Population viability analysis for a pond-breeding amphibian under future drought scenarios in the southeastern United States

Brian A. Crawford [a,*,1], John C. Maerz [b], Vanessa C.K. Terrell [b], Clinton T. Moore [c]

[a] Georgia Cooperative Fish and Wildlife Research Unit, Warnell School of Forestry and Natural Resources, University of Georgia, 180 E. Green Street, Athens, GA, USA
[b] Warnell School of Forestry and Natural Resources, University of Georgia, 180 E. Green Street, Athens, GA, USA
[c] US Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit, Warnell School of Forestry and Natural Resources, University of Georgia, 180 E. Green Street, Athens, GA, USA

ABSTRACT

Climate change effects are contributing to widespread declines of amphibians, and pond-breeding species may be particularly sensitive to future drought conditions that restrict wetland hydroperiods and decrease opportunities for successful breeding and recruitment. Pond-breeding amphibian populations can compensate for periodic droughts via episodic booms in recruitment, but studies predict that increased future drought conditions will negatively impact long-term persistence for several species. The southeastern United States is a global hotspot of amphibian biodiversity where future trends in drought conditions are uncertain. This study applied a population viability analysis (PVA) framework for an at-risk amphibian, the gopher frog (*Lithobates* [*Rana*] *capito*), to (i) explore population sensitivity to the frequency of droughts that restrict reproductive events, relative to changes in other demographic rates, and (ii) forecast future population viability over 30 years, given plausible scenarios varying in the frequency and duration of droughts adapted from recent historical patterns in the southeastern United States. Population persistence was highly sensitive to frequency of reproductive success. Persistence was fairly insensitive to all demographic parameters when reproductive success was ≥ 0.7 (i.e., ≤ 3 drought years per decade, on average), but sensitivity to survival of terrestrial stages (juvenile, adults) and initial abundance increased as reproductive success decreased. Persistence probabilities were relatively high (0.63–0.99) across a range of plausible future drought scenarios, with higher persistence probabilities (> 0.89) for all scenarios where drought years did not increase from recent historical conditions. Our results indicate gopher frog populations are likely resilient to periodic droughts that occur in 4 or fewer years per decade, but extirpation of some populations is possible if recent drought patterns repeat or increase during the next 30 years. Estimates of future risk to gopher frog populations can inform forthcoming status assessments and designation decisions of the U.S. Fish and Wildlife Service. More broadly, PVAs incorporating drought dynamics can identify climate thresholds that at-risk, pond-breeding amphibian populations can tolerate, which can inform management actions (e.g., maintaining a range of hydroperiods across proximate wetlands) that provide sufficient frequent breeding opportunities for long-term persistence even under drought conditions.

* Corresponding author.
E-mail addresses: bcrawford@compassrm.com (B.A. Crawford), jcmaerz@uga.edu (J.C. Maerz), vkinney@uga.edu (V.C.K. Terrell), ctmoore@uga.edu (C.T. Moore).
[1] Present address: Compass Resource Management, 788 Beatty St #302, Vancouver, BC V6B 2M1, Canada.

1. Introduction

Amphibian species are experiencing widespread declines due in part to multiple factors associated with climate change, which can interact with other key stressors including habitat loss and degradation, non-native invasive species, and disease (Blaustein et al., 2010; Collins and Storfer, 2003; Haggerty et al., 2019; Kissel et al., 2019; Li et al., 2013; Pechmann et al., 1991; Stuart et al., 2004). Pond-breeding amphibian species may be particularly sensitive to climate change effects related to drought frequency and intensity that restrict wetland hydroperiods and overall water availability (Blaustein et al., 2010; Cayuela et al., 2016; Kissel et al., 2019; Walls et al., 2013a). For these species, successful annual breeding and recruitment in ephemeral wetlands requires local climate conditions that allow wetlands to fill at appropriate times and hydroperiods to be sufficiently long for larval development (Chandler et al., 2017; Greenberg, 2001; Greenberg et al., 2017; Jensen et al., 2003; Snodgrass et al., 2000). Although populations can tolerate some degree of periodic recruitment failure – especially when survival rates for terrestrial life stages are sufficiently high (Semlitsch, 2003; Taylor et al., 2006; Wilbur and Rudolf, 2006) – multiple studies of pond-breeding amphibians predict negative impacts of current and future droughts on long-term population trends (Cayuela et al., 2016; Chandler et al., 2016; Davis et al., 2019; Greenberg et al., 2015; McCaffery et al., 2014; Scheele et al., 2016; Walls et al., 2013b).

The southeastern United States (hereafter, Southeast) is a global hotspot of amphibian biodiversity (Barrett et al., 2014; Graham et al., 2010; Walls, 2014) and a region with many at-risk amphibian species that are the focus of status assessments and conservation planning efforts (Crawford et al., 2020; Pickens et al., 2017; Sutherland and deMaynadier, 2012). It is also a region where predicted future trends in drought conditions are uncertain. Future climate models predict the region to experience, on average, increased precipitation, increased evaporation due to increased temperatures, and slightly drier conditions overall that are expected to increase drought frequency and intensity, especially in cooler months (November-April: Seager et al., 2009), but the range of model predictions includes some probability of wetter conditions. Keellings and Engström (2019) also predicted geographic variation in drought conditions (rainfall and number of consecutive dry days) across the Southeast region in cooler months, with some areas predicted to be wetter and some drier through 2099. However, we note the latter study did not include other climatic factors (e.g., temperature) that may influence wetland hydroperiods. Greenberg et al. (2015) found that forecasted hydroperiods for ephemeral wetlands in central Florida would reduce annual recruitment opportunities for populations of multiple amphibian species based on species-specific hydroperiod requirements related to larval development. Therefore, there is an opportunity to evaluate risk to pond-breeding amphibians of conservation concern in the Southeast across a range of plausible future drought scenarios.

Population viability analysis (PVA) can be an effective tool for predicting risk to populations (e.g., population growth rate, persistence probability) and comparing outcomes across future scenarios (Akçakaya and Sjögren-Gulve, 2000; Morris and Doak, 2002). Importantly, PVAs can produce quantitative metrics – as well as transparently capture uncertainty around those metrics – that can directly inform conservation decision-making (Beissinger and Westphal, 1998; Bonnot et al., 2011; McGowan et al., 2017). PVA models are highly customizable to species-specific life history and context-specific factors, such as mechanistic effects of environmental stressors or management interventions (Akçakaya and Sjögren-Gulve, 2000; Crawford et al., 2018; Morris and Doak, 2002; Rhodes et al., 2011; Saunders et al., 2018). PVAs often use stage-based matrices as a framework for modeling species with life histories more easily characterized by stages (e.g., juvenile, adult) rather than by ages (Caswell, 2001; Crowder et al., 1994; Lefkovitch, 1965). Numerous PVAs using stage-based models have been developed for amphibian species (Biek et al., 2002; Homyack and Haas, 2009; Trenham and Shaffer, 2005; Unger et al., 2013; Vonesh and De la Cruz, 2002), and a few recent studies have evaluated the effects of past or future droughts on reproductive opportunities and subsequent extinction risk within PVAs (Cayuela et al., 2016; Davis et al., 2019; Kissel et al., 2019; McCaffery et al., 2012; Scheele et al., 2016). To date, none have focused on at-risk amphibian species in the Southeast where future drought conditions are uncertain.

The gopher frog (*Lithobates* [*Rana*] *capito*) is a pond-breeding anuran species that is currently designated as a Species of Greatest Conservation Need in all states within the species' range (North Carolina, South Carolina, Georgia, Alabama, and Florida) and is designated for an initial status review by the U.S. Fish and Wildlife Service (USFWS) to determine a listing decision under the Endangered Species Act (Smith et al., 2018; U.S. Fish and Wildlife Service, 2016). Gopher frogs are one of many amphibian species of conservation concern in the Southeast that breed – typically in cooler months – in isolated, ephemeral or semi-permanent wetlands embedded within longleaf pine (*Pinus palustris*) forests and related xeric systems (Dodd, 1992; Enge et al., 2014; Erwin et al., 2016; Gibbons et al., 2006). Gopher frog populations encompass connected areas of upland habitat used during non-breeding seasons and one or more breeding wetlands that vary in hydrology (i.e., metapopulations: Greenberg, 2001; Humphries and Sisson, 2012; Roznik et al., 2009). At least 63 of 150 known gopher frog populations include a single known breeding wetland (multiple State agency biologists, personal communication), likely due to ongoing loss and degradation of wetlands to land use change (McCauley et al., 2013). Monitoring studies of local gopher frog populations have observed recruitment failure in certain years when all known breeding wetlands of a metapopulation have not filled or dried before larva can metamorphose (e.g., Enge et al., 2014; Greenberg, 2001; Jensen et al., 2003; Palis, 1998). Although populations of gopher frogs, like other pond-breeding amphibians, can exhibit episodic booms that allow for persistence over time despite occasional droughts (Semlitsch, 2003), the extent to which current and future drought conditions impact population growth remains unknown. This information can be used to estimate extirpation risk for gopher frogs at local and range-wide scales, which will be valuable for forthcoming listing and conservation management decisions.

This study applied a PVA modeling framework to explore the influence of future drought scenarios on reproductive failure and subsequent persistence of gopher frog populations in the Southeast. Our objectives were (i) to construct a stage-based population model for the gopher frog to examine population sensitivity to stochastic events of reproductive success or failure, and (ii) to forecast future population viability over a 30-year period, given scenarios varying in the frequency and duration of drought events adapted

from recent historical patterns in the Southeast. We modeled a gopher frog population as a simplified system without explicitly capturing processes in metapopulation models (e.g., patch-specific movement probabilities: Royle and Dorazio, 2008). In this way, our analysis represents dynamics of (a) sites with a single breeding wetland or (b) sites with multiple wetlands that we assume are relatively synchronized with regard to hydrologic conditions and drought sensitivity. We define reproductive success for a population in a given year as when wetlands fill and retain water sufficiently long for breeding and recruitment of metamorphs into the population – i.e., hydroperiods are at least 90 days (Semlitsch et al., 1995); reproductive failure represents when no wetland retains water and no recruitment occurs in the population for that year due to drought conditions (see Section 2.3 for further details). This analysis builds on previous collaborative research led by the University of Georgia and State, Federal, and other partners to estimate spatiotemporal patterns of recruitment success in gopher frog populations (B. Crawford, unpublished data). The PVA was developed and adopted for this study to support a decision-making process over the next 30 years by a "Gopher Frog Working Group" composed of multiple state, federal, academic, and non-governmental organizations (NGOs) responsible for gopher frog management across the species' range – as well as to inform the forthcoming Species Status Assessment and listing decision.

2. Materials and methods

2.1. Overview

We constructed a stage-based PVA model (Lefkovitch, 1965; Morris et al., 2002; Morris and Doak, 2002) for a gopher frog population using parameter estimates from the focal species and congeners (crawfish frog [*L. areolatus areolatus*], dusky gopher frog

Table 1

Parameter estimates used for a 30-year gopher frog (*Lithobates* [*Rana*] *capito*) population viability analysis using a stage-based, female-only matrix model.

Parameter	Mean	Range[a]	Description	Source[b]
Survival				
φ_E	0.776	0.676, 0.876	Embryo survival	Estimate from Richter et al. (2003: L. sevosus)
φ_T	-	-	Tadpole survival	Interpolated from density-dependent relationship
φ_{Tmin}	0.001	-	Minimum tadpole survival at high densities	Estimates from Kinney (2011: L. a. areolatus), Richter and Seigel (2002: L. sevosus), and Wells (2007: L. sylvaticus); affirmed by experts[c]
φ_{Tmax}	0.025	0.020, 0.030	Maximum tadpole survival at low densities	Estimates from Kinney (2011: L. a. areolatus), Richter and Seigel (2002: L. sevosus), and Wells (2007: L. sylvaticus); affirmed by experts[c]
φ_J	0.298	0.198, 0.398	Juvenile survival	Estimate from (V. Terrell, unpublished data: L. a. areolatus)
φ_{A1}	0.390	0.290, 0.490	Adult survival (1st time breeding)	Estimate from (V. Terrell, unpublished data: L. a. areolatus)
φ_{A2}	0.639	0.539, 0.739	Adult survival ($\geq$ 2nd time breeding)	Adapted from V. Terrell, unpublished data L. a. areolatus), Richter and Seigel (2002: L. sevosus)
φ_{Anb}	0.639	0.539, 0.739	Adult survival (non-breeding)	Adapted from (V. Terrell, unpublished data: L. a. areolatus), Richter and Seigel (2002: L. sevosus)
Maturity and breeding transitions				
γ_{M2}	0.250	0.150, 0.350	Probability of maturing at age 2	Adapted from (V. Terrell, unpublished data: L. a. areolatus), Richter and Seigel (2002: L. sevosus)
γ_{M3}	0.750	0.650, 0.850	Probability of maturing at age 3, given not maturing at age 2	Adapted from (V. Terrell, unpublished data: L. a. areolatus), Richter and Seigel (2002: L. sevosus)
γ_B	0.642	0.542, 0.742	Probability of individual breeding (1 - temporary emigration)	Estimate from (V. Terrell, unpublished data: L. a. areolatus)
rs	0.6	0.2, 1.0	Probability of annual reproductive success (i.e., filling of wetlands, breeding, and recruitment) in a population (1 – total recruitment failure due to drought or other catastrophes)	B. Crawford (unpublished data)
Fecundity				
k	2210	1768, 2652	Mean clutch size	Estimates from Palis (1998) and Richter et al. (2003: L. sevosus)
u	1	-	Mean clutch frequency	Estimates from Palis (1998), Greenberg (2001); affirmed by experts[c]
h	0.5	-	Proportion of embryos that are female	Assumed; affirmed by experts[c]
Abundance				
N	50	10, 200	Initial abundance of adult breeding females	Estimates from monitored populations (provided by experts[c]), Semlitsch et al. (1995), Palis (1998), Greenberg (2001)
N_{Tmax}	171496	-	Carrying capacity of tadpoles, produced from 200 adult breeding females in a population at a stable stage distribution.	Calculated as: $200 * \varphi_E * k * u * h$

[a] Range indicates values used during sensitivity analyses.

[b] Parameter estimates taken from congeners are noted; otherwise, studies estimated rates of *L. capito*.

[c] See Acknowledgments for list of experts and institutions from which oral and written communications were obtained from 2019 to 2021.

[*L. sevosus*], and wood frog [*L. sylvaticus*]) when rates were not available for gopher frogs, as well as expert review (Table 1; see Acknowledgments for list of experts and institutions from which oral and written communications were obtained from 2019 to 2021). We projected population growth and predicted persistence probability under two sets of scenarios: a set of 9 scenarios varying in probability of annual reproductive success and a set of 6 scenarios varying in patterns of potential drought frequencies and durations in the Southeast (Table 2). We ran 10,000 iterations of each scenario and projected the population for 30 years. We selected this time horizon to align with the scope of the decision-making process for management actions that this model was developed to inform. To compare the consequences of scenarios, we estimated persistence probability as the proportion of iterations (out of 10,000) that did not reach a quasi-extirpation threshold of two adult breeding females during the 30-year time horizon and recorded the time to extirpation. Although this threshold is low relative to other PVA studies, at least some gopher frog populations have been observed having between two and ten breeding adults in continuously monitored wetlands across years (Semlitsch et al., 1995), and information on genetic effects from small population sizes for this species is lacking. We also estimated the percent change in adult breeding female abundance (N) as N_{30}/N_0. Percent change in abundance was -100% when the population reached the quasi-extirpation threshold. We discuss the construction of the baseline PVA model first, followed by alterations made to reflect scenarios. We performed all statistical analyses in R version 3.5.3 (R Core Team, 2019).

2.2. PVA model construction

We adapted the female-only, post-birth matrix population model developed for crawfish frogs by V. Terrell (unpublished data) to

Table 2
Scenarios varying in annual probability of reproductive success (RS scenarios) and drought frequency and duration (D scenarios), predicted persistence probabilities, median time to extirpation, and median percent change in abundance for a 30-year gopher frog (*Lithobates* [*Rana*] *capito*) population viability analysis using a stage-based, female-only matrix model.

Scenario	Short name	Drought years (of 30)[a]	Description	Persistence prob[b]	Time to extirpation (years)	Population change[c] (%)
RS20	Reproductive success probability (*rs*) = 0.2	~24	Approximately 8 drought years per decade	0.021	15	−100.0 (−100.0, −100.0)
RS30	*rs* = 0.3	~21	Approximately 7 drought years per decade	0.118	18	−100.0 (−100.0, −96.7)
RS40	*rs* = 0.4	~18	Approximately 6 drought years per decade	0.326	20	−100.0 (−100.0, −77.6)
RS50	*rs* = 0.5	~15	Approximately 5 drought years per decade	0.586	22	−92.9 (−100.0, −43.3)
RS60	*rs* = 0.6	~12	Approximately 4 drought years per decade	0.813	23	−74.6 (−100.0, 0.0)
RS70	*rs* = 0.7	~9	Approximately 3 drought years per decade	0.936	24	−48.3 (−100.0, 52.8)
RS80	*rs* = 0.8	~6	Approximately 2 drought years per decade	0.986	25	−12.9 (−84.3, 104.3)
RS90	*rs* = 0.9	~3	Approximately 1 drought year per decade	0.997	29	24.4 (−65.0, 167.7)
RS100	*rs* = 1.0	0	No drought years	1.000	–	56.7 (−38.9, 214.3)
D1	Recent historical drought (RHD)	11	Recent historical drought patterns in previous 30 years (6 droughts [1–4 years in duration] occurring between 1990 and 2019) repeat for next 30 years	0.830	24	−76.0 (−100.0, −23.9)
D2	Decreased RHD	10	Recent historical drought patterns (1990–2019) continue, with 1 fewer drought year	0.922	26	−63.2 (−100.0, 0.0)
D3	Increased RHD	13	Recent historical drought patterns (1990–2019) continue, with 2 additional drought years	0.698	21	−85.0 (−100.0, −42.3)
D4	2-year droughts	6	A 2-year drought occurs in years 1–2 of each decade	0.987	25	−4.3 (−80.0, 115.8)
D5	3-year droughts	9	A 3-year drought occurs in years 1–3 of each decade	0.894	25	−57.1 (−100.0, 23.3)
D6	2- and 3-year droughts	15	Droughts occur in years 1–3 (3–year) and 6–7 (2-year) of each decade	0.628	21	−90.7 (−100.0, −58.6)

[a] Drought years in RS scenarios were stochastically drawn from probabilities of reproductive success, so the number of drought years varied by model iteration. Drought years were deterministic in D scenarios.
[b] Persistence probability represents the proportion of model iterations where adult breeding female abundance did not fall below a quasi-extirpation threshold of two individuals.
[c] Percent change in adult breeding female abundance in year 30, relative to initial abundance. Parentheses indicate 5th and 95th percentiles of simulation outcomes.

represent dynamics realistic for a gopher frog population (Fig. 1), given the shared life history characteristics between these species. Prior amphibian studies have found age- or stage-dependent survival, maturation, and probability of breeding (Schmidt and Anholt 1999; Frétey et al., 2004; Church et al., 2007; Muths et al., 2010). Therefore, the matrix structure used in this study combined three types of demographic rates to calculate transition rates among juvenile and adult stage classes: (1) stage-specific survival rates that varied for juveniles φ_J, first-time breeding adults φ_{A1}, second-time+ breeding adults φ_{A2}, and non-breeding adults φ_{Anb}, (2) maturity probabilities representing age of maturity for juveniles (γ_{M2}, γ_{M3}), and (3) breeding state probability of breeding or not breeding (temporary emigration, representing when females skip breeding and remain in the uplands) for mature individuals in a given year (Table 1). We only made one change to the projection matrix of V. Terrell (unpublished data). They included Markovian temporary emigration and two separate estimates of probability of breeding dependent on breeding state in the previous year, but these estimates were similar (a breeder becoming a non-breeder [γ''] = 0.377, a non-breeder remaining a non-breeder [γ'] = 0.339). Therefore, we simplified our model to have random temporary emigration ($\gamma'' = \gamma'$) and included a single probability of breeding γ_B. Gopher frogs and congeners typically mature between 2 and 4 years of age (Palis, 1998; Richter and Seigel, 2002), and we used the following maturity transition probabilities: γ_{M2} – a juvenile matures at age 2; and γ_{M3} – it matures at age 3, given it did not mature previously. Note that juveniles could mature at age 4, given they had not matured previously, which was equal to $(1 - \gamma_{M2})(1 - \gamma_{M3})$. From previous amphibian studies and expert review, survival increased as individuals grew from juvenile to adult stages, survival for first-time breeding adults was lower than second-time+ breeding adults, and survival was equivalent for second-time+ breeding adults and non-breeding adults. We also assumed juvenile survival was constant in age 1 (following metamorphosis) and through the year of first breeding (between ages 2–4). Transition probabilities between juvenile and adult stage classes were governed by combinations of annual survival, maturity, and breeding transition rates. For example, the probability a juvenile survived, matured at age 2, and bred was $\varphi_J \cdot \gamma_{M2} \cdot \gamma_B$; the probability a mature adult that has bred previously survived another year and did not breed was $\varphi_{A2} \cdot (1 - \gamma_B)$.

Fecundity was zero for the tadpole, metamorph (age 1 juvenile), non-maturing juvenile, and non-breeding adult stages. In our fecundity term, we used the mean clutch size (k), assumed an annual clutch frequency (u) of 1, and assumed half of all embryos would be female (h). The fecundity term in a given year was multiplied by a stochastic reproductive state (RS: 0 or 1), as determined by the
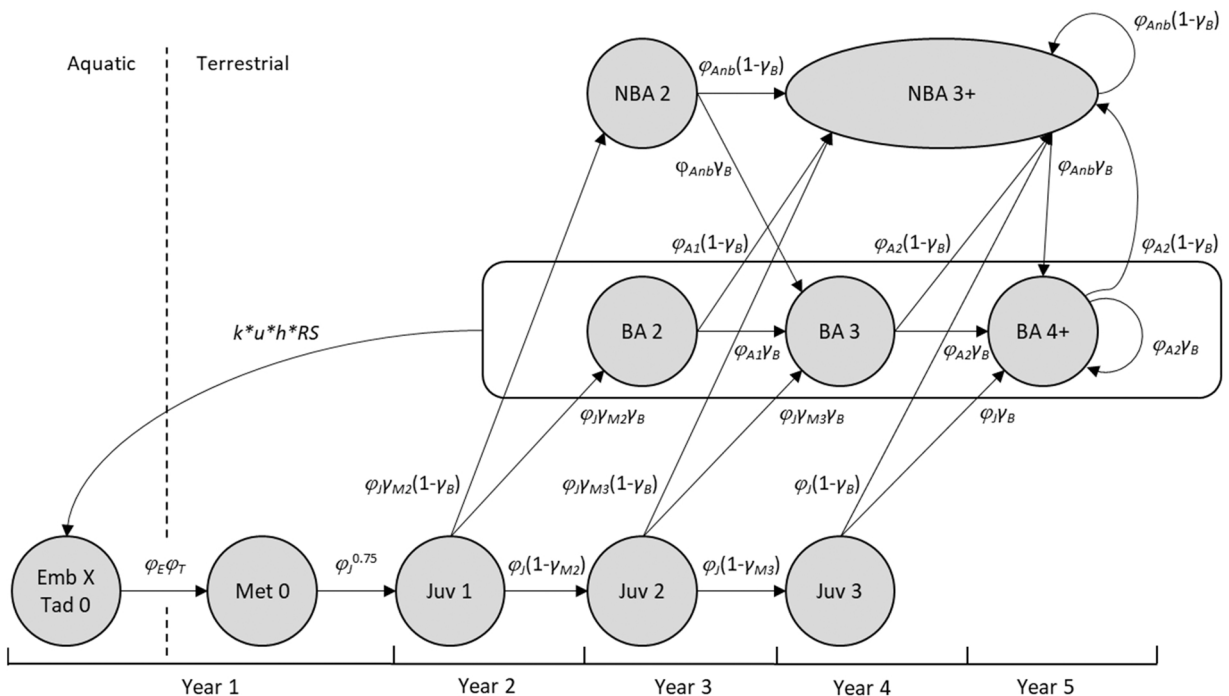

Fig. 1. Graphical depiction of a post-birth, female-only, stage-based matrix model for projecting dynamics of a gopher frog (*Lithobates* [*Rana*] *capito*) population (based on V. Terrell, unpublished data), which includes mechanisms for different ages of maturity, temporary emigration, and reproductive state (as influenced by reproductive success probability simulating seasonal drought conditions). Ovals represent life stages; symbols along arrows represent parameters. The rounded rectangle represents breeding states, where the total breeding adult abundance was multiplied by the fecundity term ($k*u*h*RS$). Life stage notations: Emb = embryos; Tad = tadpoles; Juv = juveniles; BA = breeding adults; NBA = non-breeding adults. Subscript notations: E = eggs; T = tadpoles; J = juveniles; A1 = adults (first-time breeders); A2 = adults (second+ time breeders); Anb = non-breeding adults; M2 = maturity occurs at age 2; M3 = maturity occurs at age 3; B = breeding occurs. Parameter notations: φ_E = embryo survival; φ_T = density-dependent tadpole survival; φ_J = juvenile survival; φ_{A1} = adult survival (1st time breeding); φ_{A2} = adult survival ($\geq$ 2nd time breeding); φ_{Anb} = adult survival (non-breeding); γ_{M2} = probability of maturing at age 2; γ_{M3} = probability of maturing at age 3, given not maturing at age 2; γ_B = probability of individual breeding (1 - temporary emigration); k = clutch size; u = clutch frequency; h = proportion of embryos that are female; RS = annual reproductive state (1 = success, 0 = failure), determined by reproductive success probability.

probability of reproductive success for a given scenario (see Section 2.3). The term was then multiplied by the total adult breeder abundance to calculate egg abundance in the next year. Survival through the first year was a function of egg survival φ_E, tadpole survival φ_T, and $\varphi_J{}^{0.75}$, representing surviving the remaining 9 months of the first year as a metamorph and juvenile.

To prevent projections from escalating to unrealistic abundances, we imposed a negative density-dependent effect on year-specific tadpole survival (φ_T). Density-dependent tadpole survival is well documented among amphibians and widely accepted as an important process regulating amphibian population dynamics (Vonesh and De la Cruz, 2002). Density-dependent processes during amphibian terrestrial stages has received little attention though may also be important in regulating population dynamics (Berven, 2009). There are no published studies of gopher frog tadpole survival rates; therefore, we based our tadpole survival rates on published estimates for the two most closely related species, the dusky gopher frog and the crawfish frog, that use very similar habitats for breeding. Richter and Seigel (2002) reported dusky gopher frog survival estimates from egg to metamorphs over 3 years at one site ranged from 0.00 to 0.054 (mean = 0.029), and Kinney (2011) reported tadpole survival over 5 years between two proximate wetlands ranged from 0.00 to 0.027 (mean = 0.010) and 0.00 and 0.0006 (mean = 0.0002). These tadpole survival rates were within the range reported more broadly for other congeners (Wells, 2007), though we note that a few studies have reported estimates of congeneric tadpole survival as high as 0.08. We did not include parameter stochasticity for tadpole survival; therefore, we set maximum tadpole survival at 0.025 at the lowest tadpole density and survival declined linearly with increasing tadpole density to a minimum of 0.001 at densities greater than 171,496 tadpoles female tadpoles (342,992 tadpoles total), which is the mean estimated reproduction of 200 adult breeding females under a stable stage distribution. We explored model sensitivity to a higher maximum tadpole threshold in a subsequent analysis. Experts affirmed these rates as reasonable. Preliminary model simulations with no drought years predicted stable populations fluctuating around ~80 adult breeding females per year with > 150 breeding females in some years. This pattern of breeding female density agreed with expert and stakeholder data or perception of monitored populations (multiple State agency biologists, unpublished data [see Acknowledgments]), which gave them and us confidence that our representation of tadpole survival rates and the model with density-dependence only in the tadpole stage reasonably represented dynamics for stable gopher frog populations. Additionally, model simulations with no recruitment showed < 5% of initial adult breeders survived past 8 years, in agreement with estimated longevity of congeners (6–10 years: Richter and Seigel, 2002).

The model used a 1-year time step and advanced individuals in each life stage through stochastic processes of survival, reproduction, and transition among stage classes, as well as reproductive success, using appropriate distributions (i.e., binomial, uniform) and demographic rates obtained from the literature or assumed in consultation with species experts (Table 1). Experts affirmed all demographic rates that were assumed or obtained from congener studies when gopher frog data was lacking; experts also provided population-specific adult breeding female abundance estimates from monitoring data, which we used to capture the mean and range of initial abundance. We accounted for parametric uncertainty for five parameters to which model outputs were most sensitive (see Section 3): initial abundance of adult breeding females (N), survival of metamorphs and juveniles φ_J, survival of first-time φ_{A1} and second-time+ φ_{A2} breeding adults, and survival of non-breeding adults φ_{Anb}. We drew initial abundances from a uniform distribution between 20 and 80 to capture a range of abundances expected across many currently monitored populations (multiple State agency biologists, unpublished data [see Acknowledgments]). For the four survival parameters, we drew random values each iteration from normal distributions using their mean values and a parameter-specific standard deviation that resulted in 95% of random values falling within ± 0.1 of the mean. The sampled survival parameter values for each iteration defined mean probabilities from which stochastic survival outcomes were simulated each year in the model. We kept all other rates constant across iterations and years using mean parameter values. This approach allowed us to account for uncertainty around key parameters while reducing imprecision of model predictions that enabled clearer comparison of population viability among scenarios.

2.3. Scenarios varying reproductive success and drought patterns

We implemented a mechanism in the PVA model to simulate annual population-wide reproductive success or failure due to potential catastrophic effects of drought (i.e., a population's breeding wetlands remained dry) under two sets of scenarios (Table 2). We simulated the effects of drought in both sets of scenarios by multiplying an annual reproductive state (*RS*: 1 = success, 0 = failure) by all fecundity terms so that years with reproductive failures would contribute 0 individuals that survive year 0 to be recruited into the population the next year.

In our first set of reproductive success scenarios (RS scenarios), we simulated stochastic droughts and explored the sensitivity of population outcomes to drought frequency. We created nine scenarios varying in probability of reproductive success (*rs*), which ranged from 0.2 (potential for successful recruitment every 1 of 5 years, on average) to 1.0 (potential for recruitment every year). We drew a random reproductive state each year in the model using a Bernoulli trial with these probabilities.

In our second set of drought scenarios (D scenarios), we simulated six drought patterns developed to compare population outcomes across various potential drought frequencies and durations. We assigned a deterministic series of reproductive states across years in each scenario, where the reproductive state was 0 for drought years and 1 otherwise. For each D scenario, drought patterns were deterministic, but demographic parameters could still vary as in the baseline PVA. The first drought scenario (D1) served as a status quo that assumed recent historical drought patterns would repeat over the next 30 years. We captured recent historical drought patterns using data from the U.S. Drought Monitor (Available at: https://www.drought.gov/historical-information and https://droughtmonitor.unl.edu/DmData/TimeSeries.aspx) for the Southeast Climate Region that included the gopher frog's entire range. From these time series datasets, we defined a drought year as any period greater than 6 months when more than 20% of the Southeast Climate Region was in U.S. Drought Monitor categories of "Moderate" to "Exceptional." Using these criteria, we identified six droughts

(each 1–4 years in duration) that occurred between 1990 and 2019 (11 total drought years out of 30).

The next two scenarios (D2 and D3) simulated slight decreased and increased drought conditions from D1, based on future regional climate predictions. Seager et al. (2009) assessed historic and future trends in drought using precipitation – evaporation (P-E). They found that median projections of climate models showed a ~25–33% chance of wetter conditions (P-E = 0.85 mm/day, on average) in cooler months (November–April) in the Southeast. Although gopher frog breeding can occur year-round, breeding is most common in these cooler months throughout the species' range (Enge et al., 2014; B. Crawford, unpublished data). Mean historical P-E over the period of 1950–1999 was 0.8 mm/day. Therefore, we used the ratio of mean historical P-E to number of recent historical drought years to calculate the number of drought years under the decreased drought scenario (i.e., 11 drought years in D1* [0.8/0.85] = 10 drought years in D2). We simulated reduced droughts in scenario D2 by shortening the 4-year drought in D1 by 1 year. Scenario D3 simulated increased drought conditions based on Seager et al. (2009) predictions that climate models projected a ~66–75% chance of drier conditions (P-E = 0.7 mm/day). Using the same methods from D2, we calculated 13 drought years in D3 (= 11 drought years in D1* [0.8/0.7]). We simulated increased droughts in D3 by lengthening the first 1-year drought to a 2-year drought and added a 1-year drought in the first 10 years. Different placements of the 2 additional drought years in the model time frame could have marginally changed population outcomes for this scenario, but we chose these placements to distribute drought years fairly evenly across the 30 years and also examine the effects of droughts occurring in early years when many populations may likely be small.

The final three scenarios (D4–6) simulated consistent patterns of drought each 10-year period in the model but varied the number of drought years to evaluate population resilience to multi-year drought events. In D4, we simulated 2-year droughts occurring in years 1–2 of each decade; in D5, we simulated 3-year droughts occurring in years 1–3 of each decade; and in D6, we simulated 3-year droughts occurring in years 1–3 of each decade followed by 2-year droughts occurring in years 6–7 of each decade.

2.4. Sensitivity analysis

We explored sensitivity of population persistence to variation of 11 demographic parameters (Table 1) and how sensitivity interacted with reproductive success probability (*rs*). Using *rs* values of 0.2–1.0 in turn, we first simulated baseline outcomes using
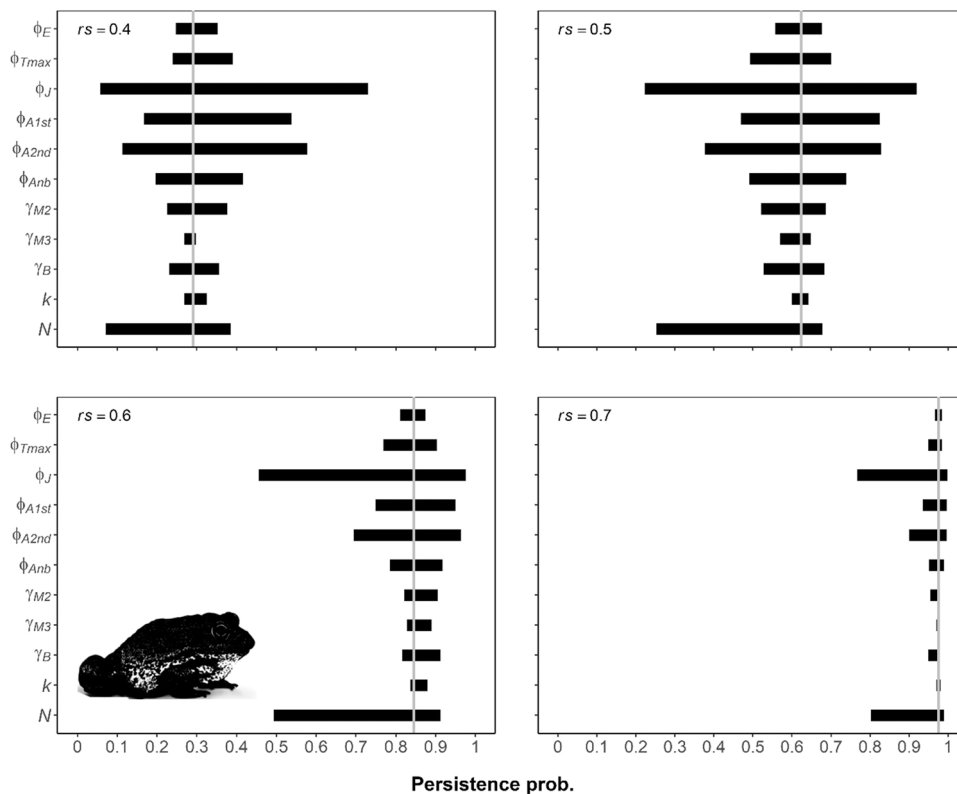
Fig. 2. Sensitivity of gopher frog (*Lithobates* [*Rana*] *capito*) population persistence probability to changes in parameter values, given different probabilities of reproductive success (*rs*), from a 30-year population viability analysis using a stage-based, female-only matrix model. Vertical grey lines indicate the persistence probability resulting from mean parameter values and each value of *rs*. Parameter notations: φ_E = embryo survival; φ_{Tmax} = maximum tadpole survival at low densities; φ_J = juvenile survival; φ_{A1st} = adult survival (1st time breeding); φ_{A2ns} = adult survival ($\geq$ 2nd time breeding); φ_{Anb} = adult survival (non-breeding); γ_{M2} = probability of maturing at age 2; γ_{M3} = probability of maturing at age 3, given not maturing at age 2; γ_B = probability of individual breeding (1 - temporary emigration); k = clutch size; N = initial abundance of adult breeding females.

mean values for all demographic parameters in the PVA model and recorded population persistence probability from 10,000 iterations (with no parametric uncertainty between iterations). Next, using each *rs* value in turn, we systematically increased and decreased baseline means of the 11 demographic parameters by values specified in Table 1 one at a time with all other parameters unaltered. We varied all survival rates with a mean of < 0.05 by 0.005 and all other survival and transition rates by 0.1. These values represented small, realistic changes to parameters (less than the standard deviation for most estimates available from the literature) and allowed for direct comparison of model outcomes. We estimated the change in population persistence probability from 10,000 runs of each model perturbation, relative to the baseline model with each *rs* probability. See Appendix A for our R code for the PVA model.

3. Results

Sensitivity analysis of the PVA model revealed that population persistence probability was highly sensitive to reproductive success (*rs*) probability, and sensitivity of model outcomes to variation in demographic rates interacted with *rs* probability. Population persistence was fairly insensitive to all demographic parameters when *rs* was ≥ 0.7 but showed greater sensitivity to varying demographic parameters as *rs* decreased (Fig. 2). At lower rates of *rs*, persistence was most sensitive to juvenile survival, followed by initial abundance of adult breeding females and adult survival for second+ and first-time breeders. Although we evaluated sensitivity using *rs* values of 0.2–1.0, we have only shown results for values between 0.4 and 0.7 in Fig. 2 to illustrate the interaction between demographic rates and *rs* probability.
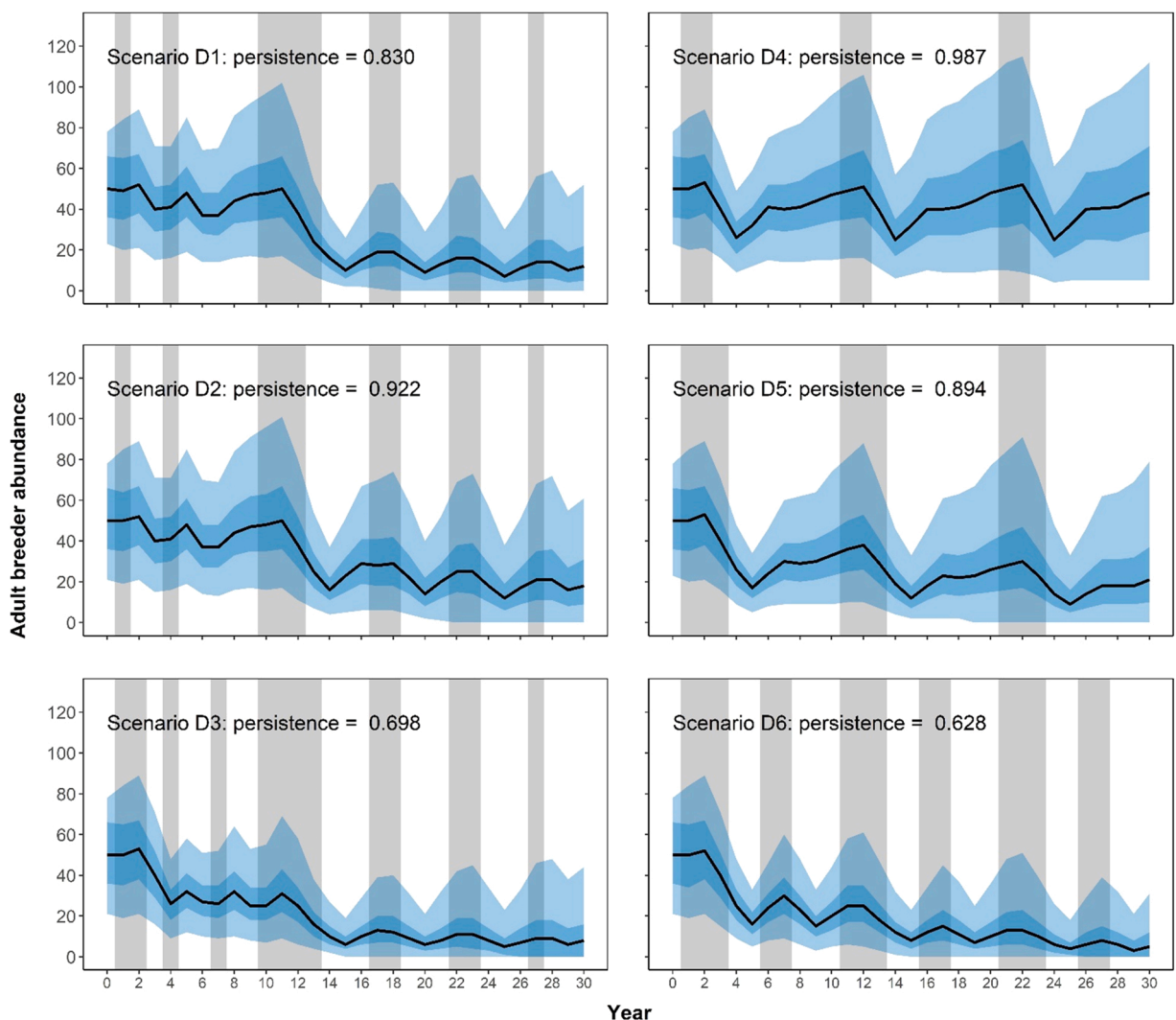

Fig. 3. Forecasted population abundance of adult breeding female gopher frogs (*Lithobates* [*Rana*] *capito*) and persistence probabilities over 30 years, given six scenarios (D1–6) varying in frequency and duration of droughts (indicated by grey panels) in the southeastern United States. Lines indicate median abundance, and confidence bands indicate the 2.5th and 97.5th (outer band) and 25th and 75th (inner band) percentiles of simulation outcomes.

The nine RS scenarios showed strong positive relationships between reproductive success and persistence probability, time to extirpation, and percent change in adult breeder abundance (Table 2). Population persistence probability was < 0.35 when there were 4 or fewer years of reproductive success per decade and > 0.95 with 8 or more years of reproductive success. The RS60 scenario (i.e., 6 or more years of reproductive success [4 or fewer years of drought] per decade) indicated threshold conditions for population persistence: this scenario resulted in populations likely persisting (persistence probability > 0.80) but declining in abundance, on average; scenarios with more drought years per decade were more likely to become extirpated and decline; scenarios with fewer drought years were more likely to persist and grow (Table 2).

Under the six D scenarios comparing specific patterns of drought durations and frequencies, persistence probabilities ranged between 0.63 and 0.99 (Table 2), and populations showed resilient patterns, where sharp declines immediately following droughts were followed by recoveries (Fig. 3). Extirpation events occurred after 10 years, usually following multi-year droughts that were preceded by additional droughts that lowered population abundance from initial values (Fig. 3). Populations would likely persist (persistence probability > 0.83) but decline under scenario D1 where recent historical drought conditions continued. Relative to D1, persistence probability was higher (0.92) in D2 where drought conditions decreased (i.e., 1 fewer drought year in the 30-year period) and was lower (0.70) in D3 where drought conditions increased (i.e., 2 more drought years). Scenarios D4–5 showed high persistence probabilities (> 0.89) where only one 2- or 3-year drought occurred per decade, but persistence probability was lowest for D6, among all drought scenarios, where both multi-year droughts occurred per decade (Table 2).

4. Discussion

Our work contributes to recent studies evaluating potential impacts of future drought conditions on viability of pond-breeding amphibian populations in a region with many at-risk amphibian species and high drought uncertainty. We also advanced previous work on gopher frogs by developing the first stage-based population model for the species using a combination of available demographic rates and expert input. This model can be improved by much-needed life history research on this species and congeners. We estimated that (i) gopher frog population persistence was highly sensitive to probability of reproductive success – representing the average frequency of annual drought events, (ii) persistence was insensitive to variation in demographic parameters when reproductive success was sufficiently frequent, and (iii) persistence probabilities varied between 0.63 and 0.99 across a range of plausible future drought scenarios, with higher persistence probabilities (> 0.89) for all scenarios where drought years did not increase from recent historical conditions. Collectively, these results indicate gopher frog populations are likely resilient to periodic droughts that occur in 4 or fewer years per decade, but extirpation of some populations is possible if recent drought patterns repeat or increase during the next 30 years.

Similar to our results, studies of gopher frogs and other pond-breeding amphibians have also predicted that long-term population outcomes were highly sensitive to current and future droughts via changes in recruitment opportunities (Cayuela et al., 2016; Greenberg et al., 2015; McCaffery et al., 2014; Scheele et al., 2016; Walls et al., 2013b). Scenarios used in our PVA revealed that populations were very likely to persist (persistence probability > 0.90) and grow with 7 or more years of reproductive success (i.e., 3 or fewer years of drought) per decade; populations were likely to persist (persistence probability > 0.80) but decline with 4 drought years per decade; and populations were less likely to persist with 5 or more drought years per decade. In a previous study, we found dynamic breeding patterns of gopher frog populations over 10 years where periods of lower probability of successful breeding and recruitment due to drier conditions were often followed and offset by episodic breeding booms in seasons with local, high rainfall events such as hurricanes (B. Crawford, unpublished data). That study estimated a mean annual probability of reproductive success of 0.68 across 67 populations, which would translate to a high persistence probability (0.81–0.94) for the average population (Table 2). The results from our previous and current work corroborate other studies suggesting that pond-breeding amphibian populations can tolerate some degree of periodic recruitment failure due to drought (Davis et al., 2019; Greenberg, 2001; Semlitsch, 2003; Semlitsch et al., 1995; Wilbur and Rudolf, 2006). We also found that population persistence was most sensitive to juvenile survival, especially with lower probabilities of reproductive success, indicating high juvenile (as well as adult) survival may help sustain populations through periods of recruitment failure. These findings agree with those from the crawfish frog PVA on which our model was based (V. Terrell, unpublished data), as well as studies of other pond-breeding anuran species (e.g., Biek et al., 2002; Davis et al., 2019; Taylor et al., 2006).

In the Southeast, future precipitation and drought patterns are uncertain but will likely restrict successful breeding opportunities for gopher frogs and other pond-breeding amphibians. This can be seen when comparing the three drought scenarios D1, D2, and D3 (the most likely scenario), which were developed from recent historical drought patterns and future climate projections. Seager et al. (2009) predicted that precipitation and evaporation will both increase through 2099, but drought conditions (using precipitation – evaporation) had a ~25–33% chance of decreasing (D2) and a ~66–75% chance of increasing (D3). Scenarios D1–3 indicated that recent drought conditions repeating, decreasing, or increasing would all result in population declines, on average, and persistence probability was substantially lower (0.70) in D3 than D1 or D2. Interestingly, Seager et al. (2009) also predicted that future precipitation may follow cyclical patterns that produce multi-year periods of drought. All six drought scenarios demonstrated patterns of steep population declines following multi-year drought events, with longer-term persistence influenced by the duration of drought events. We note that we used deterministic drought patterns in scenarios D1–6 that likely will not represent future conditions exactly. However, persistence probabilities differed by ≤ 0.04 between scenarios with random vs. deterministic drought patterns that had the same number of drought years (e.g., 12 drought years in RS70 and D5; 15 drought years in RS50 and D6: Table 2), which shows that these results are robust to variation in specific drought patterns. The potential impact of different drought durations can be seen when comparing scenarios D4 and D5: populations generally recovered and grew to initial abundances after 2-year droughts but declined to low abundances and more often became extirpated after 3-year droughts (Fig. 3). Greenberg et al. (2015) found that forecasted

drought conditions in central Florida that would reduce ephemeral wetland hydroperiods and result in recruitment failure for gopher frogs often spanned several, consecutive years. Collectively, the results from this and previous studies indicate that populations of gopher frogs and other pond-breeding amphibians – especially those at low abundances – face increased risk of extirpation if drought frequency and/or durations increase from recent conditions.

Multiple studies have demonstrated the usefulness of constructing PVAs as a transparent, initial approach for evaluating risk when conservation decisions are needed (Akçakaya and Sjögren-Gulve, 2000; Beissinger and Westphal, 1998; McGowan et al., 2017; Morris et al., 2002). Still, our PVA had limitations that should be considered when interpreting the results. Although gopher frogs are typically believed to exist in metapopulations of connected wetlands and uplands (Greenberg, 2001; Humphries and Sisson, 2012; Palis, 1998; Semlitsch et al., 1995), we simplified our PVA to use a stage-based population model that did not include mechanisms typical of metapopulation models (e.g., subpopulation-specific movement rates). No study has estimated per-capita movement rates among connected wetlands within a gopher frog metapopulation, but future research using mark-recapture or count data across known, connected breeding wetlands would inform the development of more realistic metapopulation models for this and related species. Our PVA framework made the related assumption that drought events caused total recruitment failure across the entire population (i.e., recruitment did not occur at any wetland that year). Monitoring efforts of gopher frog populations have documented recent years where all known breeding wetlands did not fill or retain water and no recruitment was observed (B. Crawford, unpublished data). Still, the relationship between drought conditions and likelihood of total recruitment failure can be evaluated with further research, which could also explore the degree that the number and hydroperiod variation (i.e., short, ephemeral to long, semi-permanent) of wetlands in a population can facilitate recruitment success even in drought years (see Davis et al., 2019; Greenberg et al., 2015). Based on feedback from experts who regularly monitor gopher frog populations, our model structure, assumptions, and predictions reasonably captured population dynamics for sites with a single known breeding wetland (at least 63 of 150 known gopher frog populations) or sites where all breeding wetland hydroperiods are relatively synchronized and would respond similarly within the same year to the same drought conditions. Sites with multiple breeding wetlands with more variable hydroperiods, including at least one breeding water body that is permanent or semi-permanent, might allow for recruitment during drought years, and we would expect increased persistence probabilities for those sites than our model currently predicts. However, we note that more permanent water bodies often support competitor and predator (e.g., fish) populations that often dramatically reduce gopher frog and other amphibian recruitment (e.g., Gregoire and Gunzburger, 2008).

We note that we used a quasi-extirpation threshold of two breeding adult females, which may appear low relative to PVAs of other taxa. A low quasi-extirpation threshold could cause an underestimation of extirpation and extinction risk, which would be a reasonable concern for rare or declining species that are high conservation priorities. However, in the case of many pond-breeding amphibians, it may be the case that any quasi-extirpation threshold requiring even one breeding female in every year is unrealistic and could lead to overestimation of extirpation. Experts who monitor gopher frog populations report it is common among small populations to have one or more consecutive years without detectable breeding by any adults before breeding resumes. These are often isolated populations where local extirpation followed by rescue from neighboring populations cannot explain the gap and subsequent restoration of breeding. Rather, this pattern likely reflects the fact that it is common for adult amphibians to skip breeding years (e.g., Cayuela et al., 2014; Muths et al., 2013) and that there was recruitment of breeding adults from juveniles that were produced several years earlier. For our model, we know that some populations were considered extirpated because fewer than two females bred in one year even though there were still non-breeding adult females and juveniles in the population that might have bred in a subsequent year. We could have removed the quasi-extirpation threshold, but that would be inconsistent with general practice. Alternatively, we could have required the quasi-extirpation threshold to be met across multiple consecutive years; however, without data on minimum viable population sizes or the relationship between breeding frequency and extirpation, the choice of a quasi-extirpation threshold is arbitrary, and it is more important to understand how this decision may affect extirpation estimates.

Estimates for many demographic rates for gopher frogs were lacking or uncertain, so we used rates from congeners with similar ecology and life histories (i.e., crawfish frogs and dusky gopher frogs) when available in consultation with experts. Using estimates from related species or expert judgment is typical in PVAs for data-limited species of conservation concern (Beissinger and Westphal, 1998; Johnson et al., 2017; Tucker et al., 2020; Wade, 2002), but careful consideration is warranted when selecting rates from ecologically-relevant species and eliciting estimates from experts (Martin et al., 2012) to reduce bias in uncertain parameters and model predictions. Ideally, these proxy rates can be replaced with those from the focal species in future PVAs as demographic studies provide improved estimates. It is also recommended to reduce bias in PVA models by accounting for uncertainty around demographic estimates (parametric uncertainty) as well as year-to-year environmental variation (stochasticity: McGowan et al., 2011; Moore et al., 2012; Wade, 2002). We included stochasticity around annual survival and transition outcomes but did not account for the uncertainty around every demographic rate, most notably tadpole survival. Instead, we used results from sensitivity analyses to include parametric uncertainty around the five demographic rates to which outcomes were most sensitive. This approach seems reasonable to achieve a balance between accounting for the most influential sources of uncertainty while reducing imprecision of model predictions that enabled easier comparison among scenarios.

PVAs like the one used in this study are an effective means for capturing uncertainty and comparing direct metrics of species risk (i. e., persistence probability) across plausible scenarios varying in stressors and management. This information can be particularly useful for many conservation decisions, including site-level management actions, allocating resources across populations, and designating species' statuses for protection (McGowan et al., 2017; Morris et al., 2002; Smith et al., 2018). Given the sensitivity of gopher frog population persistence to periodic drought events, maintaining multiple, connected breeding wetlands with a range of hydroperiods (i. e., short, ephemeral to long, semi-permanent) at a site may avoid total recruitment failure in most drought conditions and reduce the risk of population extirpation (Davis et al., 2019; Greenberg et al., 2015). Previous studies have found evidence that maintaining

open-canopied wetlands (e.g., through mechanical tree removal or prescribed fire in wetland basins and on wetland peripheries) and suitable upland habitat may mitigate effects of drought by reducing water loss to vegetation and maintaining hydroperiods sufficient for tadpole development (Greenberg, 2001) and successful recruitment (Chandler et al., 2017; Jones et al., 2018; Simpson et al., 2021). Additionally, improving upland suitability through prescribed fire (especially during summer when frog surface activity is lowest) and other habitat management actions is expected to increase gopher frog survival in terrestrial (i.e., juvenile and adult) stages (Humphries and Sisson, 2012; Roznik et al., 2009), to which population persistence was highly sensitive. However, we emphasize additional research is needed to estimate demographic rates for gopher frogs – especially juvenile and adult survival stages – that could improve the accuracy of further predictions from PVA models and subsequent conservation decisions. This work precedes research that will use the PVA model to evaluate the effects of site-specific stressors and management alternatives on population persistence as part of a range-wide conservation planning framework for the gopher frog. Using a PVA approach will provide rigorous predictions of gopher frog population persistence that capture risk and can inform State, Federal, and other partners when taking site-level management actions and allocating resources across multiple gopher frog sites in their jurisdictions. More broadly, these results can inform forthcoming status assessments and designation decisions of the USFWS.

Declaration of Competing Interest

Acknowledgments

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02119.

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