

Effects of an invasive pathogen on persistence and extinction of amphibian populations

Magdalena Merk



Supervisors

Dr. Katja Räsänen, EAWAG

Dr. R. Benedikt Schmidt, UZH

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Abstract

Emergent diseases are a major threat on biological diversity and are proposed as one of the major factors causing worldwide decline of amphibians. I used field surveys of amphibians over two time periods (2003/2004 and 2008) in combination with a model comparison approach to investigate the potential impact of the chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*), on four ecologically different amphibian species (*Bufo calamita*, *Rana temporaria*, *Triturus alpestris*, *T. helveticus*) in Switzerland. I asked two main questions: First, does *Bd* affect the distribution and extinction of these amphibian species in Switzerland? Second, what are the relative effects of *Bd* and other environmental factors (such as geographic isolation, temperature and precipitation) on the distribution patterns of these amphibian species? I found little evidence for negative effects of *Bd* on distribution and extinction probability of the investigated species. In contrast, at least under certain environmental conditions, *B.calamita* and *T.alpestris* seemed to even occur more often and/or to have lower extinction probabilities at sites where *Bd* was detected. These results suggest that *Bd* may not currently have strong negative effects on amphibian populations in Switzerland. Nevertheless, it is possible that with changing environmental conditions *Bd* may become a threat in the future.

Introduction

Global biodiversity is currently under serious threat due to human activities, which have resulted in species extinctions at a local and global scale (e.g. Dirzo & Raven 2003, Dudgeon et al. 2006, Kim & Byrne 2006, IUCN 2010). One major group that has been severely affected are amphibians, which are the most endangered vertebrate class on earth and are undergoing a global decline (e.g. Alford & Richards 1999, Stuart et al. 2004, Gewin 2008). Through their important role in the food chain, amphibians contribute substantially to the functioning of many wetland and forest ecosystems (Hamer & McDonnell 2008). The global amphibian decline might therefore have serious consequences beyond that of affecting the amphibian species per se and might even destabilize whole communities and ecosystems. Understanding the contribution of the individual factors as well as their interactions in determining amphibian distribution and persistence is crucial.

Several factors have been associated with the global decline of amphibians. These include habitat destruction, exploitation, climate change, pollution, UV radiation, introduced species and diseases (Alford & Richards 1999, Blaustein & Kiesecker 2002, Beebee & Griffiths 2005). Often however the different factors interact and the explicit reasons for decline are not clear (Alford & Richards 1999, Blaustein & Kiesecker 2002, Beebee & Griffiths 2005,). Moreover, numerous population declines have been observed in places that are apparently pristine, such as national parks (Stuart et al. 2004). Apart from climate change, infectious diseases are one reasonable explanation for this enigmatic phenomenon (Stuart et al. 2004). Especially the fungus *Batrachochytrium dendrobatidis* (*Bd*) has been linked to such declines and there is now strong evidence that *Bd* has become a major threat to amphibians (Stuart et al. 2004, Skerratt et al. 2007, Kilpatrick et al. 2010).

The main effects of *Bd* infections on amphibians range from sub-lethal damages to highly increased mortality and the effects differ between the amphibian life-stages (Kilpatrick et al. 2010). While *Bd* infection tends to induce mainly sub-lethal damages in tadpoles, it often leads to high mortality in post-metamorphic individuals (Kilpatrick et al. 2010): infected larvae may only show deformities of keratinized mouthparts (Fisher et al. 2009), whereas common symptoms for metamorphosed amphibians are an increase in both keratin production (hyperkeratosis) and proliferation of epidermal cells (epidermal hyperplasia) as well as probably upregulated skin shedding (Fisher et al. 2009). One likely cause of the death of the amphibian host following a *Bd* infection is hampered electrolyte transport of the epidermis

changes electrolyte composition of the blood, which increases the acidity of the blood and finally causes cardiac arrest (Voyles et al. 2009).

In addition to having differential effects at different life-stages, the effects of *Bd* also differ among amphibian species (Kilpatrick et al. 2010). While some of amphibian species (such as the American bullfrog *Rana catesbeiana* (Daszak et al. 2004) are hardly impacted and may act as reservoir, others (such as Australian gastric brooding frogs *Rheobatrachus sp.* or the Panamanian golden frog *Atelopus zeteki*, both extinct by now (Fisher et al. 2009)) decline rapidly by suffering nearly 100 % mortality (Blaustein et al. 2005, Kilpatrick et al. 2010). Differences in resistance to *Bd* are not observed only among species, but also among different populations of a given species. For instance, *Bd* presence may cause a decline only in some populations of a species, and while some populations may recover after a *Bd* caused decline, others fail to do so (Harris et al. 2006).

Thus *Bd* presence does not inevitably lead to population declines (Harris et al. 2006). The exact reasons for such inter- and intra-specific variation in susceptibility to *Bd* are not clear but several reasons have been proposed. These may relate to variation in the traits mediating responses to *Bd*, such as presence of antimicrobial peptides and antifungal bacteria on amphibian skin, skin shedding rate, behavior and life history (Harris et al. 2006, Kilpatrick et al. 2010) as well as genetic variation (Altizer et al. 2003).

In addition to differences in innate characteristics of the amphibian species and populations per se, amphibian susceptibility, as well as virulence and transmission efficiency of *Bd* might be influenced by variation in infectivity between different *Bd* strains, as well as by variation in the external environment (Woodhams et al. 2008, Fisher et al. 2009, Kilpatrick et al. 2010).

Bd can grow and reproduce at a wide range of environmental conditions (Kilpatrick et al. 2010). Culture temperatures between 4 and 25°C are suitable for *Bd*, with optimal growth conditions observed between 17 and 25°C and between pH 6 and 7 (Kilpatrick et al. 2010). *Bd* is resistant to freezing to some extent (Kilpatrick et al. 2010), whereas temperatures above 29°C and below 0°C, as well as prolonged desiccation, are lethal (Lips et al. 2008). Furthermore, large daily variation in temperature (diurnal range) seems to increase the probability of *Bd* occurrence (Ursina Tobler, personal communication). Moreover, at increasing temperatures *Bd* grows and develops faster, but produces fewer spores that have a shorter survival time (Woodhams et al. 2008). Such strong temperature dependency of *Bd* viability and infectivity may therefore also have crucial implications for amphibian persistence under the prospected climate change.

Amphibian declines and effects of *Bd* can clearly be highly complex and context dependent, which makes it difficult to make generalisations from findings in specific studies (Blaustein & Kiesecker 2002). Several questions remain unanswered to date. For example, is *Bd* an introduced pathogen or an endemic pathogen which has become more virulent through changing environmental conditions, genetic alteration or enhanced host susceptibility (Kilpatrick et al. 2010)? What factors control *Bd* outbreaks in amphibian populations? And finally, what factors influence the extent of amphibian population declines through *Bd* infection and thus co-decide on persistence and extinction of amphibian populations?

In this study I focused on the latter question. Specifically, I studied amphibian populations in Switzerland to gain a better understanding of the processes behind the observed amphibian declines in Switzerland and, in particular, the role of *Bd*. Compared to the situation 25 years ago, the occurrence of many amphibian species in Switzerland has declined by around 50 percent (Schmidt & Zumbach 2005). Based on the red list of endangered amphibians, suitable habitats still exist and seem intact, and – as in many other geographic areas - there does not seem to be any obvious reasons for the many population declines and extinctions (Schmidt & Zumbach 2005).

Based on Species Distribution Models, central Europe provides suitable conditions for the occurrence of *Bd* (Rödder et al. 2009). Accordingly, *Bd* was first reported in Switzerland in year 2005, when it was already widespread (Garner et al. 2005) and occurred at multiple sites across all of northern Switzerland (B.R.Schmidt, personal communication). This suggests that *Bd* might underlie or contribute to the observed amphibian declines in Switzerland. In contrast to Spain, which has an assimilable prevalence of *Bd*, no mass mortalities have been observed in Switzerland (Garner et al. 2005). It is however possible that *Bd* affects amphibian populations also in the absence of mass mortalities and spreading waves, as seen in Central and South America (Lips et al. 2008), making it crucial to investigate whether *Bd* may be a major threat for Swiss amphibians.

I used an amphibian field survey data set from two time periods (2003/2004 and 2008) on 71 sites in northern part of Switzerland, in combination with a statistical model comparison approach to address the following main questions: Has *Bd* affected the distribution and extinction of amphibians in Switzerland? Which other environmental factors (e.g. habitat characteristics and geographic isolation) explain potential changes in the distribution pattern of amphibian species over time? What is the relative role of *Bd* and other environmental

factors in determining the distribution patterns of amphibians? I focused on four ecologically distinct amphibian species that show different extents of declines in Switzerland. The natterjack toad *B. calamita* is strongly declining, and the palmate newt *T. helveticus* is declining mainly in eastern Switzerland, whereas the common frog *R. temporaria* and the alpine newt *T. alpestris* do not show signs of decline (Schmidt & Zumbach 2005). I predicted that if *Bd* indeed has a negative influence on amphibian populations, amphibian distribution should have changed and extinction probabilities increased at sites where *Bd* is present. I further predicted that the effects of *Bd* may depend on environmental factors (i.e. habitat characteristics, local climate, altitude or pond isolation) or that environmental factors may be more important than *Bd* in determining amphibian occurrence and persistence.

Material & Methods

Study sites

71 study sites from northern Switzerland (Figure 1) were used in this study. These sites were selected randomly within the known distribution of the midwife toad *Alytes obstetricans* (Grossenbacher 1988) as part of a specific study on this species (Ursina Tobler, unpublished data). The sites were surveyed during two time periods: 2003/2004 and 2008. In 2003/2004, the sites were initially surveyed for amphibian presence/absence to update the Swiss amphibian red list (Schmidt & Zumbach 2005). In 2008, the sites were re-surveyed for amphibian presence/absence and additionally for presence/absence of *Bd*.

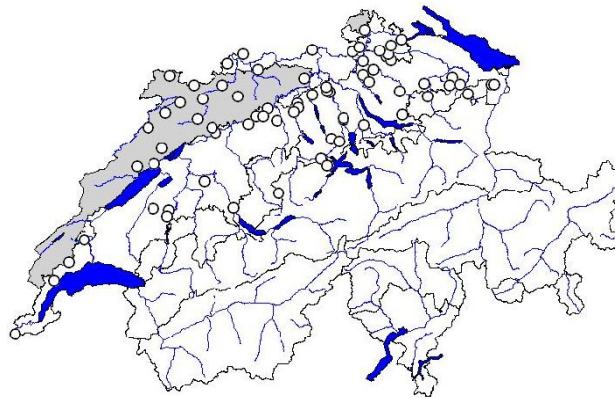


Figure 1. Map of the 71 study sites in northern part of Switzerland. The biogeographic region “Swiss Jura” is highlighted in grey.

Amphibian data

In total, 14 amphibian species (*A. obstetricans*, *Bufo bufo*, *B. calamita*, *Bombina variegata*, *Hyla arborea*, *Pelophylax esculentus* & *P. lessonae*, *Triturus alpestris*, *T. helveticus*, *T. vulgaris*, *T. cristatus*, *Rana temporaria*, *R. dalmatina* and *Salamandra salamandra*) were recorded on the study area. I focused on four species, which are ecologically different (one toad, one frog and two species of newts) and for which sufficient data was available (Table 1): *B. calamita*, *T. alpestris* (also known as *Ichthyosaura alpestris*), *T. helveticus* (also known as *Lissotriton helveticus*) and *R. temporaria*.

Table 1. Summary of the amphibian survey data for the four study species on the 71 study sites. The numbers for extinctions (loss at a site) and colonisations (new appearance at a site) are raw data and hence not adjusted for possible incomplete detection. “Species recorded at sites before 2003” equates to the predictor variable “former occurrence”, “species detected in 2003/04” equates the response variable “site occupancy (Ψ)” and “Species detected in 2003/04, but not in 2008” equates the response variable “extinction probability (ϵ)”. See section “Predictor variables”, statistical analyses and table 2 for further details.

Number of study sites where...	<i>B. calamita</i>	<i>R. temporaria</i>	<i>T. alpestris</i>	<i>T. helveticus</i>
Species recorded before 2003	32	60	61	40
Species detected in 2003/2004	18	68	61	38
Species detected in 2008	12	47	58	38
Species detected in 2003/2004, but not in 2008 (= extinctions)	9	22	6	9
Species not detected in 2003/2004, but detected in 2008 (= colonisations)	3	1	3	9

The amphibian data was provided by B. R. Schmidt and U. Tobler (Koordinationsstelle für Amphibien- und Reptilienschutz in der Schweiz, KARCH and University of Zurich). The data consists of detection-nondetection data from years 2003 or 2004 (period 2003/2004) and 2008. In contrast to presence-absence data, in detection-nondetection data a species is not necessarily assumed to be absent, even when not detected (MacKenzie et al. 2002).

Conducting several visits per site and season allows estimating detection probabilities.

Considering detection probabilities and not assuming complete detection allows for more precise site occupancy, local extinction and colonisation estimates (MacKenzie et al. 2003).

Else site occupancy is often underestimated and estimates of local extinction and colonisation probabilities are biased (MacKenzie et al. 2003).

The data were collected by several researchers. Visits were conducted during the breeding season. In 2003/2004, the sites were visited up to four times (over both two years), and in 2008 all sites except one were visited three times.

Sites were visited from March till June. During each visit all identified amphibian species, regardless of their life stage, were recorded. Amphibians were identified by eye or sound, larvae were searched for using a net. In both 2003/2004 and 2008, the first visit was done during daytime and all remaining visits during night. A species was considered as “detected” as soon as an individual belonging to any life stage was observed. The date when a species was detected the first time at any site was defined as the start of the yearly activity period, and the date when a species was detected the last time at any site as the end of the yearly activity

period. Visits before and after the yearly activity period of the species of interest were not included in data analyses so that the data meet the closure assumption of the statistical method (see below, MacKenzie et al. 2003).

Bd data

Data for *Bd* was provided by B. R. Schmidt and U. Tobler (KARCH and University of Zurich) and consists of detection-nondetection data in year 2008. In Switzerland *Bd* was not studied before the year 2005 (Garner et al. 2005) and data are therefore not available on *Bd* distribution in the years 2003/2004. I assumed that the distribution of the fungus has not changed between years 2003 and 2008: If *Bd* was found in 2008, I assumed that it had been there also before year 2003 and if *Bd* was not found in 2008, I assumed that it did not occur on the site before year 2003.

For all sites, *Bd* samples were taken from all amphibian species that were caught and from different life stages. All in all, between 10 and 30 samples were taken per site (at least 10 individuals per site were sampled). For identifying presence of *Bd*, tadpoles and metamorphosed amphibians were caught by hand or with a dip net and their skin (adults) or mouthpart (tadpoles) was swabbed. Samples were then analyzed for presence of *Bd* with real-time PCR in the laboratory (Boyle et al. 2004). Samples which exceeded the threshold value of 0.1 genomic equivalents were considered as *Bd* positive (U. Tobler, personal communication).

Response variables

To infer the effects of *Bd* and other environmental factors (see below) on amphibians, I analysed site occupancy rate (Ψ) and local extinction probability (ϵ). The program, which I applied for analysis (see below) uses extinction and colonisation probability to approximate the change in site occupancy between years and thus to fit the models to the data. But since the number of colonisations was quite low (Table 1), I kept colonisation probabilities constant in all models and thus did not investigate the effect of the environmental factors on colonisation (therefore there are no results presented concerning colonisation probabilities). The model selection approach that I used takes into account incomplete detection probabilities (p) (MacKenzie et al. 2003) and thus allows for more precise estimates of occupancy rate, extinction and colonisation probabilities. Therefore I also created predictor models to estimate detection probabilities. See statistical analyses section for details of the modelling approach.

Predictor variables

To study the factors that might influence occurrence (Ψ) and extinction (ϵ), I focused on the occurrence of *Bd* and the following abiotic factors (summarized in Table 2) that might influence amphibian distribution in Switzerland over time and space.

Table 2: The nine predictor variables that were included in the statistical data analyses on amphibian site occupancy and extinction probability.

Factors	Indicator of:	Unit*
Former occurrence	Whether the species had been detected before year 2003	Binary (Yes =1, No= 0)
Isolation	The distance to the closest site where the species of interest occurs	Continuous (meters)
Bd	Whether <i>Bd</i> has been present or absent in 2008	Binary (Yes =1, No=0)
Pond type	Whether the site is a pond-complex or a single pond	Binary (Pond complex= 1 Single pond = 0)
Gravel pit	Whether the site is a gravel pit	Binary (Gravel pit=1 Other habitat type=0)
Jura	Whether the site is located in the Swiss Jura	Binary (Jura =1 Elsewhere= 0)
Altitude	The altitude of the site	Continuous (Meters above sea level[m])
Temperature	The annual mean temperature	Continuous (°C)
Diurnal range	The daily variation in temperature	Continuous (°C)
Precipitation	The annual mean precipitation	Continuous (mm/year)

* For analysis I standardized all continuous factors using z-transformation.

Bd: The presence of *Bd* might lead to the extinction of both susceptible populations and species (Skerratt et al. 2007, Kilpatrick et al. 2010). In Switzerland *Bd* was first studied in the year 2005 and then found already to be widespread (Garner et al. 2005). Since there was no data available on *Bd* presence in 2003/2004, I assumed that the distribution of the fungus has not changed between years 2003 and 2008. Therefore, if *Bd* was found in 2008, I assumed it had been there already in/before 2003/2004 and that if *Bd* was not found in 2008, I assumed that it did not occur on the site before year 2003. This might cause some bias in the data, but since *Bd* was already widespread in 2005 (Garner et al. 2005) this assumption seems reasonable.

Former occurrence: If a species has been detected at a site in the past, the habitat is likely to be suitable for the species whereas if the species has never been recorded from a particular site before, the habitat may not be suitable for the species. I therefore used the term “former occurrence” as a general descriptor of habitat suitability and to indicate whether the species had been detected at any time before 2003/2004 at a specific study site. I obtained the data from the KARCH data base on amphibian distribution in Switzerland (www.karch.ch; Grossenbacher 1988). This data has been gathered over the last 40 years and contains all known aquatic amphibian habitats in Switzerland (>12'000), and lists all species occurring in each of the habitats.

Isolation: The extent of geographic isolation influences the occurrence and extinction probability of amphibians (Sjögren Gulve 1994, Joly et al. 2001). I therefore used the distance to the closest waterbody where the species does occur (Prugh 2009) as a measure of geographic isolation among sites. I obtained this data from the KARCH database on amphibian distribution in Switzerland (www.karch.ch; Grossenbacher 1988).

Pond type: Amphibian occurrence and persistence is expected to be higher in pond-complexes than in single ponds (Mann et al. 1991). Therefore I quantified ponds as either pond-complexes (whenever a habitat consisted of more than one pond) or as single ponds.

Gravel pit: Gravel pits consist usually of several early-successional temporary ponds, which resemble those created by braided rivers (Schmidt & Pellet 2005). They are a special kind of habitat with a high level of disturbance (Schmidt & Pellet 2005) and therefore occupancy as well as extinction probability might be different at gravel pits than at other habitat types. Moreover, some species – such as *B. calamita* – occur exclusively at gravel pits (B.R. Schmidt, personal communication).

Jura: The persistence of amphibians after outbreaks of *Bd* can be influenced by water chemistry (Bosch et al. 2001). The Swiss Jura is a mountain range in the north of Switzerland (Figure 1), which consists mainly of limestone and has an alkaline type water chemistry. I therefore used the biogeographic region “Swiss Jura” as a proxy for water chemistry.

Temperature: Temperature has fundamental direct and indirect impacts on amphibian performance (e.g. Angilletta et al. 2002, Galloy & Denoel 2010), as well as on *Bd* infections

(Woodhams et al. 2008, Walker et al. 2010). I characterized sites for temperature variation using two measures. The annual mean temperature is the average of monthly mean temperatures (since year 1950) and the mean diurnal range is the difference between monthly mean of daily maximum and daily minimum. Diurnal range was only weakly correlated with annual mean temperature (Pearson Correlation: $r = 0.31$, $N = 71$).

Altitude: Several studies show a stronger virulence as well as more frequent *Bd* outbreaks at high altitudes (Stuart et al. 2004, Woodhams et al. 2008). Moreover, high altitude sites are harsh environments (high disturbance, low temperatures) and hence also directly affect the distribution of amphibians (Oertli et al. 2002).

Precipitation: The amount of precipitation influences the hydroperiod of ponds, which may have direct effects on amphibian breeding success (Baldwin et al. 2006) as well as *Bd* infections (prolonged desiccation is lethal for *Bd*, Lips et al. 2008).

Data for temperature, diurnal range and precipitation was downloaded from the WorldClim database (<http://www.worldclim.org>) (Hijmans et al. 2005). The data arises from weather station records within the time period 1950 – 2000 and has a spatial resolution of about 1 km².

Statistical analyses

For statistical analyses I used a site occupancy model as implemented in program PRESENCE 2.4 (<http://www.mbr-pwrc.usgs.gov/software.html>). The model uses detection-nondetection data and accounts for detection probabilities smaller than one (MacKenzie et al. 2003). In contrast to presence-absence data, detection-nondetection data does not assume that a species is necessarily absent when it is not detected. The approach uses probabilistic arguments and estimates the parameters with maximum likelihood (MacKenzie et al. 2003). The model estimates occupancy, colonization, extinction and detection probabilities. Covariates can be included in the model for all probabilities (MacKenzie et al. 2003).

I ran a set of separate analyses for each species and used a model selection approach, where I formulated a set of a priori models. The model with the lowest Akaike's Information Criterion (AIC) value was in each case considered as best. If the difference between the AIC values of the best and second best model is small, the evidence for the best model is weak (Johnson & Omland 2002). The relative support for a model is expressed in its AIC weight. It is the

probability that a model is superior to the remaining investigated models (Johnson & Omland 2002).

I investigated the influence of *Bd* and other environmental variables (Table 2) on site occupancy (the presence/absence of each species) in the years 2003/2004, as well as extinction (the loss of a species) between the years 2003/2004 and 2008. Since the number of observed colonisations was for all species quite low (Table 1), I assumed a constant colonisation probability for each species over all sites (between the years 2003/2004 and 2008).

I used combinations of the different predictor variables (listed in Table 2) to create a set of candidate models for occupancy and extinction probabilities (Table 3). Each model has parameters for estimating detection probability (p), occupancy (Ψ) and extinction probability (ϵ).

Table 3: Overview of the different A) occupancy and B) extinction models. The extinction models run for *T.alpestris* are marked with “x”. I only run a subset of the models for *T.alpestris* since data were not informative enough (see text). For *R.temporaria* I run an additional occupancy model, where occupancy rate is constant (independent of all predictor variables inclusively “former occurrence”). This is, because *R.temporaria* was almost everywhere detected in years 2003/2004 (Table 1) and thus I predicted that its occupancy would not be explained by any of the predictor variables.

A) Occupancy 2003/2004 (Ψ)		B) Extinction 2003/2004 – 2008 (ϵ)		<i>T.alpestris</i> models
1	Former occurrence	<i>a</i>	Constant	×
2	Former occurrence, isolation	<i>b</i>	Isolation	×
3	Former occurrence, gravel pit	<i>c</i>	Gravel pit	×
4	Former occurrence, pond type	<i>d</i>	Pond type	×
5	Former occurrence, <i>Bd</i>	<i>e</i>	Pond type, isolation	
6	Former occurrence, <i>Bd</i> , isolation	<i>f</i>	<i>Bd</i>	×
7	Former occurrence, <i>Bd</i> , altitude	<i>g</i>	<i>Bd</i> , isolation	
8	Former occurrence, <i>Bd</i> , diurnal range	<i>h</i>	<i>Bd</i> , altitude	
9	Former occurrence, <i>Bd</i> , Jura	<i>i</i>	<i>Bd</i> , temperature	
10	Former occurrence, <i>Bd</i> , temperature	<i>j</i>	<i>Bd</i> , diurnal range	
11	Former occurrence, <i>Bd</i> , diurnal range	<i>k</i>	<i>Bd</i> , Jura	
12	Former occurrence, <i>Bd</i> , precipitation			
13	Former occurrence, <i>Bd</i> , precipitation, diurnal range			

In a first step of the analyses, I searched for a model that best explained detection probabilities while holding all the other parameters in the model constant (Exception: The predictor variable “former occurrence” was used to estimate occupancy.). I created four different design matrices for estimating detection probabilities (Table 4). The first model assumed a constant p for all visits (“Constant Model”). The second model assumed a different p for 2003/2004 and 2008 (but constant within each time period) (“Year Model”). The third model assumed a different p for each of the seven visits (“Visit Model”). The fourth model assumed that detection probability is a linear function of the calendar date (1 = 2nd of March, 2= 3rd of March etc) (“Calendar date Model”). The latter model represents the idea that during a season the number of individuals might increase/decrease and/or that they become easier/harder to detect (e.g. because of changes in behaviour) and hence the detection probability changes with time. Some models did not converge and in this case I had to fix the colonisation probability at 0 or some detection probabilities at either 0 or 1. I then used the best of these models of detection probability (as determined by AIC) to model occupancy and extinction in the second step of analyses.

Table 4: The four different design matrixes for estimating the detection probabilities (P[1,1] till P[2,3]) of the studied amphibian species. The first number is for the year (1 = 2003/2004; 2= 2008), the second for the visit within the given year. For example P[1,3] is the detection probability for the third visit within the year 2003/2004. Calendar date Model: Each calendar date was assigned a number (1= 2nd of March, 2= 3rd of March etc.). Thereafter these numbers were z-transformed. c_1 till c_7 are the estimated parameters.

For example in Model 2 $P[1,1] = 1 \cdot c_1 + 0 \cdot c_2$.

	Constant Model	Year Model		Visit Model							Calendar date Model	
	c_1	c_1	c_2	c_1	c_2	c_3	c_4	c_5	c_6	c_7	c_1	c_2
P[1,1]	1	1	0	1	0	0	0	0	0	0	1	Calendar Date
P[1,2]	1	1	0	1	1	0	0	0	0	0	1	Calendar Date
P[1,3]	1	1	0	1	0	1	0	0	0	0	1	Calendar Date
P[1,4]	1	1	0	1	0	0	1	0	0	0	1	Calendar Date
P[2,1]	1	1	1	1	0	0	0	1	0	0	1	Calendar Date
P[2,2]	1	1	1	1	0	0	0	0	1	0	1	Calendar Date
P[2,3]	1	1	1	1	0	0	0	0	0	1	1	Calendar Date

The second step of analyses consisted of candidate models for estimating occupancy and extinction (listed in Table 3). Since the program can not calculate AIC values for extinction and detection models independently of occupancy, I combined each occupancy

model (13) with each extinction model (11) and the adopted detection probability model resulting in a total amount of $13 \cdot 11 = 143$ models per species.

Occupancy models: For occupancy, model 1 assumes that former occurrence alone best explains the distribution pattern, model 2 assumes that isolation plays a major role, models 3-4 assume that habitat type plays a major role and model 5 assumes that *Bd* presence best explains occupancy. Models 6 – 13 also assume that *Bd* plays an important role, but only in combination with other factors (Table 3) Thus, these latter models include *Bd*, an environmental variable and the interaction between *Bd* and the environmental variable.

Extinction models: For extinction, model *a* assumes a constant extinction probability, models *b - e* assume habitat type and/or isolation play a major role and model *f* assumes *Bd* determines extinction probabilities. Models *g - k* assume that *Bd* determines extinction in combination with another factor. Because there were only few extinctions for most species (Table 1), I kept extinction models simple and did not consider interactions. Moreover, for *T. alpestris* less than 7 extinctions were detected (Table 1), so I only ran models explaining extinction probability with at most one predictor variable (Table 3).

Covariate information was introduced to the occupancy and extinction models using logistic regression (MacKenzie et al. 2003). For example, model 13 for occupancy can be described as follows (on the logit scale):

$$\Psi = A + B \cdot \text{former occurrence} + C \cdot \text{Bd} + D \cdot \text{precipitation} + E \cdot \text{diurnal range} + F \cdot \text{Bd} \cdot \text{precipitation} + G \cdot \text{Bd} \cdot \text{diurnal range}$$

Here A, B, C, D, E, F, G are the model parameters from the program PRESENCE estimated using maximum likelihood procedure (MacKenzie et al. 2003). As shown in the equation above, the only included interactions are 2-factor-interactions between *Bd* and environmental variables.

Next all the investigated models were ranked by their AIC score, and the model with the lowest AIC value was considered the best. In interpreting the results the predictor variable is considered to have no clear effect if the confidence interval of the related parameter included zero (e.g. it might sometimes increase extinction probability and sometimes decrease it, see results section).

Results

The “Visit Model” best explained detection probabilities for all four species and was therefore used throughout in the modeling of occupancy and extinction (Appendix 8).

Bufo calamita

For *B. calamita*, occupancy (Ψ) was best explained by model 8, which included former occurrence, Bd, and diurnal range, as well as the Bd \times diurnal range interaction (Table 5a). The confidence intervals for Bd and diurnal range included zero (Table 6a), indicating that their effect on occupancy is not significantly positive/negative. When *Bd* was present, Ψ was increased with increasing diurnal range (Figure 2a). When *B. calamita* did occur in the past and there was no *Bd*, Ψ slightly declined with increasing diurnal range, whereas when *B. calamita* did not occur in the past and there was no *Bd*, Ψ was close to zero, independent of the diurnal temperature range. Whenever *B. calamita* occurred in the past, Ψ was higher (Figure 2a).

Extinction (ϵ) of *B. calamita* was best explained by model *h*, which included Bd and altitude (Table 5a). However, the confidence intervals for both factors included zero (Table 6a), indicating that their effect on extinction is not significantly positive/negative. Extinction probability decreased with increasing altitude and when *Bd* was present (Figure 3a).

Table 5 a-d. I present the results of the five best models out of the a) 123 (*B.calamita*), b) 121 (*R.temporaria*), c) 33 (*T.alpestris*) and d) 143 (*T. helveticus*) converged models. Each model simultaneously estimates occupancy and extinction. The model with the lowest AIC score was considered best and is indicated in bold. Ψ is the probability of site occupancy, ϵ is the extinction probability, w is the Akaike weight, Δ AIC is the difference in the AIC value between the given model and the model with the lowest AIC value. # p is the number of model parameters. LogLike is the maximum value on the loglikelihood function. The words in brackets indicate the predictor variables included in the model (see Table 2). “(.)” indicates a constant estimate (independent of any factors). The AIC value is calculated as follows: $AIC = 2 \cdot \# p - 2 \cdot \text{LogLike}$

a) *B. calamita*

	AIC	Δ AIC	W	# p	-2·LogLike
Ψ (former occurrence, Bd, diurnal range) ϵ(Bd, altitude)	207.55	0.00	0.0849	16	175.6
Ψ (former occurrence, Bd, diurnal range) ϵ (Bd)	207.77	0.22	0.0761	15	177.8
Ψ (former occurrence, Bd, diurnal range) ϵ (isolation)	208.34	0.79	0.0572	15	178.3
Ψ (former occurrence, Bd, diurnal range) ϵ (.)	208.49	0.94	0.0531	14	180.5
Ψ (former occurrence, Bd, diurnal range) ϵ (Bd, isolation)	208.84	1.29	0.0446	16	176.8

b) *R.temporaria*

	AIC	Δ AIC	W	# p	-2·LogLike
Ψ (former occurrence) ϵ(pond type)	551.42	0.00	0.1617	12	527.4
Ψ (former occurrence, Bd, temperature) ϵ (pond type)	551.66	0.24	0.1434	15	521.7
Ψ (former occurrence, isolation) ϵ (pond type)	552.92	1.50	0.0764	13	526.9
Ψ (former occurrence) ϵ (pond type isolation)	552.97	1.55	0.0745	13	527.0
Ψ (former occurrence, Bd, temperature) ϵ (pond type isolation)	553.25	1.83	0.0648	16	521.2

c) *T. alpestris*

	AIC	Δ AIC	<i>W</i>	# p	-2·LogLike
Ψ (former occurrence, Bd, altitude) ϵ(.)	574.02	0.00	0.3337	14	546.0
Ψ (former occurrence, Bd, altitude) ϵ (Bd)	575.58	1.56	0.1530	15	545.6
Ψ (former occurrence, Bd, altitude) ϵ (isolation)	575.95	1.93	0.1271	15	546.0
Ψ (former occurrence, Bd, temperature) ϵ (.)	576.00	1.98	0.1240	14	548.0
Ψ (former occurrence, Bd, temperature) ϵ (Bd)	577.51	3.49	0.0583	15	547.5

d) *T. helveticus*

	AIC	Δ AIC	<i>W</i>	# p	-2·LogLike
Ψ (former occurrence) ϵ(Bd, temperature)	494.58	0.00	0.0569	13	468.6
Ψ (former occurrence, isolation) ϵ (Bd, temperature)	494.68	0.10	0.0541	14	466.7
Ψ (former occurrence, Bd, isolation) ϵ (Bd, temperature)	495.12	0.54	0.0434	16	463.1
Ψ (former occurrence) ϵ (Bd, altitude)	495.23	0.65	0.0411	13	463.1
Ψ (former occurrence, isolation) ϵ (Bd, altitude)	495.31	0.73	0.0395	14	467.3

Rana temporaria

In the year 2003/2004, *R. temporaria* was spotted everywhere except at three sites (Table 1). Because of this, I predicted that its distribution would not be explained by any of the single factors (not even former occurrence) and even less so by several factors. I therefore ran an additional occupancy model (in addition to those listed in Table 3) with a constant occupancy rate for this species (“ Ψ (.)”) and predicted that this one would perform best. However, this was not the case: occupancy was best explained by model 1, which included former occurrence (Table 5b). This result probably arose because former occurrence could explain two of the three absences and there were only 11 sites where the species has never been recorded before year 2003 (Table 1). The relationship between occupancy and former

occurrence was positive (Table 5b, Figure 2b), indicating that the species was more likely to occupy a site if it had occurred there before. However, the confidence interval for former occurrence included zero (Table 5c), indicating that its effect on occupancy is not significantly positive.

For *R. temporaria*, extinction was best explained by model *d*, which included pond type as a predictor (Table 5b): the relationship between extinction and pond complex was negative (Table 6b), indicating that extinctions were less likely in pond complexes than at single ponds.

Triturus alpestris

For *T. alpestris*, there were only six extinctions between 2003/2004 and 2008 (Table 1). Thus for this species I only ran models with at most one factor explaining extinction probability. However, even with this restricted set of models, only about half of the models converged (Appendix 7). Among them, occupancy was best explained by model 7, which included former occurrence, *Bd*, altitude and the *Bd* x altitude interaction (Table 5c).

However, the confidence intervals for all factors included zero (table 6c), indicating that their effect on occupancy is not significantly positive. Occupancy increased with higher altitude both for sites with *Bd* and without *Bd*. Above a certain altitude (approximately 500m) *T.alpestris* seemed to occur almost everywhere and seems to be even a bit more frequent at places where *Bd* is present than where *Bd* is absent (Figure 2c).

Extinction was best explained by a constant probability (model a) of five percent (Table 6c).

Table 6 a-d. The predictor variables and their parameter estimates from the best models explaining probability of site occupancy and probability of local extinction. a) *B. calamita*, b) *R. temporaria* c) *T. alpestris* and d) *T. helveticus*.

a) *B. calamita*

	Predictors	Parameter estimate (S.E.)	Confidence interval
Occupancy Ψ	intercept	-4.01 (1.19)	[-6.40, -1.62]
	Former occurrence	3.86 (1.19)	[1.48, 6.24]
	Bd	0.44 (0.86)	[-1.29, 2.17]
	diurnal range	-0.28 (0.66)	[-1.60, 1.03]
	Bd \times diurnal range	2.98 (1.24)	[0.51, 2.77]
Extinction ϵ	intercept	0.05 (1.12)	[-2.20, 2.29]
	Bd	-1.32 (1.22)	[-3.76, 1.12]
	altitude	-1.66 (1.22)	[-4.11, 0.79]

b) *R. temporaria*

	Predictors	Parameter estimate (S.E.)	Confidence Interval
Occupancy Ψ	intercept	1.53 (0.80)	[-0.07, 3.12]
	former occurrence	2.76 (1.48)	[-0.21, 5.72]
Extinction ϵ	intercept	0.05 (0.42)	[-0.79, 0.89]
	pond complex	-1.87(0.69)	[-3.25, -0.49]

c) *T. alpestris*

	Predictors	Parameter estimate (S.E.)	Confidence Interval
Occupancy Ψ	intercept	1.53 (0.80)	[-0.07, 3.12]
	former occurrence	2.28 (1.34)	[-0.39, 4.95]
	Bd	6.01(3.47)	[-0.94, 12.95]
	altitude	0.31(0.54)	[-0.77, 1.39]
	altitude \cdot Bd	7.89(3.96)	[-0.03, 15.81]
Extinction ϵ	intercept	-2.92 (0.94)	[-4.79, -1.04]

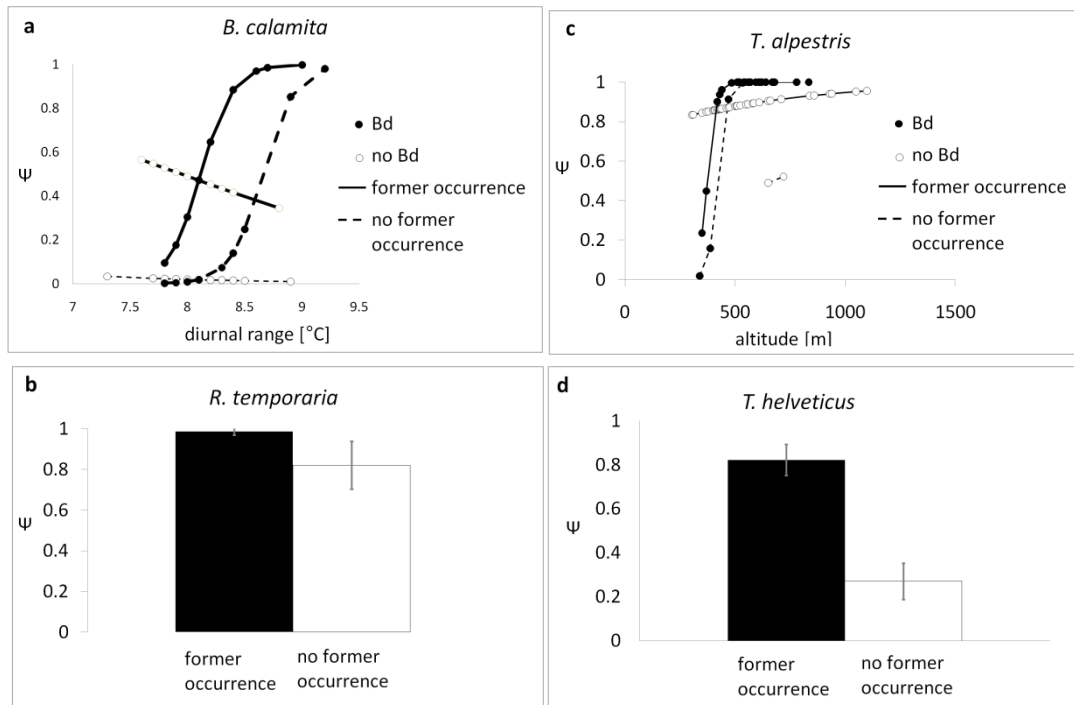
d) *T. helveticus*.

	Predictors	Parameter estimate (S.E.)	Confidence Interval
Occupancy Ψ	intercept	-0.99 (0.42)	[-1.83, -0.16]
	former occurrence	2.52 (0.63)	[1.25, 3.79]
Extinction ϵ	intercept	-2.13 (0.94)	[-4.01, -0.24]
	Bd	0.45(1.17)	[-1.88, 2.79]
	temperature	-1.05 (0.49)	[-2.04, -0.06]

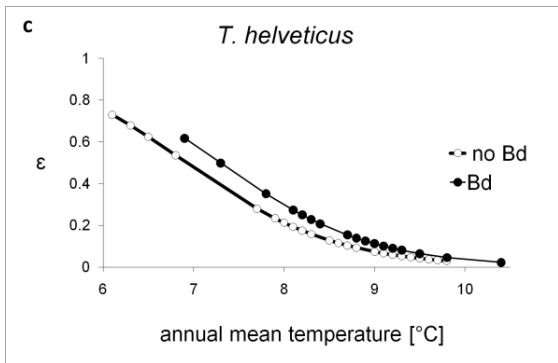
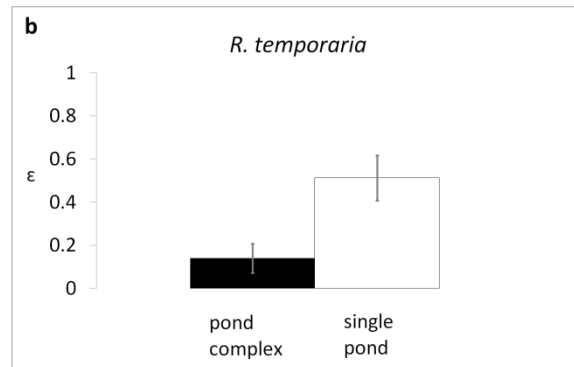
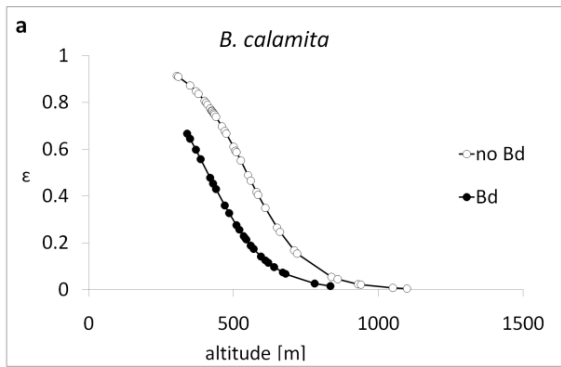
Triturus helveticus

For *T. helveticus*, occupancy was best explained by model 1 that only included former occurrence (Table 5d). The relationship between occupancy and former occurrence was positive, indicating that the species was more likely to occupy a site if it had occurred there before.

Extinction was best explained by model i, that included *Bd* and temperature as predictors (Table 5d). Extinction probability was higher if *Bd* was present and decreased with higher annual mean temperature (Figure 3c). However, the confidence intervals for the factor *Bd* included zero, (Table 6d), indicating that its effect on extinction is not significantly positive.



Figures 2a –d. Probability of site occupancy (Ψ) in relation to the most relevant environmental variables in four amphibian species. Estimates are based on the best model within each of the four species (based on AIC; see Tables 6a-d). In figures a and c, heavy lines indicate that the confidence interval for the slope does not include zero. Bars figures b and d represent probability of occupancy and their standard errors. The confidence intervals for *T. alpestris* could not be calculated since the program failed to compute the variance-covariance matrix.



Figures 3a-c. Local extinction probability (ϵ) in relation to the most relevant environmental variables in three amphibian species. Estimates are based on the best model (based on AIC; see Tables 6 a-d). For *T. alpestris* extinction was best explained by a constant probability of five percent (not shown here). In figures a and c, heavy lines indicate that the confidence interval for the slope does not include zero. Bars figure b represent probability of extinction and their standard errors.

Discussion & Conclusion

My aim was to investigate whether *Bd* presence influences occurrence and local extinction of amphibians in northern Switzerland.

If *Bd* affects the investigated populations in Switzerland the same way as populations of diverse amphibian species around the world (Berger et al. 1998, Daszak et al. 2003), one would expect that populations go extinct in presence of *Bd*. If *Bd* affected populations very recently, then one would expect an effect of *Bd* on extinction probabilities which measure the change in between 2003/2004 and 2008. If *Bd* effects occurred in the past, then one would expect to see *Bd* effects on the occupancy probability (which is for 2003/2004).

Is Bd a threat for the four studied amphibian species in northern Switzerland?

In my analysis, the model which included only *Bd* as an explanatory variable for amphibian distribution and extinction was never the best model for any species (Tables 5a-d). With the exception of *R. temporaria*, the best models for occupancy or extinction had *Bd* and an additional environmental variable (which was thought to enhance or mitigate the effects of *Bd*) as explanatory variables in them.

A model including *Bd* best explained occupancy for *T. alpestris* and *B. calamita* and best explained extinction for *T. helveticus* and *B. calamita*.

While, as expected, there was a weak trend for increased extinction probabilities in the presence of *Bd* in *T. helveticus*, the results of *B. calamita* and *T. alpestris* were neither expected nor intuitive. At sites where *Bd* occurred, occupancy rate and/or persistence (= 1 - extinction) was higher for these two species (especially if conditions were beneficial for *Bd* (i.e. high diurnal temperature range)). However, this finding does not necessarily mean that *Bd* impairs *T. helveticus*, but benefits *B. calamita* and *T. alpestris*. It is possible that there is no direct *causative* link between *Bd* presence and the presence and/or persistence of these amphibian species and that the results instead might be due to correlations with other environmental factors. For example, *Bd*, *B. calamita* and *T. alpestris* may have similar habitat preferences and temperature niches while these environmental conditions may be less suitable for *T. helveticus*. Thus the observed pattern of extinction probabilities and occupancy rates might just be a reflection of similar/dissimilar habitat preferences of amphibians and *Bd*. At least in the case of *B. calamita* it seems likely that an unknown factor(s), which might negatively influence the presence of both *B. calamita* and *Bd*. For instance, one would expect high occupancy probabilities at sites where *B. calamita* occurred in the past. Yet occupancy

probabilities for *B. calamita* were high only in presence of *Bd* and when diurnal temperature range was high (Figure 2a). When *Bd* was absent, *B. calamita* was also absent.

All in all it is possible that *T. helveticus*, *B. calamita* and *T. alpestris* might not be influenced directly by *Bd* presence at all or that two of them (*B. calamita* and *T. alpestris*) might just be more stress resistant (e.g. because of suitable environmental conditions) at places where *Bd* occurs (and thus less susceptible) (Rödder et al. 2008).

Furthermore apart from the interaction between diurnal range and *Bd* for *B. calamita*, all parameters related to the direct influences of *Bd* or interactions between *Bd* and environmental factors included zero in their confidence interval (see Tables 5c, 6c, 7c, 8c). This means, it is not significant that their effect on occupancy and extinction respectively is *positive / negative*.

Thus the observed pattern does not necessarily mean that *T. helveticus* is impaired by *Bd*, but neither does the lack of a negative relationship between *Bd* presence and occurrence/persistence of *B. calamita*, *T. alpestris* and *R. temporaria* necessarily mean that *Bd* is no major threat for them. There are different reasons why *Bd* could nevertheless affect them negatively.

Firstly, I investigated whether *Bd* presence leads to extinction of the studied amphibians. However, the effects of *Bd* might be more subtle. For example, it is probable that a population affected by *Bd* initially levels off to a smaller equilibrium population size, but does not go extinct immediately (Briggs et al. 2005). Such declines in population size would have gone undetected in my data, because I analysed occupancy rather than abundance and occupancy switches its state not before the last individual has disappeared.

Secondly, pathogens can influence the fitness of its host population through many other ways. For example, if a pathogen infects one sex more frequently than the other (e.g. Davis et al. 2009), it could change the sex ratio in the population and thus reduce the effective population size. A pathogen could also lower fecundity or resistance to other diseases/stressors (Vijendravarma et al. 2009) or change the behaviour of infected individuals (Johnson 2002). Pathogens can also be a strong selection pressure for more resistant genotypes (Altizer et. al 2003) and thereby change genotype frequencies or even lower the genetic diversity in a population. Such changes might not be of immediate concern for nature conservation, but in these ways *Bd* might alter populations cryptically, inducing consequences in the long run. Moreover, *Bd* might have a high potential for adaptation to new hosts through genetic alterations (Fisher et al. 2009). Taken together, even if *Bd* does currently not seem to affect

some amphibian populations, *Bd* presence might influence persistence of amphibian populations long-term.

On a more methodological side, I assumed in my analyses that the distribution of *Bd* did not change between years 2003/2004 and 2008. Specifically, I assumed that if *Bd* was found at a specific site in year 2008 that it was already present in years 2003/2004. However, if *Bd* exclusively caused extinctions after 2003/2004 (e.g. because it was not yet there prior or during this time period), *Bd* should only have had an influence on extinction (between years 2003/2004 and 2008), but none on occupancy in years 2003/04. I did not find any negative effect on occupancy for any of the investigated species. Therefore one could suggest that *Bd* might have spread among the study sites relatively recently and the extinctions caused by *Bd* might just have started. But this does not seem to be very probable, since *Bd* was widespread in Switzerland already in year 2005 (Garner et al. 2005).

However, according to the “emerging pathogen hypothesis” (Berger et al. 1998) extinctions might not start immediately after the arrival of *Bd*. Changing environmental conditions (for example due to climate change) or genetic alterations could trigger *Bd* outbreaks through enhanced virulence of *Bd* or increased susceptibility of amphibians (Berger et al. 1998, Skerratt et al. 2007, Bosch et al. 2007, Fisher et al. 2009).

My studies showed that *Bd* rarely had clear negative effects on the amphibians studied here. Moreover, sometimes other environmental factors were the main determinants of occupancy and/or extinction.

For example in the case of *R.temporaria*, extinction probability was best explained by the factor “pond type”. Extinction was estimated higher in habitats with a single pond compared to habitats with a pond complex. Hence the result of *R. temporaria* supports the idea that *Bd* has little to no influence, but that pond complexes favour the establishment of stable populations (Mann et al. 1991).

Temperature (diurnal range or annual mean temperature) was included in the best models for *T.helveticus*, *B.calamita* and *T.alpestris* (see Tables 5a, c, d). Because *Bd* and amphibians are both strongly influenced by temperature, and therefore potentially by climate change, it is important to consider the question: How would distribution and extinction probabilities of amphibians change, if temperatures in Switzerland would rise? According to my results, extinction probabilities of *T. helveticus* would decrease with higher annual mean temperatures and *T. helveticus* populations should become more stable. Since altitude is highly negatively correlated with temperature, my results also forecast that *B. calamita* and *T. alpestris* should become rarer and local extinction probability of *B. calamita* should increase

with increasing temperatures. Thus *T. alpestris* would be expected to retreat to higher altitudes and *B. calamita* populations would become less stable.

In conclusion I found that there are no apparent negative effects of *Bd* on amphibians in northern Switzerland despite the fact that the pathogen is currently widespread. I found some effects of *Bd*, but apart from the negative influence of *Bd* on *T. helveticus*, these were mostly not to the expected direction. This would suggest that *Bd* presence (alone) is not the main cause of extinction for the investigated amphibian populations. However, even if *Bd* does not seem to be a major threat for *B. calamita*, *T. alpestris* and *R. temporaria* in northern Switzerland, it may do so in future a result of, for instance, temperature mediated *Bd* effects.

Future research

I studied a selected subset of factors that might influence amphibian persistence and the effects of *Bd*. Future analyses could include additional factors to evaluate their effect on occupancy and extinction rate of amphibians. Firstly, these additional factors could include factors that are suspected to interact with *Bd* and promote its virulence, viability and/or distribution (e.g. the temperature at the time when amphibians undergo metamorphosis (Walker et al. 2010)) and secondly factors which influence the distribution and extinction of amphibians in absence of *Bd* (e.g. biological factors). Detailed analyses on the effects of these different factors would allow to more reliably determine the relative importance of *Bd*. For example, I only included characteristics of aquatic habitats, but amphibians also rely heavily on suitable terrestrial habitats. By considering the availability, and maybe also the quality of terrestrial habitats, one could probably make more robust predictions about site occupancy/extinction probabilities (Porej 2004). Furthermore, apart from the factor “isolation” all factors included in my study described environmental conditions on a quite local scale. For example, Van Buskirk (2005) found *R. temporaria* and *T. alpestris* to occur more often in forested landscapes, while newts occurred more often in open landscapes, avoiding urban regions. Follow up studies could therefore include more landscape level factors.

In addition to studying a broader range of factors, a larger data set would be beneficial as amphibian populations can naturally be highly dynamic (Alford & Richards 1999, Green 2003, Beebee & Griffiths 2005). For instance, observations from more than two years and on from a larger number of study sites (and maybe not exclusively habitats of *A. obstetricans*) could be included. Thereby the effects of the investigated factors on occupancy and extinction

probability might become more obvious (reducing standard errors). Moreover, if the dataset is large enough, interaction terms could be included in the extinction models as well and maybe even differences in colonization probabilities could be investigated.

Finally, in observational studies it is almost impossible to distinguish between causality and correlation. Therefore field and/or laboratory experiments would be necessary to prove the influences and interactions of *Bd* on amphibians.

Several additional questions would be interesting to address in the future. First: Since when is *Bd* present in Switzerland? An on-going study (the master thesis of Niklaus Peyer at the University of Zurich) is testing presence of *Bd* in amphibians in museum collections to address this question. Such studies could also verify the assumption that *Bd* was already present at my study sites in year 2003. Second: Which factors limit the distribution of *Bd*? This question is part of an ongoing Ph.D. study of Ursina Tobler (University of Zurich), where the the distribution of *Bd* is analysed in relation to environmental factors. If it would be known which factors limit *Bd* distribution, it would be easier to assess whether a species/ the population of a certain region might become threatened because of *Bd* or not. However, because of its poor genetic variability and yet broad spectrum of hosts and environmental niche *Bd* is assumed to be capable of further adaptations to new climates and hosts (Fisher et al. 2009).

Finally, because it is difficult to assess the threat of *Bd* for amphibian species at present and in the future, it is important to reduce the impact of known threats and to monitor amphibian populations.

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Appendix

CONTENT

- 1 Environmental variables
- 2 Isolation data of species
- 3 Former occurrences of the amphibians at the study sites
- 4 Detection- nondetection data of amphibians in years 2003/2004 and 2008
- 5 Detection – nondetection data of *Bd* in year 2008
- 6 Calendar date of visits in 2003/2004 and 2008
- 7 Overview of the models. Which were analyzed? Which did not converge?
- 8 Summary of the results
- 9 Comparison of the four detection probability models

1 ENVIRONMENTAL VARIABLES

Gravel pit 0: no gravel pit 1: gravel pit
 Jura 0: not located in Jura 1: located in Jura
 Pond type 0: single pond 1: pond complex
 Temperature: annual mean temperature

Site	diurnal range [°C]	temperature [°C]	precipitation [mm]	gravel pit	pond type	Jura	altitude [m]
AG137	8	8.6	1041	0	0	0	507
AG368	8	9.5	1039	0	1	0	370
AG388	8.3	9.8	951	1	0	0	340
AG399	7.9	9	1064	0	0	0	440
AG488	7.8	8.5	1093	0	0	0	500
AG530	8	9.5	1037	0	1	0	370
AG695	7.9	8.7	1063	0	1	1	510
AG711	7.7	8.3	1119	0	0	0	550
AG750	8	9	1038	1	0	0	470
AG755	8	9.5	1029	0	0	0	379
AI37	8.2	6.1	1208	0	0	0	1050
AI38	8.4	6.8	1175	0	0	0	930
AR2	8.2	7.9	1156	1	1	0	710
BE1052	8.5	8.7	915	0	1	0	520
BE1090	8.2	9.1	933	0	1	0	435
BE172	8.4	9.1	903	1	1	0	435

BE59	8.2	9.3	936	0	0	0	426
BE649	8	7.7	1057	0	0	1	838
BE72	8.4	8.4	945	1	1	0	570
BL173	8.4	9.8	804	0	1	0	310
BL594	8.4	9.6	839	0	0	1	350
BL77	7.9	8.5	1006	0	1	1	460
BS10	8.4	9.7	816	0	1	0	305
FR10	8.7	8.1	974	1	1	0	610
FR110	8.7	8.2	940	1	1	0	595
FR80	8.6	7.8	974	1	1	0	670
GE15	9.2	10.4	925	0	0	0	350
JU1405	8.4	8.7	951	0	1	1	540
JU1902	8	8	1025	0	0	1	560
JU5102	7.7	6.5	1232	0	1	1	860
JU5400	7.7	6.1	1296	0	0	1	1099
JU800	8.4	9.3	871	0	1	1	430
JU8700	8.5	9.2	907	0	1	1	430
LU12	7.7	9	1138	1	1	0	510
LU132	7.3	6.3	1269	0	0	0	940
LU234	7.9	9.5	1106	0	1	0	420
LU271	7.9	9.1	1120	1	1	0	544
LU582	7.8	8.8	1161	0	1	0	610
NE53	8	6.9	1165	0	1	1	835
NE58	8.8	9	922	0	0	1	432
NE70	8.3	7.3	1134	1	0	1	780
SG500	7.9	8.2	1148	0	0	0	720
SG504	8	8.2	1132	1	1	0	680
SG598	8.1	8.6	1094	0	1	0	610
SG600	8.1	8.4	1117	1	1	0	620
SG8	8.1	8.2	1130	0	1	0	650
SH31	8.4	8.3	1038	0	1	0	560
SO101	8.2	9.3	954	0	0	0	420
SO11	8.2	9.3	946	0	0	0	405
SO117	7.9	8.1	1034	0	0	1	650
SO83	8.3	9	919	0	1	1	475
TG368	8.3	9.4	972	1	0	0	420
VD232	9	9.8	966	1	0	0	420
VD80	8.9	8.7	1056	0	1	0	585
VD97	8.9	8.9	1011	0	0	0	535
ZG10	7.6	8.8	1162	1	1	0	580
ZH1205	7.9	8.2	1127	0	0	0	640
ZH148	8.1	8.9	1046	0	0	0	485
ZH169	8.1	9.2	1033	1	1	0	430
ZH304	8	8.8	1072	0	0	0	470
ZH33	8.2	9.5	995	1	1	0	400

ZH439	8.2	9.3	1017	1	1	0	387
ZH44	8.2	9.4	1000	1	0	0	410
ZH496	7.8	8.9	1093	0	1	0	485
ZH558	7.8	9.3	1105	0	1	0	425
ZH625	8.2	9.2	999	0	1	0	430
ZH636	7.8	9.2	1105	0	1	0	420
ZH706	8.2	9	1023	0	1	0	440
ZH76	7.8	9	1091	1	1	0	470
ZH764	7.8	9	1131	1	1	0	525
ZH82	7.8	8	1173	0	1	0	660

2 ISOLATION DATA

Distance [m] to the closest aquatic habitat where the species is known to exist

	<i>B.calamita</i>	<i>R.temporaria</i>	<i>T.alpestris</i>	<i>T.helveticus</i>
AG137	2885	558	558	558
AG368	394	394	394	394
AG388	4841	494	2074	2074
AG399	2500	309	214	214
AG488	1605	828	1129	1605
AG530	326	417	417	417
AG695	1811	1346	1346	1761
AG711	1256	492	1141	2789
AG750	930	930	472	930
AG755	141	141	651	651
AI37	18434	231	231	231
AI38	19761	281	281	281
AR2	15784	2081	2081	5669
BE1052	1124	422	422	422
BE1090	410	410	410	410
BE172	1304	1304	1590	2970
BE59	1632	604	604	604
BE649	576	576	576	576
BE72	1860	1012	1621	1621
BL173	1114	348	348	348
BL594	1159	1159	1159	1159
BL77	4875	1315	1315	2107
BS10	2370	667	667	2370
FR10	5367	1628	1628	2600
FR110	1154	1458	1750	1924
FR80	100	1033	1033	1141
GE15	3249	4273	3249	3249
JU1405	1977	444	444	444
JU1902	6685	1919	1857	4724

JU5102	12411	240	1077	1077
JU5400	19580	431	1191	1442
JU800	1959	1850	1722	1959
JU8700	16014	1231	943	922
LU12	1257	620	620	755
LU132	23689	901	3059	4718
LU234	414	309	468	468
LU271	922	304	900	304
LU582	5395	403	403	412
NE53	6535	1156	1156	7256
NE58	3593	604	604	1218
NE70	5267	559	559	559
SG500	11993	230	230	4797
SG504	4373	1513	1513	1751
SG598	8932	1570	1570	1570
SG600	9964	361	361	539
SG8	10522	1070	1070	1070
SH31	2279	355	355	7326
SO101	906	906	1029	1257
SO11	1288	378	1288	2205
SO117	9915	2112	2112	3809
SO83	2884	1828	2280	4370
TG368	472	472	472	8920
VD232	1687	1687	1687	1687
VD80	1523	361	361	361
VD97	1017	316	316	1017
ZG10	446	311	311	316
ZH1205	1526	609	1526	1796
ZH148	2845	585	888	5774
ZH169	150	263	263	4030
ZH304	1577	501	1577	1600
ZH33	3155	1138	1138	7254
ZH439	2405	1735	2405	2576
ZH44	801	622	457	2688
ZH496	2521	1166	1166	3202
ZH558	640	500	500	1040
ZH625	755	223	223	10134
ZH636	316	316	316	316
ZH706	444	444	444	4561
ZH76	552	552	552	552
ZH764	187	187	187	187
ZH82	1024	166	230	1024

3 FORMER OCCURRENCE OF AMPHIBIANS AT THE STUDY SITES

	<i>B.calamita</i>	<i>R.temporaria</i>	<i>T.alpestris</i>	<i>T.helveticus</i>
AG137	1	0	1	1
AG368	1	1	1	1
AG388	0	1	0	0
AG399	0	1	1	1
AG488	0	1	1	0
AG530	1	1	1	1
AG695	1	1	1	1
AG711	0	1	1	0
AG750	1	0	0	0
AG755	1	1	1	1
AI37	0	0	1	0
AI38	0	1	1	1
AR2	0	1	1	1
BE1052	0	1	1	1
BE1090	1	1	1	1
BE172	0	1	1	0
BE59	0	1	1	1
BE649	0	1	1	1
BE72	1	1	1	1
BL173	0	1	1	1
BL594	1	1	1	1
BL77	0	1	1	0
BS10	0	1	1	1
FR10	1	1	1	1
FR110	1	0	0	0
FR80	1	0	0	0
GE15	0	1	1	0
JU1405	0	1	1	1
JU1902	0	1	1	1
JU5102	0	1	1	1
JU5400	0	1	1	0
JU800	1	1	1	1
JU8700	0	1	1	1
LU12	1	1	1	0
LU132	0	1	1	1
LU234	1	1	1	1
LU271	1	1	1	1
LU582	0	0	1	0
NE53	0	1	0	0
NE58	1	1	1	1
NE70	0	1	1	0
SG500	0	1	0	0

SG504	1	1	1	1
SG598	0	1	1	1
SG600	1	1	1	1
SG8	0	1	1	1
SH31	0	1	1	0
SO101	1	1	1	1
SO11	0	1	1	1
SO117	0	1	0	0
SO83	0	1	1	1
TG368	1	1	1	0
VD232	1	1	1	1
VD80	0	1	1	1
VD97	0	1	0	0
ZG10	1	1	1	0
ZH1205	0	1	1	1
ZH148	0	1	1	0
ZH169	0	1	1	0
ZH304	0	1	0	0
ZH33	1	1	1	0
ZH439	1	0	0	0
ZH44	1	0	1	0
ZH496	0	0	1	1
ZH558	1	1	1	1
ZH625	1	1	1	0
ZH636	1	0	1	1
ZH706	1	1	1	0
ZH76	1	1	1	0
ZH764	0	1	1	0
ZH82	1	0	1	1

4 DETECTION – NONDETECTION DATA

B. calamita

	detection- nondetection data 2003/2004				detection- nondetection data 2008		
AG137	0	0	-	-	0	0	0
AG368	0	0	-	-	0	0	0
AG388	0	0	-	-	0	1	1
AG399	0	0	0	-	0	0	0
AG488	0	0	-	-	0	0	0
AG530	0	0	0	-	0	0	0
AG695	0	-	-	-	0	0	0
AG711	0	0	0	-	0	0	0
AG750	1	1	1	-	0	0	1
AG755	0	0	0	-	0	0	0
AI37	0	0	0	-	0	0	0
AI38	0	0	0	-	0	0	0

AR2	0	0	0	0	0	0	0
BE1052	0	0	-	-	0	0	0
BE1090	0	0	-	-	0	0	0
BE172	1	1	-	-	0	0	0
BE59	0	0	0	-	0	0	0
BE649	0	0	0	-	0	0	0
BE72	0	1	1	-	0	0	1
BL173	0	0	0	0	0	0	0
BL594	-	-	-	-	0	0	0
BL77	0	0	-	-	0	0	0
BS10	0	-	-	-	0	0	0
FR10	1	1	1	-	0	1	1
FR110	1	1	0	-	0	1	1
FR80	1	1	1	-	0	0	1
GE15	0	0	-	-	1	0	0
JU1405	0	0	0	-	0	0	0
JU1902	0	0	0	-	0	0	0
JU5102	0	0	0	0	0	0	0
JU5400	0	0	0	0	0	0	0
JU800	1	1	1	-	0	1	1
JU8700	0	0	0	-	0	0	0
LU12	1	1	1	-	0	1	1
LU132	0	0	0	-	0	0	0
LU234	1	1	1	-	0	0	1
LU271	0	0	0	-	0	0	0
LU582	0	0	0	-	0	0	0
NE53	0	0	-	-	0	0	0
NE58	0	0	0	-	0	0	0
NE70	0	0	-	-	0	0	0
SG500	0	0	0	0	0	0	0
SG504	1	1	-	-	0	1	1
SG598	0	0	0	0	0	0	0
SG600	0	0	-	-	0	0	0
SG8	0	0	0	0	0	0	0
SH31	0	0	0	-	0	0	0
SO101	1	0	1	1	0	0	0
SO11	0	0	0	-	0	0	0
SO117	0	-	-	-	0	0	0
SO83	0	0	-	-	0	0	0
TG368	0	1	0	-	0	0	0
VD232	1	0	-	-	0	0	0
VD80	0	0	0	-	0	0	0
VD97	1	1	-	-	0	0	0
ZG10	0	1	1	-	0	0	0
ZH1205	0	0	0	-	0	0	0
ZH148	0	0	0	0	0	0	0
ZH169	0	0	0	0	0	0	0
ZH304	0	0	0	-	0	0	0
ZH33	0	0	1	0	0	0	0
ZH439	0	-	-	-	0	0	0
ZH44	0	0	-	-	0	0	0
ZH496	0	0	0	-	0	0	0
ZH558	0	1	1	0	0	0	0

ZH625	0	1	0	-	0	0	0
ZH636	0	0	0	0	0	1	0
ZH706	0	-	-	-	0	0	0
ZH76	0	0	0	-	0	0	0
ZH764	0	0	0	-	0	0	0
ZH82	0	0	0	-	0	0	-

R.temporaria

	detection- nondetection data 2003/2004				detection- nondetection data 2008			
AG137	1	1	1	0	0	0	0	
AG368	1	1	0	0	1	1	1	
AG388	1	1	1	0	1	1	1	
AG399	1	1	1	1	1	0	0	
AG488	1	1	1	-	0	1	0	
AG530	1	1	0	0	1	0	0	
AG695	1	1	1	0	1	0	1	
AG711	1	1	1	0	1	0	0	
AG750	0	0	0	-	1	0	0	
AG755	1	0	0	0	1	1	0	
AI37	1	0	0	-	0	0	0	
AI38	1	1	1	-	0	0	0	
AR2	1	1	1	1	1	1	0	
BE1052	1	1	0	1	0	0	0	
BE1090	1	1	1	1	1	1	0	
BE172	1	1	0	1	1	1	0	
BE59	1	1	0	0	0	0	0	
BE649	1	1	1	1	1	1	0	
BE72	0	1	1	1	0	1	0	
BL173	1	1	1	0	1	0	1	
BL594	1	-	-	-	0	0	0	
BL77	1	1	0	0	0	0	0	
BS10	1	1	1	1	1	1	1	
FR10	1	0	0	0	1	1	0	
FR110	1	0	1	0	1	1	0	
FR80	1	1	1	0	0	0	0	
GE15	1	1	1	-	0	0	0	
JU1405	1	1	1	1	1	1	0	
JU1902	1	1	1	0	1	0	0	
JU5102	1	1	1	0	1	1	0	
JU5400	1	0	0	0	1	0	0	
JU800	1	1	0	1	1	0	1	
JU8700	1	1	0	0	1	1	1	
LU12	1	1	0	0	0	1	0	
LU132	1	0	0	1	0	0	0	
LU234	1	1	1	1	0	1	1	
LU271	1	1	1	1	1	1	0	
LU582	1	1	1	1	1	1	1	
NE53	1	1	1	1	0	0	1	
NE58	1	1	0	0	0	0	0	
NE70	0	1	-	-	0	0	0	
SG500	1	1	1	1	1	0	1	
SG504	1	1	0	1	1	1	0	

SG598	1	0	0	0	0	0	0
SG600	1	1	0	1	0	1	1
SG8	1	1	1	1	1	0	1
SH31	1	1	0	1	0	0	0
SO101	1	1	0	0	0	0	0
SO11	1	1	0	0	0	0	0
SO117	1	1	1	0	1	1	1
SO83	1	1	0	0	0	0	0
TG368	1	1	1	0	0	0	0
VD232	0	0	0	-	0	0	0
VD80	1	1	1	1	0	0	1
VD97	1	1	0	0	0	0	1
ZG10	1	1	0	0	1	1	1
ZH1205	1	0	0	1	1	1	1
ZH148	1	1	1	1	0	0	0
ZH169	1	1	1	1	1	0	0
ZH304	1	0	0	0	0	0	0
ZH33	1	1	1	1	1	1	1
ZH439	1	0	0	0	1	1	0
ZH44	0	0	0	-	0	0	0
ZH496	1	0	0	0	1	0	0
ZH558	1	1	1	1	0	0	0
ZH625	1	1	1	0	0	1	1
ZH636	0	1	0	0	1	1	1
ZH706	1	1	0	-	0	1	0
ZH76	1	1	1	0	1	1	0
ZH764	1	1	0	0	0	0	0
ZH82	1	1	1	-	1	0	-

T.alpestris

	detection- nondetection data 2003/2004				detection- nondetection data 2008		
AG137	0	1	1	0	0	1	1
AG368	1	1	1	0	0	1	0
AG388	0	0	0	0	0	0	0
AG399	0	0	0	0	0	0	0
AG488	0	0	0	-	0	0	0
AG530	1	1	0	0	1	1	1
AG695	0	0	1	1	0	1	0
AG711	1	1	1	1	1	1	1
AG750	0	1	0	-	0	1	1
AG755	1	1	1	0	0	0	1
AI37	1	1	1	-	1	1	1
AI38	1	1	1	-	1	0	0
AR2	1	1	1	1	0	1	0
BE1052	1	1	1	1	0	1	1
BE1090	0	1	1	1	0	1	1
BE172	1	1	1	1	0	1	1
BE59	0	1	1	1	0	0	0
BE649	0	1	0	0	0	0	0
BE72	1	1	1	1	0	1	1
BL173	1	1	1	1	1	1	1
BL594	0	-	-	-	0	0	0

BL77	0	1	1	1	1	0	0
BS10	1	1	1	1	1	1	0
FR10	1	1	1	-	1	1	1
FR110	0	0	1	1	1	1	1
FR80	1	1	1	1	0	1	1
GE15	0	0	0	-	0	0	0
JU1405	0	1	1	1	0	1	0
JU1902	0	0	0	0	0	0	0
JU5102	0	1	1	0	0	1	0
JU5400	0	1	1	0	0	0	0
JU800	1	1	1	1	0	0	1
JU8700	0	1	0	0	0	0	1
LU12	1	1	1	1	1	1	1
LU132	1	1	1	1	0	0	1
LU234	1	1	1	1	0	1	1
LU271	0	1	0	0	0	0	0
LU582	1	1	1	1	1	1	1
NE53	0	1	1	0	0	0	1
NE58	0	1	1	0	0	0	0
NE70	1	0	-	-	0	1	1
SG500	0	1	1	1	1	1	0
SG504	0	0	1	0	1	1	1
SG598	1	1	0	0	1	0	1
SG600	0	0	1	0	1	1	0
SG8	1	1	1	1	1	1	1
SH31	1	1	1	0	1	0	1
SO101	1	1	1	1	0	1	1
SO11	0	0	1	1	0	1	1
SO117	0	0	0	0	1	1	1
SO83	0	0	1	0	0	0	1
TG368	0	1	1	1	1	1	1
VD232	1	1	1	-	0	1	0
VD80	1	1	1	1	0	1	1
VD97	0	1	1	0	1	1	1
ZG10	0	1	0	0	0	1	1
ZH1205	0	1	1	1	1	1	0
ZH148	1	1	1	1	0	0	0
ZH169	0	0	0	0	0	1	1
ZH304	1	1	1	0	0	1	0
ZH33	1	1	1	1	1	0	0
ZH439	0	0	0	-	0	0	0
ZH44	0	1	0	-	1	0	0
ZH496	1	1	1	1	0	1	1
ZH558	1	1	1	1	1	1	1
ZH625	0	1	1	1	0	1	1
ZH636	1	1	1	0	0	1	0
ZH706	0	1	-	-	0	1	1
ZH76	0	0	1	1	0	0	1
ZH764	0	1	1	1	0	1	1
ZH82	0	0	0	-	1	0	-

T.helveticus

	detection- nondetection data 2003/2004				detection- nondetection data 2008		
AG137	0	1	1	1	0	0	0
AG368	1	1	1	0	1	0	0
AG388	0	0	0	0	0	0	0
AG399	0	0	0	0	0	0	0
AG488	0	0	0	-	0	0	0
AG530	1	1	0	0	1	1	1
AG695	0	0	0	0	0	0	1
AG711	0	0	0	0	0	0	0
AG750	0	0	0	-	0	0	0
AG755	1	1	1	0	0	1	0
AI37	0	0	0	-	0	1	1
AI38	0	0	0	-	1	0	0
AR2	0	0	1	0	0	0	0
BE1052	0	1	1	1	0	1	1
BE1090	0	1	1	1	0	1	1
BE172	1	0	1	1	0	1	1
BE59	0	1	1	1	1	1	1
BE649	0	1	1	1	1	1	0
BE72	0	0	1	0	0	1	1
BL173	1	1	1	1	1	1	1
BL594	0	-	-	-	0	0	1
BL77	0	0	0	0	0	0	0
BS10	0	1	1	-	1	1	0
FR10	1	1	1	-	1	1	0
FR110	0	0	0	1	1	1	1
FR80	0	1	0	0	0	0	0
GE15	0	0	0	-	0	0	0
JU1405	0	0	0	1	0	0	0
JU1902	0	1	1	1	0	0	0
JU5102	0	1	1	0	0	0	0
JU5400	0	0	1	0	0	0	0
JU800	0	1	0	1	0	0	1
JU8700	0	1	0	0	0	0	1
LU12	0	0	0	0	0	0	0
LU132	0	0	1	1	1	0	1
LU234	0	1	1	1	0	1	1
LU271	0	0	0	0	0	0	0
LU582	0	1	1	1	0	0	0
NE53	0	0	0	-	0	0	0
NE58	0	0	0	0	0	0	0
NE70	0	0	-	-	0	0	0
SG500	0	0	0	0	1	1	0
SG504	0	0	1	0	1	1	1
SG598	0	0	0	0	0	0	0
SG600	0	0	1	0	1	0	0
SG8	1	1	0	0	1	1	1
SH31	0	0	0	-	0	0	0
SO101	1	1	1	1	0	1	1
SO11	0	0	1	1	1	1	1

SO117	0	0	0	0	1	0	0
SO83	0	0	1	0	0	0	1
TG368	0	0	0	0	0	0	0
VD232	1	1	1	-	0	1	0
VD80	0	1	1	1	0	1	0
VD97	0	1	0	-	0	0	0
ZG10	0	0	0	0	0	0	0
ZH1205	0	0	1	1	1	1	0
ZH148	0	0	0	0	0	0	0
ZH169	0	0	0	0	0	0	0
ZH304	1	1	0	0	0	1	1
ZH33	0	0	0	0	0	0	0
ZH439	0	0	0	-	0	0	0
ZH44	0	0	0	-	0	0	0
ZH496	0	0	1	1	0	0	1
ZH558	0	0	0	0	0	0	0
ZH625	0	0	0	0	0	0	0
ZH636	0	0	0	0	0	1	0
ZH706	0	0	0	-	0	1	0
ZH76	0	0	0	0	0	0	0
ZH764	0	1	1	1	1	1	1
ZH82	0	0	0	-	1	1	-

5 DETECTION-NONDETECTION DATA OF BD IN YEAR 2008

Site	Bd	Site	Bd	Site	Bd	Site	Bd
AG137	0	BE72	1	LU271	1	VD97	1
AG368	0	BL173	0	LU582	1	ZG10	0
AG388	1	BL594	0	NE53	1	ZH1205	1
AG399	0	BL77	0	NE58	0	ZH148	1
AG488	0	BS10	0	NE70	1	ZH169	1
AG530	1	FR10	1	SG500	0	ZH304	1
AG695	1	FR110	1	SG504	1	ZH33	0
AG711	0	FR80	1	SG598	0	ZH439	1
AG750	1	GE15	1	SG600	1	ZH44	0
AG755	0	JU1405	1	SG8	0	ZH496	1
AI37	0	JU1902	0	SH31	1	ZH558	0
AI38	0	JU5102	0	SO101	1	ZH625	1
AR2	0	JU5400	0	SO11	0	ZH636	1
BE1052	1	JU800	1	SO117	0	ZH706	1
BE1090	0	JU8700	0	SO83	0	ZH76	0
BE172	0	LU12	0	TG368	0	ZH764	0
BE59	0	LU132	0	VD232	1	ZH82	0
BE649	0	LU234	0	VD80	0		

6 CALENDAR DATE OF VISITS IN 2003/2004 AND 2008

B.calamita

	Calendar date of visits years 2003/2004				Calendar date of visits year 2008		
AG137	09.05.2003	21.06.2003	-	-	19.04.2008	25.04.2008	01.05.2008
AG368	01.05.2003	18.06.2003	-	-	24.04.2008	09.05.2008	22.05.2008
AG388	29.05.2003	18.06.2003	-	-	26.04.2008	29.04.2008	05.05.2008
AG399	15.04.2003	18.05.2003	25.06.2003	-	25.04.2008	08.05.2008	28.05.2008
AG488	16.05.2003	25.06.2003	-	-	24.04.2008	28.04.2008	04.05.2008
AG530	28.04.2003	29.05.2003	06.06.2003	-	24.04.2008	09.05.2008	22.05.2008
AG695	21.06.2003	-	-	-	25.04.2008	08.05.2008	28.05.2008
AG711	31.03.2004	21.04.2004	08.06.2004	-	19.04.2008	24.04.2008	04.05.2008
AG750	15.04.2003	16.05.2003	23.06.2003	-	25.04.2008	28.04.2008	04.05.2008
AG755	27.04.2003	31.05.2003	13.06.2003	-	25.04.2008	09.05.2008	22.05.2008
AI37	1.4.2003	13.5.2003	25.05.2003	-	20.04.2008	12.05.2008	24.05.2008
AI38	01.04.2003	28.05.2003	04.06.2003	-	20.04.2008	12.04.2008	24.05.2008
AR2	01.04.2004	18.05.2004	30.05.2004	16.06.2004	20.04.2008	12.05.2008	24.05.2008
BE1052	20.05.2003	02.06.2003	-	-	14.04.2008	05.05.2008	15.05.2008
BE1090	05.05.2003	22.06.2003	-	-	19.04.2008	17.05.2008	23.05.2008
BE172	08.05.2003	01.06.2003	-	-	18.04.2008	08.05.2008	23.05.2008
BE59	02.04.2004	21.04.2004	03.06.2004	-	18.04.2008	27.04.2008	02.05.2008
BE649	27.04.2003	11.05.2003	15.06.2003	-	16.04.2008	24.04.2008	05.05.2008
BE72	30.04.2004	14.05.2004	25.06.2004	-	29.04.2008	05.05.2008	27.05.2008
BL173	02.04.2004	14.04.2004	09.06.2004	17.06.2004	18.04.2008	21.04.2008	27.04.2008
BL594	-	-	-	-	09.04.2008	16.04.2008	24.04.2008
BL77	02.05.2003	03.06.2003	-	-	20.04.2008	24.04.2008	01.05.2008
BS10	17.04.2003	-	-	-	23.04.2008	24.04.2008	29.04.2008
FR10	21.04.2004	28.05.2004	03.06.2004	-	27.04.2008	12.05.2008	25.05.2008
FR110	25.04.2003	23.05.2003	17.06.2003	-	20.04.2008	20.05.2008	22.05.2008
FR80	20.04.2003	31.05.2003	19.06.2003	-	20.04.2008	12.05.2008	22.05.2008
GE15	15.04.2003	29.04.2003	-	-	24.04.2008	07.05.2008	28.05.2008
JU1405	28.04.2003	31.05.2003	28.06.2003	-	17.04.2008	26.04.2008	01.05.2008
JU1902	05.05.2003	31.05.2003	28.06.2003	-	14.04.2008	23.04.2008	04.05.2008
JU5102	31.03.2004	27.04.2004	31.05.2004	30.06.2004	15.04.2008	26.04.2008	06.05.2008
JU5400	05.04.2003	29.04.2003	30.05.2003	24.06.2003	15.04.2008	06.05.2008	09.05.2008
JU800	05.05.2003	31.05.2003	28.06.2003	-	16.04.2008	24.04.2008	08.05.2008
JU8700	03.05.2003	28.05.2003	27.06.2003	-	17.04.2008	23.04.2008	01.05.2008
LU12	25.04.2003	17.05.2003	02.06.2003	-	18.04.2008	11.05.2008	21.05.2008
LU132	17.04.2003	03.06.2003	19.06.2003	-	25.04.2008	29.04.2008	15.05.2008
LU234	28.04.2003	22.05.2003	04.06.2003	-	18.04.2008	14.05.2008	21.05.2008
LU271	22.04.2003	13.05.2003	18.06.2003	-	16.04.2008	11.05.2008	26.05.2008
LU582	15.04.2004	26.05.2004	09.06.2004	-	16.04.2008	14.05.2008	26.05.2008
NE53	24.04.2003	10.06.2003	-	-	26.04.2008	04.05.2008	19.05.2008
NE58	25.04.2003	23.05.2003	20.06.2003	-	25.04.2008	09.05.2008	20.05.2008

NE70	25.04.2003	23.05.2003	-	-	26.04.2008	04.05.2008	19.05.2008
SG500	09.04.2004	12.05.2004	12.06.2004	25.06.2004	26.04.2008	08.05.2008	23.05.2008
SG504	12.05.2003	17.06.2003	-	-	26.04.2008	08.05.2008	23.05.2008
SG598	21.04.2004	12.05.2004	17.05.2004	14.06.2004	01.05.2008	14.05.2008	19.05.2008
SG600	12.05.2003	10.06.2003	-	-	26.04.2008	08.05.2008	19.05.2008
SG8	01.04.2004	29.05.2004	14.06.2004	21.06.2004	01.05.2008	14.05.2008	19.05.2008
SH31	31.03.2004	18.05.2004	08.06.2004	-	02.05.2008	13.05.2008	26.05.2008
SO101	31.03.2004	21.04.2004	08.06.2004	22.07.2004	18.04.2008	27.04.2008	02.05.2008
SO11	14.04.2003	19.05.2003	18.06.2003	-	18.04.2008	26.04.2008	02.05.2008
SO117	01.06.2003	-	-	-	14.04.2008	18.04.2008	25.04.2008
SO83	06.05.2003	19.06.2003	-	-	18.04.2008	08.05.2008	26.05.2008
TG368	05.04.2004	12.05.2004	10.06.2004	-	02.05.2008	13.05.2008	25.05.2008
VD232	14.04.2003	29.04.2003	-	-	25.04.2008	07.05.2008	28.05.2008
VD80	14.04.2004	21.05.2004	12.06.2004	-	25.04.2008	07.05.2008	25.05.2008
VD97	16.04.2003	21.05.2003	-	-	25.04.2008	07.05.2008	25.05.2008
ZG10	16.04.2003	12.05.2003	05.06.2003	-	10.04.2008	14.05.2008	20.05.2008
ZH1205	21.04.2004	19.05.2004	28.06.2004	-	27.04.2008	21.05.2008	28.05.2008
ZH148	31.03.2004	13.04.2004	10.05.2004	17.06.2004	04.05.2008	22.05.2008	29.05.2008
ZH169	31.03.2004	13.04.2004	10.05.2004	15.06.2004	04.05.2008	06.05.2008	22.05.2008
ZH304	21.04.2004	19.05.2004	28.06.2004	-	27.04.2008	21.05.2008	28.05.2008
ZH33	31.03.2004	14.04.2004	18.05.2004	15.06.2004	03.05.2008	22.05.2008	29.05.2008
ZH439	30.05.2003	-	-	-	27.04.2008	06.05.2008	27.05.2008
ZH44	18.05.2003	02.06.2003	-	-	03.05.2008	21.05.2008	29.05.2008
ZH496	21.04.2004	24.05.2004	14.06.2004	-	19.04.2008	13.05.2008	23.05.2008
ZH558	31.03.2004	22.04.2004	27.04.2004	20.05.2004	10.04.2008	07.05.2008	15.05.2008
ZH625	05.04.2004	12.05.2004	10.06.2004	-	02.05.2008	16.05.2008	26.05.2008
ZH636	08.04.2004	04.05.2004	11.05.2004	16.06.2004	10.04.2008	07.05.2008	15.05.2008
ZH706	30.05.2003	-	-	-	26.04.2008	20.05.2008	27.05.2008
ZH76	18.04.2003	01.05.2003	05.06.2003	-	19.04.2008	13.05.2008	23.05.2008
ZH764	22.04.2003	01.05.2003	03.06.2003	-	17.04.2008	06.05.2008	27.05.2008
ZH82	09.04.2004	27.04.2004	20.05.2004	-	06.05.2008	27.05.2008	-

R.temporaria

	Calendar date of visits years 2003/2004				Calendar date of visits year 2008		
AG137	21_03_2003	02_04_2003	09_05_2003	21_06_2003	19.04.2008	25.04.2008	01.05.2008
AG368	25_03_2003	28_03_2003	01_05_2003	18_06_2003	24.04.2008	09.05.2008	22.05.2008
AG388	21_03_2003	29_03_2003	29_05_2003	18_06_2003	26.04.2008	29.04.2008	05.05.2008
AG399	15_03_2003	15_04_2003	18_05_2003	25_06_2003	25.04.2008	08.05.2008	28.05.2008
AG488	13_04_2003	16_05_2003	25_06_2003	-	24.04.2008	28.04.2008	04.05.2008
AG530	28_03_2003	28_04_2003	29_05_2003	06_06_2003	24.04.2008	09.05.2008	22.05.2008
AG695	21_03_2003	02_04_2003	05_04_2003	21_06_2003	25.04.2008	08.05.2008	28.05.2008
AG711	20_03_2004	31_03_2004	21_04_2004	08_06_2004	19.04.2008	24.04.2008	04.05.2008
AG750	15_04_2003	16_05_2003	23_06_2003	-	25.04.2008	28.04.2008	04.05.2008
AG755	28_03_2003	27_04_2003	31_05_2003	13_06_2003	25.04.2008	09.05.2008	22.05.2008

AI37	01_04_2003	13_05_2003	25_05_2003	-	20.04.2008	12.05.2008	24.05.2008
AI38	01_04_2003	28_05_2003	04_06_2003	-	20.04.2008	12.04.2008	24.05.2008
AR2	01_04_2004	18_05_2004	30_05_2004	16_06_2004	20.04.2008	12.05.2008	24.05.2008
BE1052	22_03_2003	13_04_2003	20_05_2003	02_06_2003	14.04.2008	05.05.2008	15.05.2008
BE1090	21_03_2003	07_04_2003	05_05_2003	22_06_2003	19.04.2008	17.05.2008	23.05.2008
BE172	29_03_2003	03_04_2003	08_05_2003	01_06_2003	18.04.2008	08.05.2008	23.05.2008
BE59	22_03_2004	02_04_2004	21_04_2004	03_06_2004	18.04.2008	27.04.2008	02.05.2008
BE649	02_04_2003	27_04_2003	11_05_2003	15_06_2003	16.04.2008	24.04.2008	05.05.2008
BE72	27_03_2004	30_04_2004	14_05_2004	25_06_2004	29.04.2008	05.05.2008	27.05.2008
BL173	02_04_2004	14_04_2004	09_06_2004	17_06_2004	18.04.2008	21.04.2008	27.04.2008
BL594	21_03_2004	-	-	-	09.04.2008	16.04.2008	24.04.2008
BL77	10_03_2003	03_04_2003	02_05_2003	03_06_2003	20.04.2008	24.04.2008	01.05.2008
BS10	24_03_2003	31_03_2003	17_04_2003	22_07_2003	23.04.2008	24.04.2008	29.04.2008
FR10	14_03_2004	21_04_2004	28_05_2004	03_06_2004	27.04.2008	12.05.2008	25.05.2008
FR110	01_04_2003	25_04_2003	23_05_2003	17_06_2003	20.04.2008	20.05.2008	22.05.2008
FR80	30_03_2003	20_04_2003	31_05_2003	19_06_2003	20.04.2008	12.05.2008	22.05.2008
GE15	31_03_2003	15_04_2003	29_04_2003	-	24.04.2008	07.05.2008	28.05.2008
JU1405	02_04_2003	28_04_2003	31_05_2003	28_06_2003	17.04.2008	26.04.2008	01.05.2008
JU1902	30_03_2003	05_05_2003	31_05_2003	28_06_2003	14.04.2008	23.04.2008	04.05.2008
JU5102	31_03_2004	27_04_2004	31_05_2004	30_06_2004	15.04.2008	26.04.2008	06.05.2008
JU5400	05_04_2003	29_04_2003	30_05_2003	24_06_2003	15.04.2008	06.05.2008	09.05.2008
JU800	02_04_2003	05_05_2003	31_05_2003	28_06_2003	16.04.2008	24.04.2008	08.05.2008
JU8700	29_03_2003	03_05_2003	28_05_2003	27_06_2003	17.04.2008	23.04.2008	01.05.2008
LU12	15_03_2003	25_04_2003	17_05_2003	02_06_2003	18.04.2008	11.05.2008	21.05.2008
LU132	22_03_2003	17_04_2003	03_06_2003	19_06_2003	25.04.2008	29.04.2008	15.05.2008
LU234	15_03_2003	28_04_2003	22_05_2003	04_06_2003	18.04.2008	14.05.2008	21.05.2008
LU271	25_03_2003	22_04_2003	13_05_2003	18_06_2003	16.04.2008	11.05.2008	26.05.2008
LU582	22_03_2004	15_04_2004	26_05_2004	09_06_2004	16.04.2008	14.05.2008	26.05.2008
NE53	23_03_2003	24_04_2003	10_06_2003	04_07_2003	26.04.2008	04.05.2008	19.05.2008
NE58	27_03_2003	25_04_2003	23_05_2003	20_06_2003	25.04.2008	09.05.2008	20.05.2008
NE70	25_04_2003	23_05_2003	-	-	26.04.2008	04.05.2008	19.05.2008
SG500	09_04_2004	12_05_2004	12_06_2004	25_06_2004	26.04.2008	08.05.2008	23.05.2008
SG504	24_03_2003	07_04_2003	12_05_2003	17_06_2003	26.04.2008	08.05.2008	23.05.2008
SG598	21_04_2004	12_05_2004	17_05_2004	14_06_2004	01.05.2008	14.05.2008	19.05.2008
SG600	24_03_2003	07_04_2003	12_05_2003	10_06_2003	26.04.2008	08.05.2008	19.05.2008
SG8	01_04_2004	29_05_2004	14_06_2004	21_06_2004	01.05.2008	14.05.2008	19.05.2008
SH31	15_03_2004	31_03_2004	18_05_2004	08_06_2004	02.05.2008	13.05.2008	26.05.2008
SO101	31_03_2004	21_04_2004	08_06_2004	22_07_2004	18.04.2008	27.04.2008	02.05.2008
SO11	23_03_2003	14_04_2003	19_05_2003	18_06_2003	18.04.2008	26.04.2008	02.05.2008
SO117	22_03_2003	24_03_2003	01_04_2003	01_06_2003	14.04.2008	18.04.2008	25.04.2008
SO83	29_03_2003	04_04_2003	06_05_2003	19_06_2003	18.04.2008	08.05.2008	26.05.2008
TG368	22_03_2004	05_04_2004	12_05_2004	10_06_2004	02.05.2008	13.05.2008	25.05.2008
VD232	18_03_2003	14_04_2003	29_04_2003	-	25.04.2008	07.05.2008	28.05.2008
VD80	18_03_2004	14_04_2004	21_05_2004	12_06_2004	25.04.2008	07.05.2008	25.05.2008
VD97	13_03_2003	16_04_2003	21_05_2003	07_07_2003	25.04.2008	07.05.2008	25.05.2008

ZG10	17_03_2003	16_04_2003	12_05_2003	05_06_2003	10.04.2008	14.05.2008	20.05.2008
ZH1205	29_03_2004	21_04_2004	19_05_2004	28_06_2004	27.04.2008	21.05.2008	28.05.2008
ZH148	31_03_2004	13_04_2004	10_05_2004	17_06_2004	04.05.2008	22.05.2008	29.05.2008
ZH169	31_03_2004	13_04_2004	10_05_2004	15_06_2004	04.05.2008	06.05.2008	22.05.2008
ZH304	29_03_2004	21_04_2004	19_05_2004	28_06_2004	27.04.2008	21.05.2008	28.05.2008
ZH33	31_03_2004	14_04_2004	18_05_2004	15_06_2004	03.05.2008	22.05.2008	29.05.2008
ZH439	07_03_2003	07_04_2003	30_05_2003	06_07_2003	27.04.2008	06.05.2008	27.05.2008
ZH44	12_04_2003	18_05_2003	02_06_2003	-	03.05.2008	21.05.2008	29.05.2008
ZH496	27_03_2004	21_04_2004	24_05_2004	14_06_2004	19.04.2008	13.05.2008	23.05.2008
ZH558	31_03_2004	22_04_2004	27_04_2004	20_05_2004	10.04.2008	07.05.2008	15.05.2008
ZH625	29_03_2004	05_04_2004	12_05_2004	10_06_2004	02.05.2008	16.05.2008	26.05.2008
ZH636	08_04_2004	04_05_2004	11_05_2004	16_06_2004	10.04.2008	07.05.2008	15.05.2008
ZH706	07_03_2003	04_04_2003	30_05_2003	-	26.04.2008	20.05.2008	27.05.2008
ZH76	18_03_2003	18_04_2003	01_05_2003	05_06_2003	19.04.2008	13.05.2008	23.05.2008
ZH764	17_03_2003	22_04_2003	01_05_2003	03_06_2003	17.04.2008	06.05.2008	27.05.2008
ZH82	09_04_2004	27_04_2004	20_05_2004	-	06.05.2008	27.05.2008	-

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	Calendar date of visits years 2003/2004				Calendar date of visits year 2008		
AG137	21_03_2003	02_04_2003	09_05_2003	21_06_2003	19.04.2008	25.04.2008	01.05.2008
AG368	25_03_2003	28_03_2003	01_05_2003	18_06_2003	24.04.2008	09.05.2008	22.05.2008
AG388	21_03_2003	29_03_2003	29_05_2003	18_06_2003	26.04.2008	29.04.2008	05.05.2008
AG399	15_03_2003	15_04_2003	18_05_2003	25_06_2003	25.04.2008	08.05.2008	28.05.2008
AG488	13_04_2003	16_05_2003	25_06_2003	-	24.04.2008	28.04.2008	04.05.2008
AG530	28_03_2003	28_04_2003	29_05_2003	06_06_2003	24.04.2008	09.05.2008	22.05.2008
AG695	21_03_2003	02_04_2003	05_04_2003	21_06_2003	25.04.2008	08.05.2008	28.05.2008
AG711	20_03_2004	31_03_2004	21_04_2004	08_06_2004	19.04.2008	24.04.2008	04.05.2008
AG750	15_04_2003	16_05_2003	23_06_2003	-	25.04.2008	28.04.2008	04.05.2008
AG755	28_03_2003	27_04_2003	31_05_2003	13_06_2003	25.04.2008	09.05.2008	22.05.2008
AI37	01_04_2003	13_05_2003	25_05_2003	-	20.04.2008	12.05.2008	24.05.2008
AI38	01_04_2003	28_05_2003	04_06_2003	-	20.04.2008	12.04.2008	24.05.2008
AR2	01_04_2004	18_05_2004	30_05_2004	16_06_2004	20.04.2008	12.05.2008	24.05.2008
BE1052	22_03_2003	13_04_2003	20_05_2003	02_06_2003	14.04.2008	05.05.2008	15.05.2008
BE1090	21_03_2003	07_04_2003	05_05_2003	22_06_2003	19.04.2008	17.05.2008	23.05.2008
BE172	29_03_2003	03_04_2003	08_05_2003	01_06_2003	18.04.2008	08.05.2008	23.05.2008
BE59	22_03_2004	02_04_2004	21_04_2004	03_06_2004	18.04.2008	27.04.2008	02.05.2008
BE649	02_04_2003	27_04_2003	11_05_2003	15_06_2003	16.04.2008	24.04.2008	05.05.2008
BE72	27_03_2004	30_04_2004	14_05_2004	25_06_2004	29.04.2008	05.05.2008	27.05.2008
BL173	02_04_2004	14_04_2004	09_06_2004	17_06_2004	18.04.2008	21.04.2008	27.04.2008
BL594	21_03_2004	-	-	-	09.04.2008	16.04.2008	24.04.2008
BL77	10_03_2003	03_04_2003	02_05_2003	03_06_2003	20.04.2008	24.04.2008	01.05.2008
BS10	24_03_2003	31_03_2003	17_04_2003	22_07_2003	23.04.2008	24.04.2008	29.04.2008
FR10	21_04_2004	28_05_2004	03_06_2004	-	27.04.2008	12.05.2008	25.05.2008
FR110	01_04_2003	25_04_2003	23_05_2003	17_06_2003	20.04.2008	20.05.2008	22.05.2008

FR80	30_03_2003	20_04_2003	31_05_2003	19_06_2003	20.04.2008	12.05.2008	22.05.2008
GE15	31_03_2003	15_04_2003	29_04_2003	-	24.04.2008	07.05.2008	28.05.2008
JU1405	02_04_2003	28_04_2003	31_05_2003	28_06_2003	17.04.2008	26.04.2008	01.05.2008
JU1902	30_03_2003	05_05_2003	31_05_2003	28_06_2003	14.04.2008	23.04.2008	04.05.2008
JU5102	31_03_2004	27_04_2004	31_05_2004	30_06_2004	15.04.2008	26.04.2008	06.05.2008
JU5400	05_04_2003	29_04_2003	30_05_2003	24_06_2003	15.04.2008	06.05.2008	09.05.2008
JU800	02_04_2003	05_05_2003	31_05_2003	28_06_2003	16.04.2008	24.04.2008	08.05.2008
JU8700	29_03_2003	03_05_2003	28_05_2003	27_06_2003	17.04.2008	23.04.2008	01.05.2008
LU12	15_03_2003	25_04_2003	17_05_2003	02_06_2003	18.04.2008	11.05.2008	21.05.2008
LU132	22_03_2003	17_04_2003	03_06_2003	19_06_2003	25.04.2008	29.04.2008	15.05.2008
LU234	15_03_2003	28_04_2003	22_05_2003	04_06_2003	18.04.2008	14.05.2008	21.05.2008
LU271	25_03_2003	22_04_2003	13_05_2003	18_06_2003	16.04.2008	11.05.2008	26.05.2008
LU582	22_03_2004	15_04_2004	26_05_2004	09_06_2004	16.04.2008	14.05.2008	26.05.2008
NE53	23_03_2003	24_04_2003	10_06_2003	04_07_2003	26.04.2008	04.05.2008	19.05.2008
NE58	27_03_2003	25_04_2003	23_05_2003	20_06_2003	25.04.2008	09.05.2008	20.05.2008
NE70	25_04_2003	23_05_2003	-	-	26.04.2008	04.05.2008	19.05.2008
SG500	09_04_2004	12_05_2004	12_06_2004	25_06_2004	26.04.2008	08.05.2008	23.05.2008
SG504	24_03_2003	07_04_2003	12_05_2003	17_06_2003	26.04.2008	08.05.2008	23.05.2008
SG598	21_04_2004	12_05_2004	17_05_2004	14_06_2004	01.05.2008	14.05.2008	19.05.2008
SG600	24_03_2003	07_04_2003	12_05_2003	10_06_2003	26.04.2008	08.05.2008	19.05.2008
SG8	01_04_2004	29_05_2004	14_06_2004	21_06_2004	01.05.2008	14.05.2008	19.05.2008
SH31	15_03_2004	31_03_2004	18_05_2004	08_06_2004	02.05.2008	13.05.2008	26.05.2008
SO101	31_03_2004	21_04_2004	08_06_2004	22_07_2004	18.04.2008	27.04.2008	02.05.2008
SO11	23_03_2003	14_04_2003	19_05_2003	18_06_2003	18.04.2008	26.04.2008	02.05.2008
SO117	22_03_2003	24_03_2003	01_04_2003	01_06_2003	14.04.2008	18.04.2008	25.04.2008
SO83	29_03_2003	04_04_2003	06_05_2003	19_06_2003	18.04.2008	08.05.2008	26.05.2008
TG368	22_03_2004	05_04_2004	12_05_2004	10_06_2004	02.05.2008	13.05.2008	25.05.2008
VD232	18_03_2003	14_04_2003	29_04_2003	-	25.04.2008	07.05.2008	28.05.2008
VD80	18_03_2004	14_04_2004	21_05_2004	12_06_2004	25.04.2008	07.05.2008	25.05.2008
VD97	13_03_2003	16_04_2003	21_05_2003	07_07_2003	25.04.2008	07.05.2008	25.05.2008
ZG10	17_03_2003	16_04_2003	12_05_2003	05_06_2003	10.04.2008	14.05.2008	20.05.2008
ZH1205	29_03_2004	21_04_2004	19_05_2004	28_06_2004	27.04.2008	21.05.2008	28.05.2008
ZH148	31_03_2004	13_04_2004	10_05_2004	17_06_2004	04.05.2008	22.05.2008	29.05.2008
ZH169	31_03_2004	13_04_2004	10_05_2004	15_06_2004	04.05.2008	06.05.2008	22.05.2008
ZH304	29_03_2004	21_04_2004	19_05_2004	28_06_2004	27.04.2008	21.05.2008	28.05.2008
ZH33	31_03_2004	14_04_2004	18_05_2004	15_06_2004	03.05.2008	22.05.2008	29.05.2008
ZH439	07_04_2003	30_05_2003	06_07_2003	-	27.04.2008	06.05.2008	27.05.2008
ZH44	12_04_2003	18_05_2003	02_06_2003	-	03.05.2008	21.05.2008	29.05.2008
ZH496	27_03_2004	21_04_2004	24_05_2004	14_06_2004	19.04.2008	13.05.2008	23.05.2008
ZH558	31_03_2004	22_04_2004	27_04_2004	20_05_2004	10.04.2008	07.05.2008	15.05.2008
ZH625	29_03_2004	05_04_2004	12_05_2004	10_06_2004	02.05.2008	16.05.2008	26.05.2008
ZH636	08_04_2004	04_05_2004	11_05_2004	16_06_2004	10.04.2008	07.05.2008	15.05.2008
ZH706	04_04_2003	30_05_2003	-	-	26.04.2008	20.05.2008	27.05.2008
ZH76	18_03_2003	18_04_2003	01_05_2003	05_06_2003	19.04.2008	13.05.2008	23.05.2008
ZH764	17_03_2003	22_04_2003	01_05_2003	03_06_2003	17.04.2008	06.05.2008	27.05.2008

ZH82	09_04_2004	27_04_2004	20_05_2004	-	06.05.2008	27.05.2008	-
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	Calendar date of visits years 2003/2004				Calendar date of visits year 2008		
AG137	21_03_2003	02_04_2003	09_05_2003	21_06_2003	19.04.2008	25.04.2008	01.05.2008
AG368	25_03_2003	28_03_2003	01_05_2003	18_06_2003	24.04.2008	09.05.2008	22.05.2008
AG388	21_03_2003	29_03_2003	29_05_2003	18_06_2003	26.04.2008	29.04.2008	05.05.2008
AG399	15_03_2003	15_04_2003	18_05_2003	25_06_2003	25.04.2008	08.05.2008	28.05.2008
AG488	13_04_2003	16_05_2003	25_06_2003	-	24.04.2008	28.04.2008	04.05.2008
AG530	28_03_2003	28_04_2003	29_05_2003	06_06_2003	24.04.2008	09.05.2008	22.05.2008
AG695	21_03_2003	02_04_2003	05_04_2003	21_06_2003	25.04.2008	08.05.2008	28.05.2008
AG711	20_03_2004	31_03_2004	21_04_2004	08_06_2004	19.04.2008	24.04.2008	04.05.2008
AG750	15_04_2003	16_05_2003	23_06_2003	-	25.04.2008	28.04.2008	04.05.2008
AG755	28_03_2003	27_04_2003	31_05_2003	13_06_2003	25.04.2008	09.05.2008	22.05.2008
AI37	01_04_2003	13_05_2003	25_05_2003	-	20.04.2008	12.05.2008	24.05.2008
AI38	01_04_2003	28_05_2003	04_06_2003	-	20.04.2008	12.04.2008	24.05.2008
AR2	01_04_2004	18_05_2004	30_05_2004	16_06_2004	20.04.2008	12.05.2008	24.05.2008
BE1052	22_03_2003	13_04_2003	20_05_2003	02_06_2003	14.04.2008	05.05.2008	15.05.2008
BE1090	21_03_2003	07_04_2003	05_05_2003	22_06_2003	19.04.2008	17.05.2008	23.05.2008
BE172	29_03_2003	03_04_2003	08_05_2003	01_06_2003	18.04.2008	08.05.2008	23.05.2008
BE59	22_03_2004	02_04_2004	21_04_2004	03_06_2004	18.04.2008	27.04.2008	02.05.2008
BE649	02_04_2003	27_04_2003	11_05_2003	15_06_2003	16.04.2008	24.04.2008	05.05.2008
BE72	27_03_2004	30_04_2004	14_05_2004	25_06_2004	29.04.2008	05.05.2008	27.05.2008
BL173	02_04_2004	14_04_2004	09_06_2004	17_06_2004	18.04.2008	21.04.2008	27.04.2008
BL594	21_03_2004	-	-	-	09.04.2008	16.04.2008	24.04.2008
BL77	10_03_2003	03_04_2003	02_05_2003	03_06_2003	20.04.2008	24.04.2008	01.05.2008
BS10	24_03_2003	31_03_2003	17_04_2003	-	23.04.2008	24.04.2008	29.04.2008
FR10	21_04_2004	28_05_2004	03_06_2004	-	27.04.2008	12.05.2008	25.05.2008
FR110	01_04_2003	25_04_2003	23_05_2003	17_06_2003	20.04.2008	20.05.2008	22.05.2008
FR80	01_04_2003	20_04_2003	31_05_2003	19_06_2003	20.04.2008	12.05.2008	22.05.2008
GE15	31_03_2003	15_04_2003	29_04_2003	-	24.04.2008	07.05.2008	28.05.2008
JU1405	02_04_2003	28_04_2003	31_05_2003	28_06_2003	17.04.2008	26.04.2008	01.05.2008
JU1902	30_03_2003	05_05_2003	31_05_2003	28_06_2003	14.04.2008	23.04.2008	04.05.2008
JU5102	31_03_2004	27_04_2004	31_05_2004	30_06_2004	15.04.2008	26.04.2008	06.05.2008
JU5400	05_04_2003	29_04_2003	30_05_2003	24_06_2003	15.04.2008	06.05.2008	09.05.2008
JU800	02_04_2003	05_05_2003	31_05_2003	28_06_2003	16.04.2008	24.04.2008	08.05.2008
JU8700	29_03_2003	03_05_2003	28_05_2003	27_06_2003	17.04.2008	23.04.2008	01.05.2008
LU12	15_03_2003	25_04_2003	17_05_2003	02_06_2003	18.04.2008	11.05.2008	21.05.2008
LU132	22_03_2003	17_04_2003	03_06_2003	19_06_2003	25.04.2008	29.04.2008	15.05.2008
LU234	15_03_2003	28_04_2003	22_05_2003	04_06_2003	18.04.2008	14.05.2008	21.05.2008
LU271	25_03_2003	22_04_2003	13_05_2003	18_06_2003	16.04.2008	11.05.2008	26.05.2008
LU582	22_03_2004	15_04_2004	26_05_2004	09_06_2004	16.04.2008	14.05.2008	26.05.2008
NE53	23_03_2003	24_04_2003	10_06_2003	-	26.04.2008	04.05.2008	19.05.2008
NE58	27_03_2003	25_04_2003	23_05_2003	20_06_2003	25.04.2008	09.05.2008	20.05.2008

NE70	25_04_2003	23_05_2003	-	-	26.04.2008	04.05.2008	19.05.2008
SG500	09_04_2004	12_05_2004	12_06_2004	25_06_2004	26.04.2008	08.05.2008	23.05.2008
SG504	24_03_2003	07_04_2003	12_05_2003	17_06_2003	26.04.2008	08.05.2008	23.05.2008
SG598	21_04_2004	12_05_2004	17_05_2004	14_06_2004	01.05.2008	14.05.2008	19.05.2008
SG600	24_03_2003	07_04_2003	12_05_2003	10_06_2003	26.04.2008	08.05.2008	19.05.2008
SG8	01_04_2004	29_05_2004	14_06_2004	21_06_2004	01.05.2008	14.05.2008	19.05.2008
SH31	31_03_2004	18_05_2004	08_06_2004	-	02.05.2008	13.05.2008	26.05.2008
SO101	31_03_2004	21_04_2004	08_06_2004	22_07_2004	18.04.2008	27.04.2008	02.05.2008
SO11	23_03_2003	14_04_2003	19_05_2003	18_06_2003	18.04.2008	26.04.2008	02.05.2008
SO117	22_03_2003	24_03_2003	01_04_2003	01_06_2003	14.04.2008	18.04.2008	25.04.2008
SO83	29_03_2003	04_04_2003	06_05_2003	19_06_2003	18.04.2008	08.05.2008	26.05.2008
TG368	22_03_2004	05_04_2004	12_05_2004	10_06_2004	02.05.2008	13.05.2008	25.05.2008
VD232	18_03_2003	14_04_2003	29_04_2003	-	25.04.2008	07.05.2008	28.05.2008
VD80	18_03_2004	14_04_2004	21_05_2004	12_06_2004	25.04.2008	07.05.2008	25.05.2008
VD97	13_03_2003	16_04_2003	21_05_2003	-	25.04.2008	07.05.2008	25.05.2008
ZG10	17_03_2003	16_04_2003	12_05_2003	05_06_2003	10.04.2008	14.05.2008	20.05.2008
ZH1205	29_03_2004	21_04_2004	19_05_2004	28_06_2004	27.04.2008	21.05.2008	28.05.2008
ZH148	31_03_2004	13_04_2004	10_05_2004	17_06_2004	04.05.2008	22.05.2008	29.05.2008
ZH169	31_03_2004	13_04_2004	10_05_2004	15_06_2004	04.05.2008	06.05.2008	22.05.2008
ZH304	29_03_2004	21_04_2004	19_05_2004	28_06_2004	27.04.2008	21.05.2008	28.05.2008
ZH33	31_03_2004	14_04_2004	18_05_2004	15_06_2004	03.05.2008	22.05.2008	29.05.2008
ZH439	07_03_2003	07_04_2003	30_05_2003	-	27.04.2008	06.05.2008	27.05.2008
ZH44	12_04_2003	18_05_2003	02_06_2003	-	03.05.2008	21.05.2008	29.05.2008
ZH496	27_03_2004	21_04_2004	24_05_2004	14_06_2004	19.04.2008	13.05.2008	23.05.2008
ZH558	31_03_2004	22_04_2004	27_04_2004	20_05_2004	10.04.2008	07.05.2008	15.05.2008
ZH625	29_03_2004	05_04_2004	12_05_2004	10_06_2004	02.05.2008	16.05.2008	26.05.2008
ZH636	08_04_2004	04_05_2004	11_05_2004	16_06_2004	10.04.2008	07.05.2008	15.05.2008
ZH706	07_03_2003	04_04_2003	30_05_2003	-	26.04.2008	20.05.2008	27.05.2008
ZH76	18_03_2003	18_04_2003	01_05_2003	05_06_2003	19.04.2008	13.05.2008	23.05.2008
ZH764	17_03_2003	22_04_2003	01_05_2003	03_06_2003	17.04.2008	06.05.2008	27.05.2008
ZH82	09_04_2004	27_04_2004	20_05_2004	-	06.05.2008	27.05.2008	-

7 OVERVIEW OF THE MODELS. WHICH WERE ANALYZED? WHICH DID NOT CONVERGE?

Ψ : probability of site occupancy ε : local extinction probability -: constant
 nc: model did not converge ok: model did converge na: not analysed
 o: Former occurrence iso: isolation wk: pond type
 kg: gravel pit al: altitude bd: Bd ju: Jura
 te: annual mean temperature dr: diurnal range pr: precipitation

Ψ explained by ...	ε explained by ...	<i>B. calamita</i>	<i>R. temporaria</i>	<i>T. alpestris</i>	<i>T. helveticus</i>
o	-	ok	ok	ok	ok
o iso	-	ok	ok	ok	ok
o kg	-	ok	nc	ok	ok
o wk	-	ok	nc	ok	ok
o bd	-	ok	ok	ok	ok
o bd iso	-	ok	na	nc	ok
o bd al	-	ok	na	ok	ok
o bd dr	-	ok	na	ok	ok
o bd ju	-	nc	na	nc	ok
o bd te	-	ok	na	ok	ok
o bd te dr	-	ok	na	ok	ok
o bd pr	-	ok	na	ok	ok
o bd pr dr	-	ok	na	ok	ok
o	bd	ok	ok	ok	ok
o iso	bd	ok	ok	ok	ok
o kg	bd	ok	nc	ok	ok
o wk	bd	ok	nc	ok	ok
o bd	bd	ok	ok	ok	ok
o bd iso	bd	ok	na	nc	ok
o bd al	bd	ok	na	ok	ok
o bd dr	bd	ok	na	ok	ok
o bd ju	bd	nc	na	nc	ok
o bd te	bd	ok	na	ok	ok
o bd te dr	bd	ok	na	ok	ok
o bd pr	bd	ok	na	ok	ok
o bd pr dr	bd	ok	na	ok	ok
o	bd iso	ok	ok	na	ok
o iso	bd iso	ok	ok	na	ok
o kg	bd iso	ok	nc	na	ok
o wk	bd iso	ok	nc	na	ok
o bd	bd iso	ok	ok	na	ok
o bd iso	bd iso	ok	na	na	ok
o bd al	bd iso	ok	na	na	ok
o bd dr	bd iso	ok	na	na	ok
o bd ju	bd iso	nc	na	na	ok
o bd te	bd iso	ok	na	na	ok
o bd te dr	bd iso	ok	na	na	ok
o bd pr	bd iso	ok	na	na	ok

o bd pr dr	bd iso	ok	na	na	ok
o	bd al	ok	ok	na	ok
o iso	bd al	ok	ok	na	ok
o kg	bd al	ok	nc	na	ok
o wk	bd al	ok	nc	na	ok
o bd	bd al	ok	ok	na	ok
o bd iso	bd al	ok	na	na	ok
o bd al	bd al	ok	na	na	ok
o bd dr	bd al	ok	na	na	ok
o bd ju	bd al	nc	na	na	ok
o bd te	bd al	ok	na	na	ok
o bd te dr	bd al	ok	na	na	ok
o bd pr	bd al	ok	na	na	ok
o bd pr dr	bd al	ok	na	na	ok
o	bd te	ok	ok	na	ok
o iso	bd te	ok	ok	na	ok
o kg	bd te	ok	nc	na	ok
o wk	bd te	ok	nc	na	ok
o bd	bd te	ok	ok	na	ok
o bd iso	bd te	ok	na	na	ok
o bd al	bd te	ok	na	na	ok
o bd dr	bd te	ok	na	na	ok
o bd ju	bd te	nc	na	na	ok
o bd te	bd te	ok	na	na	ok
o bd te dr	bd te	ok	na	na	ok
o bd pr	bd te	ok	na	na	ok
o bd pr dr	bd te	ok	na	na	ok
o	bd dr	nc	ok	na	ok
o iso	bd dr	nc	ok	na	ok
o kg	bd dr	nc	nc	na	ok
o wk	bd dr	nc	nc	na	ok
o bd	bd dr	nc	ok	na	ok
o bd iso	bd dr	nc	na	na	ok
o bd al	bd dr	nc	na	na	ok
o bd dr	bd dr	ok	na	na	ok
o bd ju	bd dr	nc	na	na	ok
o bd te	bd dr	nc	na	na	ok
o bd te dr	bd dr	ok	na	na	ok
o bd pr	bd dr	nc	na	na	ok
o bd pr dr	bd dr	ok	na	na	ok
o	bd ju	ok	ok	na	ok
o iso	bd ju	ok	ok	na	ok
o kg	bd ju	ok	nc	na	ok
o wk	bd ju	ok	nc	na	ok
o bd	bd ju	ok	ok	na	ok
o bd iso	bd ju	ok	na	na	ok
o bd al	bd ju	ok	na	na	ok
o bd dr	bd ju	ok	na	na	ok
o bd ju	bd ju	nc	na	na	ok
o bd te	bd ju	ok	na	na	ok
o bd te dr	bd ju	ok	na	na	ok
o bd pr	bd ju	ok	na	na	ok
o bd pr dr	bd ju	ok	na	na	ok

o	wk	ok	ok	nc	ok
o iso	wk	ok	ok	nc	ok
o kg	wk	ok	nc	nc	ok
o wk	wk	ok	nc	nc	ok
o bd	wk	ok	ok	nc	ok
o bd iso	wk	ok	na	nc	ok
o bd al	wk	ok	na	nc	ok
o bd dr	wk	ok	na	nc	ok
o bd ju	wk	nc	na	nc	ok
o bd te	wk	ok	na	nc	ok
o bd te dr	wk	ok	na	nc	ok
o bd pr	wk	ok	na	nc	ok
o bd pr dr	wk	ok	na	nc	ok
o	kg	ok	ok	nc	ok
o iso	kg	ok	ok	nc	ok
o kg	kg	ok	nc	nc	ok
o wk	kg	ok	nc	nc	ok
o bd	kg	ok	ok	nc	ok
o bd iso	kg	ok	na	nc	ok
o bd al	kg	ok	na	nc	ok
o bd dr	kg	ok	na	nc	ok
o bd ju	kg	nc	na	nc	ok
o bd te	kg	ok	na	nc	ok
o bd te dr	kg	ok	na	nc	ok
o bd pr	kg	ok	na	nc	ok
o bd pr dr	kg	ok	na	nc	ok
o	iso	ok	ok	ok	ok
o iso	iso	ok	ok	ok	ok
o kg	iso	ok	nc	ok	ok
o wk	iso	ok	nc	ok	ok
o bd	iso	ok	ok	ok	ok
o bd iso	iso	ok	na	nc	ok
o bd al	iso	ok	na	ok	ok
o bd dr	iso	ok	na	ok	ok
o bd ju	iso	nc	na	nc	ok
o bd te	iso	ok	na	ok	ok
o bd te dr	iso	ok	na	ok	ok
o bd pr	iso	ok	na	ok	ok
o bd pr dr	iso	ok	na	ok	ok
o	wk iso	ok	ok	na	ok
o iso	wk iso	ok	ok	na	ok
o kg	wk iso	ok	nc	na	ok
o wk	wk iso	ok	nc	na	ok
o bd	wk iso	ok	ok	na	ok
o bd iso	wk iso	ok	na	na	ok
o bd al	wk iso	ok	na	na	ok
o bd dr	wk iso	ok	na	na	ok
o bd ju	wk iso	nc	na	na	ok
o bd te	wk iso	ok	na	na	ok
o bd te dr	wk iso	ok	na	na	ok
o bd pr	wk iso	ok	na	na	ok
o bd pr dr	wk iso	ok	na	na	ok
-	-	na	ok	na	na

-	iso	na	ok	na	na
-	kg	na	ok	na	na
-	wk	na	ok	na	na
-	wk iso	na	ok	na	na
-	bd	na	ok	na	na
-	Bd iso	na	ok	na	na
-	Bd al	na	ok	na	na
-	bd te	na	ok	na	na
-	bd dr	na	ok	na	na
-	bd ju	na	ok	na	na

8 SUMMARY OF THE RESULTS

The columns represent the studied species. N.B. For some species a reduced number of models were run since data was not informative enough. Ψ is the probability of site occupancy. ϵ is the extinction probability. γ is the colonisation probability. p is the detection probability. The words in brackets indicate the predictor variables included in the model (see Table 2). “(.)” indicates a constant estimate (independent of any factors). The “Visit Model” is illustrated in Table 3 and explained in the text. Number of deficient model outputs: number of model which did not converge properly.

	<i>B. calamita</i>	<i>R. temporaria</i>	<i>T. alpestris</i>	<i>T. helveticus</i>
Best model	Ψ (former occurrence, Bd, diurnal range) ϵ (gravel pit) γ (.) p (Visit Model)	Ψ (former occurrence) ϵ (pond type) γ (.) p (Visit Model)	Ψ (former occurrence, Bd, altitude) ϵ (.) γ (.) p (Visit Model)	Ψ (former occurrence) ϵ (Bd, temperature) γ (.) p (Visit Model)
Number of compared models	143	154	65	143
Number of adequate model outputs	123	121	33	143
Number of deficient model outputs	20	33	32	0

10 COMPARISON OF THE FOUR DETECTION PROBABILITY MODELS

Design matrixes for the models are shown in Table 4. w is the Akaike weight. Δ AIC is the difference in the AIC value between the given model and the model with the lowest AIC value. # p is the number of model parameters. LogLike is the maximum value on the loglikelihood function. AIC values are calculated as follows:

$$AIC = 2 \cdot \# p - 2 \cdot \text{LogLike}$$

	# p	<i>B. calamita</i>				<i>T. alpestris</i>			
		AIC	Δ AIC	w	-2· LogLike	AIC	Δ AIC	w	-2· LogLike
Visit Model	11	216.58	0.00	0.888	194.6	582.22	0.00	1.000	560.2
Calendar date Model	6	221.18	4.60	0.089	209.2	614.61	32.39	0.000	602.6
Year Model	6	224.09	7.51	0.021	212.1	613.73	31.51	0.000	601.7
Constant Model	5	228.72	12.14	0.002	218.7	617.08	34.86	0.000	607.1

	# p	<i>T. helveticus</i>				<i>R. temporaria*</i>			
		AIC	Δ AIC	w	-2· LogLike	AIC	Δ AIC	w	-2· LogLike
Visit Model	11	496.1	0.00	0.893	474.2	558.3	0.00	0.951	536.4
		6				8			
Calendar date Model	6	500.4	4.29	0.105	488.4	564.3	5.94	0.049	552.3
		5				2			
Year Model	6*	510.7	14.54	0.001	498.7	617.2	58.85	0.000	609.2
		0				3			
Constant Model	5*	508.9	12.80	0.002	499.0	618.5	60.13	0.000	612.5
		6				1			

**R. temporaria*: The Year Model contains only 4 and the constant model only 3 parameters, because the model converged only with parameter fixations.