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Zurich^{UZH}**

Dispersal in a Metapopulation of the Yellow-Bellied Toad: Does Conservation Action Work?



A Thesis for the Degree of Master of Science in Biology/Ecology

submitted by

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March 2015

ABSTRACT

Fragmentation of native habitats is a deeply visible result of human land exploitation. It alters population viability due to a decrease in habitat availability and an increasing isolation of each of the remaining habitat patches, reducing the connectivity between populations. More and more research has been done in order to understand the impacts of habitat fragmentation on different species and on biodiversity, but conservation measures are still often initiated on the basis of sparse data and incomplete knowledge. There is growing recognition and concern that research is rarely used in conservation leading to non-scientific/experience-based conservation. This study aimed to provide scientific evidence for a conservation project in Schwyz, Switzerland by determining the following: (1) the presence of individuals of *Bombina variegata* in newly built ponds, supposed to enhance connectivity of subpopulations of this species in the area, (2) survival probabilities among sexes and among different pond sites and (3) the dispersal rates between sites, if there are any. Data from a four-year mark recapture study was used to estimate recapture and survival. A total of 2665 adult individuals (1395 males, 895 females) were captured during the years 2011-2014 in the different pond complexes. The presence of *B. variegata* was recorded in three of the ten new pond complexes. Monthly recapture probabilities varied widely and were highest for males in all pond complexes. There was a significance influence of sex in monthly and annual survival. Monthly and annual survival was higher overall for males. There were among-site differences in monthly survival. No migration rates could be estimated due to lack of migration of individuals. The fact that seven of the ten new pond complexes remain empty requires intense analysis. Lower female survival is consistent with other studies of this and other anuran species. More long-term studies are needed for determining the effectiveness of this conservation project.

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1. INTRODUCTION

Broad-scale destruction and fragmentation of native habitats is a deeply visible result of human land exploitation all around the world (Bennett & Saunders 2010). Anthropogenic activities such as urbanisation, road and other infrastructure developments, regulation of rivers, drainage of wetlands, intensive forestry and agriculture lead to “a discontinuity in the spatial distribution of resources and conditions present in an area at a given scale” (Franklin et al. 2002). As a consequence, habitat fragmentation alters population viability due to a decrease in habitat availability and an increasing isolation of each of the remaining habitat patches, reducing the connectivity between populations. Decreasing habitat area affects local population viability by reducing population size (Joly et al. 2003) whereas isolation affects viability because it reduces migration between populations. The reduction in immigration rates has a negative effect on populations due to the fact that the demographic and genetic contributions of immigrants tend to increase the size and fitness of insular populations, thereby reducing the probability that they will become extinct (demographic rescue effects)(Brown & Kodric-Brown 1977). Habitat fragmentation also implies genetic consequences because a small population size favours genetic drift and inbreeding. These both processes result in the erosion of genetic diversity and alteration of fitness (Joly et al. 2003). Hence, habitat fragmentation has a direct effect on fitness and reproductive success of populations (Diffendorfer 1998, Hartel 2008), making them vulnerable to catastrophic mortality and inbreeding depression.

More and more research has been done in order to understand the impacts of habitat fragmentation on different species and on biodiversity (Andrén 1994, Fahrig 2003). Many conservation actions have been developed around the world as to protect potentially endangered or already endangered species. Some of the measures taken are:

increasing the size of existing fragments and the total amount of habitat in the landscape (Dolman et al. 2007), controlling degrading processes, such as the invasion of exotic plants and animals and managing the extent and impact of harvesting natural resources (e.g. timber)(Bennet & Saunders 2010). Nonetheless, one of the measures that is most used in conservation biology is the creation of habitat components that enhance connectivity in the landscape (e.g. continuous “corridors” or “stepping stones”)(Fischer & Lindenmayer 2002; Baum et al. 2004; Boscolo et al. 2008) which create linked networks of habitat, thus reducing the detrimental effects of isolation explained above (Hernández et al. 2015).

In spite of these efforts, conservation measures are still often initiated on the basis of sparse data and incomplete knowledge (Karanth et al. 2003). Theoretically, these gaps should disappear with the inclusion of scientific knowledge into conservation practice. Conservation methods and practices should be continually improved through an iterative process of incorporating the results and evidence from scientific studies (Pulliam 1995). However, in reality, conservation practitioners often rely on past experience and personal opinion rather than the scientific literature to make and improve their decisions (Walsh et al 2014). As a consequence, there is growing recognition and concern that research is rarely used in conservation and this has led to non-scientific/experience-based conservation. Therefore, there is a high need for evidence-based conservation to accurately evaluate the success of conservation projects. In the light of the current lack of scientific information in conservation actions, the present study aims to evaluate the effectiveness of a conservation project in Switzerland.

Among the taxa that would benefit the most from evidence-based conservation actions are amphibians, since their worldwide decline has been raising important conservation issues during the last decades (Houlahan et al. 2000). Nowadays, nearly one third of all

amphibian species are considered threatened (Stuart et al. 2004). Explanations for the global decline of amphibian species remain inconsistent and sometimes elusive (Warren & Büttner 2008) and cause-effect relationships are not always exactly proven (Beebee & Griffiths 2005). Several possible causes have been reported such as habitat destruction, alteration, and fragmentation, diseases, introductions of invasive species, pollution, climate change or combinations of all of these (Rodríguez-Pérez et al. 2013, Scott et al. 2013).

In the highly fragmented landscapes of Middle Europe amphibians often inhabit single ponds (Sinsch et al. 2012) and several studies have demonstrated how amphibian species richness is positively influenced by pond density and connectivity at a regional level (Ficetola et al. 2009; Jeliaskov 2014). The yellow-bellied toad *Bombina variegata* (Anura, Bombinatoridae) is an example of a declining species potentially threatened by habitat loss due to habitat fragmentation and pond isolation (Cayuela et al. 2013). Due to its dependence of well-connected small, ephemeral water bodies (Scheele et al. 2014), this species is vulnerable to land-use change including land abandonment and land-use intensification (Canessa et al. 2013) *B. variegata* is categorized as Endangered on the official IUCN Red List Switzerland (Schmidt & Zumbach 2005) and disappearances of local populations have been observed since the late 1970s. Nowadays, most of the species' populations in Switzerland have disappeared, having gone extinct in the Southern and Northern parts of the Alps as well as in the Rhône Valley and only a few populations remain in the Swiss Plateau.

The Swiss federal and regional authorities financially support the implementation of habitat connectivity measures with the aim of preventing habitat fragmentation and enhancing the exchange of individuals among populations in fragmented landscapes (Angelone & Holderegger 2009). In order to protect the remaining populations of *B.*

variegata present in the area of Schwyz, Switzerland and increase their connectivity, the project “Vernetzung Gelbbauchunken Schwyz-Ingenbohl” which started in 2008, built new pond complexes in the autumn of 2011. The areas between Goldau and Ingenbohl, in the canton of Schwyz, are the only areas in Switzerland where *B. variegata* still shows high population numbers (Schlitner et al. 2010). Due to the high importance of this area for the conservation of *B. variegata*, these new pond complexes were created for enhancing the population dynamics (e.g. emigration, immigration, survival) of the remaining populations of *B. variegata* in the area. It is also hoped to enhance the population dynamics of other amphibian species such as the Common Toad (*Bufo bufo*) and the Palmate Newt (*Triturus helveticus*) (Schlitner et al. 2010).

Population dynamics and demography are commonly analyzed using capture-mark-recapture (CMR) modeling methods (Lebreton et al. 1992). Cormack-Jolly-Seber models allow the estimation of survival and recapture probabilities between distinct locations or populations. Thus, this study aims to determine if the conservation actions undertaken by the project “Vernetzung Gelbbauchunken Schwyz-Ingenbohl” do actually work and have a positive effect on a population of *B. variegata* in Schwyz. Therefore, the objective of this study is to model the population dynamics of the population of the yellow-bellied toad in Schwyz from which CMR data have been collected over four consecutive years. This study is of high value due to the fact that, as mentioned above, although conservation action has increased globally, it still lacks meticulous and exhaustive evaluation and is still based on personal experience and/or interpretations of traditional land management practices (Pullin et al. 2004). Sutherland et al. (2004) stated “that a greater shift to evidence-based conservation would not only be highly effective, but is also likely to result in enhanced funding by actively demonstrating this effectiveness to funders and policy formers”. Demonstrating the effectiveness of

conservation actions is highly important nowadays and this study aims to provide scientific evidence for the efficacy of a conservation project.

The specific questions that I will address are:

- ▶ Are the new built ponds actually being used by individuals of *Bombina variegata*?
- ▶ Does monthly and annual survival vary between sexes and between the different pond sites?
- ▶ What are the dispersal rates between populations, if there are any?

As mentioned above, isolation affects the viability of amphibian populations because it reduces migration between them (Lenhardt et al. 2013). This reduction in migration/dispersal rates has a negative effect on populations, causing higher inbreeding and the loss of genetic diversity within populations, making them more vulnerable to catastrophic mortality and inbreeding depression. Fahrig & Merriam (1985) determined that a minimal migration between patches (which in this case would be the pond sites) results in a higher probability of population extinction in the patch, so that the probability of survival of a population in the patch will be very low. By determining survival as well as dispersal rates, it will be possible to ascertain the effectivity of the conservation project. Thus, for this project, high survival and dispersal rates hint towards enhanced connectivity, while low survival and dispersal rates hint towards little connectivity.

2. MATERIALS AND METHODS

2.1 Study species

The yellow-bellied toad (*B. variegata*) occurs in France, Belgium, the Netherlands, Luxemburg, Switzerland, Italy, Germany, many parts of the Czech Republic, Austria, Bosnia and Herzegovina, Croatia, Kosovo, Macedonia, Montenegro, Serbia, Slovenia, Bulgaria, Greece, Albania and along the arc formed by the Carpathian Mountains (Arntzen 1978).

B. variegata is well adapted to small water bodies, including those associated with human activities, such as potholes and irrigation ponds (Barandun 1990; Barandun & Reyer 1997). It shows plasticity in the number of breeding events and in the choice of spawning sites (Canessa et al. 2013). Reproduction is triggered by heavy rainfall over an extended period of time and egg-laying is distributed in time and space (Seidel 1995), which is seen as a risk-spreading strategy as the species often breeds in temporary pools which are permanently at risk of desiccation. Because of this spread egg laying the species needs a network of water habitats to breed in. Females produce several clutches per year during their prolonged breeding period and each clutch consists of 45 to 100 eggs. The hibernation period typically runs from September-October until March-May, during which time, toads overwinter in burrows, cracks, holes, and under stones and logs.

The temporary water bodies preferred by this species have limited canopy cover and high insolation, allowing high water temperatures and fast larval development, thus minimizing the threat of desiccation (Warren & Büttner 2008). These sites are also favoured since they rarely hold populations of fish, leeches, aquatic beetles, dragonfly larvae and newts which prey on the eggs and tadpoles (Hartel et al. 2007).

Despite having a wide distributional range, the yellow-bellied toad is a threatened species throughout Europe and, as mentioned above, it is recognized as an endangered species on the official Red List Switzerland (Schmidt & Zumbach 2005). The habitat range of *B. variegata* in Switzerland is limited to the northern side of the Alps and the biggest populations can be found throughout the Swiss Plateau (from Geneva to Lake Constance; Meyer et al. 2009). The species is locally extinct for the southern side of the Alps (Meyer et al. 2009).

The causes of decline not only centre on habitat fragmentation, but also on drainage or water abstraction which lowers the water table, causing the temporary breeding ponds to disappear or to dry out too quickly in summer to allow successful breeding. Eutrophication and pollution caused by leaching of nutrients from surroundings, airborne nitrogen, pesticides and other agrochemicals are also causes of population decline (Morand & Joly 1995).

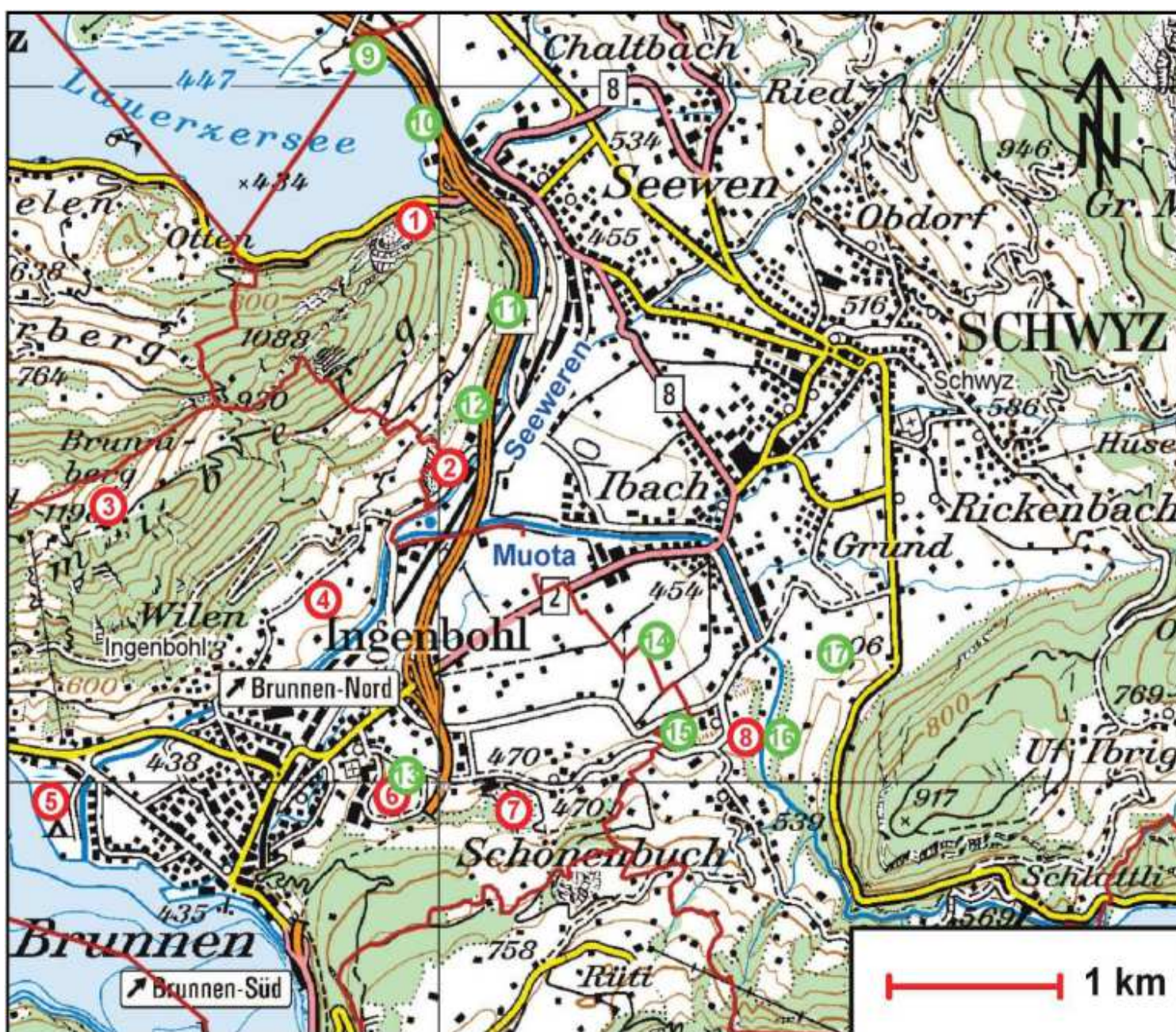
2.2-Study site

The pond complexes are located in the basin of the neighbouring municipalities of Ingenbohl (47° 0' 10.97" N, 8° 36' 42.02" E) and Schwyz (47° 1' 13.97" N, 8° 39' 29.99" E) in the canton of Schwyz, Switzerland and are flanked by a mountain belt comprising the mountains Urmiberg, Fronalpstock and the Grosser Mythen. This area is highly fragmented due to the presence of the A4 highway, the long Schwyz-Brunnen railroad, the road that connects both municipalities and the intensive farming and agriculture that takes place in the area.

The 17 pond complexes are located in quarries (e.g. Steinbruch Zingel, Steinbruch Nägeli, Steinbruch Unterschönenbuch), conservation areas (e.g. Hopfräben, Halten, Schornen, Hinter Ibach), grasslands used for agriculture and settlement zones (Fig. 1). Isolated populations of *B. variegata* have been identified in several pond complexes in

the area from historical records (red circles in Fig.1). In spring 2011 these populations were surveyed by Daniel Hasen as his Bachelor thesis (Hasen 2011). In the autumn of 2011, further pond complexes (green circles in Fig. 1) were built as part of the conservation project “Vernetzung Gelbbauchunken Schwyz-Ingenbohl”, with the aim of enhancing connectivity of these isolated subpopulations. In 2012 these new ponds, in addition to the previously existing ponds, were surveyed by Martin Jordan (Jordan 2012). The pond complexes are located between 430 m.a.m.s.l. (e.g. Hopfräben) and 1070 m.a.m.s.l (e.g. Brunniberg) and are separated by a distance of between 160 m and 1300 m. A new pond complex (690.4/208.45) around 200 m northeast from the pond complexes “Zivilschutzanlage” was created by the end of the year 2013 and was first sampled in May and July 2014.

The conservation project “Vernetzung Gelbbauchunken Schwyz-Ingenbohl“, which started in 2008 is part of an even bigger conservation project called “Vernetzung Talkessel”. This project was initiated in 2005 and aims to enhance the connectivity of other isolated species and the conservation and protection of the flora and fauna present in the area (Öko-Qualitätsverordnung, 2011).



1. Steinbruch Zingel
2. Steinbruch Nägeli
3. Brunniberg
4. Wilen
5. Hopfräben
6. Klosterweiher
7. Steinbruch Unterschönenbuch
8. Hinter Ibach
9. Schornen
10. Seemättli
11. Rossmatt
12. Zivilschutzanlage
13. Halten
14. Chrummriedmatt
15. Hasenbühl
16. Schachen Ost
17. Degenberg

Fig 1. Overview map of the study area. The old pond complexes are marked with red circles while the new pond complexes built in 2011 are marked with green circles (Jordan 2012)

2.3-Field work

Data were collected during two years (2013 and 2014). During this period all 17 ponds complexes were sampled eight times: each pond was sampled twice in May and July of each year. In addition, data from the “old” ponds was available from 2011 (3 sampling occasions in June-July 2011; Hasen 2011), and data from all ponds were available for 2012 (2 sampling occasions in July 2012; Martin 2012). The data of these surveys was also included in my data analysis. Figure 2 shows a sampling scheme over the four consecutive years.

	May	June	July
2014	10★ 11★		12★ 13★
2013	6★	7★	8★ 9★
2012			4★ 5★
2011		1★	2★ 3★

Fig 2. Sampling scheme over four consecutive years. In total, 13 sampling occasions were conducted.

Surveys were conducted during night-time to correspond with peak calling and mating activity of yellow-bellied toad individuals. Surveys started at 19.30 h the earliest and finished at 03.35 h the latest. The time spent catching individuals varied from pond to pond due to differences in site size: more time was needed for bigger ponds than for smaller ones. As a general rule, surveys ended when the number of caught individuals did not increase significantly for a long period of time (approximately 30 minutes). It was agreed that in places with a very high number of individuals catching time should not exceed two hours, because a “depletion” of the population was not possible. This decision was taken after the surveys that took place in May 2013 where some places

surveyed during that time were sampled for about three hours. The surveys that followed (July 2013 and May-July 2014) were done under the agreement mentioned above.

Adults were captured by hand and sexed, except for the individuals caught in 2012, which were not sexed by Jordan (2011). These individuals were categorized as “unknown sex” in the statistical analysis. These individuals were later sexed if some of them were recaptured in later sampling occasions. Males are easily distinguished from females by their swollen and pigmented nuptial pads on the 1st, 2nd and 3rd fingers and on the inner surface of the forearm (Barandun & Reyer 1998). A picture of the specific belly pattern of each captured individual was taken in order to allow further individual identification. Pictures were taken as follows: each frog was put into a petri dish containing a piece of foam material in its bottom half. Frogs were then put with their backs on the top half of the petri dish and then turned upside down in order to take the picture (Fig. 3). The piece of foam helped immobilize the individual while taking the picture. Pictures were taken with a Sony Cyber-shot digital camera (model DSC-T77). Adults were kept in compost containers filled with water during the surveys so as to avoid recapture of individuals and were immediately released after pictures of all the individuals were taken.



Fig. 3. Procedure for taking the pictures of the yellow-bellied toads (Jordan 2012).

2.4-Photo-Identification

Each individual can be identified individually due to the fact that the belly pattern is unique for each frog (the pattern does not change after the metamorphosis of the individuals Gollmann & Gollmann 2011). This makes the use of toe-clipping and other invasive marking methods unnecessary. The pattern is typically an irregular array of black spots on a yellow background. Since all specimens of *B. variegata* are distinguishable individually by the belly pattern, individual capture histories can be reconstructed by comparing the pictures from different capture occasions (Fig. 4).



Fig. 4. Pictures showing the belly pattern of different individuals from the study site. (Photo by Hannelore Brandt).

Capture histories of all individuals were constructed by comparison of photographs to identify recaptures. This time-consuming task was done for this project with the software Wild-ID (Version 1.0)(Bolger et al. 2011), which is a picture pattern extraction and matching program. This software uses the scale invariant feature transform algorithm (SIFT; Lowe, 2004) for pattern extraction, compares the geometric arrangement of the SIFT features of each pair of images, and calculates a match score. The most suitable photo for each individual was selected (in terms of sharpness and position of the animal) and edited. When necessary, brightness and contrast were modified, and each photo was cut in order to obtain only an image of the abdomen. The

objective of this cut was to minimize the sources of error due to the photo background and the invariant regions of individual coloration (head and extremities) (Bolger et al. 2011). Wild-ID then shows the 20 top-ranked matches for visual confirmation. All pictures taken in the years 2011, 2012, 2013 and 2014 were compared with this program, helping to generate each individual's complete capture history.

Since one of the goals of the project was to determine if the pond complexes were used as spawning areas by *B. variegata*, the presence/absence of juveniles in the pond complexes for the years 2013-2014 was recorded, but individuals were not counted.

2.5-Statistical Analysis

An initial aim of the study was to examine migration between pond complexes using multi-state mark recapture analysis. However, following construction of capture histories it became apparent that insufficient migration events occurred (3 events), thus the data were instead analysed using Cormack-Jolly-Seber CMR analysis.

2.5.1. Goodness of Fit-Test

Goodness-of-fit (GOF) was tested using programs U-CARE 2.2 (Choquet et al. 2005) and RELEASE (incorporated into MARK; Burnham et al. 1987). The U-CARE GOF-test was performed by Michael Schaub. Due to lack of migration of the individuals a single-state GOF was performed. The single-state GOF tests the assumptions of the Cormack-Jolly-Seber (CJS) model, which estimates survival and recapture probabilities under an open population framework (Pollock et al. 1985). Assumptions do not permit survival to differ between newly marked and previously marked individuals, or recapture probability to differ between animals encountered at the previous occasion and those not encountered.

2.5.2 Modelling Recapture and Survival Probabilities

A small set of candidate models for recapture probability was defined and fitted to the data. For determining the best model for recapture probability each candidate model was run while keeping the model for survival probability at the highest complexity ($\Phi(\text{sex}*\text{time}*\text{site})$).

Recapture probability was expected to be influenced by sex of the individuals. Barandun et al. (1997) determined higher capture and recapture rates of males demonstrating that males tend to be more active and in higher numbers in spawning areas compared to females. Therefore, recapture probability was expected to be higher for males than for females in this study. Recapture probability was also expected to be influenced by the pond site of the individuals, since the probability of recapturing individuals from smaller populations and smaller pond complexes is higher compared to bigger populations and bigger pond complexes. I also expected recapture probability to be influenced by time. Based on these expectations the following set of candidate models was created (notations follow Lebreton et al. (1992): “sex”= variation between males, females and unknown sex, “t”=time dependence (i.e. monthly variation), “site”= variation among pond sites, “.”=constant probability):

- 1) $p(\text{sex}*t*\text{site})$
- 2) $p(\text{sex}*\text{site})$
- 3) $p(\text{sex})$
- 4) $p(\text{site})$
- 5) $p(t)$
- 6) $p(.)$
- 7) $p(t*\text{site})$
- 8) $p(\text{sex}+t+\text{site})$

9) $p(t+site)$

Model 1) is the most general model allowing differences of p between sexes, in every month (t) and all pond sites ($site$) with interaction. Model 2) tested if p was influenced by the sex and pond site of the individuals, while models 3) and 4) tested if p was influenced only by sex or pond site of the individuals, respectively. Model 5) tested a fully time-dependency of p , while model 6) set p to be constant in time. Model 7) tested for an interaction of time and pond site influencing p , model 8) tested for additive effects of sex, time and population on p , while model 9) tested for additive effect of time and site. The candidate model with the lowest AICc value was selected for further analysis. The analysis of the models accounted for unequal time intervals between capture events (the difference of time between capture events ranged from 2 weeks to 10 months). Due to sparse data and to avoid overparameterization, the factor time was grouped as follows: variables $t_1, t_2, t_3, t_4, t_5, t_6, t_7$ for which capture probabilities were defined as equal for the capture occasions that took place during the same months within the same year. Hence t_1 refers to the sampling occasions in July 2011, t_2 to the sampling occasions in July 2012, t_3 to the ones in May 2013, t_4 to the ones in June 2013, t_5 to the ones in July 2013, t_6 to the ones in May 2014 and t_7 to the sampling occasions that took place in July 2014. There were a total of 13 capture occasions.

Survival rate (Φ) is a measure of the probability that a frog survives and is present in the sampling area. I wanted to test whether survival rates (Φ) differ among sexes (sex) and among pond sites (site), as well as over time, either alone or in an interactive (*) or an additive (+) manner. A set of candidate models was created and fitted to the data, using the previously identified best model for recapture probability. The candidate models were the following:

- 1) $\Phi(\text{sex}*\text{t}*\text{site})$
- 2) $\Phi(\text{sex}+\text{site})$
- 3) $\Phi(\text{sex}+\text{t})$
- 4) $\Phi(\text{sex})$
- 5) $\Phi(\text{site})$
- 6) $\Phi(\text{t})$
- 7) $\Phi(.)$
- 8) $\Phi(\text{t}*\text{site})$

2.5.3. Model Selection

Program R (R Development Core Team 2012) and the package RMark (Laake 2013), as well as program MARK (Version 7.1; White and Burnham 1999) were used for analysing the data. I used the small sample correction of Akaike's Information Criterion (AICc) (Akaike 1973, Hurvich & Tsai 1989) and Akaike weights (ω_i) for determining which model best described the data (Burnham & Anderson 2002). The AIC is calculated as follows

$$\text{AIC} = -2 \ln(L) + 2K$$

where L is the model likelihood and K is the number of parameters in the model. AICc accounts for model likelihood and number of parameters used in such a way that higher model likelihood and fewer parameters result in lower AICc's. Hence, the best model always has the lowest AICc. Akaike weights are derived from AICc differences (ΔAICc) and indicate the relative support of a model, given the data and the set of candidate models.

A Cormack-Jolly-Seber capture-mark-recapture model (Brownie et al. 1993, Schwarz et al. 1993) was used for determining and modelling monthly survival and recapture probabilities. Only data from adult individuals was used. The SS model is composed of two parameters: recapture probability (p) and survival probability (Φ). The recapture probability is a measure of the probability that a frog, which was caught previously, is caught again. The survival rate is a measure of the probability that a frog survives and is present in the sampling area. In this study we were interested to determine if survival rates differ among sexes and the different pond complexes.

A step-down approach (Lebreton et al. 1992) was used for guiding the modelling. First, the top model for recapture probability was determined by comparing the models in the candidate set while keeping the complexity of the other model component (Φ) high. After determining the best model for recapture probability, that model was used to compare each of the candidate models for survival rate. After having run the models, AICc and Akaike weights (ω_i) were used to determine which model best described the data. The model with the lowest AICc and the highest ω_i was chosen as the model which best fitted the data. Parameter estimates of recapture and survival probabilities were obtained using RMark. Annual survival probabilities were calculated as:

$$\text{Monthly survival probability}^{12} = \text{Annual survival probability}$$

3. RESULTS

3.1 Capture Data

A total of 2665 adult individuals (1395 males, 895 females and 375 individuals who were not sexed in the year 2012) were captured during the years 2011-2014 in the different pond complexes. At six of the pond complexes (Klosterweiher, Schornen, Seemättli, Halten, Schachen Ost and Degenberg) no individuals were captured during the surveys. Of the sites at which individuals were seen, the largest number of captures occurred at the Hinter Ibach complex, which is an old pond complex, whereas Rossmatt (new pond complex) presented the fewest (Table 3.1). Postmetamorphic juveniles were recorded as present in the sites Brunniberg, Hinter Ibach, Hopfräben, Nägeli, Unterschönenbuch and Zingel.

3.2 Statistical Analysis

3.2.1 Goodness of Fit-Test

The goodness-of-fit (GOF) tests ran with U-CARE and RELEASE showed that the assumptions of the Cormack-Jolly-Seber (CJS) model were met and that the model with sex, pond site and time-specific survival and recapture probabilities ($\Phi(\text{sex}*\text{site}*t)p(\text{sex}*\text{site}*t)$) fitted the data well ($\chi^2_{\text{U-CARE}}=218.3$, $df=243$, $p=0.871$; $\chi^2_{\text{RELEASE}}=179.9$, $df=207$, $p=0.913$).

3.2.2 Model Selection

Modelling Recapture and Survival Probabilities

The model selection analysis showed that recapture probability was best described by the model that included the additive effects of sex, time and pond site (Akaike weight=1.00)(Table 3.2a) and survival probability was best described by the model that

Table 3.1. Number of captured individuals over four consecutive years. A *-sign indicates that the pond site did not exist for a specific year.

Pond site	Sex	Year				Total
		2011	2012	2013	2014	
Brunniberg	Males	2	1	2	14	19
	Females	3	3	4	36	46
	Undefined	0	21	0	0	21
Chrummriedmatt	Males	*	0	7	3	10
	Females	*	0	2	1	3
	Undefined	*	3	0	0	3
Hasenbühl	Males	*	0	0	0	0
	Females	*	0	0	0	0
	Undefined	*	7	0	0	7
Hopfräben	Males	6	0	0	8	14
	Females	1	0	0	1	2
	Undefined	0	1	0	0	1
Hinter Ibach	Males	103	3	52	270	428
	Females	189	9	34	201	433
	Undefined	0	66	0	0	66
Nägeli	Males	41	3	65	213	322
	Females	13	0	19	77	109
	Undefined	0	52	0	3	55
New Site	Males	*	*	*	2	2
	Females	*	*	*	1	1
	Undefined	*	*	*	0	0
Rossmatt	Males	*	0	0	0	0
	Females	*	0	0	0	0
	Undefined	*	1	0	0	1
Unterschönenbuch	Males	4	0	22	356	382
	Females	21	3	23	170	217
	Undefined	0	116	33	0	149
Wilén	Males	14	1	66	110	191
	Females	2	0	23	30	55
	Undefined	0	36	2	0	38
Zingel	Males	13	1	0	1	15
	Females	8	5	0	0	13
	Undefined	0	14	0	0	14
Zivilschutzanlage	Males	*	0	3	9	12
	Females	*	0	6	10	16
	Undefined	*	18	2	0	20
Total	Males	183	9	217	986	1395
	Females	237	20	111	527	895
	Undefined	0	335	37	3	375

included the additive effects of sex and pond site, but excluded time effects (Akaike weight=1.00)(Table 3.2b).

Table 3.2. Ranking of the different models in the candidate set for modelling a) recapture probability (p) and b) survival probability (Φ) in different pond sites of *Bombina variegata*. The ranking is based on AICc values. Model notation follows Lebreton et al. (1992). The variable “t” refers to time dependence (monthly variation), “site” refers to variation among pond sites and “sex” refers to variation between males and females. Table entries are the number of estimated parameters (np), the AICc values, the difference of the AICc value of the current model and of the best model (Δ AICc), the Akaike weight (Weight) and the deviance of the model (Dev). All models for modelling recapture probability were built with $\Phi(\text{sex} * t * \text{site})$, all models for modelling survival probability were built with $p(\text{sex} + t + \text{site})$.

a)

Model	np	AICc	Δ AICc	Weight	Dev
$p(\text{sex} + t + \text{site})$	421	7449.45	0.00	1.00	1701.59
$p(t + \text{site})$	419	7485.32	35.87	0.00	1742.71
$p(t * \text{site})$	540	7565.41	115.96	0.00	1491.28
$p(t)$	408	7658.24	208.79	0.00	1944.40
$p(\text{sex} * \text{site})$	429	7942.12	492.67	0.00	2173.18
$p(\text{site})$	408	7942.68	493.23	0.00	2228.84
$p(\text{sex})$	399	8099.3	649.85	0.00	2408.83
$p(.)$	397	8157.51	708.06	0.00	2472.22
$p(\text{sex} * t * \text{site})$	792	8188.23	738.77	0.00	1320.94

b)

Model	np	AICc	Δ AICc	Weight	Dev
$\Phi(\text{sex} + \text{site})$	35	7014.45	0.00	1.00	2161.24
$\Phi(\text{sex} + t)$	35	7060.85	46.40	0.00	2207.64
$\Phi(\text{sex})$	24	7073.43	58.98	0.00	2242.62
$\Phi(\text{site})$	33	7148.42	133.97	0.00	2299.29
$\Phi(t)$	33	7206.69	192.24	0.00	2357.56
$\Phi(t * \text{site})$	165	7232.39	217.95	0.00	2102.48
$\Phi(.)$	22	7232.76	218.31	0.00	2406.01
$\Phi(\text{sex} * t * \text{site})$	417	7534.23	519.78	0.00	1796.87

Recapture probabilities were higher for males than for females. Recapture probability was highest for the capture occasions of July 2014 and May 2014 (in that order) and lowest for the capture occasions in May 2013 (Table 3.3). There were among-site differences in recapture probabilities. Recapture probability was highest in the pond complexes “Chrummriedmatt”, “Steinbruch Zingel” and “Zivilschutzanlage and lowest

for the pond sites “Hinter Ibach”, “Steinbruch Unterschönenbuch” and “Steinbruch Nägeli” (Appendix, Figure A.1).

TABLE 3.3. Beta-estimates (and 95% confidence intervals) on the logit scale of recapture probability for individuals of *Bombina variegata*. Estimates are based on the model $\Phi(\text{sex} + \text{site})p(\text{sex} + \text{time} + \text{site})$. The variables t1, t2, t3, t4, t5, t6, t7 refer to the grouping made for capture probabilities by the variable “time” due to sparse data: capture probabilities were defined as equal for the capture occasions that took place during the same months within the same year. Hence t1= June 2011, t2= July 2011, t3=July 2012, t4= May 2013, t5=July 2013, t6= May 2014, t7= July 2014. Pond complexes: CHR= Chrummriedmatt, HAS= Hasenbühl, HOP= Hopfräben, IBA= Hinter Ibach, NAG= Steinbruch Nägeli, NEW= New Site, ROS= Rossmatt, UNT= Steinbruch Unterschönenbuch, WIL= Wilen, ZIN= Steinbruch Zingel, ZIV= Zivilschutzanlage.

Factor	Recapture probability (95% confidence interval) (logit scale)
Intercept	-3.73 (-5.23, -2.22)
Sex (Males)	0.50 (0.30, 0.70)
Sex (Unknown)	0.47 (-0.08 0.94)
t1	0.84 (-0.77, 2.44)
t2	2.59 (1.07, 4.11)
t3	3.17 (1.66, 4.67)
t4	1.72 (0.19, 3.26)
t5	2.49 (1.20, 4.19)
t6	3.69 (2.20, 5.18)
t7	3.94 (2.46, 5.43)
site (CHR)	0.72 (-0.76, 2.20)
site (HAS)	-0.76 (-49.84, 48.32)
site (HOP)	-0.20 (-2.37, 1.97)
site (IBA)	-1.94 (-2.29, -1.59)
site (NAG)	-1.19 (-1.56, -0.82)
site (NEW)	-11.86 (-3238.80, 3215.08)
site (ROS)	14.70 (-2242.93, 2272.33)
site (UNT)	-1.35 (-1.70, -0.99)
site (WIL)	-1.76 (-2.17, -1.34)
site (ZIN)	0.35 (-0.66, 1.35)
site (ZIV)	0.12 (-0.42, 0.65)

Monthly recapture probabilities were highest for males in all pond complexes. Monthly recapture probabilities for males were highest in the pond complex “Chrummriedmatt”, where values ranged from 0.31-0.81, while the lowest male recapture probabilities were for the pond complex “Hinter Ibach”, where values ranged from 0.01-0.23 (Appendix, Figure A.1b and A.1d). Recapture probabilities for females was also highest in

“Chrummriedmatt”, with values ranging from 0.22-0.72, while the lowest female recapture probabilities were for the pond complexes “Hinter Ibach” and “Wilén”, with values ranging from 0.01-0.15 and 0.01-0.18, respectively (Appendix, Figure A.1b, A.1d and A.1g).

Survival probability was higher overall for males. There were among-site differences in monthly survival (Table 3.4). For most pond sites, survival was around 0.91-0.98, but for the pond sites “Chrummriedmatt”, “Hopfräben” and “New Site” survival was substantially lower (Fig. 3.1).

TABLE 3.4. Beta-estimates (and 95% confidence intervals) on the logit scale of survival probability for individuals of *Bombina variegata*. Estimates are based on the model $\Phi(\text{sex} + \text{site})p(\text{sex} + \text{time} + \text{site})$. Pond complexes: CHR= Chrummriedmatt, HAS= Hasenbühl, HOP= Hopfräben, IBA= Hinter Ibach, NAG= Steinbruch Nägeli, NEW= New Site, ROS= Rossmatt, UNT= Steinbruch Unterschönenbuch, WIL= Wilén, ZIN= Steinbruch Zingel, ZIV= Zivischutzanlage.

Factor	Survival probability (95% confidence interval) (logit scale)
Intercept	3.55 (3.08, 4.02)
Sex (Males)	0.32 (-0.01, 0.65)
Sex (Unknown)	-2.32 (-2.72 -1.92)
site (CHR)	-3.13 (-4.36, -1.90)
site (HAS)	-2.03 (-101.72, 97.67)
site (HOP)	-3.32 (-6.90, 0.26)
site (IBA)	0.09 (-0.42, 0.61)
site (NAG)	-0.92 (-1.47, -0.37)
site (NEW)	-6.64 (-2692.00, 2678.72)
site (ROS)	-0.20 (-3.50, 3.10)
site (UNT)	0.12 (-0.43, 0.67)
site (WIL)	-0.66 (-1.32, 0.00)
site (ZIN)	-1.20 (-1.87, -0.53)
site (ZIV)	-0.42 (-1.17, 0.32)

Monthly survival was highest for males in the pond complexes “Brunniberg”, “Hinter Ibach” and “Steinbruch Unterschönenbuch” with a value of 0.98 for all three complexes (Fig. 3.1). Survival probability for males was lowest in the pond complex “New Site” with

a value of 0.06. Monthly survival for females was highest in the pond complexes “Steinbruch Unterschönenbuch” (0.98), “Brunniberg” (0.97) and “Hinter Ibach” (0.97) and lowest in the complex “New Site”, with a value of 0.04 (Fig. 3.1).

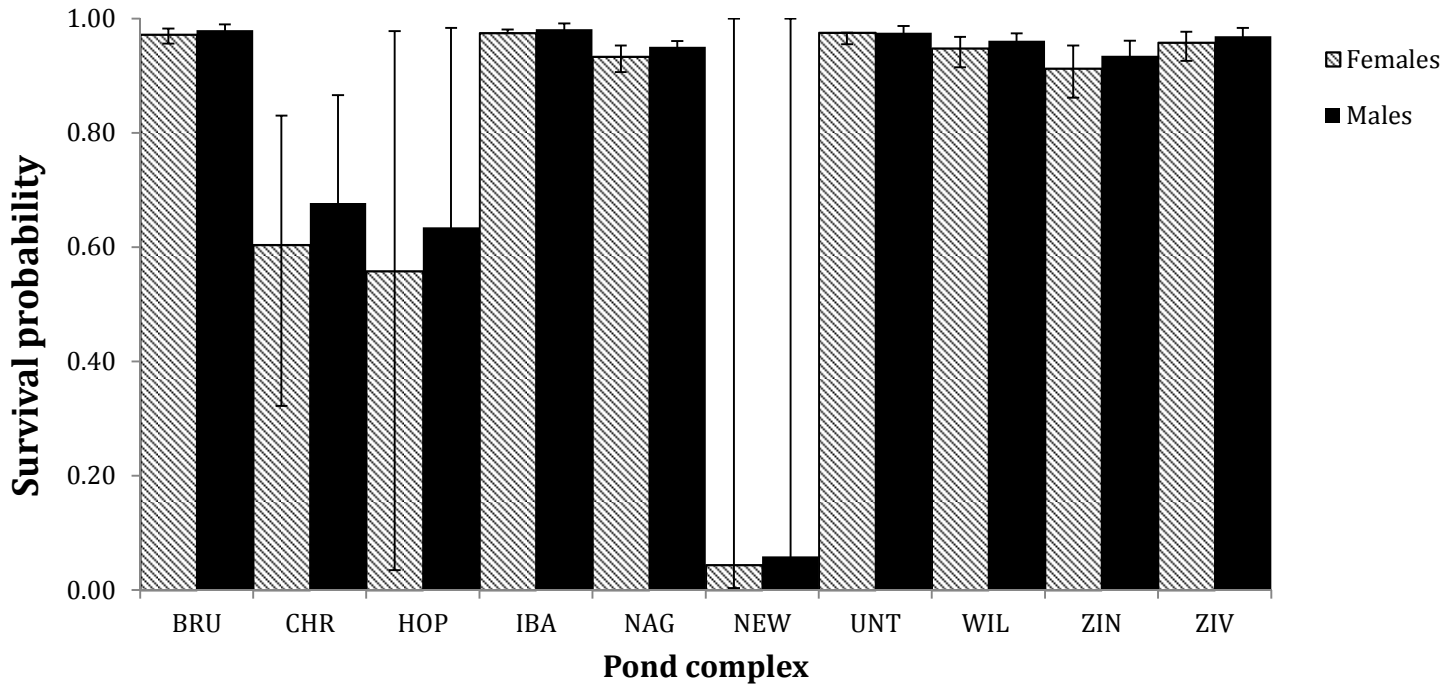


FIGURE 3.1. Estimates (mean and 95% confidence interval), based on the model $\Phi(\text{sex} + \text{site})p(\text{sex} + \text{time} + \text{site})$ of monthly survival probabilities of males and females of *Bombina variegata* in twelve pond complexes. Pond complexes: BRU= Brunniberg, CHR= Chrummriedmatt, HAS= Hasenbühl, HOP= Hopfräben, IBA= Hinter Ibach, NAG= Steinbruch Nägeli, NEW= New Site, ROS= Rossmatt, UNT= Steinbruch Unterschönenbuch, WIL= Wilen, ZIN= Steinbruch Zingel, ZIV= Zivilschutzanlage.

Annual survival was highest for males in the pond complexes “Hinter Ibach” (0.80), “Brunniberg” (0.78) and “Steinbruch Unterschönenbuch” (0.74)(Fig. 3.2). Annual survival probability for males was lowest in the pond complexes “Chrummriedmatt” (0.01), “New Site” and “Hopfräben”, both with a value of 0.01. Annual survival for females was highest in the pond complexes “Steinbruch Unterschönenbuch” (0.74), “Hinter Ibach” (0.73) and “Brunniberg” (0.71) and lowest in the pond complexes “Chrummriedmatt”, “New Site” and “Hopfräben”, all with a value of 0.00 (Fig. 3.1).

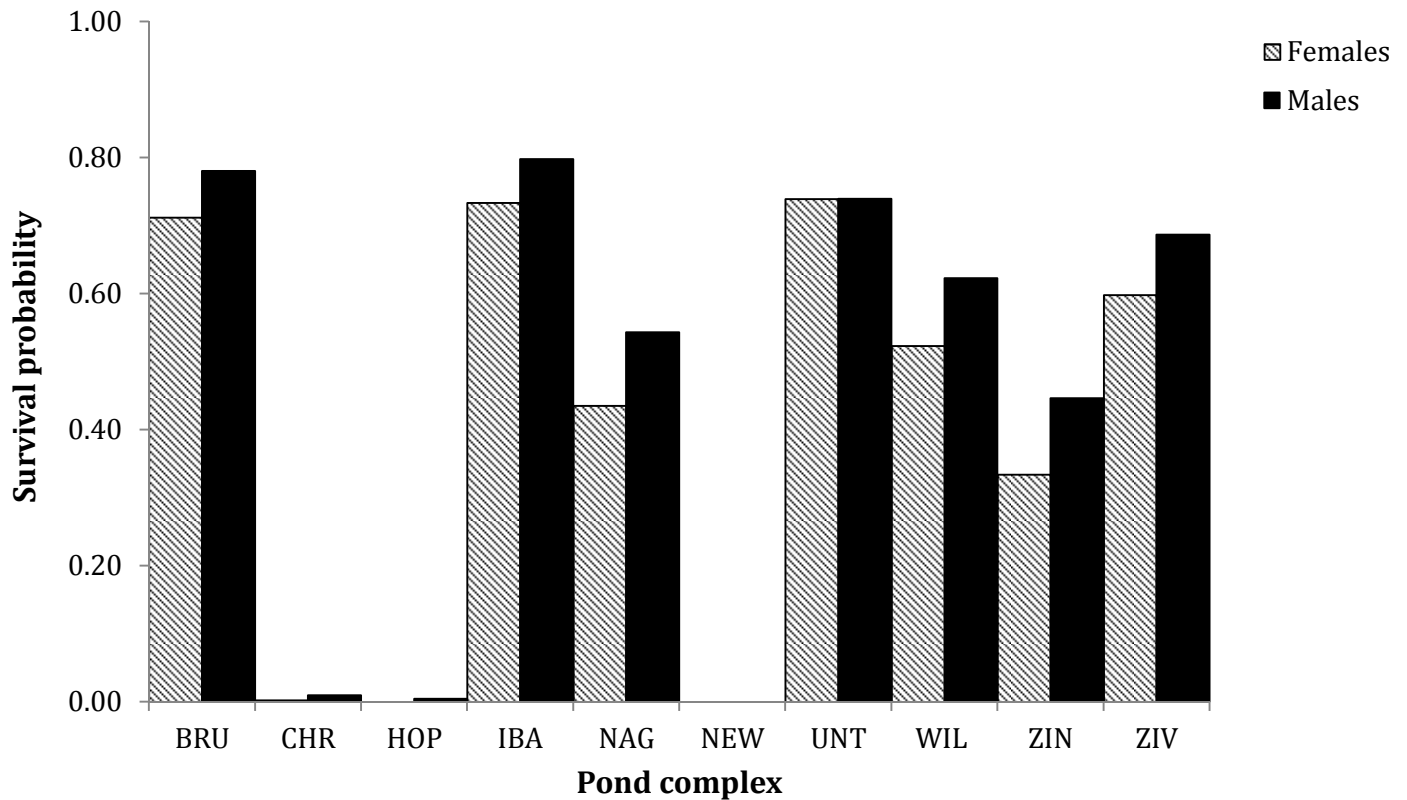


FIGURE 3.2. Estimates, based on the model $\Phi(\text{sex} + \text{site})p(\text{sex} + \text{time} + \text{site})$ of annual survival probabilities of males and females of *Bombina variegata* in twelve pond complexes. Pond complexes: BRU= Brunniberg, CHR= Chrummriedmatt, HAS= Hasenbühl, HOP= Hopfräben, IBA= Hinter Ibach, NAG= Steinbruch Nägeli, NEW= New Site, ROS= Rossmatt, UNT= Steinbruch Unterschönenbuch, WIL= Wilen, ZIN= Steinbruch Zingel, ZIV= Zivilschutzanlage.

4. DISCUSSION

The analysis of mark-recapture data of yellow-bellied toads showed that there was substantial variation in recapture probabilities among sexes, months and pond sites as well as substantial variation in survival probabilities among sexes and pond sites.

Recapture probabilities

Recapture probabilities varied over the different capture occasions in the field and between sexes, in such a way that males showed higher recapture probabilities than females. This result could have arisen from the fact that males are easier to detect than females and hence, males get caught more often than female individuals. When in the field at night, singing male individuals are not only used as reference points for finding the ponds but are also detected faster and more easily, since they keep singing even when torchlight is directed straight towards them (*pers. obs.*). Females, on the other hand, remain silent and floating around the singing males, hidden within the pond's vegetation, making their detection more difficult.

The differences in recapture probabilities between months can be explained by differences in capture effort. Although it was not possible to incorporate capture effort in the statistical analysis, it is possible that this factor explains at least part of the variation in recapture probabilities due to the following: many of the sampling occasions in the year 2013 were conducted by myself alone, which can explain the low recapture probabilities for those seasons, while the sampling occasions in 2011, 2012 and 2014 were always conducted by at least two people. Sampling by three people was not uncommon in the year 2014. In addition, the month May 2013 was a very cold month, with an average temperature of 8.4 °C and a maximum temperature of 18.2 °C (website: rp5.md), compared with May 2014, which had an average temperature of 9.9 °C and a

maximum temperature of 23.5 °C. The sampling occasions of the years 2011 and 2012 took place in the months of June-July 2011 and July 2012, which had higher temperatures. The period of June-July 2011 had an average temperature of 17.2°C, with a maximum temperature of 31.7 °C, while the month of July 2012 had an average temperature of 18.4 °C and a maximum temperature of 30.6 °C (website: rp5.md). For successful sampling occasions of amphibians, Schlüpmann & Kupfer (2009) recommend performing the sampling with minimum temperatures of 12-13 °C. In addition, Zweifel (1959) found a strong positive correlation of calling rate of male individuals of *B. variegata* with temperature. Lower temperatures mean lower calling rates, making the detection of individuals harder. Thus, lower average temperatures and a lower number of sampling persons may have had influenced the recapture probabilities of the year 2013.

The differences of recapture probabilities between sites can also be explained by different habitat characteristics among pond complexes. The pond complex that had the highest recapture rates between males and females was “Chrummriedmatt”, which was built in 2011 and comprises five plastic basins between 1.3-2.0m long, 1.0m wide and between 25-38cm deep, arranged in one group of three basins positioned 190 m away from a second group of two (Schlitner & Hertach, 2012). The sampling area of this pond complex is very small and the vegetation around the basins is low-cut grass, which facilitates the detection and capture of individuals, even if they swim to the bottom of the basin when disturbed. The other pond complex that showed high recapture probabilities was “Zivilschutzanlage”, which shares similar characteristics with “Chrummriedmatt” (six concrete troughs between 0.5-2.0m long x 0.5 m x 0.5 m, separated by a few meters and with no vegetation around besides low grass). The pond complexes that showed the lowest recapture probabilities (“Hinter Ibach”, “Steinbruch

Unterschönenbuch", "Wilen") are characterized by their large areas (0.9 ha, 0.2 ha and 0.3 ha respectively (Hasen 2011)) and numerous little ponds, which make sampling and capturing more difficult.

Despite these habitat characteristics and differences in sampling effort and temperature between sampling occasions, the hypothesis that capture heterogeneity may also provide relevant biological information, revealing underlying biological traits (e.g. social structure) of wild populations has been receiving increasing support (Crespin et al. 2008). Cayuela et al. (2014) also found fluctuating recapture probabilities according to capture session in a population of *B. variegata* in northeastern France. In their study, they explained heterogeneity in recapture probability as a result of differing habitat characteristics among ponds, which influenced either capture effectiveness or the amount of time an individual spent in a pond in a given year, influencing their availability for being captured. Hence, more studies are needed to define if the observed differences in recapture probabilities in my study exist due to biological traits of *Bombina variegata* (intrinsic heterogeneity as called by Crespin et al. 2008) in addition to heterogeneity induced by the study design itself.

Survival probabilities

Monthly and annual survival probabilities were higher for males than for females, independent of the pond complex, which is consistent with results reported for *B. variegata* by Barandun et al (1997). Lower female survival has been also found in the wood-frog (*Rana sylvatica*; Berven 1981), the afro-tropical pig-nosed frog (*Hemisus marmoratus*; Grafe et al. 2004) and the common toad (*Bufo bufo*; Loman & Madsen 2010). Thus, lower female survival may be a general phenomenon in anurans. One explanation for these differences may be related to differences in costs of breeding

between sexes and the “trade-off” theory, which studies the relationship between the reproductive effort of females in one season and the probability that she will survive to the next season. Following this theory, females and males differ in their survival probabilities due to the fact that the overall energy cost of sexual reproduction is higher in females than in males (oogenesis is costlier than spermatogenesis), causing lower survival probabilities for females (Yanagi & Miyatake 2009). Cayuela et al. (2014) also cite escaping unwanted sexual attention and injuries inflicted by males during attempts at amplexus as factors that may reduce female survival. As mentioned above, lower survival probabilities in females of *B. variegata* were reported by Baradun et al. (1997). Nevertheless, they also found that the annual individual reproductive output for females is very low (average clutch sizes of 40-70 eggs) compared to most other aquatic spawning anurans (average clutch sizes of 120-300 eggs). This lower reproductive output may have a positive influence on female survival, which may explain the small differences in survival between the sexes in this study.

Survival probabilities were found to be highest in the pond complexes that presented a bigger sampling area, the highest numbers of caught individuals and the biggest water bodies, like “Hinter Ibach”, “Steinbruch Unterschönenbuch”, “Wilen” and “Steinbruch Nägeli”. This can be explained by the fact that yellow-bellied toads prefer water bodies with large water volume and high water temperature, which ensure the longest water periods (Cayuela et al. 2011). These conditions not only promote rapid larval development, but it has been found that survival of amphibians can be negatively affected by a water deficit because excessive water loss by evaporation through the skin increases mortality (Wardziak et al. 2013). As a consequence, individuals of *B. variegata* may avoid places where water loss is high and select places which present large water volumes, like “Hinter Ibach” and “Wilen”. This would also explain why no individuals

were found at the new places “Hasenbühl” and “Schachen Ost”, since its ponds were dry in the years 2012 and 2013 and partially dry in the year 2014. Low survival probabilities can also be explained by the presence of predators (not only of adults but also of tadpoles and juvenile individuals) in the pond sites. For example, the area “Hopfräben” is a mire and natural reserve protected by the canton, and the presence of fish, ducks and swans, which may be potential predators (Abbühl 1997), was recorded there.

Non-colonised pond complexes

The absence of *B. variegata* in seven of the ten new pond complexes (“Schornen”, “Seemättli”, “Rossmatt”, “Halten”, “Schachen Ost”, “Hasenbühl” and “Degenberg”) may be explained by several reasons. For most populations, monthly survival was high and larger than 90% (i.e. pond sites “Brunniberg”, “Hinter Ibach”, “Steinbruch Nägeli”, “Steinbruch Unterschönenbuch”, “Wilen”, “Steinbruch Zingel” and “Zivilschutzanlage”). Because this is apparent survival, this represents the probability that the toad survived and did not emigrate from the site. As a consequence, this implies low emigration rates from one pond site to the others. Another reason that may explain the non-colonisation of some pond complexes is the large distances of some of these pond complexes (“Schornen”, “Seemättli”, “Rossmatt”, “Halten”, “Schachen Ost”, “Hasenbühl” and “Degenberg”) from those with the biggest populations which may therefore serve as “source” ponds (the old places “Hinter Ibach”, “Steinbruch Unterschönenbuch”, “Wilen” and “Steinbruch Nägeli”). Hartel (2008) showed that the average between-pond distances covered by individuals of *B. variegata* for the study period of three years was 161 m for males and 172 m for females. Although another study conducted in 1980 showed shorter distances for both sexes (males moved in average 63.8 m, while females moved 20.0 m over a period of one year (Beshkov & Jameson 1980)), it is clear that *B.*

variegata is not a species that presents great dispersal distances. Jordan (2012) determined the linear distance of those new pond complexes that were as a maximum 1.5 km away from the “source” ponds. From the new pond complexes, “Schornen”, “Seemättli” and “Degenberg” were more than 1.5 km away from their nearest “source” complex, while the pond complexes “Rossmatt”, “Zivilschutzanlage”, “Chrummriedmatt” and “Hasenbühl” showed distances of 300m (“Nägeli” <-> “Zivilschutzanlage”), 800m (“Rossmatt” <-> “Zingel”, “Chrummriedmatt” <-> “Hinter Ibach”), 1200m (“Hasenbühl” <-> “Steinbruch Unterschönenbuch”) and exactly 1500m (“Wilen” <-> “Zivilschutzanlage”). The proximity of these new pond complexes to the bigger, older ones may have facilitated their colonisation by individuals of *B. variegata*.

Nevertheless, proximity to “source” water bodies is not the only factor that plays a crucial role in site colonisation by yellow-bellied toads. Pond characteristics, such as limited canopy cover and high insolation (allowing high water temperatures and fast larval development (Warren & Büttner 2008)), as well as pond area and longer water periods, determine if the pond will be selected or not by individuals of *B. variegata* as spawning areas (Canessa et al. 2013, Cayuela et al. 2011). As mentioned above, the new sites “Schachen Ost” and “Hasenbühl” were dry during the sampling for this study, which makes them unsuitable for yellow-bellied toads. The places “Seemättli”, “Halten” and “Degenberg” presented considerable more vegetation growth compared to the other ones. This vegetation growth impedes high insolation of the water, probably rendering the water too cold for the spawning of individuals of *B. variegata*. As mentioned above, a combination of many factors make certain places suitable or not suitable for colonisation by the yellow-bellied toad. Although in the sites “Klosterweiher” and “Rossmatt” the presence of yellow-bellied toads was reported in the past studies, no individuals were found in 2013 nor 2014. All these two places showed very high

vegetation growth (which in addition prevented an optimal sampling), algae growth and deep waters, which may be factors that prevented colonisation by *B. variegata*.

Conclusion

This study aimed to assess the effectiveness of conservation actions by providing scientific evidence of the outcomes of a conservation project in Schwyz, Switzerland.

It was shown that there was substantial variation in recapture probabilities among sexes, months and sites as well as substantial variation in survival probabilities among sexes and sites of the species *B. variegata* in the region of Schwyz, Switzerland. The differences in recapture probabilities may be explained not only by variation induced by the study design itself, but also by biological traits of the species (i.e. differences in sex ratios not only in the spawning areas but also in the surroundings, influence of weather condition in calling activity of males and thus, in their detectability). These biological traits have not been studied for this species in this area, and thus, it is strongly recommended that future analyses take them into consideration. Although reasons why survival probabilities differed between sexes and sites were presented here, many variables which may explain these variations more accurately (i.e. individual size, presence and number of egg clutches per pond, exact pond area, distance in meters between ponds) were not measured for this study. Therefore, it is recommended that these variables should be measured in the future.

The fact that seven of the ten new pond complexes remain empty, while the other three were colonized one year after their construction requires intense analysis. As mentioned before, *B. variegata* is not a species that wanders long distances, thus, the creation of an adequate density of ponds within a small radius may decrease the isolation by distance

between the fragmented aquatic habitats, enhancing connectivity and easing the individuals' movements through the landscape.

More studies like this one are needed in future years to provide accurate scientific evidence for the effectiveness not only of this conservation project, but of conservation actions all around the world.

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6. ACKNOWLEDGEMENTS

Special thanks to Benedikt Schmidt, Arpat Ozgul and Sam Cruickshank for their advice and helpful comments. To Daniela Flück, Laurent Montagano, Joaquim Golay, Alejandro Marín, Ranluca Bancila, Hedwig Ens, Marco Plebani and Benedikt Schmidt for helping me in the field. To the Tierpark Goldau for letting me and the people that helped me stay in the Interns' Rooms, so we did not have to drive back to Zürich late at night after each sampling occasion. And last but not least, to my parents for giving me the opportunity to make an academic degree and for their support over all the years at university.

7. APPENDIX

Figure A.1. Estimates (mean and 95% confidence interval), based on the model $\Phi(\text{sex} + \text{site})p(\text{sex} + \text{time} + \text{site})$ of monthly recapture probabilities of males (■) and females (△) of *Bombina variegata* in the pond complexes a) Brunniberg, b) Chrummriedmatt, c) Hopfräben, d) Hinter Ibach, e) Steinbruch Nägeli, f) Steinbruch Unterschönenbuch, g) Wilen, h) Steinbruch Zingel, i) Zivilschutzanlage. The variables t1, t2, t3, t4, t5, t6, t7 refer to the grouping made for capture probabilities by the variable “time” due to sparse data: capture probabilities were defined as equal for the capture occasions that took place during the same months within the same year. Hence t1= July 2011, t2= July 2012, t3=May 2013, t4= June 2013, t5=July 2013, t6= May 2014, t7= July 2014.

