Estimation of breeding probability can make monitoring data more revealing: a case study of amphibians

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Abstract. Monitoring programs serve to detect trends in the distribution and abundance of species. To do so, monitoring programs often use static state variables. Dynamic state variables that describe population dynamics might be more valuable because they allow for a mechanistic understanding of the processes that lead to population trends. We fit multistate occupancy models to data from a country-wide multispecies amphibian occupancy monitoring program and estimated occupancy and breeding probabilities. If breeding probabilities are determinants of occupancy dynamics, then they may serve in monitoring programs as state variables that describe dynamic processes. The results showed that breeding probabilities were low and that a large proportion of the populations had to be considered to be non-breeding populations (i.e., populations where adults are present but no breeding occurs). For some species, the majority of populations were non-breeding populations. We found that non-breeding populations have lower persistence probabilities than populations where breeding occurs. Breeding probabilities may thus explain trends in occupancy but they might also explain other ecological phenomena, such as the success of invasive species, which had high breeding probabilities. Signs of breeding, i.e., the presence of eggs and larvae, were often hard to detect. Importantly, non-breeding populations also had low detection probabilities, perhaps because they had lower abundances. We suggest that monitoring programs should invest more in the detection of life history stages indicative of breeding, and also into the detection of non-breeding populations. We conclude that breeding probability should be used as a state variable in monitoring programs because it can lead to deeper insights into the processes driving occupancy dynamics.

Key words: amphibian; breeding probability; monitoring; occupancy; population dynamics.

INTRODUCTION

Population declines are the first step toward the loss of species, both locally and globally. Therefore, conservation biologists monitor populations to quantify and to explain how and why populations grow and shrink. Customarily, monitoring programs are used to describe changes in the size of animal and plant populations through time (Buckland et al. 2005, Marsh and Trenham 2008, Geijzendorffer et al. 2016). The growth rate of a population, λ , can be described by the simple ratio of two successive population sizes (N_t ; Turchin 1999)

$$\lambda = N_{t+1}/N_t.$$

The analyses of time-series data can inform about trends in abundance and can lead to valuable insights into the ecology and conservation of species (Inchausti and Halley 2003, Leung et al. 2017). However, such data are less suitable for understanding the processes that lead to population declines because these data contain no information on demographic mechanisms. It is more informative to decompose population growth into its demographic components and to determine how the relative contributions of gains and losses contributes to population trends (Nichols et al. 2000, Bjørnstad and Grenfell 2001). The canonical equation of population ecology decomposes population growth into its demographic components. The equation states that changes in population size (N) through time (t) depend on gains to the population through births and immigration and on the loss of individuals from the populations through death and emigration (Pulliam 1988)

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$$N_{t+1} = N_t + \text{births}_t + \text{immigrants}_t - \text{deaths}_t - \text{emigrants}_t.$$

There is a consensus among population ecologists that analyses of population dynamics that include an explicit modeling of vital rates and phenotypic traits yield deeper insights into the processes driving population dynamics (Clutton-Brock and Sheldon 2010, Zipkin et al. 2014, Clements and Ozgul 2016, Coulson et al. 2017, Plard et al. 2019) and metapopulation dynamics where vital rates may vary among populations (MacKenzie et al. 2003, Runge et al. 2006, Gurevitch et al. 2016). Similarly, in species distribution modeling, researchers are increasingly aware that although presence/absence or presence-only data may yield predictions of habitat suitability, these predicted suitabilities may not reflect the performance of individuals (Kearney 2006, Thuiller et al. 2014, Unglaub et al. 2018). Modeling the dynamic processes underlying distribution patterns is likely to be more informative than static analyses (Schmidt and Pellet 2005, Keith et al. 2008, Kéry et al. 2013, Yackulic et al. 2015). For example, adding data on vital rates that determine dynamic processes (e.g., data on reproductive performance [births in the equation above]) improved the predictive value of distribution models for conservation (Titeux et al. 2007, Brambilla and Ficetola 2012, Searcy and Shaffer 2016, Bacon et al. 2017). This is perhaps not surprising if we remind ourselves that species may be present in sink habitats where population growth rates (λ) are less than 1, perhaps because there is no successful reproduction (Pulliam 1988, 2000).

Consequently, species monitoring programs that focus on the essential biodiversity variables “species distribution” and “species abundance” (sensu Jetz et al. 2019) may benefit from data on breeding (e.g., anything ranging from the presence of eggs and larval stages to recruitment rates; our operational definition in this study is explained in *Methods*). To date, however, many species monitoring programs collect data on the abundance, distribution, and richness of species but not breeding (Buckland et al. 2005, Marsh and Trenham 2008, Geijzendorffer et al. 2016). The relevance of a monitoring program for species management can be increased if there are also data on the processes that lead to changes in the distribution or abundance of species (Nichols and Williams 2006, Martin et al. 2009, Green et al. 2013, Schmeller et al. 2018). Data on where breeding occurs and on trends in breeding, for example, in the number of sites with successful reproduction, would be very valuable for species conservation. These kinds of data could lead to a better understanding of the drivers of population change and could lead to more insightful analyses of the effectiveness of conservation actions (Schmidt et al. 2019).

We used data from a nation-wide amphibian monitoring program (Bergamini et al. 2019) to estimate and compare the occurrence of adults and the occurrence of

breeding for multiple species. Amphibians are a suitable class for this type of analysis for two reasons. The global decline of amphibians is an ongoing phenomenon (Houlahan et al. 2000, Grant et al. 2016, Leung et al. 2017, Falaschi et al. 2019). While there are many known causes contributing to declines (e.g., pathogens, overharvesting, habitat loss; Stuart et al. 2004, Grant et al. 2016), the demographic processes underlying the declines are not yet sufficiently understood (Marsh and Trenham 2001, Schmidt et al. 2005, Muths et al. 2017). Obviously, the possible lack of successful breeding could be one factor that can contribute to population decline. For example, Vredenburg (2004) showed that frog populations recovered quickly after fish were removed because there was no longer fish predation on larvae. Furthermore, it is well known that successful reproduction does not occur in all years in amphibian populations (Shoop 1974, Bell and Lawton 1975, Sinsch 1992, Greenberg et al. 2017) and that many populations appear to be sink populations without or with little offspring production (i.e., metamorphs; Gill 1978, Sinsch 1992, Hels 2002, Peterman et al. 2018). An increasing number of studies have reported the absence of reproductive stages at sites where adults appear to thrive (Green et al. 2013, Unglaub et al. 2015, Tournier et al. 2017, Gould et al. 2019, Schmidt et al. 2019).

We use multistate occupancy models (Nichols et al. 2007) to estimate both occurrence and breeding probabilities (given occurrence) and the detection probabilities of the species overall and of breeding life stages (i.e., eggs or larvae). We do so for the entire assemblage of pond-breeding amphibians in Switzerland. The estimates can inform the feasibility of monitoring the occurrence of breeding. If the detectability of breeding (i.e., detectability of eggs and tadpoles) is low, then uncertainty will be large and parameter estimates of limited value (Schmidt et al. 2019). Nevertheless, reliable estimates of breeding probability as a state variable in a monitoring program may add value to it because the lack of breeding may be an early warning signal of impending population declines. We discuss the implications of the results for the design of monitoring programs and the conservation biology of amphibians.

MATERIALS AND METHODS

The monitoring program

We used data collected by the Swiss national monitoring program “Monitoring the Effectiveness of Habitat Conservation in Switzerland” (“Wirkungskontrolle Biotopschutz Schweiz”) (WBS; Bergamini et al. 2019; program details *available online*).⁶ The 240 sites included in the monitoring program are amphibian breeding sites of national importance and were selected by a stratified random procedure from all amphibian breeding sites of

⁶<https://biotopschutz.wsl.ch/en/index.html>

national importance (Schmidt and Zumbach 2019). Sites are visited according to a rotating panel design (McDonald 2003) such that each of the 240 sites is visited once every six years (40 sites visited every year). For our analyses, we used data collected from 2011 to 2016 at 233 of the 240 sites (data from some sites was not available). Monitoring continued after 2016 and we used data from 73 sites that were re-surveyed in 2017 and 2018 to analyze the effects of earlier occupancy status (i.e., absent, present but no breeding, present and breeding) upon population persistence. The sites re-surveyed in 2017 and 2018 were first visited in 2011 and 2012.

Survey protocols for the national program include four visits during the breeding season (March–June) for every site targeted for a visit in a given year. The survey window spans four months in order to include the breeding seasons of all amphibians in the assemblage (Appendix S1: Table S1). Repeated visits to a site allow imperfect detection to be accounted for when estimating site occupancy and breeding probabilities (MacKenzie et al. 2002, Nichols et al. 2007). At each visit, the goal is to detect all species and all life history stages (eggs, larvae, adults, calling males) that are present. Methods include visual encounter surveys, aural surveys and dip-netting (Dodd 2009). Surveys are limited to 1 h, independent of the size of the site. If a site is large, then surveyors are instructed to focus on the areas that seem most suitable for amphibians. In any given year, 16–29 professional herpetologists are given mandates to conduct the surveys; with each person surveying one to four sites. To ensure population closure, we carried out data set filtering following the recommendations of MacKenzie et al. (2002). For each species, we removed survey data from surveys carried out before the first sighting of a species within the year, and after the final sighting within that year.

Statistical analyses

We used single-season multistate occupancy models to analyze the data (Nichols et al. 2007). Multistate occupancy models estimate the probability that a pond is occupied (ψ) and the probability that breeding occurs (given occupancy; r). The three (latent) states were: (1) species absent ($1 - \psi$), (2) species present but no breeding ($\psi(1 - r)$), and (3) species present and breeding (ψr). We used the estimates of occurrence (ψ) and breeding probability (r) to estimate the number of sites with breeding and non-breeding populations.

The data matrix (i.e., the raw data) contains the observed states. Because detection is imperfect, observed states can differ from the true state. An observation was given a 1 (observed state, species absent) if the species was not detected. If only adults were detected, then the observed state was 2 (observed state, species present but there is no breeding). If eggs or larvae were detected, this was noted as 3 (observed state, species present and breeding). The model uses this information to estimate

the probability of detecting adults (but not breeding signs) and the probability of detecting breeding. These detection probabilities are then used to estimate the true (latent) states. For details on the model, see Nichols et al. (2007) and Kéry and Royle (2020, which includes code to fit the models to the data). Here, we only provide a description of the detection matrix in Table 1. It is important to note that the model differentiates between the true state of a population and the probability of detecting that true state. That is, it differentiates between the absence of breeding (i.e., absence of eggs or tadpoles) and non-detection of breeding (i.e., non-detection of eggs or tadpoles).

In a second analysis, we asked whether the state in the years 2011–2016 had an effect on occupancy in 2017–2018. For this analysis, we used data from all sites surveyed in 2011–2016 and 73 sites resurveyed in 2017 or 2018 (which were first surveyed in 2011 and 2012). The sites surveyed only once lead to greater precision of the estimates of the states of the sites in 2011 and 2012. For this analysis, we combined a multistate model and a two-state (species present or absent; MacKenzie et al. 2002) occupancy model. We first modeled the state in the years 2011 and 2012 using the multistate model. Then we used the estimated states as predictor variables for occupancy in the two-state occupancy model, using a single vague prior on detection probability across all sites in this second analysis (code for this latter model can be found in Kéry and Schaub [2011]).

We had no data on habitat characteristics that could be used in a reliable way to model occupancy or breeding probabilities (e.g., from remote sensing; Cruickshank et al. 2020; see also Appendix S1: Section S3). Therefore,

TABLE 1. Description of the detection matrix used in the multistate occupancy models.

True state	Observed state		
	Absent	Species present but no breeding detected	Species present and breeding detected
Absent	1	0	0
Species present, no breeding	$1 - p_{2,2}$	$p_{2,2}$	0
Species present and breeding	$1 - p_{3,2} - p_{3,3}$	$p_{3,2}$	$p_{3,3}$

Notes: The detection matrix is a 3×3 matrix in which rows represent the true states of the populations and columns represent the observed states. The parameter $p_{2,2}$ is the probability that a population that is in state “species present but there is no breeding” is detected (i.e., adults only); $p_{3,2}$ is the probability that only adults are detected in a population that is in state “species present and breeding”; $p_{3,3}$ is the probability that signs of breeding (eggs or larvae) are detected in a population that is in state “species present and breeding.” The zeroes in the matrix indicate that model assumes that there are no false positives. The probabilities in a row sum to one.

these parameters, as well as detection probabilities for each state were modeled as constant.

Some species have restricted ranges in Switzerland and occur only in southern Switzerland (*Hyla intermedia*, *Rana latastei*, *Triturus carnifex*). For these species, we used only the sites from this region in the analysis.

All models were run in JAGS (Plummer 2003) using the R package jagsUI (Kellner 2016). All models were run using a burn-in of 5,000, three chains, and thinning 1 in 10, with 50,000 iterations. Convergence was assessed using the Brooks-Gelman-Rubin statistic (Kéry and Schaub 2011). We used uninformative priors for all parameters (based on the code in Kéry and Schaub (2011) and Kéry and Royle (2020)).

RESULTS

Detection probability

Species were easier to detect in sites in which they did breed than in sites in which they did not breed ($p_{3,2} + p_{3,3} > p_{2,2}$; Fig. 1). The probability that breeding signs were detected ($p_{3,3}$) was low for most species and for many species substantially lower than the probability of detecting only adults in breeding populations ($p_{3,2}$; Fig. 1). The exceptions were *Alytes obstetricans*, *Bufo bufo*, and *Epidalea calamita* as well as the *Rana* frogs. The latter probably had very high detection probabilities for breeding signs because they are mostly detected through egg masses (while adults can be hard to detect because males call underwater).

Breeding probability

The multistate model showed that breeding probabilities were substantially lower than 1 (Fig. 2). For most species, the ratio of breeding to non-breeding populations was between 3:1 and 5:1 (Fig. 3). However, there were species where there were only few non-breeding populations (e.g., *Rana temporaria*, *Ichthyosaura alpestris*) while for other species (e.g., *Hyla arborea*, *Triturus cristatus*) the majority of sites had non-breeding populations. The 95% credible intervals for the number of non-breeding populations were often wide, particularly for species that were either rare (e.g., *R. latastei*) or have low detection probabilities (*L. vulgaris*).

The effect of breeding state upon subsequent occupancy

Population status during the years 2011–2016 (absent, present but no breeding, present and breeding) had a strong effect on occupancy in 2017–2018 (Fig. 4). The results, however, have to be interpreted cautiously because the number of sites included in this analysis is small and therefore 95% credible intervals are wide. Across all species, colonizations were observed (i.e., some sites that were unoccupied in 2011–2012 were occupied in 2017 or 2018, Fig. 4, bars labelled

“Unoccupied”). With the exception of *H. arborea*, populations of all species in state “present but not breeding” in 2011–2012 had lower occupancy probabilities in 2017–2018 than populations in state “present and breeding,” indicating that populations where breeding occurred were more likely to persist.

DISCUSSION

The analysis of breeding probabilities in an assemblage of amphibians based on data from a national monitoring program revealed that there is no breeding in many amphibian populations (Figs. 2, 3), that non-breeding populations are less likely to persist than breeding populations (Fig. 4), and that non-breeding populations are harder to detect than breeding populations (Fig. 1). A particularly striking case is the tree frog *H. arborea* where only one-quarter of the populations seem to be breeding populations (i.e., eggs and tadpoles were absent from most sites). Because the data were collected at a large number of sites and over more than half a decade, results are unlikely to be caused by a single year with unfavorable conditions, lending confidence to our results.

Reproductive success varies among years in amphibian populations (Shoop 1974, Bell and Lawton 1975, Sinsch 1992, Green et al. 2013, Greenberg et al. 2017) and many populations are apparently sink populations with insufficient reproduction to persist without immigration (Gill 1978, Sinsch 1992, Hels 2002), perhaps because of low habitat quality (Sjögren 1991, Unglaub et al. 2015, Gould et al. 2019, Schmidt et al. 2019). Our results show that breeding probabilities are substantially smaller than one and we show that in a country where declines of rare and common species have been reported (Cruickshank et al. 2016, Petrovan and Schmidt 2016), there are a number of species for which non-breeding populations outnumber breeding populations. Whether a population was breeding or non-breeding was related to persistence (Fig. 4), corroborating the qualitatively similar results of Green et al. (2013) and Tournier et al. (2017). Breeding populations were less likely to go extinct than non-breeding populations. Moreover, non-breeding populations had lower detection probabilities than breeding populations. Low detection probability can indicate higher extinction risk (Alpizar-Jara et al. 2004) because detectability is often correlated to population size (Tanadini and Schmidt 2011), further suggesting that the population is at risk (i.e., less likely to persist).

One might expect that species breeding in temporary ponds may be less affected by low breeding probabilities because they are adapted to intermittent breeding success (e.g., through bet-hedging life history strategies involving longer lifespans and reduced annual investment into reproduction; Wilbur and Rudolf 2006). Population models suggest that temporary-pond breeding species can persist despite the absence of reproduction in

FIG. 1. The probability of detections at breeding sites and non-breeding sites. Green bars denote the detection of adults (and no breeding signs), purple bars denote detections that include the detection of breeding signs. The total height of the bars gives the overall probability that the species is identified at breeding or non-breeding sites. Bars show posterior means. Estimates shown are for the WBS data set 2011–2016. The estimates and the 95% credible intervals are also presented in Appendix S1: Fig. S1. Genera are *Alytes* (*A. obstetricans*), *Bombina* (*B. variegata*), *Bufo* (*B. bufo*), *Epidalea* (*E. calamita*), *Hyla* (*H. arborea*, *H. intermedia*), *Ichthyosaura* (*I. alpestris*), *Lissotriton* (*L. helveticus*, *L. vulgaris*), *Pelophylax* (*P. ridibundus*), *Rana* (*R. dalmatina*, *R. latastei*, *R. temporaria*), and *Triturus* (*T. cristatus*, *T. carnifex*).

some years as long as the frequency of “bad” years does not increase too much (Stevens and Baguette 2008). However, a difference in breeding probabilities between species preferring different pond hydroperiod lengths was not clearly supported by the data. This can be seen by comparing the species that are typical temporary-pond breeding species (*E. calamita*, *B. variegata*, and

H. arborea) to the other species that are more likely to breed in permanent ponds (Van Buskirk 2003). The results in Fig. 4 therefore suggest that a preference for short or long hydroperiods does not appear to predict breeding probabilities. It would be important to assess the relationship between the viability of a metapopulation and the proportion of populations in a

FIG. 2. Estimates of breeding probabilities. The bars show posterior means. Error bars show 95% credible intervals.

metapopulation network that produce offspring. Green and Bailey (2015) found that a metapopulation of the Wood frog *Lithobates sylvatica* was viable if >16% of the populations produce offspring. Unfortunately, similar analyses do not exist for the species that we studied. Furthermore, it would be worthwhile to study how often populations transition between the states “breeding population” to “non-breeding population” because this determines their functional importance in a metapopulation network (Peterman et al. 2018, Gould et al. 2019). Ideally, such an analysis should also include an assessment of structural and functional connectivity (Semlitsch 2000, Baguette et al. 2013, Cruickshank et al. 2020).

Low breeding probabilities may affect metapopulations dynamics through changes in connectivity. Connectivity is known to affect patch occupancy in amphibian populations because many populations depend on immigration (Sjögren 1991, Sinsch 1992, Cruickshank et al. 2020). Immigration depends, amongst other things, on the number of emigrants produced by neighboring populations (Hanski 1994). Commonly used metapopulation connectivity metrics are thought to reflect this number and are pragmatically calculated using the distance between sites and the size (area) of the sites. The size of a patch is thought to reflect the number of emigrants (Hanski 1994). However, when only a subset of populations are breeding populations, connectivity measures that

FIG. 3. The numbers of occupied sites at which breeding is occurring and in which the species is present but no breeding is occurring, within the WBS data set (years 2011–2016). The colored bars show posterior means. Error bars are 95% credible intervals.

acknowledge that non-breeding populations do not produce dispersing individuals should be preferred. Assuming that non-breeding populations produce no emigrants, one might thus add an indicator variable to the equation that states whether a population is a breeding or a non-breeding population (e.g., one and zero). Such a change would be easy to implement and Hamer and Mahony (2010) showed that such a modeling approach can predict occupancy and turnover of amphibians. Ideally, such an approach should be combined with recent improvements in the estimation of connectivity in metapopulations where the number of dispersers is estimated from data (Sutherland et al. 2012, Howell et al. 2018, Duarte et al. 2020). For example, Howell et al.

(2020) modeled the probability of immigration, π , between the focal pond i and the neighboring pond m as $\pi_{i,m} = \exp(-\rho \times d_{i,m})$, where ρ describes how the dispersal probability declines with distance and d is the distance between ponds i and m . This equation might be expanded to $\pi_{i,m} = \exp(-\rho \times d_{i,m} \times b)$, where b is an indicator of breeding that equals 1 if pond m is a breeding population and 0 if it is a non-breeding population. Modeling connectivity and the number of dispersers in such a way and might lead to more realistic estimates of connectivity and might explain why connectivity is sometimes found to be unimportant for amphibian metapopulation dynamics (Marsh and Trenham 2001, Prugh et al. 2008). Moreover, distance d between ponds may further include

FIG. 4. Effect of breeding status in the first round of surveys (absent, present but no breeding, present and breeding) upon the occupancy status of sites in the second round of surveys (absent, present).

information on the landscape resistance to colonization (Howell et al. 2018).

It would be important to understand the reasons why breeding probabilities are low. Lacking biologically relevant data, we could not undertake an analysis of the determinants of breeding probability, but such an analysis would clearly be worthwhile. In particular, joint analyses of habitat and occupancy dynamics might prove valuable (Miller et al. 2012, Gould et al. 2019). Predictor variables of particular interest would include habitat quality (Unglaub et al. 2015, Schmidt et al. 2019), invasive species (Miller et al. 2012, Manenti et al. 2020), and population size (e.g., Allee and density dependent

effects; Cayuela et al. 2019, Boualit et al. 2020). Furthermore, one might also partition breeding probability into the probabilities that eggs, larvae and/or metamorphs are present (Green et al. 2013) and link these probabilities to explanatory variables. Ultimately, one should use estimates of breeding probabilities to determine the contribution of populations to the metapopulation and whether they should be classified as sources or sinks (Runge et al. 2006).

We suggest that breeding probabilities should be regularly assessed because they affect occupancy dynamics. Distinguishing between breeding and non-breeding populations contributes to a more mechanistic

understanding of occupancy dynamics and thereby increases the value of a monitoring program that tracks these dynamics. Importantly, recording the observation of eggs and larvae in our monitoring program did not lead to additional costs because these life stages could be detected while looking for adults. However, the 95% credible intervals of occupancy and detectability parameters were wide. This was partly because the number of species occurrences was low. This is known to lead to imprecise estimates, particularly in multistate models (Kéry and Royle 2020). The precision of estimates would increase with higher detection probabilities. Green et al. (2013), for example, reported for wood frogs high detection probabilities of eggs and tadpoles of 0.94 and 0.96, respectively. Detection probabilities were much lower in our study but could be increased if surveyors were instructed to search more intensively for eggs, larvae, and possibly metamorphs. This might increase costs, however.

An unexpected result with implications for monitoring was that detection probabilities for non-breeding populations were low (Fig. 3). As discussed above, low detection probabilities may be caused by small population size (Tanadini and Schmidt 2011). Low detection probabilities imply that many non-breeding populations may have been overlooked. For example, a non-breeding population of the common frog *R. temporaria* had a detection probability of 0.14. Thus, the cumulative detection probability after four site visits is 0.45, suggesting that many non-breeding populations were missed. Therefore, additional site visits may be necessary to detect non-breeding populations (Tanadini and Schmidt 2011). Detection of non-breeding populations would be important because extinction risk could be decreased through species-specific habitat management.

The monitoring of breeding probabilities has applications beyond occupancy and trend estimation. Issues in conservation biology such as the success of invasive species could be traced with such data. For example, *T. carnifex* had higher breeding probabilities than *T. cristatus* (Fig. 1) and the former is invasive in some areas in northern Switzerland and has supplanted the native *T. cristatus* (Dufresnes et al. 2016). A higher breeding propensity may have contributed to propagule pressure and to the spread of this invasive species.

Although we began the discussion with the statement that the absence of reproduction in many amphibian populations is a reason for concern, we want to end the discussion with a positive message for amphibian conservation. Lack of breeding is a conservation problem that is actionable because the probability of breeding can be quantified through monitoring programs and because breeding probabilities can be increased through pond management, possibly using adaptive management (Canessa et al. 2019) or based on the knowledge compiled in the conservation evidence data base (Smith and Sutherland 2014). For example, breeding may be restored through the removal of nonnative fish

(Vredenburg 2004) or ponds with hydroperiods that maximize reproductive success can be constructed (Schmidt et al. 2015). If we focus on problem solving, then conservation action may lead to the recovery of amphibian populations despite the many gloomy reports of worldwide declines (Grant et al. 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2357/full>

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Data (Cruickshank et al. 2021) are available from EnviDat at <https://doi.org/10.16904/envodat.216>.