

Master-Thesis submitted to the Faculty of Mathematics and Natural Sciences of the University of Zurich

Describing the ecological niche of Rana dalmatina considering metapopulation theory and source-sink model

submitted by Mario Lippuner

supervised by Dr. Benedikt R. Schmidt and Prof. Dr. Heinz-Ulrich Reyer

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University of Zurich
Institute of Evolutionary Biology and Environmental Studies

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Abstract

The ecological niche model is a fundamental property of a species and determines its distribution. However, niche model treat all sites where a model species occurs as suitable and all sites where species does not occur as unsuitable, even though the source-sink model and the metapopulation theory suggest that occupied sites may be unsuitable (sink presences) and unoccupied sites may be suitable (metapopulation absences). I therefore analysed the ecological niche of *Rana dalmatina* using an approach that considered the source-sink model and metapopulation theory. New statistical methods have made it possible to obtain reliable inferences about the process of change in the occurrence of a model species on the basis of repeated detection/non-detection data, and therefore, probabilities of occupancy, colonisation and extinction can be estimated. In addition to analysing metapopulation dynamics, I also examined which factors explain spatial variation in reproduction and abundance. Colonisation events with reproduction showed that not all suitable ponds were always occupied (i.e., there were metapopulation absences). Extinction and the fact that reproduction did not occur in all occupied ponds, showed that not all ponds had self-sustaining populations and might be sinks. Different combinations of ecological factors best explained the probabilities of occupancy, colonisation, extinction, reproduction and abundance. Pond drying and the availability of structures for egg attachment had a positive effect on occupancy. Ponds that were close to woodland were more likely to be occupied than ponds farther away. Colonisation was determined by a positive effect of connectivity. Small populations were more likely to become extinct than larger ones. Pond drying also had a positive effect on reproduction. Exposure to sunlight, the availability of structures for egg attachment and connectivity had a positive effect on abundance in a pond. The distance between pond and woodland affected abundance negatively. Based on the analysis, I conclude that reproduction describes the ecological niche better than occupancy or abundance and that reproduction is determined by pond drying. Therefore pond drying was the most important ecological factor. Along with reproduction, colonisation and extinction were also important to verify metapopulation absence and sink presence. Therefore, further niche models should be described by reproduction, colonisation and extinction instead of occupancy and abundance.

Zusammenfassung

Das Modell der ökologischen Nische beschreibt als fundamentale Eigenschaft die Verbreitung von Arten. Das Modell geht davon aus, dass alle Habitats, in denen eine Art vorkommt, geeignet sind und alle Habitats, in denen eine Art fehlt, ungeeignet sind. Das Source/Sink-Modell und das Metapopulationsmodell zeigen aber, dass besetzte Habitats ungeeignet (Sink-Präsenzen) und unbesetzte Habitats geeignet sein können (Metapopulationsabsenzen). Deshalb analysierte ich die ökologische Nische von *Rana dalmatina* anhand eines Ansatzes, der das Source/Sink-Modell und das Metapopulationsmodell berücksichtigt. Neue statistische Methoden ermöglichten mir, auf der Basis wiederholter Präsenz- und Absenzuntersuchungen Vorkommens-, Kolonisierungs- und Aussterbewahrscheinlichkeiten zu schätzen und damit dynamische Populationsprozesse zu beschreiben. Weiter wurde untersucht, welche Faktoren die Reproduktion und Abundanz bestimmen. Kolonisierungsereignisse mit Reproduktion zeigten, dass nicht alle günstigen Gewässer besetzt waren (Metapopulationsabsenzen). Aussterbeereignisse und die Tatsache, dass nicht in allen besetzten Gewässern Reproduktion stattfand, zeigten, dass nicht alle Vorkommen selbst erhaltend waren, was für Sinks spricht. Die Wahrscheinlichkeiten für Vorkommen, Kolonisieren, Aussterben und Reproduktion sowie die Abundanz konnten durch unterschiedliche Kombinationen von Habitatfaktoren qualitativ beschrieben werden. Die Vorkommenswahrscheinlichkeit wurde durch die Faktoren Gewässeraustrocknung und Aufhängestrukturen für Laichballen positiv, durch die Distanz zwischen Gewässer und Wald hingegen negativ beeinflusst. Die Kolonisierungswahrscheinlichkeit wurde positiv beeinflusst durch die Konnektivität. Kleine Populationen zeigen eine höhere Aussterbewahrscheinlichkeit als größere. Für die Reproduktionswahrscheinlichkeit war entscheidend, dass Gewässer gelegentlich austrocknen. Die Abundanz wurde durch die Faktoren Sonnenexposition, Aufhängestrukturen für Laichballen und Konnektivität positiv, durch die Distanz zwischen Gewässer und Wald hingegen und negativ beeinflusst. Aus den Analysen kann geschlossen werden, dass Reproduktion die Ökologische Nische besser beschreibt als Vorkommen und Abundanz, und dass Reproduktion ermöglicht wird, wenn Gewässer ab und zu austrocknen. Deshalb war der Faktor Gewässeraustrocknung der wichtigste Nischenfaktor. Um Metapopulationsabsenzen und Sink-Präsenzen zu verifizieren waren nebst der Reproduktion auch Kolonisieren und Aussterben wichtig. Nischenmodelle sollten demzufolge künftig durch Reproduktion sowie durch Kolonisation und Aussterben beschrieben werden und nicht durch Vorkommen und Abundanz.

1 INTRODUCTION

1.1 Conceptual basis

Hutchinson (1957) defined the ecological niche of a species as an “ n -dimensional hypervolume”, which is determined by complex relations between environmental factors and resources. Hutchinson made the distinction between fundamental (in terms of Grinnell 1917) and realised niches. The fundamental niche describes the full range of environmental conditions (biological and physical) under which an organism can exist (Figure 1). As a result of pressure from other organisms and interactions, species are usually forced to occupy a niche which is narrower than the fundamental niche. This is termed the realised niche (Figure 2). Since then, Hutchinson’s formalisation of the niche concept has become central to ecological theory, and has become a fundamental property of species which is often described using distribution models (Hutchinson 1957, Begon et al. 1998, Pulliam 2000, Soberón & Nakamura 2009).

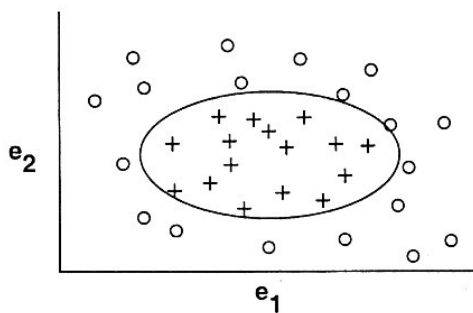


Figure 1 Fundamental niche model in terms of Grinnell (1917). The solid oval refers to the fundamental niche, e_1 and e_2 are environmental factors or resources. Pluses are occupied sites, circles unoccupied sites. Thus, a species occurs everywhere where conditions are suitable. (Figure taken from Pulliam 2000).

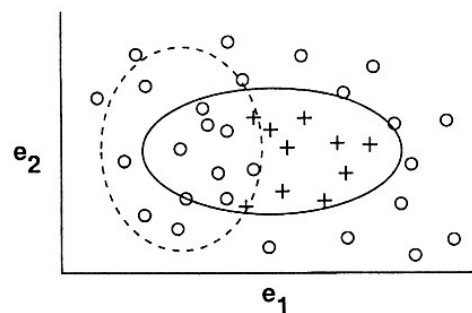


Figure 2 Realised niche model (Hutchinson 1957). Hutchinsonian realised niche postulates that a species will be absent for those portions of the niche spaces that are utilised by a dominant competitor or by a predator. The dashed oval refers to habitats influenced by competitors or predators. (Figure taken from Pulliam 2000).

However, niche and distribution models imply a problem – all sites where model species occur count as suitable and all sites where species do not occur count as unsuitable (e. g. Skelly et al. 1999, Pulliam 2000, Hamer et al. 2002, Houlahan & Findlay 2003, Knapp et al. 2003, Schmidt & Pellet 2005, Denoël & Ficetola 2008, Hartel et al. 2008, Hooper et al. 2008 Elith and Leathwick 2009, Holt 2009). This assumption may be unrealistic. The source-sink model (Pulliam 1988) and the metapopulation theory (e. g. Hanski 1989, 1991, Hanski & Gyllenberg 1993) show the occupied sites may be unsuitable and unoccupied sites may be suitable, respectively. Therefore, a distinction must be made between sink presence (mortality > natality, species persists in an unsuitable habitat as a consequence of immigration) and source presence

(mortality < natality, species is self-sustainable). For absence, it must be differentiated between metapopulation absence in a suitable habitat and absence in an unsuitable habitat (Kadmon & Pulliam 1993, 1995, Hanski et al. 1994, Schmidt & Pellet 2005, Pulliam 2000, Holt 2009) (Figure 3). Apart from this, ‘overlooking’ a species, i.e. not

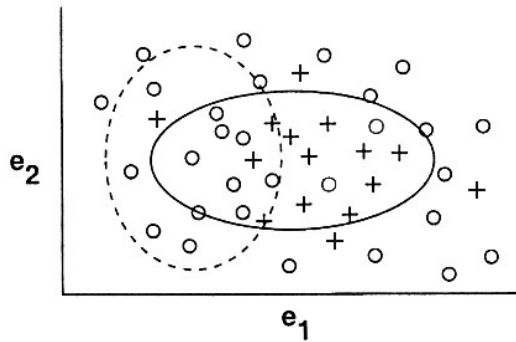


Figure 3 Modified realised niche with source-sink dynamics and metapopulation absence. Pluses outside the lined oval are sink populations (because of unsuitable habitat), pluses inside the dashed oval are sinks (because of competitors or competitors plus unsuitable habitat). Pluses inside the lined oval (but outside the dashed oval) are sources, circles in the same part denote metapopulation absence. The rest of the circles represent absence because of unsuitability of habitat or/and predators’ influence. (Figure taken from Pulliam 2000 and modified)

finding a species which is present, has generally not been taken into consideration, and may also result in “false” absence (Royle et al. 2005).

The goal of my master thesis is to build an ecological niche model that avoids some of these problems. While most distribution models only use presence/absence data (i. e. detection/non-detection data), I use data from a long-term study (Lippuner 2000, Lippuner and Rohrbach 2007, 2009) to build a better distribution model considering the source-sink model (Pulliam 1988) and the metapopulation theory. With the long-term data, I can differentiate between various kinds of presence/absence data:

- presence where the species persists,
- presence where the species becomes extinct,
- absence where the species’ absence persists,
- absence where the species colonises,
- presence where the species is rare or common,
- presence where the species reproduces.

These data allow estimates of occupancy, colonisation, extinction, reproduction and abundance. Colonisation, together with reproduction, shows metapopulation absence. Occupancy and reproduction provide information about sources. Occupancy without reproduction shows sink populations. Different combinations of best explaining covariates for probability of occupancy, colonisation, extinction, reproduction and abundance show me the importance of the

dynamic approach and I can reach the main possible approximation to what is suitable for *R. dalmatina*.

New methods allow direct estimation of occupancy, colonisation, local extinction and detection probability from repeated detection/non-detection surveys. These methods have made it possible to obtain more reliable inferences about the process of change in species occurrence (MacKenzie et al. 2003, 2006, 2009, Royle and Kéry 2007).

1.2 Model species and biological derivation of niche factors

R. dalmatina seems to be a suitable model species for my topic. The data basis is rather large, and the spatio-temporal dynamics appear to be relatively high (Grossenbacher et al. 2002, Lippuner & Rohrbach 2009). Most literature which describes habitats of *R. dalmatina* (mentioned in the paragraph below) are not based on empirical data (except Hartel 2008, 2009, 2010 and Zanini et al. 2009). Therefore, scientific results about the niche of *R. dalmatina* are needed. The resulting knowledge is required for conservation programs.

R. dalmatina shows a few biological peculiarities. Thus, potential niche factors for my investigation can be easily derived. In comparison to the phenologically similar *Rana temporaria*, development of eggs and larvae of *R. dalmatina* is slower (Lippuner 2000, Bühler et al. 2007). The aquatic period of development is therefore, comparatively long, and eggs and larvae are exposed to aquatic predators over a longer period of time. Furthermore, females of *R. dalmatina* produce comparatively few eggs (Günther et al 1996). I therefore assume that warm water, a low density of predacious invertebrates and absence of fish populations are important for reproduction (→ niche factors: exposure to sunlight, pond drying). Exposure to sunlight ensures warm water, while pond drying inhibits fish populations and reduces some other aquatic predators (e. g. Barandun 1995, 1996, Skelly 1996, Wellborn et al. 1996, Snodgrass et al. 2000). Together with a good supply of food, these factors ensure a reduction on the aquatic development period with a reduced risk of predation. Furthermore, the presence of structures for egg attachment could be relevant for reproduction (→ niche factor: structures for egg attachment). Typically, *R. dalmatina* attaches its egg masses individually to structures such as reed stalks or branches (e. g. Günther 1996, Grossenbacher 1997 b, Hartel 2003) only a few centimetres beneath the water surface in middle deep riparian zones. If such structures are missing, egg masses are placed on the bottom of ponds in shallow water, where newts (i. e. *Ichthyosaura alpestris*) prefer to eat (ML pers. obs.). *I. alpestris* occurs in large

numbers in most ponds of *R. dalmatina* in north-east Switzerland (Lippuner & Rohrbach 2009). This habit of attaching and distributing the egg masses contrasts with *R. temporaria*'s strategy of concentrating all egg masses together into high density aggregations in shallow riparian zone.

Characteristic summer and breeding habitats of *R. dalmatina* show a huge biological diversity (Lippuner & Rohrbach 2009). Therefore, ponds of *R. dalmatina* are colonised by a comparatively high number of other amphibians (Geisselmann et al. 1971, Podloucky 1985, Lippuner & Rohrbach 2009). Direct interspecific competition would be most likely with *R. temporaria* (→ niche factor: abundance of *R. temporaria*). As already mentioned, larvae of *R. temporaria* and *R. dalmatina* develop in a similar time period. *R. dalmatina* reaches a small advantage over *R. temporaria* because of an earlier migration and breeding time, but as a result of comparatively slow development of eggs and larvae, *R. dalmatina* loses this head start, and the hatchlings leave egg masses at approximately the same time as those of *R. temporaria* (ML pers. obs.). The larvae of both species then live together for a 2 or 3 months, but larvae of *R. temporaria* reach metamorphosis 2-3 weeks earlier (Lippuner 2000, Bühler et al. 2007).

In contrast to other mid European species of amphibians whose populations are often widespread (Grossenbacher 1988), *R. dalmatina* often lives in high densities in smaller disjunct areas (Gasc 1997, Grossenbacher 1997a) with a high density of suitable ponds (Lippuner 2000). Hence, a strong connectivity between local populations could be important. Zanini et al. (2009) demonstrate the importance of connectivity for *R. dalmatina* (→ niche factor: connectivity).

R. dalmatina is a characteristic species of woodland areas. Summer habitats are located almost only in well-lit woods (e. g. Blab 1978, 1986, Grossenbacher 1988, Ahlén 1997, Fog 1997, Podloucky 1997, Lippuner et al. 2001, Stümpel & Grosse 2005). Thus, the species' occurrence is dependent on woods in close neighbourhood to the ponds (→ niche factor: distance between pond and woodland). Because all ponds outside woods are surrounded by arable land, such as fields and grassland without refuges, migration between ponds (which are located far away from the woods) and woodland could be very dangerous and not enough individuals survive to allow occurrence or a high abundance (e. g. Schneeweiss and Schneeweiss 1997, Becker et al. 2007). Another reason for occupancy and abundance being more likely in ponds close to or in woodlands could be that *R. dalmatina* generally avoids areas without trees.

1.3 Hypotheses

I supposed that different ecological factors determine probability of occupancy, colonisation, extinction, reproduction and abundance. That indicates the importance of a dynamic approach. In the following paragraphs I define my assumptions for the factors best explaining each probability.

Occupancy: Factors that positively affect occupancy are pond drying (PD), exposure to sunlight (ETS), structures for egg attachment (SFEA) and connectivity (CON). I expect that distance to woodland (DTW) and abundance of *R. temporaria* (RATE) negatively affect occupancy. As described in paragraph “Reproduction” below factors pond drying, exposure to sunlight and structures for egg attachment allow reproduction, and therefore, they have an indirect effect on occupancy.

Colonisation: Factors that negatively affect colonisation are distance to woodland (DTW) and connectivity (CON), i.e. the combined effect of the distance to the next colonised ponds and their population size, with a positive effect.

Extinction: Factors that affect extinction are connectivity (CON), abundance in 1997 (ABU97) and abundance in 2004 (ABU04). All three parameters show a negative effect.

Reproduction: Factors that positively affect reproduction are pond drying (PD), exposure to sunlight (ETS), structures for egg attachment (SFEA) and abundance (ABU10). Pond surface (PSF) and *R. temporaria* population size (RATE) affect reproduction negatively. These are the factors which have an effect inside ponds. I include abundance in 2010 (ABU10) and pond surface as control variables (pond surface could have an influence on detecting larvae; in large ponds reproduction could therefore be underrated).

Abundance: Factors that positively affect abundance are abundance in 2004 (ABU04), pond drying (PD), exposure to sunlight (ETS), structures for egg attachment (SFEA) and connectivity (CON). Distance to woodland (DTW) affects abundance negatively. As described in paragraph “Reproduction”, pond drying, exposure to sunlight and structures for egg attachment allow reproduction, and therefore, they have an indirect effect on abundance. Abundance in the previous investigation (ABU04) is included as a control variable.

2 METHODS

2.1 Study area

The study area is part of *R. dalmatina*'s distribution area in the Lake Constance region. I investigated ponds to the south of the River Rhine in Cantons Zurich and Thurgau. The altitude ranges from 343 m at Flaach to 591 m on the Rodenberg. The average temperature is 17.8 °C for July, -1.0 °C for January and 8.5 °C on average throughout the year (arithmetic mean of the years 1961-1990 at the weather station near Schaffhausen, at the border to the study area; MeteoSchweiz 2006). Total yearly precipitation is 883 mm (weather station Schaffhausen). Bedrock and soil are in most places neutral or slightly alkaline (mixed substratum of moraines of the glacial Rhine glacier, molasses and fluvio-glacial brash). The density of ponds is much higher than in most other parts of Switzerland. Characteristic and common are "Sölle" (developed by ice relicts as the glaciers melted, Hofmann 1967) in undulating parts and backwaters along the Rivers Rhine and Thur. Along with a high density of ponds, the study area is also known for its relatively dry and warm habitats (Hofmann 1967).

2.2 Data collection and niche parameters

I studied 76 ponds (Appendix I). These are 2/3 of all ponds in the previously described study area. These ponds were chosen randomly.

Detection/non-detection and abundance: My study consists of three primary sampling periods (1997, 2004, 2010), between which changes in site occupancy may have occurred. Usually three site visits were undertaken each year. *R. dalmatina* was detected by searching egg masses. Egg masses were counted to obtain an estimate of abundance; a female usually produces a single egg mass (Günther et al. 1996). For the distribution analyses (occupancy, colonisation and extinction), number of egg masses was reduced to presence (1) and absence (0) data.

Reproduction: To determine whether reproduction was successful, I conducted dip net surveys in June and July 2010 when tadpoles were close to metamorphosis (i. e., when they had hind limbs and sometimes forelimbs). In every pond I sampled four transects (high/low density vegetation [or other structures] once in sunny and once in shady parts each transect five minutes) from shallow to deeper water. Reproduction was defined based on the presence of larvae which were close to metamorphosis.

Niche factors: Most niche factors were determined while sampling for occurrence of *R. dalmatina*. Specific information about investigation of the niche factors is shown in Table 1.

Table 1 Investigated parameters with methodical information.

Factors	Classification	Definition/method
Pond drying (PD)	Never (0), every few years (1), every year (2), more than once a year (3). For analysis of abundance and reproduction combining 2 and 3 was required.	Empirical value over 13 years field work, considering droughts as in 1998 and 2003.
Exposure to sunlight (ETS)	Degree in percent	Temporal or partial degree of sunlight over a day.
Structures for egg attachment (SFEA)	None (0), few (1), many (2)	Estimation of abundance of reed stalks, branches et cetera in relation to the water surface.
Distance to woodland (DTW)	Distance in metres	Measured in map 1 : 25'000.
Connectivity (CON)	Resulting value on a metric scale.	Combined effect of the distance to the next colonised ponds and their population size calculated by equation $c = \sum_{j \neq i} \exp\{-d(ij)\}A$ where d denotes for distance between ponds i and j . A denotes for abundance (Prugh 2009)
Pond surface (PSF)	Area in square meters.	Estimated in the field.
Abundance of <i>Rana temporaria</i> (RATE)	Absent (0), small (1), medium (2), large (3), very large (4). For analysis of abundance and reproduction combining 3 and 4 was required.	Egg mass count; classification into size classes based on Grossenbacher 1988.
Abundance of <i>Rana dalmatina</i> 1997/2004/2010 (ABU97, ABU04, ABU10)	Count	Number of egg masses. Determined in field.
Reproduction of <i>Rana dalmatina</i> (REP)	No (0), yes (1)	Sampling of four transects (high/low density vegetation, sunny/shady) with dip net, each transect five minutes.

2.3 Data analysis

2.3.1 Occupancy, colonisation, local extinction and detection probability

I used the multiseason site occupancy model of MacKenzie et al. (2003). Occupancy ψ was estimated for first primary sampling period in 1997, and colonisation γ and local extinction ε were estimated for the following primary sampling periods in 2004 and 2010. The model accounts for imperfect detection (Appendix II equation four). The detection history for each of the three primary sampling periods can be expressed as vectors of 1's and 0's, indicating de-

tection and non-detection of the species, respectively. If a site was investigated three times in all three primary sampling periods, the detection history of *R. dalmatina* for that site could be e. g. 101 010 000. The probability of observing the detection history at the three primary sampling periods $t = 1$, $t = 2$ and $t = 3$ can be modelled as follows:

$$\Pr(\mathbf{X}_{i,1} = 101) = \psi_1 p_{1,1}(1 - p_{1,2}) p_{1,3},$$

$$\Pr(\mathbf{X}_{i,2} = 010) = \psi_1 p_{1,1}(1 - p_{2,1}) p_{2,2}(1 - p_{2,3}),$$

$$\Pr(\mathbf{X}_{i,3} = 000) = (1 - \varepsilon_1) \prod_{j=1}^3 (1 - p_{3,j}) + \varepsilon_1.$$

ψ_1 shows the probability that a pond is occupied by *R. dalmatina* and $p_{i,j}$ shows the probability of detecting, given presence, in survey j within primary period t , and ε is the probability that a site occupied at $t + 1$ is unoccupied at $t + 2$ (local extinction). The detection history for the surveys for site i at a primary period t is denoted as $\mathbf{X}_{i,t}$. The product of all three equations shows the probability of observing the full detection history (Appendix II).

Estimates of the parameters occupancy, colonisation and local extinction probabilities were calculated using an application of likelihood theory. Relationships between covariates and parameters were calculated by the logistic model of following equation:

$$\theta = \frac{\exp(Y\beta)}{1 + \exp(Y\beta)}.$$

θ is the probability of interest, Y is the matrix of covariate information, and β is the vector of logistic coefficients. I therefore included my niche factors as covariates in the models for ψ , γ and ε . For detection probability ρ no covariates were included. According to experience, detection of egg clusters is more or less independent of environmental conditions (Lippuner 2007, 2009) and my results show that detection probability is very high.

With the previous framework I tested my hypotheses (chapter 1.3). After that, I excluded the weakest factors (variables whose confidence interval include zero) step by step until the best model was reached. Further models were built as controls, excluding all factors for each parameter. Information-theoretic methods (Akaike's Information Criterion AIC, Δ AIC and AIC weight) were used to select the better models (Burnham and Anderson 2002). Models with lower AIC and Δ AIC values and higher Akaike weights fit the data better than models with higher AIC and Δ AIC or lower Akaike weights. I used the statistics program PRESENCE 3.0 (www.mbr-pwrc.usgs.gov/software/presence.html).

2.3.2 Abundance and reproduction probability

I used poisson regression and generalised linear models. These models allow use of my several predictor variables which are either continuous or categorical. Poisson distribution with zero inflation (with log link function) (Martin et al. 2005, Kéry 2010) was required for my analyses of abundance, binomial error distribution (with logit link function) was required for my analyses of reproduction.

In the first model of reproduction I tested all parameters included in my hypotheses. Then, I excluded the weakest parameters (variable with the highest p -value) step by step until the best model was reached. Information-theoretic methods (Akaike's Information Criterion AIC and Δ AIC) were used to select the better models (Burnham and Anderson 2002). Model goodness improves with decreasing AIC and Δ AIC. For abundance, model selection was not required because all factors included in the hypothesis were significant except one factor. The abundance and reproduction were analysed in statistics program R 2.8.0 (R Development Core Team, 2008).

2.3.3 Correlation

I tested the correlation between all independent factors with the purpose of achieving a better interpretation of the results of the model selections. Because my data consist of categorical and numerical factors, I assessed relationships between independent factors in three different ways. I used 1) correlation analysis if both factors were continuous, 2) ANOVA if one factor was categorical and the other continuous, and 3) χ^2 if both factors were categorical. All three analyses were calculated in statistics program R 2.8.0 (R Development Core Team 2008).

3 RESULTS

3.1 Occupancy, colonisation, local extinction and detection probability

Eight models were built for the probabilities of occupancy, colonisation and local extinction (Table 2). The first model includes all eight covariates as described in chapter 1.3. The model that was best supported by the data included the variables pond drying (PD), exposure to sunlight (ETS), structures for egg attachment (SFEA) and distance to woodland (DTW) for occurrence ψ , connectivity (CON) for colonisation γ , and abundance in 1997 (ABU97) plus abundance in 2004 (ABU04) for extinction ε (Tables 2-4). Pond drying, exposure to sunlight and structures for egg attachment were positive correlated with ψ , distance to woodland was negative correlated (Tables 3 and 4, Figures 4-7). Connectivity was positive correlated with γ (Table 4, Figure 8). Abundance in 1997 and abundance in 2004 was negative correlated with ε

(Table 4, Figures 9 and 10). The confidence interval of the variable exposure to sunlight included zero but the models without exposure to sunlight were less well supported by the data. The detection probability was 94.20 % per site visit, so we can say that nearly all occupied sites had been detected during the visits.

Table 2 Summary of model selection procedure for occupancy, colonisation and local extinction.

Model	AIC	Δ AIC	AICwgt
$\psi(\text{PD,ETS,SFEA,DTW}), \gamma(\text{CON}), \varepsilon(\text{ABU97,ABU04}) p(\cdot)$	324.45	0.00	0.4299
$\psi(\text{PD,ETS,SFEA,DTW,CON}), \gamma(\text{CON}), \varepsilon(\text{ABU97,ABU04}), p(\cdot)$	324.87	0.42	0.3484
$\psi(\text{PD,SFEA,DTW}), \gamma(\text{CON}), \varepsilon(\text{ABU97,ABU04}), p(\cdot)$	326.23	1.78	0.1765
$\psi(\text{PD,ETS,SFEA,DTW,CON,RATE}), \gamma(\text{DTW,CON}), \varepsilon(\text{CON,ABU97,ABU04}), p(\cdot)$	329.35	4.90	0.0371
$\psi(\text{PD,ETS,SFEA,DTW}), \gamma(\cdot), \varepsilon(\text{ABU97,ABU04}), p(\cdot)$	332.41	7.96	0.0080
$\psi(\cdot), \gamma(\text{CON}), \varepsilon(\text{ABU97,ABU04}), p(\cdot)$	344.13	19.68	0.0000
$\psi(\text{PD,ETS,SFEA,DTW}), \gamma(\text{CON}), \varepsilon(\cdot), p(\cdot)$	354.72	30.27	0.0000
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	378.05	53.60	0.0000

Table 3 Parameter estimates (on the logit scale) of the best model (Table 2).

Coefficients			Estimate	Standard error	Confidence interval
A1	occupancy	ψ	0.545	0.309	-0.061, 1.151
A2	occupancy	ψ PD	0.722	0.342	0.052, 1.392
A3	occupancy	ψ ETS	0.594	0.323	-0.039, 1.227
A4	occupancy	ψ SFEA	0.686	0.312	0.074, 1.298
A5	occupancy	ψ DTW	-1.000	0.386	0.244, 1.756
B1	colonisation	γ	-1.139	0.330	0.493, 1.785
B2	colonisation	γ CON	0.957	0.327	0.317, 1.597
C1	local extinction	ε	-4.168	1.506	-1.215, -7.121
C2	local extinction	ε ABU97	-11.614	4.191	-3.400, -19.828
C3	local extinction	ε ABU04	-10.921	4.795	-1.524, -20.318
D1	detection	p	2.787	0.276	2.246, 3.328

Notes: Confidence interval was calculated by standard error \times 1.96.

Table 4 Summary of the results.

	PD	ETS	SFEA	DTW	CON	RATE	ABU97	ABU04	ABU10
Occupancy	+	×	+	-	×	×			
Colonisation				×	+				
Extinction					×		-	-	
Reproduction	+	×	×		×	×			+
Abundance	×	+	+	-	+	×		+	

Notes: Plus shows a positive influence, minus a negative influence. Crosses are factors which were included in the hypotheses but which are not significant or whose confidence interval includes zero, respectively.

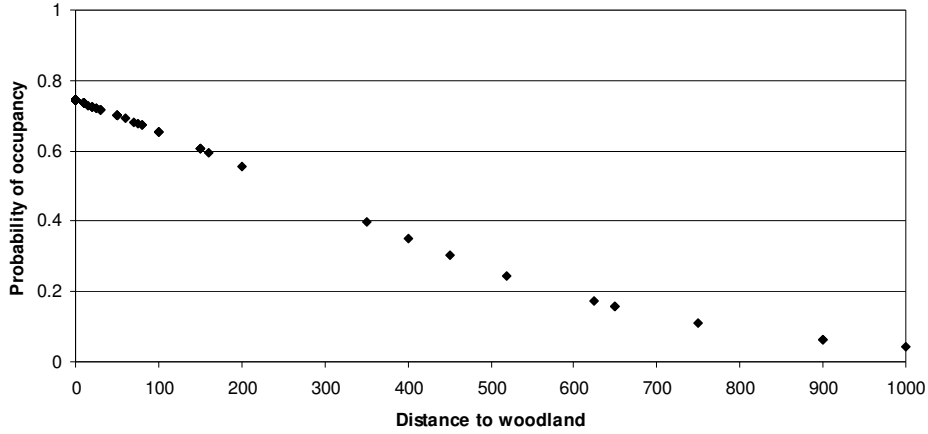


Figure 4 Relationship between the probability of occupancy and distance to woodland (in meters). The dots show the relationship when all other factors in the model are held at their mean.

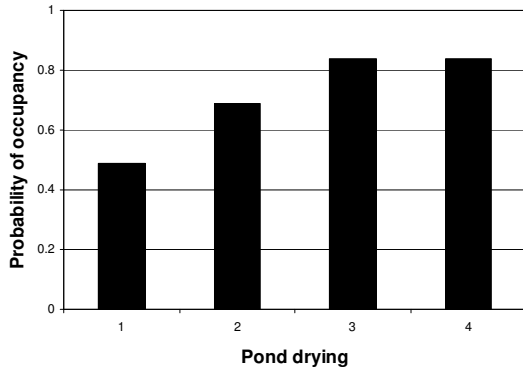


Figure 5 Relationship between occupancy and pond drying. Scale of pond drying: 1 = never; 2 = every few years; 3 = every year; 4 = more than once a year. The bars show the relationship when all other factors in the model are held at their mean.

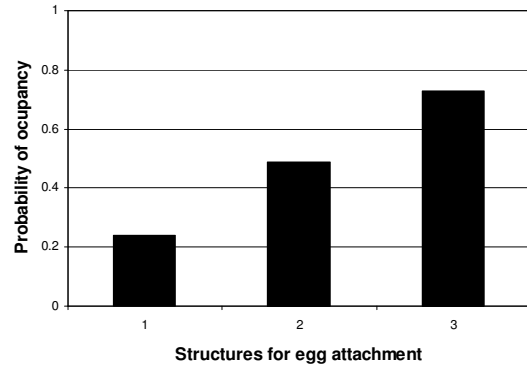


Figure 6 Relationship between occupancy and structures for egg attachment. Scale of structures for egg attachment: 1 = none; 2 = few; 3 = many. The bars show the relationship when all other factors in the model are held at their mean.

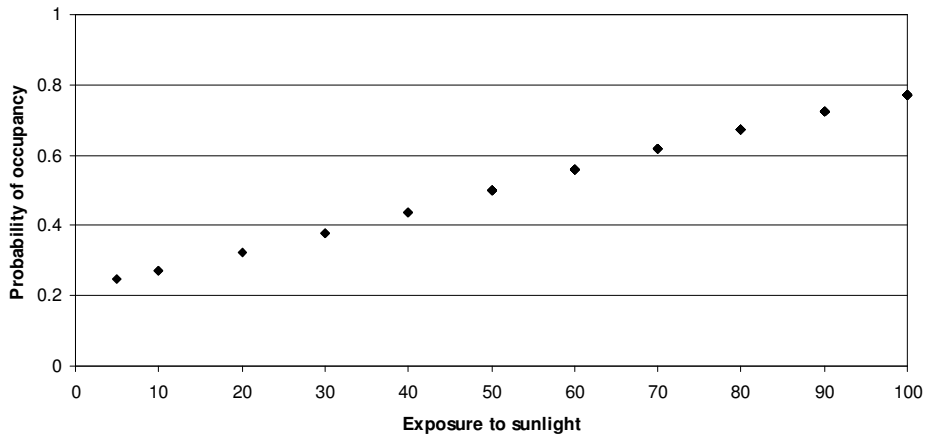


Figure 7 Relationship between probability of occupancy and exposure to sunlight in percent. The dots show the relationship when all other factors in the model are held at their mean.

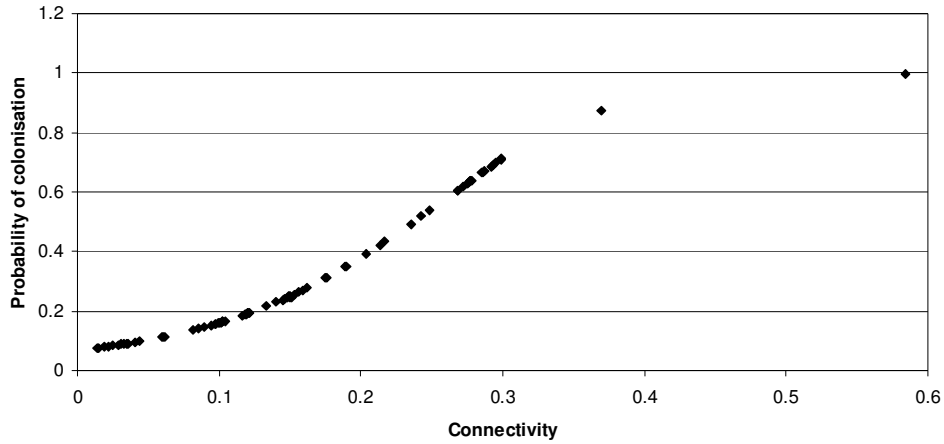


Figure 8 Relationship between probability of colonisation and connectivity. The dots show the relationship when all other factors in the model are held at their mean.

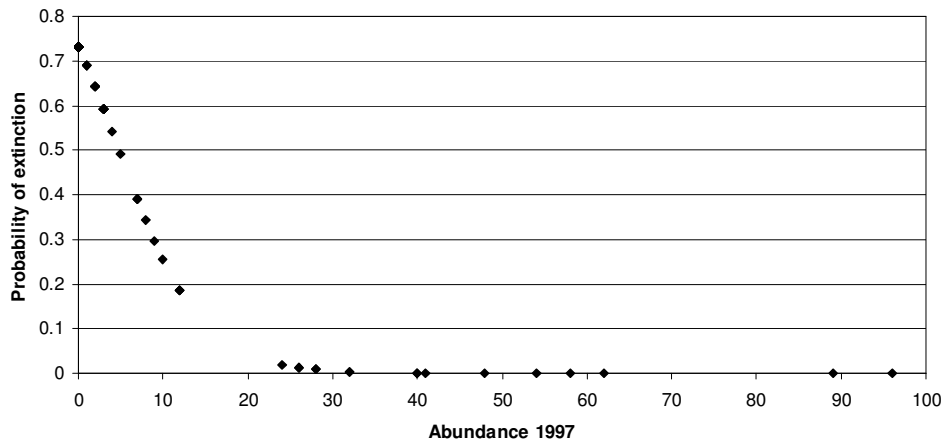


Figure 9 Relationship between probability of extinction and abundance in 1997. The dots show the relationship when all other factors in the model are held at their mean. The probability of extinction reaches nearly zero if the abundance was greater than 25 egg masses.

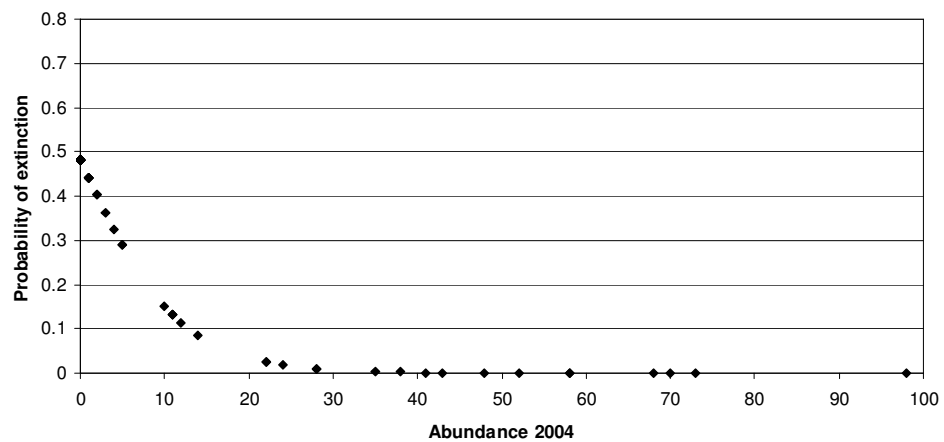


Figure 10 Relationship between probability of extinction and abundance in 2004. The dots show the relationship when all other factors in the model are held at their mean. The probability of extinction reaches nearly zero if the abundance was greater than 20 egg masses.

3.2 Reproduction probability

Six covariates were tested for an effect on the probability of reproduction (Table 5). The strongest model includes the factors abundance in 2010 (ABU10), pond drying (PD) and pond surface (PSF) (Tables 4 and 5). Abundance in 2010 and pond drying were positive correlated, pond surface was negative correlated with reproduction (Tables 4 and 6, Figures 11-13). Abundance in 2010 was included as a control variable.

Table 5 Summary of model selection procedure for reproduction.

Model	AIC	Δ AIC
REP~ABU10+PSF+PD	36.42	0.00
REP~ABU10+PSF+PD+ETS	37.40	0.98
REP~ABU10+PSF+PD+ETS+SFEA	39.39	2.97
REP~ABU10+PSF+PD+ETS+SFEA+RATE	41.96	5.54

Table 6 Parameter estimates (on the logit scale) and test statistics for the best model (table 5).

	Estimate	Standard error	z value	Pr(> z)
Intercept	4.854	2.523	1.924	0.054
ABU10	25.431	8.709	2.920	0.004
PSF	-1.453	0.847	-1.716	0.086
PD.f [T1]	3.968	1.657	2.395	0.017
PD.f [T2]	3.692	1.682	2.195	0.028

Note: PD.f [T1] shows the term pond drying “once every few years”, PD.f [T2] shows pond drying “every year” or “more than once a year”. I took pond drying “never” as reference.

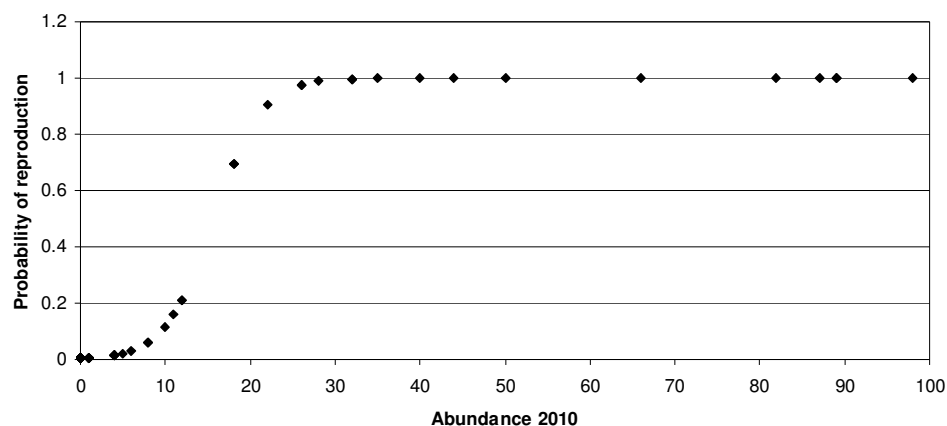


Figure 11 Relationship between reproduction and abundance. The dots show the relationship when all other factors in the model are held at their mean. The probability of reproduction reaches nearly 100 % if abundance is greater than 25 egg masses.

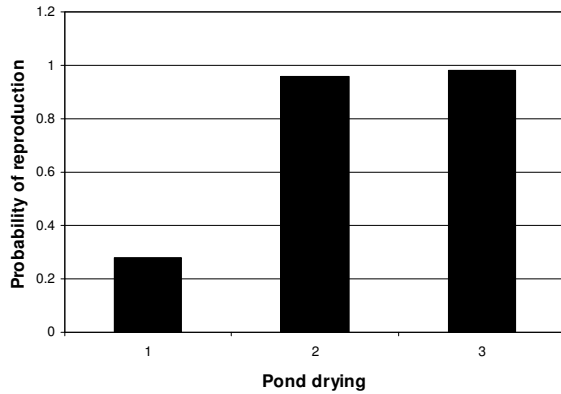


Figure 12 Relationship between reproduction and pond drying. Scale of pond drying: 1 = never; 2 = every few years; 3 = every year or more than once a year. The bars show the relationship when all other factors in the model are held at their mean.

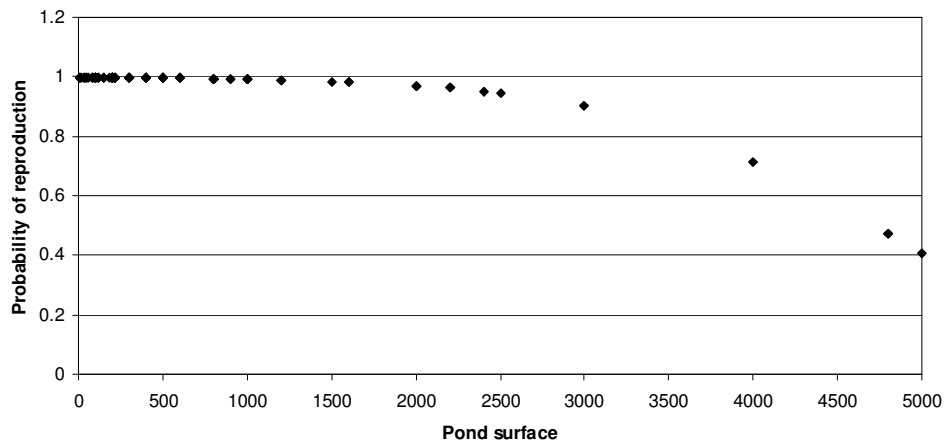


Figure 13 Relationship between reproduction and pond surface. The dots show the relationship when all other factors in the model are held at their mean.

3.3 Abundance

Factors abundance in 2004, exposure to sunlight, structures for egg attachment, distance to woodland and connectivity showed a significant relationship with abundance (Tables 4 and 7). Abundance in 2004, exposure to sunlight, structures for egg attachment and connectivity were positive correlated with abundance, distance to woodland was negative correlated (Tables 4 and 7, Figures 14-18). Significant variable abundance in 2004 shows a very small estimate. Abundance in 2004 and pond surface were included as a control variables.

Table 7 Parameter estimates (on the log scale) and test statistics for the best model.

	Estimate	Standard error	z value	Pr(> z)
Intercept	0.100	0.407	0.245	0.807
ABU04	0.050	0.013	3.836	< 0.010
PD.f [T1]	-0.009	0.066	-0.139	0.890
PD.f [T2]	-0.035	0.076	-0.460	0.646
ETS	0.656	0.059	11.052	< 0.010
HUS.f [T1]	2.074	0.463	5.151	< 0.010
HUS.f [T2]	2.458	0.395	6.218	< 0.010
DTW	-1.877	0.162	-11.646	< 0.010
CON	0.515	0.014	16.732	< 0.010

Note: PD.f [T1] shows the term pond drying “once every few years”, PD.f [T2] shows pond drying “every year” or “more then once a year”. I took pond drying “never” as reference.

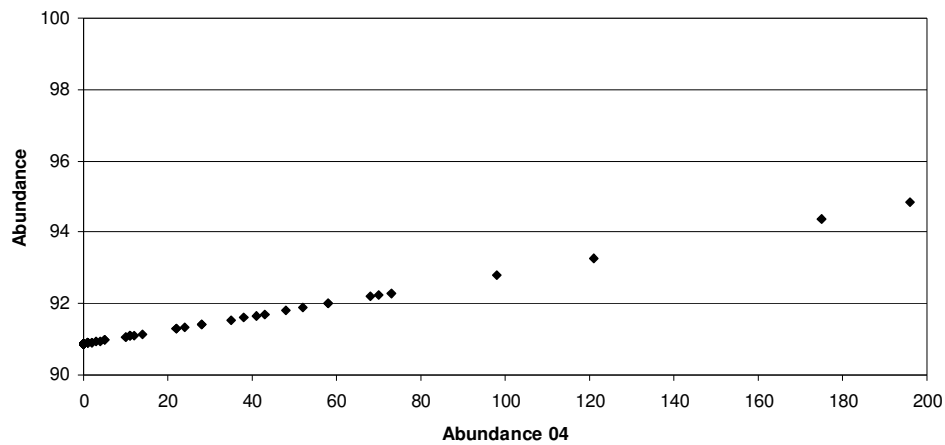


Figure 14 Relationship between abundance in 2010 and abundance in 2004. The dots show the relationship when all other factors in the model are held at their mean.

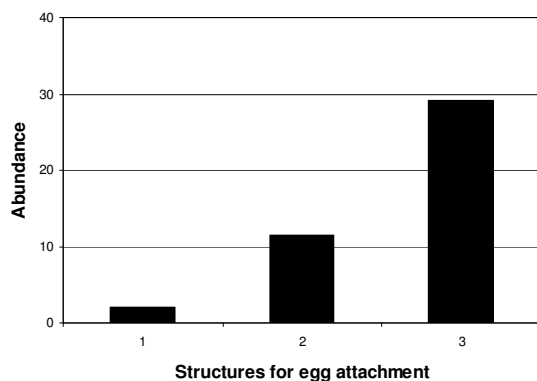


Figure 15 Relationship between abundance and structures for egg attachment. Scale of structures for egg attachment: 1 = none; 2 = few; 3 = many. The bars show the relationship when all other factors in the model are held at their mean.

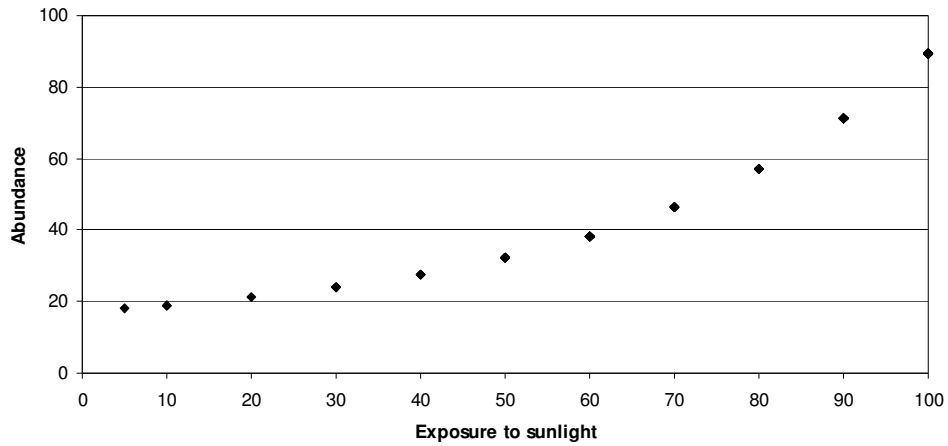


Figure 16 Relationship between abundance in 2010 and exposure to sunlight. The dots show the relationship when all other factors in the model are held at their mean.

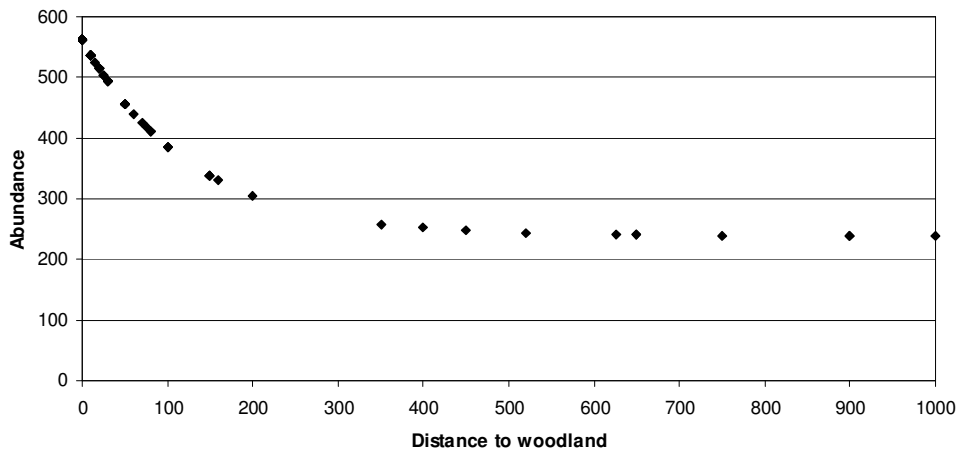


Figure 17 Relationship between abundance in 2010 and distance to woodland. The dots show the relationship when all other factors in the model are held at their mean.

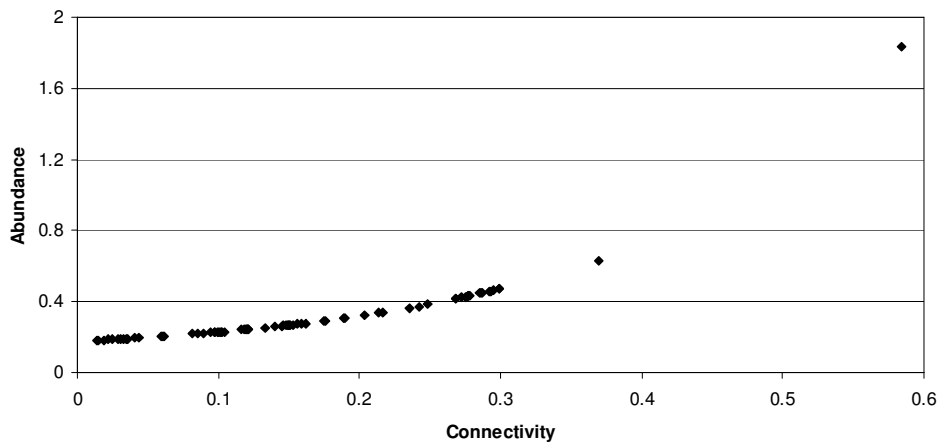


Figure 18 Relationship between abundance in 2010 and connectivity. The dots show the relationship when all other factors in the model are held at their mean.

3.4 Correlation

Some pairs of parameters show a strong correlation. The strongest correlations exist between the three abundance parameters (ABU97, ABU04 and ABU10), and between connectivity and abundance parameters (Table 8) and distance to woodland, respectively. Furthermore, some dependent and independent parameters, which show a strong connection in my abundance and reproduction models, also show a strong correlation (ABU10~CON, REP~PD, REP~SFEA).

Table 8 Correlations between continuous variables.

	ABU04	ABU10	ABU97	CON	PSF	DTW
ABU10	0.37					
ABU97	0.73	0.41				
CON	0.34	0.62	0.31			
PSF	0.33	0.12	0.33	-0.03		
DTW	-0.13	-0.15	-0.16	-0.36	0.08	
ETS	0.19	0.21	0.19	0.24	0.18	0.19

Note: Correlation is shown by the correlation coefficient r .

Table 9 Association between categorical variables calculated by χ^2 test.

	HUS	PD	RATE
PD	34.45		
RATE	5.21	21.01	
REP	16.99	24.00	9.50

Note: Association is shown by the χ^2 coefficient.

Table 10 Association between continuous and categorical variables calculated by variance analysis.

	ABU97	ABU04	ABU10	CON	PSF	DTW	ETS
HUS	0.05	0.06	0.06	0.09	0.04	0.15	0.04
PD	0.16	0.09	0.09	0.09	0.09	0.02	0.11
RATE	0.15	0.09	0.24	0.15	0.04	0.01	0.04
REP	0.16	0.13	0.18	0.16	0.05	0.11	0.07

Note: Association is shown by the coefficient of determination R^2 .

4 DISCUSSION

Because niche and distribution models treat all sites where a model species occurs as suitable and all sites where species does not occur as unsuitable, I built a model which considers the source-sink model (Pulliam 1988) and metapopulation theory (e. g. Hanski 1989, 1991, Hanski & Gyllenberg 1993). The source-sink model and the metapopulation theory show the occupied sites may be unsuitable (sink presences) and unoccupied sites may be suitable (meta-

population absences), respectively. New methods (MacKenzie et al. 2003, 2006, 2009, Royle and Kéry 2007) have made it possible to obtain reliable inferences about the process of change in the occurrence of a model species. These methods allowed me to directly estimate occupancy, colonisation and local extinction from repeated detection/non-detection data. In addition to analysing metapopulation dynamics, I also tested which factors explain spatial variation in reproduction and abundance. The fact that different combinations of ecological factors best explain probability of occupancy, colonisation, extinction, reproduction and abundance, shows the importance of the dynamic approach. Thus, I reach a better picture of the ecological niche. Colonisation showed together with reproduction and survival metapopulation absence. Occupancy and reproduction provided information about sources. Presence without reproduction and with tendency for changes between colonisation and extinction showed sink populations.

4.1 Interpretation of resulting models and parameters

In chapter 1.3 hypotheses for occupancy, colonisation, extinction, reproduction and abundance were formulated. Expectedly, occupancy was positively affected by pond drying and structures for egg attachment, distance to woodland affected occupancy negatively (Table 3). Distance to woodland was the most important parameter. Exposure to sunlight (whose confidence interval included zero), connectivity and abundance of *R. temporaria* did not show the expected influence on occupancy. Colonisation was best explained by a positive effect of the connectivity (Table 3), as formulated in the hypothesis, but the second parameter, distance to woodland, only explained the colonisation poorly. Extinction was best explained by a negative effect of abundance in previous investigations (factors ABU97 and ABU04) (Table 3). The third factor included in the hypothesis, connectivity, did not show the expected influence on extinction. Reproduction was best explained by pond drying (besides the control variables abundance and pond surface) (Table 5). All three parameters were positively correlated with reproduction (Table 6). Exposure to sunlight, structures for egg attachment, and abundance of *R. temporaria* did not show the expected influence on reproduction. Abundance was strongly correlated with exposure to sunlight, structures for egg attachment, distance to woodland and connectivity (Table 7). Distance to woodland affected abundance negatively, the other significant parameters affected abundance positively. Pond drying did not show the expected influence. In the following, every tested ecological factor is discussed individually.

Pond drying: Pond drying had a positive effect on occupancy and reproduction (Tables 3 and 6, Figures 5 and 12). I expected that the impact of this factor – no noteworthy occurrence of

fish and a reduced density of other aquatic predators (i.e. predacious invertebrates) (e. g. Barandun 1995, 1996, Skelly 1996, Wellborn et al. 1996, Snodgrass et al. 2000) – are essential for reproduction and development of enough larvae to maintain a population of *R. dalmatina*. Therefore, pond drying has a direct effect on reproduction and an indirect effect on occupancy. Pond drying did not show the expected influence on abundance may because of the strong association with structures for egg attachment (Table 9), which may outweigh the power of the effect. The ephemeral ponds in the study area usually dry out in late summer or autumn (M. Lippuner, pers. obs.). Drying during the development period of the larvae only takes place as an exception. Kuhn et al. (1997), Rohrbach & Kuhn (1997), Laufer et al. (1997), Cabela et al. (2001), Lippuner 2002, Van Buskirk (2003) and Lippuner & Rohrbach (2009) described ponds of *R. dalmatina* which regularly dry out. Out of the mentioned literature above, only the results of Lippuner (2002), Van Buskirk (2003) and Lippuner and Rohrbach (2009) are confirmed by statistic analyses. Barandun (1995) described the importance of the factor pond drying for *Bombina variegata*, Barandun (1996) for *Hyla arborea*.

Exposure to sunlight: Abundance of *R. dalmatina* was positively correlated with exposure to sunlight (Tables 3 and 7, Figures 7 and 16). Exposure to sunlight indicates whether a pond is cold or warm. *R. dalmatina* shows a preference for sunny and warm areas in summer habitat at the border of or inside woods (e. g. Ahlén 1997, Fog 1997, Lippuner et al. 2001, Stümpel & Grosse 2005). Therefore, a preference for sunny and warm breeding habitat can also be assumed. The positive influence on reproduction due to faster development of eggs and larvae, and therefore, a shorter exposure to aquatic predators as suggested in my hypothesis, could not be verified (Table 5). If I had tested the abundance of larvae instead of presence/absence of larvae, I probably would have received a significantly positive correlation with exposure to sunlight. The analyses in Lippuner and Rohrbach 2009 explained that models are much stronger if abundance (egg masses) were taken instead of presence/absence data. I still suppose that exposure to sunlight implies an effect on reproduction. The fact that exposure to sunlight affected occupancy and abundance supports the mentioned assumption.

Structures for egg attachment: This factor affected occupancy and abundance strongly (Tables 3 and 7, Figures 6 and 15). I assume that structures for egg attachment are required to protect eggs from predation by *I. alpestris*. If structures for egg attachment are missing, egg masses are placed on the bottom of the pond where most eggs are eaten by *I. alpestris* (M. Lippuner pers. obs.). Therefore, structures for egg attachment affected occupancy and abun-

dance indirectly. Contrary to what I had expected, structures for egg attachment did not show a strong influence in reproduction models. I assume that testing abundance of larvae would result in a significant value of structures for egg attachment. The abundance of larvae may also be strongly connected to abundance and occupancy of adults. Another reason for discussed factor not showing a strong influence on reproduction, could be that it is more difficult to find and catch larvae in ponds with a high density of mentioned structures. Hartel et al. (2009) show a significant correlation between abundance of *R. dalmatina* and occurrence of macrophyte cover. In most ponds, structures for egg attachment are macrophytes. Hence, the result of Hartel et al. (2009) is comparable with my result of structures for egg attachment. Furthermore, structures for egg attachment also function as refuges for larvae for hiding from predators. I had recorded refuges for larvae but I finally excluded it from my hypotheses, because nearly all ponds were well provided by refuges for larvae (macrophytes, last year's leaves, stones etc.).

Distance to woodland: Distance to woodland showed a strong negative influence on occupancy and abundance (Tables 3 and 7, Figures 4 and 17). In the model for occupancy, distance to woodland showed the strongest influence of all parameters. A small distance to woodland allows a safe migration between summer habitat and pond. Because all ponds outside woods are surrounded by arable land, such as fields and grassland without refuges, migration between ponds (which are located far away from the woods) and woodland could be very dangerous and not enough individuals survive to allow occurrence and a high abundance (e. g. Schneeweiss and Schneeweiss 1997, Becker et. al. 2007). I had recorded refuges between pond and woodland but I finally excluded this factor from my hypotheses, because nearly all areas between ponds and woods do not include refuges. Another reason for occupancy and abundance being more likely in ponds close to or in woodlands, could be that *R. dalmatina* generally avoids areas without trees. Lippuner (2003), Lippuner and Rohrbach (2009) and Hartel et al. (2010) mentioned also a negative association between occurrence of *R. dalmatina* and distance to woodland. Contrary to my results and the results of Hartel et al. (2010), in the analyses of Zanini et al. (2009) the woodland factor (forest) did not show a strong influence on the occurrence of *R. dalmatina*, but Zanini et al. (2009) used a different method. The area of woodland within a radius of 100 to 3000 meters was tested, not the distance between ponds and woodland only. Hence, area of woodland in a circle and distance between pond and woodland probably were correlated. I finally excluded the recorded factor

area of woodland from my hypotheses because of a strong correlation between the factors distance of woodland and area of woodland.

Connectivity: Connectivity (i. e. the combined effects of the distance to the next colonised ponds and their population size) was the determining parameter for colonisation (Table 3, Figure 8) and it also played a role for abundance (Table 7, Figure 18). A positive effect was detected for both probabilities. Thus, if reproducing populations in ponds are large (source) and the distance between colonised and “empty” ponds is small, more colonising adults reach “empty” ponds or other populations, resulting in colonisation or higher abundance respectively. The fact that connectivity was important for colonisation but not important for occupancy, indicates that local populations are separated strongly. On the other hand, connectivity affected abundance positively which indicate that individuals interchange between ponds. This is a contradiction which may can be explained by the strong correlations between the factors distance to woodland, connectivity and abundance in 2004 (Abundance in 2004 is included in abundance models only). In the analysis of Zanini et al. (2009) connectivity affected abundance of *R. dalmatina* strongly.

Abundance of R. temporaria: In contrast to my hypothesis, abundance of *R. temporaria* did not show a negative effect on occupancy and reproduction of *R. dalmatina* (Table 2 and 5). It seems to be unlikely, however, that no competition takes place between these both species which live often syntopic. It is not well known how larvae live and which food they prefer. In contrast to *R. temporaria*, larvae of *R. dalmatina* can rarely be observed in the riparian zone (Lippuner 2000, Bühler et al. 2007). Van Buskirk (2002) shows that larvae of *R. temporaria* move more actively than larvae of *R. dalmatina* which could result in protection from predators for *R. dalmatina* larvae, although it is possible that at high density of *R. temporaria* the negative effects of density may outweigh the protective effect. Breeding of *R. dalmatina* and *R. temporaria* takes place nearly in a similar period of time. The relationship between both species should be subjected to deeper investigation.

4.2 The dynamic realised niche model

The identified niche factors suggest the following mechanism in a metapopulation of *R. dalmatina*: Colonisation takes place if ponds are well connected, i.e. if the combined effects of the distance to the next colonised ponds and their population size are strong. The population can persist at a colonised site when reproduction takes place and/or the abundance is high.

Reproduction takes place when ponds dry out regularly. High abundance can be reached if ponds are located in or near woodland, well connected to other large local populations, exposed to sunlight and contain many structures for egg attachment. Populations do not survive when abundance is small.

Therefore, I gained substantial information about dynamic population processes of *R. dalmatina*. Without considering the dynamic approach, the results suggest that occurrence is determined by positive effects of pond drying and the presence of structures for egg attachment and the negative effect of distance to woodland (Table 4). A more comprehensive analysis that includes colonisation, extinction, reproduction and abundance shows that other factors affect habitat suitability as well: connectivity, population size and exposure to sunlight (Table 4). The factor connectivity which affects colonisation and abundance positively implies that occupancy and a high abundance of *Rana dalmatina* at a pond alone is no indication of species niche according my definition; a pond may be occupied simple because it is close to a source population. Hence, sink presence is included and metapopulation absence is not considered. In some cases, “empty” ponds had been colonised and reproduction was later detected. On the other hand, some local extinction was observed. That indicates that metapopulation absence and sink presence exist, and therefore, not all absence shows unsuitable habitats and not all presence shows suitable habitats. Sinks represented presence without reproduction and with tendency for changes between colonisation and extinction. Metapopulation absence was represented by colonisation and subsequent reproduction and surviving. Thus, including the parameters reproduction, colonisation and extinction was essential.

In comparison to my old analyses (Lippuner 2002, Lippuner and Rohrbach 2009) considering occupancy and abundance only, I get further important knowledge about the niche of *R. dalmatina*. I know more about the mechanisms in a metapopulation of *R. dalmatina*. Hence, occupancy and abundance can be a result of a strong connectivity only, and abundance is the determining factor for extinction. Van Horne (1983) mentions examples that abundance and habitat quality are not positively correlated. Therefore, models for occupancy and abundance in Lippuner (2002) and Lippuner and Rohrbach (2009) could imply factors which do not describe habitat suitability. Reproduction provides strongest evidences for suitable ponds, and reproduction is the determining parameter to verify source-sink presence and metapopulation absence. Thus, the resulting factor pond drying describes the niche of *R. dalmatina* very strong. Additionally, the factor connectivity determines the colonisation and the factor abun-

dance, which is a result of reproduction and connectivity determines the survival of populations.

4.3 Conclusions

With my dynamic approach that considered the source-sink model and metapopulation theory, I found that different combinations of ecological factors best explained the probability of occupancy, colonisation, extinction, reproduction and abundance. That showed me the importance of the dynamic approach and I reached a better picture of the ecological niche. Colonisation events with reproduction showed that not all suitable ponds were always occupied (i.e., there were metapopulation absences). Extinctions and the fact that reproduction did not occur in all ponds showed that not all ponds had self-sustaining populations and which might be sinks. Based on the analysis, I conclude that reproduction describes the ecological niche better than occupancy or abundance and that reproduction is determined by pond drying. Therefore pond drying was the most important ecological factor. Along with reproduction, colonisation and extinction were also important to verify metapopulation absence and sink presence. Therefore, further niche models should be described by reproduction, colonisation and extinction instead of occupancy and abundance.

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Appendix

Appendix I: Investigated ponds and covariates with standardised values.

Laichgebiet	PD	ETS	HUS	DTW	CON	RATE	PSF	CL97	CL04	CL10
Kg Mittlerboden ost	0.336108137	1.131051443	0.678995098	-0.09314399	1.58169252	0.743827056	-0.62898744	2.594774688	2.583459604	1.244030434
Kg Mittlerboden west	0.336108137	1.131051443	0.678995098	-0.177167054	1.542650343	-0.247942352	-0.54725886	-0.444858613	-0.375422009	0.032780537
Stauweiher Dachsen	-0.824992701	-2.579448256	-0.884751188	-0.513259313	-0.518575355	-0.247942352	-0.50639457	-0.444858613	-0.375422009	-0.407673971
Teiche hinter Strandbad	-0.824992701	-2.167170512	0.678995098	-0.513259313	-1.339872365	-0.247942352	-0.58812315	-0.444858613	-0.375422009	-0.407673971
Uhwiesenweiher	-0.824992701	0.718773699	0.678995098	2.217490291	-1.076636144	-0.247942352	3.37571287	-0.444858613	-0.375422009	-0.407673971
Seewadelgrab	0.336108137	0.718773699	0.678995098	-0.387224716	4.60926623	2.72736587	-0.71071601	1.137172754	1.451234497	7.162637887
Quarzwirk Benken	0.336108137	0.306495955	-0.884751188	-0.303201651	1.376725436	-0.247942352	-0.77609887	-0.391531713	-0.375422009	-0.393909768
Waldweiher bei Quarzwirk	-0.824992701	-0.930337278	0.678995098	-0.513259313	-0.497516458	1.735596463	1.169041273	-0.444858613	-0.375422009	-0.407673971
Stauweiher bei Saustall	-0.824992701	-1.754892767	0.678995098	-0.471247781	-0.043302644	-0.247942352	-0.80061745	-0.302653547	-0.375422009	-0.407673971
Eschenriet	0.336108137	0.718773699	0.678995098	-0.429236248	1.376725436	0.743827056	3.048798559	4.941158289	7.112360032	1.02380318
St. Katharimental	1.497208975	-0.10578179	0.678995098	-0.09314399	0.60807567	-1.239711759	-0.62898744	0.408371787	-0.31503667	0.032780537
Waldweiher bei Rhein	-0.824992701	-0.518059534	-0.884751188	-0.513259313	1.355666538	0.743827056	-0.13861597	-0.32042918	0.047275364	1.381672468
Baggerweiher Chleewis	-0.824992701	0.306495955	-0.884751188	-0.513259313	0.450133938	-0.247942352	-0.05688739	0.017307854	0.500165407	-0.297560344
Ober Weiher	-0.824992701	-0.518059534	-0.884751188	-0.471247781	0.744958505	-1.239711759	-0.84148174	-0.32042918	-0.34522934	-0.393909768
Ziegeleigrube	-0.824992701	0.306495955	0.678995098	-0.471247781	1.281960396	-1.239711759	0.433484074	0.05285912	0.349202059	0.720990706
Teichlein Fenisbergmulde	-0.824992701	-0.930337278	0.678995098	-0.471247781	0.302721654	-0.247942352	-0.80879031	-0.444858613	-0.375422009	-0.407673971
Hangried bei Unterschlatt	-0.824992701	-1.342615023	-0.884751188	-0.19817282	1.471490475	-0.247942352	-0.85374102	-0.444858613	-0.375422009	-0.407673971
Enteler-Weiher	1.497208975	-0.10578179	-0.884751188	-0.513259313	1.071371419	2.72736587	1.169041273	1.261602188	-0.194265992	-0.407673971
Riet	1.497208975	1.131051443	0.678995098	-0.177167054	-0.897635514	-0.247942352	3.212255715	1.634890488	1.104018797	-0.104861497
Grube Hüttenboden	1.497208975	1.131051443	0.678995098	-0.303201651	1.471490475	-0.247942352	-0.62898744	-0.444858613	-0.375422009	-0.325088751
Mösli	0.336108137	-0.518059534	-0.884751188	-0.513259313	-1.213518979	-0.247942352	-0.54725886	-0.37375608	-0.360325674	-0.352617158
Trutiker Ried	-0.824992701	1.131051443	0.678995098	-0.261190119	-1.38199016	-0.247942352	-0.57995029	-0.444858613	-0.375422009	-0.407673971
Hegi	-0.824992701	-0.518059534	0.678995098	-0.513259313	-0.465928111	0.743827056	1.169041273	-0.26710228	-0.375422009	0.197950978
Kleinweiher bei Brüggli	-0.824992701	-0.10578179	0.678995098	-0.471247781	-0.139515197	0.743827056	-0.30207312	-0.409307347	-0.375422009	-0.407673971
Teich im Sand	-0.824992701	0.306495955	-0.884751188	1.167201981	-1.276695672	-0.247942352	-0.85374102	-0.444858613	-0.375422009	-0.407673971
Blauseeli Rodenberg	-0.824992701	0.718773699	0.678995098	-0.471247781	-0.065809055	-0.247942352	0.147434053	-0.32042918	-0.360325674	-0.407673971
Hohlenbaum Dyonislißöll	0.336108137	-2.785587128	0.678995098	2.637605614	-1.392519609	-1.239711759	-0.13861597	-0.444858613	-0.375422009	-0.407673971
Sammelbecken Furt	0.336108137	1.131051443	0.678995098	-0.219178587	-0.276398032	-0.247942352	-0.71071601	-0.42708298	-0.360325674	-0.352617158
Waldweiher Sepling	-0.824992701	-0.930337278	-0.884751188	-0.513259313	0.38169252	-0.247942352	0.351755497	-0.409307347	-0.375422009	-0.338852954
Seewädeli	1.497208975	1.131051443	0.678995098	-0.387224716	0.029134568	0.743827056	3.37571287	0.58612812	-0.299940335	2.496572942

Laichgebiet	PD	ETS	HUS	DTW	CON	RATE	PSF	CL97	CL04	CL10
Tongrube Fälmi	0.336108137	1.131051443	-2.448497473	3.687893923	-1.308284018	0.743827056	-0.13861597	-0.444858613	-0.375422009	-0.407673971
Teich Rodmüli	-0.824992701	0.306495955	0.678995098	3.2677786	-0.687046537	-0.247942352	-0.05688739	-0.409307347	-0.375422009	-0.407673971
Kg Heva	-0.824992701	0.718773699	-0.884751188	2.217490291	-1.10822449	-0.247942352	0.351755497	-0.444858613	-0.375422009	-0.407673971
Mettschlatt	-0.824992701	0.306495955	-0.884751188	1.67134037	-0.887106065	0.743827056	-0.80879031	-0.444858613	-0.375422009	-0.407673971
Waldweiher Hamenberg	-0.824992701	-0.930337278	-0.884751188	-0.513259313	-0.486987009	0.743827056	-0.66985172	-0.391531713	-0.375422009	-0.407673971
Weiher ne Rudolffingen	-0.824992701	-1.342615023	0.678995098	-0.513259313	-1.160871735	-0.247942352	1.169041273	-0.444858613	-0.375422009	-0.407673971
Pfaffensee	1.497208975	0.718773699	0.678995098	-0.429236248	0.02107378	0.743827056	0.59694123	0.283942354	0.198238712	0.81734013
Mördersee	0.336108137	-0.930337278	-0.884751188	-0.513259313	0.028955984	-1.239711759	-0.54725886	-0.284877913	-0.209362327	-0.393909768
Birchwissee	-0.824992701	0.718773699	0.678995098	-0.471247781	-0.002632362	-0.247942352	1.98632705	-0.42708298	-0.375422009	-0.407673971
Lochsee	-0.824992701	0.718773699	-0.884751188	0.326971334	2.302284018	-1.239711759	-0.46553028	-0.444858613	-0.375422009	-0.393909768
Altwasserest östlich Thurhus	-0.824992701	0.718773699	-0.884751188	-0.303201651	1.618902759	0.743827056	0.147434053	0.26616672	0.409587398	0.94121796
Mittlere Altwasser Thurhus ne	2.658309813	0.718773699	-2.448497473	-0.303201651	1.534667168	-1.239711759	0.760398385	0.123961654	-0.164073323	-0.297560344
Altlauf Inseln	2.658309813	-0.10578179	0.678995098	-0.471247781	1.482019924	-0.247942352	-0.3838017	-0.409307347	-0.013109975	-0.022276277
Elliker Auen (Steipis)	0.336108137	0.718773699	0.678995098	-0.450242015	1.008194726	0.743827056	-0.30207312	4.034600989	0.047275364	1.271558841
Heinrichsee	1.497208975	0.718773699	0.678995098	-0.303201651	0.060544331	-1.239711759	-0.36745599	-0.409307347	-0.224458662	-0.256267734
Bucketensee	0.336108137	0.718773699	0.678995098	-0.09314399	0.102662126	-0.247942352	-0.30207312	0.657230654	-0.209362327	0.500763452
Steiniggrundsee	-0.824992701	0.718773699	0.678995098	0.95714432	-0.276398032	-0.247942352	0.760398385	-0.444858613	-0.375422009	-0.407673971
Cholgruebsee	0.336108137	1.131051443	0.678995098	-0.408230482	-0.318515827	-0.247942352	-0.13861597	-0.231551013	-0.209362327	0.142894164
Kiesgrube Müllersbuck	1.497208975	1.131051443	-2.448497473	0.116913672	-0.265868583	-1.239711759	-0.7515803	-0.444858613	-0.375422009	-0.407673971
Kiesgrube Steinacker	0.336108137	1.131051443	-2.448497473	0.158925205	-1.234577876	1.735596463	-0.77609887	-0.444858613	-0.375422009	-0.407673971
Stauweiher Fosenacker	-0.824992701	-0.518059534	-0.884751188	-0.387224716	-1.192460081	0.743827056	-0.3838017	-0.444858613	-0.375422009	-0.407673971
Ölweiher	-0.824992701	-0.930337278	-0.884751188	2.11246146	-1.171401183	-0.247942352	0.351755497	-0.444858613	-0.375422009	-0.407673971
Linggisee	0.336108137	0.306495955	0.678995098	0.116913672	0.460663387	-1.239711759	-0.22034455	-0.018243413	0.273720386	-0.242503531
Folienweiher unter Rindisburg	-0.824992701	-0.930337278	-2.448497473	-0.513259313	0.934488585	-0.247942352	-0.86600031	-0.444858613	-0.375422009	-0.407673971
Ried Örlingen	-0.824992701	1.131051443	0.678995098	1.377259643	-0.47645756	2.72736587	-0.79244459	-0.391531713	-0.375422009	-0.407673971
Wolfzeichen	0.336108137	-0.10578179	0.678995098	-0.513259313	-0.465928111	-0.247942352	-0.46553028	-0.231551013	-0.375422009	-0.297560344
Söll Schneitenberg	-0.824992701	-0.518059534	0.678995098	-0.513259313	-0.550163702	-0.247942352	-0.05688739	-0.42708298	-0.375422009	-0.407673971
Söll Speck	0.336108137	-0.518059534	0.678995098	-0.513259313	-0.276398032	2.72736587	0.760398385	-0.391531713	-0.375422009	-0.270031937
Mittlerer Räubrichsee	0.336108137	-0.518059534	0.678995098	-0.513259313	-0.602810946	-0.247942352	-0.13861597	3.359126922	0.651128755	0.032780537
Nördlicher Räubrichsee	1.497208975	-1.342615023	-0.884751188	-0.513259313	-0.644928741	-1.239711759	-0.13861597	-0.231551013	0.152949707	-0.242503531
Chli Au	-0.824992701	0.718773699	0.678995098	-0.429236248	-1.908164962	-0.247942352	-0.79244459	-0.355980447	-0.043302644	-0.15991831
Stauweiher Moosrain	-0.824992701	-0.518059534	0.678995098	-0.471247781	-0.444869213	1.735596463	-0.7515803	-0.444858613	-0.375422009	-0.407673971
Altlauf Stuck	-0.824992701	-1.754892767	0.678995098	-0.513259313	-0.265868583	1.735596463	0.351755497	-0.444858613	-0.375422009	-0.407673971
Tü e Präuselen (Voreng)	-0.824992701	0.306495955	0.678995098	-0.408230482	-0.518575355	-0.247942352	-0.54725886	-0.444858613	-0.330133005	-0.407673971

Laichgebiet	PD	ETS	HUS	DTW	CON	RATE	PSF	CL97	CL04	CL10
Weiherr Präuselen	-0.824992701	0.306495955	0.678995098	-0.513259313	1.284254385	-1.239711759	1.577684162	-0.444858613	-0.299940335	-0.049804683
Präuselen	0.336108137	0.718773699	0.678995098	-0.471247781	1.387254885	-0.247942352	-0.220344455	0.017307854	0.243527716	0.81734013
Thurhus ost	1.497208975	0.718773699	0.678995098	-0.387224716	1.629432208	-1.239711759	0.270026919	0.26616672	0.681321424	-0.049804683
Altwasserest nw Thurhus	0.336108137	1.131051443	0.678995098	0.116913672	1.324078192	-1.239711759	-0.79244459	0.123961654	0.500165407	0.280536198
Altwasser Thurspitz	-0.824992701	0.306495955	0.678995098	-0.513259313	0.134250473	-0.247942352	-0.05688739	0.05285912	2.266436574	0.074073147
Kiesgrube Buchbrunnen	1.497208975	1.131051443	0.678995098	3.2677786	0.039485433	-1.239711759	-0.13861597	-0.444858613	-0.34522934	-0.352617158
Teiche beim Zeltplatz	-0.824992701	-0.518059534	0.678995098	-0.513259313	-0.286927481	-0.247942352	-0.62898744	-0.444858613	-0.043302644	-0.352617158
Steubisalmend/Rüdlinger Feld	2.658309813	-2.579448256	-2.448497473	-0.513259313	0.165838819	-0.247942352	-0.79244459	-0.444858613	-0.375422009	-0.407673971
Tümpel im Ried bei Alten	0.336108137	0.306495955	-0.884751188	-0.429236248	0.018426535	-0.247942352	-0.77609887	-0.444858613	-0.360325674	-0.15991831
Thurhau	0.336108137	-0.930337278	0.678995098	-0.513259313	0.313251103	-0.247942352	-0.83330888	-0.391531713	-0.360325674	-0.407673971
Flutmulde bei Thurhau	-0.824992701	-0.518059534	-0.884751188	-0.513259313	-0.29745693	-0.247942352	-0.220344455	-0.444858613	-0.360325674	-0.407673971
Grube Präuselen	0.336108137	-0.10578179	0.678995098	-0.513259313	1.366195987	0.743827056	0.433484074	0.515025587	0.726610428	0.789811723

Appendix II: Sampling detection histories, X_i , and the associated probability of observing them, $\Pr(X_i)$. According to equation one *R. dalmatina* was detected at the site i during first (t) and second ($t + 1$) primary periods. *R. dalmatina* was not detected during the third primary period and during the second survey at t and at the first and the third surveys at $t + 1$. According to equation two *R. dalmatina* was detected at the site in the first (t) and third ($t + 2$) primary periods (t , during the first and third surveys and at $t + 2$, during all surveys), but the species was never detected in the second primary period ($t + 1$). Hence, there are two possibilities that would result in the species not being detected at $t + 1$: either it was present and remained undetected, or it became locally extinct. According to equation three, *R. dalmatina* was never detected at the site. Equation four shows a detection history with missing observations in primary sampling periods two and three (“_” indicates a missing observation) (principle according to MacKenzie 2003 and extended to three primary sampling periods).

X_i	$\Pr(X_i)$
101 010 000	$\Phi_0 D(p_{101,1}) \Phi_1 p_{010,2} \Phi_2 p_{000,3}$ $= [\psi_1 \quad 1 - \psi_1] \begin{bmatrix} p_{1,1}(1 - p_{1,2})p_{1,3} & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} 1 - \varepsilon_1 & \varepsilon_1 \\ \gamma_1 & 1 - \gamma_1 \end{bmatrix} \begin{bmatrix} (1 - p_{2,1})p_{2,2}(1 - p_{2,3}) \\ 0 \end{bmatrix} \begin{bmatrix} 1 - \varepsilon_2 & \varepsilon_2 \\ \gamma_2 & 1 - \gamma_2 \end{bmatrix}$ $\times \begin{bmatrix} (1 - p_{3,1})(1 - p_{3,2})(1 - p_{3,3}) \\ 0 \end{bmatrix}$ $= \Psi_1 p_{1,1}(1 - p_{1,2})p_{1,3}(1 - \varepsilon_1)(1 - p_{2,1})p_{2,2}(1 - p_{2,3}) \left\{ (1 - \varepsilon_2) \prod_{j=1}^3 (1 - p_{3,j}) + \varepsilon_2 \right\}$
101 000 111	$\Phi_0 D(p_{101,1}) \Phi_1 p_{000,2} \Phi_2 p_{111,3}$ $= [\psi_1 \quad 1 - \psi_1] \begin{bmatrix} p_{1,1}(1 - p_{1,2})p_{1,3} & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} 1 - \varepsilon_1 & \varepsilon_1 \\ \gamma_1 & 1 - \gamma_1 \end{bmatrix} \begin{bmatrix} \prod_{j=1}^3 (1 - p_{2,j}) \\ 1 \end{bmatrix} \begin{bmatrix} 1 - \varepsilon_2 & \varepsilon_2 \\ \gamma_2 & 1 - \gamma_2 \end{bmatrix} \begin{bmatrix} \prod_{j=1}^3 p_{3,j} \\ 0 \end{bmatrix}$ $= \Psi_1 p_{1,1}(1 - p_{1,2})p_{1,3} \left\{ (1 - \varepsilon_1) \prod_{j=1}^3 (1 - p_{2,j}) + \varepsilon_1 \right\} (1 - \varepsilon_2) \prod_{j=1}^3 p_{3,j}$
000 000 000	$\Phi_0 D(p_{000,1}) \Phi_1 p_{000,2} \Phi_2 p_{000,3}$ $= [\psi_1 \quad 1 - \psi_1] \begin{bmatrix} \prod_{j=1}^3 (1 - p_{1,j}) & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 1 - \varepsilon_1 & \varepsilon_1 \\ \gamma_1 & 1 - \gamma_1 \end{bmatrix} \begin{bmatrix} \prod_{j=1}^3 (1 - p_{2,j}) \\ 1 \end{bmatrix} \begin{bmatrix} 1 - \varepsilon_2 & \varepsilon_2 \\ \gamma_2 & 1 - \gamma_2 \end{bmatrix} \begin{bmatrix} \prod_{j=1}^3 (1 - p_{3,j}) \\ 1 \end{bmatrix}$ $= \Psi_1 \prod_{j=1}^3 (1 - p_{1,j}) \left\{ (1 - \varepsilon_1) \prod_{j=1}^3 (1 - p_{2,j}) + \varepsilon_1 \right\} + (1 - \Psi_1) \left\{ \gamma_1 \prod_{j=1}^3 (1 - p_{2,j}) + (1 - \gamma_1) \right\}$
101 0_0_10	$\Phi_0 D(p_{101,1}) \Phi_1 p_{0_0,2} \Phi_2 p_{_10,3}$ $= [\psi_1 \quad 1 - \psi_1] \begin{bmatrix} p_{1,1}(1 - p_{1,2})p_{1,3} & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} 1 - \varepsilon_1 & \varepsilon_1 \\ \gamma_1 & 1 - \gamma_1 \end{bmatrix} \begin{bmatrix} (1 - p_{2,1})(1 - p_{2,3}) \\ 0 \end{bmatrix} \begin{bmatrix} 1 - \varepsilon_2 & \varepsilon_2 \\ \gamma_2 & 1 - \gamma_2 \end{bmatrix} \begin{bmatrix} p_{3,2}(1 - p_{3,3}) \\ 0 \end{bmatrix}$ $= \Psi_1 p_{1,1}(1 - p_{1,2})p_{1,3}(1 - \varepsilon_1)(1 - p_{2,1})(1 - p_{2,3})(1 - \varepsilon_2)p_{3,2}(1 - p_{3,3})$