigma)$  change according to (4), (5) and (6), respectively.

Parameter	Value	Description	Citation
$\omega$	24 eggs/egg mass	Eggs per egg mass	Kats et al. (2013)
$\gamma$	2.5 egg masses/female	Number of egg masses per female newt per lay	Kats et al. (2013)
$\alpha = \gamma \omega$	60 eggs/female	Eggs per female newt per lay	Kats et al. (2013)
$T_J$	0.025	Annual probability of transition from egg to juvenile	Sever et al. (1986)
$\sigma$	0.91	Annual probability of newt survivorship	Twitty (1966)
$P_j(\sigma)$	0.7917	Annual probability of juvenile persistence	Calculated, (4)
$T_A(\sigma)$	0.1183	Annual probability of transition from juvenile to adult	Calculated, (5)
$P_A(\sigma)$	0.8984	Annual probability of adult persistence	Calculated, (6)
$\beta(r)$	varies (female newts)	Number of female adults where half of female newts can lay eggs	Fit, (8)

data analysis estimates that the adult newt population declined from 1025 adult newts in 2000 to 572 in 2013.

We develop the parameter values for our model (1) from literature, calculations, and personal observation as summarized in Table 1. Adult newts lay 2–3 egg masses (Brame, 1968, Ritter, 1897) with 15–30 eggs per egg mass (Kats et al., 2013), which yields between 30 and 90 eggs per female. Therefore, we assume an average of 60 eggs per female newt, defined as parameter  $\alpha$ , which corresponds to 2.5 egg masses per female containing 24 eggs each. As represented by  $T_J$ , approximately 2.5% of eggs survive through hatching into larvae and metamorphosing into juveniles due to larval density-dependent survival, native and invasive predation of larvae, and newt cannibalism of larvae when other prey are not abundant (Elliott et al., 1993). This agrees with the egg-to-juvenile survivorship estimates for tiger salamanders (*Ambystoma tigrinum*) by Sever et al. (1986). Twitty (1966) conducted a mark-recapture study of a *Taricha rivularis* population with approximately 20,000 individuals at Pepperwood Creek in Mendocino County, California that concluded that the annual survivorship of adult newts is 91%. We use  $\sigma = 0.91$  as our best estimate of annual survivorship and calculate the persistence and transition probabilities of juveniles and adults,  $P_j$ ,  $T_A$ , and  $P_A$ , using (4), (5) and (6), respectively.

Our study is motivated by field observations of California newts during years with both above and below average rainfall (Kats et al., 2013). These observations include years with heavy rainfall due to events such as El Niño storms as well as the most recent years marked by severe drought. The number of egg masses laid in years with below average rainfall is substantially fewer than the number of eggs laid in years with above average rainfall (Kats et al., 2013). Because adult newts require stream permanence to lay eggs, we assume the number of egg masses laid is limited by the available breeding habitat, which depends upon annual precipitation. Other factors that could also contribute to a reduction in newt egg-laying, such as decreased adult migration to streams, are not overtly modeled. However, their effects, if present in the data, are accounted for in our upcoming parameter fits. Fig. 2 extends the results from Kats et al. (2013) and juxtaposes observed egg masses per year and recorded annual precipitation from 2000 to 2015 (WRCC, 2015). We incorporate annual rainfall measurements for a given year based on monthly recordings from September of the previous year through August of the current year. Therefore, we explore a possible relationship between annual precipitation,  $r$ , and available stream space for adult egg-laying,  $\beta(r)$ .

Based on our model (1a), an increase in the adult population will increase egg production, but the rate of increase will slow as the newt population saturates the available stream space. In our derivation of the egg production model (1a), we define  $\beta(r)$  as the number of adult female newts at which the stream habitat allows for half of the females to lay eggs. Thus, the parameter  $\beta(r)$  controls the degree to which limited habitat inhibits egg-laying by adults. We use  $\beta_t$  to indicate an observed value for a particular year and rainfall level and  $\beta(r)$  to represent the function fit to observed  $\beta_t$  data points across precipitation levels,  $r$ , as discussed later. We estimate  $\beta_t$  for each year  $t$  by solving

(1a) for  $\beta$ , and substituting observed egg masses and adult data for each year  $t$ . That is,

$$\beta_t = \frac{A_t E_t}{\alpha A_t - 2 E_t}, \quad (7)$$

where  $E_t$  is the number of eggs ( $\omega \times$  recorded egg masses) from year  $t$  and  $A_t$  is the adult population estimated for year  $t$  at Cold Creek based on mark-recapture methods. The annual estimates for  $\beta_t$  are displayed along with observed egg mass counts and precipitation in Fig. 2. We note that low values of  $\beta_t$ , or less space for egg-laying, correspond with years of below average precipitation and fewer observed egg masses. Higher values of  $\beta_t$ , or increased space for egg-laying, correspond with years of above average precipitation and a greater number of observed egg masses. Fig. 3a displays our annual estimates of  $\beta_t/L_t$  versus annual precipitation  $r$ , where  $L_t$  is the total length of stream space surveyed in year  $t$ . These values are calculated by substituting annual adult and egg densities,  $A_t/L_t$  and  $E_t/L_t$ , for  $A_t$  and  $E_t$ , respectively.

A logistic curve ( $R^2 = 0.426$ ) best fits our estimates for  $\beta_t/L_t$  versus other fits including linear ( $R^2 = 0.2723$ ) and exponential ( $R^2 = 0.1777$ ) fits. Fig. 3a shows the best fit logistic curve

$$\beta(r)/L = \frac{0.3668}{1 + 88.61e^{-0.1771r}}, \quad (8)$$

which quantifies a relationship between space for egg-laying and annual precipitation,  $r$ . We observe that the fit  $\beta(r)$  saturates with increasing precipitation and that the space available does not increase significantly in years with 50 cm of precipitation or greater. Fig. 3b shows that the trend of the values of  $\beta(r)$  given by (8) match the annual estimates  $\beta_t$  given by (7).

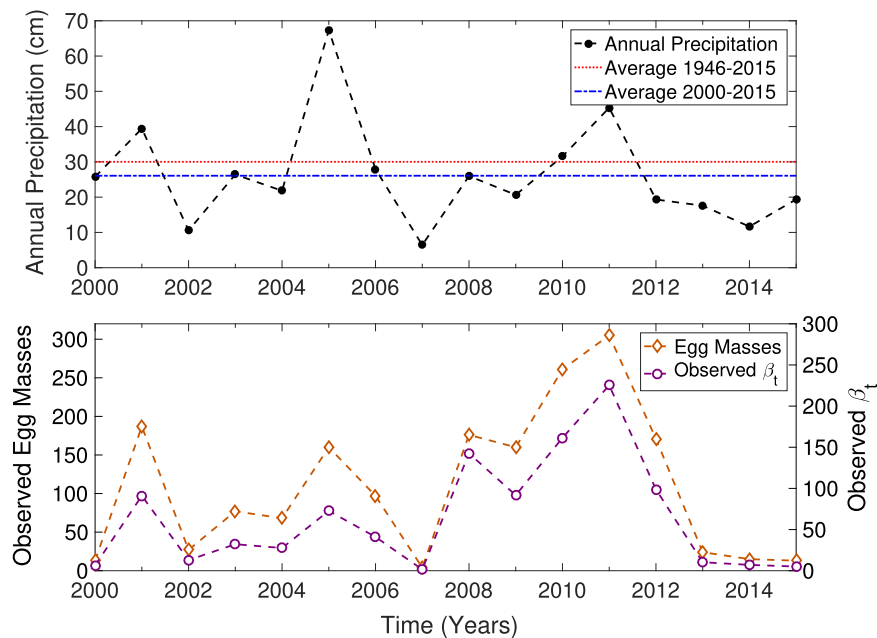
## 2.6. Sensitivity to parameters

We determine the relative contribution of each individual parameter value to the simulated adult population dynamics (1c) by varying a single parameter at a time and leaving the rest of the parameter values as reported in Table 1. An analysis of the outcomes from simulations that vary each parameter is then used to compare the importance of different demographic parameters within a life cycle.

Fig. 4 shows egg production (1a) versus number of adults (1c) for values of  $\beta(r)$  that range from 0 to 150 female newts. Note that for small values of  $\beta(r)$ , i.e., low precipitation, egg production is limited. For large values of  $\beta(r)$ , i.e., high precipitation, egg production is close to the linear approximation of (1a),  $E_t \approx \frac{1}{2} \alpha A_t$ , which corresponds to unlimited habitat for egg-laying,  $\beta(r) = \infty$ .

Fig. 5 shows the number of adults versus time for values of  $T_J$  that range from 0.005 to 0.095 as well as values of  $\sigma$  that range from 0.8 to 0.99. As exhibited by the graph, we find the adult population to be more sensitive to the likelihood of an egg surviving and transitioning into the juvenile stage,  $T_J$ , than to juvenile and adult annual survivorship,  $\sigma$ . This sensitivity analysis suggests that successful transition from egg to juvenile plays an important role in driving the persistence of the population.





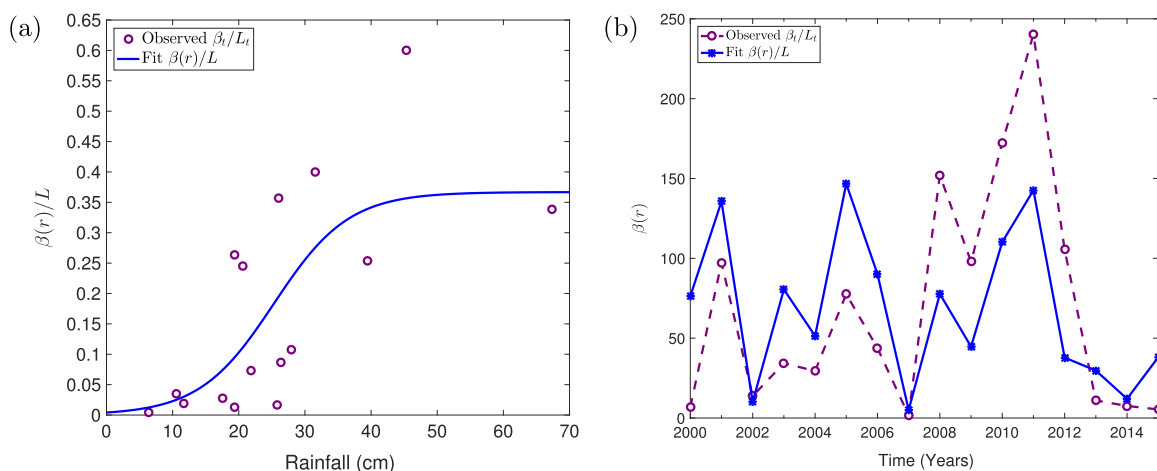
**Fig. 2.** (Top) Annual precipitation in cm recorded at Los Angeles International Airport from 2000 to 2015 (WRCC, 2015). The horizontal lines indicate the historical average annual precipitation from 1946 to 2015 and the recent average annual precipitation from 2000 to 2015. (Bottom) Observed egg masses in a 400 m section of upper Cold Creek and annual field data estimates for  $\beta_t$ , which is the number of female newts in year  $t$  for which the stream habitat allows half of these females to lay eggs (Kats et al., 2013).

### 3. Results

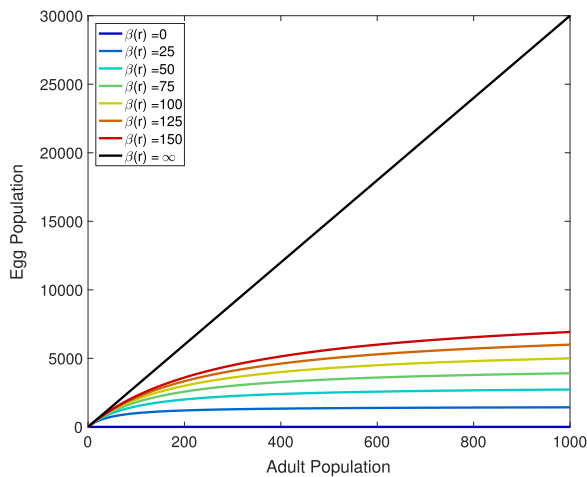
We use our stage-based model (1) to explore the implications of drought on the newt population in Cold Creek or a similar stream. We validate our model by comparing the simulated newt adult population decline to adult population estimates from mark-recapture data taken at Cold Creek from 2000 to 2015. We also find equilibrium solutions in the case where annual precipitation, and therefore  $\beta(r)$ , is constant. This allows us to address questions such as what is the percentage of population decline under current drought conditions as well as under extended periods of severe drought. We use simulations to explore the effect of severe drought on the persistence of the local newt population and to predict the annual precipitation levels required for long-term newt persistence. In all simulations we use the parameters from Table 1 unless otherwise stated. We also assume that the length of the stream is 400 m so that results will correspond with Cold Creek surveys, and we initialize our simulations with 1025 adults, the estimated number of adults in the 400 m section of Cold Creek for 2000.

#### 3.1. Model validation

We validate our model results by comparing estimated newt adult population decline predicted by our model to mark-recapture data from 2000 to 2015. We simulate egg, juvenile, and adult populations under current rainfall conditions using measured annual precipitation at Los Angeles International Airport from 2000 to 2015 (WRCC, 2015). Mark-recapture data estimates indicate that the newt population in Cold Creek declined 44.2% from 1025 adults in 2000 to 572 adults by 2013 (Bucciarelli et al., unpublished). As seen in Fig. 6a, our model similarly predicts a 35.0% decline from 1025 to 666 adult newts from 2000 to 2013. The model predicts a total 38.3% decline to 632 newts by 2015. Small differences in simulated and estimated newt population numbers could be due to natural variation in mark-recapture data estimates or fluctuation in juvenile and adult annual survivorship in drought versus non-drought conditions (Muncy et al., 2014). We also validate estimates of egg masses predicted by our model to observed egg masses recorded in field surveys from 2000 to 2015. The average



**Fig. 3.** (a) Annual estimates of observed  $\beta_t/L_t$  values (female newts/m) as given by (7) versus annual precipitation, and the best fit curve  $\beta(r)$  as given by (8) with  $R^2 = 0.426$ . Here,  $L_t$  is the annual survey length of Cold Creek. (b) Annual estimates of the observed  $\beta_t$  values (female newts/m) each year as given by (7) and the corresponding fit value of  $\beta(r)$  from 2000 to 2015.



**Fig. 4.** Egg production (1a) versus adult population (1c) for values of  $\beta(r)$  that range from 0 to 150 female newts. Note that egg production is limited for all values of  $\beta(r)$ . For large values of  $\beta(r)$ , i.e. high precipitation, egg production approaches the linear approximation ( $\beta(r) = \infty$ ).

number of egg masses observed in Cold Creek from 2000 to 2015 is 113 egg masses. As seen in Fig. 6b, our model similarly predicts 128 egg masses. The differences in predicted and recorded egg masses could be due to stochasticity in newt egg-laying or documented effects of multiyear rainfall deficits and past breeding events on future breeding events (Cayuela et al., 2014) that we do not account for in our model (1).

### 3.2. Analysis and predictions

By setting the populations of eggs, juveniles, and adults in year  $t + 1$  equal to those in year  $t$  in (1), we find that the equilibrium solution for adults is

$$A = 2\beta(r) \left( \frac{\frac{1}{2}\alpha T_A T_J}{(1 - P_J)(1 - P_A)} - 1 \right). \quad (9)$$

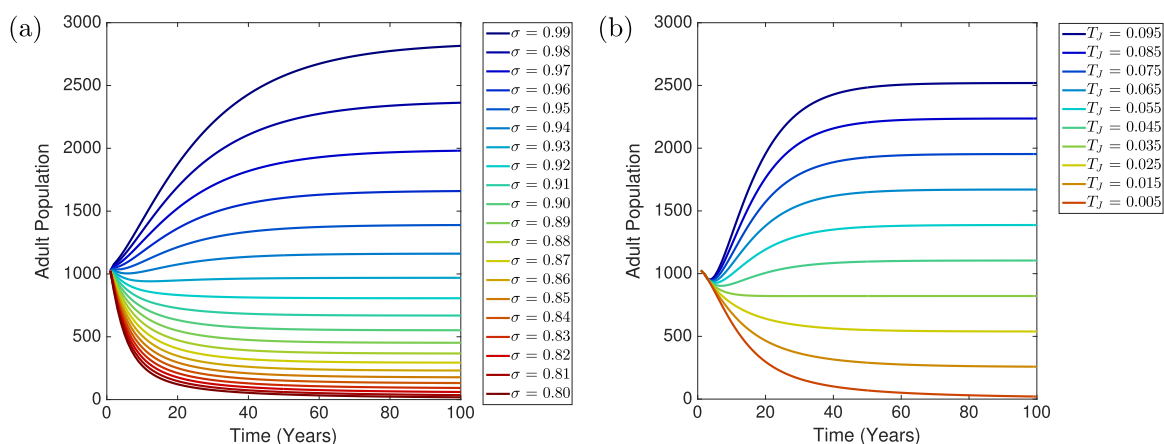
The adult equilibrium is directly proportional to  $\beta(r)$ , which accounts for the amount of stream space available for egg-laying and varies with annual precipitation.

Fig. 7 displays simulations of the adult newt population that begin with 1025 individuals in 2000, incorporate historical annual precipitation from 2000 to 2015, and continue beyond 2015 for a range of

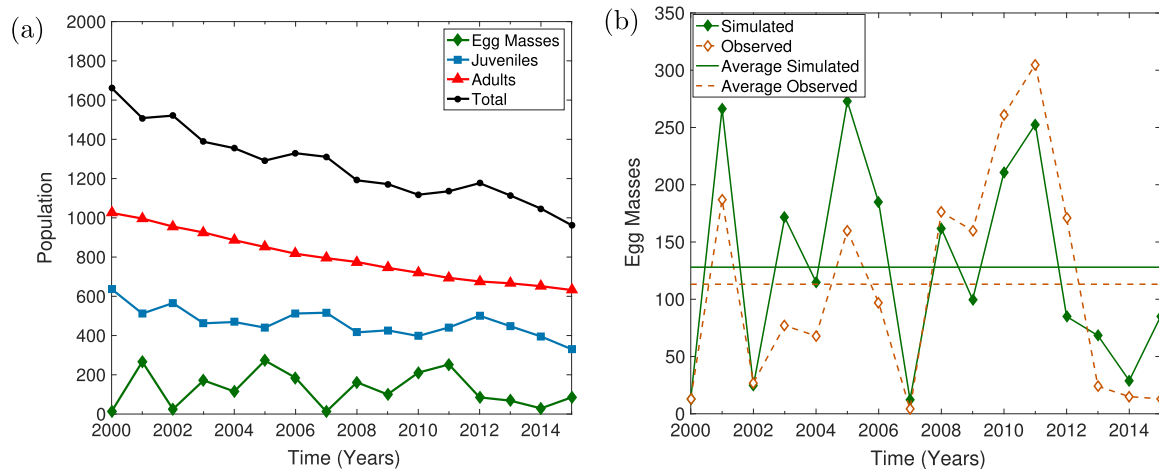
constant annual precipitation, and therefore constant  $\beta(r)$ , values. These simulations approach the equilibrium values (9) for constant values of  $\beta(r)$ . If average annual precipitation were to increase to 30 cm, the average annual precipitation from 1946 to 2015, we predict that the long-term adult newt population will increase to 651 individuals, a 5.5% increase from 2015. Given the current drought conditions of 26 cm, the average annual precipitation from 2000 to 2015, we predict that the adult newt population will decline in the long-term to 497 individuals, a 19.6% decrease from 2015. A species is considered critically endangered if it declines 90% or more from the initial population size after three generations (approximately 54 years with a generation time of 18 years) (IUCN, 2016). We predict that the long-term adult newt population will become critically endangered, less than 100 individuals by 2054, if the average annual precipitation falls to 11 cm or less.

Our simulation and results shown in Fig. 7a have assumed that the annual survivorship of juveniles and adults,  $\sigma = 0.91$ , does not vary with above and below average precipitation levels. Some studies have concluded that the annual survivorship of salamanders decreases significantly during periods of drought (Muncy et al., 2014, Cayuela et al., 2014, 2016). We account for this documented effect of drought conditions in Fig. 7b by allowing  $\sigma$  to decrease in consecutive years with below average annual precipitation by 0.01 per year down to a minimum of  $\sigma = 0.86$  in years with  $r < 30$  cm. With this adjustment to  $\sigma$ , we predict that under current drought conditions of an average annual precipitation of 26 cm, the long-term adult newt population will decline to 173 individuals, an 83.1% decrease from 2000 or a 72.6% decrease from 2015. We further predict that given this adjustment the adult newt population will become critically endangered, less than 100 individuals by 2054, if the average annual precipitation falls to 19 cm or less.

We now consider predictions of the impact on the adult newt population of extended periods of severe drought followed by a rebound to average precipitation levels. We initialize the simulations with 1025 adult newts in 2000 and use the historical annual precipitation at Los Angeles International Airport from 2000 to 2015. Beginning in 2016, we consider periods of extreme drought that range from 0 to 30 years with an annual precipitation of 10 cm, an average of the three worst drought years from 2000 to 2015. For the years following the severe drought, the constant annual precipitation rebounds to 30 cm, the average annual precipitation from 1946 to 2015 (WRCC, 2015). In our simulations we assume a fixed annual survivorship,  $\sigma = 0.91$ . The results are shown in Fig. 8a. **We predict the adult newt population will become critically endangered following an extended period of extreme drought of 29 years or longer.** Below the critically endangered population size, our model may not be predictive due to stochastic effects for



**Fig. 5.** (a) Total adult newt population versus time for varying probabilities of juvenile and adult annual survivorship,  $\sigma$ . Note that as we vary  $\sigma$ , the values of  $P_J$ ,  $T_A$ , and  $P_A$  are updated using (4), (5) and (6), respectively. (b) Total adult newt population versus time for varying probabilities of transition to juveniles,  $T_J$ . The model is more sensitive to the parameter  $T_J$  than  $\sigma$  because small changes in  $T_J$  have a greater effect on the long-term adult newt population.



**Fig. 6.** (a) Number of egg masses, juveniles, adults, and total newts (juveniles plus adults) from a simulation of (1) using a stream length of 400 m and precipitation measured at Los Angeles International Airport from 2000 to 2015. (b) A comparison of the number of simulated egg masses (1a) and observed egg masses in a 400 m section of upper Cold Creek from 2000 to 2015.

small population sizes. In contrast, due to the long adult lifespan, our model predicts that the newt population will recover from an extreme drought that lasts up to 28 years. It is important to note that these results assume some newts can survive longer than 30 years even if rarely. In periods of extended drought, few if any newts successfully reproduce (Cayuela et al., 2014), and thus the rebound in our model is generated by aging newts once again being able to reproduce.

In Fig. 8b we also account for the impact of drought on annual survivorship by decreasing  $\sigma$  by 0.01 annually to a lower limit of  $\sigma = 0.86$  during the extended periods of drought. With this adjustment to  $\sigma$ , we predict the adult newt population will become critically endangered following an extended period of extreme drought of 17 years or longer. In this case we predict that the newt population is able to recover from an extended period of drought of 16 years or less. Thus, adult survivorship can have a significant effect on the newt population's ability to recover.

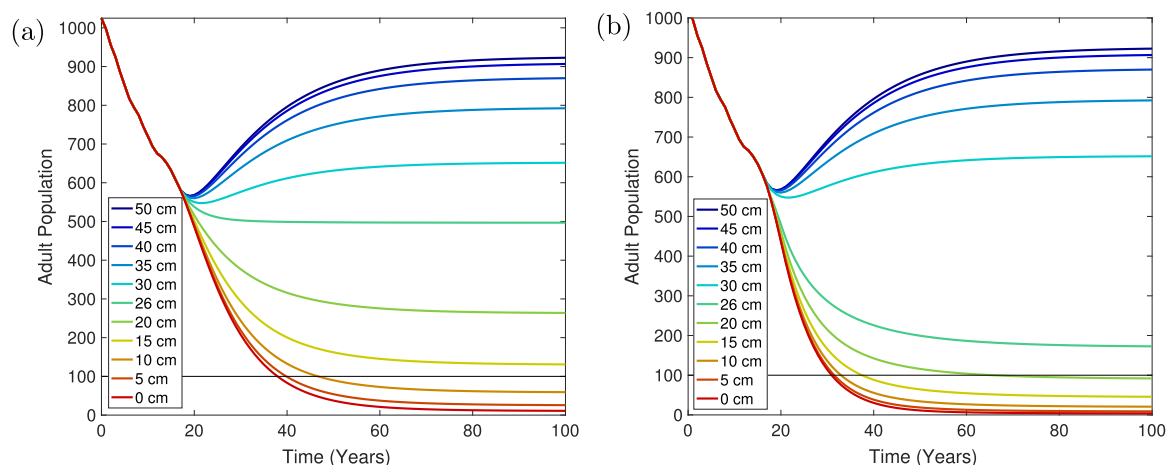
#### 4. Discussion

We have constructed a stage-structured mathematical model (1) of a California newt population that enables us to explore the impact of California's extreme drought upon newt persistence in Santa Monica

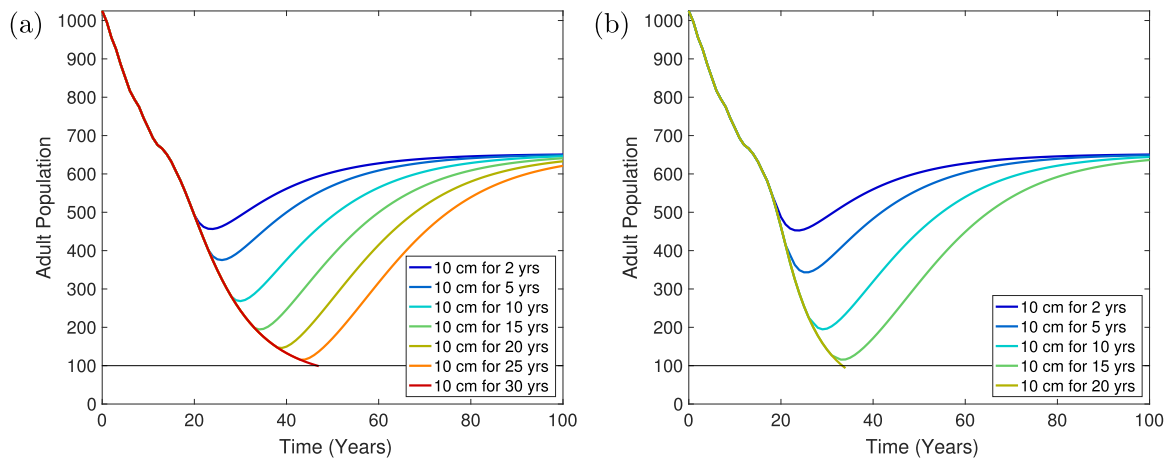
Mountain streams. We account for the impact of drought by incorporating a data-driven newt egg-laying term (1a) that depends upon variable annual precipitation. Our simulations of egg, juvenile, and adult populations that incorporate historical values of annual precipitation accurately capture adult and egg population dynamics from 2000 to 2015, as shown in Fig. 6. Small differences in simulations versus observations of newt population sizes may be attributed to natural variation, uncertainty in mark-recapture data estimates, and additive effects of multiyear drought (Cayuela et al., 2014, 2016).

We present a data-driven mathematical model to capture key biological interactions. However, modeling inherently simplifies environmental dynamics, and thus modeling results should be confirmed with biological observation and experimentation. Our model may not be predictive for very small population sizes due to stochastic effects as well as the simplifying assumptions associated with deriving the persistence and transition probabilities. As a result, our model does not enforce a strict lifespan for individual newts, which could affect estimates of the longest drought period after which the newt population could still recover, as seen in Fig. 8. This is consistent with known limitations of discrete stage-structured models (Caswell, 2001).

Simulations from our model forecast newt population dynamics in future years given a variety of precipitation levels and regimes. If



**Fig. 7.** Simulations of adult newt populations versus time for varying amounts of constant annual precipitation in a 400 m stream. The simulations begin with 1025 adults in 2000 and incorporate historical annual precipitation from 2000 to 2015 (WRCC, 2015). Beginning in 2016, we vary the constant annual precipitation,  $r$ , between 0 and 50 cm, and therefore the value of  $\beta(r)$  ranges from 1.644 to 145. The black line at 100 adults represents the threshold for critical endangerment, which is defined as a 90% decline from the initial newt population size within three generations (54 years). (a) The annual survivorship of juveniles and adults is fixed at  $\sigma = 0.91$ . (b) The annual survivorship,  $\sigma$ , decreases annually by 0.01 down to a minimum of  $\sigma = 0.86$  in years with  $r < 30$  cm. This respectively decreases the persistence and transition probabilities to  $P_j = 0.7649$ ,  $T_A = 0.0951$ , and  $P_A = 0.8555$  as calculated using (4), (5) and (6).



**Fig. 8.** Simulations of adult newt populations versus time during and following extended periods of severe drought in a 400 m stream. The simulations begin with 1025 adults in 2000 and incorporate historical annual precipitation from 2000 to 2015 (WRCC, 2015). Beginning in 2016, the constant annual precipitation,  $r$ , is set to 10 cm, which is the average of the three worst drought years from 2000 to 2015, for a drought period that ranges from 0 to 30 years. For the years following the drought, the constant annual precipitation,  $r$ , is set to 30 cm, the average annual precipitation from 1946 to 2015. The black line at 100 adults represents the threshold for critical endangerment which is defined as a 90% decline from the initial newt population size within three generations (54 years). (a) The annual survivorship of juveniles and adults is fixed at  $\sigma = 0.91$ . (b) The annual survivorship,  $\sigma$ , decreases annually by 0.01 for each drought year down to a minimum of  $\sigma = 0.86$ . This respectively decreases the persistence and transition probabilities to  $P_j = 0.7649$ ,  $T_A = 0.0951$ , and  $P_A = 0.8555$  as calculated using (4), (5) and (6).

current drought conditions persist, as shown in Fig. 7a, the newt population is predicted to become critically endangered if the average annual precipitation falls below 11 cm. However, if annual survivorship of adults decreases due to additional drought stresses, as shown in Fig. 7b, the newt population is predicted to become critically endangered if the average annual precipitation falls to 19 cm or less. For reference, the average recorded rainfall was 26 cm from 2000 to 2015, but the average recorded rainfall from 2012 to 2015 during extreme drought was 17 cm (WRCC, 2015). Given that multiple studies project that future drought periods could increase in duration and severity (Cook et al., 2015; Diffenbaugh et al., 2015; Underwood, 2015), our model predicts that California newt population sizes will continue to decline, possibly to critically endangered levels.

If the current drought is temporary and is followed by a rebound to the historical average annual precipitation, as shown in Fig. 8b, we predict that land life stages help newts to persist through short-term droughts. That is, if extreme drought continues for up to 16 years and is followed by a rebound to the historical average annual precipitation, the newt population theoretically rebounds to sustained long-term levels. However, following an extended period of severe drought of 17 years or longer, the newt population is predicted to become critically endangered. This assumes that the annual survivorship of adults decreases in successive years of extreme drought.

When considering restorative measures to preserve the California newt population, we note that the model is most sensitive to the parameter  $T_j$ , the probability of surviving from the egg to juvenile stage. This underscores the importance of protecting the critical aquatic newt life stages potentially most affected by drought.

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