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CONSERVATION BIOLOGY OF AMPHIBIANS

## Assessing the success of ponds created for amphibian conservation



**Master Thesis** submitted by Stéphanie Vuichard<sup>1</sup> in 2015

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## Abstract

The aim of this thesis was to assess the success of a conservation project, aimed to support local amphibian populations by providing suitable breeding habitats in Emmental, Switzerland. I evaluated the effects of different factors on occupancy probability and abundance of all amphibian species in the breeding ponds in 2015, as well as on colonisation and extinction probabilities between 2010 and 2015. Factors were measured on the aquatic level (i.e. pond level), terrestrial level and level of meta-population. Ponds were visited three to seven times a season. I used multi-season and single-season occupancy models and binomial mixture models to estimate abundance. All models corrected for imperfect species detectability. Model selection was used to rank potential models for their power to explain the data. Five species were surveyed: midwife toad (*Alytes obstetricans*), common toad (*Bufo bufo*), common frog (*Rana temporaria*), alpine newt (*Ichthyosaura alpestris*) and palmate newt (*Lissotriton helveticus*). The alpine newt and common frog colonised over 90% of the 36 ponds surveyed, common toad and palmate newt around 50% and midwife toad over a third. On the aquatic level, abundance of some amphibian species was affected by pond size (negative effect on both newts, positive effect on common frog), steepness of the shoreline (negative effect on common frog, positive effect on palmate newt), water temperature (negative effect on both newts and common frog), water conductivity (positive effect on common frog and palmate newt), and predation risk (negative effect on alpine newt, positive effect on common frog and palmate newt). On the terrestrial level, solar exposure of the breeding ponds had effects only on the abundance of all species but the common toad: positive effects for midwife toad and palmate newt, negative effects for common frog and alpine newt. The degree of forestation in a 100m surrounding had a positive effect on the colonisation probability of the midwife toad. Quality of the terrestrial habitat, which was only tested for the midwife toad, had a positive effect on abundance, occupancy and colonisation probabilities of the midwife toad. In a 1'000m surrounding, forestation, the development of settlements, water surface and stone area had no effect on none of the surveyed species. On a meta-population level, the age of a pond had a positive effect on the abundance of the midwife toad and the common frog. Connectivity to other occupied ponds had a positive effect on occupancy probability of the palmate newt and a positive effect on abundance of both newts, but a negative effect on abundance of the common frog. The fact that a species demonstrably reproduced as well as the high abundance of a species in 2010 had no effect on its extinction probability between 2010 and 2015. No factor on water level increased the probability that the midwife toad occupied a pond, but terrestrial habitat and meta-population levels did. For the common toad, no site preferences could be found. These results show that amphibian

species have clearly different preferences on their habitat. There is not one model pond that suits all amphibian species together, pond creation need to be tailored to particular needs of single species. This re-emphasizes the importance of high variability of ponds and their surroundings for amphibian conservation projects, if the target is high amphibian species richness. Results showed often not what was expected from the literature. Some variables had even a contrary effect, but it needs to be considered that studies are difficult to compare as methods and side effects can vary from one survey to the other.

**Keywords:**

Amphibian conservation, *Alytes obstetricans*, *Bufo bufo*, *Rana temporaria*, *Ichthyosaura alpestris*, *Lissotriton helveticus*, multi-season and single-season occupancy model, N-mixture model, abundance, AIC-based model selection, water level, terrestrial level, meta-population level

**Abbreviations:**

- MWT: midwife toad (*Alytes obstetricans*)
- CT: common toad (*Bufo bufo*)
- CF: common frog (*Rana temporaria*)
- AN: alpine newt (*Ichthyosaura alpestris*)
- PN: palmate newt (*Lissotriton helveticus*)

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# 1 Introduction

Assessing the success of conservation action is rarely done in a scientific way. Conservation projects are often not monitored in a scientifically sound way and without replication. This leads to decisions in practical conservation that are rather based on personally gained experience or anecdotal sources rather than evidence-based. It is not always clear, which conservation actions resulted from scientifically sound experiments and which arose just from a single experience or even a simple assumption. Not properly evaluated methods can lead to a wrong dogma. In worst case, conservation work could even have detrimental effects to nature. Hence, more evidence-based studies for conservation are needed (Sutherland, et al., 2004).

A common species conservation action is building new ponds for amphibians (Baillie, et al., 2004). It got important because amphibians are the most threatened vertebrate group on earth (Stuart, et al., 2004). They are endangered due to multiple reasons. However, a major reason is habitat destruction (Beebee & Griffiths, 2005; Collins & Storer, 2003). For example in Swiss lowlands, 90% of wetlands got drained in the last 150 years and destroyed important habitat for pond-breeding amphibians (Hintermann, 1992). Therefore, a relatively simple but crucial way to counteract amphibian decline seems to be the construction of new ponds with suitable terrestrial habitats around. But how successful are these pond-creating conservation actions? Are ponds and natural surroundings sufficient to stop the decline of amphibians?

## 1.1 Aim and research questions

My Master thesis aims to evaluate an extensive amphibian conservation project in a scientific way. This conservation project was mainly implemented for the midwife toad (*Alytes obstetricans*) in Emmental, Canton of Berne, Switzerland. For the same study area, a similar study was already done by Kröpfl (2011) in 2010. She looked at occupancy and abundance of amphibian species in the new created ponds, evaluated the success for the midwife toad and examined different factors influencing its population. Using her data enabled me to evaluate not only colonisation and abundance in 2015 but also the changes, i.e. colonisations and extinctions, between 2010 and 2015. To know the factors that influence colonisation and extinction helps to better understand meta-population dynamics of amphibians. As a further step, conservation can better prevent extinction and forward colonisation. I assessed if all amphibian species profited from the conservation work in the same way. Thus, I did not only look at population dynamics of a single species but on the five species regularly occurring in these new ponds: midwife toad (*Alytes obstetricans*),

common toad (*Bufo bufo*), common frog (*Rana temporaria*), alpine newt (*Ichthyosaura alpestris*) and palmate newt (*Lissotriton helveticus*).

The pond creation project in Emmental will be evaluated by analysing different factors and their influence on amphibian populations. Factors influencing populations may vary from species to species (Hazell, et al., 2001). Thus, aim was to find out which factors were successful for which amphibian species. Finding the right factors is not easy, due to the complex life cycle of amphibians with an aquatic larval stage and a semi-aquatic adult stage. Semlitsch (2002) mentioned three levels that influence colonisation: aquatic level (i.e. pond level), terrestrial level around the pond and level of meta-population. Most factors I measured were on aquatic level, as it is the place where reproduction occurs and therefore crucial. For the terrestrial level, only solar exposition and for the midwife toad the quality and structures of the terrestrial habitat were measured, because this species seems to have more specific requirements on its terrestrial habitat (Grossenbacher, 1988; Mermod, et al., 2010). Additionally, I could use measured factors by Kröpfli (2011) in 2010 including variables describing land use at large spatial scales, to assess changes between 2010 and 2015. For the level of meta-population, I looked at the connectivity to other occupied ponds, age of ponds and for extinction probability I included abundance and occurrence of reproduction of a species in 2010.

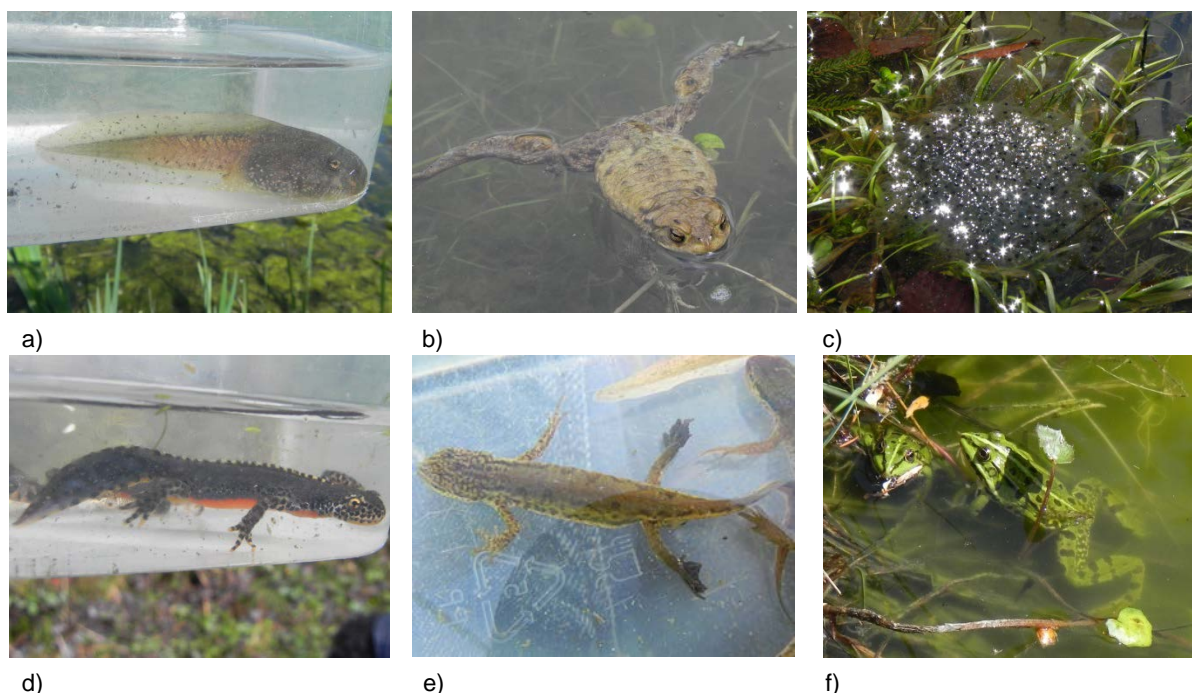
I examined the different factors by evaluating if they had positive, negative or no effects on each study species. Often, it is not just one factor that is the most important but their combination and interactions (Semlitsch, 2002; Van Buskirk, 2005). Thus, I tested also models with more than one factor and searched for the model that explained population dynamics best for each species separately.

The aim of this thesis was to find out whether all amphibian species profit from conservation projects equally or if it needs to be tailored to particular needs of single species. What factors influence which species populations in what way? In the end, I tried to give some scientifically investigated advices for conservation work, how to build ponds to have a higher chance they get occupied by amphibians.

## 2 Material and methods

### 2.1 Study species

Six amphibian species can be found in ponds in the study area (Figure 1). The endangered midwife toad (MWT) *Alytes obstetricans* (Laurenti, 1768) breeds in permanent ponds that offer refuges for the tadpoles. Other ponds characteristics seem to be not important. The requirements on the terrestrial habitat of this species seem to be more specific or the habitat of adults may be simply known better than the ones for the tadpoles. MWTs like terrestrial habitats with stony structures, sun exposure, sandy grounds and steep slopes lacking vegetation. They breed up to three times in spring and early summer time. Tadpoles often hibernate and can survive in frosty ponds (Grossenbacher, 1988; Ryser, et al., 2003). The common toad (CT) *Bufo bufo* (Linnaeus, 1758) is an early spawner who disappears again after a few days. Their tadpoles are often in permanent, sunny, big and deep waters. Adult CTs prefer forest area but can also be found in agricultural or urban areas with natural elements. The common frog (CF) *Rana temporaria* (Linnaeus, 1758) has the same spawning rhythm as CT and can only be seen in ponds for a



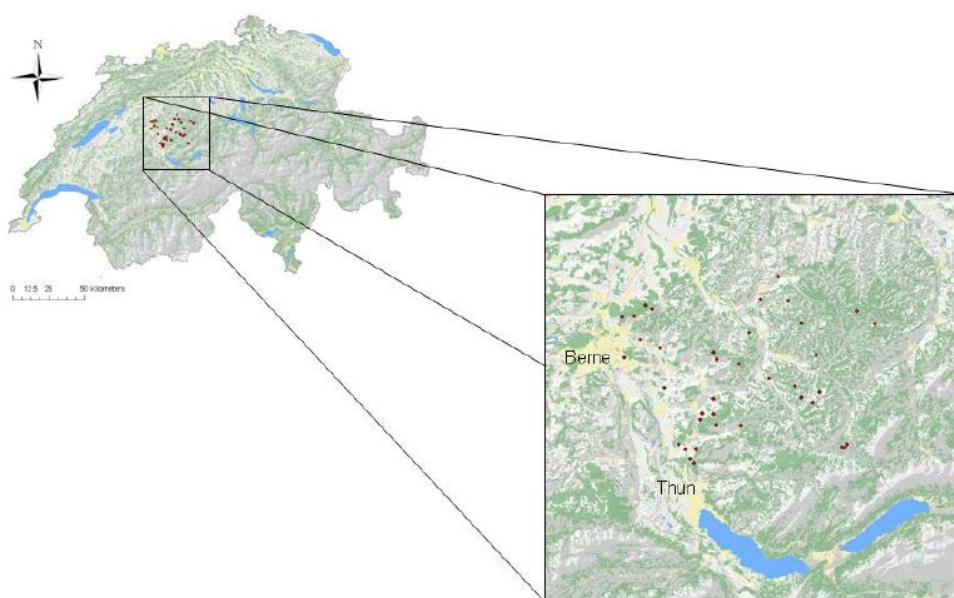
**Figure 1:** There are six amphibian species that occur in the survey ponds. a) Midwife toads (MWT) *Alytes obstetricans* were mostly found as tadpoles in this study. b) Common toads (CT) *Bufo bufo* were detected equally as adults and spawn strings. c) Common frogs (CF) *Rana temporaria* were mostly detected as spawn mass. d) Alpine newts (AP) *Ichthyosaura alpestris* were mostly detected as adults. e) Palmate Newt (PM) *Lissotriton helveticus* were also mostly detected as adults. f) Green frog complex (*Pelophylax* sp.) were not often found but always as adults.



few days. The CF occurs nearly across whole Switzerland. It occurs also in quite shady and small ponds. It only avoids really dry or intense and monotonous landscapes. However, it can rapidly colonise artificial ponds. The alpine newt (AN) *Ichthyosaura alpestris* (Laurenti, 1768) is wide spread on the northern side of the Alps. ANs occur in all kind of water ponds from small pools to lakeshores and in artificial ponds. It only avoids ponds inhabited by fish. The palmate newt (PM) *Lissotriton helveticus* (Razoumowsky, 1789) prefers smaller ponds than the AN. The PN often occurs in shady woodlands or low-moor bog but rarely in urban area. It also avoids ponds inhabited by fish. PN and AN both move to the ponds in early spring, but stay in the ponds at least till early summer in May or June. Members of the green frog complex (*Pelophylax sp.*) are a rare sight in Emmental. And it is nearly impossible to identify the native species in the field. Therefore, green frogs were excluded from data collection during field surveys (Grossenbacher, 1988; Meyer, et al., 2009).

## 2.2 Study area

The Emmental pond creation project (EPCP) in the Canton of Berne, Switzerland, aims to maintain the resident populations of endangered amphibians, mainly the midwife toad. To offer new breeding sites to local amphibians, new ponds were constructed in locations, where there were no ponds before (Beatrice Lüscher, pers. comm.). The EPCP can be seen as a natural experiment on colonisation patterns of pond-breeding amphibians. Emmental is a hilly countryside mainly with forest area and agriculture land. There are a lot of single farm houses outside the villages (Ryser, et al., 2003).



**Figure 2:** Spatial arrangement of study ponds in the Bernese Emmental. The distance between Berne and Thun is approximately 30 km. Map: Kröpfl (2011)

There has already been a survey on factors influencing colonisation by the midwife toad (Kröpfli, 2011). Choosing the same study design as Kröpfli enables me to compare and jointly analyse her field data from 2010 with my data from 2015. This way, I may trace back the colonisation speed and patterns of amphibian species. Kröpfli looked at 38 ponds that were built between 1985 and 2009 (Figure 2). Two ponds needed to be delisted in 2015, because one totally dried out and for the other one, we were not allowed to visit the pond any more at the owner's request. Hence, I looked at 36 ponds.

### 2.3 Sampling design and data collection

Field work was done with my fellow master student Aaron Pereira from 25<sup>th</sup> of March to 26<sup>th</sup> of June 2015. Ponds were visited in a clustered way, so that we had to drive as few as possible. We started with ponds in the lower altitude from east to west and then ponds in higher altitude.

Imperfect detection is crucial to account for, as not doing it can result in “false absence”, biased estimators and spurious conclusions (e.g. Bailey & Adams, 2005; Kéry & Schmidt, 2008; Mazerolle, et al., 2007). Therefore, each site needed to be surveyed repeatedly. It is not necessary that all ponds are visited equal times. Detection probability of a species may vary among sites due to survey characteristics (e.g. different weather conditions) or site characteristics (e.g. different habitat structures as refuges). Therefore, observation covariates and the two site covariate pond size and water depth were used to model detection probability.

All equipment was disinfected with Virkon S (Antec International – a DuPont Company) after every visit to avoid the spread of the amphibian pathogen *Bd* and other pathogens (Schmidt, et al., 2009).

#### 2.3.1 Amphibian survey

We recorded two response variables: 1) Detection / non-detection of every amphibian species in each pond. 2) Abundance of tadpoles of MWTs, adult ANs and PNs by dip-netting, adult CTs by sight and egg clutches of the CF by sight (Dodd Jr., 2009).

Ponds were first visited in the beginning of the amphibian season between end of March and end of April to detect the early spawners CF and CT, which leave ponds again after a few days. We counted the number of egg clutches of the CF. One female CF lays one egg clutch. Thus, abundance of females can be concluded. For CTs, we recorded detection / non-detection of spawn string and abundance of seen adults. Depending on the size of the pond, we took between four and ten sweeps with a dip-net (24cm wide) to record the

number of MWT tadpoles and adults of AN and PN. Some sites have more than one pond, thus could have a total of more than 10 sweeps per site.

In the second part of field work, ponds were visited two or more times from beginning of May till end of June to improve detection / non-detection probability especially for MWT, AN and PN. We dip-netted until we caught twenty ANs and twenty tadpoles of MWT or for maximum 1.25 hour. We used two dip-nets, of which one had a bigger net to improve chance of catching something. Again, we recorded the number of MWT tadpoles and adults of the two newts.

During the whole field work, we recorded detection / non-detection of *Pelophylax sp* to know the distribution of all amphibian species occurring in the study site and to submit the data to CSCF (Swiss centre for the cartography of the fauna).

If we were not able to detect any MWTs during the daytime visits, we visited the sites once at night between the 27<sup>th</sup> of May and 22<sup>nd</sup> of June. MWTs are more active at night. Calling males can be detected acoustically and they may be found easier by sight as they come more likely out of their hiding places at night. Night time visits started at dusk and did not last longer than 01:40 am. We surveyed the sites for 20 minutes and recorded the number of calling males and seen adults (Dodd Jr., 2009). At sites, where the noise of a stream made it hard to hear calling adults, we stayed up to 30 minutes.

### 2.3.2 Observation covariates

For every visit, we recorded following explanatory variables to model detection probability:

- No. of sweeps: How many sweeps per visit we took or how long we were dip-netting for. I rated one hour of dip-netting equally to 180 sweeps.
- Date: Which day of year we were at the pond.
- Time: Day time, when we started dip-netting.
- Weather: If it was (partly) rainy, (partly) cloudy or sunny during day time visits or if it was at night. Sights were only visited at night, when it was not raining.
- Method: If we were dip-netting and searching by sight or listening during the night time visit.
- Difficulty dip-netting: For every pond, we assessed over three levels how difficult it was to dip-net: easy (mainly mud on the pond ground), medium (plants like reeds in the way or some stones on the bottom of the pond) or difficult (a lot of stones on the bottom of the pond where amphibians can hide and not get caught by our dip-nets).

### 2.3.3 Site covariates

Nine explanatory variables to model occupancy and abundance of amphibian species were measured. Variables for aquatic habitat and terrestrial habitat were measured between mid of May and end of June 2015. Level of metapopulation were examined by calculating the connectivity of ponds:

- **pond size:** Pond size seems to be an important factor determining habitat choice of different amphibians. Parris (2006) found an increase in amphibian species richness with increasing pond size. On the other hand, Porej & Hetherington (2005) found no effect of pond size on amphibian species richness. Indermaur, et al. (2010) found out that CT and CF prefer bigger ponds. The importance of pond size for occupancy of amphibians could lay in their differential productivity. However, PNs seem to prefer smaller ponds, whereas the MWT and AN seem to have no preference (Grossenbacher, 1988). The hypothesis is that the effect of pond size on occupancy and abundance is species specific, positive for CT and CF, negative for PN and non-effective for AN and MWT. We determined pond area [m<sup>2</sup>] by multiplying the length and width of the pond measured in the field.
- **water depth:** Some species prefer shallow ponds, others even the opposite (Indermaur, et al., 2010). However, the study of Porej & Hetherington (2005) shows a strong positive effect of shallow littoral zones on amphibian species richness. A shallow pond heats up much faster than a deep one. MWT and AN seem to have no preference, as they can also occur in colder ponds (Grossenbacher, 1988). It seems to be species specific. The hypothesis is similar as for pond size but maybe less distinct: Deeper ponds have a positive effect on occupancy and abundance of CT and CF whereas PN prefers shallow ones and MWT and AN do not have any preference. Water depth [m] was measured at a distance of one meter from the shore. I took the mean of four measurements per pond.
- **water temperature:** In the study of Indermaur et al. (2010) toads preferably used warmer ponds whereas frogs selected ponds independently from temperature. For tadpoles of MWTs, water temperature of 22 to 25° C is favoured, which is less than other amphibian species prefer (Meyer, et al., 2009). This indicates that water temperature can be an influencing factor for occupancy and abundance of amphibian species. PN prefer shadier ponds than AN (Grossenbacher, 1988). Pond shading has a negative influence on water temperature (Hamer & Parris, 2011), thus PN may prefer colder ponds. The hypothesis is that warmer ponds have a positive effect on occupancy and abundance of CTs and a negative effect on PN. However, CF, AN and MWT seem to have no preference. We measured water

temperature [C°] using temperature loggers (HOBO 8K Pendant® Temperature/Alarm (Waterproof) Data Logger Part # UA-001-08). We put one logger per site at a water depth of 25 cm. However, depth fluctuated due to sinking water levels during warm periods. Temperature was measured every half hour. The loggers were set in place between 12<sup>th</sup> of May and 26<sup>th</sup> of June and stayed in the water for one to three weeks. For each pond, we then calculated the mean of the water temperature during one week that was closest to the mean date of water temperature measuring, the 6<sup>th</sup> of June 2015. Unusual temperature fluctuations due to possible water level change were excluded.

- **conductivity:** Conductivity measures the amount of ions dissolved in the water. It positively correlates with concentrations of P, NO<sup>3-</sup>, NH<sup>4+</sup> and can be used as an indicator for eutrophication (Zampella, 1994). Fertiliser is known to harm amphibians (Beebee & Griffiths, 2005). Thus, high conductivity can have negative effects on amphibian species (Stumpel & van der Voet, 1998; Hamer & Parris, 2011). I evaluated the hypotheses that higher conductivity in a pond has a negative effect on occupancy and abundance of all five study species. I cannot make more precise prognoses for each species. Conductivity [ $\mu$ S/cm] was measured at a depth of 25cm using the conductivity meter CONSORT K511. I took the mean of four measurements per pond.
- **predation:** Invertebrate predators can have an influence on occupancy and abundance of amphibian species. Some few species as AN and CT occur more likely in ponds with high predation risk, whereas other species are negatively effected by predation (Indermaur, et al., 2010; Van Buskirk, 2005). My hypotheses is that predation risk has a negative effect on occupancy and abundance of MWT, CF and PN, whereas AN and CT are even effected slightly positive. To estimate predation risk, we counted larvae and adults of the great diving beetle (*Dytiscus marginalis*, Linnaeus, 1758) that we caught during the whole dip-netting season. Additionally, we dip-netted each pond once using four to ten sweeps per pond and recorded the number of caught dragonfly larvae of the genus *Anax sp.* and *Aeshna sp.* that were longer than 3cm. Then, we calculated the average number of caught predators per sweep as a factor for predation density.
- **solar exposition:** In the study of Van Buskirk (2005), anurans are more frequently present in sunny ponds, whereas newts prefer woodland ponds. The hypothesis is that sunny ponds have a positive effect on occupancy and abundance of CF and especially of CT, because toads also prefer warmer ponds, which is linked with solar exposition. On the other hand, sunny ponds have a negative effect on AN and especially on PN. Again, tadpoles of MWTs seem to have no preference.

However, adults are said to prefer sunny habitats. Meaning that chance is higher that adults come to spawn. Thus, solar exposition has a positive effect on occupancy and abundance of MWT. I measured solar exposition using a spherical densitometer that gives the percentage of sun reaching the ground. I took the mean of solar expositions at the north, east, south and west side of the pond.

- **terrestrial habitat:** Terrestrial habitat is said to be important especially for MWTs (Grossenbacher, 1988; Mermod, et al., 2010). The other four study species may not as strong influenced by it as the MWT. Thus, I tested if terrestrial habitat has a positive effect on MWTs, but did not test the influence on the other study species. Ryser, et al. (2003) found various terrestrial habitat structures that were used by MWTs in Emmental: loose substrate, slopes, natural hollows in the ground like mouse holes, artificial stone walls, flagstones or cellars, or wood piles. It didn't seem that some structures were preferred. That is why we did not look at what specifically kinds of structure MWT occurred but how many different types of structures were around. We recorded the presence and kind of structure types occurring within an area up to 50 meters away from the shore of the pond. The six structures we were looking for were: dry stone wall, stone heaps, open rock / gravel, slopes with open soils, garden with suitable microhabitat and wood heaps (Appendix A). No matter how big a structure was, we noted 1 for each structure type found and 0 for nothing found. Thus, six is the biggest number a site could get.
- **pond age:** The age of a pond can be an important factor for colonisation. The colonising speed of amphibians is different among species. Some species are quick colonisers while others are slow, which indicates an optimum pond age regarding species diversity (Stumpel & van der Voet, 1998). MWTs are said to be bad colonisers (Laan & Verboom, 1990), which need 1-5 years till a pond gets colonised (Ryser, et al., 2003). Thus, age could have a positive effect on occupancy and abundance of MWT. The other four study species may be faster colonisers, so that pond age has less or even no influence on their occupancy and abundance. Construction years and thus age of the surveyed ponds are known.
- **connectivity:** Persistence of populations in a metapopulation depends on their isolation. Isolation refers to distances to other possible source populations. Isolation has a negative effect on occupancy of species (Hanski, 1999). However, bad colonisers as the MWT (Laan & Verboom, 1990) are more affected by isolation than others. The hypothesis is that connectivity (i.e. opposite of isolation) has a positive effect on occupancy and abundance of all study species, especially of the MWT. Demographic connectivity is a species-specific measure. I calculated the distances to the next occupied ponds including a factor of relative migration distance

of 500m (Prugh, 2009). 500m is a default number as migration distances of species is not known very well but 1km could already be a too long distance (Laan & Verboom, 1990). I considered only those ponds, where a certain species was detected no longer than ten years ago. Data of all ponds in the study area with a list when which species was detected the last time at a certain site was kindly provided by CSCF (Swiss centre for the cartography of the fauna).

Various other explanatory variables were discussed which are said to have an influence on amphibian occurrence, for example refuges for tadpoles, or water chemistry like pH, NO<sub>x</sub> or chlorophyll. However, it was not possible to measure all variables as water chemistry fluctuates too much to measure it in a simple way that was feasible in this time period. Additionally, we concentrated on the variables that seem to have strong arguments in literature.

#### **2.3.4 Covariates for multi-season survey**

The site covariates explained above were used to estimate occupancy and abundance probability of one season in 2015. To examine dynamics in meta-population, more than one season has to be considered. Thus, I combined my data with those from 2010 by Kröpfli (2011) to analyse if there were any changes between 2010 and 2015 and which variables influenced it. I only used variables that were measured in 2010 by Kröpfli (2011). The following variables were considered: pond size, water depth, age, forest area within 100m surrounding, and for landscape scale: forest, stone, water and settlement area within 1'000m surrounding. Landscape influence is supposed to be important for several amphibian species (Van Buskirk, 2005). Furthermore, for every study species, I used their abundance and their presence-absence of reproduction in 2010 as site covariates. For the MWT, connectivity in 2010 and habitat quality within 100m surrounding (i.e. is there good habitat yes/no) was included as well. As observation covariate, I could use the two variables, year (2010 or 2015) which in this case is the same as observer, and if observation was done during day or night time.

I expected that the effect of pond size, water depth and age on the species will be the same as for the single-season occupancy probability. In addition, age may have a positive effect on colonisation probability for the bad coloniser MWT, but less or no positive effect on the other study species. I expect that habitat quality will affect occupancy and colonisation probability of MWT positively, because the terrestrial habitat is important for adult MWTs (Ryser, et al., 2003). Hypothesis is that forest area within a radius of 100m has no effect at all on all study species (Porej & Hetherington, 2005). However, forest area within a surrounding of 1'000m can have positive or negative influences on species. It has more

permeability and a low road density, which may help dispersing individuals. CF and AN occur more frequently and in higher abundance in forested area. In contrast, other species were found in lower densities in ponds in forested landscape (Van Buskirk, 2005). PN and CT are also more likely in forested area (Grossenbacher, 1988). Thus, I expected forest area within a 1'000m surrounding having a positive effect on occupancy and colonisation of AN, PN, CF and CT and no effect on extinction probability. However, forest coverage may have a negative effect on occupancy and especially on colonisation probability and maybe a positive effect on extinction probability for MWTs, as adults prefer sunny places and forest areas is said to be avoided (Grossenbacher, 1988). Another hypothesis is that settlement area has a negative influence on occupancy and colonisation and a positive influence on extinction probability for all study species, because amphibian richness negatively correlates with urbanisation and density of roads (Lehtinen, et al., 1999; Parris, 2006). Water surface was expected to have no effect on study species, as it depends on quality rather than quantity of water surface (Boyer & Grue, 1995). Stones are said to be important structures for adult MWT (Grossenbacher, 1988; Ryser, et al., 2003). The other study species seem to have no preference for stone structures. Thus, hypothesis is that occupancy and colonisation probability of MWT is positive affected by stone structures, but the other species are not affected by it. The abundance of a study species in 2010 was used to examine, if little population extinct more likely than bigger populations (Carlson & Edenhamn, 2000; Schmidt & Pellet, 2005). For abundance in 2010, I had the number of adults but never larvae or eggs of a species. For MWTs, the number of calling adults was recorded. Reproduction of the examined species in 2010 was used, to ask, if it is less likely a population get extinct, when there was reproduction in 2010. This assumption is derived from the source-sink theory and that reproduction occurs more likely where the habitat is suitable (Pulliam, 1988). Connectivity (data only available for MWT) was tested, if it helps against getting extinct and if it has a positive effect on occupancy and colonisation probability.

### 2.3.5 Summary of all site-covariates and their expected effects

Table 1 shows overview of all site-covariates and which covariate is expected to have an effect on which study species.

**Table 1:** Summary of all covariates tested and what effects were expected on occupancy, abundance, colonisation and extinction probability of all five study species.

⊕ : positive effect

⊕ : only a small positive effect

⊖ : negative effect

⊖ : only a small negative effect

X : no effect



Variable	MWT	CT	CF	AN	PN
<b>Occupancy <math>\Psi</math> 2015</b>					
pond size	X	+	+	X	-
water depth	X	+	+	X	-
water temperature	X	+	X	X	-
conductivity	- / -	- / -	- / -	- / -	- / -
predation	-	+	-	+	-
solar exposition	+	+	+	-	-
terrestrial habitat	+				
pond age	+	+ / X	+ / X	+ / X	+ / X
connectivity	+	+	+	+	+
<b>Abundance 2015</b>					
pond size	X	+	+	X	-
water depth	X	+	+	X	-
water temperature	X	+	X	X	-
conductivity	- / -	- / -	- / -	- / -	- / -
predation	-	+	-	+	-
solar exposition	+	+	+	-	-
terrestrial habitat	+				
pond age	+	+ / X	+ / X	+ / X	+ / X
connectivity	+	+	+	+	+
<b>Multi-season 2010 / 2015 – occupancy <math>\Psi</math></b>					
pond size	X	+	+	X	-
water depth	X	+	+	X	-
habitat 100m	+				
forest 100m	X	X	X	X	X
forest 1'000m	-	+	+	+	+
stone 1'000m	+	X	X	X	X
water 1'000m	X	X	X	X	X
settlement 1'000m	-	-	-	-	-
age	+	+ / X	+ / X	+ / X	+ / X
connectivity	+				
<b>Multi-season 2010 / 2015 – colonisation <math>\gamma</math></b>					
habitat 100m	+				
forest 100m	X	X	X	X	X

forest 1'000m	-	+	+	+	+
stone 1'000m	+	X	X	X	X
water 1'000m	X	X	X	X	X
settlement 1'000m	-	-	-	-	-
age	+	+ / X	+ / X	+ / X	+ / X
connectivity	+				
<b>Multi-season 2010 / 2015 – extinction <math>\epsilon</math></b>					
forest 100m	X	X	X	X	X
forest 1'000m	+	X	X	X	X
water 1'000m	X	X	X	X	X
settlement 1'000m	+	+	+	+	+
abundance	-	-	-	-	-
reproduction	-	-	-	-	-
connectivity	-				

## 2.4 Statistical analysis

Statistical analyses were done using R (R Core Team, 2015). I used the package unmarked by Fiske & Chandler (2011) for all models explained below. It is a common package used for population analysis that deals with imperfect detection of unmarked animals (Mazerolle, 2015). Numerical variables were mean-standardised before analysing. All models I used accounted for imperfect detection to correct occupancy and abundance probability.

### 2.4.1 Models used

The single-season site occupancy model developed by MacKenzie, et al. (2002) aims to estimate the true distribution of a species. I examined the occupancy probability ( $p$ ) of all survey species using detection / non-detection data from every visit. Observation covariates, which influence detection probability ( $p$ ) and site covariates, which influence occupancy probability ( $\psi$ ) of the surveyed species can be included in the model (Kéry, 2010; MacKenzie, et al., 2006).

The binomial mixture model, also called N-mixture model, by Royle (2004) estimates species abundance using count data. I examined the abundance of tadpoles of MWTs, adult ANs and PNs caught by dip-netting as well as adult CTs and egg clutches of the CF detected by sight. While site occupancy models refer only to presence-absence of populations, the N-mixture model estimates the number of individuals in populations. Thus, it can

model more precisely the current situation of a population, i.e. if a population is big or so small that it is threaten by extinction. It corrects imperfect detection from replicated counts instead of detection / non-detection data as the site-occupancy model does. The N-mixture model estimates the count  $y_{ij}$  at a site  $i$  during a survey  $j$ . The model assumes that there are biological processes (i.e. site covariates) which distribute animals among sites  $j$ . Thus, there is a site-specific abundance  $N_i$ . Like in the occupancy model, site and observations covariates can be included in the model (Kéry, 2010).

The two models described above are single-season models. To examine also colonisation ( $\gamma$ ) and extinction ( $\epsilon$ ) patterns, I used a second data set from 2010 by Kröpfli (2011). That is why I surveyed the same ponds as Kröpfli did. For this multi-season occupancy model, I used detection / non-detection data from 2010 by Kröpfli and from 2015 from my survey. For observation and site covariates, I used a different data set only with variables measured in 2010. This is because the state of 2010 is causing the population dynamics that happened until 2015. The multi-season site occupancy model by MacKenzie, et al. (2003) estimates probabilities of colonization ( $\gamma$ ) and local extinction ( $\epsilon$ ). It assesses detection probability ( $p$ ) and occupancy probability ( $\psi$ ), too. Site and observations covariates can be included in the model as in the single-season models (Fiske & Chandler, 2011; MacKenzie, et al., 2006).

#### **2.4.2 Model selection strategy**

All five study species were evaluated separately how they respond to explanatory variables. For each species, all three models (single- and multi-season occupancy and N-mixture model) were used. For each model in turn, I fitted a number of candidate-models that represent biological hypotheses. I compared the candidate-models using model selection, which is an alternative to null-hypothesis testing. The Akaike Information Criterion (AIC) compares the different models and computes the strength of evidence for each model. The model with the lowest AIC-value is considered the best of them (Burnham & Anderson, 1998). One needs to be careful, as the best AIC-value does not imply that this model is a good one. It is simply the best one of the chosen ones but it could still be a poor model in terms of explaining the data. To judge if a model is a good one or not, it helps to look at the estimate and confidence interval of the variable in the model; i.e. if zero is included in the 95% confidence interval, then there is too much uncertainty. Model selection helps certainly to deal with too many explanatory variables and determine the most suitable model. It needs to be considered, that a model with too few variables will get biased, but a model with too many variables will be less precise (Burnham, et al., 2011; Franklin, et al., 2001; Mazerolle, 2006).

Analysis was done stepwise. First, I only determined the factors that best explain detection probability. Then, I combined the best model for detection probability with several candidate-models for occupancy, abundance, colonisation or extinction (Burnham & Anderson, 2002).

As observation covariates for detection probability (Table 2), I tested the model of no variable and models with following variables separately: date, time, weather, method, pond size and water depth (described in chapter 2.3 Sampling design and data collection). The two variables No. of sweeps and difficulty dip-netting were only for MWT and newts, as CF and CT were mostly recorded by sight and not with a dip-net. For detection probability, no models with more than one variable were created. For the multi-season occupancy model, I tested three models: no variable, variable year (i.e. also observer) and variable day.night (i.e. if the visit was during day or night time).

**Table 2:** Models tested for detection probability ( $p$ ) for single-season occupancy model and N-mixture model. Variables were tested separately including the model without any variable. The model with the best AIC-value was then taken for further analysis.

Model	Comment
$p$ (.)	no variable
$p$ (no. sweeps)	only for MWT and newts
$p$ (date)	
$p$ (time )	
$p$ (weather)	
$p$ (method)	
$p$ (difficulty dip-net)	only for MWT and newts
$p$ (pond size )	
$p$ (water depth)	

For candidate-models examine occupancy or abundance probability (Table 3), I primarily tested simple models with one variable which support biological hypotheses. One model was the model of no variable and the other models tested had following variables separately: pond size, water depth, water temperature, solar exposition, conductivity, predation, pond age, connectivity and only for MWT the terrestrial habitat (described in chapter 2.3.3 Site covariates). In addition, one model had water temperature together with calendar week, when the water temperature was measured. The model, which had the best AIC-value, was then gradually getting more complex by adding one to two more models. It was added once with the second, once with the third, once with the fourth best model and once with the second and third best model together. If the model of no variable was the

second to fourth best model, it was excluded and the fifth best model with a variable was taken. Then, I examined again, if the AIC-value got lower (i.e. better) with the new, complex models. These complex models had never more than three variables to explain occupancy or abundance probability as too complex models are not precise either.

**Table 3:** Models tested for occupancy probability ( $\Psi$ ) in single-season occupancy model and N-mixture model. All models include the best model for detection probability ( $p$ ), tested before. Step 1: The model of no variable, nine models with one variable and one model with the two variables water temperature and its calendar week were tested. Step 2: The model with the best AIC-value was tested including the model with the second, respectively third or fourth best model (exclusive the model of no variable) and one model with the best, second and third best model, thus a model with three variables.

Model	Comment
$\Psi$ (.)	step 1 (no variable)
$\Psi$ (pond size)	step 1
$\Psi$ (water depth)	step 1
$\Psi$ (water temperature)	step 1
$\Psi$ (water temperature + calendar week)	step 1
$\Psi$ (solar exposition)	step 1
$\Psi$ (conductivity)	step 1
$\Psi$ (predation)	step 1
$\Psi$ (pond age)	step 1
$\Psi$ (connectivity)	step 1
$\Psi$ (terrestrial habitat)	step 1 (only for MWT)
$\Psi$ (best variable + second best)	step 2: depending on results of step 1
$\Psi$ (best variable + third best)	step 2: depending on results of step 1
$\Psi$ (best variable + fourth best)	step 2: depending on results of step 1
$\Psi$ (best variable + second best + third best)	step 2: depending on results of step 1

For multi-season models examine occupancy ( $\psi$ ), colonisation ( $\gamma$ ), and extinction ( $\epsilon$ ) probabilities, I primarily tested simple models with one or no variable, too (Table 4). As I could only use those variables, that were measured in 2010 by Kröpfli (2011), there are other factors tested in multi-season models. There were ten variables: pond size, water depth, age, forest area (100 m surrounding), forest area (1'000m), stone area (1'000m), water area (1'000m) and settlement area (1'000m), abundance of examined species in 2010 and the presence-absence of reproduction of examined species in 2010. For the MWT, I had also the data for connectivity and habitat quality (100 m surrounding).

For pond size and water depth, there was only one model for  $\psi$ , because these two variables seem to have no influence on  $\gamma$  or  $\epsilon$ . The variables age, forest 100m, forest 1'000m, stone 1'000m, water 1'000m, settlement 1'000m and for MWT also habitat 100m and connectivity had each one model only for  $\psi$ , one only for  $\gamma$  and one for  $\psi + \gamma$ . These variables may have influence on occupancy as well as on colonisation probability. Additionally, the seven variables forest 100m, forest 1'000m, water 1'000m, settlement 1'000m, abundance, reproduction and connectivity (for MWT) had each a model only for  $\epsilon$ .

The model, which had the best AIC-value, was then gradually getting more complex by adding one to two more models. The best model was added once with the second best model, once with the third or rather fourth best model and once with the second and third best model. The model of no variable was not accounted for the second to fourth best model. Then, the AIC-values of the models were compared again.

**Table 4:** Models tested for occupancy ( $\Psi$ ), colonisation ( $\gamma$ ) and extinction ( $\epsilon$ ) probability for multi-season occupancy models. All models include the best model for detection probability ( $p$ ), tested before. Step 1: The model of no variable and simple models with one variable were tested. There were variables which were either used for  $\Psi$ ,  $\gamma$ ,  $\Psi + \gamma$ , or  $\epsilon$ . For MWT, additionally the variables connectivity and habitat quality were available. Step 2: The model with the best AIC-value was tested including the model with the second, respectively third or fourth best model (exclusive the model of no variable) and one model with the best, second and third best model.

Model	Comment
$\Psi$ (.), $\gamma$ (.), $\epsilon$ (.)	step 1 (no variable)
$\Psi$ (pond size), $\gamma$ (.), $\epsilon$ (.)	step 1
$\Psi$ (water depth), $\gamma$ (.), $\epsilon$ (.)	step 1
$\Psi$ (age), $\gamma$ (.), $\epsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (age), $\epsilon$ (.)	step 1
$\Psi$ (age), $\gamma$ (age), $\epsilon$ (.)	step 1
$\Psi$ (forest 100m), $\gamma$ (.), $\epsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (forest 100m), $\epsilon$ (.)	step 1
$\Psi$ (forest 100m), $\gamma$ (forest 100m), $\epsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (.), $\epsilon$ (forest 100m)	step 1
$\Psi$ (forest 1'000m), $\gamma$ (.), $\epsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (forest 1'000m), $\epsilon$ (.)	step 1
$\Psi$ (forest 1'000m), $\gamma$ (forest 1'000m), $\epsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (.), $\epsilon$ (forest 1'000m)	step 1
$\Psi$ (stone 1'000m), $\gamma$ (.), $\epsilon$ (.)	step 1

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$\Psi$ (.), $\gamma$ (stone 1'000m), $\varepsilon$ (.)	step 1
$\Psi$ (stone 1'000m), $\gamma$ (stone 1'000m), $\varepsilon$ (.)	step 1
$\Psi$ (water 1'000m), $\gamma$ (.), $\varepsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (water 1'000m), $\varepsilon$ (.)	step 1
$\Psi$ (water 1'000m), $\gamma$ (water 1'000m), $\varepsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (.), $\varepsilon$ (water 1'000m)	step 1
$\Psi$ (settlement 1'000m), $\gamma$ (.), $\varepsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (settlement 1'000m), $\varepsilon$ (.)	step 1
$\Psi$ (settlement 1'000m), $\gamma$ (settlement 1'000m), $\varepsilon$ (.)	step 1
$\Psi$ (.), $\gamma$ (.), $\varepsilon$ (settlement 1'000m)	step 1
$\Psi$ (.), $\gamma$ (.), $\varepsilon$ (abundance)	step 1
$\Psi$ (.), $\gamma$ (.), $\varepsilon$ (reproduction)	step 1
$\Psi$ (habitat 100m), $\gamma$ (.), $\varepsilon$ (.)	step 1 (only for MWT)
$\Psi$ (.), $\gamma$ (habitat 100m), $\varepsilon$ (.)	step 1 (only for MWT)
$\Psi$ (habitat 100m), $\gamma$ (habitat 100m), $\varepsilon$ (.)	step 1 (only for MWT)
$\Psi$ (connectivity), $\gamma$ (.), $\varepsilon$ (.)	step 1 (only for MWT)
$\Psi$ (.), $\gamma$ (connectivity), $\varepsilon$ (.)	step 1 (only for MWT)
$\Psi$ (connectivity), $\gamma$ (connectivity), $\varepsilon$ (.)	step 1 (only for MWT)
$\Psi$ (.), $\gamma$ (.), $\varepsilon$ (connectivity)	step 1 (only for MWT)
best model + second best model	step 2: depending on results of step 1
best model + third best model	step 2: depending on results of step 1
best model + fourth best model	step 2: depending on results of step 1
best model + second best model + third best model	step 2: depending on results of step 1

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### 3 Results

36 ponds were visited during field work. For the multi-season site occupancy model only 35 ponds were compared, as one pond had wrong coordinates in 2010. On average, ponds were visited 4.86 times (range 3 to 7 visits) in 2015. All models and their AIC values are found in the appendix B.

The symbols in Table 5 to Table 26 mean following:

- AIC: Akaike's Information Criterion
- delta: Difference between the AIC of the model and AIC of the highest ranked model
- AICwt: Akaike weight: Chance of being the best model among all tested ones. All AICwt added together gives 1.00
- cumltvWt: cumulated Akaike weight (cumltvWt of next better model + AICwt of model)
- $p$ : detection probability
- $\Psi$ : occupancy probability
- $\gamma$ : colonisation probability
- $\varepsilon$ : extinction probability

#### 3.1 Midwife toad

##### Pond occupancy in 2015

We detected MWTs at 13 sites. This gives a naïve site occupancy (i.e. without considering detection probability) of 36.1%. The highest ranked model for detection probability included no. of sweeps taken (Table 5). It had an average detection probability of 39.8%  $\pm$  7.6%. The average occupancy probability corrected for detection probability with the model  $p(\text{no.sweeps}) \Psi(\cdot)$  was 39.2%  $\pm$  8.9%.

**Table 5:** Two models for detection probability of occupancy of MWT had delta AIC value < 3.00.

model	AIC	delta	AICwt	cumltvWt
$p(\text{no. sweeps}) \Psi(\cdot)$	124.42	0.00	0.6430	0.64
$p(\text{date}) \Psi(\cdot)$	125.91	1.49	0.3058	0.95

The model for occupancy in 2015 with the lowest AIC value (i.e. the best among the tested ones) was the one including solar exposition as site-covariate (Table 6). It was the only model that had a lower AIC value than the model of no variable, but the estimate of the



regression coefficient for the effect of solar exposition in the best models was imprecise, and the 95% confidence interval for the regression coefficients included 0. Estimates of regression coefficients for all explanatory variables included 0 in their 95% confidence intervals.

**Table 6:** Fourteen models for occupancy probability of MWT had delta AIC value < 3.00. But only one model had lower AIC value than the model of no variable.

model	AIC	del ta	AICwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(\text{sol ar. exp})$	124.31	0.00	0.119	0.12
$p(\text{no. sweeps}) \Psi(.)$	124.42	0.11	0.112	0.23
$p(\text{no. sweeps}) \Psi(\text{age})$	124.71	0.40	0.097	0.33
$p(\text{no. sweeps}) \Psi(\text{sol ar. exp+depth})$	124.75	0.44	0.095	0.42
$p(\text{no. sweeps}) \Psi(\text{depth})$	124.86	0.55	0.090	0.51
$p(\text{no. sweeps}) \Psi(\text{sol ar. exp+age})$	125.12	0.81	0.079	0.59
$p(\text{no. sweeps}) \Psi(\text{sol ar. exp+si ze})$	125.67	1.36	0.060	0.65
$p(\text{no. sweeps}) \Psi(\text{si ze})$	125.84	1.53	0.055	0.71
$p(\text{no. sweeps}) \Psi(\text{connect})$	125.84	1.53	0.055	0.76
$p(\text{no. sweeps}) \Psi(\text{sol ar. exp+age+depth})$	125.94	1.63	0.052	0.81
$p(\text{no. sweeps}) \Psi(\text{conduct})$	126.33	2.02	0.043	0.86
$p(\text{no. sweeps}) \Psi(\text{terr. hab})$	126.39	2.08	0.042	0.90
$p(\text{no. sweeps}) \Psi(\text{water. temp})$	126.40	2.09	0.042	0.94
$p(\text{no. sweeps}) \Psi(\text{predator})$	126.42	2.11	0.041	0.98

### Abundance at occupied ponds in 2015

Ten sites (27.8%) had at least once a detection of MWT tadpoles (range 0 to 24 tadpoles per visit). The highest ranked model for detection probability included no. of sweeps taken (Table 7). It had an average detection probability of  $10.5\% \pm 1.7\%$ .

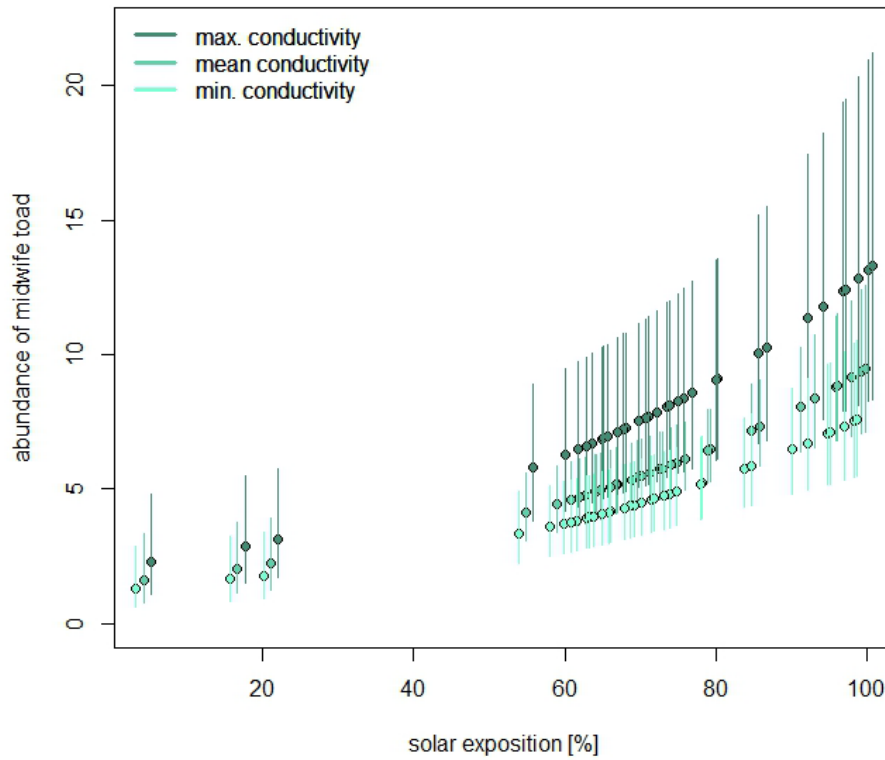
**Table 7:** One model for detection probability of abundance of MWT tadpoles had delta AIC value < 3.00.

model	AIC	del ta	AICwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(.)$	636.48	0.00	1.0	1.00

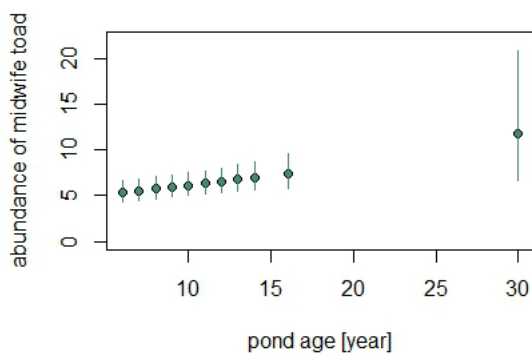
The highest ranked model for abundance of MWT tadpoles in 2015 included solar exposition and conductivity but there was uncertainty in model selection as several models had very similar AIC values, thus explained occupancy probability equally well (Table 8). In the best model (Figure 3), solar exposition had a positive effect on abundance (effect on the log scale:  $0.41 \pm 0.21$ ) as well as conductivity (effect on the log scale:  $0.154 \pm 0.152$  95% CI). Other than that, the two variables age (effect on the log scale:  $0.15 \pm 0.12$  95% CI, Figure 4) and the number of terrestrial habitat types (effect on the log scale:  $0.17 \pm 0.16$  95% CI, Figure 5) had positive effects on abundance of MWT tadpoles.

**Table 8:** Five models for abundance prediction of MWT tadpoles had delta AIC value < 3.00.

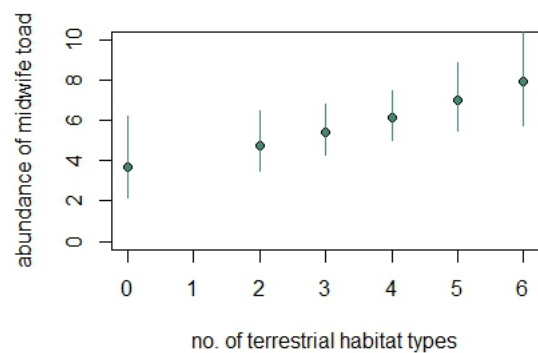
model	AIC	del ta	AICwt	cuml tvWt
$\rho(\text{no. sweeps}) \Psi(\text{sol ar. exp+conduct})$	621.89	0.000	0.27	0.27
$\rho(\text{no. sweeps}) \Psi(\text{sol ar. exp+age+terr. hab})$	621.92	0.024	0.27	0.54
$\rho(\text{no. sweeps}) \Psi(\text{sol ar. exp+age})$	621.93	0.034	0.27	0.81
$\rho(\text{no. sweeps}) \Psi(\text{sol ar. exp})$	623.88	1.991	0.1	0.91
$\rho(\text{no. sweeps}) \Psi(\text{sol ar. exp+terr. hab})$	624.10	2.204	0.09	1.00



**Figure 3:** The highest ranked model for abundance of MWT tadpoles was  $\rho(\text{no. sweeps}) \Psi(\text{solar exp} + \text{conduct})$ . In this model, solar exposition and conductivity had both a positive effect on abundance.



**Figure 4:** Pond age had a positive effect on abundance of MWT tadpoles.



**Figure 5:** The no. of terrestrial habitat types had a positive effect on abundance of MWT tadpoles.

### Pond occupancy, colonisation and extinction 2010 - 2015

16 of 35 sites (45.7%) had at least once a detection of MWT in 2010 or 2015. There were detections at 10 sites in 2010 (naïve occupancy probability: 27.8%) and at 13 sites in 2015 (naïve occupancy probability: 37.1%). At six sites, MWTs were detected in 2015 where no detection was made in 2010 (naïve colonisations probability of 24.0%). However, at three sites, we did not find any MWTs in 2015 where they were found in 2010 (naïve extinction probability of 30.0%). The highest ranked model for detection probability included the variable if it was a day or a night time visit (Table 9). It had an average detection probability of  $63.8\% \pm 6.0\%$ . Using this model  $\Psi(.) \gamma(.) \varepsilon(.) p(\text{day.night})$ , the average occupancy probability for 2010 was  $28.6\% \pm 7.7\%$  and for 2015  $38.8\% \pm 14.6\%$ , colonisation probability was  $24.4\% \pm 8.7\%$  and extinction probability was  $28.8\% \pm 14.7\%$ .

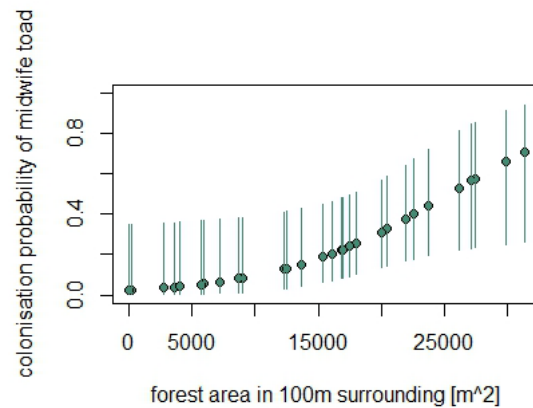
**Table 9:** For the MWT, one model for detection probability for multi-season models had delta AIC value < 3.00.

model	AIC del ta	AI Cwt	cuml tvWt
$\Psi(.) \gamma(.) \varepsilon(.) p(\text{day. ni ght})$	223. 64	0. 00	0. 99303

The highest ranked multi-season model for 2010 to 2015 included habitat quality in a 100m surrounding for occupancy and colonisation probability and the variable forest area in 100m surrounding for extinction probability (Table 10). Forest area had no certain effect on extinction probability in this model, as its 95% confidence interval included 0. For occupancy probability, habitat quality in a 100m surrounding had a positive effect (effect on the logit scale:  $2.54 \pm 1.84$  95% CI). Connectivity had no certain positive effect, as its 95% confidence interval included 0. However, if looking only at significance, it had a small significance of  $p < 0.1$ . For colonisation probability, habitat quality in a 100m surrounding (effect on the logit scale:  $4.59 \pm 3.16$  95% CI) and forest area in a 100m surrounding (effect on the logit scale:  $1.48 \pm 1.476$  95% CI, Figure 6) had a positive effect. Forest in a 1'000m surrounding had no certain positive effect, as its confidence interval included 0. However, if looking only at significance, it had a small significance of  $p < 0.1$ . For extinction probability, regression coefficients of all tested explanatory variables included 0 in the 95% confidence intervals. Because age had a slightly negative effect on colonisation probability, the model  $\Psi(\text{age} + \text{l}(\text{age}^2)) \gamma() \varepsilon() p(\text{day.night})$  was tested additionally to see if age has an optimum age for colonisation. However, there was still no effect.

**Table 10:** Only one model for multi-season predictions for the MWT had delta AIC value < 3.00.

model	AIC del ta	AI Cwt	cuml tvWt
$\Psi(\text{habi tat. 100m. 2010}) \gamma(\text{habi tat. 100m. 2010})$ $\varepsilon(\text{forest. 100m. 2010}) p(\text{day. ni ght})$	197. 81	0. 00	0. 95



**Figure 6:** Forest area in 100m surrounding had a positive effect on colonisation probability of the MWT.

### 3.2 Common toad

#### Pond occupancy in 2015

CTs were detected at 16 sites, giving a naïve occupancy probability of 44.4%. The highest ranked model for detection probability included weather (Table 11). It had an average detection probability of  $66.2\% \pm 4.8\%$ . The mean occupancy probability from the model  $p(\text{weather}) \Psi(\cdot)$  was  $54.1\% \pm 10.9\%$ .

**Table 11:** One model for detection probability of occupancy of CT had delta AIC value  $< 3.00$ .

model	AIC	del ta	AI Cwt	cuml tvWt
$p(\text{weather}) \Psi(\cdot)$	131.25	0.00	0.99	0.99

The highest ranked model for occupancy in 2015 included water temperature as site-covariate (Table 12). It was the only model that had a lower AIC value than the model of no variable, but the estimate of the regression coefficient for the effect of water temperature in the best model was imprecise, and the 95% confidence interval included 0. Estimates of regression coefficients for all explanatory variables included 0 in their 95% confidence intervals.

**Table 12:** Ten models for occupancy probability of CT had delta AIC value  $< 3.00$ . But only one model had lower AIC value than the model of no variable.

model	AIC	del ta	AI Cwt	cuml tvWt
$p(\text{method}) \Psi(\text{water. temp})$	131.23	0.000	0.14	0.14
$p(\text{weather}) \Psi(\cdot)$	131.25	0.015	0.14	0.28
$p(\text{weather}) \Psi(\text{depth})$	131.29	0.056	0.14	0.41
$p(\text{weather}) \Psi(\text{age})$	131.56	0.328	0.12	0.53
$p(\text{weather}) \Psi(\text{water. temp} + \text{CW})$	131.65	0.420	0.11	0.65

$p(\text{weather})\Psi(\text{size})$	131.67	0.439	0.11	0.76
$p(\text{weather})\Psi(\text{sol ar})$	132.70	1.466	0.067	0.83
$p(\text{weather})\Psi(\text{connect})$	132.85	1.623	0.062	0.89
$p(\text{weather})\Psi(\text{predator})$	132.99	1.757	0.058	0.95
$p(\text{weather})\Psi(\text{conduct})$	133.17	1.937	0.053	1.00

### Abundance at occupied ponds in 2015

Only the first two visits were considered, as nearly no CTs were found afterwards. During these first two visits, six sites (16.7%) had at least once a detection of an adult CT (range 0 to 34 adults per visit). However, only during ten visits, an adult CT was detected, which is 13.9% of all visits. Because there were not enough counts, no analysis on abundance of CT was done.

### Pond occupancy, colonisation and extinction 2010 – 2015

29 of the 35 sites (82.9%) had at least once a detection of CT in 2010 or 2015. In 2010, 25 sites had detection (naïve occupancy probability: 71.4%) and in 2015, there were detections at 16 sites (naïve occupancy probability: 45.7%). In 2015, four sites had detection, where there was none in 2010 (naïve colonisation rate of 40.0%) and 13 sites had no detection of the CT in 2015 where there was detection in 2010 (naïve extinction probability of 52.0%). The highest ranked model for detection probability included the variable, if the visit was at day or night time (Table 13). It had an average detection probability of  $47.6\% \pm 5.3\%$ . Using the model  $\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{day.night})$ , the mean occupancy probability was  $73.3\% \pm 7.9\%$  in 2010 and  $57.5\% \pm 25.9\%$  in 2015, colonisation probability was  $48.4\% \pm 20.7\%$  and extinction probability was  $39.2\% \pm 13.3\%$ .

**Table 13:** For the CT, one model for detection probability for multi-season models had delta AIC value < 3.00.

model	AIC del ta	AICwt	cuml tvWt
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{day. ni ght})$	352.32	0.00	0.9932
			0.99

The highest ranked multi-season model for 2010 to 2015 included forest area in a 1'000m surrounding for colonisation and for extinction probabilities (Table 14). However, the estimates of the regression coefficient for the effects of this model were imprecise, and the 95% confidence intervals for the regression coefficients included 0. Estimates of regression coefficients for all explanatory variables included 0 in their 95% confidence intervals.

**Table 14:** Three models for multi-season predictions for the CT had delta AIC value < 3.00.

model	AIC del ta	AICwt	cuml tvWt
$\Psi(\cdot) \gamma(\text{forest. 1000m}) \varepsilon(\text{forest. 1000m}) p(\text{day. ni ght})$	340.59	0.00	0.46130
			0.46

$\Psi(\text{forest. 1000m})$	$\gamma(\text{forest. 1000m})$	341.49	0.90	0.29462	0.76
$\varepsilon(\text{forest. 1000m})$	$p(\text{day. ni ght})$				
$\Psi(.)$	$\gamma(\text{forest. 1000m})$	342.89	2.29	0.14654	0.90
$\varepsilon(\text{forest. 1000m+water. 1000m})$	$p(\text{day. ni ght})$				

### 3.3 Common frog

#### Pond occupancy in 2015

35 of 36 sites had detection of CF, giving a naïve occupancy probability of 97.2%. There were not enough ponds without any CFs for comparison, thus no occupancy analysis for CF was done.

#### Abundance at occupied ponds in 2015

Only the first two visits were considered for the abundance of egg clutches of CF, as nearly no more eggs were found afterwards. 33 of 36 sites (91.7%) had at detection of egg clutches (range 0 to 511 egg clutches per visit). The highest ranked model for detection probability included pond size (Table 15). It had an average detection probability of 36.4%  $\pm$  1.3%.

**Table 15:** One model for detection probability of abundance of CF egg clutches had delta AIC value < 3.00.

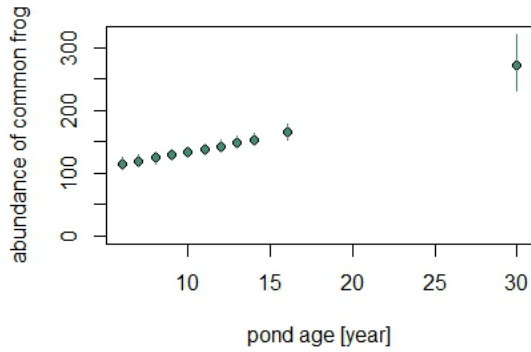
model	AIC	delta	AICwt	cumltvWt
$p(\text{size})\Psi(.)$	2707.95	0.00	1.0	1.00

The highest ranked model for abundance of CF egg clutches in 2015 included water temperature, the calendar week when water temperature was measured, and pond size (Table 16). In this model, pond size had a positive (effect on log scale:  $1.10 \pm 0.10$  95% CI) and water temperature a negative (effect on log scale:  $-0.70 \pm 0.06$  95% CI) effect on abundance. All explanatory variables had a certain effect on abundance of CF egg clutches. Four variables had positive effects on abundance of CF egg clutches: pond age (effect on log scale:  $0.16 \pm 0.04$  95% CI, Figure 7), pond size (effect on log scale:  $1.05 \pm 0.04$  95% CI, Figure 8), conductivity (effect on log scale:  $0.42 \pm 0.05$  95% CI, Figure 9), and predation (effect on log scale:  $0.16 \pm 0.04$  95% CI, Figure 10). Following variables had negative effects on abundance: water temperature (effect on log scale:  $-0.67 \pm 0.05$  95% CI, Figure 11), water temperature when including calendar week (effect on log scale:  $-0.65 \pm 0.05$  95% CI), water depth (effect on log scale:  $-0.08 \pm 0.04$  95% CI, Figure 12), solar exposition (effect on log scale:  $-0.08 \pm 0.04$  95% CI, Figure 13), and connectivity (effect on log scale:  $-0.29 \pm 0.06$  95% CI, Figure 14). To clarify that bigger ponds were not colder because they needed more time to warm up, correlation of pond size and water tempera-

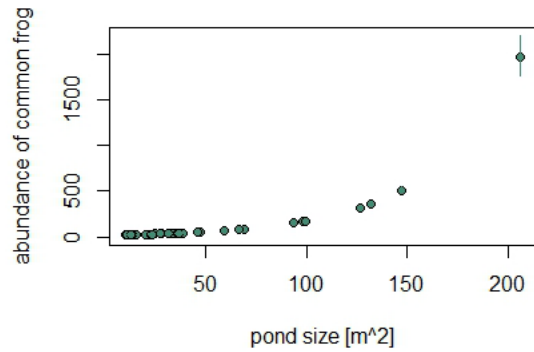
ture was tested and correlation was bad ( $r = 0.08$ ), also shown in Figure 15. Pond size and water temperature were both independent factors that influenced abundance of CF.

**Table 16:** Only one model for abundance probability of CF egg clutches had delta AIC value < 3.00.

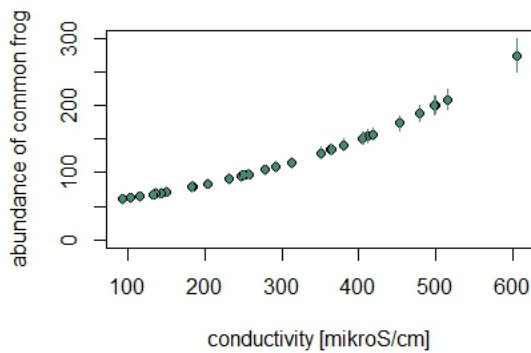
model	AIC	delta	AICwt	cumltvWt
$p(\text{size})\Psi(\text{water. temp}+\text{CW}+\text{size})$	1549.35	0.00	1.0	1.00



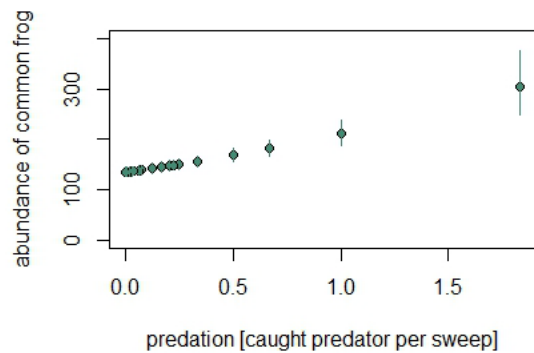
**Figure 7:** Pond age had a positive effect on abundance of CF egg clutches.



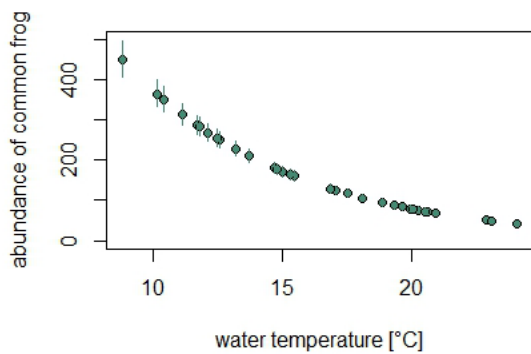
**Figure 8:** Pond size had a positive effect on abundance of CF egg clutches.



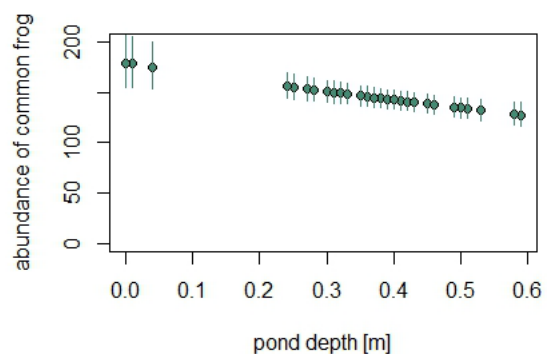
**Figure 9:** Conductivity in water had a positive effect on abundance of CF egg clutches.



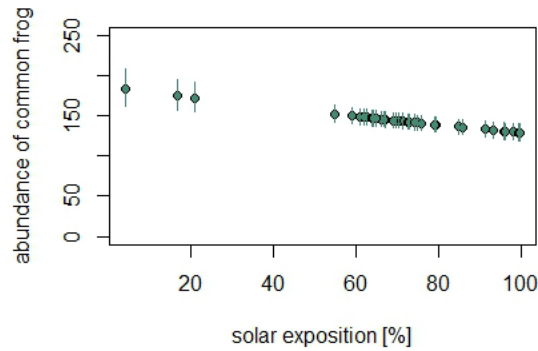
**Figure 10:** Predation risk had a positive effect on abundance of CF egg clutches.



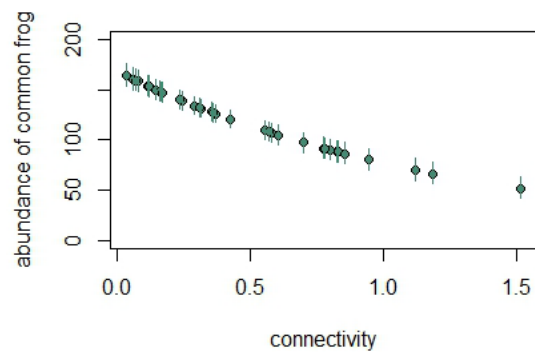
**Figure 11:** Water temperature had a negative effect on abundance of CF egg clutches. The colder the water, the better for them.



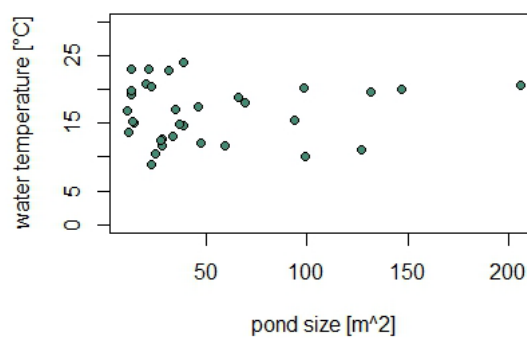
**Figure 12:** Water depth at 1m from shoreline had a negative effect on abundance of CF egg clutches.



**Figure 13:** Solar exposition had a negative effect on abundance of CF egg clutches.



**Figure 14:** The connectivity to other occupied ponds had a negative effect on abundance of CF egg clutches.



**Figure 15:** A bigger pond did not automatically have colder water temperature. Pond size and temperature did not correlate.

### Pond occupancy, colonisation and extinction 2010 – 2015

34 of 35 sites (97.1%) had at least once a detection of CF in 2010 or 2015. In 2010, 27 sites had detection (naïve occupancy probability: 77.1%) and in 2015, 34 of 35 ponds had detection (naïve occupancy probability: 97.1%). Seven sites had detection in 2015, where there was none in 2010, giving a naïve colonisation probability of 70.0%. All 27 sites, that had detection in 2010 had again detection in 2015, there was no local extinction (0%). Because nearly all ponds were occupied in both seasons and no site went extinct, no analysis of occupancy and extinction probability was done. However, as naïve colonisation probability was 70%, analysis for colonisation probability was done. The highest ranked model for detection probability included the variable if it was a day or a night time visit (Table 17). It had an average detection probability of 66.4% ± 4.2%. Using the model  $\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{day.night})$  gave an colonisation probability of 87.3% ± 11.9%.

**Table 17:** For CF, two models for detection probability for multi-season models had delta AIC value < 3.00.

model	AIC	del ta	AI Cwt	cuml tvWt
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{day.ni ght})$	361.05	0.00	0.65486	0.65
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{year})$	362.33	1.28	0.34502	1.00



Only six models analysing colonisation probability were tested. Among them, the highest ranked model included only the explanatory variable age (Table 18). However, the estimate of the regression coefficient for the effect of age in the best model was imprecise, and the 95% confidence interval included 0. Estimates of regression coefficients for all explanatory variables included 0 in the 95% confidence intervals.

**Table 18:** Five models for colonisation probability of CF had delta AIC value < 3.00.

model	AIC	del ta	AICwt	cuml tvWt
$\Psi(\cdot) \gamma(\text{age}) \varepsilon(\cdot) p(\text{day. ni ght})$	357.16	0.00	0.365	0.37
$\Psi(\cdot) \gamma(\text{age+forest. 100m}) \varepsilon(\cdot) p(\text{day. ni ght})$	359.11	1.95	0.138	0.50
$\Psi(\cdot) \gamma(\text{age+stones. 1000m}) \varepsilon(\cdot) p(\text{day. ni ght})$	359.17	2.00	0.134	0.64
$\Psi(\cdot) \gamma(\text{age+water. 1000m}) \varepsilon(\cdot) p(\text{day. ni ght})$	359.17	2.00	0.134	0.77
$\Psi(\cdot) \gamma(\text{forest. 100m}) \varepsilon(\cdot) p(\text{day. ni ght})$	360.07	2.91	0.085	0.86

### 3.4 Alpine newt

#### Pond occupancy in 2015

33 of 36 ponds had at least once a detection of ANs, giving a naïve occupancy probability of 91.7%. Because nearly all ponds were occupied and not enough ponds were without detection of ANs, no occupancy analysis was done.

#### Abundance at occupied ponds in 2015

31 of 36 (86.1%) sites had adult ANs caught by dip-netting (range of 0 to 36 adults per visit). The highest ranked model for detection probability included the no. of sweeps taken (Table 19). It had an average detection probability of  $22.3\% \pm 2.3\%$ .

**Table 19:** One model for detection probability of abundance of adult ANs had delta AIC value < 3.00.

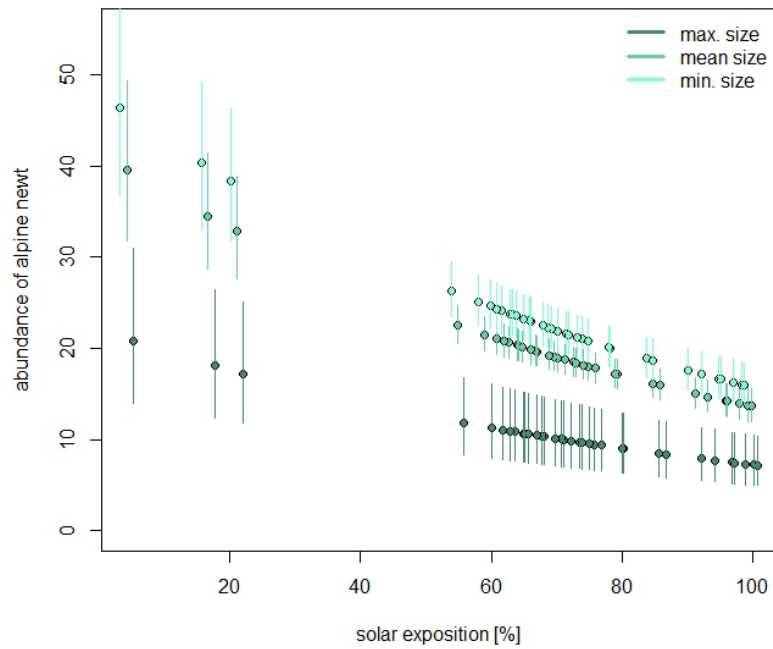
model	AIC	del ta	AICwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(\cdot)$	817.65	0.00	1.0	1.00

The highest ranked model for abundance of adult ANs in 2015 included solar exposition and pond size as site-covariates (Table 20, Figure 16). In the best model, solar exposition (effect on log scale:  $-0.25 \pm 0.07$  95% CI) and pond size (effect on log scale:  $-0.19 \pm 0.10$  95% CI) had both a negative effect. Following variables had a negative effect on abundance of adult ANs: water temperature (effect on log scale:  $-0.18 \pm 0.08$  95% CI, Figure 17), pond size (effect on log scale:  $-0.17 \pm 0.10$  95% CI), solar exposition (effect on log scale:  $-0.24 \pm 0.07$  95% CI), and predation (effect on log scale:  $-0.10 \pm 0.09$  95% CI, Figure 18). Conductivity had no certain negative effect, as its 95% confidence intervals in-

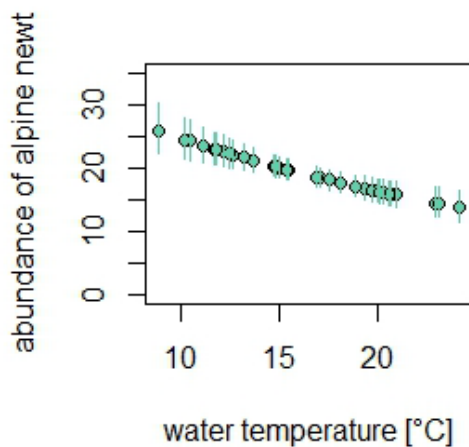
cluded 0. However, if looking only at significance, it had a small significance of  $p < 0.1$ . Connectivity had a positive effect (effect on log scale:  $0.12 \pm 0.08$  95% CI, Figure 19).

**Table 20:** Only one model for abundance prediction of adult ANs had delta AIC value < 3.00

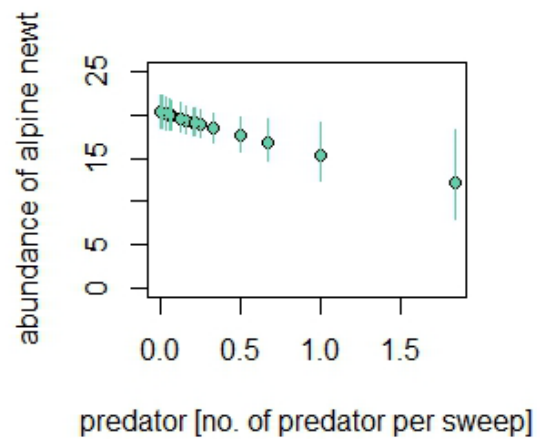
model	AIC del ta	AI Cwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(\text{sol ar. exp+si ze})$	765.70	0.00	0.99



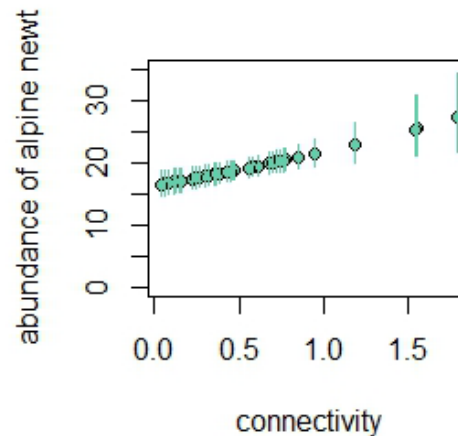
**Figure 16:** Solar exposition and pond size had both a negative effect on abundance of adult ANs.



**Figure 17:** Water temperature had a negative effect on abundance of adult ANs.



**Figure 18:** Predation had a negative effect on abundance of adult ANs.



**Figure 19:** Connectivity to other occupied ponds had a positive effect on abundance of adult ANs.

### Pond occupancy, colonisation and extinction 2010 - 2015

All 35 sites had at least once a detection of AN in 2010 or 2015. In 2010, all 35 sites had detection (occupancy probability: 100%), whereas in 2015, 32 sites had detection (naïve occupancy probability: 91.4%). There could be no colonisation (0%) as all sites were already occupied in 2010. However, three ponds had no more detection in 2015, giving a naïve extinction probability of 8.6%. The occupancy and colonisation probabilities are too high and the extinction probability too low, thus no analyses on meta-population dynamic probabilities were done.

## 3.5 Palmate newt

### Pond occupancy in 2015

At 16 of 36 sites, PNs were detected, giving a naïve site occupancy of 44.4%. The highest ranked model for detection probability of PN included no. of sweeps taken (Table 21). It had an average detection probability of  $19.9\% \pm 9.4\%$ . The average occupancy probability of PN using the model  $p(\text{no. sweeps}) \Psi(\cdot)$  was  $54.6\% \pm 11.9\%$ .

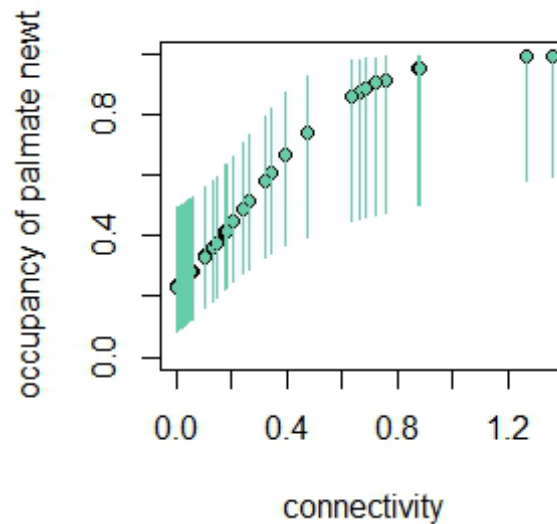
**Table 21:** One model for detection probability of PN had delta AIC value  $< 3.00$ .

model	AIC del ta	AI Cwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(\cdot)$	89.37	0.00	1.0

The highest ranked model for occupancy in 2015 included connectivity to other occupied ponds (Table 22). Connectivity was the only variable that had a certain effect on occupancy of PN, which was positive (effect on logit scale:  $1.75 \pm 1.53$  95% CI, Figure 20).

**Table 22:** Three models for occupancy of PN had delta AIC value < 3.00.

model	AIC	del ta	AI Cwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(\text{connect})$	81.06	0.00	0.44	0.44
$p(\text{no. sweeps}) \Psi(\text{connect}+\text{conduct})$	82.32	1.26	0.24	0.68
$p(\text{no. sweeps}) \Psi(\text{connect}+\text{sol ar. exp})$	82.68	1.62	0.20	0.88

**Figure 20:** Connectivity to other occupied ponds had a positive effect on occupancy of PN in 2015.

### Abundance at occupied ponds in 2015

15 of 36 sites (41.7%) had at least once detection of adult PN caught by dip-netting (range 0 to 29 newts per visit). The highest ranked model for detection probability of abundance of adult PN included no. of sweeps taken (Table 23). It had an average detection probability of  $3.1\% \pm 1.4\%$ .

**Table 23:** One model for detection probability of the abundance of adult PN had delta AIC value < 3.00.

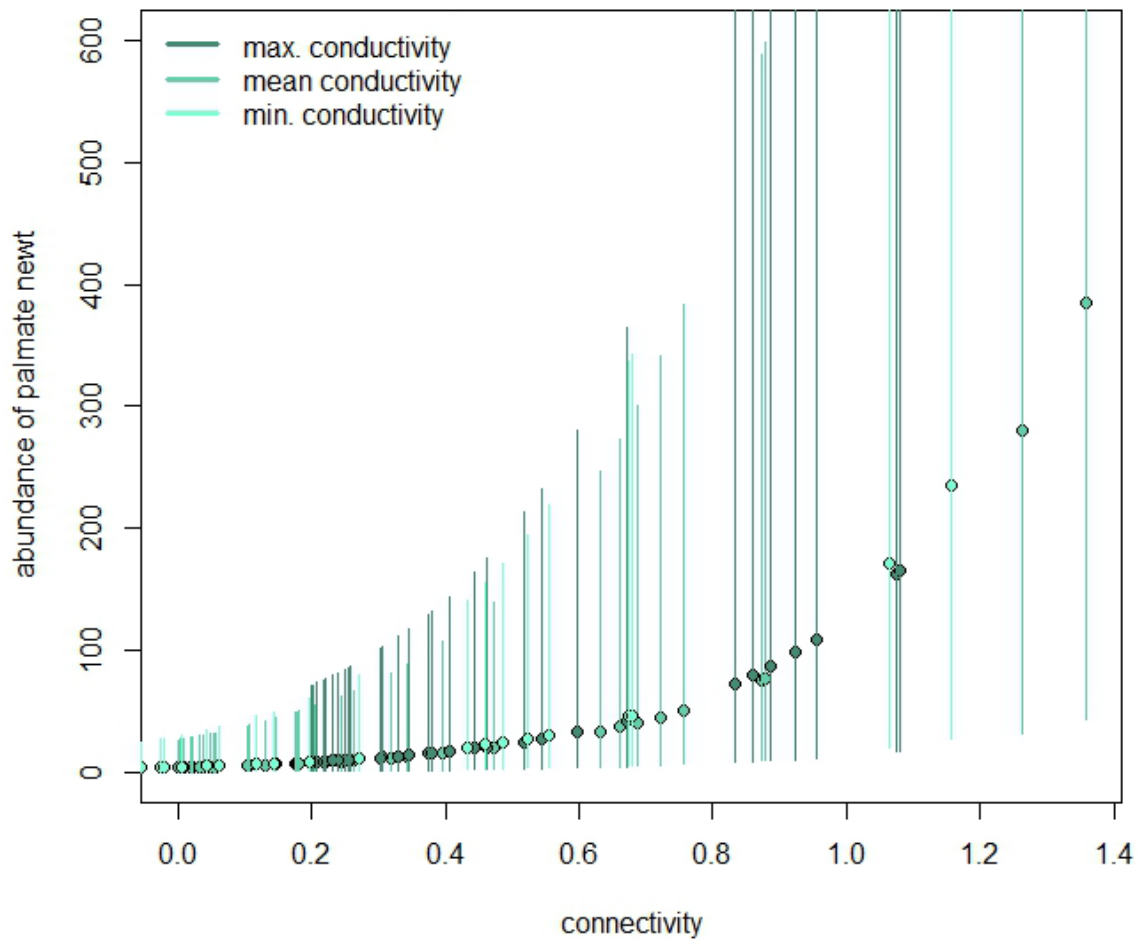
model	AIC	del ta	AI Cwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(.)$	351.56	0.00	1.00	1.00

The highest ranked model for abundance of adult PN in 2015 included connectivity, water temperature, the calendar week when water temperature was measured, and conductivity (Table 24, Figure 21). In the best model, connectivity (effect on log scale:  $0.92 \pm 0.29$  95% CI) and conductivity (effect on log scale:  $0.34 \pm 0.25$  95% CI) had a positive effect. However, effect of water temperature in the best model was imprecise, and its 95% confidence interval included 0. Following variables had negative effects on the abundance: Water temperature (effect on log scale:  $-0.32 \pm 0.20$  95% CI, Figure 22) and pond size (effect on log scale:  $-0.55 \pm 0.34$  95% CI, Figure 23). Following variables had positive effects on abundance: water depth (effect on log scale:  $0.53 \pm 0.31$  95% CI, Figure 24), conductivity (effect on log scale:  $0.64 \pm 0.19$  95% CI, Figure 25), solar exposition (effect on log scale:

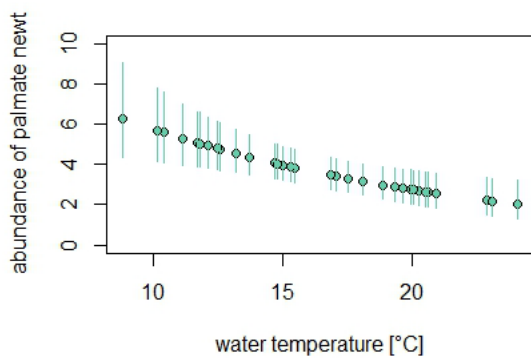
0.25 ± 0.248 95% CI, Figure 26), predation (effect on log scale: 0.21 ± 0.14 95% CI, Figure 27), and connectivity (effect on log scale: 1.13 ± 0.25 95% CI, Figure 21).

**Table 24:** Only one model for abundance prediction of adult PN had delta AIC value < 3.00.

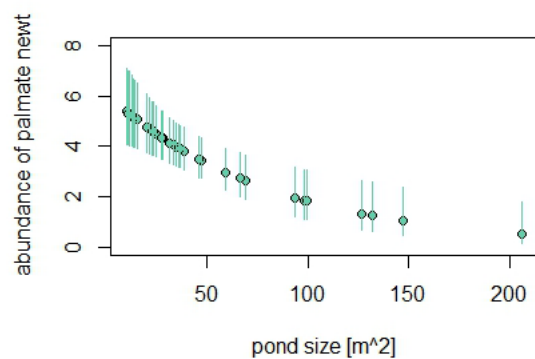
model	AIC	delta	AI Cwt	cuml tvWt
$p(\text{no. sweeps})\Psi(\text{connect}+\text{water. temp}+\text{CW}+\text{conduct})$	145.96	0.00	0.82	0.82



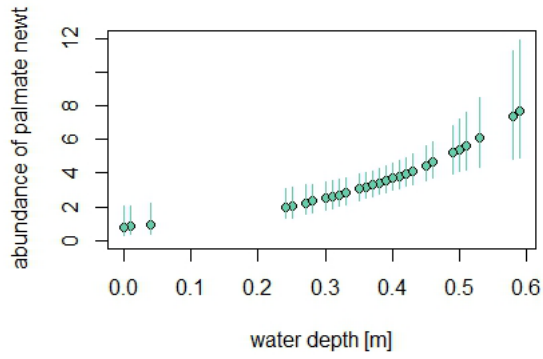
**Figure 21:** Connectivity to other occupied ponds and conductivity [ $\mu\text{S}/\text{cm}$ ] had both a positive effect on abundance of adult PNs.



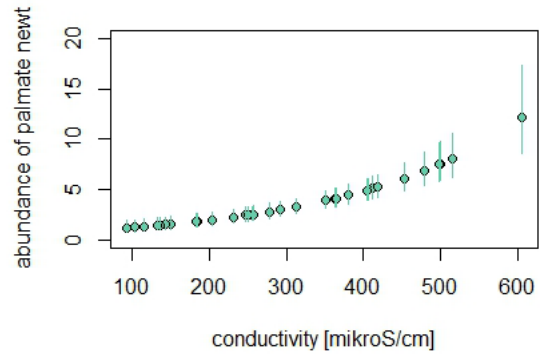
**Figure 22:** Water temperature had a negative effect on abundance of adult PNs.



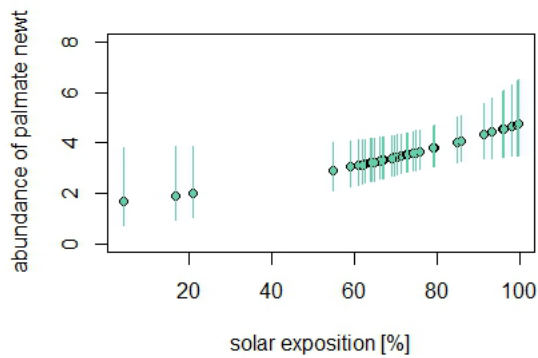
**Figure 23:** Pond size had a negative effect on abundance of adult PNs.



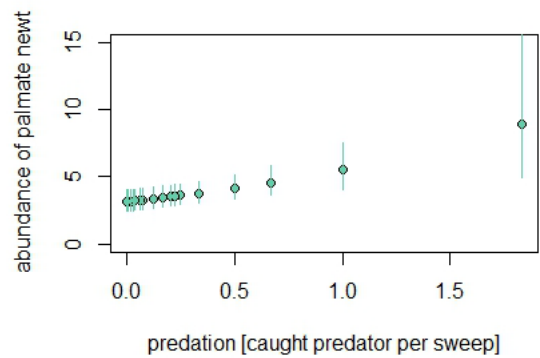
**Figure 24:** Water depth at 1m from shoreline had a positive effect on abundance of adult PNs.



**Figure 25:** Conductivity had a positive effect on abundance of adult PNs.



**Figure 26:** Solar exposition had a positive effect on abundance of adult PNs.



**Figure 27:** Predator density had a positive effect on abundance of adult PNs.

**Pond occupancy, colonisation and extinction 2010 - 2015**

28 of 35 sites (80.0%) had at least once a detection of a PN in 2010 or 2015. In 2010, 18 sites had detection of PN (naïve occupancy probability: 51.4%) and in 2015, 15 sites had detection (naïve occupancy probability: 42.9%). Five sites had detection in 2015, where there was none in 2010, giving a naïve colonisation probability of 27.8%. On the other hand, eight sites had detection of PN in 2010 that had none in 2015, giving a naïve extinction probability of 44.4%. The highest ranked model for detection probability of PN included the variable, in which year the visit was done (Table 25). It had an average detection probability of  $26.4\% \pm 5.9\%$ . Using the model  $\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{year})$  gives a mean occupancy probability in 2010 of  $85.3\% \pm 9.3\%$  and in 2015  $69.8\% \pm 50.3\%$ , a colonisation probability of  $6.6 \pm 47.9$  and an extinction probability of  $19.3 \pm 26.2$ .

**Table 25:** For the PN, all three models for detection probability for multi-season models had delta AIC value < 3.00.

model	AIC del ta	AICwt	cuml tvWt
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{year})$	326.21	0.00	0.47
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\cdot)$	326.79	0.58	0.82
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{day. ni ght})$	328.10	1.89	1.00

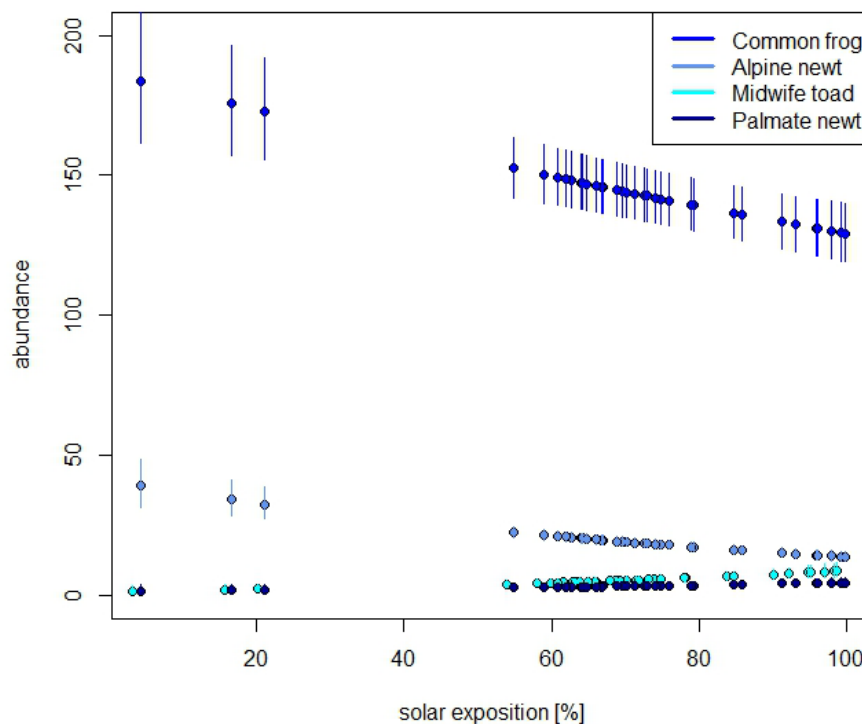
The highest ranked multi-season model for 2010 to 2015 included forest area in a 1'000m surrounding for occupancy and extinction probability (Table 26). However, the estimates of the regression coefficients for the effects of the explanatory variables in the best model were imprecise, and their 95% confidence intervals included 0. Estimates of regression coefficients for all explanatory variables included 0 in their 95% confidence intervals.

**Table 26:** Three models for multi-season predictions for PN had delta AIC value < 3.00.

model	AIC	del ta	AI Cwt	cuml tvWt
$\Psi(\text{forest. 1000m}) \gamma(.) \varepsilon(\text{forest. 1000m}) p(\text{year})$	315.11	0.00	0.46756	0.47
$\Psi(\text{forest. 1000m}) \gamma(\text{forest. 1000m}) \varepsilon(\text{forest. 1000m}) p(\text{year})$	316.84	1.74	0.19631	0.66
$\Psi(\text{forest. 1000m}) \gamma(.) \varepsilon(\text{water. 1000m}) p(\text{year})$	317.48	2.37	0.14280	0.81

### 3.6 Summary of all variables and their effects

The factor that effected most amphibian species was solar exposition, with twice a negative and twice a positive effect on abundance in 2015 (Figure 28). Table 2 shows an overview of all site-covariates and which covariate had an effect on which study species.



**Figure 28:** Solar exposition had a negative effect on abundance of CF and AN, but a positive effect on MWT and PN in 2015.

**Table 27:** Summary of all covariates tested and if they had an effect on occupancy, abundance, colonisation and extinction probability for all five study species.

+ : positive effect

+ : positively significant ( $p < 0.1$ ), but zero is in 95% CI

- : negative effect

- : negatively significant ( $p < 0.1$ ), but zero is in 95% CI

X : no effect

? : no analysis done

Variable	MWT	CT	CF	AN	PN
<b>Occupancy <math>\Psi</math> 2015</b>					
modelled mean $p$ [%]	39.8 $\pm$ 7.6	66.2 $\pm$ 4.8	?	?	19.9 $\pm$ 9.4
naïve $\Psi$ [%]	36.1	44.4	97.2	91.7	44.4
modelled mean $\Psi(\cdot)$ [%]	39.2 $\pm$ 8.9	54.1 $\pm$ 10.9	?	?	54.6 $\pm$ 11.9
pond size	X	X	?	?	X
water depth	X	X	?	?	X
water temperature	X	X	?	?	X
water temperature (incl. calendar week)	X	X	?	?	X
conductivity	X	X	?	?	X
predation	X	X	?	?	X
solar exposition	X	X	?	?	X
terrestrial habitat	X				
pond age	X	X	?	?	X
connectivity	X	X	?	?	+
<b>Abundance 2015</b>					
modelled mean $p$ [%]	10.5 $\pm$ 1.7	?	36.4 $\pm$ 1.3	22.3 $\pm$ 2.3	3.1 $\pm$ 1.4
sites with counted data [%]	27.8	16.7	91.7	86.1	41.7
caught individuals per visit	0 - 24	0 - 34	0 - 511	0 - 36	0 - 29
pond size	X	?	+	-	-
water depth	X	?	-	X	+
water temperature	X	?	-	-	-
water temperature (incl. calendar week)	X	?	-	-	X
conductivity	X	?	+	-	+
predation	X	?	+	-	+
solar exposition	+	?	-	-	+
terrestrial habitat	+				
pond age	+	?	+	X	X



connectivity	X	?	-	+	+
<b>Multi-season 2010 / 2015 – occupancy <math>\Psi</math></b>					
modelled mean $\rho$ [%]	63.8 ± 6.0	47.6 ± 5.3	66.4 ± 4.2	?	26.4 ± 5.9
naïve $\Psi$ [%] 2010	27.8	71.4	77.1	100.0	51.4
modelled mean $\Psi(.)$ [%] 2010	28.6 ± 7.7	73.3 ± 7.9	?	?	85.3 ± 9.3
naïve $\Psi$ [%] 2015	37.1	45.7	97.1	91.4	42.9
modelled mean $\Psi(.)$ [%] 2015	38.8 ± 14.6	57.5 ± 25.9	?	?	69.8 ± 50.3
pond size	X	X	?	?	X
water depth	X	X	?	?	X
habitat 100m	+				
forest 100m	X	X	?	?	X
forest 1'000m	X	X	?	?	X
stone 1'000m	X	X	?	?	X
water 1'000m	X	X	?	?	X
settlement 1'000m	X	X	?	?	X
age	X	X	?	?	X
connectivity	+				
<b>Multi-season 2010 / 2015 – colonisation <math>\gamma</math></b>					
naïve $\gamma$ [%]	24.0	40.0	70.0	0.0	27.8
modelled mean $\gamma(.)$ [%]	24.4 ± 8.7	48.4 ± 20.7	87.3 ± 11.9.	?	6.6 ± 47.9
habitat 100m	+				
forest 100m	+	X	X	?	X
forest 1'000m	+	X	X	?	X
stone 1'000m	X	X	X	?	X
water 1'000m	X	X	X	?	X
settlement 1'000m	X	X	X	?	X
age	X	X	X	?	X
connectivity	X				
<b>Multi-season 2010 / 2015 – extinction <math>\varepsilon</math></b>					
naïve $\varepsilon$ [%]	30.0	52.0	0.0	8.6	44.4
modelled mean $\varepsilon(.)$ [%]	28.8 ± 14.7	39.2 ± 13.3	?	?	19.3 ± 26.2
forest 100m	X	X	?	?	X

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forest 1'000m	X	X	?	?	X
water 1'000m	X	X	?	?	X
settlement 1'000m	X	X	?	?	X
abundance	X	X	?	?	X
reproduction	X	X	?	?	X
connectivity	X				

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## 4 Discussion

I surveyed occupancy, abundance, colonisation and extinction of five amphibian species in ponds that were mainly created for the endangered species MWT to assess the success of this conservation project. I evaluated the success of the project for every species separately analysing factors and their effects on amphibian population dynamics to give advice for further pond-creating conservation work.

### 4.1 Species occupancy and abundance

#### Midwife toad

Occupancy probability of MWT in 2015 was  $39.2\% \pm 8.9\%$ , thus MWT were present in more than a third of the ponds. Considering, that it is an endangered species which decreased continuously over the last 20 years in Emmental (Ryser, et al., 2003) and that it is said to be a bad coloniser (Laan & Verboom, 1990), it is a good result. Six sites were colonised between 2010 and 2015, while MWT went extinct in three out of 10 sites. One of these three extinct ponds silted up and nearly no water was in the pond anymore. For the other two ponds, no clear change was found. At one pond, the landowner told that MWTs got constantly less in this region over the last thirty years and totally disappeared during the last years, not knowing what the reason for the decline and extinction could be. These high colonisation ( $24.4\% \pm 8.7\%$ ) and extinction ( $28.8\% \pm 14.7\%$ ) probabilities between 2010 and 2015 show a dynamic meta-population. Ryser, et al. (2003) experienced already high dynamics of the MWT. It is possible that the colonisation processes in this study area are not finished yet. This non-stable distribution state suggests that meta-population processes are important factors.

Nevertheless, the number of structure types as a terrestrial factor had positive effects on occupancy and abundance of MWTs in 2015. Grossenbacher (1988) and Mermod, et al. (2010) pointed out the various structure types that are preferred by the MWT. This study indicates that not only one of these structure types might be important, but also a mixture of them. Solar exposition and ponds age had also a positive effect on abundance in 2015. Surprisingly, forest area in a 100m surrounding had a positive effect on colonisation, which was thought to have no or in a 1'000m surrounding even a negative effect. What sticks out is that no factors on aquatic level had an effect. Not even predation risk and conductivity had an effect, although they were predicted to have a negative effect. These results confirm that MWTs do not have preferences for ponds. It is more the preferences of terrestrial and meta-population factors which matter.

## Common toad

Occupancy probability of CT in 2015 was  $50.5\% \pm 9.9\%$ . Thus, around half of the ponds were occupied. That is good compared to the fact that in most cantons 25% - 45% of the ponds are occupied (Grossenbacher, 1988). Between 2010 and 2015, colonisation ( $48.4\% \pm 20.7\%$ ) and extinction ( $39.2\% \pm 13.3\%$ ) probabilities maintained more or less a balance. However, four sites were colonised between 2010 and 2015, while CT went extinct in 13 sites. Despite considering different detection probabilities, as methods were different in 2010 and 2015, it indicates a quite dynamic meta-population for the CT.

Unfortunately, there were not enough counts to determine effects on the abundance as most adults have already left the ponds when we arrived. CT is said to be in big, deep and sunny ponds and in forest area (Grossenbacher, 1988). However, in my survey no such factor had an effect on occupancy in one and two seasons, as well as colonisation and extinction probabilities.

## Common frog



**Figure 29:** The biggest pond with over  $200\text{m}^2$  had 47 and 60 egg clutches.



**Figure 30:** The site having the most egg clutches (511 and 465 clutches) consists of two ponds, giving a pond size of  $127\text{m}^2$ .

Occupancy probability of CF in 2015 was  $\geq 97.2\%$ . This species definitely profited from the pond-creation project. Between 2010 and 2015, colonisation probability ( $87.3\% \pm 11.9\%$ ) clearly outweighed extinction probability (0.0%). On meta-population level, this species seems to be in good condition showing even an increasing trend. CF did not have any special preferences to start spawning at a site, which confirms the common opinion about this wide spread species (Grossenbacher, 1988). Although it seems that this species can occupy any kind of pond, there are important factors influencing its abundance. Thus, there are factors influencing the success of establishing at a new pond with a high number of individuals. In 2015, the abundance of

CF was especially affected by water temperature and pond size. There were big changes in abundance, having over 400 additional individuals from smallest to biggest, respectively

from warmest to coldest pond (see Results, Figure 8 and Figure 11). The biggest pond with a size of 206m<sup>2</sup> had 47 and 60 egg clutches (Figure 29). The pond having by far the highest abundance had 511 and 465 egg clutches (Figure 30). This site had two ponds that increased pond size to 127m<sup>2</sup>. The spawn of CF is relatively big compared to the other study species. Thus, it is logic, that a bigger pond has more space for egg clutches, whereas a small pond cannot be filled with hundreds of egg clutches. The preference of big ponds confirms the results from Indermaur, et al. (2010). ANs, which are more abundant in smaller ponds, eat eggs of CF. Thus, it could be a reason, that CFs thrive more in bigger ponds, where the predation risk of ANs is lower. I have not modelled species-co-occurrence but this could be interesting for future research. However, the study of Indermaur, et al. (2010) says that CF has no preference of water temperature were my results show a clear preference for colder ponds.

### Alpine Newt

Occupancy probability of AN in 2015 was  $\geq 91.7\%$ . As the CF, also the AN profited from the pond-creation project. Between 2010 and 2015, colonisation (0.0%) and extinction (~8.6%) probabilities showed a slightly decrease between 2010 and 2015. However, all ponds were occupied in 2010, thus colonisation probability had to be 0%. AN were not detected anymore at only three ponds in 2015, which all nearly desiccated and had not much water left anymore in 2015 (Figure 31). Thus, disappearing at these three sites was not surprising.



**Figure 31:** Three ponds nearly desiccated in 2015. These were also the only three ponds where the AN disappeared in 2015.

As the CF, the AN occupied nearly all ponds in 2010 and 2015, which shows that this species did not have any habitat preferences for occupancy. This confirms the common opinion about this wide spread species (Grossenbacher, 1988). Although this species seem to occupy almost all kinds of pond, this study showed that there are important factors influencing its abundance. As for the CF, there are factors influencing the success of the AN to establish at a new pond with a high number of individuals. In 2015, abundance of the AN was especially influenced by solar exposition and pond size. ANs preferred

shady and, in contrary to CFs, smaller ponds. One could think that more newts were caught in smaller ponds because it is easier to dip-net for them, as they cannot hide in the middle of the pond, where the dip-net does not reach. However, size was tested as a covariate for detectability and it had bad explanatory value. The size itself seems to be a reason for higher abundance. ANs clearly avoid ponds inhabited by fish (Grossenbacher, 1988). As fish are more likely to be in bigger ponds, it could be that this is a reason that ANs consciously avoid bigger ponds.

### **Palmate Newt**

Occupancy probability of PN in 2015 was  $54.6\% \pm 11.9\%$ . Around half of the ponds were occupied. Between 2010 and 2015, colonisation ( $6.6\% \pm 47.9\%$ ) and extinction ( $19.3\% \pm 26.2\%$ ) probabilities had huge uncertainty. This might be due to much lower detection probability ( $p$ ) of PN ( $p$  in single-season occupancy model:  $19.9\% \pm 9.4\%$ ;  $p$  in N-mixture model  $3.1\% \pm 1.4\%$ ;  $p$  in multi-season occupancy model:  $26.4\% \pm 5.9\%$ ) than of the other species ( $p$  in single-season occupancy model: MWT had second lowest  $p$  with  $39.8\% \pm 7.6\%$ ;  $p$  in N-mixture model: MWT had second lowest  $p$  with  $10.5\% \pm 1.7\%$ ;  $p$  in multi-season occupancy model: CT had second lowest  $p$  with  $47.6\% \pm 5.3\%$ ). However, it is the only surveyed species showing a decreasing trend. Five sites were colonised between 2010 and 2015, while PN went extinct in eight sites. This indicates a dynamic metapopulation, as it seems also for MWT and CT.

The PN was the only species whose occupancy probability in 2015 was affected by a factor. That was connectivity which had a positive effect. For the abundance in 2015, connectivity (positive), conductivity (positive) and water temperature (negative) together had the highest effect. Overall, connectivity seems to be a remarkable positive factor for PN. Water temperature was expected to be negative, as PN is said to prefer shady and thus colder ponds (Grossenbacher, 1988). In the contrary, I found a positive effect of solar exposure on abundance of PN.

## **4.2 Variables and their effects**

### **Aquatic level**

Pond size had a huge positive effect on abundance of CFs and negative effects on ANs and PNs. Interestingly, it was the opposite for water depth. CFs preferred shallow pond edges and PNs steeper ones. If high amphibian species richness is the target, different kinds of pond need to be created. Then, big ponds need shallow shorelines and small ponds can have steep shorelines. Small ponds with deep water will also desiccate or silt up slower.

Water temperature had a negative influence on abundance of CFs, ANs and PNs but no positive effect to any other species. Indermaur et al. (2010) interpreted that warmer ponds produce more food for larvae, which would be a counter-argument for my results. Tadpoles tend to be in warmer waters if they can select. However, they can acclimate to different temperature, also depending on the season (Lucas & Reynolds, 1967). These poikilothermic animals are able to survive in colder waters. Thus, water temperature does not need to have a negative effect. However, it explains not why colder waters had even a positive effect in my survey. Though, results should be interpreted with caution. Water temperature was measured at only one point of the pond and ponds had big differences in order of daily fluctuations.

Conductivity was expected to have negative effect on species richness (Stumpel & van der Voet, 1998; Hamer & Parris, 2011). Surprisingly, CFs and PNs were positively affected by it. Conductivity is said to increase from fertiliser in agricultural land or from chemical contaminants of roads and other surface runoffs in urban areas which all have negative effects on amphibian species (Zampella, 1994; Paul & Meyer, 2001). However, also other factors may increase conductivity, which have no negative influence on amphibian species richness and abundance. Conductivity is just an indirect factor, making it hard to find explanations for its positive effects in my study. Reasons for positive effects of conductivity are not known and may be subject for further research.

Predation had a negative effect on abundance of AN, but a positive effect on abundance of CF and PN. In contrary, Indermaur, et al (2010) had an opposite result for CF. This indicates that predation risk does not necessarily have a compulsory effect on abundance of amphibian species. It depends on the habitat. A good habitat for dragonfly larvae and great diving beetle increasing their abundance can also be a good habitat for amphibian species. For example, higher productivity of a pond can increase predation risk but it can simultaneously outweigh the negative effect of higher predation risk (Thurnheer & Reyer, 2001). Or predation risk can firstly decrease the abundance of their prey but the survivors will have more resources left for them (Peacor, 2002).

Factors on aquatic level had an effect on abundance of both newts and CFs. These species were sometimes contrary effected. This leads to the conclusion, that there is not one model pond that suits all amphibian species the same.

### **Terrestrial level**

Solar exposition had a negative effect on CFs and ANs and a positive effect on MWTs and PNs. That was contrary to expectation, because in the study of Van Buskirk (2005), newts preferred shady ponds and anurans sunny ones. CFs and PNs are the other side

around in my results. Sunny ponds can have more vegetation and thus more food and refuges for larvae (Van Buskirk, 2005), which was positive for the less abundant species MWT and PN. On the other hand, CFs and ANs had may have too high abundances, so that some more food and some more refuges was not enough to have a benefit for them. Results confirm that different terrestrial habitats are needed to support several amphibian species.

Evaluating the multi-season models, only forest in 100m surrounding and habitat quality had an effect, but only for MWT. It confirms that especially for the MWT the terrestrial habitat is important. Thus, natural surroundings and different structures should be included in conservation work for the MWT.

### **Meta-population level**

The youngest ponds in my survey were already six years old. Stumbel & Van (1998) found an optimum pond age after three years. That could be a reason why ANs, PNs and CTs were not affected by pond age anymore. As there were no negative effects of age, it is probably a good advice to keep older ponds and maintaining them to avoid desiccation or siltation.

Interestingly, the abundance of CFs was negatively affected by connectivity. Maybe, the CF is already that much wide-spread that close connection to other occupied ponds may increase intraspecific competition. Denoël & Lehmann (2006) found out that the effect of connectivity on abundance depends on the quality of the surrounding ponds. Surrounding ponds that were occupied by PNs had a positive effect on abundance of PNs in the given ponds. However, if abundance in surrounding ponds was very high, the effect turned and connectivity got a negative effect. Then, terrestrial factors got more important than the level of meta-population. Thus, in my survey, effect of connectivity on abundance of CFs might be negative, because the surrounding ponds had high abundance of CFs, too. Although, connectivity is said to be an important factor against isolation, studies showed a weak effect on occupancy and abundance in natural surroundings. Negative effects of connectivity on occupancy probability has already been found by Schmidt & Pellet (2005). Connectivity seems to get only important in highly developed areas (Marsh & Trenham, 2001; Pellet, et al., 2007; Prugh, et al., 2008). This result enforce that connectivity is an important factor when conservation work is done in areas which are highly developed.

The high population dynamics of MWT, CT and PN indicate that the meta-population level has a huge effect on colonisation and extinction processes which may be difficult to manage for conservation targets. Unfortunately, it is the amphibian species on the red list that have high population-dynamics (MWT: endangered; CT and PN: vulnerable) (Schmidt &



Zumbach, 2005). In general, most effects were shown in abundance of species but occupancy, colonisation and extinction probabilities were rarely affected by factors. This indicates that the size of populations is a better response variable than occupancy. Unfortunately, no effect on extinction probability was found. It is still not always quite clear, why some species decline and disappear. Further studies on causes for extinction probabilities are needed. Meanwhile, it is important to focus on increasing the abundance of existing populations and helping colonise new ponds. Results showed often not what was expected from the literature. Some variables had even a contrary effect, but it needs to be considered that studies are difficult to compare as methods and side effects can vary from one survey to the other.

### **4.3 Conservation implications**

All five species colonised ponds of the conservation project in Emmental. For MWT, CT and PN, the meta-population level seemed to be important. MWT also reacted to factors of the terrestrial habitat. CF, AN and PN reacted strongly to aquatic level factors. There cannot be one perfect pond, which has positive effects on all species equally. Ponds need to be tailored to particular needs of single species. If the target of a conservation project is to generally increase amphibian species richness, several kinds of ponds need to be created. Thus, for higher species richness, a mixture of big ponds having a shallow shoreline and small but deeper ponds seems to be a good choice. A mix of shady and sunny places, where there are more sunny than shady ones, is preferable. Connectivity to other ponds should be considered in conservation work especially in highly developed areas. Older ponds need to be maintained. They may desiccate briefly to reduce predation risk but should be re-constructed soon. For the MWT, it is important to have a natural surrounding (i.e. also forest) with high solar exposition and a lot of structure types around the pond. To conserve only the PN, small, steep and sunny ponds and a high connectivity are good. Results strongly support that high variability of ponds and their surroundings need to be created to increase amphibian species richness. There is not one model pond that suits all amphibian species together.

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## **Appendix**

### **Image sources:**

Cover picture: view from pond “Holzweid”, taken by Stéphanie Vuichard in 2015

All other pictures: Taken by Stéphanie Vuichard in 2015

**Appendix A:** Six habitat structure types

**Appendix B:** All models analysed

**Appendix A: Six habitat structure types**

Pictures from: Mermod, M. et al., 2010. *Praxismerkblatt Artenschutz - Geburtshelferkröte Alytes obstetricans*, Neuenburg: karch.

Dry stonewall:



Stone heaps:



Open rock or gravel:



Slopes with open soils



Garden with loose soil:



Wood heap:





## Appendix B: All models analysed

AIC: Akaike's Information Criterion

delta: Difference between the AIC of the model and AIC of the highest ranked model

AICwt: Akaike weight: Chance of being the best model among all tested ones. All AICwt added together gives 1.00

cumltvWt: cumulated Akaike weight (cumltvWt of next better model + AICwt of model)

$p$ : detection probability

$\Psi$ : occupancy probability

$\gamma$ : colonisation probability

$\epsilon$ : extinction probability

For single-season models and N-mixture model (abundance): no.sweeps: no. of sweeps taken; date: date of visit; time: time when we started dip-netting; weather: weather during visit; method: if visit was at day or night time; difficulty dip-net: if it was easy, middle or difficult to dip-net; size: pond size; depth: water depth at 1m from shore; water.temp: water temperature; CW: calendar week when water temperature was measured; conduct: conductivity in water; predation: predation risk; solar.exp: solar exposition; terr.hab: no. of terrestrial habitat structures; age: age of the pond; connect. connectivity to other occupied ponds

For multi-season models: day.night: if it was a day or night time visit; year: the year the visit took place; size: pond size; depth: max. water depth; age: age of pond; habitat100: if there was good terrestrial habitat for the midwife toad in a 100m surrounding; forest 100: forest area in a 100m surrounding; forest1000: forest area in a 1'000m surrounding; stone1000: stone area in a 1'000m surrounding; water1000: water surface in a 1'000m surrounding; settlement1000: settlement area in a 1'000m surrounding; abu: high abundance of analysed species in 2010; repro: if there was reproduction of the analysed species in 2010

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### Midwife toad – occupancy – detection probability

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model	AIC	del ta	AICwt	cuml tvWt
$p(\text{no. sweeps})\Psi(\cdot)$	124.42	0.00	0.6430	0.64
$p(\text{date})\Psi(\cdot)$	125.91	1.49	0.3058	0.95
$p(\cdot)\Psi(\cdot)$	132.00	7.58	0.0145	0.96
$p(\text{depth})\Psi(\cdot)$	132.66	8.24	0.0104	0.97
$p(\text{method})\Psi(\cdot)$	133.15	8.73	0.0082	0.98
$p(\text{time})\Psi(\cdot)$	133.80	9.38	0.0059	0.99
$p(\text{size})\Psi(\cdot)$	133.94	9.52	0.0055	0.99
$p(\text{diffi culty di p-net})\Psi(\cdot)$	133.99	9.57	0.0054	1.00
$p(\text{weather})\Psi(\cdot)$	136.78	12.36	0.0013	1.00

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### Midwife toad – occupancy

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model	AIC	del ta	AICwt	cuml tvWt
$p(\text{no. sweeps})\Psi(\text{solar. exp})$	124.31	0.00	0.119	0.12
$p(\text{no. sweeps})\Psi(\cdot)$	124.42	0.11	0.112	0.23
$p(\text{no. sweeps})\Psi(\text{age})$	124.71	0.40	0.097	0.33
$p(\text{no. sweeps})\Psi(\text{solar. exp+depth})$	124.75	0.44	0.095	0.42
$p(\text{no. sweeps})\Psi(\text{depth})$	124.86	0.55	0.090	0.51
$p(\text{no. sweeps})\Psi(\text{solar. exp+age})$	125.12	0.81	0.079	0.59
$p(\text{no. sweeps})\Psi(\text{solar. exp+size})$	125.67	1.36	0.060	0.65
$p(\text{no. sweeps})\Psi(\text{size})$	125.84	1.53	0.055	0.71
$p(\text{no. sweeps})\Psi(\text{connect})$	125.84	1.53	0.055	0.76
$p(\text{no. sweeps})\Psi(\text{solar. exp+age+depth})$	125.94	1.63	0.052	0.81
$p(\text{no. sweeps})\Psi(\text{conduct})$	126.33	2.02	0.043	0.86
$p(\text{no. sweeps})\Psi(\text{terr.hab})$	126.39	2.08	0.042	0.90
$p(\text{no. sweeps})\Psi(\text{water. temp})$	126.40	2.09	0.042	0.94
$p(\text{no. sweeps})\Psi(\text{predator})$	126.42	2.11	0.041	0.98
$p(\text{no. sweeps})\Psi(\text{water. temp+ CW})$	128.12	3.81	0.018	1.00

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Midwife toad – abundance – detection probability				
model	AIC	delta	AICwt	cumltvWt
$p(\text{no. sweeps})\Psi(\cdot)$	636.48	0.00	1.0	1.00
$p(\text{date})\Psi(\cdot)$	833.02	196.54	2.1e-43	1.00
$p(\text{method})\Psi(\cdot)$	936.68	300.19	6.5e-66	1.00
$p(\text{weather})\Psi(\cdot)$	937.65	301.16	4.0e-66	1.00
$p(\text{time})\Psi(\cdot)$	959.28	322.80	8.0e-71	1.00
$p(\text{difficulty.dipnet})\Psi(\cdot)$	972.24	335.76	1.2e-73	1.00
$p(\text{depth})\Psi(\cdot)$	990.49	354.01	1.3e-77	1.00
$P(\cdot)\Psi(\cdot)$	990.59	354.10	1.3e-77	1.00
$p(\text{size})\Psi(\cdot)$	992.23	355.75	5.6e-78	1.00

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Midwife toad – abundance				
model	AIC	delta	AICwt	cumltvWt
$p(\text{no. sweeps})\Psi(\text{sol ar. exp+conduct})$	621.89	0.000	0.27	0.27
$p(\text{no. sweeps})\Psi(\text{sol ar. exp+age+terr. hab})$	621.92	0.024	0.27	0.54
$p(\text{no. sweeps})\Psi(\text{sol ar. exp+age})$	621.93	0.034	0.27	0.81
$p(\text{no. sweeps})\Psi(\text{sol ar. exp})$	623.88	1.991	0.1	0.91
$p(\text{no. sweeps})\Psi(\text{sol ar. exp+terr. hab})$	624.10	2.204	0.09	1.00
$p(\text{no. sweeps})\Psi(\text{age})$	633.55	11.657	0.0008	1.00
$p(\text{no. sweeps})\Psi(\text{terr. hab})$	634.32	12.431	0.0005	1.00
$p(\text{no. sweeps})\Psi(\cdot)$	636.48	14.592	0.0002	1.00
$p(\text{no. sweeps})\Psi(\text{conduct})$	637.09	15.199	0.0001	1.00
$p(\text{no. sweeps})\Psi(\text{water. temp})$	637.51	15.621	0.0001	1.00
$p(\text{no. sweeps})\Psi(\text{predator})$	638.02	16.129	8.5e-05	1.00
$p(\text{no. sweeps})\Psi(\text{connect})$	638.42	16.526	7.0e-05	1.00
$p(\text{no. sweeps})\Psi(\text{size})$	638.48	16.584	6.8e-05	1.00
$p(\text{no. sweeps})\Psi(\text{depth})$	638.48	16.585	6.8e-05	1.00
$p(\text{no. sweeps})\Psi(\text{water. temp+ CW})$	639.51	17.620	4.1e-05	1.00

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Midwife toad – multi-season – detection probability				
model	AIC	delta	AICwt	cumltvWt
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{day. ni ght})$	223.64	0.00	0.99303	0.99
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{year})$	233.66	10.02	0.00662	1.00
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\cdot)$	239.51	15.87	0.00036	1.00

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Midwife toad – multi-season				
model	AIC	delta	AICwt	cumltvWt
$\Psi(\text{habi tat. 100m. 2010}) \gamma(\text{habi tat. 100m. 2010}) \varepsilon(\text{forest. 100m. 2010}) p(\text{day. ni ght})$	197.81	0.00	0.95	0.95
$\Psi(\text{habi tat. 100m}) \gamma(\text{habi tat. 100m}) \varepsilon(\cdot) p(\text{day. ni ght})$	203.80	5.99	0.048	1.00
$\Psi(\cdot) \gamma(\text{habi tat. 100m}) \varepsilon(\cdot) p(\text{day. ni ght})$	211.35	13.54	0.0011	1.00
$\Psi(\text{habi tat. 100m}) \gamma(\cdot) \varepsilon(\cdot) p(\text{day. ni ght})$	216.07	18.26	0.0001	1.00
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\text{forest. 100m}) p(\text{day. ni ght})$	217.65	19.85	4.7e-05	1.00
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\text{repro}) p(\text{day. ni ght})$	218.14	20.33	3.7e-05	1.00

$\Psi(\text{forest. 100m}) \gamma(\text{forest. 100m}) \varepsilon(.)$ $p(\text{day. ni ght})$	218.46	20.65	3.1e-05	1.00
$\Psi(.) \gamma(\text{settlement. 1000m}) \varepsilon(.)$ $p(\text{day. ni ght})$	219.40	21.60	1.9e-05	1.00
$\Psi(.) \gamma(\text{forest. 100m}) \varepsilon(.)$ $p(\text{day. ni ght})$	219.41	21.60	1.9e-05	1.00
$\Psi(\text{settlement. 1000m}) \gamma(\text{settlement. 1000m}) \varepsilon(.)$ $p(\text{day. ni ght})$	221.37	23.56	7.3e-06	1.00
$\Psi(\text{age}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	221.60	23.80	6.5e-06	1.00
$\Psi(\text{connect}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	221.70	23.89	6.2e-06	1.00
$\Psi(.) \gamma(\text{forest. 1000m}) \varepsilon(.)$ $p(\text{day. ni ght})$	221.74	23.93	6.0e-06	1.00
$\Psi(\text{forest. 1000m}) \gamma(\text{forest. 1000m}) \varepsilon(.)$ $p(\text{day. ni ght})$	222.05	24.24	5.2e-06	1.00
$\Psi(\text{age}) \gamma(\text{age}) \varepsilon(.)$ $p(\text{day. ni ght})$	222.23	24.42	4.7e-06	1.00
$\Psi(.) \gamma(.) \varepsilon(\text{abu})$ $p(\text{day. ni ght})$	222.31	24.51	4.5e-06	1.00
$\Psi(\text{forest. 100m}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	222.69	24.89	3.8e-06	1.00
$\Psi(.) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	223.64	25.83	2.3e-06	1.00
$\Psi(\text{connect}) \gamma(\text{connect}) \varepsilon(.)$ $p(\text{day. ni ght})$	223.68	25.88	2.3e-06	1.00
$\Psi(\text{forest. 1000m}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	223.95	26.14	2.0e-06	1.00
$\Psi(.) \gamma(\text{water. 1000m}) \varepsilon(.)$ $p(\text{day. ni ght})$	224.17	26.37	1.8e-06	1.00
$\Psi(\text{stones. 1000m}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	224.22	26.41	1.8e-06	1.00
$\Psi(.) \gamma(\text{age}) \varepsilon(.)$ $p(\text{day. ni ght})$	224.27	26.46	1.7e-06	1.00
$\Psi(\text{si ze}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	224.53	26.72	1.5e-06	1.00
$\Psi(.) \gamma(.) \varepsilon(\text{connect})$ $p(\text{day. ni ght})$	224.64	26.83	1.4e-06	1.00
$\Psi(.) \gamma(.) \varepsilon(\text{settlement. 1000m})$ (day. ni ght)	224.76	26.95	1.3e-06	1.00
$\Psi(.) \gamma(.) \varepsilon(\text{forest. 1000m})$ $p(\text{day. ni ght})$	224.90	27.09	1.2e-06	1.00
$\Psi(.) \gamma(.) \varepsilon(\text{water. 1000m})$ $p(\text{day. ni ght})$	225.34	27.53	1.0e-06	1.00
$\Psi(\text{water. 1000m}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	225.54	27.74	9.0e-07	1.00
$\Psi(\text{depth}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	225.56	27.75	9.0e-07	1.00
$\Psi(.) \gamma(\text{stones. 1000m}) \varepsilon(.)$ $p(\text{day. ni ght})$	225.57	27.76	8.9e-07	1.00
$\Psi(.) \gamma(\text{age} + \text{I}(\text{age}^2)) \varepsilon(.)$ $p(\text{day. ni ght})$	225.58	27.78	8.8e-07	1.00
$\Psi(\text{settlement. 1000m}) \gamma(.) \varepsilon(.)$ $p(\text{day. ni ght})$	225.60	27.80	8.8e-07	1.00
$\Psi(.) \gamma(\text{connect}) \varepsilon(.)$ $p(\text{day. ni ght})$	225.62	27.82	8.7e-07	1.00
$\Psi(\text{water. 1000m}) \gamma(\text{water. 1000m}) \varepsilon(.)$ $p(\text{day. ni ght})$	226.08	28.27	6.9e-07	1.00
$\Psi(\text{stones. 1000m}) \gamma(\text{stones. 1000m}) \varepsilon(.)$ $p(\text{day. ni ght})$	226.15	28.34	6.7e-07	1.00

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Common toad – occupancy – detection probability

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model	AIC	del ta	AI Cwt	cuml tvWt
$p(\text{weather}) \Psi(.)$	131.25	0.00	0.99	0.99
$p(\text{method}) \Psi(.)$	142.05	10.80	0.0045	1.00
$p(\text{si ze}) \Psi(.)$	142.37	11.12	0.0038	1.00
$p(.) \Psi(.)$	147.98	16.74	0.0002	1.00
$p(\text{depth}) \Psi(.)$	149.39	18.14	0.0001	1.00
$p(\text{ti me}) \Psi(.)$	149.45	18.20	0.0001	1.00
$p(\text{date}) \Psi(.)$	149.77	18.53	9.4e-05	1.00

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Common toad – occupancy

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model	AIC	del ta	AI Cwt	cuml tvWt
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$p(\text{method})\Psi(\text{water. temp})$	131.23	0.000	0.14	0.14
$p(\text{weather})\Psi(.)$	131.25	0.015	0.14	0.28
$p(\text{weather})\Psi(\text{depth})$	131.29	0.056	0.14	0.41
$p(\text{weather})\Psi(\text{age})$	131.56	0.328	0.12	0.53
$p(\text{weather})\Psi(\text{water. temp} + \text{CW})$	131.65	0.420	0.11	0.65
$p(\text{weather})\Psi(\text{size})$	131.67	0.439	0.11	0.76
$p(\text{weather})\Psi(\text{solar})$	132.70	1.466	0.067	0.83
$p(\text{weather})\Psi(\text{connect})$	132.85	1.623	0.062	0.89
$p(\text{weather})\Psi(\text{predator})$	132.99	1.757	0.058	0.95
$p(\text{weather})\Psi(\text{conduct})$	133.17	1.937	0.053	1.00
$p(\text{weather})\Psi(\text{water. temp}+\text{age})$	148.72	17.493	2.2e-05	1.00
$p(\text{weather})\Psi(\text{water. temp}+\text{depth})$	148.77	17.543	2.2e-05	1.00
$p(\text{weather})\Psi(\text{water. temp}+\text{depth}+\text{age})$	149.50	18.270	1.5e-05	1.00

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Common toad – multi-season – detection probability

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model	AIC del ta	AICwt	cuml tvWt
$\Psi(.) \gamma(.) \varepsilon(.) p(\text{day. ni ght})$	352.32	0.00	0.9932
$\Psi(.) \gamma(.) \varepsilon(.) p(.)$	362.95	10.62	0.0049
$\Psi(.) \gamma(.) \varepsilon(.) p(\text{year})$	364.83	12.51	0.0019

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Common toad – multi-season

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model	AIC del ta	AICwt	cuml tvWt
$\Psi(.) \gamma(\text{forest. 1000m}) \varepsilon(\text{forest. 1000m}) p(\text{day. ni ght})$	340.59	0.00	0.46130
$\Psi(\text{forest. 1000m}) \gamma(\text{forest. 1000m}) \varepsilon(\text{forest. 1000m}) p(\text{day. ni ght})$	341.49	0.90	0.29462
$\Psi(.) \gamma(\text{forest. 1000m}) \varepsilon(\text{forest. 1000m}+\text{water. 1000m}) p(\text{day. ni ght})$	342.89	2.29	0.14654
$\Psi(.) \gamma(.) \varepsilon(\text{forest. 1000m}) p(\text{day. ni ght})$	345.97	5.37	0.03141
$\Psi(.) \gamma(\text{forest. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	346.45	5.86	0.02463
$\Psi(.) \gamma(.) \varepsilon(\text{forest. 1000m}+\text{water. 1000m}) p(\text{day. ni ght})$	348.50	7.91	0.00883
$\Psi(.) \gamma(.) \varepsilon(\text{water. 1000m}) p(\text{day. ni ght})$	348.91	8.31	0.00722
$\Psi(\text{forest. 1000m}) \gamma(\text{forest. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	350.02	9.43	0.00414
$\Psi(.) \gamma(.) \varepsilon(\text{forest. 100m}) p(\text{day. ni ght})$	350.23	9.63	0.00373
$\Psi(\text{forest. 100m}) \gamma(\text{forest. 100m}) \varepsilon(.) p(\text{day. ni ght})$	351.40	10.80	0.00208
$\Psi(.) \gamma(.) \varepsilon(.) p(\text{day. ni ght})$	352.32	11.73	0.00131
$\Psi(\text{stones. 1000m}) \gamma(.) \varepsilon(.) p(\text{day. ni ght})$	352.60	12.01	0.00114
$\Psi(.) \gamma(.) \varepsilon(\text{abu}) p(\text{day. ni ght})$	352.76	12.17	0.00105
$\Psi(\text{water. 1000m}) \gamma(.) \varepsilon(.) p(\text{day. ni ght})$	352.82	12.23	0.00102
$\Psi(.) \gamma(\text{age}) \varepsilon(.) p(\text{day. ni ght})$	352.82	12.23	0.00102
$\Psi(\text{size}) \gamma(.) \varepsilon(.) p(\text{day. ni ght})$	352.84	12.25	0.00101
$\Psi(\text{forest. 1000m}) \gamma(.) \varepsilon(.) p(\text{day. ni ght})$	353.17	12.58	0.00086
$\Psi(.) \gamma(\text{settlement. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	353.36	12.77	0.00078
$\Psi(\text{age}) \gamma(.) \varepsilon(.) p(\text{day. ni ght})$	353.46	12.87	0.00074
$\Psi(.) \gamma(\text{water. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	353.53	12.94	0.00072
$\Psi(.) \gamma(\text{stones. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	353.62	13.02	0.00069

$\Psi(\cdot) \gamma(\cdot) \varepsilon(\text{repro}) p(\text{day, ni ght})$	353.79	13.20	0.00063	1.00
$\Psi(\text{depth}) \gamma(\cdot) \varepsilon(\cdot) p(\text{day, ni ght})$	353.90	13.31	0.00059	1.00
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\text{settlement, 1000m}) p(\text{day, ni ght})$	353.92	13.33	0.00059	1.00
$\Psi(\text{stones, 1000m}) \gamma(\text{stones, 1000m}) \varepsilon(\cdot) p(\text{day, ni ght})$	353.94	13.34	0.00058	1.00
$\Psi(\text{water, 1000m}) \gamma(\text{water, 1000m}) \varepsilon(\cdot) p(\text{day, ni ght})$	354.04	13.45	0.00055	1.00
$\Psi(\text{settlement, 1000m}) \gamma(\cdot) \varepsilon(\cdot) p(\text{day, ni ght})$	354.04	13.45	0.00055	1.00
$\Psi(\text{age}) \gamma(\text{age}) \varepsilon(\cdot) p(\text{day, ni ght})$	354.05	13.46	0.00055	1.00
$\Psi(\text{forest, 100m}) \gamma(\cdot) \varepsilon(\cdot) p(\text{day, ni ght})$	354.30	13.71	0.00049	1.00
$\Psi(\text{settlement, 1000m}) \gamma(\text{settlement, 1000m}) \varepsilon(\cdot) p(\text{day, ni ght})$	355.03	14.44	0.00034	1.00
$\Psi(\cdot) \gamma(\text{forest, 100m}) \varepsilon(\cdot) p(\text{day, ni ght})$	355.29	14.70	0.00030	1.00

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Common frog – abundance – detection probability

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model	AIC	del ta	AICwt	cuml tvWt
$p(\text{si ze}) \Psi(\cdot)$	2707.95	0.00	1.0	1.00
$p(\text{ti me}) \Psi(\cdot)$	3382.14	674.20	4.0e-147	1.00
$p(\text{weat her}) \Psi(\cdot)$	3388.07	680.12	2.1e-148	1.00
$p(\text{date}) \Psi(\cdot)$	3401.18	693.24	2.9e-151	1.00
$p(\text{depth}) \Psi(\cdot)$	3434.57	726.63	1.6e-158	1.00
$p(\cdot) \Psi(\cdot)$	3438.94	730.99	1.9e-159	1.00

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Common frog – abundance

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model	AIC	del ta	AICwt	cuml tvWt
$p(\text{si ze}) \Psi(\text{water, temp}+\text{CW}+\text{si ze})$	1549.35	0.00	1.0	1.00
$p(\text{si ze}) \Psi(\text{water, temp}+\text{CW}+\text{conduct})$	1687.24	137.89	1.1e-30	1.00
$p(\text{si ze}) \Psi(\text{water, temp}+\text{CW})$	1802.75	253.40	9.4e-56	1.00
$p(\text{si ze}) \Psi(\text{water, temp})$	1807.75	258.40	7.7e-57	1.00
$p(\text{si ze}) \Psi(\text{conduct})$	2367.67	818.32	2.0e-178	1.00
$p(\text{si ze}) \Psi(\text{si ze})$	2553.64	1004.29	8.3e-219	1.00
$p(\text{si ze}) \Psi(\text{connect})$	2594.23	1044.88	1.3e-227	1.00
$p(\text{si ze}) \Psi(\text{age})$	2649.80	1100.45	1.1e-239	1.00
$p(\text{si ze}) \Psi(\text{predator})$	2660.51	1111.16	5.2e-242	1.00
$p(\text{si ze}) \Psi(\text{sol ar, exp})$	2691.11	1141.76	1.2e-248	1.00
$p(\text{si ze}) \Psi(\text{depth})$	2697.65	1148.30	4.5e-250	1.00
$p(\text{si ze}) \Psi(\cdot)$	2707.95	1158.60	2.6e-252	1.00

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Common frog – multi-season – detection probability

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model	AIC	del ta	AICwt	cuml tvWt
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{day, ni ght})$	361.05	0.00	0.65486	0.65
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\text{year})$	362.33	1.28	0.34502	1.00
$\Psi(\cdot) \gamma(\cdot) \varepsilon(\cdot) p(\cdot)$	378.21	17.16	0.00012	1.00

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Common frog – multi-season (only colonisation!)

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model	AIC	del ta	AICwt	cuml tvWt
$\Psi(\cdot) \gamma(\text{age}) \varepsilon(\cdot) p(\text{day, ni ght})$	357.16	0.00	0.365	0.37

$\Psi(.) \gamma(\text{age+forest. 100m}) \varepsilon(.) p(\text{day. ni ght})$	359.11	1.95	0.138	0.50
$\Psi(.) \gamma(\text{age+stones. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	359.17	2.00	0.134	0.64
$\Psi(.) \gamma(\text{age+water. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	359.17	2.00	0.134	0.77
$\Psi(.) \gamma(\text{forest. 100m}) \varepsilon(.) p(\text{day. ni ght})$	360.07	2.91	0.085	0.86
$\Psi(.) \gamma(\text{age+forest. 100m+water. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	361.12	3.95	0.051	0.91
$\Psi(.) \gamma(\text{water. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	362.45	5.28	0.026	0.93
$\Psi(.) \gamma(\text{stones. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	362.47	5.31	0.026	0.96
$\Psi(.) \gamma(\text{forest. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	362.76	5.60	0.022	0.98
$\Psi(.) \gamma(\text{settlement. 1000m}) \varepsilon(.) p(\text{day. ni ght})$	363.02	5.86	0.020	1.00

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Alpine newt – abundance – detection probability

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model	AIC	del ta	AI Cwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(.)$	817.65	0.00	1.0	1.00
$p(\text{date}) \Psi(.)$	1540.65	723.00	1.0e-157	1.00
$p(\text{weather}) \Psi(.)$	1950.54	1132.90	9.9e-247	1.00
$p(\text{depth}) \Psi(.)$	1971.65	1154.00	2.6e-251	1.00
$p(\text{di ffi cul ty. di pnet}) \Psi(.)$	1986.89	1169.24	1.3e-254	1.00
$p(\text{method}) \Psi(.)$	1993.11	1175.47	5.6e-256	1.00
$p(\text{si ze}) \Psi(.)$	2010.74	1193.09	8.4e-260	1.00
$p(\text{ti me}) \Psi(.)$	2013.08	1195.44	2.6e-260	1.00
$p(.) \Psi(.)$	2018.95	1201.30	1.4e-261	1.00

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Alpine newt - abundance

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model	AIC	del ta	AI Cwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(\text{solar. exp+si ze})$	765.70	0.00	0.99	0.99
$p(\text{no. sweeps}) \Psi(\text{solar. exp+water. temp})$	775.37	9.67	0.0078	1.00
$p(\text{no. sweeps}) \Psi(\text{solar. exp+water. temp+ CW})$	776.78	11.08	0.0039	1.00
$p(\text{no. sweeps}) \Psi(\text{solar. exp})$	780.23	14.53	0.0007	1.00
$p(\text{no. sweeps}) \Psi(\text{water. temp})$	801.08	35.38	2.1e-08	1.00
$p(\text{no. sweeps}) \Psi(\text{water. temp+CW})$	802.13	36.43	1.2e-08	1.00
$p(\text{no. sweeps}) \Psi(\text{si ze})$	805.56	39.86	2.2e-09	1.00
$p(\text{no. sweeps}) \Psi(\text{connect})$	810.34	44.64	2.0e-10	1.00
$p(\text{no. sweeps}) \Psi(\text{predator})$	814.15	48.45	3.0e-11	1.00
$p(\text{no. sweeps}) \Psi(\text{conduct})$	816.86	51.16	7.7e-12	1.00
$p(\text{no. sweeps}) \Psi(.)$	817.65	51.95	5.2e-12	1.00
$p(\text{no. sweeps}) \Psi(\text{depth})$	818.13	52.43	4.1e-12	1.00
$p(\text{no. sweeps}) \Psi(\text{age})$	819.63	53.93	1.9e-12	1.00

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Palmate newt – occupancy – detection probability

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model	AIC	del ta	AI Cwt	cuml tvWt
$p(\text{no. sweeps}) \Psi(.)$	89.37	0.00	1.0	1.00
$p(\text{date}) \Psi(.)$	105.02	15.65	0.0004	1.00
$p(\text{weather}) \Psi(.)$	115.13	25.76	2.5e-06	1.00
$p(\text{method}) \Psi(.)$	118.90	29.53	3.9e-07	1.00
$p(.) \Psi(.)$	124.49	35.13	2.4e-08	1.00

$p(\text{size})\Psi(\cdot)$	125.35	35.99	1.5e-08	1.00
$p(\text{depth})\Psi(\cdot)$	125.43	36.07	1.5e-08	1.00
$p(\text{time})\Psi(\cdot)$	125.74	36.37	1.3e-08	1.00
$p(\text{difficulty, dlnet})\Psi(\cdot)$	127.77	38.40	4.6e-09	1.00

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 Palmate newt – occupancy
 

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model	AIC	delta	AICwt	cumltvWt
$p(\text{no. sweeps})\Psi(\text{connect})$	81.06	0.00	0.44	0.44
$p(\text{no. sweeps})\Psi(\text{connect+conduct})$	82.32	1.26	0.24	0.68
$p(\text{no. sweeps})\Psi(\text{connect+sol ar. exp})$	82.68	1.62	0.20	0.88
$p(\text{no. sweeps})\Psi(\text{connect+size+sol ar. exp})$	84.25	3.19	0.09	0.97
$p(\text{no. sweeps})\Psi(\cdot)$	89.37	8.31	0.0070	0.97
$p(\text{no. sweeps})\Psi(\text{size})$	89.82	8.76	0.0056	0.98
$p(\text{no. sweeps})\Psi(\text{sol ar. exp})$	90.78	9.72	0.0034	0.98
$p(\text{no. sweeps})\Psi(\text{conduct})$	90.90	9.84	0.0032	0.99
$p(\text{no. sweeps})\Psi(\text{depth})$	91.07	10.01	0.0030	0.99
$p(\text{no. sweeps})\Psi(\text{predator})$	91.17	10.11	0.0028	0.99
$p(\text{no. sweeps})\Psi(\text{water. temp})$	91.32	10.26	0.0026	1.00
$p(\text{no. sweeps})\Psi(\text{age})$	91.36	10.30	0.0026	1.00
$p(\text{no. sweeps})\Psi(\text{water. temp} + \text{CW})$	92.05	10.99	0.0018	1.00
$p(\text{no. sweeps})\Psi(\text{connect+size})$	115.13	34.07	1.8e-08	1.00

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 Palmate newt – abundance – detection probability
 

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model	AIC	delta	AICwt	cumltvWt
$p(\text{no. sweeps})\Psi(\cdot)$	351.56	0.00	1.00	1.00
$p(\text{date})\Psi(\cdot)$	495.34	143.78	6.0e-32	1.00
$p(\text{weather})\Psi(\cdot)$	553.29	201.74	1.6e-44	1.00
$p(\text{difficulty, dlnet})\Psi(\cdot)$	621.27	269.72	2.7e-59	1.00
$p(\text{depth})\Psi(\cdot)$	623.35	271.79	9.6e-60	1.00
$p(\text{size})\Psi(\cdot)$	630.64	279.09	2.5e-61	1.00
$p(\text{time})\Psi(\cdot)$	642.68	291.12	6.1e-64	1.00
$p(\text{method})\Psi(\cdot)$	642.93	291.37	5.4e-64	1.00
$p(\cdot)\Psi(\cdot)$	643.73	292.17	3.6e-64	1.00

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 Palmate newt – abundance
 

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model	AIC	delta	AICwt	cumltvWt
$p(\text{no. sweeps})\Psi(\text{connect+water. temp+CW+conduct})$	145.96	0.00	0.82	0.82
$p(\text{no. sweeps})\Psi(\text{connect+conduct})$	150.40	4.44	0.089	0.91
$p(\text{no. sweeps})\Psi(\text{connect+water. temp+CW})$	150.82	4.86	0.072	0.98
$p(\text{no. sweeps})\Psi(\text{connectivity})$	154.50	8.54	0.011	1.00
$p(\text{no. sweeps})\Psi(\text{connect+size})$	156.47	10.51	0.0043	1.00
$p(\text{no. sweeps})\Psi(\text{water. temp+CW})$	276.35	130.40	4.0e-29	1.00
$p(\text{no. sweeps})\Psi(\text{conduct})$	307.26	161.31	7.7e-36	1.00
$p(\text{no. sweeps})\Psi(\text{size})$	338.53	192.57	1.3e-42	1.00
$p(\text{no. sweeps})\Psi(\text{depth})$	342.06	196.10	2.1e-43	1.00

$p(\text{no. sweeps})\Psi(\text{water. temp})$	343.28	197.32	1.2e-43	1.00
$p(\text{no. sweeps})\Psi(\text{predator})$	345.97	200.02	3.0e-44	1.00
$p(\text{no. sweeps})\Psi(\text{sol ar. exp})$	349.29	203.33	5.8e-45	1.00
$p(\text{no. sweeps})\Psi(.)$	351.56	205.60	1.9e-45	1.00
$p(\text{no. sweeps})\Psi(\text{age})$	353.48	207.52	7.1e-46	1.00

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 Palmate newt – multi-season – detection probability
 

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model	AIC del ta	AICwt	cuml tvWt
$\Psi(.)\gamma(.)\varepsilon(.)\ p(\text{year})$	326.21	0.00	0.47
$\Psi(.)\gamma(.)\varepsilon(.)\ p(.)$	326.79	0.58	0.82
$\Psi(.)\gamma(.)\varepsilon(.)\ p(\text{day. ni ght})$	328.10	1.89	1.00

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 Palmate newt – multi-season
 

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model	AIC del ta	AICwt	cuml tvWt
$\Psi(\text{forest. 1000m})\gamma(.)\varepsilon(\text{forest. 1000m})\ p(\text{year})$	315.11	0.00	0.46756
$\Psi(\text{forest. 1000m})\gamma(\text{forest. 1000m})\varepsilon(\text{forest. 1000m})\ p(\text{year})$	316.84	1.74	0.19631
$\Psi(\text{forest. 1000m})\gamma(.)\varepsilon(\text{water. 1000m})\ p(\text{year})$	317.48	2.37	0.14280
$\Psi(\text{forest. 1000m})\gamma(.)\varepsilon(.)\ p(\text{year})$	319.10	3.99	0.06361
$\Psi(\text{forest. 1000m})\gamma(.)\varepsilon(\text{forest. 100m})\ p(\text{year})$	319.82	4.71	0.04439
$\Psi(.)\gamma(.)\varepsilon(\text{forest. 1000m})\ p(\text{year})$	320.94	5.83	0.02537
$\Psi(\text{forest. 1000m})\gamma(\text{forest. 1000m})\varepsilon(.)\ p(\text{year})$	321.20	6.09	0.02225
$\Psi(.)\gamma(.)\varepsilon(\text{forest. 100m})\ p(\text{year})$	323.38	8.27	0.00749
$\Psi(.)\gamma(.)\varepsilon(\text{water. 1000m})\ p(\text{year})$	324.40	9.29	0.00450
$\Psi(\text{age})\gamma(\text{age})\varepsilon(.)\ p(\text{year})$	324.88	9.77	0.00353
$\Psi(.)\gamma(\text{age})\varepsilon(.)\ p(\text{year})$	324.95	9.84	0.00341
$\Psi(.)\gamma(.)\varepsilon(.)\ p(\text{year})$	326.21	11.10	0.00182
$\Psi(.)\gamma(.)\varepsilon(\text{abu})\ p(\text{year})$	326.24	11.13	0.00179
$\Psi(\text{water. 1000m})\gamma(.)\varepsilon(.)\ p(\text{year})$	326.30	11.20	0.00173
$\Psi(\text{age})\gamma(.)\varepsilon(.)\ p(\text{year})$	326.82	11.71	0.00134
$\Psi(\text{forest. 100m})\gamma(\text{forest. 100m})\varepsilon(.)\ p(\text{year})$	326.95	11.84	0.00125
$\Psi(\text{size})\gamma(.)\varepsilon(.)\ p(\text{year})$	327.37	12.26	0.00102
$\Psi(.)\gamma(\text{stones. 1000m})\varepsilon(.)\ p(\text{year})$	327.64	12.53	0.00089
$\Psi(\text{stones. 1000m})\gamma(.)\varepsilon(.)\ p(\text{year})$	327.65	12.55	0.00088
$\Psi(.)\gamma(.)\varepsilon(\text{repro})\ p(\text{year})$	327.69	12.58	0.00087
$\Psi(.)\gamma(\text{settlement. 1000m})\varepsilon(.)\ p(\text{year})$	327.74	12.63	0.00084
$\Psi(\text{settlement. 1000m})\gamma(.)\varepsilon(.)\ p(\text{year})$	327.77	12.66	0.00083
$\Psi(\text{depth})\gamma(.)\varepsilon(.)\ p(\text{year})$	327.84	12.74	0.00080
$\Psi(\text{forest. 100m})\gamma(.)\varepsilon(.)\ p(\text{year})$	327.85	12.75	0.00080
$\Psi(.)\gamma(.)\varepsilon(\text{settlement. 1000m})\ p(\text{year})$	327.86	12.76	0.00079
$\Psi(\text{water. 1000m})\gamma(\text{water. 1000m})\varepsilon(.)\ p(\text{year})$	328.15	13.04	0.00069
$\Psi(.)\gamma(\text{forest. 1000m})\varepsilon(.)\ p(\text{year})$	328.20	13.10	0.00067
$\Psi(.)\gamma(\text{water. 1000m})\varepsilon(.)\ p(\text{year})$	328.21	13.10	0.00067
$\Psi(\text{stones. 1000m})\gamma(\text{stones. 1000m})\varepsilon(.)\ p(\text{year})$	329.26	14.15	0.00040
$\Psi(\text{settlement. 1000m})\gamma(\text{settlement. 1000m})\varepsilon(.)\ p(\text{year})$	329.46	14.35	0.00036
$\Psi(.)\gamma(\text{forest. 100m})\varepsilon(.)\ p(\text{year})$	329.56	14.45	0.00034



