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Perspective

Benefits and limits of comparative effectiveness studies in evidence-based conservation

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ABSTRACT

Conservation action aims at halting the erosion of biodiversity. Assessing the outcome of a conservation intervention is thus key to improving its efficiency. This is often done by comparing an intervention to a control. Comparative effectiveness studies, on the other hand, compare multiple conservation interventions among each other. In doing so, one can determine which are the most beneficial interventions despite the lack of a control and a formal experimental design. We use an amphibian conservation study to discuss the benefits and limits of this approach. We used the comparative effectiveness approach to evaluate the outcome of a pond creation project. We measured habitat variables at three spatial scales (pond, terrestrial microhabitat, and landscape) and used multistate occupancy and N-mixture models to account for imperfect detection and to relate the explanatory variables to pond colonization, species abundance and the presence of tadpoles (i.e., evidence for successful reproduction). Although characteristics of the created ponds mattered, the availability of suitable terrestrial microhabitat (such as dry stone walls) was even more important in terms of conservation success as measured by colonization and abundance. This case study shows that successful amphibian conservation action depends on landscape complementation, i.e., the paired availability of suitable aquatic and terrestrial microhabitat. We conclude that comparative effectiveness studies can be used to provide critical information for improved conservation action. However, small sample size and a lack of randomization may a priori represent an impediment to strong inference. Nevertheless, comparative effectiveness studies can provide valuable guidance for evidence-based conservation.

1. Introduction

Conservation biologists have the dual task of identifying the causes of biodiversity erosion, and to provide recommendations to halt or reverse it (Soulé, 1985; Sodhi et al., 2011) and even to initiate conservation action that may lead to species recovery (Arlettaz et al., 2010). Therefore, assessing the uptake and effectiveness of existing conservation strategies and recommendations should be an integral component of the conservation process (Sutherland et al., 2004; Ferraro and Pattanayak, 2006; Arlettaz et al., 2010). Despite the clear mandate, a surprisingly small proportion of conservation science papers offer solutions to real-world problems (Godet and Devictor, 2018). For example, Canessa et al. (2019 – this issue) looked at the vast research on an emerging disease which threatens amphibian diversity and found that only a few studies offered solutions. Here, we use an amphibian conservation case study to suggest that comparative effectiveness studies (as defined by Smith et al., 2014), part of the toolkit of evidence-based conservation (Sutherland et al., 2004), should be used more often to improve the effectiveness of conservation action.

Effectiveness of conservation actions is often, but not always, measured and reported (Smith and Sutherland, 2014). Many studies compare a treatment (i.e., management action) to a control where no management was undertaken or they use a before-after design (Margoluis et al., 2009; Smith et al., 2014). With this approach, one can tell whether management action was successful. For example, Waddle et al. (2013) compared the occurrence of amphibians in restored

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wetlands to occurrence in unmanaged wetlands in agricultural land. They found that amphibians were more likely to occur in restored wetlands than in wetlands in agricultural lands (for a review on wetland restoration, see Sievers et al., 2018). Comparative effectiveness studies go one step further because they compare results across different conservation interventions simultaneously (Smith et al., 2014). Comparative effectiveness studies are conceptually similar to Diamond's (1983) “natural experiments”. Comparative effectiveness studies differ from natural experiments because the “experiment” is not natural but rather the outcome of man-made conservation action. The direct comparison of multiple management interventions is important because generally several conservation actions or ways of implementation could be entertained (e.g., Heard et al., 2018). Thus, one can go beyond the dichotomy success/no success and use comparative effectiveness studies to rank the success rate of management interventions. Rannap et al. (2009), for example, compared the use by amphibians of unmanaged, restored and newly created ponds (i.e., two types of conservation interventions). They also identified characteristics of the ponds, such as presence of submerged aquatic vegetation, which favoured colonization by amphibians and could deliver clear recommendations for future pond restoration and creation projects.

We use a case study to illustrate the comparative effectiveness approach. The focus of the case study is on the creation of new breeding habitats for amphibians. Habitat loss and degradation are the principal drivers of the ongoing erosion of biodiversity (Cushman, 2006; Hanski, 2011; Ceballos et al., 2015). In contrast to other drivers of biodiversity decline such as climate change and emerging infectious diseases, the effects of habitat loss are, at least in theory, comparatively easier to mitigate because conservation action can be implemented locally and because the habitats of many species can be restored or created by humans (Dobson et al., 1997). Amphibians – the most highly endangered class of vertebrates (Stuart et al., 2004) – are a taxon that is negatively affected by habitat loss and degradation (Stuart et al., 2004; Cushman, 2006; Gardner et al., 2007), but habitat management and creation can counteract declines (Rannap et al., 2009; Beebee, 2014; Pilliod and Scherer, 2015; Schmidt et al., 2015). This is possible because many amphibian species inhabit both natural and human-made wetlands and ponds (Knutson et al., 2004; Ruhi et al., 2012; Sievers et al., 2019), so breeding sites can be restored or built (Porej and Hetherington, 2005; Beebee, 2014; Calhoun et al., 2014b).

However, given imperfect knowledge of the ecology of a species, conservation action is not immune to errors in design and implementation, with unanticipated negative effects on target species (Beebee, 2014). Comparative effectiveness studies investigating the outcome of multiple conservation interventions can help to determine the most effective methods to guide future habitat restoration and creation. In our case study, we compare constructed ponds with different habitat characteristics (e.g., depth, size), with or without terrestrial microhabitats and in different landscape settings. Such a comparison may allow us to learn which characteristics (pond, terrestrial microhabitat, landscape) determine the success of conservation action (Stumpel and van der Voet, 1998; Shulse et al., 2010; Porej and Hetherington, 2005; Smith et al., 2014).

The focal species of the pond creation project and study was the midwife toad, *Alytes obstetricans*, which is Red Listed in many European countries because of population declines and whose status is “unfavourable” in many reports on the implementation of the European Habitats Directive (Barrios et al., 2012). In Switzerland, the species is ranked as endangered because about 50% of the populations are estimated to have gone extinct in the past quarter century (Schmidt and Zumbach, 2005; Cruickshank et al., 2016). Habitat loss and degradation are thought to be the main causes for the decline while emerging disease does not seem to be important (Borgula and Zumbach, 2003; Tobler et al., 2012). In order to counter the regional decline and to try to reinforce the metapopulation in the Swiss Emmental, the distribution of the species was thoroughly mapped (Ryser et al., 2003). Extant habitats were restored or managed and new ponds created. The goal of pond construction was to strengthen the existing network of sites through the addition of new populations and an increase in overall connectivity. Within the identified network, ponds were constructed in places were landowners allowed to build them and included both aquatic and terrestrial microhabitats (Mermod et al., 2010). Adult midwife toads need sunny terrestrial microhabitats such as stone piles, dry stone walls, or similar rock structures or taluses offering bare ground (Ryser et al., 2003; Mermod et al., 2010; Böll et al., 2011).

For the case study, we selected newly constructed ponds in places where there were previously no ponds and no populations of *Alytes obstetricans*. The availability of a large number of newly created ponds allowed us to properly evaluate the success of the conservation project while avoiding three common deficiencies of conservation assessments. Firstly, lack of replication, which reduces explanatory power (Hurlbert, 1984; Sutherland et al., 2004). Secondly, imperfect detection (Preston, 1979; Pollock et al., 2002; Schmidt, 2005) that leads to biased species-habitat relationships (Kéry and Schmidt, 2008; Gu and Swihart, 2004; Mazerolle et al., 2005). Thirdly, we used multiple metrics to assess success because the conclusion may depend on the metric that is being chosen (Gascon et al., 2009; Unglaub et al., 2015). The first metric was colonization rate (i.e., how many ponds were colonized by the toad). Yet, the mere presence of a species at a pond (i.e., colonization of) does not provide strong evidence for “success” if the population functions as a sink, with little or no successful reproduction and recruitment (Pulliam, 1988; Nichols et al., 2007). Previous studies showed that absence of reproductive stages is common in amphibian populations (Green et al., 2013; Unglaub et al., 2015; Bancila et al., 2017). To investigate this possibility, we also documented the occurrence of tadpoles in colonized ponds. The third metric was the size of the adult population at colonized ponds. From a conservation perspective it matters whether a small or large population became established at a newly created pond but high abundance does not necessarily indicate high habitat quality (Van Horne, 1983). Because amphibians have a complex life cycle, we used explanatory variables describing the ponds, the surrounding terrestrial habitat, connectivity within the metapopulation and the wider landscape context to explain spatial variation in colonization, occurrence of tadpoles (i.e., signs of successful breeding), and abundance. These spatial scales affect distribution and abundance of species and the success of conservation projects (Stumpel and van der Voet, 1998; Van Buskirk, 2005; Carvell et al., 2011). Our comparative analysis provides evidence-based recommendations to enhance restoration action plans for this declining amphibian species and can be interpreted as a case study for the fine-tuning of conservation action based on effectiveness.

2. Methods

2.1. Study area

Newly created ponds (n = 38) were located and surveyed in the Emmental region (central coordinates 62.2°N; 19.6°E) of Switzerland. The study area covers c. 2800 km^2 and is dominated by hilly, wooded country, with nonforested areas mostly used as pastures and agricultural crops.

2.2. Amphibian survey

To obtain occurrence and abundance data, every site was visited three times during the midwife toad's breeding season in 2010 (April–June) and all life stages (tadpoles, adults, calling males) were recorded as detection/nondetection data for occupancy analysis. During every site visit, we counted the number of calling males. Midwife toad males call on land close to their burrows. The number of calling males serves as a proxy for abundance of males. Site visits started at dusk and finished before 03:00 a.m. The pond shores and their surroundings were also systematically searched for additional adults during 20 min using a strong torch light. To collect data on breeding, two daytime dip netting surveys for tadpoles were conducted at every site in all types of pond microhabitats. To avoid the spread of pathogens, field equipment and boots were disinfected using Virkon S ($2\,g\,l^{-1}$, Antec International – A DuPont Company, Sudbury, Great Britain) after every site visit (Schmidt et al., 2009).

2.3. Habitat variables

To avoid model overfitting (Anderson et al., 2001), we selected a small number of variables that are potentially easy to modify by conservation action, and which are thought to be important for the success of midwife toad conservation (based on our own experience and the amphibian conservation literature; Mermod et al., 2010). Variables describe both the aquatic and terrestrial microhabitat and connectivity to other local populations in the metapopulation. Other factors that affect the distribution and abundance of amphibians, such as the presence of fish, were not included because at the time of the survey only one of the ponds contained fish. We measured the surface area (6 to 400 m^2) and depth of ponds (maximum depth ranged from 0.1 to 1.5 m; water levels do not fluctuate much) in the field. Pond age was also included in the analysis (range: 1 to 25 years). To describe the terrestrial habitat, we assessed whether there were dry stone walls, piles of stones and taluses with bare ground (Fig. 1). Presence/absence of those habitat variables was assessed directly in the field within a circle with a radius of 100 m. We used the "Vector25" GIS data set provided by the Swiss Federal Office of Topography (Bundesamt für Landestopographie swisstopo, 2018) to measure the percentage (0–99%) of forests within a radius of 100 m around the pond. We used a simplified version of Hanski's (1994) formula to calculate connectivity, $C_i = \Sigma \exp(d_{ij})$, where d_{ij} is the straight-line distance between ponds i and j. Data on the location of the ponds in the study area was obtained from the data base of Swiss Amphibian and Reptile Conservation Programme (Info Fauna Karch) and our own observations. Connectivity ranged from 0.142 to 3.388. The correlation between pond size and depth was 0.52. All other correlations between continuous explanatory variables were smaller than $|0.27|$.

2.4. Statistical analysis

We used multistate occupancy to estimate occupancy and reproduction, and N-mixture point count models to estimate abundance of calling males (Nichols et al., 2007; Royle and Dorazio, 2008). All models adjust estimates of occupancy, reproduction or abundance for imperfect observation. The multistate occupancy model had three states: species absent, species present but no breeding, species present and breeding. Multistate occupancy models estimate the probability that a pond is occupied and the probability that reproduction occurs (given occupancy). Because all ponds were created, occupancy implies colonization of the new pond. In the multistate occupancy model, reproduction means that offspring are produced and tadpoles present at a given site; it is therefore a characteristic of the population rather than of individuals. Detection probabilities in multistate occupancy models are specific for each state.

We fitted a single multistate model to the data. All six covariates were used to model both occupancy and reproduction probabilities. Continuous covariates were normalized prior to analysis (mean = 0, standard deviation = 1). Detection probability was held constant. We also explored different modelling strategies (e.g., one explanatory variable at a time) and found that results were qualitatively similar.

The N-mixture model estimates abundance from the temporally repeated counts. The model assumes a closed population size during the counts. To study the relationship between abundance and site-specific habitat variables we used the same approach as for the multistate occupancy model. We fitted one model with all six habitat variables for abundance and kept detection probability constant. All continuous habitat variables were normalized prior to analysis.

We used the R package jagsUI to fit models to the data in a Bayesian framework in JAGS (Kéry and Schaub, 2012; model code and an in-depth description of the models can be found in this book). Vague uniform priors were used for all model parameters. We ran three parallel Markov chains of which the first 20% of samples were deleted until convergence was reached (as judged by the Gelman-Rubin-Brooks statistic $\widehat{R}$; Kéry and Schaub, 2012). Habitat variables were judged to be important when 95% of the posterior distribution was either larger or smaller than zero (Wade, 2000).

3. Results

The probability of detection at a site without reproduction was 0.113 (95% credible interval [CRI]: 0.043, 0.216; all detection probabilities are per visit). The probability that the species was not detected at a site with reproduction was 0.297 (95% CRI: 0.155, 0.458). The probability that the species is detected at a site with reproduction while reproduction is not observed (i.e., the state misclassification probability) was 0.530 (95% CRI: 0.360, 0.706). The probability that the species was detected and reproduction observed was 0.173 (95% CRI, 0.064, 0.320; those three latter probabilities sum to 1).

Parameter estimates of the regression coefficients are shown in Table 1. In our analysis, credible intervals were wide. We believe that this is partly due to the fact that we used multistate models. We repeated the analysis using single-state occupancy models (MacKenzie et al., 2002) and found the results regarding the probability of occupancy were similar, but with much narrower credible intervals.

3.1. Occupancy

Using the model, 15.7 sites (95% CRI: 10.0, 20.0) were unoccupied, 14.6 sites (95% CRI: 11.0, 20.0) were occupied but there was no reproduction and 6.6 sites (95% CRI: 6.0, 7.0) were occupied with reproduction. Whether a pond was colonized (i.e., occupied) depended on

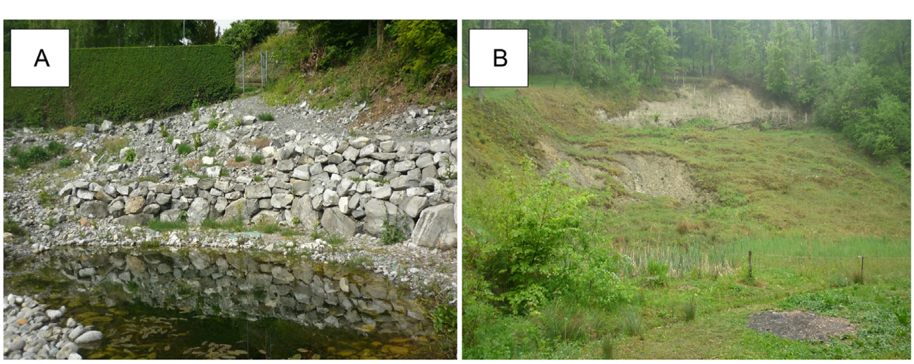

Fig. 1. (A) A newly constructed pond where terrestrial habitat (a dry stone wall) was built. Adult toads are commonly found in dry stone walls. (B) Midwife toad habitat in an abandoned quarry. The talus with bare ground serves as terrestrial habitat for adult toads. Both sites are not located in the study area but are representative for the species and conservation action. Pictures were taken by Benedikt Schmidt.

Table 1
Parameter estimates of multistate occupancy models (probabilities of occupancy and reproduction) and N-mixture models (for abundance). The table entries show the mean of the posterior and the limits of the 95% credible interval. f is the proportion of the posterior which is either larger or smaller than zero (depending on the sign of the mean).

Variable	Mean	Lower limit of 95% credible interval	Upper limit of 95% credible interval	f
Occupancy probability				
Intercept	−3.052	−11.656	8.530	0.751
Pond size	−7.456	−20.212	4.449	0.925
Pond depth	−8.608	−20.911	−0.237	0.981
Terrestrial habitat	10.588	−1.104	25.567	0.961
Forest cover	−0.691	−7.126	8.433	0.654
Connectivity	2.016	−4.489	9.853	0.736
Pond age	10.678	−0.213	26.362	0.970
Reproduction probability				
Intercept	−7.294	−19.862	7.871	0.861
Pond size	−2.996	−18.286	12.912	0.652
Pond depth	8.637	−2.480	21.895	0.928
Terrestrial habitat	−2.177	−17.001	11.053	0.604
Forest cover	−15.773	−27.917	−5.674	1.000
Connectivity	−0.741	−10.491	9.935	0.576
Pond age	5.362	−1.393	15.689	0.927
Abundance				
Intercept	−1.789	−2.607	−1.038	1.000
Pond size	−0.216	−0.667	0.172	0.853
Pond depth	0.398	0.071	0.733	0.991
Terrestrial habitat	3.358	2.663	4.098	1.000
Forest cover	−1.478	−1.935	−1.081	1.000
Connectivity	−0.160	−0.409	0.086	0.902
Pond age	0.022	−0.185	0.216	0.586

pond depth and age, and the availability of suitable terrestrial habitat. Depth had a negative effect on colonization whereas age and terrestrial habitat had positive effects (Table 1, Fig. 2). Pond size had a negative effect on colonization but the evidence was weaker because less than 95% of the posterior distribution was negative (Table 1). Connectivity had the expected positive effect but the 95% credible interval overlapped zero. Forest cover did not seem to affect colonization.

3.2. Reproduction

The probability that breeding occurred (i.e., tadpoles were present) at an occupied site was 0.32 (95% CRI: 0.24, 0.39). The probability of reproduction was negatively affected by forest cover (Fig. 3). Pond depth and age had positive effects on reproduction but the evidence was weaker because less than 95% of the posterior distribution were positive (Table 1). The other variables did not seem to have an effect.

3.3. Abundance

Detection probability was 0.392 (95% CRI: 0.260, 0.520). Estimated abundance was positively affected by pond depth and the presence of dry stone walls or taluses with bare ground, and negatively by the amount of forest cover (Fig. 4). Pond size, connectivity and pond age did not seem to have an effect.

4. Discussion

We used a comparative effectiveness approach to better understand the characteristics that determine the use of created ponds by a threatened amphibian such that we can provide guidance for improved future conservation action. Although variables measured at the three scales (pond, nearby terrestrial microhabitat; landscape) drove responses, the most striking result was that terrestrial microhabitat appeared to be much more important than the characteristics of the aquatic habitat. Fig. 4 shows that estimated abundance is essentially zero in the absence of suitable terrestrial microhabitat in the pond surroundings. Thus, the comparative effectiveness approach allowed us to determine the key determinants of the success of conservation actions.

4.1. Determinants of successful amphibian conservation

Pond characteristics such as depth affected both colonization and abundance, but effects were opposite. While shallower ponds (less than 1 m deep) were more likely to be colonized by toads, deeper ponds harbored larger populations; an effect of depth on reproduction was weakly supported. Shallow ponds may be better for successful colonization because they are warmer. Pond temperature determines the length of larval period (Thiesmeier, 1992) and shorter larval periods increase population growth rates in amphibian species with overwintering tadpoles (Govindarajulu et al., 2005). Thus, shallow ponds may increase the likelihood of successful colonization for this species because they enhance population growth rate when populations are still small just after colonization. Once a population is well established at a pond, the benefits of short larval periods may be of lesser importance and deeper ponds may become more favorable (e.g., carrying capacity might be larger).

The presence of suitable terrestrial microhabitat affected colonization, reproduction and abundance, with consistent strong positive effects on all metrics; in contrast, forest cover negatively affected all metrics. This pattern largely corroborates our knowledge of the natural history of the midwife toad (Böll et al., 2011). Adults are often observed in dry stone walls and similar terrestrial habitat types. Terrestrial shelters should be sunny (Mermod et al., 2010) and forest cover may lead to too much shading. However, midwife toads use forest edges as terrestrial microhabitat (Ryser et al., 2003; Böll et al., 2011). As this study looked only at the total forest cover surrounding pond sites, more detailed investigations would be worthwhile. For example, one might analyze the spatial configuration of forest patches and the length of forest edges (primarily sunny, south-facing edges).

We identified several habitat characteristics that increased the likelihood of pond conservation success for the midwife toad. It is important to note that it may take five to ten years after pond construction until a reproducing population establishes at a pond (Fig. 2; see Travis, 1996 for a general discussion). Based on our models (Figs. 2, 3, 4), we suggest that suitable terrestrial microhabitat is of prime importance and forest cover in a circle with 100 m radius should not exceed 33%. Ponds with a surface area up to 100 m^2 appear better than larger ponds. However, the number of large ponds in our study area was small and one of those contained fish. Deep ponds (more than 0.8 m) seem better for reproduction and abundance but are colonized more slowly. Our description here of an optimal pond based on our model matches rather well the traditional "Feuerweiher" that farmers in the Emmental used to build close to their farms and which were commonly used by midwife toads (Ryser et al., 2003).

We wish to stress that it is not always possible to create ponds in the most suitable locations, especially on private land where the owners have the final word. This implies that ponds may not make the greatest possible contribution to metapopulation viability because the location in the network may not be optimal (Runge et al., 2006; Pellet et al., 2006; Altermatt and Ebert, 2010; Green and Bailey, 2015; Scroggie et al., 2019 – this issue). Nevertheless, we believe that positive interactions with landowners and other stakeholders are crucial because they make a conservation program more successful in the long term (Calhoun et al., 2014a; Hartel et al., 2019 – this issue).

In our view, the result that the availability of terrestrial habitat had a stronger effect than the characteristics of the ponds themselves on population abundance, is certainly one of the main lessons of this study.

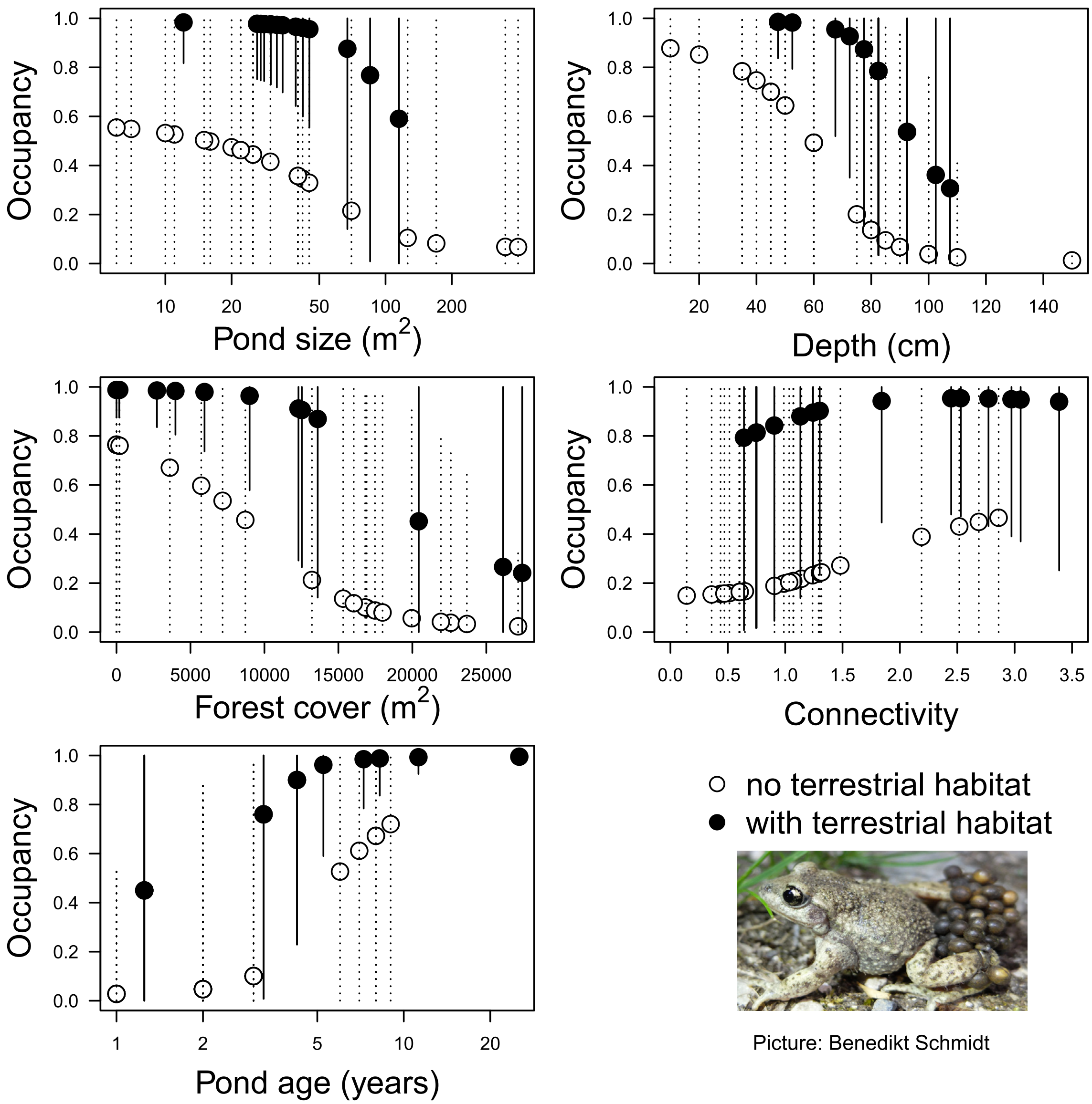

Fig. 2. Estimated occupancy probabilities as a function of habitat characteristics and the presence/absence of terrestrial habitat (because all ponds were created, occupancy implies colonization of the new pond). Open and closed symbols show predictions made for observed values of habitat characteristics. Error bars are 95% credible intervals. Predictions are based on a model with all explanatory variables. When making predictions for one variable, the other variables were fixed at their mean (which was zero after normalization). To improve readability, symbols were slightly horizontally jittered or a logarithmic x-axis was used. The picture shows an adult male midwife toad carrying eggs.

Our results corroborate other studies which found that amphibian distributions are often best predicted by combinations of aquatic and terrestrial habitat variables (i.e., landscape complementation; Van Buskirk, 2005; Pope et al., 2000; Denoël and Ficetola, 2008). Our study also confirms the expert-based view that midwife toads need stone piles, dry stone walls, or similar rock structures or taluses offering bare ground because this is a terrestrial microhabitat preferentially used by adult midwife toads (Ryser et al., 2003; Mermod et al., 2010; Böll et al., 2011) and it confirms the recommendations for the conservation management of midwife toads that more emphasis should be put on the terrestrial rather than the details of the aquatic habitat (assuming that there are no fish; Borgula and Zumbach, 2003; Mermod et al., 2010). While the removal of nonnative fish which prey on tadpoles can lead to the recovery of amphibian populations (Knapp et al., 2016), other recovery programs and conservation strategies for amphibians have also stressed the importance of terrestrial habitat conservation and management (Denton et al., 1997; Trenham and Shaffer, 2005; Hamer and McDonnell, 2008). A likely reason for this may be that the survival of postmetamorphic juveniles is a main determinant of population growth rate in pond-breeding amphibians (Petrovan and Schmidt, 2019 – this issue). The availability of suitable terrestrial microhabitat may thus have a strong effect on amphibian population dynamics through its effect of juvenile survival (see Patrick et al., 2008 for a case study).

Costs of pond construction are largely independent of the habitat characteristics that we measured because they depend primarily on whether an artificial liner is necessary, the access to the site and the type of excavator which can be used. Construction of a terrestrial microhabitat can be costly if it is a dry stone wall (Fig. 1A) but is cheaper when a simple stone pile or suitable terrestrial microhabitat restored (e.g. removal of scrub).

4.2. Benefits and limits of comparative effectiveness studies

Smith et al. (2014) argued that comparative effectiveness assessments are useful when evaluating the outcome of conservation projects. Just as we learn from natural and quasi-experiments (Diamond, 1983;

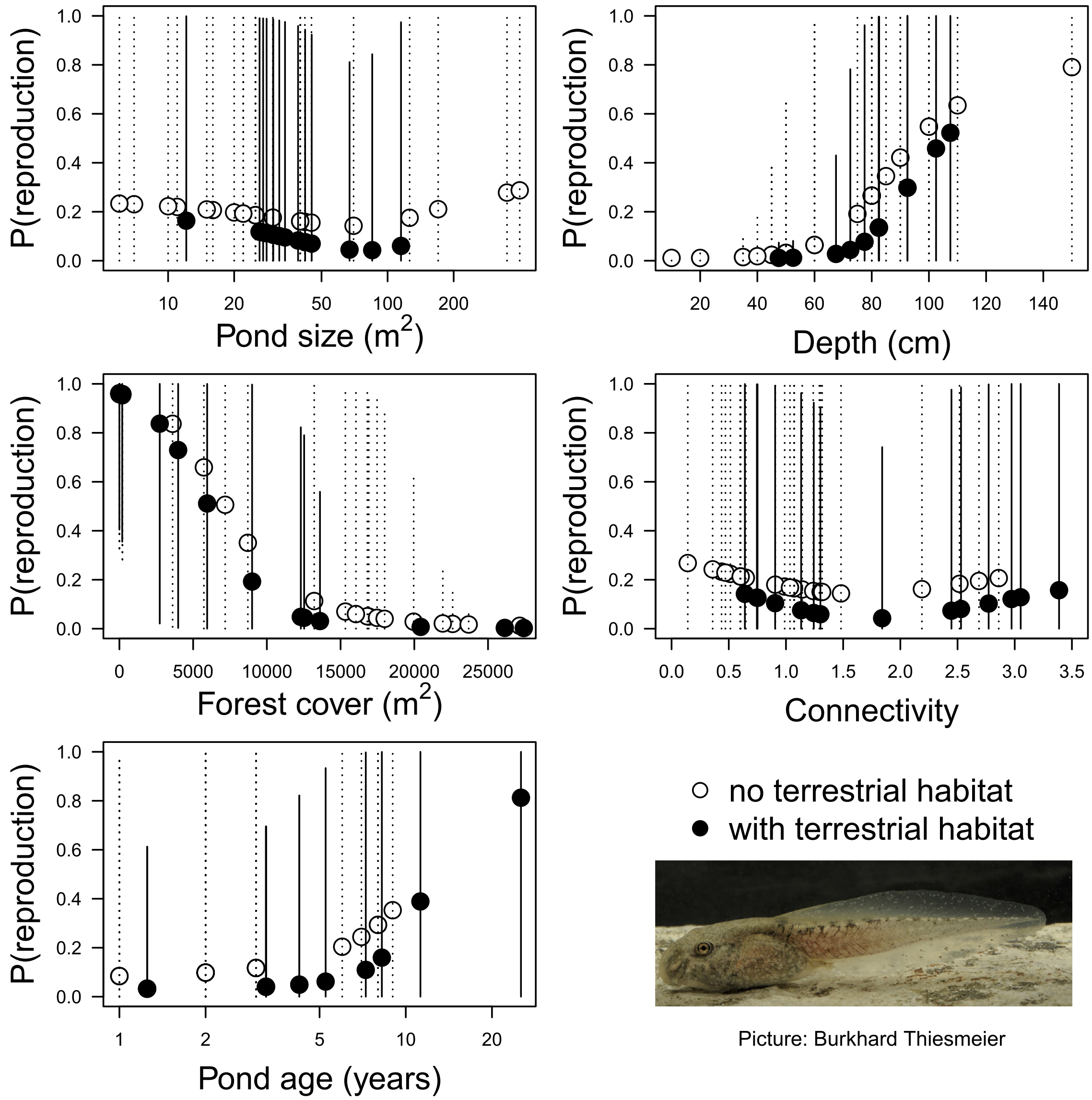

Fig. 3. Estimated reproduction probabilities, given that a site was occupied, as a function of habitat characteristics and the presence/absence of terrestrial habitat. Open and closed symbols show predictions made for observed values of habitat characteristics. Error bars are 95% credible intervals. Predictions are based on a model with all explanatory variables. When making predictions for one variable, the other variables were fixed at their mean (which was zero after normalization). To improve readability, symbols were slightly horizontally jittered or a logarithmic x-axis was used. The picture shows a second-year tadpole the midwife toad.

Margoluis et al., 2009), we can learn from the analysis of conservation action, which can be seen as "conservation experiments". Although true experiments are to be preferred because inference from experiment is stronger than from any other type of study (Diamond, 1983; Margoluis et al., 2009), experiments are not always feasible in conservation (but see Semlitsch et al., 2009; Shulse et al., 2012). Still, the observational approach of comparative effectiveness studies is powerful because multiple treatments (i.e., conservation actions) are compared such that the outcome of different interventions can be compared and the rate of success can be ranked. One strength of the approach is that no control is required even though a control may be useful for certain questions. Furthermore, comparative effectiveness studies look at conservation actions that were already implemented and thereby allows for rapid learning and development of recommendations. An experiment would have to be set up and it may take years until results are obtained.

We would, however, be remiss to ignore the limitations of such an approach. Many of these limits of comparative effectiveness studies are related to the constraints of study design. For example, comparative effectiveness studies are correlational. Causation cannot be established in the context of a comparative effectiveness study; other, possibly correlated variables may be important. For example, Zanini et al. (2008) found that road density had a positive effect on amphibian pond occupancy and argued that this was a spurious effect because roads fragment amphibian habitat and because amphibians get killed on roads. We suggest that if there is a clear biological mechanism why a factor should be important, then we can have more confidence that there is an underlying causality. Generally, we concur with the suggestion of Anderson et al. (2001) that explanatory variables should be selected carefully and reasons for the selection should be defined a priori.

Furthermore, in our case, and probably in general, conservationists did not decide randomly where to build which type of pond. First, sites were not selected randomly but rather where previous experience suggested that success was likely and where landowners allowed building new ponds. While those facts put constraints on inference, interactions with land owners and stakeholders are likely to make a conservation program successful (Calhoun et al., 2014a; Hartel et al., 2019 – this issue). Second, pond characteristics such as pond depth

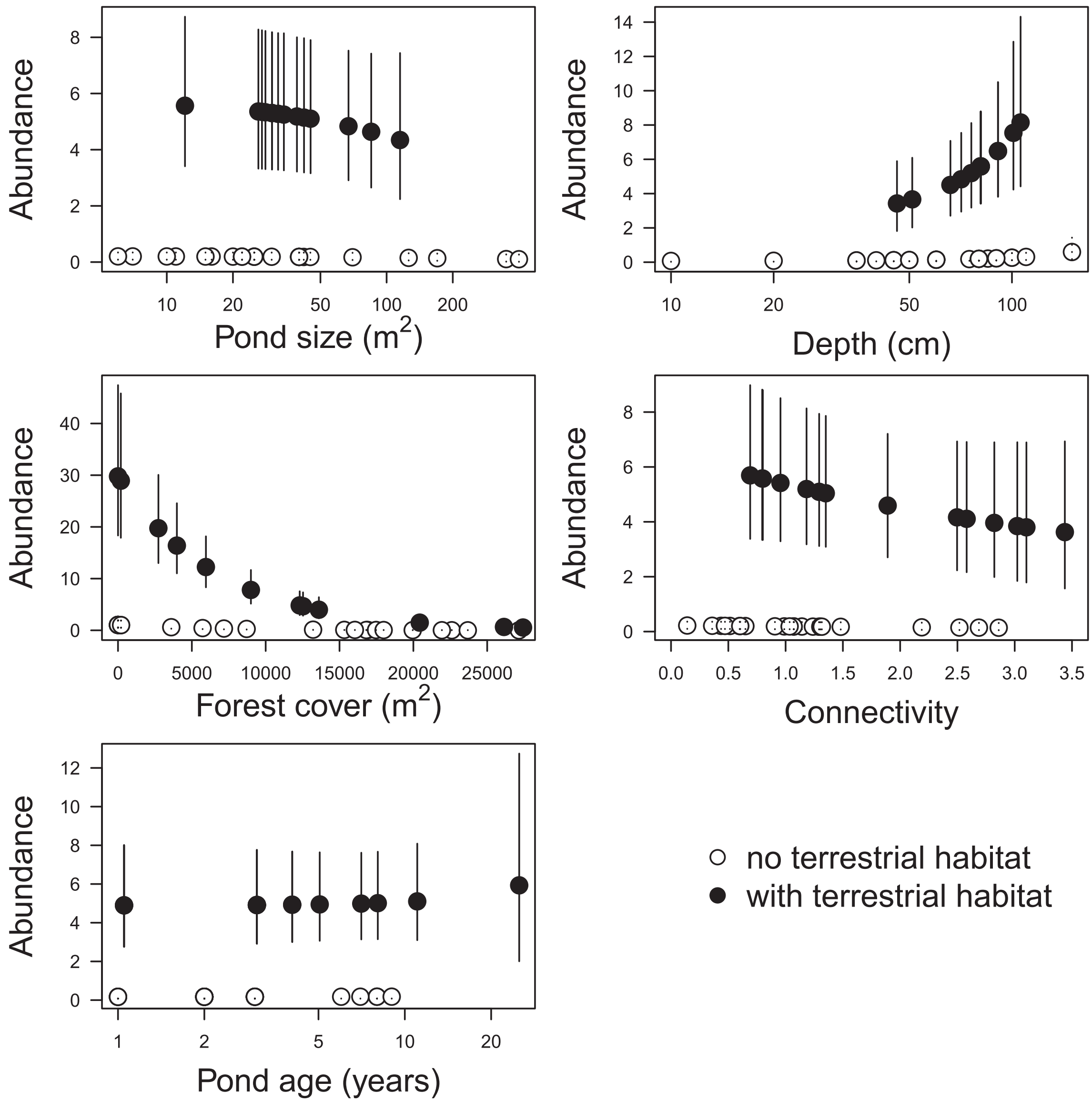

Fig. 4. Estimated abundance as a function of habitat characteristics and the presence/absence of terrestrial habitat. Open and closed symbols show predictions made for observed values of habitat characteristics. Error bars are 95% credible intervals. Predictions are based on a model with all explanatory variables. When making predictions for one variable, the other variables were fixed at their mean (which was zero after normalization). To improve readability, symbols were slightly horizontally jittered or a logarithmic x-axis was used.

were not assigned randomly to locations. The lack of randomization limits inference and means that generalizations are difficult. Third, the lack of variation in conservation action limits inference. Conservationists only undertake actions that they think will be successful. For example, if only deep ponds are created, then one cannot assess the effect of pond depth (see Eigenbrod et al., 2011, for further discussion). If some treatment combinations do not exist (e.g. deep, small ponds), then we cannot disentangle the effects of such conservation-action induced correlation of pond characteristics (e.g., small, shallow ponds vs. large, deep ponds).

Finally, sample size may limit strong inference. Using a set of 38 newly created ponds, we asked which ponds were most successful and provided evidence that different factors drive colonization, reproduction and abundance. We used simple models but some credible intervals were wide (particularly for the effects on the presence of tadpoles, Fig. 3). This created ambiguous results. Even though 38 ponds are a lot in terms of both conservation action and the field work necessary to collect the data, sample size remains small for statistical analysis. Because we wanted to avoid models that are too complex for our data, we only used a small set of explanatory variables. Many other variables may be important and one might also study interactions and non-linear relationships. Lack of sufficient replication for comparative effectiveness studies may not be uncommon in today's real world conservation For instance, using time series data from all British natterjack toad populations, Buckley et al. (2014) could not unambiguously determine whether populations with management had higher population growth rates than unmanaged populations. Given the high number of habitat variables that can affect habitat use by amphibians, one would need very large data sets to gain a full understanding of the factors that determine the success of conservation projects. Such large data sets are rarely available or it may not be possible to study all ponds for logistic reasons. If a conservation project has clear objectives, however, scientists can identify the most important variables which merit study through discussions with conservationists and other stakeholders (Converse, 2019 – this issue) and select the most important characteristics to consider (Canessa et al., 2015).

Uncertainty about the best state variables which should be used to measure success can be another limit of comparative effectiveness. We used multiple state variables (occupancy, abundance, reproduction) to quantify success. While some variables were important for all state variables, other variables only affect a single state variable. This type of uncertainty about success could be solved if the conservation project has clear objectives (Converse and Grant, 2019 – this issue). Once clear objectives are defined, the choice of state variables becomes easier (Converse and Grant, 2019 – this issue). The choice of metrics could also be determined using ecological sensitivity analysis. That is, one could ask which life history stage has the greatest effect on population growth. For amphibians, the fate of postmetamorphic juveniles appears to drive population dynamics (Petrovan and Schmidt, 2019 – this issue). Thus, it seems worthwhile to include this stage in future studies.

5. Conclusion

Created ponds were most successful at attracting and maintaining populations of the threatened midwife toad if suitable terrestrial microhabitat neighboring the pond was available. We were able to discern this important result using a comparative effectiveness approach. If conservation scientists use comparative effectiveness more often, then they could rapidly build up a solid evidence base for conservation. By doing so, they could ensure that more solutions to conservation problems are published and the gap between science and practice is reduced (Arlettaz et al., 2010; Godet and Devictor, 2018). A comparative effectiveness approach allows one to learn while doing conservation on the ground. This is clearly a step forward in conservation because there is no need to do research first and delay conservation action until a system is fully understood (Grant et al., 2013; Nichols et al., 2015).

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Author contributions

BRS, RA and MK conceived the study. BL provided data and expert advice that was necessary to conduct the study. MK collected data in the field and analysed the data with help from BRS and MS. BRS led the writing. All authors contributed to the writing.

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