

Demographic effects of prolonged drought on a nascent introduction of a semi-aquatic snake

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Abstract Faced with a nascent introduction of a non-native species, conservationists need to quickly determine how a population performs in its new environment. Although correlative models can predict environmental suitability at a coarse scale, they often neglect short-term climatic variability, instead relying on long-term averages. Accurately projecting the fate of any particular introduction requires demographic data on how a population responds to a novel environment. The recent introduction of watersnakes (genus *Nerodia*) poses a risk to California's already imperiled aquatic vertebrate fauna. Despite inhabiting a seemingly suitable climate, a non-native *Nerodia sipedon* population in central California is likely to have been affected by a prolonged extreme drought from 2012 to 2015. We studied the only known population of *N. sipedon* in California for 3 years from 2013 to 2015, and estimated its abundance and annual survival. Its abundance declined from a peak of 218 (95% Credible Interval 149–313) in August 2013 to 97 (80–119) in July 2015. Annual survival of *N. sipedon* from 2013 to 2014 (0.23, 0.13–0.39) and from 2014 to 2015 (0.29, 0.18–0.41) was lower than survival estimates reported from native populations. Snake body condition, the abundance of large adult females, and prey availability all declined throughout the study.

We conclude that the population of *N. sipedon* declined from 2013 to 2015, likely due to decreasing habitat and prey availability from the prolonged regional drought. This study highlights the importance of the effect of climatic extremes on the trajectory of introduced populations in a novel environment.

Keywords Invasive species · Population ecology · Conservation · Climate change · Watersnake · Extreme drought

Introduction

There is considerable interest in predicting the risk non-native species pose in establishing and spreading across novel environments. The extent to which a non-native species can establish, grow in number, and spread depends on whether it has been introduced to an area of suitable abiotic and biotic conditions such that it not only survives, but thrives. Many published studies predict invasion risk using correlative models based on climatic factors like estimated average temperature or precipitation (e.g., BIOCLIM data, Hijmans et al. 2005) in the native and non-native ranges (Ficetola et al. 2007; Villemant et al. 2011). Short-term climatic variability and climatic extremes like droughts or prolonged high or low temperatures, however, may also affect whether a non-native species can thrive in a new environment (Drake et al. 2006;

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Fernández et al. 2012). To successfully invade, a small non-native population must avoid stochastic extinction (Lockwood et al. 2005; Simberloff 2009a), increase in abundance, and expand its range in a new environment (Williamson and Fitter 1996; Richardson et al. 2000). Infrequent climatic events such as droughts, fires, floods, and extreme temperatures present threats to the persistence of nascent introduced populations (Sax and Brown 2000). Thus, while correlative models based on average environmental conditions can provide coarse estimates of regional invasion risk for a species, predicting the trajectory of any particular non-native population requires understanding the demographic response to stochastic environmental variability.

Obtaining precise, unbiased estimates of key population metrics is difficult for many species due to low probability of capture. Capture-mark-recapture (CMR) models that account for imperfect detection have become increasingly vital as biologists have recognized their potential to improve inference in wild populations (White 2005). Modeling variation in capture probability with CMR models is especially useful for studying herpetofauna (Mazerolle et al. 2007), and snakes in particular, because their low detection probability can otherwise limit inferences about population parameters (Parker and Plummer 1987; Willson et al. 2011). CMR models are commonly used to estimate the temporal and spatial patterns in the abundance of wildlife populations (e.g., Semlitsch et al. 2014), but data on abundance alone, however, are not sufficient to properly understand population trends. Negligible change in the abundance of a non-native species over a short period of time may not indicate a low risk of invasion, as the population could simply be in an early “lag phase” that precedes exponential growth (Crooks and Soulé 1999). To know what drives the decline or growth of a population, information is needed on vital rates such as survival, fecundity, and individual growth (Van Horne 1983; Todd and Rothermel 2006). Along with estimates of abundance and vital rates, changes in the size structure of a population can be useful for inferring underlying processes such as growth and mortality (Smith et al. 1998), and changes in individual body condition can signal a decline before changes in abundance are apparent (Madsen and Stille 1988). Although it may take many years to collect data for a time series of abundance, data on vital rates, size

structure, and body condition can give insights into the trajectory of a population more quickly. Determining the status of a non-native population quickly, and with confidence, will allow conservation and management agencies to best allocate limited resources to deal with invasive species.

The introduction of common watersnakes, *Nerodia sipedon*, to Roseville, California presents an opportunity to study the response of a non-native species exposed to novel climatic extremes. A species distribution model based on average temperatures and the availability of aquatic habitat predicts extensive suitable habitat for this species in central California (Rose and Todd 2014). Nevertheless, the Mediterranean climate of central California with its hot, dry summers is different from the climate typical of much of this species' native range in eastern North America. Historically, many wetlands in the Central Valley of California were seasonal, and native semi-aquatic reptiles were adapted to spend large portions of the year aestivating or brumating in terrestrial habitat (Rathbun et al. 2002; Halstead et al. 2015). Seasonally-variable aquatic habitat in California could present a problem to *N. sipedon*, which, although a habitat generalist (Gibbons and Dorcas 2004), is usually associated more with permanent than ephemeral wetlands (Roe et al. 2004). While the pre-European environment in central California may not have been ideal for *N. sipedon*, California's flow regimes have been greatly altered by the construction of dams (Poff et al. 2007), often to the benefit of non-native species that thrive in less variable aquatic systems (Marchetti and Moyle 2001; Fuller et al. 2011; Kiernan et al. 2012). Even with these anthropogenic changes to California's aquatic habitats, the severe drought experienced by central and southern California from 2012 to 2015 (Robeson 2015) was likely to stress non-native as well as native wildlife populations.

The recent, historic drought in California provided an opportunity to study how short-term climatic fluctuations influence the establishment success of non-native species. Here, we studied a nascent population of *N. sipedon* in central California to examine the demographic response of this non-native species to extreme climatic variation not captured by typical bioclimatic datasets. This study had three main objectives: (1) to estimate trends in the abundance of *N. sipedon* over time in response to changes in its wetland habitat, (2) to estimate the annual survival rate

of *N. sipedon* during 2013–2015, and (3) to measure the response of individual growth rates, body condition, and the size distribution of watersnakes to extreme environmental conditions. The information presented here will be useful to those concerned by the nascent invasion of *Nerodia* in California, as well as to researchers interested more broadly in the response of invaders to novel climatic regimes.

Methods

Study site

The non-native population of *N. sipedon* in Roseville, California inhabits a narrow, shallow wetland in a suburban green space. Emergent vegetation in the wetland is dominated by cattails (*Typha sp.*) and water primrose (*Ludwigia hexapetala*). The wetland decreased in size from 2013 to 2015 during this study as California experienced an exceptional drought (Robeson 2015). The wetland is subsidized by runoff from the suburban neighborhoods and thus did not dry completely at any point during the study. The primary prey species for watersnakes at this wetland are other non-native vertebrates, including American bullfrogs (*Lithobates catesbeianus*), western mosquitofish (*Gambusia affinis*), and sunfish (*Lepomis sp.*).

Mark-recapture study

We sampled the *N. sipedon* population during five periods from August 2013–August 2015. We used three types of aquatic funnel traps to capture *N. sipedon*: approximately 50% of traps were plastic (Model 700, Gator Buckets), 25% were metal (Gee's minnow trap, Tackle Factory), and 25% were vinyl-coated steel traps (Torpedo trap, Frabill). We set 158 aquatic funnel traps for 10 nights in August 2013, 8 nights in August 2014, and 8 nights in September 2014. Because the area of the wetland decreased substantially between 2014 and 2015, we set only 110 traps during July 2015 (8 nights) and 103 traps in August 2015 (7 nights). Each year, we attempted to sample all areas with standing water that could accommodate traps. The area of the wetland declined over the course of the study, from approximately 4100 m² in August 2013, to 1200 m² in August–September 2014, and 450 m² in July 2015. As a

consequence of wetland size, trap-density increased from approximately 0.04 traps/m² in 2013, to 0.13 traps/m² in 2014 and 0.24 traps/m² in 2015.

Aquatic funnel traps are an effective method for capturing watersnakes and have been commonly used in CMR studies in part because they allow standardization of capture effort when estimating detection probability (Durso et al. 2011; Rose et al. 2013). We set aquatic funnel traps along the bank of the wetland and in emergent vegetation where watersnakes forage. We did not bait traps, but traps naturally accumulated anuran larvae and small fish over time. We checked traps once per day and measured, weighed, and determined the sex of all captured snakes. We gave snakes unique marks by branding ventral scales (Winne et al. 2006). We released snakes within 2 h of capture.

Robust-design CMR model

We used robust-design CMR models to estimate the capture probability, p , of snakes in the population during each sampling occasion (primary and secondary), the apparent survival rate, ϕ , between primary sampling periods, and the abundance, N , during each primary period. The inclusion of several secondary sampling periods within each primary period allows for better estimation of capture probability at each time, and therefore more precise estimates of abundance, N (Pollock 1982; Kendall et al. 1995). The population is assumed to be closed to birth, death, immigration, and emigration within each primary period, but open between the longer intervals that separate primary periods. The five primary periods were August 2013, August 2014, September 2014, July 2015, and August 2015, and consisted of 10, 8, 8, 8, and 7 secondary sampling occasions respectively. Because snakes were removed from the population upon capture in the last sampling period of August 2015, we used these data only to estimate apparent survival from September 2014 to July 2015, and do not report an estimate of N from this period. We can only estimate apparent survival—and not true survival—because without auxiliary data such as dead recoveries, our CMR model cannot distinguish between mortality and permanent emigration from the population.

Some variation in abundance among years could be attributable to the timing of sampling relative to the

pulse of neonates entering the population. To account for this sampling artifact, we report estimates of N for adults and juveniles (≥ 225 mm SVL), and neonates (< 225 mm SVL) separately (King 1986; Weatherhead et al. 1999). We estimated the finite growth rate of the population, λ , between primary periods by dividing N_{t+1} by N_t . We also estimated the abundance of snakes > 600 mm SVL during each primary period to track the abundance of adult females over time. Females in this population reach sexual maturity at approximately 600 mm (Rose et al. 2013), whereas males rarely reach this size (one individual out of 128 in 4 years of sampling). We modified code from Schofield and Barker (2011), which allowed us to include snake snout-vent-length (SVL) as an individual time-varying covariate, and to estimate the latent size distribution during each primary period. For snakes that were not captured and measured during a given primary sampling period, we imputed their SVL using a somatic growth model based on growth rate data from the Roseville population, described below.

All models included a random effect for individual heterogeneity in capture probability, as failure to account for differences in capture probability among individuals leads to underestimates of abundance (Williams et al. 2002). We modeled heterogeneity using a logistic-normal continuous mixture, where the individual-level random effect on capture probability was normally distributed with a mean of 0. The random effect was added to the population mean before being transformed using the logistic function to scale capture probability between 0 and 1 (Coull and Agresti 1999).

We defined a set of candidate models that were biologically plausible with a set hierarchical effects structure for temporal variation in apparent survival and capture probability (Table 1). We modeled

variation in capture probability among primary periods using a fixed effect, as the wetland area and the density of traps differed among primary periods. Within primary periods, we included a random effect of secondary period (day) on capture probability. We modeled apparent survival, ϕ , between primary periods using a fixed effect, as the time between primary periods varied from 1 month (August to September 2014) to 1 year (August 2013 to August 2014). We included linear and quadratic effects of size on survival, based on a study from Ontario, Canada that found intermediate-sized *N. sipedon* had higher survival than small and large individuals (Brown and Weatherhead 1999a). We also included linear and quadratic effects of size on capture probability because our earlier capture data indicated both large and small individuals were less likely to be captured in aquatic funnel traps (Rose et al. 2013). We did not include models with a behavioral effect (trap-response), as a previous study of this population strongly supported equal probabilities of capture and recapture (Rose et al. 2013).

We built CMR models in R (version 3.2.0, R Core Team 2015) and analyzed them in JAGS (Plummer 2003) using the R2jags package (Su and Yajima 2015). We used parameter-expanded data augmentation to fit models with varying estimates of N by adding 800 all-zero capture histories to the observations (Royle and Dorazio 2012). We fit all models with uninformative, Uniform(0, 1) priors for survival and capture probability within a primary period, and weakly informative Cauchy-distributed priors (location = 0, scale = 2.5) for the size covariates on capture probability and survival (Gelman et al. 2008; Schofield and Barker 2011).

We tested for the importance of including an effect of snake size (SVL) on apparent survival and capture probability using the indicator variable selection method of Kuo and Mallick (1998). In brief, the parameters for the size-effects on apparent survival and capture probability are multiplied by a binary indicator variable that determines whether the size effect is turned on (1) or off (0) in a given model iteration. In this way, we can tabulate the number of model iterations in which a parameter is turned on, and use this as a measure of how important the effect of that parameter is in fitting the observed data. Each indicator variable, w , had a Bernoulli distributed prior with a probability of 0.5; in that way, we assigned each size-effect parameter an equal prior probability of

Table 1 Model comparison of top five candidate robust-design capture-mark-recapture models. SVL indicates a linear effect of snake SVL on a parameter, SVL² indicates a quadratic effect. All models include time-varying (t) estimates of p and ϕ

Model	p	ϕ	k	Posterior probability
1	$t + \text{SVL}$	t	16	0.39
2	$t + \text{SVL}$	$t + \text{SVL}$	17	0.38
3	$t + \text{SVL}^2$	t	17	0.12
4	$t + \text{SVL}^2$	$t + \text{SVL}$	18	0.06
5	$t + \text{SVL}$	$t + \text{SVL}^2$	18	0.04

being included in the model. To improve model convergence and sampling of parameter space, we standardized snake SVL by subtracting the mean SVL from each value, and then dividing by the standard deviation. We ran our model with five independent chains for 200,000 iterations each, with the first 100,000 iterations discarded as burn-in and the remaining 100,000 iterations thinned by 1/10 to remove serial autocorrelation among sequential samples. This resulted in a posterior distribution for each parameter composed of 50,000 samples, 10,000 from each chain. We inspected each chain visually using trace plots to ensure that all chains were well mixed. We measured model convergence with the Gelman-Rubin diagnostic (\hat{R}), which compares within chain variance to between chain variance, and approaches 1 as the posterior distribution of each parameter converges to a stationary distribution (Gelman and Rubin 1992). We ran models until \hat{R} was <1.01 for all parameters. We evaluated the goodness of fit of the most general CMR model (including size effects on p and ϕ) using a Bayesian p value (Gelman et al. 1996); a value near 0.5 indicates the model adequately fits the observed data, whereas values near 0 or 1 indicate poor fit (Kéry and Schaub 2012). We calculated a Bayesian p -value using the Freeman-Tukey statistic as a discrepancy measure (Freeman and Tukey 1950; Brooks et al. 2000). For each parameter of interest, we report the mean of the posterior distribution, along with a 95% Credible Interval (CRI) based on the 2.5th and 97.5th % of the posterior distribution.

Growth rate and body condition

Somatic growth rates of *N. sipedon* are variable among populations in its native range, but in all populations they show a strong negative relationship with SVL (Feaver 1977; Brown and Weatherhead 1999b; King et al. 2006b). We measured the SVL of all individuals upon capture and calculated growth rate by subtracting initial SVL from SVL at the second capture, dividing by the number of days between captures. To estimate the relationship between growth rate and SVL, we fit two linear regression models of growth rate on initial SVL with and without a fixed effect of sex on the y-intercept using the “rethinking” package (McElreath 2015) in R. We compared models using the

Widely Applicable Information Criterion (WAIC, Watanabe 2010). For the growth rate regressions, we only included captures that took place at least 250 days apart and we scaled growth rates to be averaged over 365 to ensure results were comparable to previously published growth rate data.

To measure trends in the condition of individual snakes over time, we calculated a body condition index (BCI) based on their length and mass. We first regressed the natural log of snake body mass on natural log SVL for all snakes captured from 2011 to 2015, including 47 days of removal sampling from July to September 2011, before the drought (Rose et al. 2013), and 46 additional days of removal sampling conducted by the California Department of Fish & Wildlife from August to October 2015. We then took the residuals from this regression and divided by the predicted (fitted) mass to calculate relative BCI for each individual (Blouin-Demers et al. 2005). A BCI of zero indicates a snake is an average mass for its length, a positive BCI indicates a snake that is heavier than average for its length, and a negative BCI indicates a snake is lighter than average for its length. To test for differences in BCI among sexes and years, we fit a set of four biologically plausible mixed-effects models. Candidate models include fixed effects of sex and year separately, additive effects of sex and year, and an interactive effect of sex and year on BCI. Each model had a random effect for individual because some snakes were measured in multiple years. We excluded females longer than 550 mm SVL from this analysis because the mass of gravid females may not reflect their body condition in terms of stored lipids and protein (Coates et al. 2009). The final BCI data set included 308 measures of BCI from 255 snakes. We fit all linear models using the “rethinking” package (McElreath 2015) in R, with uninformative priors for all parameters, and compared models using WAIC (Watanabe 2010). After model comparison, we calculated model-averaged parameter estimates by taking WAIC weighted samples from the posterior.

Prey capture rate

The two most abundant prey species for *N. sipedon* at the study site were the western mosquitofish, *Gambusia affinis*, and the American bullfrog, *Lithobates catesbeianus*. As a simple index of the abundance of these prey species, we recorded the presence or

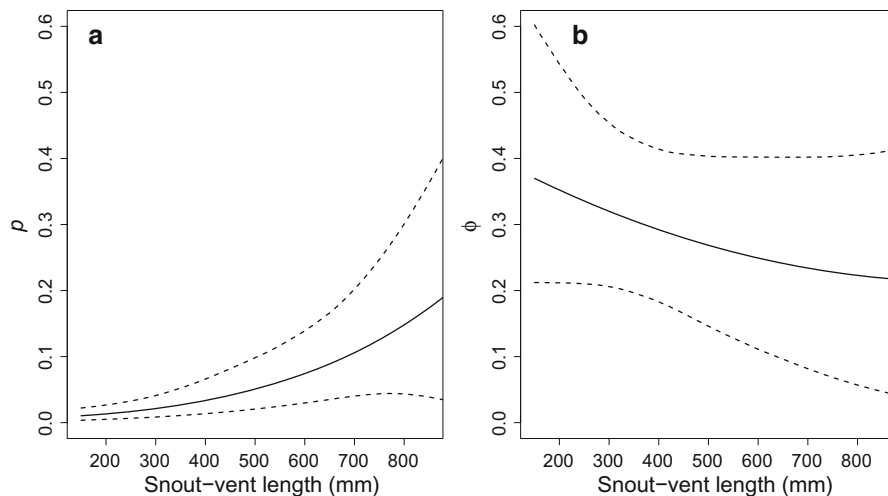


Fig. 1 The effect of snake size on **a** capture probability (p) and **b** apparent survival (ϕ). Relationships are based on model-averaged parameter estimates. *Solid lines* represent the mean relationship, and *dashed lines* represent 95% credible intervals.

absence of mosquitofish and bullfrogs from a subset of trap-nights in 2011 ($n = 275$), 2013 ($n = 31$), 2014 ($n = 398$), and 2015 ($n = 110$). We tested for a difference in the capture rate of prey over time by building linear models with a fixed effect of year on the binomial response using the “rethinking” package in R as above (McElreath 2015). We constructed separate models for mosquitofish and bullfrogs (adults and tadpoles combined). We compared the estimated capture rates from 2013, 2014, and 2015 to a pre-drought reference in 2011. We calculated the difference in parameter estimates among years and considered a difference significant if $\geq 95\%$ of the posterior probability was above or below 0.

Results

We made a total of 377 captures of 180 snakes over 41 sampling days of the Roseville *N. sipedon* population from 2013 to 2015. In August 2013, we captured 70 snakes a total of 99 times in 10 days of trapping. In August 2014, we captured 52 snakes a total of 78 times in 8 days, five of which were snakes marked in 2013. In September 2014, we captured 27 snakes (13 marked) a total of 36 times over 8 days. Capture rates were highest in July 2015, when we captured 63 snakes (21 marked) a total of 146 times in 8 days. August 2015, when all snakes were removed from the

population upon capture, had the fewest captures—just 18 snakes (12 marked) over 7 days. Of the 180 snakes captured, 75 were male, 94 were female, and 11 individuals could not be sexed because their small size prevented cloacal probing. The sex ratio of captured snakes did not differ significantly from 1:1 (Fisher’s exact test, $p = 0.33$).

The two top ranked CMR models had nearly equal posterior probability, and a positive, linear effect of snake size on capture probability. The top model had no effect of size on survival, the second best model included a linear, negative effect of size on survival (Table 1). Averaging over all models, snake size had a clear, positive effect on capture probability (Fig. 1a). The model-averaged relationship between snake size and apparent survival had greater uncertainty, but exhibited a slight decline in apparent survival with increasing size (Fig. 1b). Below, we present ensemble parameter estimates based on model-averaging using the posterior probability of each model. The full CMR model appeared to adequately fit the observed data based on our goodness-of-fit test (Bayesian p -value = 0.26).

Mean capture probability, p , was consistent during the first three primary sampling periods, from August 2013 ($\bar{p}_1 = 0.023$, 95% CRI 0.009–0.045) to August 2014 ($\bar{p}_2 = 0.033$, 0.013–0.065) and September 2014 ($\bar{p}_3 = 0.022$, 0.009–0.044). Capture probability was much greater in July 2015 ($\bar{p}_4 = 0.16$, 0.085–0.25)

Intercepts are from **a** capture probability in August 2014 and **b** apparent survival from 2014 to 2015 adjusted for a 12 month interval

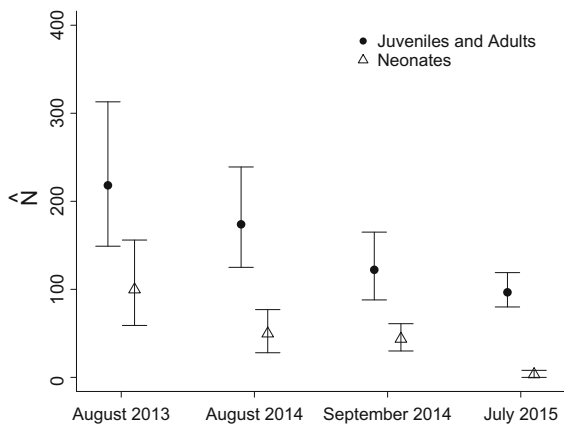


Fig. 2 Trends in estimated abundance of *N. sipedon* over four sampling periods from 2013 to 2015. Points represent posterior means and error bars are 95% credible intervals

than in the three prior primary sampling periods. Average apparent survival was lowest from August 2013 to August 2014 ($\hat{\phi} = 0.23$, 0.13–0.39). Survival over the 11 month period from August 2014 to July 2015 was similar; multiplying our survival estimate from August–September 2014 by our estimate from September 2014–July 2015, and adjusting this survival over an 11 month period to a 12 month interval ($\hat{\phi}^{12/11}$) gave an annual survival estimate of $\hat{\phi} = 0.29$ (0.18–0.41) for 2014–2015.

The combined abundance of juvenile and adult *N. sipedon* (≥ 225 mm SVL) declined over the course of our study, from a high of 218 snakes (149–313) in August 2013 to 174 (125–239) in August 2014, 122 (88–165) in September 2014, and a low of 97 (80–119) in July 2015 (Fig. 2). The abundance of juvenile and adult watersnakes did not change substantially from August 2013 to August 2014, as the estimated growth rate of the population widely overlapped 1 ($\hat{\lambda} = 0.83$, 0.50–1.31). In contrast, abundance of juveniles and adults declined sharply from August 2014 to July 2015 ($\hat{\lambda} = 0.57$, 0.40–0.79). The abundance of neonates (< 225 mm SVL) declined from August 2013 to August 2014 ($\hat{\lambda} = 0.51$, 0.22–1.02; Fig. 2). The abundance of adult females exhibited the sharpest decline according to our CMR model, from an estimated 23 (17–31) snakes > 600 mm SVL in August 2013 to 12 (8–17) in August 2014 and 1 (0–2) in July 2015.

The majority of snakes captured were 200–600 mm SVL during all sampling periods, but the size

distribution of captured snakes changed throughout the study, with fewer large snakes captured in 2014 and 2015 than in 2013 (Fig. 3). Snakes were roughly uniformly distributed between 200 and 600 mm SVL in August 2013, whereas in August 2014 there was a large increase in the number of individuals between 250 and 350 mm SVL and a decrease in the number of snakes larger than 450 mm SVL (Fig. 3a, b). In July 2015, the abundance of captured snakes in the 250–450 mm size range was similar to August 2014, but there were no individuals < 200 mm or > 600 mm SVL captured (Fig. 3d).

We were able to estimate the growth rate for 14 male and 17 female snakes. Intervals between measurements varied from 299 to 769 days, and growth rate ranged from -0.02 to 0.47 mm/day. Growth rate declined as snake SVL increased for both males and females. Models with and without an effect of sex on growth rate received equivocal support. The model with an effect of sex on the intercept of the relationship between growth rate and snake SVL received 52% of the model weight according to WAIC, with males having slightly lower growth rates than females (female = 0.20 mm/day, male = 0.15 mm/day for a snake of 400 mm SVL). There was also substantial support for a model with no effect of sex on the growth rate-size relationship (Δ WAIC = 0.2, WAIC weight = 0.48).

The most parsimonious model for explaining variation in BCI included an interaction between snake sex and year, although a model with additive effects of sex and year and a model with a year-effect only also had substantial model weight (Table 2). Model-averaged estimates of BCI based on model WAIC weights were qualitatively similar to those from the highest ranked model. The average body condition of snakes of both sexes was much lower in 2015 than in 2011, the last year before the drought (Fig. 4). In contrast, average BCI in 2013 and 2014 did not differ from 2011. The year-by-sex interaction is manifested in males having greater body condition on average than females in 2011 and 2015, whereas in 2013 and 2014 males had slightly lower average BCI than females (Fig. 4).

The capture rate of western mosquitofish was highest in 2011, when 65% of traps contained at least one mosquitofish ($\hat{p} = 0.65$, 95% CRI = 0.59–0.71). The capture rate of mosquitofish was lower in 2013 (0.42, 0.25–0.59) and 2014 (0.46, 0.41–0.51) than in 2011, with no difference between 2013 and 2014. The

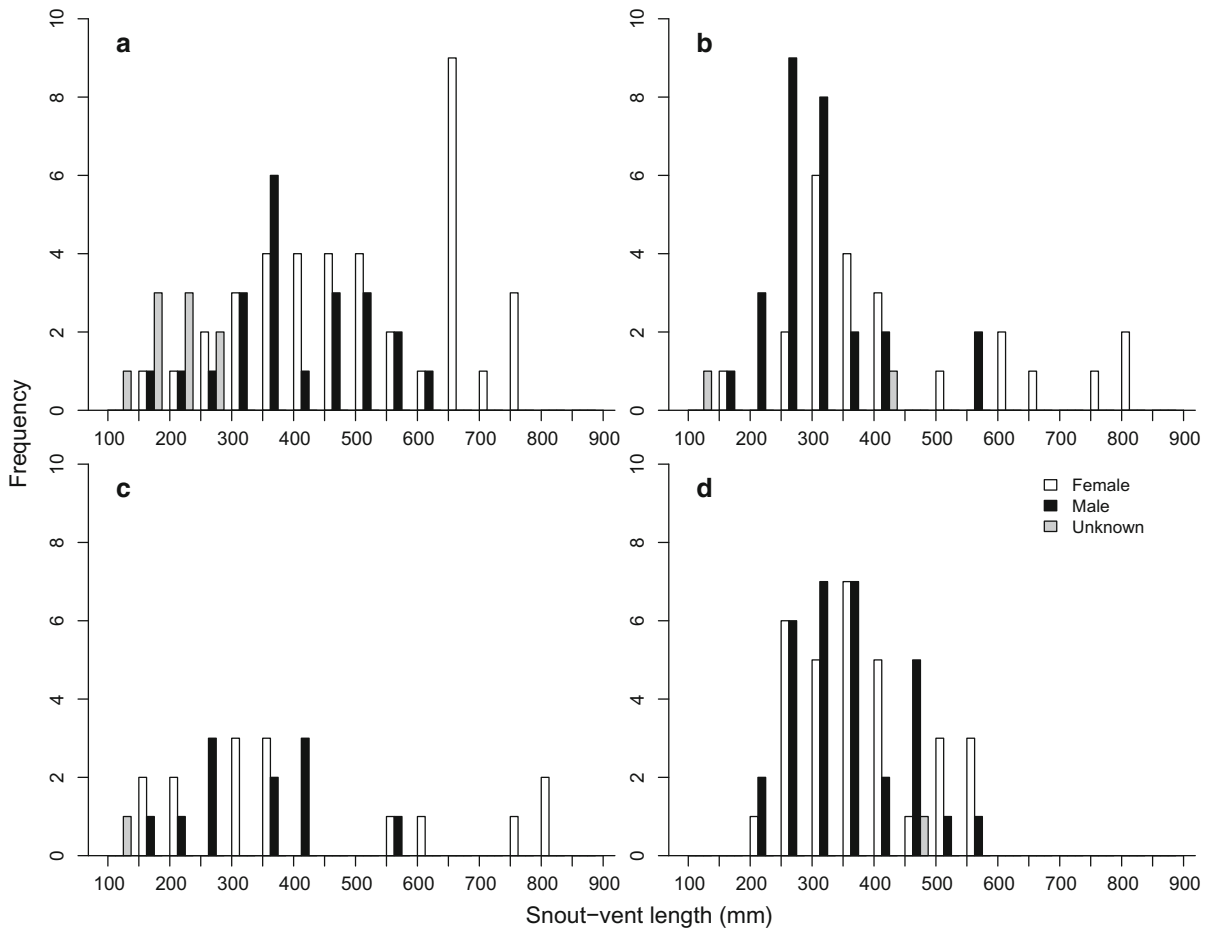


Fig. 3 Size-frequency histograms of *N. sipedon* captured in **a** August 2013, **b** August 2014, **c** September 2014, and **d** July 2015 by sex

Table 2 Candidate set of models for variation in body condition index (BCI). Models listed in order of ascending Watanabe–Akaike Information Criterion (WAIC). pWAIC represents the effective number of parameters in the model

Model	Specification	WAIC	pWAIC	Δ WAIC	Weight
1	Sex \times year	-791.5	42.9	0	0.51
2	Sex + year	-790.3	42.2	1.2	0.28
3	Year	-789.7	33	1.8	0.21
4	Sex	-736.4	53.9	55.1	0

capture rate of mosquitofish was lowest in 2015 (0.29, 0.21–0.38), which was significantly lower than 2011 and 2014 but not 2013 (Fig. 5a). More than 90% of the posterior weight supported a lower capture rate in 2015 than 2013, but there was great uncertainty about the capture rate in 2013 because of the small sample

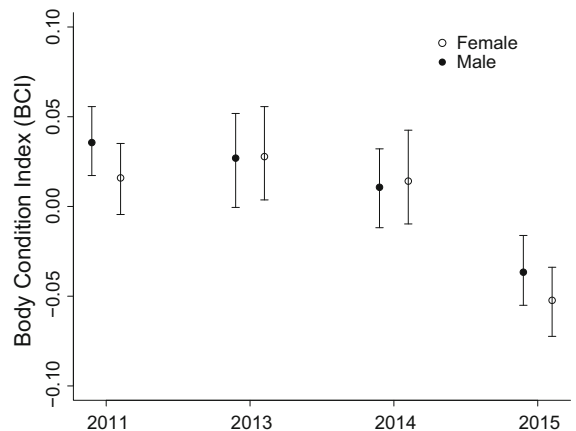


Fig. 4 Change in *N. sipedon* body condition from 2011 to 2015. Estimates of average body condition index (BCI) each year for male and female snakes from an ensemble of models with effects of sex and year on BCI. Points represent posterior means and error bars are 95% credible intervals

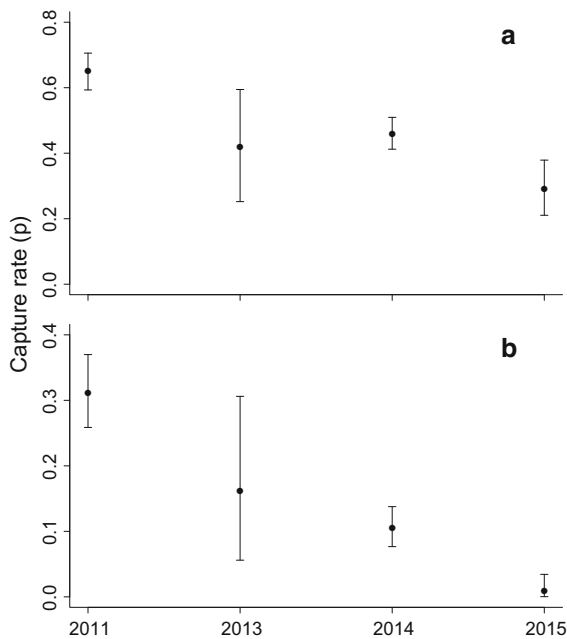


Fig. 5 Estimates of capture rate of **a** western mosquitofish (*Gambusia affinis*) and **b** American bullfrogs (*Lithobates catesbeianus*) over time from a linear model with a binomial response of captured or not captured in each trap. Points represent posterior means and *error bars* are 95% credible intervals

size that year. The pattern for American bullfrogs was similar, with the highest rate of capture in 2011 (0.31, 0.26–0.37), and lower capture rates in 2013 (0.16, 0.06–0.31) and 2014 (0.11, 0.08–0.14). In 2015, only a single bullfrog was captured in a trap, resulting in a significantly lower capture rate (0.01, 0–0.03) than any of the previous 3 years (Fig. 5b).

Discussion

Our study suggests that an incipient invasion of watersnakes in California may have been stymied by an exceptional drought, a factor seldom captured in environmental data used to create species distribution models. Multiple lines of evidence pointed to an overall decline in what was previously believed to be a well-established population of non-native *N. sipedon* (Rose et al. 2013), including low survival from 2013 to 2015, slowed somatic growth, declining body condition, and the loss of large adult females over time. Because fecundity scales with body size in *N. sipedon* (Weatherhead et al. 1999), the loss of large females

from 2013 to 2015 likely resulted in low recruitment in subsequent years. Along with the decline in *N. sipedon*, the capture rates of western mosquitofish and American bullfrogs declined during the drought, suggesting parallel declines in the abundance of these prey species. Despite the declining trend in this watersnake population, the fast life-history (Feaver 1977) and broad climatic tolerances (Rose and Todd 2014) of *N. sipedon* suggest the potential for rapid population growth should conditions become more favorable, and thus it should still be considered a potentially invasive species in California.

The decline of this non-native population of *N. sipedon* is most likely due to the loss of wetland habitat during the drought, resulting in decreased survivorship. The wetland area decreased by 75% from August 2013–August 2014, and declined an additional 60% from August 2014–July 2015. During each of these years, <30% of snakes survived. It is possible this is an underestimate of true survival if a substantial portion of the population did not die, but instead left the wetland in search of new habitats. The closely related *N. fasciata* exhibited declines at an isolated population in response to extreme drought in South Carolina, with many individuals dispersing over land in search of new habitat (Seigel et al. 1995; Willson et al. 2006), and two individuals moving between wetlands approximately 3.1 km apart (Luhring et al. 2011). Inter-wetland dispersal was rare for *N. sipedon* in Ohio and Michigan, but individuals in that region inhabited stable, permanently-filled wetlands (Roe et al. 2004). Thus, some *N. sipedon* may have dispersed to colonize new habitats as our study wetland dried. However, it is unlikely many snakes successfully dispersed to new wetlands because trapping and environmental DNA surveys of wetland habitats within 4 km of this study site in 2015 failed to detect any *N. sipedon* (Rose and Todd unpubl. data) and the spatial extent of the drought reduced the availability of wetland habitat across the region. Therefore, the estimates of apparent survival from 2013 to 2015 likely reflect low true survival, given that the wetland we sampled is the only known location occupied by this non-native species in the area. Our estimates of average survival of non-native *N. sipedon* in California were lower than size-dependent survival estimates from a stable population in Ontario, which varied from approximately 0.4 in juveniles to 0.64 in sub-adults (Brown and Weatherhead 1999a). Our estimates are also lower than

survival of radio-tracked individuals in Michigan and Ohio (0.71, Roe et al. 2013) and Indiana (0.46, Roe et al. 2015), although these studies estimated survival from adult snakes only.

The trends in abundance of non-native *N. sipedon* from 2013 to 2015 raise an interesting question: if survival was nearly equal from 2013 to 2014 as it was from 2014 to 2015, why did the population size remain nearly stable during the former period and decline during the latter? The explanation is apparent from changes in the size distribution of captures over time. Snakes were fairly uniformly distributed in August 2013, with several large adult females captured. In contrast, the size distribution shifted in August 2014 to be dominated by juvenile and sub-adult snakes, and by July 2015 was truncated with no large females. Between August 2014 and July 2015, the population decline was likely due to a lack of recruitment to balance losses due to mortality and/or emigration; lower recruitment from 2014 to 2015 would have resulted from the decline in the number of mature females (>600 mm SVL) from 2013 to 2014. While the number of juvenile and sub-adult snakes captured in July 2015 was similar to August 2014, the higher capture probability in July 2015 ($4.9 \times$ greater than 2014) shows the actual abundance of 1 year old individuals was lower during this period, as reflected also in the declining abundance estimates of neonates from 2013 to 2014. Indeed, without accounting for capture probability in a CMR framework, we would erroneously conclude based on counts alone that the population was stable from 2014 to 2015.

There is ample reason to suspect that survival of adult female *N. sipedon* in particular was greatly affected by the drought. Both the number of captures and estimated abundance of large adult females declined from 2013 to 2015. Furthermore, the second ranked CMR model included a negative effect of snake size on survival—suggesting larger snakes survived at a lower rate than smaller snakes. We documented a decrease in captures of mosquitofish and bullfrogs relative to pre-drought conditions, suggesting that prey resources declined after 2011. Drought and other extreme environmental conditions that limit food availability have been shown to exert the greatest effect on the survival of the largest individuals in squamate populations (Madsen and Stille 1988; Wikelski 2005; Winne et al. 2010). Large individuals have greater absolute metabolic demands

than small individuals (Bennett 1982; Andrews and Pough 1985), and in times of scarcity, large animals' energetic demands can be difficult to meet (Winne et al. 2010). *Nerodia sipedon* exhibits female-biased sexual size dimorphism (King 1986; Brown and Weatherhead 1999b), and thus adult females are likely to be most affected by times of scarcity. A study of another aquatic natricine snake with female-biased sexual size dimorphism, *Seminatrix pygaea*, in South Carolina found reduced maximum body sizes in females following a drought, likely due to increased mortality of large individuals (Winne et al. 2010).

Further evidence for the effect of California's drought on *N. sipedon* can be seen in the lower body condition of snakes captured in 2015 than in previous years, and in the low somatic growth rate compared to native populations. The decrease in body condition we observed is not a result of the loss of very large individuals (>600 mm SVL) from the population between 2013 and 2015, as female snakes >550 mm SVL were excluded from our analysis of body condition and only one male had an SVL >600 mm. Also, the average growth rate of snakes in the non-native population ranged from 0.27 mm/day for small snakes (200 mm SVL) to 0.09 mm/day for large females (600 mm SVL). These growth rates are about half what has been reported for *N. sipedon* in its native range. After scaling to give an equivalent number of growth-days among studies (averaging growth over a 365-day year), Brown and Weatherhead (1999b) reported mean growth rates of 0.47 and 0.21 mm/day for small and large female snakes in Ontario, Canada, while King et al. (2006b) found growth rates of 0.53 and 0.28 mm/day for Lake Erie watersnakes, *N. sipedon insularum* in Ohio, and Feaver (1977) reported fast growth (0.6 and 0.27 mm/day) in a Michigan population. Increased competition for food among snakes occupying a shrinking wetland is one potential explanation for the decreased body condition and low growth rates we observed. An experimental study of intraspecific competition in *N. sipedon* found snakes exhibited lower growth when forced to share limited prey resources with conspecifics (Himes 2003). Poor body condition could lead to increased over-winter mortality, as demonstrated for neonate *N. sipedon* in Ontario (Kissner and Weatherhead 2005). Lower survival in snakes with poor body condition could also be a result of increased time spent foraging and therefore higher predation risk, as seen in

European adders, *Vipera berus* (Madsen and Shine 1993) and Texas ratsnakes, *Pantherophis obsoletus* (Sperry and Weatherhead 2008).

The recent decline of non-native *N. sipedon* in Roseville, California is a positive development, as it presents an excellent opportunity to begin systematic eradication efforts. Small, declining populations are particularly susceptible to extinction (Caughley 1994), especially if human-caused mortality acts synergistically with other drivers of decline (Brook et al. 2008). Drought conditions in California may directly facilitate watersnake removal. The capture probability of *N. sipedon* increased sharply in July 2015, when the wetland had shrunk to its smallest size and consequently trap-density was greatest. The higher capture probability in 2015 might be due in part to the low abundance of prey; reduced prey abundance was correlated with higher trap capture rates for Brown tree snakes, *Boiga irregularis*, on Guam (Gragg et al. 2007). Two of the hallmarks of successful eradications are the invasive population having a limited spatial extent, and a quick response following detection of a nascent invasion (Simberloff 2009b; Pluess et al. 2012). We suggest that conservationists should also respond quickly to capitalize on fortuitous, stochastic events such as climatic extremes that stress non-native populations.

Despite the trends seen in this population from 2013 to 2015, we caution against concluding that *N. sipedon* does not pose a risk as an invasive species in California. Growth rates are highly variable in many reptiles, and in favorable conditions individuals can exploit resources to rapidly increase in size (Andrews 1982). The plasticity of growth in *N. sipedon* was clearly demonstrated by the Lake Erie watersnake, *N. sipedon insularum*, in the last 20 years. This endemic subspecies of *N. sipedon* was listed as threatened under the United States Endangered Species Act in 1999 due to its restricted distribution and declining abundance (Fazio and Szymanski 1999). Only a few years after its listing, researchers reported that snakes had begun to feed heavily on non-native round gobies, *Neogobius melanostomus*, and as a result, individuals grew more rapidly and produced larger litters than before this abundant food source was introduced (King et al. 2006b, 2008). Increased growth and fecundity, in conjunction with habitat protection and public outreach, led to rapid population recovery (King et al. 2006a) and delisting of the species in 2011 (U.S. Fish

and Wildlife Service 2011). That conservation success story, along with the knowledge that *N. sipedon* is widely distributed in eastern North America (Gibbons and Dorcas 2004) where it tolerates human disturbance (Attum et al. 2008; Pattishall and Cundall 2009), points to the potential for this non-native snake to become invasive in California if given a respite from eradication efforts.

The present study demonstrates that the non-native population of *N. sipedon* in Roseville, California declined from 2013 to 2015. The decline over this period was characterized by low survival, slow growth, poor body condition, and the loss of large adult female snakes, and was potentially driven in part by increased intraspecific competition for declining prey resources. More broadly, this study illustrates the importance of climatic variability in predicting how non-native species will respond to novel environments. The decline in *N. sipedon* occurred at the same time that central California experienced a prolonged drought that resulted in decreased water availability throughout the region. If its wetland habitat had remained stable during this time period, it is likely that the non-native population of *N. sipedon* would have grown, as high temperatures alone are not stressful to this broadly distributed species. The effect of the drought has likely made this population especially susceptible to extirpation at this point in time. The recent declines in *N. sipedon* should motivate immediate action by state and federal wildlife agencies to try to eradicate this potentially invasive species, before it has a chance to recover.

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