

# **Factors influencing colonization of created habitats by an endangered amphibian species**

## **Master Thesis**

der philosophisch-naturwissenschaftlichen Fakultät der  
Universität Bern

vorgelegt von  
Madeleine KROEPFLI<sup>1</sup>  
2011

Leiter der Arbeit

Dr. Benedikt R. Schmidt<sup>2;3</sup>

Prof. Dr. Raphaël Arlettaz<sup>1;4;5</sup>

<sup>1</sup> Institute of Ecology and Evolution – Division of Conservation Biology,  
University of Bern, Erlachstrasse 9a, CH-3012 Bern, Switzerland

<sup>2</sup> Institute of Evolutionary Biology and Environmental Studies, University of Zürich,  
Winterthurststrasse 190, CH-8057 Zürich, Switzerland

<sup>3</sup> karch, Passage Maximilien-de-Meuron 6, CH-2000 Neuchâtel, Switzerland

<sup>4</sup> Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

<sup>5</sup> Swiss Ornithological Institute, Valais Field Station, Nature Centre, CH-3970 Salgesch, Switzerland

## Abstract

1. The success of conservation projects is rarely assessed and therefore decisions are often not evidence based. We assessed the success of an amphibian conservation project. We assessed whether 38 ponds that were created specifically for the endangered midwife toad *Alytes obstetricans* were indeed used by the species.
2. Imperfect detection and three different biodiversity metrics such as colonization, abundance and reproduction, were taken into account. Four different groups of covariates affecting the use of the ponds were measured at four different scales: pond and water characteristics, habitat characteristics in a 10 m and 100 m radius around the pond and landscape characteristics. We used multistate occupancy models and N-mixture count models to analyze the data.
3. Our results support species ability to colonize created sites. 28.9% of all sites were colonized by the species. Yet, we found evidence for reproduction at only 54.4% of the colonized sites.
4. Pond characteristics and the immediate surroundings did not seem to affect colonization, reproduction and abundance. The amount of ponds at a site influenced colonization and abundance in a positive way. Pond age, however, showed a positive influence on colonization and on reproduction. In contrast, characteristics of the terrestrial habitat were important. Among the habitat characteristics within a 100 m radius around the pond the availability of a stonewall or a hangslide had a positive and

constructions a negative effect on colonization and on abundance. Forest influenced reproduction and abundance in a negative way. At the landscape scale, the amount of stony area, including rocks and gravel influenced colonization in a negative way. Connectivity had a positive effect on abundance which suggests that abundance may not be a good metric for evaluation the success of conservation projects.

5. *Synthesis and application.* Our study provides essential information regarding the use of created habitats. It sets the basis of future efficient conservation programs providing a set of evidence-based recommendations to optimize habitat creation for an endangered amphibian species.

**Words: 322**

**Keywords:** Abundance, *Alytes obstetricans*, Bayesian statistics, colonization, detection probability, evidence-based conservation, habitat creation, multi-state occupancy model, occurrence estimation, Switzerland

## Introduction

The success of conservation projects is rarely assessed and consequently management decisions are often not based on scientific facts (Sutherland *et al.* 2004). We assessed the success of a large conservation project –creation of new ponds for an endangered amphibian species- while trying to avoid three common deficiencies. First, success of pond creation is generally assessed without replication (e.g., one new pond at a time). However, an evaluation without replication has limited explanatory power (Hurlbert 1984; Quinn & Keough 2002). To avoid the problem, replicates are necessary. Replications reduce effects from random variation (Hurlbert 1984). Second, we accounted for imperfect detection of species because imperfect detection may bias inference (MacKenzie *et al.* 2002; MacKenzie *et al.* 2003; MacKenzie 2005; Pellet & Schmidt 2005; Kéry & Schmidt 2008). Species detection is always imperfect (Schmidt 2005). Therefore failing to account for imperfect detectability can lead to wrong inference, namely underestimation of biodiversity metrics and even bias model estimates such as i.e. species-habitat relationships (MacKenzie *et al.* 2002; MacKenzie *et al.* 2003; Gu & Swihart 2004; MacKenzie 2005). Third, we used different metrics to assess success because the answer may depend on the metric that is being chosen (Heino, Mykra & Kotanen 2008; Gascon, Boix & Sala 2009). Usually, one would assess which species have colonized newly created habitat. However, this approach may be too simple. We believe that multiple metrics that describe success should be used. To define habitat quality, demographic data (e.g. reproduction) and abundance of species occupying that site

have to be considered (Van Horne 1983). Therefore, we assessed whether reproduction occurred in colonized sites. The distinction of occupied sites with and without reproduction matters when dealing with thoughts of sink and source sites (Pulliam 1988) or in other words with contributions of sites to metapopulation dynamics (Hanski 1994; Runge, Runge & Nichols 2006). Moreover it helps to clarify site quality based on a species fitness constituent such as reproduction (Franklin *et al.* 2000). As the third metric for evaluating success, we quantified abundance. It clearly matters whether a small or large population established at a newly created pond. However, one has to be careful when defining high quality sites by assuming that abundance relates to high-quality habitat (Van Horne 1983).

We chose a pond creation project for our assessment of conservation success because ponds and wetlands have been and are destroyed at an alarming rate (Imboden 1976) even though they may be hotspots of biodiversity in landscapes (Davies *et al.* 2008). To counter the negative effects of pond loss on wildlife, the creation of new ponds is often the only possibility to be up to the marks of the habitat requirements and to conserve the species (Goldberg & Waits 2009; Brand & Snodgrass 2010; Shulse *et al.* 2010). Amphibians are characteristic and endangered inhabitants of ponds. Habitat loss is a major reason for the worldwide decline of amphibians (Stuart *et al.* 2004; Gardner, Barlow & Peres 2007). Amphibians are facing an extinction crisis (Wake & Vredenburg 2008) to the extent that the class Amphibia is the most endangered vertebrate class on Earth (Stuart *et al.* 2004). With 70% of all native amphibian species being red-listed, Switzerland has cause to be concerned as well (Schmidt & Zumbach 2005). In order to be able to stop

and reverse the negative trends, we have to improve our understanding of the factors that determine distribution, abundance of the amphibians, the causes of declines and the ways to promote population recovery. The successful persistence and conservation of amphibians depend on informed planning and well-founded conservation management regarding the factors that determine persistence or decline (Schmidt & Pellet 2005). In this study we investigated the factors affecting the use of newly created breeding ponds by an endangered amphibian species, the midwife toad, *Alytes obstetricans*. To halt the decline of the species which was partly caused by habitat loss (Borgula & Zumbach 2003; Mermod *et al.* 2010), new ponds were created. We studied the factors determining the success of the pond creation project. We used different population metrics to assess conservation success: colonization (i.e., presence and absence at the new ponds), abundance, and reproduction. Our analysis provides a set of scientifically explored management and conservation guidelines regarding creation of new habitats to improve amphibian conservation.

## Material and methods

### Study Species

Midwife toad (*Alytes obstetricans*) populations are typically found in floodplains or close to ponds with sun exposed, lightly sloping banks with diggable ground and sparse vegetation (Mermod *et al.* 2010). The different pond types that are used by midwife toads often include permanent watercourses (natural and anthropogenic) and sometimes even water reservoirs (used by the fire brigade in earlier times) (Borgula & Zumbach 2003; Mermod *et al.* 2010).

In the past 25 years, almost 50% of the known midwife toad populations disappeared in Switzerland (Schmidt & Zumbach 2005). Reasons for the decline are unknown but probably include the destruction of terrestrial habitats and the disappearance of breeding ponds (Borgula & Zumbach 2003; Schmidt & Zumbach 2005; Mermod *et al.* 2010).

New ponds constructed for amphibian conservation in the study area are rarely colonized (B. Lüscher, personal communication). This might be a reason why the species shows no signs of recovery from the declines. However, scientifically confirmed reasons are lacking.

### Study area

Study sites were located in the Bernese Emmental (central coordinates 46.2 °N; 7.6 °E), Switzerland, which is a core distribution area of the species in Switzerland (Ryser *et al.* 2003). The study area covers an area of approximately 2800 km<sup>2</sup> and is dominated by hilly country with numerous forested areas. The main part of the unforested area is used for agriculture (mainly pasture land and crop production). Outside of the

villages, single barnyard settlements are the most common housing scheme (Ryser *et al.* 2003).

From 1985 until 2009, ponds were created using expert-based knowledge to match the demands of midwife toads as closely as possible (Mermod *et al.* 2010). The primary goal was to construct a network of suitable new sites, usually including both terrestrial habitats and breeding ponds, such that a well-connected metapopulation might form. 38 ponds were chosen as study sites where prior to pond construction neither amphibians nor ponds were present (B. Lüscher personal communication). No translocations of individuals took place.

## **Sampling design**

### Amphibian survey

To obtain presence/absence and abundance data, every site was visited three times during the midwife toad's breeding season in 2010 (April-June). During every site visit, the number of calling males was counted. Site visits started at dusk and lasted no longer than 03:00 a.m. The pond shores and their surroundings were searched systematically for 20 min, using a strong torch (Mag-Lite<sup>®</sup>, Maginstrument RX4019E, California, USA). All amphibians recognized visually (number of adults) and acoustically (number of callers) were recorded.

To get reproduction data, the sampling above was complemented by a number of standardized dip net sweeps during day time (Sztatecsny *et al.* 2004). Two surveys for larvae were conducted at every site.

To avoid the spread of pathogens, field equipment and boots were disinfected, using Virkon S (2 g l<sup>-1</sup>, Antec Interational – A DuPont



Company, Sudbury, Great Britain) after every site visit (Schmidt *et al.* 2009).

### Habitat analysis

We selected 19 covariates (Table 1) believed to affect colonization, reproduction and population sizes at the created ponds. The focus was on covariates with that can be manipulated by conservation authorities.

The covariates were either measured in the field, calculated using a geographic information system using arcGIS ([www.esri.com](http://www.esri.com), Environmental Systems Research Institute, California) or obtained from the database of the Swiss Biological Records Center (CSCF).

The covariates were divided into four groups. Assignment of covariates to groups depended on the spatial scale of the covariates. The first group included covariates that were measured at the scale of the pond. This group included abiotic pond and water characteristics, to estimate design features of the pond. The second and third group included covariates that were measured within 10 m from the shoreline of the pond or within a circle with a radius of 100 m, respectively. Both groups were used to analyze habitat characteristics of the terrestrial surroundings at two different scales. In the last group, landscape characteristics were measured within a circle with a radius of 1000 m, to analyze placements of ponds in the landscape.

### Statistical Analysis

We used occupancy and N-mixture point count models to analyze the data (MacKenzie *et al.* 2002; Royle 2004; Royle & Dorazio 2006; Nichols *et al.* 2007). Specifically, in order to estimate the proportion of colonized

sites, the proportion of sites where reproduction occurred and detection probabilities we used multistate occupancy models (Nichols *et al.* 2007). These models allow for multiple states, i.e. categories of occupancy (Nichols *et al.* 2007). The states were: "the site was not colonized", "the site was colonized", and "the site was colonized and reproduction occurred". These multistate models account for uncertainty in state classification (Nichols *et al.* 2007). Further to explore at which sites larger populations were present we used the N-mixture models developed by Royle (2004), which allow the estimation of population sizes (abundance) without the marking of and identification of individuals. In both modeling approaches covariates can be inserted separately for detection, occupancy and population sizes, respectively. The multistate models assume closed sites, that is no change in the occupancy state of the site during the study. Each site is either colonized or not (MacKenzie *et al.* 2002). The N-mixture models assume the populations being sampled are closed, that is, no colonization, emigration or mortality is taking place (Royle 2004).

All models were fitted in a Bayesian framework (Wade 2000; Ellison 2004) using the software WinBUGS (Kéry 2010) and R (R Development Core Team 2010) using the library R2WinBUGS (Sturtz, Ligges & Gelman 2005).

Each model was started with the simplest case, in which occupancy probabilities and detection probabilities were kept constant (intercept models). In a second step, a set of a priori defined, more complex models were tested. Each model set included one of the four group's covariates.

We checked for correlations between covariates. If the correlation coefficient was  $r > 0.7$ , then we fitted two models to the data, one with each correlated covariate each. In case of no convergence of the model ( $\hat{R} > 1.01$ ), the models were simplified by excluding further covariates (Brooks & Gelman 1998). Prior to statistical analysis, covariates were standardized. The models for each of the four groups of covariates were developed separately. We did not combine covariates of different groups, to avoid comparison between the design features, the habitat characteristics and the landscape characteristics (Shulze *et al.* 2010). Covariates were considered important when their 95% credible interval (CRI) did not include zero (Kéry 2010). For all analysis we run three Markov-chain Monte Carlo chains (Kéry 2010) in parallel. For the multistate models we run 10000 iterations discarding the first 1000 as burn-in and thinned out such that every fifth value was retained. For the N-mixture models we run 100000 iterations, discarding the first 10000 as burn-in and thinned out such that every fifth value was retained.

## Results

### Multistate occupancy model

At 11 sites we found either adults or larvae, leading to an observed occupancy rate of 28.9%. At six sites out of the 11 colonized sites (54.4%), evidence for reproduction (i.e., tadpoles) was detected.

To account for imperfect detectability, all multistate models included the covariates temperature, date and rain. "Date" had the greatest influence on detection probability. The estimates for the detectabilities of the different states based on a model with no explanatory variables are shown in (Table 2).

P1 corresponds to the detectability of colonization, if the true state is "colonized". It is estimated at 0.403 (95% CRI 0.193 – 0.616) (Table 2).

P2[1] corresponds to the detectability of colonization, given that the true state is "colonized with reproduction". It is estimated at 0.278 (95% CRI 0.141 – 0.438) (Table 2). P2[2] corresponds to the detectability of reproduction, given the true state of a site is "colonized with reproduction". It is estimated at 0.564 (95% CRI 0.384 – 0.733) (Table 2). P2[3] corresponds to the probability of not detecting the species, given the true state would be "colonized with reproduction" (Table 2).

The parameter estimates of the 10 candidate models that were fitted to the data are shown in tables 2 to 6. Based on model 1 (Table 2)  $\psi$ , the probability of colonization (regardless of its reproductive state) was estimated at 0.318 (95% CRI 0.177 – 0.484).  $R$ , the proportion of colonized sites where reproduction occurred was estimated at 0.524 (95% CRI 0.257 – 0.791) (Table 2).  $\text{Occ}[1]$ , the estimated number of colonized sites, was estimated at 5.522 (95% CRI 4.0 – 9.0) (Table 2).

Occ[2] the estimated number of colonized sites where reproduction occurred was estimated at 6.153 (95% CRI 6.0 – 7.0) (Table 2). Occ[3], the estimated number of uncolonized sites was estimated at 26.325 (95% CRI 23 – 27) (Table 2).

Among the pond and water characteristics that were included as explanatory variables in the model (Table 1), the amount of ponds had a positive effect on colonization (model 3) (Table 3, Fig. 6) In model 2, the effect of number of ponds was similar, but the credible interval was wider (Table 3). None of the covariates of this group had an effect on reproduction. Out of the habitat characteristics in a 100 m radius around the pond, none had an effect on colonization, population size or reproduction (models 4, 5, and 6) (Table 4). Among the habitat characteristics in a 100 m radius around the pond (Table 1), constructions had a negative effect and the availability of a stonewall or a hangslide with no or sparse vegetation had a positive effect on colonization (model 7) (Table 5, Fig. 6). Forest had a negative effect on reproduction (models 7 and 8) (Table 5, Fig. 4). Among the landscape characteristics (Table 1), stones had a negative effect (models 9 and 10) (Table 6, Fig. 3) on colonization. Age had a positive effect on colonization (model 9) (Table 6, Fig. 2) and on reproduction (models 9 and 10) (Table 6, Fig. 2).

### **N-Mixture Model**

At 28 sites, no individuals were heard calling. If males were heard calling at least once (10 sites), then maximum caller counts varied from 1 to 20.

To model detection probability, we included temperature as a covariate. Models that included rain or date as covariates for detection probability never converged. Hence, these two variables were not considered any further. Population sizes at the 38 study sites ( $N$ ) estimated by this model were between 0 ( $\pm 0$ ) and 20 ( $\pm 0$ ) (Table 7). These estimates are mostly equal to the maximal counts per sites.

Among the pond and water characteristics (Table 1), the amount of ponds had a positive effect on population sizes (models 2 and 3) (Table 8, Fig. 6). Among the habitat characteristics in a 10 m radius, none had an effect (models 4, 5 and 6) (Table 9).

Out of the habitat characteristics in a 100 m radius (Table 1), the availability of a stonewall or a hangslide with no or sparse vegetation (model 7) (Table 10, Fig. 6) had a positive effect, constructions and stones had a negative effect on population sizes (model 7) (Table 10, Fig. 1 & Fig. 3).

Among the landscape characteristics (Table 1), connectivity had a positive effect on population sizes (models 8 and 10) (Table 11, Fig. 5).

## Discussion

For the survival of many amphibian species it is not enough to save and preserve current occupied sites (Goldberg & Waits 2009). In many situations, it is urgent to create new ponds to counter the loss of wetlands and ponds. This study evaluated the success and the determinants of success of a pond building conservation project. Our results highlight the importance of using different population metrics when evaluating conservation management projects. The explanatory variables that determined success depending on the metric that was chosen to measure success. Our analysis revealed which factors determined colonization, population size and reproduction of newly created ponds (Table 12).

Almost one third of the study ponds (28.9%) were colonized by the targeted amphibian species. This result demonstrates the species' ability to colonize newly created, previously unoccupied sites. Midwife toads are known as a species with low dispersal capacity (Tobler, Garner & Schmidt in preparation). Given this widely held belief, the proportion of colonized sites is remarkable. We found evidence for a maximum colonization distance up to 2.388 km.

Most estimated population sizes were rather small, and the majority of the estimations were equal to the maximum counts per site (Table 7). It is known that most amphibian populations are considerably larger than assumed from the census population counts (Vucetich, Waite & Nunney 1997; Green 2003). Therefore, we have to interpret these numbers with caution. Hence, the relevant estimation of quantities describing the population sizes at each site could be evaluated.

Tadpoles occurred at a low proportion of the colonized sites: 0.52 ( $\pm 0.139$ ), i.e. only at about half of the colonized sites reproduction occurred (Table 2). This result shows that even if a site is colonized, there may be no reproduction. Therefore, the population might not be self sustainable but may be a sink population. This status may change, since reproduction was more likely to occur in older ponds (Table 6, Fig. 2). The species, once it has colonized the site, needs time to start reproducing.

*Pond and water characteristics.* Out of the models including the pond and water characteristics, only the number of ponds influenced colonization and abundance in a positive way (Table 3, Fig. 6). The other characteristics did not show any effects, neither on colonization or population size nor on reproduction. Our results suggest that *Alytes obstetricans* seem to show that the characteristics of the pond itself may not matter much. Rather, the terrestrial habitat may matter.

*Habitat characteristics within a 10 m radius around the pond.* None of these measured characteristics had an effect on any of the response metrics. A 10 m radius around the pond might be a too small scale, which might not have a detectable impact on our metrics, even though *Alytes obstetricans* used the immediate surroundings of the breeding pond as their terrestrial habitat (Mermod *et al.* 2010).

*Habitat characteristics within a 100 m radius around the pond.* Out of this set of habitat characteristic, constructions had a negative effect on colonization (Table 5, Fig. 1) and on abundance (Table 10, Fig. 1). Different studies propose negative associations with building development, e.g. limitation of dispersal (Marsh & Trenham 2001). Constructed ponds surrounded by human settlements such as e.g.



garden ponds are less achievable because colonization is less likely, as well as population sizes are smaller. No effect is shown on reproduction, meaning once the species colonized a site, reproduction is not affected by the surrounded constructions (Table 5). Further several studies suggest the importance of forested areas for amphibians, but rather as terrestrial habitats (Van Buskirk 2005; Eigenbrod, Hecnar & Fahrig 2008). This seems not to be the case for our targeted taxon, because to we did not found an effect on colonization. Our models confirmed that forested area is negative for reproduction (Table 5, Fig. 4) as well as on population size (Table 10, Fig. 4). Moreover, stone walls and hangslides with no or sparse vegetation bear on colonization in a positive way (Table 5). These types of surroundings are often used by the adults as their terrestrial habitats (Meyer *et al.* 2009; Mermod *et al.* 2010). Hence, their need and positive effect on site use is underlined by our results (Table 5 & Table 10, Fig. 6).

*Landscape characteristics.* *Alytes obstetricans* stand to benefit from stone quarries. Probably due to the optimal terrestrial habitat found in this habitat type. However, we found a negative effect of stones on colonization (Table 6, Fig. 3). The variable as measured in this study (Table 1) was not congruent with the used habitat of the species (Kordges 2003). One post-hoc explanation might be that we considered every different kind of stones into our covariate. We suggest differentiating various sizes of stones in order to obtain differentiated results regarding stone structures. Various studies revealed influences of pond age on amphibians, whereas the occurrence of the species relates in a positive or negative way, depending on the species (Stumpel & Van der Voet 1998). Pond age, the simple time a pond is available as a

breeding site, but it is also an indicator of succession, meaning of changing pond conditions. Colonization of created habitats by midwife toads and reproduction are positively correlated with age (Table 6, Fig. 2), meaning older ponds are better. As it seems that Midwife toads are flexible regarding the spectrum of used ponds (Kordges 2003), we conclude that mostly the time itself plays the crucial role. This matches the assumption, that the target species is not particularly mobile (Mermod *et al.* 2010) therefore, dispersal and colonization need time. The density of nearby populations is depending on the available breeding sites (Van Horne 1983). Not well connected sites effect longer colonization times (Travis 1994). Connectivity is suggested to be a crucial factor regarding pond use (Marsh & Trenham 2001). Surprisingly, we found no evidence for an impact of connectivity on colonization (Table 6), but rather on population sizes (Table 11, Fig. 5). Well connected sites are important for the creation of larger populations. However the simple population sizes of species at a certain site cannot be related with high quality sites (Van Horne 1983), as this partly different, important metrics, evaluated by the different models. Sink populations can hold larger population sizes due to a high number of immigrants from a source population (Van Horne 1983).

## **Conservation Implications**

The ecological restoration program was causative for establishing new sites colonized by the midwife toad. The proof of success of a conservation project has to be performed at various sites, include various biodiversity metrics and take imperfect detection into account.

Emphasis for further efforts should be put on providing suitable sites because we were able to prove that spontaneous colonization occurs. We suggest the construction of several ponds per site, rather than only one. Based on our results, the characteristics of the pond do not appear to matter much. Beside the availability of multiple ponds the terrestrial habitat is of major importance. Therefore management plans should not only focus on constructing and conserving ponds. Each breeding pond should be surrounded by suitable terrestrial habitat according to the identified habitat characteristics. The availability of a stone wall or a hangslide with no or sparse vegetation is a contribution for the use of a constructed pond. As constructions had a negative effect on colonization and on population size, sites should not be placed near human settlements. Ponds within forested area, namely forested area within a radius of 100 m around the pond should be avoided.

In the broader landscape, connectivity had an influence on population size. New ponds have to be set in close proximity to ensure a high connectivity of metapopulations.

Based on the identification of influencing factors regarding pond colonizations, population size and reproduction, this study provides the first scientifically-based implications to improve conservation management of wetland structures for *Alytes obstetricans* and their colonization of created habitats. Further studies are needed to determine clearer habitat features and dispersal abilities, because this could be essential for more accurate habitat management practice of colonized sites. However, this study sets the basis for constructing new ponds reaching high colonization probabilities such that the benefit for species conservation can be maximized while minimizing financial costs.

## **Acknowledgements**

I am grateful to Dr. Benedikt R. Schmidt for his supervision and his valuable support. Further I thank Prof. Dr. Raphaël Arlettaz for co-supervision. Funding was provided by the University of Bern, Institute of Ecology and Evolution, Conservation Biology and the Environmental office, Division of nature advancement, canton of Bern, Switzerland. Great thanks to Michael Schaub for his helpful discussions and support developing the multi-state winBUGs code. We thank to the "Swiss Biological Records Center" (CSCF) to provide access to its data.

## References

- Borgula, A. & Zumbach, S. (2003) Verbreitung und Gefährdung der Geburtshelferkröte (*Alytes obstetricans*) in der Schweiz. *Zeitschrift für Feldherpetologie*, **10**.
- Brand, A.B. & Snodgrass, J.W. (2010) Value of artificial habitats for amphibian reproduction in altered landscapes. *Conservation Biology*, **24**, 295-301.
- Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7**, 434-455.
- Davies, B.R., Biggs, J., Williams, P.J., Lee, J.T. & Thompson, S. (2008) A comparison of the catchment sizes of rivers, streams, ponds, ditches and lakes: implications for protecting aquatic biodiversity in an agricultural landscape. *Hydrobiologia*, **597**, 7-17.
- Eigenbrod, F., Hecnar, S.J. & Fahrig, L. (2008) The relative effects of road traffic and forest cover on anuran populations. *Biological Conservation*, **141**, 35-46.
- Ellison, A.M. (2004) Bayesian inference in ecology. *Ecology Letters*, **7**, 509-520.
- Franklin, A.B., Anderson, D.R., Gutierrez, R.J. & Burnham, K.P. (2000) Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs*, **70**, 539-590.
- Gardner, T.A., Barlow, J. & Peres, C.A. (2007) Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. *Biological Conservation*, **138**, 166-179.
- Gascon, S., Boix, D. & Sala, J. (2009) Are different biodiversity metrics related to the same factors? A case study from Mediterranean wetlands. *Biological Conservation*, **142**, 2602-2612.
- Goldberg, C.S. & Waits, L.P. (2009) Using habitat models to determine conservation priorities for pond-breeding amphibians in a privately-owned landscape of northern Idaho, USA. *Biological Conservation*, **142**, 1096-1104.
- Green, D.M. (2003) The ecology of extinction: population fluctuation and decline in amphibians. *Biological Conservation*, **111**, 331-343.
- Gu, W.D. & Swihart, R.K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation*, **116**, 195-203.
- Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151-162.
- Heino, J., Mykka, H. & Kotanen, J. (2008) Weak relationships between landscape characteristics and multiple facets of stream macroinvertebrate biodiversity in a boreal drainage basin. *Landscape Ecology*, **23**, 417-426.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187-211.
- Imboden, C. (1976) *Leben am Wasser: Kleine Einführung in die Lebensgemeinschaften der Feuchtgebiete*. Schweizerischer Bund für Naturschutz, Basel.
- Kéry, M. (2010) *Introduction to WinBUGS for ecologist; Bayesian approach to regression, ANOVA, mixed models and related analysis*. Academic Press.
- Kéry, M. & Schmidt, B.R. (2008) Imperfect detection and its consequences for monitoring for conservation. *Community Ecology*, **9**, 207-216.
- Kordges, T. (2003) Zur Biologie der Geburtshelferkröte (*Alytes obstetricans*) in Kalksteinbrüchen des Niederbergischen Landes (Nordheim-Westfalen). *Zeitschrift für Feldherpetologie*, **10**, 1-24.
- MacKenzie, D.I. (2005) Was it there? Dealing with imperfect detection for species presence/absence data. *Australian & New Zealand Journal of Statistics*, **47**, 65-74.

- Mackenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**, 2200-2207.
- Mackenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248-2255.
- Marsh, D.M. & Trenham, P.C. (2001) Metapopulation dynamics and amphibian conservation. *Conservation Biology*, **15**, 40-49.
- Mermod, M., Zumbach, S., Borgula, A., Lüscher, B., Pellet, J. & Schmidt, B.R. (2010) Praxismerkblatt Artenschutz Geburtshelferkröte *Alytes obstetricans*. Neuenburg.
- Meyer, A., S., Z., B.R., S. & J.C., M. (2009) *Auf Schlangenspuren und Krötenpfaden, Amphibien und Reptilien der Schweiz*. Haupt Verlag, Bern. Stuttgart. Wien.
- Nichols, J.D., Hines, J.E., Mackenzie, D.I., Seamans, M.E. & Gutierrez, R.J. (2007) Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology*, **88**, 1395-1400.
- Pellet, J. & Schmidt, B.R. (2005) Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. *Biological Conservation*, **123**, 27-35.
- Prugh, L.R. (2009) An evaluation of patch connectivity measures. *Ecological Applications*, **19**, 1300-1310.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652-661.
- Quinn, G.P. & Keough, M.J. (2002) *Experimental design and data analysis for biologist*. Cambridge University Press.
- R Development Core Team (2010) R: a language and environment for statistical computing. *R Foundation for Statistical Computing Vienna, Austria*.
- Royle, J.A. (2004) N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, **60**, 108-115.
- Royle, J.A. & Dorazio, R.M. (2006) Hierarchical models of animal abundance and occurrence. *Journal of Agricultural Biological and Environmental Statistics*, **11**, 249-263.
- Runge, J.P., Runge, M.C. & Nichols, J.D. (2006) The role of local populations within a landscape context: defining and classifying sources and sinks. *American Naturalist*, **167**, 925-938.
- Ryser, J., Lüscher, B., Neuenschwander, U. & Zumbach, S. (2003) Geburtshelferkröten im Emmental, Schweiz. *Zeitschrift für Feldherpetologie*, **10**, 27-35.
- Schmidt, B.R. (2005) Monitoring the distribution of pond-breeding amphibians when species are detected imperfectly. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **15**, 681-692.
- Schmidt, B.R., Furrer, S., Kwet, A., S., L., Rödder, D., Sztatecsny, M., Tobler, U. & Zumbach, S. (2009) Desinfektion als Massnahme gegen die Verbreitung der Chytridiomykose bei Amphibien. *Zeitschrift für Feldherpetologie*, **15**, 229-241.
- Schmidt, B.R. & Pellet, J. (2005) Relative importance of population processes and habitat characteristics in determining site occupancy of two anurans. *Journal of Wildlife Management*, **69**, 884-893.
- Schmidt, B.R. & Zumbach, S. (2005) *Rote Liste der gefährdeten Amphibien der Schweiz*. BAFU & karch, Bern.
- Shulse, C.D., Semlitsch, R.D., Trauth, K.M. & Williams, A.D. (2010) Influences of design and landscape placement parameters on amphibian abundance in constructed wetlands. *Wetlands*, **30**, 915-928.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783-1786.

- Stumpel, A.H.P. & Van der Voet, H. (1998) Characterizing the suitability of new ponds for amphibians. *Amphibia-Reptilia*, **19**, 125-142.
- Sturtz, S., Ligges, U. & Gelman, A. (2005) R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software*, **12**, 1-16.
- Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology & Evolution*, **19**, 305-308.
- Sztatecsny, M., Jehle, R., Schmidt, B.R. & Arntzen, J.W. (2004) The abundance of premetamorphic newts (*Triturus cristatus*, *T-marmoratus*) as a function of habitat determinants: an a priori model selection approach. *Herpetological Journal*, **14**, 89-97.
- Tobler, U., Garner, T. & Schmidt, B.R. (in preparation) Comparative population genetic analysis of toad populations in regions.
- Travis, J. (1994) Calibrating our expectations in studying amphibian populations. *Herpetologica*, **50**, 104-108.
- Van Buskirk, J. (2005) Local and landscape influence on amphibian occurrence and abundance. *Ecology*, **86**, 1936-1947.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893-901.
- Vucetich, J.A., Waite, T.A. & Nunney, L. (1997) Fluctuating population size and the ratio of effective to census population size. *Evolution*, **51**, 2017-2021.
- Wade, P.R. (2000) Bayesian methods in conservation biology. *Conservation Biology*, **14**, 1308-1316.
- Wake, D.B. & Vredenburg, V.T. (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11466-11473.

## Tables

**Table 1** Description of the covariates.

<b>covariates</b>	<b>range</b>	<b>description</b>
<i>detection</i>		
temperature	4.9-19.4 °C	temperature during the survey
date	2010-04-19 - 2010-07-09	Julian date
rain	categorical	rain or no rain during the day of the survey
<i>pond and water characteristics</i>		
size	6-365m <sup>2</sup>	watersurface
depth	10-150m	maximal water depth
interlayer	categorical	interlayer for waterproofing the pond
pH	6.308-10.089	pH
pH <sup>2</sup>	39.790-101.806	pH squared
#ponds	categorical	one or more ponds at a site
<i>habitat characteristics</i>		
<i>10m radius</i>		
forest	0-85	% of forest (and hedges)
grass	10-100	% of grass
stones	0-50	% of stones, gravel, rocks
open soil	0-75	% of open soil
<i>habitat characteristics</i>		
<i>100m radius</i>		
constructions	0-13857.522	m <sup>2</sup> of settlements
forest	0-31374.21	m <sup>2</sup> of forest (and hedges)
stonewall or open	categorical	stonewall or open hangslide
hangslide		with sparse or no vegetation
<i>landscape</i>		
distance_km	0.091-2.388	km to the next population (Prugh 2009)
connectivity	0.142-3.388	$S_i = \sum p_j \exp(-d_{ij})$ (Hanski 1994)
constructions	5844.278-1099528	m <sup>2</sup> of settlements
waterbodies	0-76479	m <sup>2</sup> of waterbodies
forest	232619.9-2551189	m <sup>2</sup> of hedges and forest
stones	0-86336.46	m <sup>2</sup> of stones, gravel, rocks
age	1-25	age of the pond in years



**Table 2** Parameter estimates of the multistate models for the pond and water covariates,  $psi$  stands for the probability of colonization,  $r$  stands for the probability of reproduction, given a site is colonized,  $p1$  stands for detectability of colonization, given the true state is "colonized",  $p2[1]$  stands for detectability of colonization, given the true state would be "occupied with reproduction",  $p2[2]$  stands for the detectability of reproduction, given the true state is "occupied with reproduction",  $occ[1]$  stands for the estimated number of colonized,  $occ[2]$  stands for the estimated number of sites which are colonized and reproduction occurs,  $occ[3]$  stands for the estimated number of uncolonized sites, CRI stands for credible interval.

#	estimates	mean	lower limit 95% CRI	upper limit 95% CRI
1	$psi$	0.318	0.177	0.484
	$r$	0.524	0.257	0.791
	$p1$	0.403	0.193	0.616
	$p2[1]$	0.278	0.141	0.438
	$p2[2]$	0.564	0.384	0.733
	$occ[1]$	5.522	4.000	9.000
	$occ[2]$	6.153	6.000	7.000
	$occ[3]$	26.325	23.000	27.000

**Table 3** Parameter estimates of the multistate models for the pond and water characteristics,  $p1$  stands for detectability of colonization, given the true state is "colonized",  $p2[1]$  stands for detectability of colonization, given the true state would be "occupied with reproduction",  $p2[2]$  stands for the detectability of reproduction, given the true state is "occupied with reproduction", CRI stands for credible interval.

#	covariates	mean	lower limit 95% CRI	upper limit 95% CRI
2	<i>detection p1</i>			
	intercept	1.053	-0.163	2.346
	temp	-0.711	-1.909	0.377
	<b>date</b>	<b>-0.634</b>	<b>-1.398</b>	<b>-0.096</b>
	rain	0.712	-0.976	2.450
	<i>detection p2[1]</i>			
	intercept	0.353	-1.110	1.987
	temp	0.010	-1.237	1.350
	date	1.077	-1.147	2.793
	rain	-0.244	-2.025	1.643
	<i>detection p2[2]</i>			
	intercept	0.701	-0.849	2.370
	temp	0.066	-2.016	2.073
	date	0.027	-1.111	1.096
	rain	0.373	-1.400	2.191
	<i>colonization</i>			
	intercept	-1.042	-1.917	-0.211
	size	-0.203	-1.099	0.653
	max_depth	0.031	-0.786	0.865
	interlayer	-0.151	-1.390	1.056
	#pond	1.128	-0.235	2.487
	<i>reproduction</i>			
	intercept	0.025	-1.272	1.341
	size	-0.917	-2.292	0.437
	max.depth	0.960	-0.445	2.389
	interlayer	-0.277	-1.876	1.351
	#pond	0.707	-0.944	2.385
3	<i>detection p1</i>			
	intercept	1.041	-0.199	2.334
	temp	-0.724	-1.919	0.375
	<b>date</b>	<b>-0.636</b>	<b>-1.391</b>	<b>-0.096</b>
	rain	0.706	-0.994	2.452
	<i>detection p2[1]</i>			
	intercept	0.349	-1.133	2.007
	temp	0.019	-1.226	1.332
	date	1.062	-1.191	2.802
	rain	-0.250	-2.031	1.652
	<i>detection p2[2]</i>			
	intercept	0.682	-0.870	2.328
	temp	-0.053	-2.046	2.084
	date	-0.030	-1.110	1.102
	rain	0.367	-1.399	2.170
	<i>colonization</i>			
	intercept	-1.165	-1.962	-0.417
	size	-0.071	-0.955	0.799
	max.depth	-0.105	-0.972	0.768
	pH	-0.398	-1.825	1.006
	pH <sup>2</sup>	-0.183	-1.618	1.245
	<b>#pond</b>	<b>1.282</b>	<b>0.026</b>	<b>2.571</b>
	<i>reproduction</i>			
	intercept	-0.074	-1.339	1.241
	size	-0.965	-2.331	0.428
	max.depth	0.935	-0.529	2.456
	pH	0.227	-1.261	1.734
	pH <sup>2</sup>	0.210	-1.300	1.720

---

#pond	0.005	-1.931	1.986
-------	-------	--------	-------

---

**Table 4** Parameter estimates of the multistate models for the habitat characteristics in a 10 m radius around the pond,  $p1$  stands for detectability of colonization, given the true state is "colonized",  $p2[1]$  stands for detectability of colonization, given the true state would be "occupied with reproduction",  $p2[2]$  stands for the detectability of reproduction, given the true state is "occupied with reproduction", CRI stands for credible interval.

#	covariates	mean	lower limit 95% CRI	upper limit 95% CRI
4	<i>detection p1</i>			
	intercept	1.059	-0.167	2.370
	temp	-0.723	-1.913	0.347
	<b>date</b>	<b>-0.648</b>	<b>-1.459</b>	<b>-0.095</b>
	rain	0.705	-1.010	2.454
	<i>detection p2[1]</i>			
	intercept	0.332	-1.153	1.983
	temp	0.010	-1.234	1.341
	date	1.066	-1.140	2.799
	rain	-0.239	-1.995	1.662
	<i>detection p2[2]</i>			
	intercept	0.694	-0.848	2.332
	temp	-0.062	-2.058	2.117
	date	-0.022	-1.112	1.116
	rain	0.384	-1.391	2.229
	<i>colonization</i>			
	intercept	-8.809	-1.489	-0.803
	forest	0.064	-1.895	2.035
	stones	0.004	-1.967	1.969
	<i>reproduction</i>			
intercept	0.161	-0.898	1.224	
forest	-0.059	-2.005	1.894	
stones	0.011	-1.940	1.974	
5	<i>detection p1</i>			
	intercept	1.054	-0.176	2.388
	temp	-0.721	-1.906	0.346
	<b>date</b>	<b>0.651</b>	<b>-1.464</b>	<b>-0.095</b>
	rain	0.707	-0.994	2.444
	<i>detection p2[1]</i>			
	intercept	0.342	-1.138	1.975
	temp	-1.08E-4	-1.243	1.307
	date	1.075	-1.104	2.792
	rain	-0.254	-2.043	1.666
	<i>detection p2[2]</i>			
	intercept	0.692	-0.860	2.335
	temp	-0.075	-2.056	2.069
	date	-0.018	-1.087	1.129
	rain	0.371	-1.394	2.189
	<i>colonization</i>			
	intercept	-0.809	-1.491	-0.179
	forest	0.068	-1.896	2.018
	open soil	0.015	-1.942	1.986
	<i>reproduction</i>			
intercept	0.169	-0.888	1.253	
forest	-0.062	-2.019	1.870	
open soil	0.017	-1.942	1.980	
6	<i>detection p1</i>			
	intercept	1.044	-0.207	2.365
	temp	-0.725	-1.928	0.356
	<b>date</b>	<b>-0.658</b>	<b>-1.489</b>	<b>-0.102</b>
	rain	0.697	-1.011	2.438
	<i>detection p2[1]</i>			
	intercept	0.367	-1.125	2.002
	temp	-1.4E-6	-1.242	1.302

---

date	1.051	-1.110	2.771
rain	-0.238	-2.037	1.667
<i>detection p2[2]</i>			
intercept	0.678	-0.871	2.311
temp	-0.057	-2.046	2.094
date	-0.021	-1.086	1.100
rain	0.379	-1.402	2.215
<i>colonization</i>			
intercept	-0.843	-1.543	-0.175
grass	-0.365	-1.057	0.309
stones	-0.025	-1.987	1.935
<i>reproduction</i>			
intercept	0.281	-0.835	1.462
grass	0.481	-0.587	1.635
stones	0.018	-1.978	1.962

---

**Table 5** Parameter estimates of the multistate models for the habitat characteristics in a 100 m radius around the pond,  $p1$  stands for detectability of colonization, given the true state is "colonized",  $p2[1]$  stands for detectability of colonization, given the true state would be "occupied with reproduction",  $p2[2]$  stands for the detectability of reproduction, given the true state is "occupied with reproduction", CRI stands for credible interval.

#	covariates	mean	lower limit 95% CRI	upper limit 95% CRI
7	<i>detection p1</i>			
	intercept	0.971	-0.348	2.332
	temp	-0.673	-1.876	0.411
	<b>date</b>	<b>-0.658</b>	<b>-1.531</b>	<b>-0.102</b>
	rain	0.656	-1.091	2.433
	<i>detection p2[1]</i>			
	intercept	0.518	-1.018	2.229
	temp	-0.008	-1.303	1.342
	date	0.741	-1.470	2.631
	rain	-0.150	-1.997	1.800
	<i>detection p2[2]</i>			
	intercept	0.653	-0.886	2.303
	temp	0.001	-2.007	2.149
	date	-0.098	-1.262	1.087
	rain	0.356	-1.408	2.171
	<i>colonization</i>			
	intercept	-1.161	-2.093	-0.346
	<b>constructions</b>	<b>-0.525</b>	<b>-1.342</b>	<b>-0.021</b>
	forest	-0.057	-0.137	0.019
	<i>reproduction</i>			
intercept	-0.058	-1.694	1.632	
constructions	0.093	-1.578	1.718	
<b>forest</b>	<b>-0.451</b>	<b>-1.646</b>	<b>-0.048</b>	
8	<i>detection p1</i>			
	intercept	0.955	-0.377	2.309
	temp	-0.668	-1.885	0.427
	<b>date</b>	<b>-0.667</b>	<b>-1.560</b>	<b>-0.101</b>
	rain	0.645	-1.092	2.416
	<i>detection p2[1]</i>			
	intercept	0.536	-1.023	2.239
	temp	0.004	-1.286	1.359
	date	0.690	-1.513	2.648
	rain	-0.110	-1.951	1.837
	<i>detection p2[2]</i>			
	intercept	0.618	-0.916	2.262
	temp	0.012	-2.000	2.194
	date	0.111	-1.299	1.059
	rain	0.378	-1.389	2.218
	<i>colonization</i>			
	intercept	-1.656	-2.698	-0.748
	constructions	0.460	-1.246	0.008
	forest	-0.055	-0.137	0.024
	<b>stonewall/hangslide</b>	<b>1.423</b>	<b>0.267</b>	<b>2.616</b>
<i>reproduction</i>				
intercept	-0.094	-1.796	-0.100	
constructions	0.107	-1.600	1.809	
<b>forest</b>	<b>-0.477</b>	<b>-1.689</b>	<b>-0.037</b>	
stonewall/hangslide	0.168	-1.569	1.936	

**Table 6** Parameter estimates of the multistate models for the landscape characteristics (in a 1000 m radius around the pond),  $p1$  stands for detectability of colonization, given the true state is "colonized",  $p2[1]$  stands for detectability of colonization, given the true state would be "occupied with reproduction",  $p2[2]$  stands for the detectability of reproduction, given the true state is "occupied with reproduction", CRI stands for credible interval.

#	covariates	mean	lower limit 95% CRI	upper limit 95% CRI
9	<i>detection p1</i>			
	intercept	1.046	-0.186	2.346
	temp	-0.713	-1.899	0.366
	<b>date</b>	<b>-0.650</b>	<b>-1.453</b>	<b>-0.103</b>
	rain	0.699	-1.016	2.467
	<i>detection p2[1]</i>			
	intercept	0.336	-1.142	1.989
	temp	0.005	-1.247	1.335
	date	1.074	-1.104	2.780
	rain	-0.244	-1.999	1.651
	<i>detection p2[2]</i>			
	intercept	0.691	0.858	2.340
	temp	-0.060	-2.061	2.093
	date	-0.017	-1.074	1.121
	rain	0.379	-1.398	2.211
	<i>colonization</i>			
	intercept	-1.045	-2.092	-0.316
	distance_km	-0.700	-1.613	0.130
	constructions	-0.383	-1.341	0.500
	waterbodies	-0.039	-0.125	0.026
	forest	-0.309	-1.166	0.524
	<b>stones</b>	<b>-0.081</b>	<b>-0.222</b>	<b>-0.001</b>
	<b>age</b>	<b>9.946</b>	<b>0.018</b>	<b>2.054</b>
	<i>reproduction</i>			
	intercept	0.261	-1.466	1.993
	distance_km	-0.160	-1.482	1.162
	constructions	-0.588	-2.122	0.860
waterbodies	0.239	-0.070	0.775	
forest	-0.350	-1.902	1.182	
stones	-0.049	-0.616	0.474	
<b>age</b>	<b>1.474</b>	<b>0.105</b>	<b>3.094</b>	
10	<i>detection</i>			
	intercept	1.031	-0.214	2.327
	temp	-0.733	-1.900	0.341
	date	-0.636	-1.402	-0.100
	rain	0.676	-1.021	2.414
	<i>colonization</i>			
	intercept	-1.143	-2.105	-0.310
	connectivity	0.790	-0.036	1.703
	constructions	-0.519	-1.540	0.414
	waterbodies	-0.028	-0.106	0.037
	forest	-0.322	-1.185	0.515
	<b>stones</b>	<b>-0.084</b>	<b>-0.232</b>	<b>-0.002</b>
	age	0.701	-0.221	1.768
	<i>reproduction</i>			
	intercept	0.308	-1.405	2.055
	connectivity	0.692	-0.514	1.928
	constructions	-0.658	-2.216	0.796
	waterbodies	0.275	-0.041	0.829
	forest	-0.245	-1.825	1.300
	stones	0.010	-0.539	0.527

---

**age****1.516****0.143****3.106**



**Table 7** Parameter estimates of the N-mixture model (constant model). N stands for population sizes for each site,  $\psi$  ( $\lambda$ ) stands for the averaged population size over all sampled sites,  $p$  stands for the detectability of the species, CRI stands for credible interval.

#	estimates	mean	lower limit 95% CRI	upper limit 95% CRI
1	$\psi$ ( $\lambda$ )	2.607	2.594	3.216
	$p$	0.589	0.590	0.664
	N[1]	3.448	3	5
	N[2]	0.186	0	1
	N[3]	0.184	0	1
	N[4]	0.187	0	1
	N[5]	0.185	0	1
	N[6]	0.186	0	1
	N[7]	0.190	0	1
	N[8]	3.356	3	5
	N[9]	0.186	0	1
	N[10]	0.187	0	1
	N[11]	0.191	0	1
	N[12]	1.339	1	3
	N[13]	0.188	0	1
	N[14]	0.191	0	1
	N[15]	0.190	0	1
	N[16]	16.640	16	19
	N[17]	0.186	0	1
	N[18]	0.188	0	1
	N[19]	0.184	0	1
	N[20]	0.187	0	1
	N[21]	11.5	11	13
	N[22]	0.187	0	1
	N[23]	20.14	20	22
	N[24]	6.553	6	8
	N[25]	4.185	4	5
	N[26]	5.848	6	8
	N[27]	0.187	0	1
	N[28]	0.186	0	1
	N[29]	0.192	0	1
	N[30]	20.89	21	23
	N[31]	0.187	0	1
	N[32]	0.191	0	1
	N[33]	0.183	0	1
	N[34]	0.188	0	1
	N[35]	0.191	0	1
	N[36]	0.189	0	1
	N[37]	0.188	0	1
	N[38]	0.19	0	1
	N[tot]	99.15	99	110

**Table 8** Parameter estimates of the N-mixture models for the pond and water characteristics. CRI stands for credible interval.

#	covariates	mean	lower limit 95% CRI	upper limit 95% CRI
2	<i>detection</i>			
	intercept	-1.217	-1.563	-0.993
	temp	-0.067	-0.235	0.075
	<i>abundance</i>			
	intercept	-0.976	-1.825	-0.227
	size	-0.417	-1.209	0.185
	max_depth	-0.252	-0.829	0.310
	interlayer	0.547	-0.310	1.417
	<b>#pond</b>	<b>1.660</b>	<b>0.700</b>	<b>2.648</b>
3	<i>detection</i>			
	intercept	-1.275	-1.693	-1.017
	temp	-0.067	-0.242	0.084
	<i>abundance</i>			
	intercept	-0.823	-1.586	-0.113
	size	-0.319	-1.090	0.275
	max.depth	-0.230	-0.856	0.374
	pH	-0.611	-5.861	4.848
	pH <sup>2</sup>	0.040	-5.674	5.521
	<b>#pond</b>	<b>1.436</b>	<b>0.444</b>	<b>2.456</b>

**Table 9** Parameter estimates of the N-mixture models for the habitat characteristics in a 10 m radius around the pond, CRI stands for credible interval.

#	covariates	mean	lower limit 95% CRI	upper limit 95% CRI
4	<i>detection</i>			
	intercept	-1.189	-1.483	-0.986
	temp	-0.062	-0.218	0.075
	<i>abundance</i>			
	intercept	-0.146	-0.597	0.304
	forest	0.408	-9.212	9.349
5		0.878	-9.192	9.529
	<i>detection</i>			
	intercept	-1.185	-1.478	-0.983
	temp	-0.063	-0.218	0.072
	<i>abundance</i>			
	intercept	-0.173	-0.623	0.281
6	forest	-0.092	-0.482	0.318
	opensoil	0.670	-13.880	14.15
	<i>detection</i>			
	intercept	-1.083	-1.329	-0.917
	temp	-0.044	-0.180	0.071
	<i>abundance</i>			
intercept	-0.323	-0.780	0.115	
grass	-0.027	-0.436	0.404	
stones	0.683	-13.91	14.13	

**Table 10** Parameter estimates of the N-mixture models for the habitat characteristics in a 100 m radius around the pond, CRI stands for credible interval.

#	covariates	mean	lower limit 95% CRI	upper limit 95% CRI
7	<i>detection</i>			
	intercept	-1.424	-2.195	-1.041
	temp	-0.059	-0.228	0.086
	<i>abundance</i>			
	intercept	-2.080	-3.670	-0.765
	<b>constructions</b>	<b>-0.671</b>	<b>-1.788</b>	<b>-0.084</b>
	<b>forest</b>	<b>-0.094</b>	<b>-0.146</b>	<b>-0.047</b>
	<b>stonewall/hangslide</b>	<b>2.189</b>	<b>1.243</b>	<b>3.314</b>

**Table 11** Parameter estimates of the N-mixture models for the landscape characteristics covariates in a 1000 m radius around the pond, CRI stands for credible interval.

#	covariates	mean	lower limit 95% CRI	upper limit 95% CRI
8	<i>detection</i>			
	intercept	-1.220	0.002	-0.987
	temp	-0.081	-0.245	0.056
	<i>abundance</i>			
	intercept	-0.303	-0.826	0.208
	<b>connectivity</b>	<b>0.584</b>	<b>0.189</b>	<b>0.969</b>
	constructions	-0.224	-0.705	0.156
age	0.068	-0.254	0.4845	
9	<i>detection</i>			
	intercept	-1.202	-1.521	-0.988
	temp	-0.060	-0.218	0.078
	<i>abundance</i>			
	intercept	-0.195	-0.672	0.285
	distance_km	-0.362	-0.813	0.061
	waterbodies	-2.963	-9.739	8.212
10	<i>detection</i>			
	intercept	-1.226	-1.561	-1.001
	temp	-0.079	-0.241	0.059
	<i>abundance</i>			
	intercept	-0.267	-0.773	0.239
	<b>connectivity</b>	<b>0.527</b>	<b>0.153</b>	<b>0.897</b>
age	0.032	-0.280	0.433	

**Table 12** Summary of the results. "Plus" stands for a positive influence, "minus" stands for a negative influence on colonization, reproduction or abundance, respectively. "Cross" stands for evaluated covariates which included zero in their CRI.

<b>covariates</b>	<b>colonization</b>	<b>reproduction</b>	<b>abundance</b>
<i>pond and water characteristics</i>			
size	X	x	x
depth	X	x	x
interlayer	X	x	x
pH	X	x	x
pH <sup>2</sup>	X	x	x
#ponds	<b>+</b>	x	<b>+</b>
<i>habitat characteristics 10m</i>			
<i>radius</i>			
forest	X	x	x
grass	X	x	x
stones	X	x	x
open soil	X	x	x
<i>habitat characteristics 100m</i>			
<i>radius</i>			
constructions	-	x	-
forest	X	-	-
stonewall or open hangslide	<b>+</b>	x	<b>+</b>
<i>landscape</i>			
distance_km	X	x	x
connectivity	X	x	<b>+</b>
constructions	X	x	x
waterbodies	X	x	x
forest	X	x	x
stones	-	x	x
age	<b>+</b>	<b>+</b>	x

## Figure captions

**Fig. 1** Effects of constructions on observed (dots) and expected (line) on occupancy probability (A) and abundance (B).

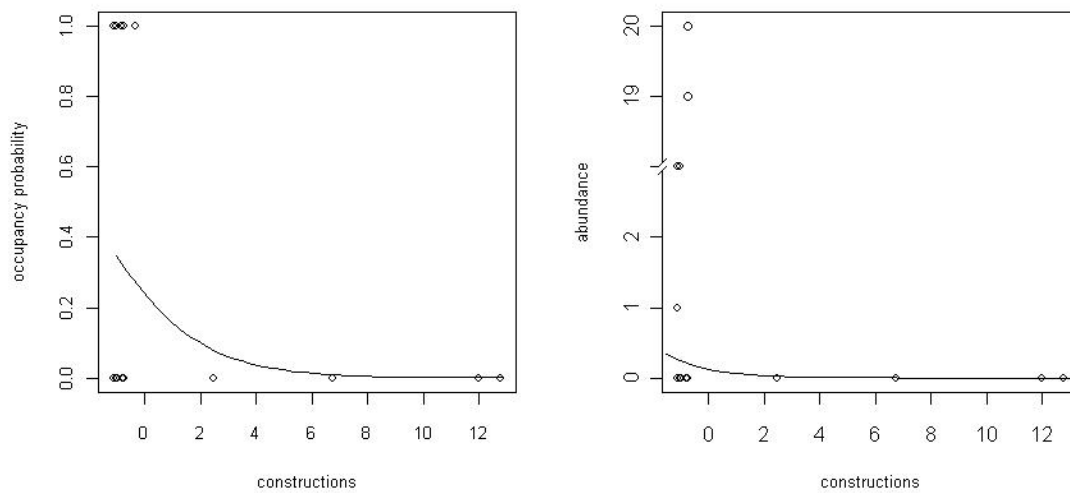
**Fig. 2** Effects of age on observed (dots) and expected (line) on occupancy probability (A) and reproduction (B).

**Fig. 3** Effects of stones on observed (dots) and expected (line) on abundance (A) and reproduction (B).

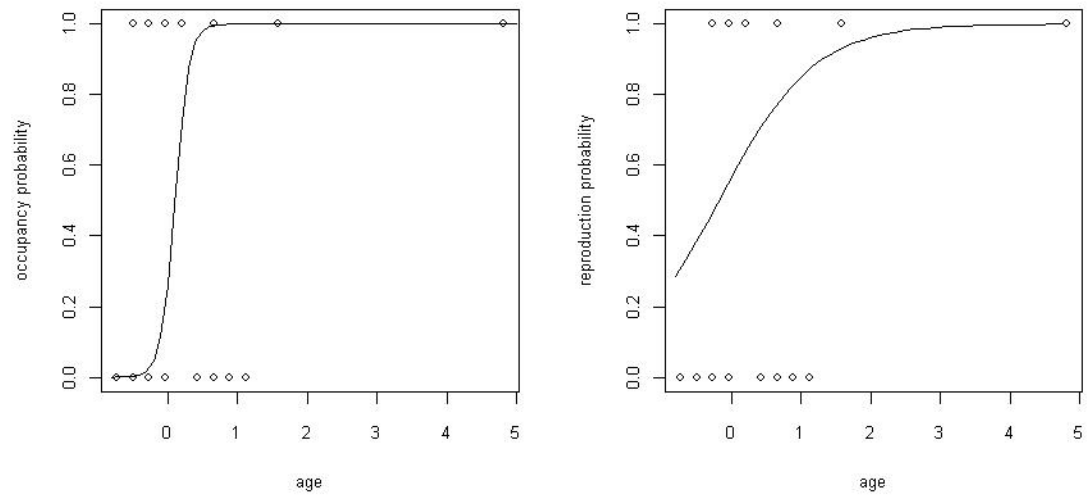
**Fig. 4** Effects of forest on observed (dots) and expected (line) on occupancy (A) and abundance (B).

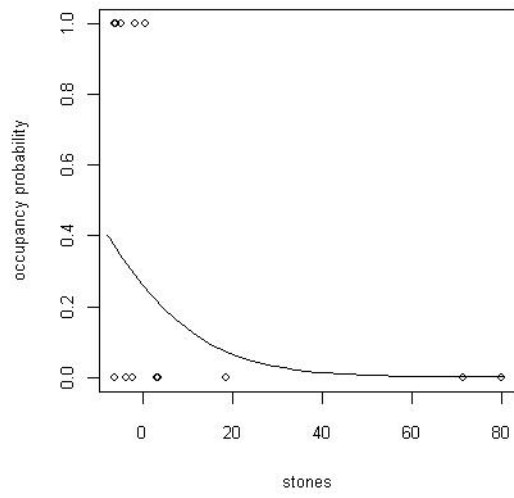
**Fig. 5** Effects of connectivity on observed (dots) and expected (line) on abundance.

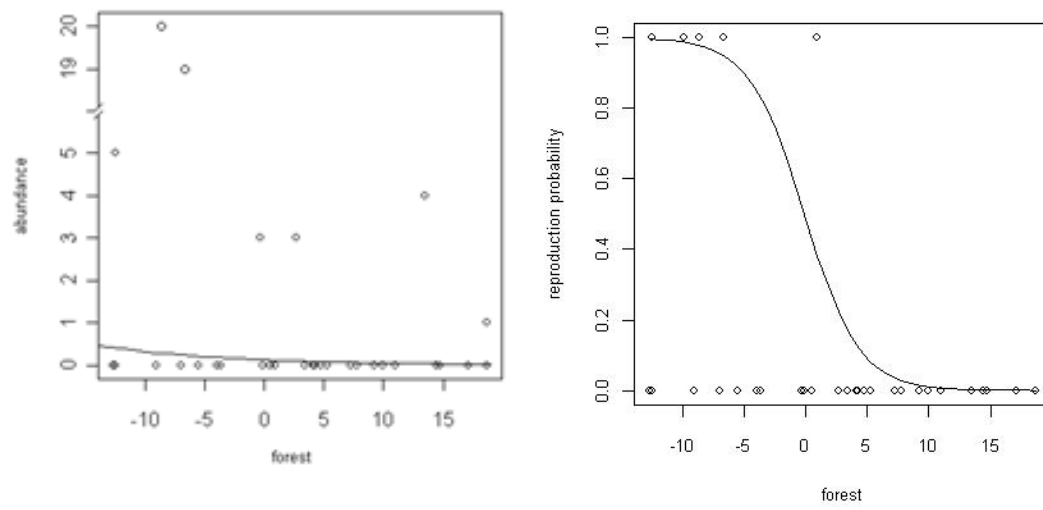
**Fig. 6** A: One pond per site (0) and more than one pond per site (1) related to the expected occupancy probability. B: No stonewall or hangslide (0) and a stonewall or hangslide per site (1) related to the expected occupancy probability.

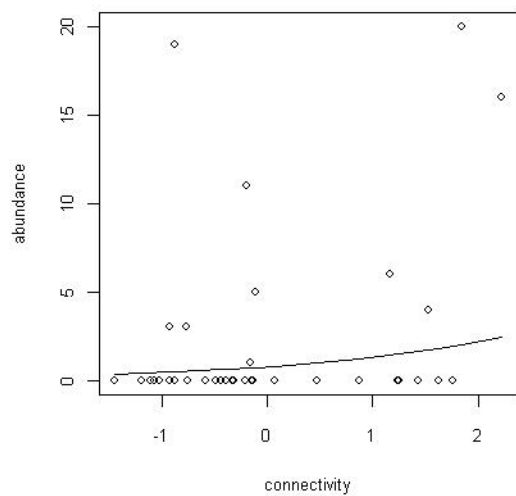
**Fig. 1**

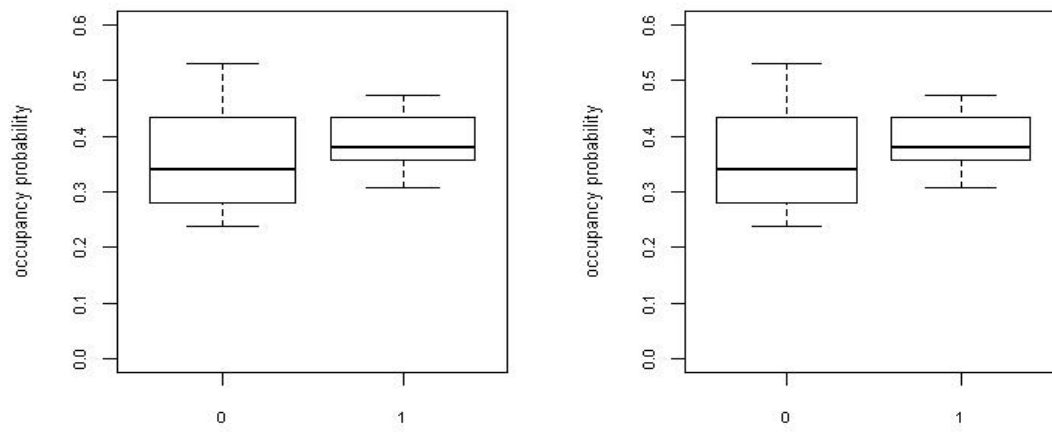


**Fig. 2**

**Fig. 3**

**Fig. 4**

**Fig. 5**

**Fig. 6**

## Appendix

### R and winBUGS code 1: Multistate model

```
# multistate occupancy model: all parameters constant

# define model
sink("model.txt")
cat("
model
{

# prior distribution
p1 ~ dunif(0,1)
psi ~ dunif(0,1)
r ~ dunif(0,1)
  for (i in 1:3)
  {
    beta[i] ~ dgamma(1,1) # induce Dirichlet distribution
    p2[i] <- beta[i]/sum(beta[])
  }

# define the detection matrix
# order of indices: true state, time, observed state
  for (t in 1:nvisit)
  {
    p[1,t,1] <- p1
    p[1,t,2] <- 0
    p[1,t,3] <- 1- p1
    p[2,t,1] <- p2[1]
    p[2,t,2] <- p2[2]
    p[2,t,3] <- p2[3]
    p[3,t,1] <- 0
    p[3,t,2] <- 0
    p[3,t,3] <- 1
  }

# define the state vector
  for (s in 1:nsite)
  {
    # probability of colonization, no reproduction
    phi[s,1] <- psi * (1-r)
    # probability of colonization with reproduction
    phi[s,2] <- psi * r
    # probability of no colonization
    phi[s,3] <- 1 - psi
  }

# state-space-likelihood
# state equation: model true states (z)
  for (s in 1:nsite)
  {
    z[s] ~ dcat(phi[s,])
  }

# observation equation
  for (s in 1:nsite)
  {
    for (t in 1:nvisit)
```

```

        {
          Y[s,t] ~ dcat(p[z[s],t, ])
        } # t
      } # s

# derived quantities
  for (s in 1:nsite)
  {
    occ1[s] <- equals(z[s], 1) # colonized
    occ2[s] <- equals(z[s], 2) # colonized with reproduction
    occ3[s] <- equals(z[s], 3) # uncolonized
  }

occ[1] <- sum(occ1[]) # number of sites with true state 1
occ[2] <- sum(occ2[]) # number of sites with true state 2
occ[3] <- sum(occ3[]) # number of sites with true state 3

} # model

", fill=TRUE)
sink()

# bundle data
win.data <- list(Y=as.matrix(Y, ncol=dim(Y)[2], nrow=dim(Y)[1],
byrow=T), nvisit= dim(Y)[2], nsite= dim(Y)[1])

# intits function
inits <- function () { list(z=rep(1, dim(Y)[1]), psi= runif(1, 0,
1), r=runif(1, 0, 1))}

# parameters to estimate
params <- c("p1", "p2", "psi", "r", "occ")

# MCMC settings
nc=3
nb=1000
ni=10000
nt=5

# start Gibbs sampler
out<-
bugs(win.data,inits,params,"model.txt",n.chains=nc,n.iter=ni,n.burn=
nb,n.thin=nt,debug=TRUE,bugs.directory=bugs.dir,
working.directory=getwd())

```

---



---

```

# multistate occupancy model: colonization and detectability
parameters modelled with covariates

sink("model.txt")
cat("

model
{

# prior distribution
  for (s in 1:nsite)
  {
    for (t in 1:3)
    {

```

```

        logit(p1[t,s]) <-
        a[1]+a[2]*temp[s,t]+a[3]*rain[s,t]+a[4]*Date[s,t]
    } #t

    for (t in 4:5)
    {
        logit(p1[t,s])<-a[4]* Date[s,t]+A[t-3]
    } # t
} # s

for (s in 1:nsite)
{
    for (t in 1:nvisit)
    {
        lpp2[t,s] ~ dnorm(0,0.001)
        pp2[3,t,s] <- 1/(1+exp(-lpp2[t,s]))
    }#t

    for (t in 1:3)
    {
        logit(pp2[1,t,s])<-
        c[1]+c[2]*temp[s,t]+c[5]*Date[s,t]+c[7]*rain[s,t]
        logit(pp2[2,t,s])<-
        c[3]+c[4]*temp[s,t]+c[6]*Date[s,t]+c[8]*rain[s,t]
    }#t

    for (t in 4:5)
    {
        logit(pp2[1,t,s])<- c[5]*Date[s,t]+B[t-3]
        logit(pp2[2,t,s])<- c[6]*Date[s,t]+C[t-3]
    }#t
}#s

for (s in 1:nsite)
{
    for (t in 1:nvisit)
    {
        for (i in 1:3)
        {
            p2[i,t,s] <- pp2[i,t,s]/sum(pp2[ ,t,s])
        }#i
    }#t
}#s

for (s in 1:nsite)
{
    logit(psi[s]) <- b[1] + b[2] * X2[s]+ b[3] * X3[s]+ b[4]
    * X4[s]+ b[5] * X5[s]+ b[6] * X6[s] +b[7] * X8[s]
    logit(r[s]) <- d[1] + d[2] * X2[s]+d[3] * X3[s] +d[4] *
    X4[s]+ d[5] * X5[s]+ d[6] * X6[s]+ d[7] * X8[s]
}#s

for (i in 1:7)
{
    b[i] ~ dnorm(0,1)
    d[i] ~ dnorm(0,1)
}

for (i in 1:4)
{
    a[i] ~ dnorm(0,1)
}

```



```
for (i in 1:8)
  {
    c[i] ~ dnorm(0,1)
  }

for (i in 1:2){
  A[i] ~ dnorm(0,1)
}

for (i in 1:2)
  {
    B[i] ~ dnorm(0,1)
  }

for (i in 1:2)
  {
    C[i] ~ dnorm(0,1)
  }

# define the detection matrix
# indices: true state, time, observed state
for (s in 1:nsite)
  {
    for (t in 1:nvisit)
      {
        p[1,t,s,1] <- p1[t,s]
        p[1,t,s,2] <- 0
        p[1,t,s,3] <- 1- p1[t,s]
        p[2,t,s,1] <- p2[1,t,s]
        p[2,t,s,2] <- p2[2,t,s]
        p[2,t,s,3] <- p2[3,t,s]
        p[3,t,s,1] <- 0
        p[3,t,s,2] <- 0
        p[3,t,s,3] <- 1
      } # for t
    }# for s

# define the state vector
for (s in 1:nsite)
  {
    phi[s,1] <- psi[s] * (1-r[s])
    phi[s,2] <- psi[s] * r[s]
    phi[s,3] <- 1-psi[s]
  }

# state-space-likelihood
# state equation: model true states (z)
for (s in 1:nsite)
  {
    z[s] ~ dcat(phi[s,])
  }

# observation equation
for (s in 1:nsite)
  {
    for (t in 1:nvisit)
      {
        Y[s,t] ~ dcat(p[z[s],t,s, ])
      } # t
    } # s

# derived quantities
```

```
    for (s in 1:nsite)
    {
      occ1[s] <- equals(z[s], 1)
      occ2[s] <- equals(z[s], 2)
      occ3[s] <- equals(z[s], 3)
    }

occ[1] <- sum(occ1[]) # number of sites with true state 1
occ[2] <- sum(occ2[]) # number of sites with true state 2
occ[3] <- sum(occ3[]) # number of sites with true state 3

} # model

", fill=TRUE)
sink()

# bundle data
win.data <- list(Y=as.matrix(Y, ncol=dim(Y)[2], nrow=dim(Y)[1],
byrow=T), X2=(X2-mean(X2))/sd(X2), X3=(X3-mean(X3))/sd(X3), X4=(X4-
mean(X4))/1000, X5=(X5-mean(X5))/sd(X5), X6=(X6-mean(X6))/1000,
X8=(X8-mean(X8))/sd(X8), rain=as.matrix(rain, ncol=dim(rain)[1],
nrow=dim(rain)[2], byrow=T), temp= as.matrix((temp-
mean(temp))/sd(temp), ncol=dim(temp)[1], nrow=dim(temp)[2],
byrow=T), Date= as.matrix((Date-mean(Date))/sd(Date),
ncol=dim(Date)[1], nrow=dim(Date)[2], byrow=T), nvisit= dim(Y)[2],
nsite= dim(Y)[1])

# intits function
inits <- function () { list(z=rep(1, dim(Y)[1]), b= runif(7,-1,1),
d=runif(7,-1,1), a=runif(4,-1,1), A=runif(2,-1,1), B=runif(2,-1,1),
C=runif(2,-1,1), c=runif(8,-1,1) )}

# parameters to estimate
params<-c("a", "A", "B", "C", "b", "d", "c", "occ")

# MCMC settings
nc=3
nb=1000
ni=10000
nt=5

# start Gibbs sampler
out<-
bugs(win.data, inits, params, "model.txt", n.chains=nc, n.iter=ni, n.burn=
nb, n.thin=nt, debug=TRUE, bugs.directory=bugs.dir, working.directory=ge
twd())
```

---

---

## R and winBUGS code 2: N-mixture model

```
# N-mixture model: all parameters constant

# define model
sink("model2.txt")
cat("
model
{

# priors distribution
lambda ~ dunif(0, 10)
p ~ dunif(0, 1)

# likelihood
# biological model for true abundance
  for (i in 1:nsite)
  {
    N[i] ~ dpois(lambda)
  }#i

# observation model for replicated counts (detection)
  for (i in 1:nsite)
  {
    for (s in 1:nvisit)
    {
      C[i,s] ~ dbin(p, N[i])
    }#s
  }#i

# derived quantities
totalN <- sum(N[]) # total pop. size across all sites

}#model

",fill=TRUE)
sink()

# bundle data
win.data <- list(C=C, nsite=38, nvisit=3)

# inits function
Nst <- apply(C,1,max)+1 # maximum count per site, +1 to avoid 0
inits <- function()list(N = Nst)

# parameters to estimate
params <- c("lambda", "p", "N", "totalN")

# MCMC settings
nc <- 3
nb <- 10000
ni <- 100000
nt <- 5

# start Gibbs sampler
out<-
bugs(win.data,inits,params,"model2.txt",n.chains=nc,n.iter=ni,n.burn
=nb,n.thin=nt,debug=TRUE,bugs.directory=bugs.dir,
working.directory=getwd())
```

---

---

**# N-mixture model: Abundance and detectability parameters modelled with covariates****# define model**

```
sink("model2.txt")
cat(""
```

```
model
{
```

**# priors**

```
a ~ dunif(-15, 15)
b ~ dunif(-15, 15)
c ~ dunif(-15, 15)
e ~ dunif(-15, 15)
f ~ dunif(-15, 15)
k ~ dunif(-15, 15)
l ~ dunif(-15, 15)
```

**# likelihood****# biological model for true abundance**

```
  for (i in 1:nsite)
  {
    N[i] ~ dpois(lambda[i])
    log(lambda[i]) <- a + b* cov1[i]+ c* cov2[i]+e* cov4[i]
    +f* cov5[i]
  }#i
```

**# observation model for replicated counts (detection)**

```
  for (i in 1:nsite)
  {
    for (s in 1:nvisit)
    {
      C[i,s] ~ dbin(p1[i,s], N[i])
      p1[i,s] <- min(0.99999, max(p[i,s],0.00001))
      p[i,s]<-exp(lp[i,s])/(1-exp(lp[i,s]))
      lp[i,s]<-k+l*temp[i,s]
    } #s
  } #i
```

**# derived quantities**

```
totalN <- sum(N[]) # total pop. size across all sites
```

```
}#model
```

```
",fill=TRUE)
```

```
sink()
```

**# bundle data**

```
win.data <- list(C=C, cov1=cov1, cov2=cov2, cov4=cov4,
cov5=cov5,temp=temp,nsite=38, nvisit=3)
```

**# inits function**

```
Nst <- apply(C,1,max)+1 # maximum count per site, +1 to avoid 0
inits <- function()list(N = Nst, a=dunif(1,-1,1), e=dunif(1,-1,1),
k=dunif(1,-1,1), l= dunif(1,-1,1),c=dunif(1,-1,1), f=dunif(1,-1,1),
b= dunif(1,-1,1))
```

**# parameters to estimate**

```
params <- c("N", "totalN", "a","b","c","e","f","k","l")
```

**# MCMC settings**

```
nc <- 3
nb <- 10000
ni <- 100000
nt <- 5
```

**# start Gibbs sampler**

```
out<-
bugs(win.data,inits,params,"model2.txt",n.chains=nc,n.iter=ni,n.burn
=nb,n.thin=nt,debug=TRUE,bugs.directory=bugs.dir,
working.directory=getwd())
```



**Fig. S1** Location of the study 38 study sites.