Breeding Population Dynamics of Threatened Crawfish Frogs Inform Targets for Habitat Management

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We used data from a five-year study at two focal breeding wetlands of a single Crawfish Frog (*Rana areolata*) population to demonstrate the relative importance and potential of tadpole survival as a target for population management. We concurrently estimated 11 vital rates in the field and used a females-only matrix projection model to estimate elasticities of demographic rates. We then simulated stochastic population dynamics at each wetland with and without immigration to estimate the intrinsic capacity for each focal breeding wetland to sustain a Crawfish Frog breeding population and the likelihood of breeding population persistence at each wetland. Elasticity of tadpole survival was second only to juvenile survival elasticity and 1.34–2.04 times greater than adult survival elasticity. Projections indicated that the Crawfish Frog population was not at risk of extinction but only one breeding site was capable of self-sustaining a breeding population. Because of low tadpole survival, the other breeding site was completely dependent on immigration to persist and was functioning as a population sink. Despite higher variability compared to terrestrial vital rates, larval survival did have a strong effect on population growth. Tadpole survival at the more productive breeding site was density dependent and likely related to wetland vegetation and predator and competitor abundance. Two additional findings were that annual survival of frogs following their first known breeding event was 48% lower compared to survival of frogs that had bred in two or more prior years, and adult temporary emigration from the breeding population was moderately high. Our study demonstrates the benefits of using population models that integrate density-dependent processes, temporary emigration from the breeding population, and state-specific adult survival, to identify larval habitats that function as population sinks and limit current population size and persistence probability. We contend that tadpole survival is an important and feasible habitat management target within broader conservation strategies for Crawfish Frogs and other amphibian species.

AMPHIBIANS are recognized as model species with complex life cycles dependent on multiple, complementary habitats. An estimated 60–80% of amphibians worldwide, including most native North American anurans, breed in lentic habitats such as ponds or wetlands but grow, forage, and overwinter as juveniles and adults in terrestrial habitats (Semlitsch, 2003). While ecologists understand the interaction between and dual importance of aquatic and terrestrial stages, limited resources or competing priorities often constrain comprehensive management of amphibian populations. Constraints create a need to prioritize actions, which has driven investigations into those life stages for which population growth is most responsive and would make the most efficient targets for management (e.g., Biek et al., 2002).

There is a substantial body of research that provides a general theoretical understanding of North American pond-breeding amphibian population dynamics (reviewed by Semlitsch, 2003). In short, many species are dependent on isolated, open-canopy wetlands with short to intermediate hydroperiods. High primary production and periods with few predators and low competition within these wetlands increases the production of large-sized juveniles, resulting in episodic booms in population growth (Semlitsch, 2003). However, the variable hydroperiod and community composition of isolated wetlands lead to highly variable larval success including frequent catastrophic larval mortality (Pechmann et al., 1989; Taylor et al., 2006); therefore, adult and juvenile survival is important for sustaining populations through periods of larval failure.

Typically, evaluations of the relative importance of amphibian life stages and vital rates to population growth are aided by the use of matrix population projection models and elasticity and sensitivity analyses (Mills, 2007). The models are used to evaluate which life stages and associated vital rates are most likely to affect population growth and be targets for population restoration (e.g., Biek et al., 2002). However, informing management actions also requires determining which life stages and vital rates are sufficiently variable and responsive to management (de Kroon et al., 2000; Manlik et al., 2018). Prior studies have found that amphibian population growth appears more sensitive to

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changes in terrestrial survival, particularly among adults (Taylor and Scott, 1997; Biek et al., 2002; Schmidt et al., 2005; Trenham and Shaffer, 2005; Taylor et al., 2006; Kissel et al., 2014), while other studies have found population growth is most responsive to factors affecting larval survival or larval carry-over effects on juvenile survival and age or size at first reproduction (Berven, 1990, 1995; Biek et al., 2002; Altwegg, 2003; Altwegg and Reyer, 2003; Govindarajulu et al., 2005; Matthews et al., 2013). Even in cases where elasticities of population growth are higher among terrestrial stages, low and highly variable larval survival may have large effects on population growth and may be an important and effective target for management (Biek et al., 2002).

The objectives of our study were to (1) simultaneously estimate embryonic, larval, juvenile, and adult survival, age at first reproduction, fecundity, and temporary immigration and emigration from the breeding population at two wetlands used by a Crawfish Frog (*Rana areolata*) population within a managed landscape, (2) estimate the relative importance of aquatic and terrestrial stages to population growth (λ), and (3) model the dynamics and probability of breeding population persistence at each site intrinsically (without immigration from other breeding sites) and with immigration. Crawfish Frogs are one of four species within the *Nenirana*, which includes Gopher Frogs (*R. capito*) and Dusky Gopher Frogs (*R. sevosa*), that are high priority species for management due to range-wide population declines (Jensen and Richter, 2005; Parris and Redmer, 2005; Richter and Jensen, 2005; Thurgate and Pechmann, 2007; Engbrecht and Lannoo, 2010; IUCN, 2011). The loss and degradation of isolated wetlands and suitable terrestrial habitats from agricultural and mining activities (Lannoo et al., 2009), urban and exurban development, fire suppression (Enge et al., 2014), pollution, and disease (Kinney et al., 2011) are identified as contributing factors to the endangerment of species of *Nenirana*. A common habit of *Nenirana* is their strong dependence on the terrestrial burrows of other animal species or stump holes for post-metamorphic survival (e.g., see references in Smith et al., 2021). For example, Crawfish Frogs are obligate inhabitants of terrestrial crayfish burrows (Thompson, 1915; Heemeyer and Lannoo, 2012; Heemeyer et al., 2012). For this reason, conservation efforts for Crawfish Frogs and other *Nenirana* often focus on the restoration and management of terrestrial habitats, particularly for the keystone species or ecosystem engineers upon which these frogs and other wildlife depend. There have been no evaluations of the potential importance of aquatic habitat management to Crawfish Frog population growth, and information on most stage-specific vital rates are limited (Wright and Myers, 1927; Bragg, 1953; Parris and Semlitsch, 1998; Redmer, 2000; Parris and Redmer, 2005; Kinney, 2011).

MATERIALS AND METHODS

Study site

Our field site was located on the western portion of Hillenbrand Fish and Wildlife Area (HFWA-W) in Greene County, Indiana. HFWA-W comprises 729 hectares of what was historically eastern deciduous forest containing scattered pocket prairies converted to agricultural fields prior to being surface mined for coal (described in detail in Lannoo et al., 2009, 2017). Following post-mining soil re-contouring and

vegetative recovery, HFWA-W was purchased by the state as a fish and wildlife area and is currently managed by the Indiana Department of Natural Resources' (IDNR) Division of Fish and Wildlife. HFWA-W contains several bodies of water ranging from ephemeral wetlands through seasonal and semi-permanent wetlands to large final-cut lakes. Terrestrial habitats are managed as native grassland using prescribed burns, tree removal, and herbicide application (Lannoo et al., 2009). More detailed descriptions of habitat structure are available in Heemeyer et al. (2012) and Terrell et al. (2014). The source population for Crawfish Frog recolonization of HFWA-W is not known. The entire area surrounding the study site is private agricultural lands. The closest known population is 5 km away from the study site. It is also not known whether there are or were more proximate populations.

This study was part of a larger, longer-term study of a single Crawfish Frog population that breeds among eight wetlands that vary in hydroperiod and vegetation (Lannoo et al., 2009, 2017; Heemeyer et al., 2012; Nunziata et al., 2013; Terrell et al., 2014; Stiles et al., 2020). The focus of this study was Crawfish Frog breeding population dynamics between 2009 and 2013 at two wetlands (Nate's Pond and Cattail Pond) where a large portion of the adult Crawfish Frogs were known to breed and where we could logistically install complete drift fences. Crawfish Frog breeding events at five of the other ponds on site were generally small and irregular, and the sixth pond was too large for monitoring as part of this study. There may be additional breeding sites that were not yet known at the time of this study. Observations of juvenile and adult dispersal from Nate's Pond and adult movements among all wetlands began in 2012 and are summarized by Lannoo et al. (2017).

Though proximate to one another (0.9 km), there were significant differences in vegetation between the two focal breeding wetlands. Cattail Pond was dominated by invasive hybrid cattails (*Typha* x *glauca*) throughout the duration of our study. Nate's Pond was dominated by bulrushes (*Scirpus* spp.); however, by the fall of 2012, woody vegetation including willows (*Salix* spp.), Eastern Cottonwoods (*Populus deltoides*), raspberries (*Rubus* spp.), and invasive Amur Honeysuckle (*Lonicera maackii*) had encroached Nate's Pond from the upland and was subsequently removed. In 2013, invasive hybrid cattails rapidly increased within a portion of Nate's Pond and were removed. Both ponds typically filled in winter. Nate's Pond generally dried by August, and Cattail Pond generally dried by late fall, though it did hold water through one winter into the next breeding season during our study. The relative abundances of other amphibians varied among sites and years (Lannoo et al., 2009; Kinney et al., 2010; Kinney, 2011; Terrell et al., 2014). Small-Mouthed (*Ambystoma texanum*) and Marbled Salamanders (*A. opacum*) and Southern Leopard Frogs (*Rana sphenocephala*) were abundant in some years at both Nate's and Cattail Pond (Lannoo et al., 2009; Terrell et al., 2014). There was concurrent upland management on site during our study. Food plots were present in 2009 and 2010, but abandoned after, and in 2011 the DNR instituted a no-plow policy. The area around Nate's Pond was burned in the early spring of 2010 and 2015, which might have reduced female migration to breeding sites (Engbrecht and Lannoo, 2012; Lannoo et al., 2017).

Field methods

In 2009, we enclosed Nate's and Cattail Ponds with 270 and 280 m, respectively, of 1 m tall woven polypropylene composite or monofilament fabric buried 10–15 cm below ground and 5 m from the wetland edge with support stakes every 5 m and hardware cloth instead of fabric in sections along drainage areas (see also Heemeyer et al., 2010; Lannoo et al., 2017). We installed 25 and 26 pairs of pitfall traps, respectively, made from 15 L white square buckets placed every 10 m along the inside and outside of the fencing. Buckets were covered with a half lid (open side closest to the fence) to provide shade for trapped animals and deter predators, and contained an aged, wetted sponge to help prevent desiccation of animals during dry periods and serve as a floating substrate when buckets flooded. We placed a wooden stake in each bucket so small mammals could escape. We opened pitfall traps from 5 March–16 October (2009), 1 March–19 August (2010), 23 February–11 August (2011), 27 February–6 July (2012), and 15 March–12 August (2013). We checked pitfall traps minimally once daily—immediately after sunrise—and repeatedly during warm rainy nights when Crawfish Frogs migrated. For logistical reasons, from 2014–2016 pitfall traps were only open during spring immigration of adults to the breeding sites but were not to monitor adult emigration from breeding sites or to capture emerging juveniles in the summer. No juveniles were marked after 2013. Therefore, we only used data from 2009–2013 to estimate larval and adult survival, but we were able to use data from 2009–2016 to estimate juvenile survival to first breeding. We also use data presented by Lannoo et al. (2017) and Lannoo (unpubl. data) to summarize the number of presumed new, non-natal immigrants between 2012 and 2015 when immigrant status could reasonably be assigned to breeding adults.

Captured frogs were weighed to the nearest 0.1 g (Pesola® spring scale), measured (snout–vent length [SVL]; mm), and sexed (adults). We marked individual adults by inserting a Passive Integrated Transponder (PIT) tag subcutaneously (Christy, 1996); from 2009–2011 adults were also marked with a toe-clip indicating the first year they were known to have bred (Richter and Seigel, 2002). We marked emigrating metamorphic frogs using cohort-specific toe clips indicating their natal pond and year they metamorphosed. We saw no evidence of partially regenerated toes on recaptured adult frogs and the toe-clips we did observe were unambiguous.

Field estimation of vital rates

Female fecundity and embryonic and larval survival.—Throughout the breeding seasons in 2010 and 2011, we surveyed wetlands for Crawfish Frog egg masses. New egg masses were flagged and monitored daily to determine whether any egg masses failed to hatch. In 2010, we haphazardly selected five egg masses that had fully hatched and counted the number of embryos that failed to hatch. To estimate the number of eggs deposited each year in each pond, we estimated the clutch size for each spent female captured using published relationships between female SVL and mean clutch size (Redmer, 2000; equation: clutch size = –10,974.3 + 172.4 × SVL). We then summed those estimated clutch sizes to determine the number of eggs deposited. We divided the mean number of eggs that failed to hatch by the mean estimated clutch size in 2010 to estimate embryonic

mortality (Richter et al., 2003). We multiplied the estimated embryonic survival by the estimated total number of eggs deposited to estimate the number of tadpoles input into each pond each year. To estimate tadpole survival, we divided the number of metamorphs captured emigrating at the drift fence by the estimated number of tadpoles in each pond each year.

Juvenile survival and age at first reproduction.—We used the following approach to estimate mean annual juvenile survival. Because of low numbers of metamorphs at Cattail Pond, juvenile survival is only based on data from metamorphs at Nate's Pond. Based on other studies that measured sex ratios of ranid metamorphs (Berven, 1990), we assumed half the estimated number of metamorphs within a cohort were female. Juvenile mortality is likely highest in the days or weeks immediately post-metamorphosis; however, because the juvenile life stage of amphibians is generally latent, for estimation purposes, we had to assume that juvenile annual survival (Φ) was constant with age. Crawfish Frogs typically mature between 2 and 4 years of age, and mean age at maturity can differ between sexes and be variable among years. Therefore, we estimated the probability, p, that a juvenile would mature at age 2 and the probability, q, that if a juvenile did not mature at age 2, it would mature at age 3. Therefore the probability a juvenile would first breed age at 3 was $((1-p) \cdot q)$ and at age 4+ was $((1-p) \cdot (1-q))$. Using these probability statements, we used the estimated number of metamorphs (x) to predict the number of individuals (y) we would expect to capture as adults breeding for the first time at age (y_i) for each yearly cohort:

$$y_2 = x \cdot p \cdot \Phi^{1.75}$$

$$y_3 = x \cdot (1 - p) \cdot q \cdot \Phi^{2.75}$$

$$y_4 = x \cdot (1 - p) \cdot (1 - q) \cdot \Phi^{3.75}$$

From a related study, we know that some juveniles disperse to other wetlands before breeding the first time (Lannoo et al., 2017), and we needed to account for this dispersal in our estimate of juvenile survival; however, we lacked a means to estimate that rate directly. Lannoo et al. (2017) reported that between 2012 and 2016, 28.1% of juveniles born at Nate's Pond were observed breeding at other sites. This is a minimum "estimate" of dispersal rate with no measure of uncertainty or variability and which does not account for imperfect detection due to incomplete and inconsistent sampling and the use of other techniques (minnow traps) at other wetlands. We believe it is most likely that dispersal occurs as an adult during the animal's first breeding event. Therefore, we used our estimates of temporary breeding emigration (see next section on *Adult survival and temporary emigration*), which was greater than but not too dissimilar to the dispersal rate of Lannoo et al. (2017), as a proxy for adult breeding dispersal to estimate the number of juveniles that likely survived to breed at any site based on the number known to have survived and returned to breed at their natal site. We provided both the observed and estimated likely number of juveniles that survived to breed (Supplemental Table S1; see Data Accessibility). We used the *GRG Nonlinear Solver* function in Excel (v 15.24, ©2016, Microsoft Corpo-

ration) to determine the most likely values of Φ, p, and q that minimized the sum of the squared differences between the estimated likely number of individuals we captured breeding for the first time and the predicted number of individuals. This is analogous to a maximum likelihood approach without assuming a probability distribution of residuals. We generated estimates for males and females for each yearly cohort of metamorphs. Because of the large differences in the number of metamorphs in the 2009 cohort compared to the 2010 and 2011 cohorts, we used weighted means for p, q, and Φ for parameterizing our population models.

Adult survival and temporary emigration.—We used a robust capture–mark–recapture design to estimate survival and temporary emigration among adult breeding classes (Kendall et al., 1997). We defined temporary emigration as the probability an individual was alive but did not breed at the focal wetland and therefore was not available to be sampled. The robust design assumes populations are open between primary periods (years in this study) and closed between secondary periods, which we considered the entry and exit events during the breeding period within each year. While breeding season duration could last for several weeks, individual females and males only remained at the site for an average of 8 ($\pm$ 8 = 1 SD) and 18 ($\pm$ 10) days, respectively (Kinney, 2011). While it is possible that there were some deaths while breeding, our capture data of spent females exiting the wetland relative to the number that entered the wetland indicated that this was negligible (Supplemental Table S2; see Data Accessibility) and the assumption of closure during the secondary events was reasonable.

We developed multiple Robust Design models in the rMark package (Laake, 2013) in Program R version 3.5.3 (R Core Team, 2019), and we assessed the fit of each candidate model using Akaike's Information Criteria (AIC; Akaike, 1973) with adjustment for small-sample bias (AIC$_c$; Hurvich and Tsai, 1989). We used Akaike weights (w_i) to compare the relative fit of each candidate model (Burnham and Anderson, 2002). We performed multi-model inference using AIC$_c$ in three stages that separately examined potential effects on 1) capture and recapture, 2) survival, and 3) temporary emigration parameters most supported by our data. For each stage, we tested candidate models where the parameter in question varied while all others were held constant, and the effects for a parameter supported by the top-ranked model in one stage were retained for that parameter in every model in subsequent stages. In the first stage, we specified four models where capture (p) and recapture (c) rates varied by between immigrating and emigrating from the wetland and year or were constant. We originally included models with separate effects for p and c, but any model of this kind yielded unreliable estimates, likely because of overparameterization. Therefore, we set p and c equal in all candidate models and tested year- and time-specific effects on capture probability. In the second stage, we specified seven candidate models to explore the individual and additive effects of breeding site, sex, year, and a dichotomous breeding status variable on survival. Because breeding is a risky and a highly energetically demanding event and first-time breeders are generally smaller than animals known to have bred previously, we hypothesized that survival rate was lower following first breeding. We specified an individual's known status each year if it was captured for the first time as a breeding adult or

if it was known to have bred previously. In the third and final stage, we specified four models where temporary emigration parameters varied by year or were constant. We included models where temporary emigration was treated as Markovian and represented by two parameters (γ'' and γ') used to estimate the probabilities that an individual emigrated out of the breeding population in a year or, if already emigrated, remained out of the breeding population that year. We also specified temporary random emigration ($\gamma' = \gamma''$) in candidate models while specifying different time-specific effects between models. We performed model averaging of the third set of candidate models to obtain final estimates where parameters were rescaled based on the Akaike weights of their models as described by Burnham and Anderson (2002).

Population modeling and analyses

Projection model and elasticity and sensitivity analysis.—We used our field-based estimates of 11 vital rates to parameterize a females-only, post-birth projection matrix with an annual projection interval (Lefkovitch, 1965; Caswell, 2001; Biek et al., 2002; Mills, 2007; Fig. 1). Because prior amphibian studies and our own results showed age or state-dependent survival, maturation, and probability of breeding (Schmidt and Anholt, 1999; Frétey et al., 2004; Church et al., 2007; Muths et al., 2010), our matrix structure retained juveniles and adults in age and breeding status-specific classes (first-time vs. repeated breeder, breeder vs. non-breeder [aka, "temporary emigrant"]; Fig. 1). The matrix contained 21 unique, non-zero transition probabilities and nine non-zero fecundity terms based on unique combinations of the 11 estimated vital rates with many vital rates shared among stages. For example, we used the same stochastic temporary emigration and reimmigration rates for all adult stages regardless of age or prior breeding status, and adult survival rates for first-time or repeat breeders were assumed to be the same for breeders and emigrants within the same year. Fecundity was zero for the tadpole, juvenile, and emigrant stages. In our fecundity term, we used the mean clutch size, and we assumed half of all embryos would be female and that survival rates were not different for female and male embryos. We also assumed terrestrial stage vital rates were density independent among years. All estimated vital rates used in our models are listed in Table 1. We did not have data on the sources of immigrants, or whether their larval, juvenile, or adult survival or dispersal rates differ from our frogs at our focal wetlands. Therefore, we would have had to assume that those rates were the same among immigrants and natal frogs and the inclusion of an immigrant life stage would have no effect on our estimates of elasticities. We did include immigrants in our *Stochastic population projections* (see next section). We calculated the elasticities and sensitivities of mean vital rates following Caswell (2001) using the package 'popbio' (Stubben and Milligan, 2007) in R (R Core Team, 2019). Importantly, the elasticity and sensitivity estimates from this analysis are proportional and, therefore, subject to misinterpretation about the relative importance of vital rates that differ greatly in scale (e.g., fecundity v. adult survival v. tadpole survival) and natural variability (Manlik et al., 2018). To address this, for each vital rate, we plotted the percent change in λ only across the range of natural variation we observed or estimated for that vital rate, and we used that to guide our inferences related to how vital rates affected

A   Crawfish Frog, post-birth, females-only stage model to accommodate age or state-specific transition probabilities within stages and individuals that skip reproduction or emigrate to breed at other sites.
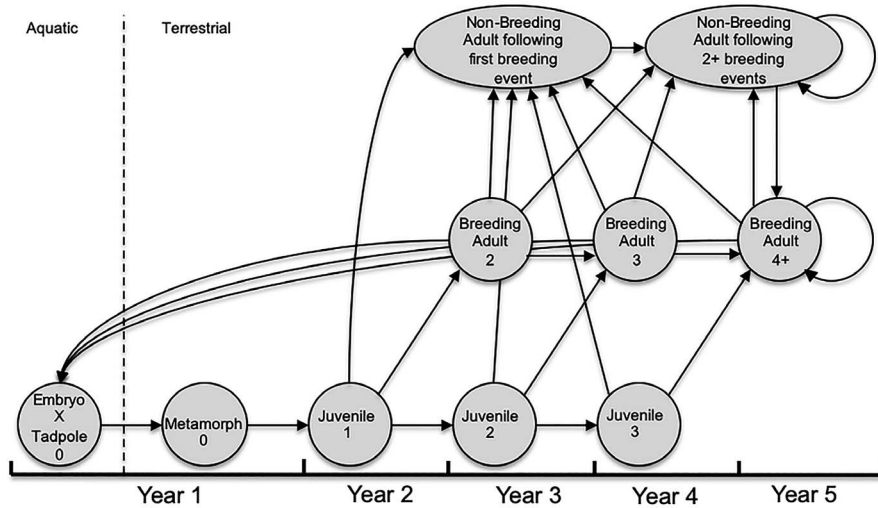
B   Crawfish Frog female population projection matrix.

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          Year 1        Year 2              Year 3                                        Year 4/5+
            0        [Sⱼ·p·(1-γ″)·C]  [Sⱼ·q·(1-γ″)·C]  [Sₐ₁·p·(1-γ″)·C]  [Sₐ₁·p·(1-γ)·C]   [Sⱼ·(1-γ″)·C]  [Sₐ₁·(1-γ″)·C]  [Sₐ₁·(1-γ″)·C]  [Sₐ₁·(1-γ)·C]  [Sₐ₂·(1-γ)·C]
 [Sₑ·Sₜ·Sⱼ^0.75]       0                0                0                0                0              0              0              0              0
      0          [Sⱼ·(1-p)]            0                0                0                0              0              0              0              0
      0          [Sⱼ·p·(1-γ″)]         0                0                0                0              0              0              0              0
      0          [Sⱼ·p·γ″]             0                0                0                0              0              0              0              0
      0             0            [Sⱼ·(1-q)]             0                0                0              0              0              0              0
      0             0            [Sⱼ·q·(1-γ″)]          0                0                0              0              0              0              0
      0             0                0          [Sₐ₁·(1-γ″)]      [Sₐ₁·(1-γ)]            0              0              0              0              0
      0             0            [Sⱼ·q·γ″]              0                0                0              0              0              0              0
      0             0                0          [Sₐ₁·γ″]          [Sₐ₁·γ]               0              0              0              0              0
      0             0                0                0                0          [Sⱼ·(1-γ″)]    [Sₐ₁·(1-γ″)]   [Sₐ₂·(1-γ″)]   [Sₐ₁·(1-γ″)]   [Sₐ₂·(1-γ″)]
      0             0                0                0                0          [Sⱼ·γ″]            0              0              0              0
      0             0                0                0                0              0        [Sₐ₁·γ″]       [Sₐ₂·γ″]       [Sₐ₁·γ]        [Sₐ₂·γ]
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Fig. 1. (A) Post-birth, females-only, stage matrix model of Crawfish Frogs that accommodates age and state-specific transition probabilities and the "temporary emigration" of individuals that skip breeding or breed at other sites. (B) Projection matrix of the model used to estimate elasticities and sensitivities of vital rates. Parameters in the matrix model: embryonic survival (S_e), tadpole survival (S_t), metamorph and juvenile survival (S_j), adult survival following the first breeding event (S_{a1}), adult survival following two or more breeding events (S_{a2}), probability that a one-year-old juvenile matures at age 2 (p), probability that a two-year-old juvenile matures at age 3 (q), the probability that a mature individual emigrates to become a non-breeding individual (γ''), probability that a non-breeding individual remains a non-breeding individual (γ'), and clutch size multiplied by 0.5 to represent half of all eggs developing into females (C). We assumed that all individuals mature by age 4. Individuals that emigrate to become a non-breeding individual may either skip reproduction or breed at another site.

Crawfish Frog population dynamics and were potential targets of habitat management.

Stochastic population projections.—We constructed a female-only, post-birth matrix population model (Lefkovitch, 1965; Morris and Doak, 2002; Morris et al., 2002) that represented realistic dynamics for a Crawfish Frog population (Fig. 1) and used that model to independently project the population growth and extinction probability for Nate's and Cattail Ponds over a 50-year period with and without immigration present. This and 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), so our matrix structure combined three types of demographic rates to calculate transition rates among juvenile and adult stage classes: stage-specific survival rates that varied for juveniles (S_j), adults who had bred only once (S_{a1}), and adults who had bred two or more times; probabilities of juveniles maturing at age 2 (p) or at age 3 (q) (we assumed all frogs mature by age 4);

and the probability of emigrating from the breeding population at that wetland (γ'') and the probability of returning to breed at that wetland after having emigrated out of the breeding population (γ'). Transition probabilities between juvenile and adult stage classes were governed by combinations of annual survival, probability of maturing, and probability of emigrating out of or into the breeding population (Fig. 1). Fecundity was zero for the tadpole, juvenile year 1 ("metamorph"), non-maturing juvenile, and emigrated ("non-breeding") adult stages. For our fecundity term, we used the mean clutch size and assumed half of all embryos would be female. Survival through first year was a function of egg survival (S_e), tadpole survival (S_t), and juvenile survival ($S_j^{0.75}$). Embryonic survival was fixed at 0.98 while tadpole and juvenile survival were stochastic based on field estimated rates. Juvenile survival was raised to the power 0.75 to represent nine months of the first year as a post-metamorphic juvenile.

Without density-dependent processes, our projections would be prone to increasing unrealistically. Density-depen-

Table 1. Estimated vital rates and transition probabilities estimated for Crawfish Frogs from a site located in southwest Indiana, USA between 2009–2016, some of which were used to parameterize a females only, stage matrix model to simulate population dynamics at two breeding wetlands. Data and parameter estimation are detailed in Tables S1, S2, S3, and S4 available online in Supporting Information (see Data Accessibility).

	Mean	Median	SD	Range
Vital rates				
Embryo survival	0.980			
Tadpole survival[a]				
Nate's Pond	0.012[a]	0.010[a]	±0.012[a]	0.00005–0.0273
Cattail Pond	0.0003[a]	0.0002[a]	±0.0002[a]	0.0001–0.0006
Metamorph and juvenile survival[b]	0.298		±0.114	0.135–0.361
Adult survival				
1st time breeding	0.390	0.300	±0.266	0.181–0.689
$\geq$2nd time breeding	0.639	0.614	±0.207	0.445–0.857
Probability of age at first reproduction[bc]				
Females				
p	0.125		±0.276	
q	0.408		±0.212	
Age 2 (p)	0.125			
Age 3 (1–p)*q	0.357			
Age 4+ (1–p)*(1–q)	0.518			
Males				
p	0.175		±0.058	
q	0.553		±0.338	
Age 2 (p)	0.175			
Age 3 (1–p)*q	0.466			
Age 4+ (1–p)*(1–q)	0.369			
Temporary emigration probabilities				
Breeder becoming a non-breeder (γ'')	0.377	0.384	±0.053	0.290–0.426
Non-breeder remaining a non-breeder (γ')	0.339	0.358	±0.061	0.218–0.384
Fecundity				
Estimated mean clutch size	6181	6477	±1027	4238–7633
Proportion of embryos that are female[d]	0.500			

[a] Represents the weighted mean or median value assuming that there was some tadpole survival. Does not factor in the probability of catastrophic larval failure. Nate's Pond failed to have any tadpoles survive in 1 of 5 years, and Cattail Pond failed to have any tadpoles survive in 2 of 5 years.

[b] Represents the mean value weighted by the number of metamorphs in the cohort used to estimate the parameter.

[c] Probability only reflects probability of age at first reproduction. The probability does not include survival; therefore, the probabilities do not reflect the ratio of individuals expected to survive to and breed for the first time at a given age.

[d] This rate was assumed based on literature.

dent larval survival is well documented among amphibians and widely accepted as an important process regulating amphibian population dynamics (Berven, 1990, 1995; Vonesh and De la Cruz, 2002). Density-dependent processes during amphibian terrestrial stages might also occur but are poorly documented (Berven, 2009). Based on our observations of larval survival rates, we imposed a negative density-dependent effect on year-specific larval survival for Nate's Pond. Tadpole survival rates at Cattail Pond were always too low to show any density-dependent pattern. Therefore, for Cattail Pond, we randomly determined the tadpole survival rate using a Beta distribution based on the observed median and standard deviation of larval survival among years. Among the four years of data we had for Nate's Pond, tadpole survival showed a negative but highly variable relationship with the number of females that bred that year (Supplemental Fig. S1; see Data Accessibility). We used likelihood estimation to fit a negative sigmoid function to our observed tadpole survival ($S_{t\ Nate's}$) and the number of breeding females, and then we used that function with a stochastic error term (ε) to vary $S_{t\ Nate's}$ as a function of the number of females that bred (N; Supplemental Fig. S1; see Data Accessibility).

$$s_{t\ Nate's} = 0.0346/(1 + e^{(0.085*(N-27)} + \varepsilon)$$

ε was modeled as a Gaussian function with $a = 0.008$, $b = 25$, and $c = 9$, with a lower bound of 0 and an upper bound of 0.35.

The model used a one-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. For each time step in our simulation, we randomly and independently varied tadpole, juvenile, and adult survival rates with one exception. Because first-time breeding and older breeding adult survival estimates were highly positively correlated among the three years, we had those two adult survival rates covary in the model based on their bivariate correlation. With the exception of larval survival and the number of immigrants, all other vital rates were randomly sampled from a normal distribution based on the mean and variance for that rate (Table 1). Rates were bounded between

0.15 and 0.70 for adult survival following the first-time breeding (S_{a1}), 0.20 and 0.85 for adult survival following the second time breeding (S_{a2}). We used a two-step process to vary larval survival. First, we randomly determined whether there would be complete tadpole failure because a site failed to hold water long enough for tadpole development. Based on field observations, we assumed this probability was 0.2. When a site held water long enough for tadpoles to complete development, tadpole survival was determined using the probability functions described previously. For simulations with immigration, we fit a negative binomial distribution to four years (2012–2015) of data on the known number of new, breeding female immigrants to Nate's Pond (Lannoo et al., 2017; Lannoo, unpubl. data). Those values were 3, 13, 5, and 8 immigrant females, respectively. Using that negative binomial function, for each iteration we drew 100 randomly selected numbers of potential immigrant females and selected the first number that did not exceed the highest number of immigrants ever observed (13). This number of immigrants was added as first-time breeding adults prior to multiplying by the fecundity term to calculate the total number of tadpoles deposited each year.

We ran 1,000 simulations for each wetland and estimated persistence probability as the proportion of iterations (out of 1,000) that did not result in complete extinction in all individual life stages and classes. Other population viability analyses typically assign a non-zero quasi-extinction threshold often based on the number of breeding females; however, we did not assign a non-zero extinction threshold because amphibian populations can routinely have few or no breeding adults in some years even though adults persist in terrestrial habitats and there may be several cohorts of juvenile persisting in terrestrial habitats (Taylor et al., 2006). We performed all statistical analyses in Program R version 3.5.3 (R Core Team, 2019) and the code is available for public download (https://github.com/jcmaerz3/Crawfish-Frog-PVA.git).

RESULTS

Female fecundity and embryonic and larval survival.—We monitored 53 egg masses in 2010 and 2011 and every clutch had nearly all eggs hatch. Among the five egg masses for which we counted unhatched eggs, we estimated that 98% of embryos hatched. In contrast, larval survival to metamorphosis was low and highly variable. We observed complete larval failure due to early drying at both Nate's Pond and Cattail Pond in 1 of 5 years. We observed complete larval failure at Cattail Pond in one other year even though the wetland held sufficient water. Among years with successful metamorphosis, metamorph cohort sizes at Nate's Pond ranged between 8 and 3,122 individuals compared to 11 and 30 at Cattail Pond, and estimated tadpole survival at Nate's Pond was 25–46 times greater than tadpole survival at Cattail Pond (Table 1; Supplemental Table S2; see Data Accessibility). Larval survival rate at Nate's Pond was negatively correlated with the number of breeding females and the numbers of metamorphosing predatory ambystomatid salamanders and congeneric frogs during that year (Supplemental Figs. S1, S2; see Data Accessibility). In addition, there was a negative relationship among years between the number of metamorphs produced and mean wet mass of metamorphs (Supplemental Fig. S3; see Data Accessibility).

Juvenile survival and age at first reproduction.—We never observed a metamorph from Cattail Pond return as a breeding adult. For metamorphs from Nate's Pond, known age at first reproduction and estimated juvenile survivorship from metamorphosis to first reproduction differed among years and sexes (Supplemental Table S1; see Data Accessibility). Weighted mean annual juvenile survival was similar for males and females (Table 1). Among the three metamorph cohorts for which we could follow for 5–7 years, 48% of males were first observed breeding at age 2, 40% at age 3, and 12% at age 4 or older. We did not observe any males breeding for the first time older than age 4. For females, 28% were first observed breeding at age 2, 54% at age 3, 15% at age 4, and 3% at age 5 or older (we observed one female breeding for the first time at age 5 and one at age 6). For frogs that survived to reproduce, the probability that their age at first reproduction was 2, 3, and 4+ years of age was of 0.175, 0.466, and 0.369 for males and 0.125, 0.357, and 0.518 for females, respectively (Table 1).

Adult survival and temporary emigration.—We captured 354 individual adult Crawfish Frogs (192 males, 162 females). The number of Crawfish Frogs that bred at Nate's Pond was approximately twice as large as the population at Cattail Pond and varied among years (Supplemental Table S2; see Data Accessibility). Capture and recapture rates were high, varied slightly among years, and differed moderately between initial capture during immigration into the breeding wetland and recapture during emigration from the breeding wetland the same year (mean capture = 0.912, 95% CI = 0.872–0.951; mean recapture = 0.720, 95% CI: 0.612–0.825). The longest gap between capture events of any adult frog was three years. Estimated adult survival varied by year and breeding status (first known breeding event versus having bred prior) but not as a function of breeding site (Supplemental Table S3; see Data Accessibility). Model-averaged survival estimates for adults known to have bred at least twice were between 24% and 146% higher than survival estimates for first-time breeders (Table 1). Mean mass and SVL of females known to have bred at least twice (mean ± 1 SD, mass [g]: 92.8±20.2, SVL [mm]: 104.0±5.64) were 14% and 4% larger, respectively, compared to first-time breeding females (mass [g]: 81.4±23.7, SVL [mm]: 99.8±7.43). Mean mass and SVL of males known to have bred at least twice (mass [g]: 107.0±17.7, SVL [mm]: 99.1±5.98) were 17% and 6% larger, respectively, compared to first-time breeding males (mass [g]: 91.8±21.9, SVL [mm]: 93.1±7.40). The size differences between first-time breeders and adults that were known to have bred two or more times is likely an underestimate because some individuals considered first-time breeders in the first few years of the study likely had bred previously. Among the three years for which we had estimates of survival for first-time breeding (S_{1st}) and prior-breeding adults (S_{2nd+}), survival estimates were highly positively correlated ($R^2 = 0.967$).

The top model of temporary emigration was non-Markovian and constant across years of the study (Supplemental Table S4; see Data Accessibility); although, we also found support, indicated by model weights, for two additional models where emigration was random but varied by year and emigration was Markovian (i.e., $\gamma'' \neq \gamma'$) but constant across years. The model-averaged estimate of the temporary emigration rate out of the breeding population (γ'') was

Table 2. Elasticity and sensitivity of estimated Crawfish Frog female vital rates and transition probabilities of a population located in southwest Indiana, USA, 2009–2013.

Transition or vital rate	Rate	Elasticity	Sensitivity
Embryo survival (S_e)	0.980	0.255	0.276
Tadpole survival (S_t)	0.012	0.255	24.489
Juvenile survival (S_j)	0.298	0.622	2.209
Adult survival following first breeding (S_{a1})	0.390	0.125	0.338
Adult survival following ≥ second breeding (S_{a2})	0.639	0.190	0.314
Probability of becoming a non-breeding adult (γ'')	0.337	−0.124	−0.347
Probability of remaining a non-breeding adult (γ')	0.339	−0.024	−0.075
Probability that a one-year old juvenile matures at age 2 (p)	0.125	0.100	0.850
Probability that a two-year old juvenile matures at age 3 (q)	0.408	0.069	0.179
Clutch size	6180	0.255	<0.001

0.377, and the probability that an adult that had emigrated from the breeding population would return to the breeding population (1−γ') was 0.661 (Table 1).

Population elasticity and sensitivity analysis.—The total elasticity of all eight terrestrial vital rates (1.213) was 2.4 times greater than the elasticity of the two aquatic vital rates (0.510; Table 2). We considered clutch size a terrestrial vital rate because it is likely determined by female growth and foraging success in the terrestrial environment. Juvenile survival had the highest elasticity of any other vital rate by more than double (Table 2). However, the elasticities of embryonic and tadpole survival were second only to juvenile survival and equal to clutch size (Table 2), and because tadpole survival was low but varied by several orders of magnitude, it affected instantaneous population growth twice as much as did variation in juvenile survival during this study (Fig. 2). Across the range of natural variation we

observed or estimated, we estimated that tadpole survival had the greatest potential to cause declines or growth in Crawfish Frog populations.

Without immigration, the median (± lower 90% credible interval–upper 90% credible interval) stochastic λ was 1.154 (1.060–1.285) and 0.500 (0.358–0.500) for Nate's Pond and Cattail Pond, respectively. With immigration, the median stochastic λ was 1.093 (1.034–1.154) and 1.087 (1.037–1.145) for Nate's Pond and Cattail Pond, respectively. Without immigration, simulations of Cattail Pond seldom had years of positive population growth and the predicted probability of breeding population extinction at Cattail Pond over 50 years was 100% with a mean time to extinction of eight years; however, with immigration, the probability of extinction at Cattail Pond was only 2.3% and female breeding population sizes fluctuated between 5 and 21 individuals, which was highly consistent with the range (7–21) and dynamics observed at Cattail Pond between 2009 and 2013 (Supplemental Table S2, Supplemental Fig. S4; see Data Accessibility). Without immigration, the predicted probability of breeding population extinction at Nate's Pond was 3.4% with a mean time to extinction of 50 years, and with immigration, this probability of extinction declined to 0% (Supplemental Fig. S4; see Data Accessibility). Without immigration, simulations predicted relatively stable breeding population at Nate's Pond with a median adult female breeding population of 33 individuals (± lower 90% credible interval–upper 90% credible interval = 7–65) fluctuating between a minimum of 0 and a maximum of 150 breeding females (Supplemental Fig. S4; see Data Accessibility). Simulated dynamics of female breeding population sizes were similar with immigration, with a median adult female breeding population of 42 individuals (± lower 90% credible interval–upper 90% credible interval = 19–75) fluctuating between a minimum of 5 and a maximum of 180 breeding females (Supplemental Fig. S4; see Data Accessibility). Simulated population growth with or without immigration at Nate's Pond was characterized by episodic "booms" of high growth (λ > 2) followed by intervals of low recruitment due to stochastic failure or negative larval density-dependent survival (Fig. 3, Supplemental Fig. S4; see Data Accessibility). With and without immigration, there was positive population growth at Nate's Pond during 46.3% and 42.2% of simulated years, respectively, and the positive correlation between larval survival and lambda for Nate's Pond was similar with or without immigration in the simulation (Fig. 3).
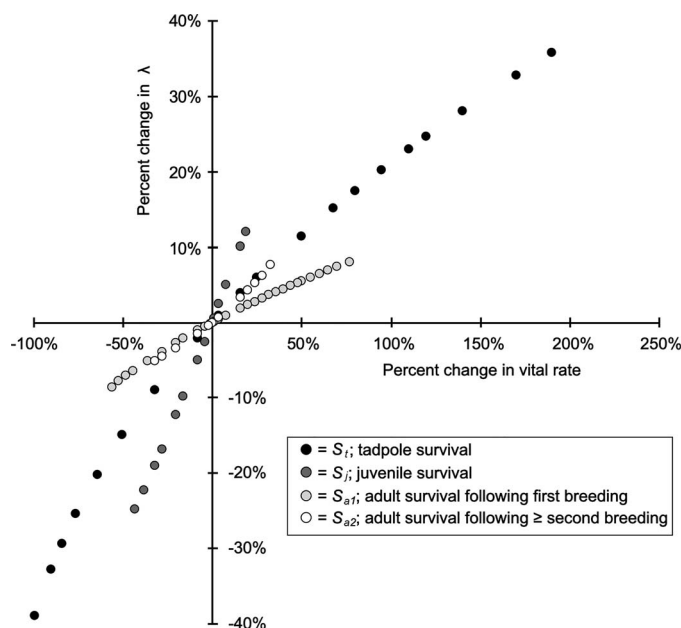

Fig. 2. Percent change in the instantaneous population growth rate (λ) in response to a percent change in female Crawfish Frog tadpole, juvenile, or adult survival rates for a population located in southwest Indiana, USA, between 2009–2013. Percent change in each vital rate represents the general range of that vital rate observed in this study. Change was estimated by varying the focal rate while holding all other rates constant.
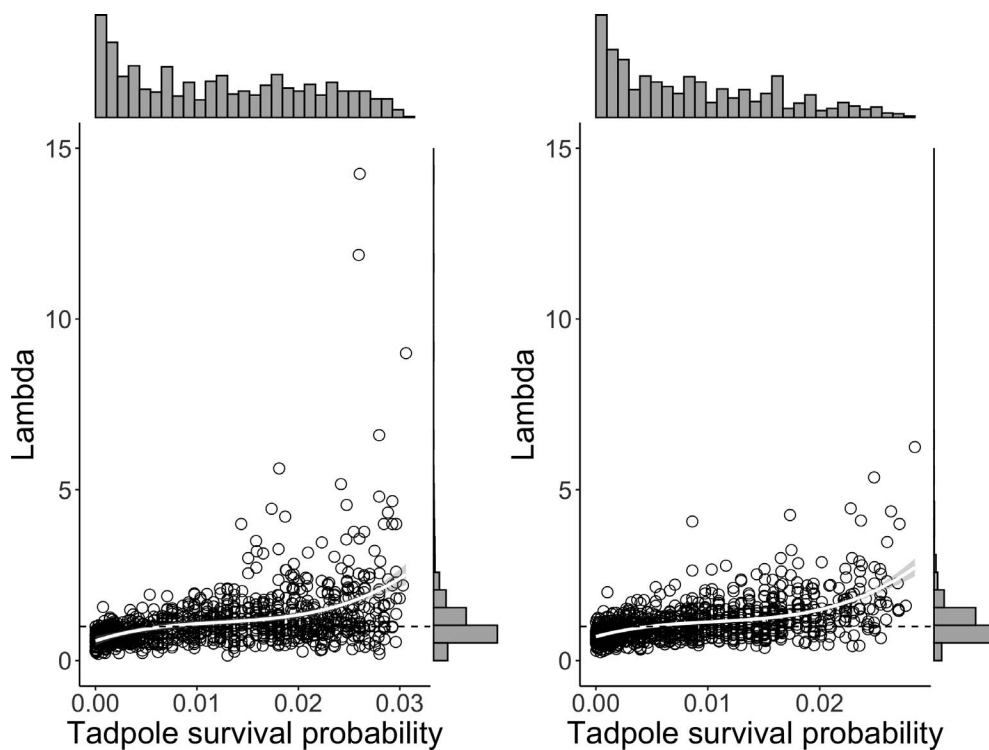
Fig. 3. Correlation between tadpole survival and the instantaneous population growth rate (λ) for 1,000 points drawn randomly from 1,000 simulations of stochastic population simulations of Nate's Pond with (left panel) and without (right panel) immigration included in the simulation model. The white line is a third order polynomial function fitted to the data, and the gray band represents the 95% confidence interval. The horizontal dashed line indicates a λ of 1. The distributions of tadpole survival rates and λ values are provided as marginal plots.

DISCUSSION

All vital rates of all life stages are important to population growth and, therefore, would ideally be the focus of management. However, when limited resources, knowledge, or other factors constrain comprehensive management, it is important to determine what actions targeting specific life stages should be prioritized and whether ignoring some life stages will compromise management efforts (e.g., Govindarajulu et al., 2005; Kissel et al., 2014; Schmidt et al., 2019). Evolutionary theory predicts a negative relationship between variability in a vital rate and its influence on population dynamics (high elasticity; Pfister, 1998). For many amphibians with complex life cycles, larval survival in aquatic environments is likely to be more variable than post-metamorphic terrestrial vital rates. This would suggest larval survival should not have a relatively strong effect on amphibian population dynamics compared to terrestrial stages and, therefore, might not make an effective priority for management compared to actions targeting survival of terrestrial stages. However, in the case of pond-breeding amphibians, studies of amphibians have found that population growth is strongly affected by highly variable vital rates including larval survival or larval carry-over effects on juvenile survival and age and size at first reproduction (Berven, 1990, 1995; Biek et al., 2002; Altwegg, 2003; Altwegg and Reyer, 2003; Govindarajulu et al., 2005; Matthews et al., 2013; Kissel et al., 2014). In this study, we found relatively small temporal variation among juvenile and adult survival compared to tadpole survival, which varied by several orders of magnitude within and between proximate breeding sites. Tadpole survival was important in affecting Crawfish Frog population growth at this site and differences in tadpole survival between two main breeding wetlands can explain breeding population dynamics at the two wetlands. Our results indicate that one of two focal

breeding wetlands, Cattail Pond, with a relatively stable and persistent adult breeding population is incapable of being self-sustaining and entirely dependent on immigration for its persistence. In further support of this conclusion, we note that between 2009 and 2016, no juvenile from Cattail Pond has ever been recovered as a breeding adult at Cattail Pond or any other breeding site (Lannoo et al., 2017). Solely because of poor tadpole survival in that wetland, Cattail Pond is functioning as a population sink and—assuming no terrestrial density dependence—limiting the overall population size of Crawfish Frogs at HFWA-W.

In contrast, we demonstrate that solely because of higher tadpole survival rates, Nate's Pond is likely self-sustaining and a potential source wetland for other sites such as Cattail Pond. Lannoo et al. (2017) reported that at least 28% of Crawfish Frog juveniles from Nate's Pond were detected breeding at another wetland, with 36% of those Nate's Pond juveniles dispersing as breeding adults to Cattail Pond. These results further support the conclusion that restoration of Cattail Pond from a sink habitat would likely increase the total Crawfish Frog population size at this site, which would in-turn increase overall population viability.

Though we found support for the relative importance of tadpole survival on Crawfish Frog population growth at this site, our model and other studies still likely underestimate the true relative influence of the aquatic environment on amphibian population dynamics. First, negative density dependence in the larval stage serves as a check on the influence of the adult population size on population growth (this study in addition to Berven, 1990, 1995; Scott, 1994; Vonesh and De la Cruz, 2002; Altwegg, 2003; Altwegg and Reyer, 2003). Models that do not integrate larval negative density dependence will overestimate the importance of adult survival to population growth. Field estimates of the strength of density dependence on population growth are limited and likely vary among populations and species.

Going forward, such estimates will be important for more robust projection models that describe population dynamics and inform management. Second, numerous studies demonstrate that larval environments have carry-over effects on amphibian terrestrial vital rates including juvenile and adult survival, age and size at first reproduction, and fecundity (Semlitsch et al., 1988; Berven, 1990, 1995; Scott, 1994; Scott et al., 2007). The strongest carry-over effects are generally the effect of size at and timing of metamorphosis on juvenile survival shortly after metamorphosis (Altwegg, 2002, 2003; Altwegg and Reyer, 2003; Chelgren et al., 2006; however, see Earl and Semlitsch, 2013), which multiple studies identify as having the largest effect on population dynamics (this study in addition to Berven, 1990, 1995; Altwegg, 2003; Altwegg and Reyer, 2003; Govindarajulu et al., 2005). We observed limited variation in our estimates of mean annual juvenile survival among our three metamorph cohorts; however, we caution that our study was not designed to estimate carry-over effects on juvenile survival and our results are inadequate to judge whether larval carry-over effects occurred. If there were negative density-dependent or other environmental larval carry-over effects on juvenile survival or other vital rates, then elasticities associated with "terrestrial" habitats such as juvenile survival would underestimate the relative importance of the aquatic environment to Crawfish Frog population dynamics at our study site. We advocate for increased efforts to estimate natural carry-over effects of the larval environment on terrestrial vital rates to improve models that inform habitat management for amphibians.

Larval survival within and between our study wetlands varied consistently with factors already well known to affect larval performance. Larval amphibian survival, growth, and size and timing at metamorphosis are primarily related to resource availability, which is affected by hydroperiod, predator and competitor identity and density, and plant quantity and quality (Pechmann et al., 1989; Berven, 1990; Pechmann and Wilbur, 1994; Skelly, 1994; Richter et al., 2003; Daszak et al., 2005; Maerz et al., 2010; Cohen et al., 2012). Short hydroperiods and high predator density are both known to contribute to high larval amphibian mortality (Pechmann and Wilbur, 1994; Skelly, 1994; Richter, 2000; Cohen et al., 2012). During our study, complete larval mortality at both breeding sites was associated with drought. We also found that larval survival at Nate's Pond was negatively dependent on the number of breeding females and potentially with interspecific competitor and predatory salamander abundance. However, at Cattail Pond, competitor and predator abundance and hydroperiod were insufficient to explain the consistently low rates of larval Crawfish Frog survival including complete tadpole mortality in one year with a sufficient hydroperiod. Within the past decade, an emerging body of research demonstrates that the quality of plant resources within the wetland is an important factor determining amphibian larval performance and community dynamics (e.g., Maerz et al., 2010; Cohen et al., 2012; Stephens et al., 2013; Burrow and Maerz, 2021). Some plant species may also contain secondary metabolites that can be lethal to some tadpole species (e.g., Maerz et al., 2005; Watling et al., 2011). Notably, cattails and other plants that are low in nitrogen or phosphorus leaf content tend to support poor tadpole growth and survival (Maerz et al., 2010; Cohen et al., 2012; Stephens et al., 2013). In addition, plant species such as cattails that produce dense stands can support greater abundances of predatory invertebrates that may reduce tadpole survival (Woodward, 1983). In contrast, herbaceous grasses, bulrushes, and sedges that are typically richer in nitrogen and phosphorus support higher larval survival, faster growth, and larger size at metamorphosis. The difference we observed in tadpole survival between the two main breeding sites was consistent with differences in the dominant emergent vegetation, and we hypothesize that the consistently low tadpole survivorship observed at Cattail Pond was the result of the dense stands of hybrid cattails.

Two relatively novel dimensions of our projection model were the estimation and integration of temporary emigration and differential adult survival into our projections. Few amphibian projection models account for temporary emigration from breeding populations. Most models assume that all females breed annually or assume the proportion that breed is independent of age or some other state (e.g., breeding history). Seldom are temporary emigration rates estimated. Yet the exclusion of temporary emigration from models biases parameter estimates (e.g., survival) and the relative importance of those parameters to population growth. Moderate to high rates of temporary emigration and re-immigration are now reported for several amphibian species and appear to be the norm rather than the exception (this study in addition to Schmidt and Anholt, 1999; Bailey et al., 2004; Frétey et al., 2004; Church et al., 2007; Muths et al., 2010, 2013). A moderate to high probability of skipping breeding reduces the likelihood an adult amphibian will have multiple breeding events (Church et al., 2007), which reduces the influence of adult survival on population growth relative to survival of other life stages. Importantly, in our study and in others, we do not know whether "temporary emigration" represents individuals skipping reproduction or emigrating to other breeding sites in some years. Because capture–recapture is logistically challenging and resource intensive, few amphibian population studies adequately cover more than a few breeding sites; therefore, estimating the separate probabilities of skipping breeding and dispersal among breeding sites is difficult (Bailey and Muths, 2019). Trenham et al. (2001) estimated annual movements among ponds by adult California Tiger Salamanders (*A. californiense*) are between 0.13 and 0.33 among first-time breeders and older adults, respectively. However, Church et al. (2007) estimated that male and female Eastern Tiger Salamanders (*A. tigrinum*) show relatively low annual probabilities of movement among breeding ponds (0.03–0.06) but relatively high probabilities of skipping breeding the year following breeding (males > 0.50, females > 0.70). Petranka et al. (2004) did not estimate individual dispersal or breeding probabilities but found inversely correlated breeding population sizes of Wood Frogs (*R. sylvatica*) and Spotted Salamanders (*A. maculatum*) among local wetlands, suggesting that adults may be dispersing among breeding sites between years. At our study site between 2012–2016, 11% of adult Crawfish Frogs that were born and known to have first bred at Nate's Pond were known to have switched to another breeding site (Lannoo et al., 2017), but because of different and inconsistent capture methods and effort at other wetlands, we cannot estimate annual adult dispersal among breeding wetlands. We only know that it did occur. We also know that the longest interval between captures of an adult Crawfish Frog breeding at Nate's Pond was three years without observing

that female breeding at another site. Again, we do not know confidently whether this female bred elsewhere during the intervening two breeding seasons. The apparent level of adult dispersal among wetlands over five years (>11%) seems insufficient to account for most of the >30% annual temporary emigration from the breeding population at our two focal breeding sites, but this remains to be examined. We believe it is likely that at least a modest number of adults skip breeding some years. Skipping breeding would presumably be related to replenishing energy reserves (Bull and Shine, 1979) or a response to recent terrestrial disturbances that reduce breeding migration such as prescribed burns shortly before the breeding migration period (Engbrecht and Lannoo, 2012).

We also estimated that subsequent survival of presumed first-time breeders was 21–60% lower compared to adults that had bred in prior years. Schmidt and Anholt (1999) also report 24–57% lower survival among common toads (*Bufo bufo*) the first year following breeding compared to the year following second breeding. We are not aware of any other studies of amphibians that address differential survival among breeding adults as a function of breeding age or prior breeding experience, but other studies suggest differential survival between breeding and non-breeding adults is possible when conditions during breeding are particularly stressful (Church et al., 2007). Because reproduction requires large energetic expenditures by both males (for calling) and females (for egg production), we would expect higher post-breeding mortality among younger, first-time breeding adults assuming that age is related to body condition. In our study, first-time breeders were smaller and weighed less than individuals known to have bred previously. We suspect that high mortality following first breeding is common among amphibians though poorly documented. Differential survival of different ages or sizes of breeding adults can affect estimates of the importance of adult survival to population growth relative to other vital rates. Because most individuals in a Crawfish Frog breeding population will be first-time breeders, using a single mean adult survival rate for all individuals would overestimate survival rates for these individuals and thereby inflate the importance of adult survival to population growth. When modeling amphibian population dynamics, this could also apply to different survival rates for other classes of individuals such as breeding adults versus non-breeding adults or translocated versus naturally recruited adults (e.g., Duarte et al., 2017).

Finally, our study in conjunction with Lannoo et al. (2017) confirms the importance of dispersal and immigration in amphibian population dynamics. Even though we estimate that Nate's Pond is self-sustaining, 12–33% of breeding females at Nate's Pond each year were immigrants, and minimally, 29% of juveniles produced at Nate's Pond dispersed to breed at other wetlands. The stable breeding population at Cattail Pond is entirely composed of immigrants.

This study demonstrates the need to integrate wetland management to complement upland management for Crawfish Frogs and similar amphibian species to achieve management goals. Survival of terrestrial amphibian stages is critical for sustaining populations through episodic larval failure (i.e., drought), so terrestrial habitat degradation that reduces juvenile and adult terrestrial survival can and

would likely cause population declines and extinction. However, we show that in an area with adequately managed uplands that support "high" terrestrial survival, wetland conditions alone can create population sinks that limit the overall population size and, thereby, increase the risk of local extinction. Without intervention in 2012 and 2013 to prevent encroachment of shrubs and hardwoods and hybrid cattail invasion, Nate's Pond would have shifted to conditions similar to Cattail Pond and a vital breeding site that was self-sustaining and a major source of immigrants to other breeding sites might have been lost. A failure to manage complementary habitats can compromise other management efforts to restore and sustain amphibian populations (Thurgate and Pechmann, 2007; Schmidt et al., 2019).

We recommend the restoration of wetlands, like Cattail Pond, to increase the carrying capacity for Crawfish Frogs at HFWA-W and other sites. Short and intermediate hydro-period wetlands dry regularly, which will reduce the abundances of some predators and competitors and will facilitate vegetation management such as the penetration of prescribed fire into wetlands. We recommend mechanical removal and the use of fire during dry seasons to control encroachment of cattails, shrubs, and hardwoods and maintain open canopies, grasses, and sedges within wetland basins (Liner et al., 2008; Kirkman et al., 2012). These are similar to recent habitat recommendations for the federally protected Dusky Gopher Frog (Thurgate and Pechmann, 2007). The management of other native predators or competitors is a greater challenge for conservation efforts for Crawfish Frogs and other priority amphibian species. Research and efforts to manage predator communities that threaten amphibian population recovery have largely focused on the removal of introduced predatory fish (Lannoo, 1996; Knapp and Matthews, 2000; Vredenburg, 2004). There are few studies of the effectiveness of controlling native amphibians as a management strategy. Predatory and competing amphibian species could be managed at focal sites using drift fences to intercept breeding adults or cull emigrating metamorphs, as has been recommended for controlling invasive Bullfrog populations (Govindarajulu et al., 2005). It is also possible to use biocides to manage amphibians with multiannual larvae (e.g., Bullfrog tadpoles) that would compete with or prey upon the larvae of priority species. We recognize the sensitivity around management of other native amphibian species, but a temporary cull of other larval amphibian species may be justified when intervention needs are critical and other native species are locally secure. The timing and frequency of management of other native species should be carefully considered. Finally, our results provide indirect support for the value of captive larval rearing programs to augment or restore threatened amphibian populations (Stiles et al., 2016). Captive-reared larvae can have survival rates orders of magnitude greater than natural rates, which our results indicate should have large effects on population growth. Currently, recovery and management guidelines for other *Nenirana*, including populations of the federally endangered Dusky Gopher Frog and federally petitioned Gopher Frog, include captive rearing and head-starting programs (Mississippi Gopher Frog Recovery Action Plan, 2009; USFWS, 2010).

DATA ACCESSIBILITY

ACKNOWLEDGMENTS

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