Factors influencing colonization of created habitats by an endangered amphibian species

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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.

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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 sliding hangsides 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 62.2 °N; 19.6 °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^2 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®, 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^{-1}, 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, 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 (Rhat > 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 (Shulse *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 detecability 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 it's 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). 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 (±0) and 20 (±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 preperation). 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 (±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 o f 100 m around the pond should be avoided.

In the broader landscape, connectivity had an influence on population size. New ponds have to be setin 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.

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Tables

Table 1 Description of the covariates.

covariates	**range**	**description**
detection		
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
pond and water characteristics		
size	6-365m^2	watersurface
depth	10-150m	maximal water depth
interlayer	categorical	interlayer for waterproofing the pond
pH	6.308-10.089	pH
pH^2	39.790-101.806	pH squared
#ponds	categorical	one or more ponds at a site
habitat characteristics 10m radius		
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
habitat characteristics 100m radius		
constructions	0-13857.522	m^2 of settlements
forest	0-31374.21	m^2 of forest (and hedges)
stonewall or open hangslide	categorical	stonewall or open hangslide with sparse or no vegetation
landscape		
distance_km	0.091-2.388	km to the next population (Prugh 2009)
connectivity	0.142-3.388	$S_i=\Sigma\ p_i \exp(-d_{ij})$ (Hanski 1994)
constructions	5844.278-1099528	m^2 of settlements
waterbodies	0-76479	m^2 of waterbodies
forest	232619.9-2551189	m^2 of hedges and forest
stones	0-86336.46	m^2 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	*detection p1*			
	intercept	1.053	-0.163	2.346
	temp	-0.711	-1.909	0.377
	date	**-0.634**	**-1.398**	**-0.096**
	rain	0.712	-0.976	2.450
	detection p2[1]			
	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
	detection p2[2]			
	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
	colonization			
	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
	reproduction			
	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	*detection p1*			
	intercept	1.041	-0.199	2.334
	temp	-0.724	-1.919	0.375
	date	**-0.636**	**-1.391**	**-0.096**
	rain	0.706	-0.994	2.452
	detection p2[1]			
	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
	detection p2[2]			
	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
	colonization			
	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^2	-0.183	-1.618	1.245
	#pond	**1.282**	**0.026**	**2.571**
	reproduction			
	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^2	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	*detection p1*				
		intercept	1.059	-0.167	2.370
		temp	-0.723	-1.913	0.347
		date	**-0.648**	**-1.459**	**-0.095**
		rain	0.705	-1.010	2.454
	detection p2[1]				
		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
	detection p2[2]				
		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
	colonization				
		intercept	-8.809	-1.489	-0.803
		forest	0.064	-1.895	2.035
		stones	0.004	-1.967	1.969
	reproduction				
		intercept	0.161	-0.898	1.224
		forest	-0.059	-2.005	1.894
		stones	0.011	-1.940	1.974
5	*detection p1*				
		intercept	1.054	-0.176	2.388
		temp	-0.721	-1.906	0.346
		date	**0.651**	**-1.464**	**-0.095**
		rain	0.707	-0.994	2.444
	detection p2[1]				
		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
	detection p2[2]				
		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
	colonization				
		intercept	-0.809	-1.491	-0.179
		forest	0.068	-1.896	2.018
		open soil	0.015	-1.942	1.986
	reproduction				
		intercept	0.169	-0.888	1.253
		forest	-0.062	-2.019	1.870
		open soil	0.017	-1.942	1.980
6	*detection p1*				
		intercept	1.044	-0.207	2.365
		temp	-0.725	-1.928	0.356
		date	**-0.658**	**-1.489**	**-0.102**
		rain	0.697	-1.011	2.438
	detection p2[1]				
		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
detection p2[2]			
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
colonization			
intercept	-0.843	-1.543	-0.175
grass	-0.365	-1.057	0.309
stones	-0.025	-1.987	1.935
reproduction			
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	*detection p1*				
		intercept	0.971	-0.348	2.332
		temp	-0.673	-1.876	0.411
		date	**-0.658**	**-1.531**	**-0.102**
		rain	0.656	-1091	2.433
	detection p2[1]				
		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
	detection p2[2]				
		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
	colonization				
		intercept	-1.161	-2.093	-0.346
		constructions	**-0.525**	**-1.342**	**-0.021**
		forest	-0.057	-0.137	0.019
	reproduction				
		intercept	-0.058	-1.694	1.632
		constructions	0.093	-1.578	1.718
		forest	**-0.451**	**-1.646**	**-0.048**
8	*detection p1*				
		intercept	0.955	-0.377	2.309
		temp	-0.668	-1.885	0.427
		date	**-0.667**	**-1.560**	**-0.101**
		rain	0.645	-1.092	2.416
	detection p2[1]				
		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
	detection p2[2]				
		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
	colonization				
		intercept	-1.656	-2.698	-0.748
		constructions	0.460	-1.246	0.008
		forest	-0.055	-0.137	0.024
		stonewall/hangslide	**1.423**	**0.267**	**2.616**
	reproduction				
		intercept	-0.094	-1.796	-0.100
		constructions	0.107	-1.600	1.809
		forest	**-0.477**	**-1.689**	**-0.037**
		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	*detection p1*			
	intercept	1.046	-0.186	2.346
	temp	-0.713	-1.899	0.366
	date	**-0.650**	**-1.453**	**-0.103**
	rain	0.699	-1.016	2.467
	detection p2[1]			
	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
	detection p2[2]			
	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
	colonization			
	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
	stones	**-0.081**	**-0.222**	**-0.001**
	age	**9.946**	**0.018**	**2.054**
	reproduction			
	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
	age	**1.474**	**0.105**	**3.094**
10	*detection*			
	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
	colonization			
	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
	stones	**-0.084**	**-0.232**	**-0.002**
	age	0.701	-0.221	1.768
	reproduction			
	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* (lamda) 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 (lamda)*	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	*detection*			
	intercept	-1.217	-1.563	-0.993
	temp	-0.067	-0.235	0.075
	abundance			
	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
	#pond	**1.660**	**0.700**	**2.648**
3	*detection*			
	intercept	-1.275	-1.693	-1.017
	temp	-0.067	-0.242	0.084
	abundance			
	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^2	0.040	-5.674	5.521
	#pond	**1.436**	**0.444**	**2.456**

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	*detection*			
	intercept	-1.189	-1.483	-0.986
	temp	-0.062	-0.218	0.075
	abundance			
	intercept	-0.146	-0.597	0.304
	forest	0.408	-9.212	9.349
	stones	0.878	-9.192	9.529
5	*detection*			
	intercept	-1.185	-1.478	-0.983
	temp	-0.063	-0.218	0.072
	abundance			
	intercept	-0.173	-0.623	0.281
	forest	-0.092	-0.482	0.318
	opensoil	0.670	-13.880	14.15
6	*detection*			
	intercept	-1.083	-1.329	-0.917
	temp	-0.044	-0.180	0.071
	abundance			
	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	*detection*				
		intercept	-1.424	-2.195	-1.041
		temp	-0-059	-0.228	0.086
	abundance				
		intercept	-2.080	-3.670	-0.765
		constructions	**-0.671**	**-1.788**	**-0.084**
		forest	**-0.094**	**-0.146**	**-0.047**
		stonewall/hangslide	**2.189**	**1.243**	**3.314**

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	*detection*			
	intercept	-1.220	0.002	-0.987
	temp	-0.081	-0.245	0.056
	abundance			
	intercept	-0.303	-0.826	0.208
	connectivity	**0.584**	**0.189**	**0.969**
	constructions	-0.224	-0.705	0.156
	age	0.068	-0.254	0.4845
9	*detection*			
	intercept	-1.202	-1.521	-0.988
	temp	-0.060	-0.218	0.078
	abundance			
	intercept	-0.195	-0.672	0.285
	distance_km	-0.362	-0.813	0.061
	waterbodies	-2.963	-9.739	8.212
10	*detection*			
	intercept	-1.226	-1.561	-1.001
	temp	-0.079	-0.241	0.059
	abundance			
	intercept	-0.267	-0.773	0.239
	connectivity	**0.527**	**0.153**	**0.897**
	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.

covariates	**colonization**	**reproduction**	**abundance**
pond and water characteristics			
size	X	x	x
depth	X	x	x
interlayer	X	x	x
pH	X	x	x
pH^2	X	x	x
#ponds	**+**	x	**+**
habitat characteristics 10m radius			
forest	X	x	x
grass	X	x	x
stones	X	x	x
open soil	X	x	x
habitat characteristics 100m radius			
constructions	**-**	x	**-**
forest	X	**-**	**-**
stonewall or open hangslide	**+**	x	**+**
landscape			
distance_km	X	x	x
connectivity	X	x	**+**
constructions	X	x	x
waterbodies	X	x	x
forest	X	x	x
stones	**-**	x	x
age	**+**	**+**	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 on 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.

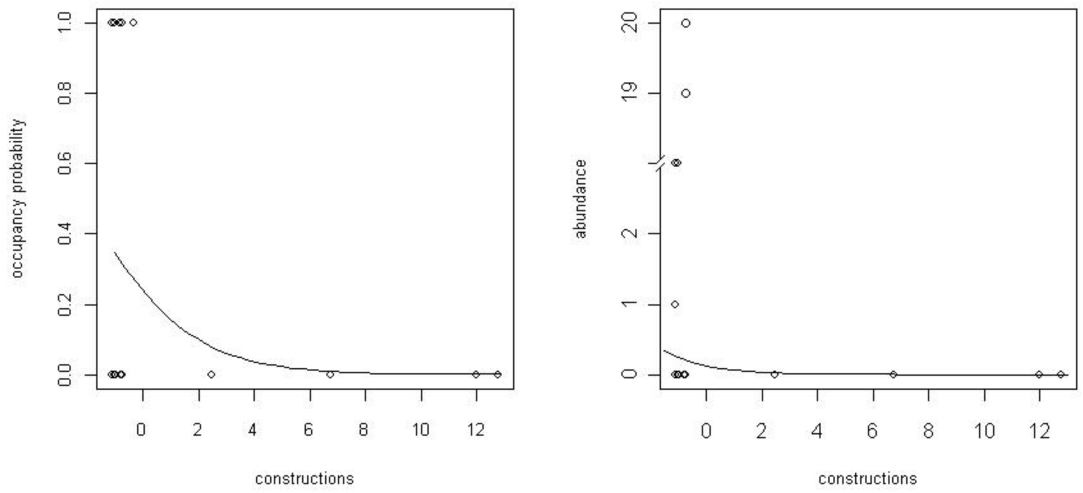
occupancy probability
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
constructions
abundance
20
19
2
1
0
0
2
4
6
8
10
12
constructions

Fig. 1

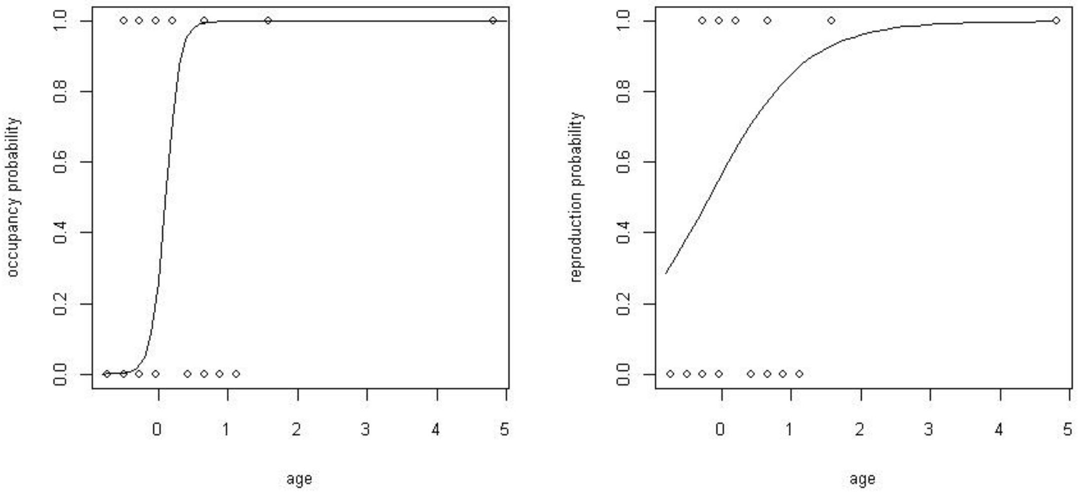
occupancy probability
reproduction probability
age
age
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
5

Fig. 2

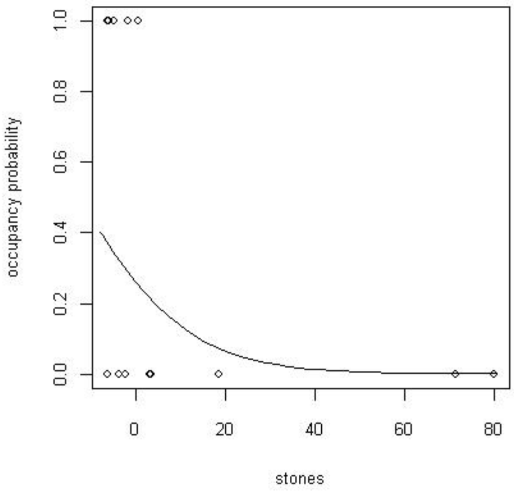

Fig. 3

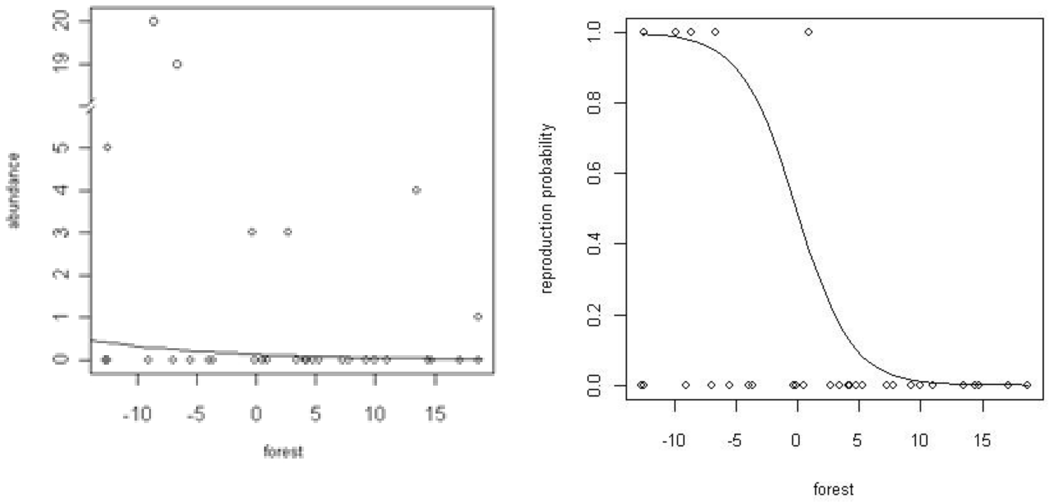

Fig. 4

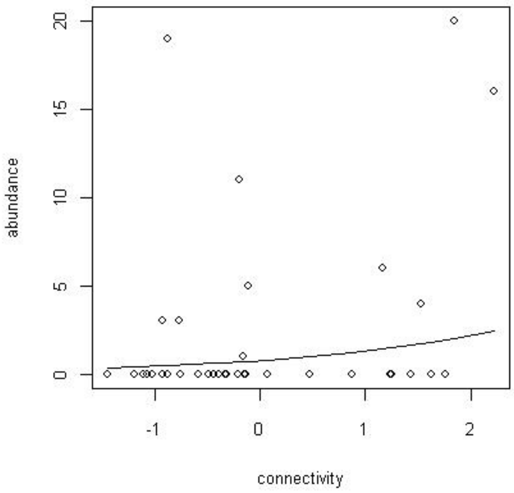

Fig. 5

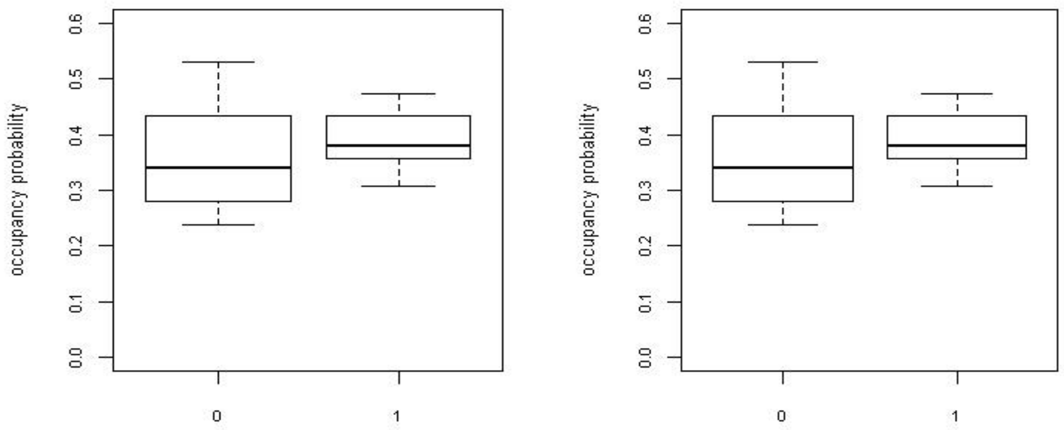
occupancy probability
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
1
occupancy probability
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
1

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.