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Beaver as an Ecosystem Engineer that Creates Habitat for Amphibians



Gabriela Patricia Gschwend

Supervision by:

Dr. Benedikt Schmidt, KARCH & University of Zurich

Prof. Dr. Arpat Ozgul, University of Zurich

Institute of Evolutionary Biology and Environmental Sciences
University of Zurich, Switzerland

Zusammenfassung

Interaktionen zwischen Organismen sind ein wichtiger Bestimmungsfaktor in der Verteilung und Abundanz von Arten. Diese Interaktionen können inter- und intraspezifische Konkurrenz für biotische und abiotische Ressourcen, Prädation, Parasitismus und Mutualismus sein, aber auch das Erschaffen, Verändern und Aufrechterhalten von Habitaten sind darin enthalten. Ein Organismus, der durch seine Anwesenheit oder seine Aktivität seine physikalische Umwelt oder den Fluss von Ressourcen verändert, wird Ökosystem Ingenieur genannt (Jones *et al.* 1994).

Menschen sind Ökosystem Ingenieure *per se* (Jones *et al.* 1994). Sie sind die primären Agenten des Klimawandels in den meisten Regionen der Erde (Naiman 1988). Anthropozentrische Aktivitäten führen zum Verlust und zur Abwertung von Feuchtgebieten; mit Verlusten, die regional 75% überschreiten (Lehtinen *et al.* 1999). Die verbleibenden Feuchtgebiete sind oft durch umliegende Gebiete, die kultiviert oder als Wohngebiet genutzt werden, isoliert (Lehtinen *et al.* 1999).

Biber (*Castor spp.*) sind weitere bekannte Beispiele für Ökosystem Ingenieure (Jones *et al.* 1994). Die Aktivitäten der Biber resultieren in aufgestauten Fließgewässern, gefällten Bäumen und unterspülter Vegetation, führen zur Veränderung von biotischen und abiotischen Verhältnissen und beeinflussen somit das Habitat für andere Arten (Dalbeck *et al.* 2007, Rosell *et al.* 2005). Viele Beispiele zeigen den positive Einfluss des Bibers auf die Biodiversität (Harthun 1999, Dalbeck 2011, Schlüter *et al.* 2008). Andererseits sind Biber mutmassliche Ursachen für menschliche Sicherheits-, Eigentums- und Landwirtschaftskonflikte (Organ & Ellingwood 2000). Diese Konflikte sind vor allem dadurch verursacht, dass sich Biber an Kulturpflanzen verpflegen, Entwässerungsgräben aufstauen, Gebiete unterhöhlen oder Teiche in Siedlungsgebieten oder Kläranlagen besiedeln (Halley & Rosell 2002). Für Landwirte bedeutet die Stauaktivität der Biber, dass das geflutete Land der Landwirtschaftszone verloren geht und zu einem Feuchtgebiet umfunktioniert wird (Hood 2006).

Während der Nutzen des Bibers als Ökosystem Ingenieur für die Biodiversität im Wald gut dokumentiert ist, fehlen diesbezüglich Studien im Landwirtschaftsland. Diese wären aber für eine Beurteilung der Sachlage bei Nutzungskonflikten notwendig. Die

vorliegende Arbeit untersucht den Nutzen des Bibers für eine gefährdete Artengruppe, die Amphibien, im Landwirtschaftsland.

Amphibien haben den grössten Anteil gefährdeter Arten innerhalb der Wirbeltiere (Stuart *et al.* 2004). Amphibien sind besonders von Zerstörung und Fragmentation von Feuchthabitaten betroffen, weil sie für die Reproduktion an Gewässer gebunden, aber als Adulttiere von geeignetem terrestrischem Habitat abhängig sind (Dalbeck & Weinberg 2009). Zahlreiche Amphibienarten in Mitteleuropa pflanzen sich vorzugsweise in sonnigen stehenden Gewässern fort; dauerhaften oder temporären Feuchtgebieten, wie sie auch vom Biber hervorgebracht werden (Dalbeck *et al.* 2007). Studien, durchgeführt in Deutschland (*Castor fiber*) und Kanada (*Castor canadensis*), fanden, dass die durch Biber veränderte Umgebung wichtige Habitate für verschiedene Amphibienarten sind (Dalbeck *et al.* 2007, Stevens *et al.* 2007). Aufgrund ihrer Resultate, folgerten Dalbeck *et al.* (2007), dass Biber eine entscheidende Rolle im Amphibienschutz spielen.

Ich habe in dieser Studie das Vorkommen von Amphibien an 70 Biberdämmen im Kanton Zürich und Thurgau untersucht, wobei aufgrund geringer Datenmenge nur die Daten vom Grasfrosch (*Rana temporaria*) statistisch ausgewertet werden konnten. Um Herauszufinden, welche habitat-spezifischen Merkmale (Table 1) das Vorkommen des Grasfrosches beeinflussen, erstellten wir eine Liste mit Kandidatenmodellen (Appendix 3) und wandten „Belegungsmodelle“ nach MacKenzie *et al.* (2003) an. Die gesammelten Zählraten von Grasfrosch-Laichballen wurden mit „Generalized Linear Mixed Effect Models (GLMMs)“ analysiert, wobei eine Poisson-Regression angewendet wurde (Kéry 2010). Die GLMMs erlaubten es uns, die durchschnittliche Abundanz von Grasfrosch-Laichballen für einen einzelnen Weiher zu schätzen und die potentiellen Effekte der Kovariablen (Table 1) zu untersuchen.

Die Resultate zeigten, dass der Grasfrosch das neue Habitat an Biberdämmen im Wald, wie auch auf dem Landwirtschaftsland, tatsächlich nutzt. Die Variable, welche beschreibt, ob sich der Weiher im Wald oder aus Landwirtschaftsland befindet, war nicht im besten Modell enthalten. Das heisst, dass die Lokalität des Weihers weder Einfluss auf das Vorkommen, noch auf die Abundanz des Grasfrosches hat und sowohl Weiher im Wald als auch Weiher auf Landwirtschaftsland gleichermassen als Habitat geeignet sind. Weiter

konnte ich aufgrund meiner Beobachtungen zeigen, dass auch gefährdete Arten (Schmidt & Zumbach 2005) von dem von Bibern erschaffenen Habitat profitieren (Table 3).

Das beste Modell zum Vorkommen des Grasfrosches beinhaltete die Kovariable, die beschreibt, wieviel Prozent des Weihers von Schilf bedeckt ist, als erklärende Variable. Der Effekt war jedoch nicht signifikant, weil das Vertrauensintervall 0 beinhaltete (Table 5). Schilfdeckung war neben Wasserpflanzen, Holzablagerungen, Deckung des Kronendachs, Fläche mit seichtem Wasser und Präsenz von Fischen, auch im besten Modell zur Abundanz des Grasfrosches enthalten (Table 7). Alle Variablen, ausser Wasserpflanzen hatten einen positiven Effekt auf die Abundanz des Grasfrosches (Figure 3).

Im Vorfeld der vorliegenden Arbeit konnte bereits gezeigt werden, dass Schilf und andere aquatische Vegetation gute Indikatoren sind, um Vorkommen und Abundanz des Grasfrosches (Reid *et al.* 2014) und anderer Amphibien (Hartel *et al.* 2007, Sztatecsny *et al.* 2004) vorherzusagen. Die architektonischen Modifikationen, welche die Diversität des Habitats beinhaltet, bieten Strukturen für Laichanlagerungen, erhöhtes Nahrungsangebot, aber auch Verstecke vor Räubern. Letzteres begünstigt die Koexistenz von Amphibien und Fischen (Dalbeck & Weinberg 2009, Stott *et al.* 1998), was auch in den hier vorliegenden Resultaten bestätigt wurde. Auch die Präferenz des Grasfrosches für Weiher mit seichtem Wasser, die in der vorliegenden Arbeit gefunden wurde, wird durch die Literatur unterstützt (Dalbeck *et al.* 2007, Savage 1962). Während der Feldarbeit fiel mir auf, dass die Grenzen von geflutetem Grasland auf Landwirtschaftsland eine hohe Dichte an Laichballen und Larven des Grasfrosches beherbergten. Hier könnten die wärmeren Bedingungen durch das Fehlen von Schatten durch Bäume eine Rolle spielen (Savage 1962, Dalbeck *et al.* 2007, Stevens *et al.* 2006). Im besten Modell dieser Studie wird jedoch höhere Abundanz für zunehmende Deckung des Kronendaches vorhergesagt.

Die vorliegende Arbeit zeigte, dass die Aktivität von Bibern zu wertvollen Erschaffungen und Veränderungen der Umgebung für Amphibienarten führt. Wie auch bereits von anderen Studien (Cunningham *et al.* 2007, Dalbeck *et al.* 2007, Stevens *et al.* 2006) vorgeschlagen, könnten Biber eine wichtige Rolle im Amphibienschutz inne haben. Wir konnten die Bedeutsamkeit eines Ökosystem Ingenieurs, des Bibers, für den Schutz anderer Arten aufzeigen und unterstützen somit die Empfehlung Ökosystem Ingenieure im Artenschutz und Management-Plänen zu berücksichtigen.

Abstract

Beavers (*Castor spp.*) are familiar examples for ecosystem engineers. The ecosystem engineering of beavers results in impounded streams, felled trees and submerged vegetation. Beavers are presumable cause of human safety, property and agricultural conflicts. While the benefits of beaver as ecosystem engineer for biodiversity in the forest are well documented, studies in agricultural land are lacking. However, these would be necessary for an assessment of the situation of land use conflicts. The present study took a look on the benefits of beavers as an ecosystem engineer to an endangered class, the amphibians, on agricultural land. I investigated the distribution and the abundance of amphibians in new beaver-constructed habitats at agricultural streams and which habitat features determined the distribution of amphibians. A set of candidate models was applied to detection/non-detection data of the Common Frog (*Rana temporaria*) and occupancy models were run. Abundance data, *i.e.* counts of egg masses of the Common Frog, was analysed with generalized linear mixed effects models. The model best explaining the occurrence data for the Common Frog incorporated the linear and quadratic effect of percentage of pond covered by reed as covariate to explain occupancy. Furthermore, it included date of visit as covariate for detection probability. Abundance of the Common Frog was best explained by the percentage of the pond covered by aquatic plants, reed, woody debris, riparian canopy cover, area of shallow water and presence of fish, whereby only aquatic plants had a primarily negative effect.

Our results showed that the Common Frog indeed breed in beaver ponds both in the forest and in agricultural areas without a significant difference. Thus, whether the pond was located in the forest or on agricultural land did not have a significant effect, neither on occupancy nor on abundance of the Common Frog. Conclusively, the present study shows that beavers as an ecosystem engineers play a role in the conservation of the Common Frog by means of providing suitable habitat.

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1. Introduction

Interactions between organisms are a major determinant of the distribution and abundance of species. These interactions are inter- and intraspecific competition for biotic and abiotic resources, predation, parasitism and mutualism, but they also include the role of organisms in creating, modifying and maintaining habitats. An organism whose presence or activity alters its physical environment or changes the flow of resources, thereby creating, modifying or maintaining habitats, is called an ecosystem engineer (Jones *et al.* 1994).

Humans are ecosystem engineers *per se* and not showing any fundamental differences in function to other ecosystem engineers (Jones *et al.* 1994). People are the primary agents of environmental change in most areas of the world (Naiman 1988). People build dams and skyscrapers, clear forests, dredge and canalise water courses, which results in altered physical environments and modified resource flow to other species (Jones *et al.* 1994). Anthropogenic measures, as contamination, nutrient loading, drainage, sinking of water table and destruction of wetlands, caused massive changes in water bodies in the recent history (Czech & Lisle 2003). Human activities led to a loss and degradation of wetlands; with losses exceeding 75% regionally (Lehtinen *et al.* 1999). The remaining wetlands are often isolated due to the surrounding areas that are cultivated or residential (Lehtinen *et al.* 1999).

Beavers (*Castor spp.*), another well-known examples for ecosystem engineers (Jones *et al.* 1994) create wetlands and it has been shown that areas with beaver dams contained 60% more water during a dry period than the same area previously to the immigration of beavers (Hood 2006). The ecosystem engineering of beavers results in impounded streams, felled trees and submerged vegetation. This ecosystem engineering leads to changes of biotic and abiotic conditions, i.e. species composition, course of succession, hydrology, geomorphology, water chemistry and temperature, and thereby also affects the habitat for other species (Dalbeck *et al.* 2007, Rosell *et al.* 2005). There are numerous examples of beaver ecosystem engineering showing positive effects on biodiversity (Harthun 1999, Dalbeck 2011, Schlüter *et al.* 2008). Impounded water bodies and branches at beaver dams provide biotopes with shelter and food for various fish species. In turn, fish-eating species as ducks, otters or storks profit of an improved food supply. Further, beavers have an impact on forest ecology due to the flood-caused die back of less water-tolerant trees. The latter again

provide habitat for insects and woodpeckers and moreover improved food supply also for bats (Schlüter *et al.* 2008).

The Eurasian beaver (*Castor fiber*), as many other species, had to suffer persecution by humans in the last centuries. After near eradication of the Eurasian beaver in the 19th century, beaver populations recovered due to protection and reintroduction programs in the 20th century (Halley & Rosell 2002). Today it is more important to understand the ecological roles of those returnees and people now have to face different challenges of cohabitation. Beavers are presumable cause of human safety, property and agricultural conflicts (Organ & Ellingwood 2000). These conflicts are mainly caused by beavers feeding on cultivated plants, impounding drainage channels, undermining areas or colonise ponds in settlements or sewage works (Halley & Rosell 2002). For farmers it means that beavers promote water retention in agricultural areas, by implication that the flooded land is removed from the agricultural zone in means of its transformation into a wetland.

While the benefits of beaver as ecosystem engineer for biodiversity in the forest are well documented, studies in agricultural land are lacking. However, these would be necessary for an assessment of the situation of land use conflicts. The present study takes a look on the benefits of this ecosystem engineer for an endangered class, the amphibians, on agricultural land. In that, I investigate the distribution and the abundance of amphibians in new beaver-constructed habitats at agricultural streams and by which habitat features that distribution of amphibians is determined. If amphibians indeed colonise beaver ponds on agricultural land, it could be concluded that beavers play an important role in amphibian conservation.

Amphibians have the highest proportion of endangered species among vertebrates and suffered of a massive decline in the last decades (Stuart *et al.* 2004). The study subjects, the amphibians are particularly affected by destruction and fragmentation of wetland habitats, because they are tied to water bodies for reproduction and as adults also dependent on suitable land habitats (Dalbeck & Weinberg 2009). Numerous amphibian species of Central Europe preferably reproduce in sunny stagnant water bodies; permanent or temporary wetlands as they are also created by beavers (Dalbeck *et al.* 2007). Thus, amphibians are likely to be in favour of the redesigned habitat. Studies conducted in Germany on the Eurasian Beaver (*Castor fiber*) as well as on the North American Beaver

(*Castor canadensis*) in Canada found that beaver-altered environments are important habitats for several amphibian species (Dalbeck *et al.* 2007, Stevens *et al.* 2007). A comparative study of artificial versus beaver ponds found that both ponds supported the same amphibian species, but the species were more abundant at ponds created by beavers (Dalbeck & Weinberg 2009). Dalbeck *et al.* concluded in 2007, that the increase in habitat heterogeneity caused by beaver activity led to an increase in amphibian species in their study area and further that beavers may therefore play a crucial role for the conservation of amphibians.

The above-mentioned and other studies on beaver and amphibians were conducted on beaver ponds in forests. The colonisation of streams in agricultural areas by beavers is only recent and has not been considered in studies yet. However, this colonisation is assumed to be highly important for amphibian conservation, because the beaver ponds on agricultural land could provide additional habitat to amphibians. Observations could already confirm that amphibian species are immigrating at beaver ponds located on agricultural land (personal communication with Christof Angst, CSCF). The aim of the present study is to provide further knowledge about beavers and amphibians in Switzerland and provide research-based evidence to mitigate the conflict of land use between beavers and farmers. Precisely, I will test whether there are benefits of beavers for amphibians in agricultural areas and provide information about amphibian habitat preferences. For farmers, this means that there are also positive consequences when beavers colonise their land.

I expect to confirm the colonisation of beaver ponds on agricultural land by amphibians. However, the different species are not expected to occur uniformly at different ponds due to species-specific habitat requirements and rarity. I expect the Common Frog to be the most abundant in ponds on agricultural land as well as in the forest, because the species is widespread and has low habitat requirements compared to other amphibian species (Savage 1962). Pond age might play a role, since habitat heterogeneity is more diverse at older ponds. Habitat heterogeneity, *i.e.* aquatic plants, reed, woody debris, but also the area of shallow water and connectivity of a pond are expected to play a major role in habitat features.

2. Methods

2.1 Study subjects

For this study, all amphibian species that require lentic water bodies for reproduction or as adults and are present in Switzerland were of interest. Thus, I familiarised myself previous to the fieldwork with the following species: Common Frog (*Rana temporaria*), Edible Frog (*Pelophylax esculentus*), Pool Frog (*Pelophylax lessonae*), Marsh Frog (*Pelophylax ridibundus*), Agile Frog (*Rana dalmatina*), Common Toad (*Bufo bufo*), Natterjack Toad (*Bufo calamita*), Midwife Toad (*Alytes obstetricians*), Yellow-bellied Toad (*Bombina variegata*), Palmate Newt (*Lissotriton helveticus*), Smooth Newt (*Lissotriton vulgaris*), northern Crested Newt (*Triturus cristatus*), Alpine Newt (*Ichthyosaura alpestris*). The Common Frog (*Rana temporaria*) is known to colonise new ponds very quickly (Gollmann *et. al* 2002). It is therefore expected to be the most widespread and abundant amphibian species at the beaver ponds surveyed in this study. However, beaver ponds are also known to be suitable for more rare species (Dalbeck *et al.* 2007).

Beavers (*Castor fiber*) live in families of three generations and are territorial. Their territories have multiple dams, lodges, earth constructions and ponds. The fieldwork was conducted in 15 different territories in the cantons Zurich and Thurgau that were chosen randomly out of a list provided by the Beaver consulting service of the Swiss Biological Records Center (CSCF). These territories contained a total of 70 beaver dams, of which 23 were located in the forest and 47 on agricultural land. Every water body behind a beaver dam with reduced flow was decided to be a pond.

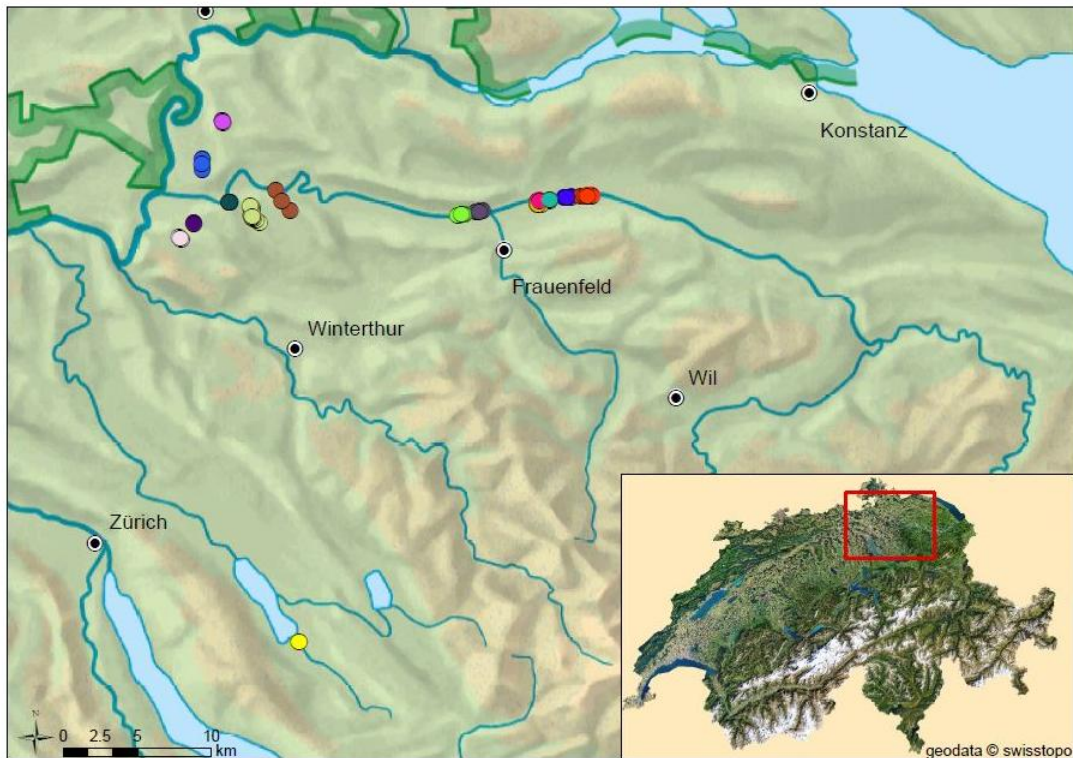


Figure 1: The map shows the 15 randomly chosen territories; each one represented by an individual colour. The points represent a single beaver pond.

2.2 Data collection

I wanted to analyse how the distribution of amphibian species is influenced by the beaver pond-related factors (Table 1). Amphibians were surveyed on three visits to each beaver pond at daytime towards the end of the breeding season of *Rana temporaria* (March). Egg masses of the Common Frog (*Rana temporaria*) were counted and detection/nondetection data were recorded for adult amphibians by walking around the edge of each beaver pond. In a second phase, each pond was visited three times at nights from April onwards to get detection/nondetection data on larvae and adult amphibian species. I used visual encounter surveys and call surveys to record detection/nondetection data (Dodd 2009). I was always accompanied by a field assistant during the field excursions at nights. A species was noted as present when at least one individual of a species could be detected auditory or visually within a 15 minutes observation at a pond. Detection probability is highly influenced by weather conditions; therefore, I only went to the field when it was not raining at the time of observation. An example of the original protocol can be found in the appendix (the protocol was supplemented by separate notes for an additional visit at daytime and another additional visit at nights) (Appendix 1).

2.3 Explanatory variables

Explanatory variables were chosen according to previous studies and general knowledge about amphibians. A complete list of all covariates and what was measured is shown in Table 1. In order to examine whether there are differences in colonisation between ponds situated on agricultural land and in forests, the location of the pond (LAND) was recorded as a binary variable. When recording the location, only the immediate vicinity of the pond was considered. The point of this examination is to show that amphibian species do indeed colonise habitat on agricultural land, despite vast literature showing that agricultural land tends to influence amphibian population negatively (Van Buskirk 2005). However, ponds on agricultural land might be highly attractive to amphibians, because of the adults' preferences for warmer breeding sites (Skelly & Freidenburg 2000, Stevens *et al.* 2006). Because amphibian species differ in their habitat preferences with respect to forest cover (Van Buskirk 2005), it is expected that different amphibian species occur at different frequencies in the two habitat types, *i.e.* the diversity of amphibian species is richer in the forest.

Connectivity of ponds (CONNEC) is assumed to be a major factor that is positively related to the presence/absence and abundance of amphibian species (Cushman 2006). The following assumptions according to Hanski (1999) are applied to connectivity (Figure 2), except the assumptions for the area for a pond. "A" was unknown and set equal 1.

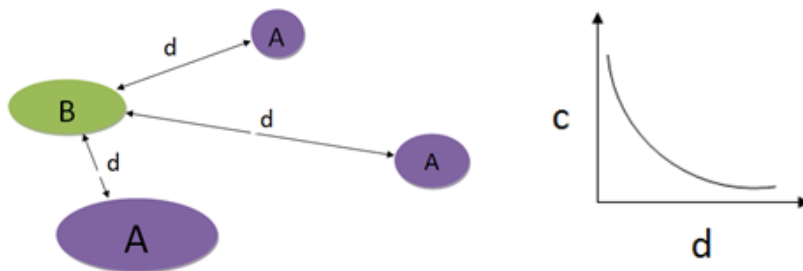


Figure 2: Assumptions applied for connectivity. On the left: Simplified illustration of the situation in the field. B=beaver pond, A=Amphibian pond. On the right: Negative exponential relation between distance (d) and connectivity (c).

The age of a pond is expected to be related to the variables explaining vegetation structure. Generally, amphibian species are expected to be more abundant at older ponds, where canopy cover is reduced by beavers to a higher extent (Stevens *et al.* 2006), aquatic

plants, reed and woody debris is more frequent (Dalbeck *et al.* 2007) and the dam itself is wider and higher. Older ponds might even better allow coexistence of fish and amphibians (Dalbeck & Weinberg 2009). The Beaver consulting service of the Swiss Biological Record Center (CSCF), the nature station “Silberweide” and Mathis Müller kindly provided me data about the age of the ponds (AGEP). The age of a territory then corresponds the age of the oldest pond in the territory (AGET). Riparian canopy cover (CANCOV) was estimated by means of a template (provided by Christof Angst (CSCF), Appendix 2) that was compared to the shade pattern on the water surface of a pond. Aquatic plant cover (APCOV), reed cover (RCOV) and woody debris cover were estimated according to the proportion of covered pond surface. Dam width (DAMW) and height (DAMH) were measured by a folding yardstick. Fish were noted as present in a pond when an individual could be observed during any of the six field visits.

Sztatecsny *et al.* (2004) found a negative correlation of the pond area and amphibian abundance. Hence, the area of a pond (POSI) and the area of shallow water (SHAWAT) of a pond were calculated by measuring the length and width of the surface of a pond area. Additionally, I noted whether the water surface area was completely stagnant or flowing (WAFLO). Moreover, the presence of amphibians in other ponds (not beaver ponds) or on land (AOSUR) in the vicinity of the beaver ponds was recorded as well in order to investigate whether this has an influence on the probability to colonise a beaver pond by amphibian species. Last but not least, it was noted whether the beavers are still active at a pond. Beaver activity (BACT) was positive when fresh beaver tracks or a beaver itself could be monitored. To account for the dependency of ponds within the same territory, a species-specific term (generally ADT) was added to every model, that described the presence of a species in a territory; *e.g.* RtDT for the analysis of the occurrence data for *Rana temporaria*.

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Table 1: List of explanatory variables with explanations and what was measured for each variable. Note that only part of them was incorporated in each of the candidate models.

ABBREVIATION	EXPLANATION	MEASURE
<i>Surrounding</i>		
LAND	Location of pond = Landscape	Forest or Agriculture
CONNEC	Connectivity of pond	$c = \sum e^{-d \cdot A} = \sum e^{-d \cdot 1}$
AOSUR	Amphibians observed in the surrounding of the pond	Yes/No
ADT	Amphibians detected in the territory of the pond	Yes/No
VISIT	Date of visit; observation covariate	1-35
TER_NO	Territory number; random effect	1-15
<i>Pond characteristics</i>		
AGEP	Age of the pond	1 to 23 years
AGET	Age of the territory of the pond	1 to 23 years
BACT	Beaver activity at the pond (fresh beaver tracks or not)	Yes/No
CANCOV	% of pond area covered by canopy	10% - 100%
APCOV	% of pond covered by aquatic plants	10% - 100%
RCOV	% of pond covered by reed	10% - 100%
WDCOV	% of pond covered by woody debris	10% - 100%
DAMW	Width of the beaver dam	Widest point $\pm 0.5m$
DAMH	Height of the beaver dam	Deepest point in the centre $\pm 0.1m$
SHAWAT	Area of pond with shallow water (<30cm)	m^2
POSI	Pond size	m^2
WAFLO	Flow of the pond water	Yes/No
FISH	Presence of fish in the pond	Yes/No

2.4 Data analysis

The candidate models (Table 2) represent biological hypotheses based on published research or observations during fieldwork (Appendix 3). The simplest model assumed random distribution of amphibians among ponds; *i.e.* amphibians do not prefer any of the pond characteristics described by the chosen variables. In a first step, univariate models were run. Further, the list of candidate models was supplemented by models containing combinations of explanatory variables we expect to be biologically the most relevant among all recorded variables. Quadratic terms of continuous variables were added to investigate whether the relation of explanatory and response variables were nonlinear. Two dams had to be excluded from data analysis, because they were too different in area to the 68 other dams.

The same set of candidate models was applied to occurrence and abundance data. All continuous explanatory variables were z-standardised.

Table 2: Composition of candidate models. List of the explanatory variables that were combined to model occupancy and abundance of amphibian species at beaver ponds.

Model-no.	Model Covariates
00	No covariate
01	VISIT (Observation covariate)
02	ADT (independency of ponds)
03	TER_NO (random effect)
<i>Univariate models</i>	
1	LAND
2	AGEP
3	AGEP + AGE ²
4	AGET
5	AGET + AGET ²
6	CONNEC
7	CONNEC + CONNEC ²
8	AOSUR
9	ADT
10	BACT
11	CANCOV
12	CANCOV + CANCOV ²
13	SHAWAT
14	SHAWAT + SHAWAT ²
15	POSI
16	POSI + POSI ²
17	WAFLO
18	FISH

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19	APCOV
20	APCOV + APCOV ²
21	RCOV
22	RCOV + RCOV ²
23	WDCOV
24	WDCOV + WDCOV ²
25	DAMW
26	DAMW + DAMW ²
27	DAMH
28	DAMH + DAMH ²
<i>Landscape models</i>	
29	LAND + AGEP + AGET
30	LAND + AGEP + AGEP ² + AGET + AGET ²
31	LAND + CONNEC
32	LAND + CONNEC + CONNEC ²
33	LAND + AGEP + AGET + BACT
34	LAND + AGEP + AGEP ² + AGET + AGET ² + BACT
35	LAND + AGEP + AGET + BACT + CANCOV + SHAWAT + FISH
36	LAND + AGEP + AGEP ² + AGET + AGET ² + BACT + CANCOV + CANCOV ² + SHAWAT + SHAWAT ² + FISH
37	LAND + AOSUR + ADT
<i>Pond age models</i>	
38	AGEP + AGET
39	AGEP + AGEP ² + AGET + AGET ²
40	AGEP + AGET + CANCOV
41	AGEP + AGEP ² + AGET + AGET ² + CANCOV + CANCOV ²
42	AGEP + AGET + AOSUR + ADT
43	AGEP + AGEP ² + AGET + AGET ² + AOSUR + ADT
<i>Vegetation structure models</i>	
44	APCOV + RCOV + WDCOV
45	APCOV + APCOV ² + RCOV + RCOV ² + WDCOV + WDCOV ²
46	APCOV + RCOV + WDCOV + SHAWAT
47	APCOV + APCOV ² + RCOV + RCOV ² + WDCOV + WDCOV ² + SHAWAT + SHAWAT ²
48	APCOV + SHAWAT
49	APCOV + APCOV ² + SHAWAT + SHAWAT ²
50	RCOV + SHAWAT
51	RCOV + RCOV ² + SHAWAT + SHAWAT ²
52	WDCOV + SHAWAT
53	WDCOV + WDCOV ² + SHAWAT + SHAWAT ²
54	APCOV + RCOV + WDCOV + SHAWAT + WAFLO + FISH
55	APCOV + APCOV ² + RCOV + RCOV ² + WDCOV + WDCOV ² + SHAWAT + SHAWAT ² + WAFLO + FISH
56	APCOV + RCOV + WDCOV + CANCOV
57	APCOV + APCOV ² + RCOV + RCOV ² + WDCOV + WDCOV ² + CANCOV + CANCOV ²
58	APCOV + RCOV + WDCOV + CANCOV + SHAWAT + FISH
59	APCOV + APCOV ² + RCOV + RCOV ² + WDCOV + WDCOV ² + CANCOV + CANCOV ² + SHAWAT + SHAWAT ² + FISH

2.4.1 Detection/nondetection data

I used the R package “unmarked” to fit occupancy models to the data (Fiske & Chandler 2011, MacKenzie *et al.* 2002). The occupancy models enabled me to estimate occupancy and detection probability and to investigate potential effects of explanatory variables on each of these parameters. Detection probability was modelled with the covariate “visit”, which contains the date of visit. The candidate models (Table 2) were fitted to the data and ranked using Akaike weights. Occupancy analysis could be done only for the Common Frog, as too few detection events were observed for all other species.

2.4.2 Abundance data

The maximum value over all field visits of counts of egg masses of the Common Frog (*Rana temporaria*) were analysed with generalized linear mixed effects models, whereby I used a Poisson distribution of errors (Kéry 2010). The GLMMs enabled me to estimate the mean abundance of egg masses of the Common Frog per pond and to investigate potential effects of covariates on this parameter. The territory (TER_NO) was added as random effect in all models, because the ponds in the same territory are not independent. The candidate models (Table 2) were run and ranked according to their Akaike weights. Data analysis was performed in R (Version 3.1.2; R Core Team (2014)).

3. Results

3.1 Occupancy

Species present at beaver ponds were the Common Frog (*Rana temporaria*), Edible Frog (*Pelophylax esculentus*), Pool Frog (*Pelophylax lessonae*), Marsh Frog (*Pelophylax ridibundus*), Common Toad (*Bufo bufo*), Midwife Toad (*Alytes obstetricians*) and Yellow-bellied Toad (*Bombina variegata*). However, only the Common Frog could be observed in a sufficient number to perform statistics on (Table 3). Interestingly, the other (rare) species were observed mainly at the two ponds that had to be excluded from the analysis due to their striking difference to the other 68 ponds in pond size (five and one hectare, respectively). Newts could not be observed at any of the beaver ponds.

Table 3: Summary of the night visits per species and what stage (LAI=spawns, LAR=larvae, ADU=Adults, X=not detected) was observed. Total Ponds=Number of different ponds at which the species could be observed. Larvae of the genus *Pelophylax* could not be distinguished and are therefore not considered. Visit 4, Visit 5 and Visit 6 were the three visits to the field sites at nights.

Common name	Scientific name	Visit 4	Visit 5	Visit 6	Total Ponds
Common Frog	<i>Rana temporaria</i>	LAI, LAR	LAR, ADU	LAR, ADU	28
Edible Frog	<i>Pelophylax esculentus</i>	X	ADU	ADU	2
Pool Frog	<i>Pelophylax lessonae</i>	ADU	ADU	ADU	5
Marsh Frog	<i>Pelophylax ridibundus</i>	ADU	X	ADU	3
Agile Frog	<i>Rana dalmatina</i>	X	X	X	0
Common Toad	<i>Bufo bufo</i>	ADU	LAR	LAR, ADU	4
Natterjack Toad	<i>Bufo calamita</i>	X	ADU	X	1
Midwife Toad	<i>Alytes obstetricians</i>	ADU	X	ADU	1
Yellow-bellied Toad	<i>Bombina variegata</i>	ADU	ADU	X	2
Palmate Newt	<i>Lissotriton helveticus</i>	X	X	X	0
Smooth Newt	<i>Lissotriton vulgaris</i>	X	X	X	0
Northern crested Newt	<i>Triturus cristatus</i>	X	X	X	0
Alpine Newt	<i>Ichthyosaura alpestris</i>	X	X	X	0

The model best explaining the occurrence data for the Common Frog (*Rana temporaria*) had an Akaike weight of 0.71 (Table 4). It incorporated the linear and quadratic effect of percentage of pond covered by reed (RCOV) and the term (*Rana temporaria* detected in the territory), the variable used to account for pond dependency within a territory, as covariates for occupancy. Furthermore, it included visit (date of visit) as covariate for detection probability.

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Table 4: The five top ranked occupancy models from the candidate model list for *Rana temporaria*. nPars give the degrees of freedom, delta is the delta AIC and AICwt is the Akaike weight of the model. The only variable describing detection probability is “visit”, whereas all other variables describe occupancy.

Model-no.	Model	nPars	delta	AICwt
242	RCOV + RCOV ² , visit	6	0.00	0.71
241	RCOV + RCOV ²	5	2.36	0.22
51	APCOV+ APCOV ² + RCOV+ RCOV ² + WDCOV+ WDCOV ²	9	5.84	0.038
23	RCOV	4	7.08	0.021
37	LAND+AGEP+AGEP ² +AGET+AGET ² +BACT+CANCOV+ CANCOV ² +SHAWAT+SHAWAT ² +FISH	14	10.32	0.004

All covariates had a non-significant effect and large standard errors (Table 5). However, the top ranked model was substantially better (evidence ratio=0.71/0.00000041) than the null model with no covariates.

Table 5: Estimates, standard errors and p-values for the covariates contained in the top ranked occupancy model for *Rana temporaria*. RtDTyes= positive detection of *Rana temporaria* in the territory.

Parameter	Explanatory Variable	Estimate	Std. Error	p-value
Occupancy	Intercept	-8.00	16.48	0.627
	Reed cover	4.37	4.09	0.285
	Reed cover ²	-3.25	3.98	0.414
	RtDTyes	11.91	17.19	0.488
Detection probability	Intercept	-0.378	0.380	0.320
	Date of visit	-0.039	0.019	0.040

The date of visit had a negative effect on detection probability. Detection probability was the highest at the beginning of the season, which is consistent with the fact that adult individuals of the Common Frog migrate from the breeding sites to terrestrial habitats in this period (Savage 1962).

3.2 Abundance

The number of egg masses of the Common Frog observed at one pond ranged from 0 to 109. The model best explaining the abundance data for the Common Frog (*Rana temporaria*) had an Akaike weight of 0.99 (Table 6).

Table 6: The five top ranked abundance models from the candidate model list for *Rana temporaria*. df give the degrees of freedom, delta is the delta AIC and AICwt is the Akaike weight of the model.

Model-no.	Model	df	delta	AICwt
59	APCOV+APCOV2+RCOV+RCOV2+WDCOV+WDCOV2+CANCOV+CANCOV2+SHAWAT+SHAWAT2+FISH	13	0.00	0.99
57	APCOV+APCOV2+RCOV+RCOV2+WDCOV+WDCOV2+CANCOV+CANCOV2	10	27.29	<0.001
55	APCOV+APCOV2+RCOV+RCOV2+WDCOV+WDCOV2+SHAWAT+SHAWAT2+WAFLO+FISH	12	31.99	<0.001
47	APCOV+APCOV2+RCOV+RCOV2+WDCOV+WDCOV2+SHAWAT+SHAWAT2	10	44.05	<0.001
45	APCOV+APCOV2+RCOV+RCOV2+WDCOV+WDCOV2	8	60.65	<0.001

The best model incorporates the linear and quadratic effects of percentage of pond covered by aquatic plants (APCOV), reed (RCOV), woody debris (WDCOV), riparian canopy cover (CANCOV), area of shallow water (SHAWAT) and presence of fish (FISH) as covariates for fixed effects (Table 7); whereby all variables show a significant linear and quadratic effect.

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Table 7: Coefficients and p-values for the covariates contained in the top ranked abundance model for *Rana temporaria*.

Parameter	Explanatory Variable	Coefficient	Std. Error	p-value
Fixed Effects	Intercept	0.906	1.031	0.380
	Aquatic plant cover	-1.591	0.192	<0.001
	Aquatic plant cover ²	0.359	0.049	<0.001
	Reed cover	4.063	0.313	<0.001
	Reed cover ²	-3.951	0.366	<0.001
	Woody debris cover	0.777	0.171	<0.001
	Woody debris cover ²	-0.005	0.129	0.970
	Canopy cover	0.594	0.162	<0.001
	Canopy Cover ²	0.426	0.145	0.003
	Shallow water	0.595	0.218	0.006
	Shallow water ²	-0.022	0.060	0.713
	Fish present	0.861	0.351	0.014
Random Effects	Intercept	10.4	3.226	

The relationship between abundance of the Common Frog and explanatory variables is shown in Figure 3.

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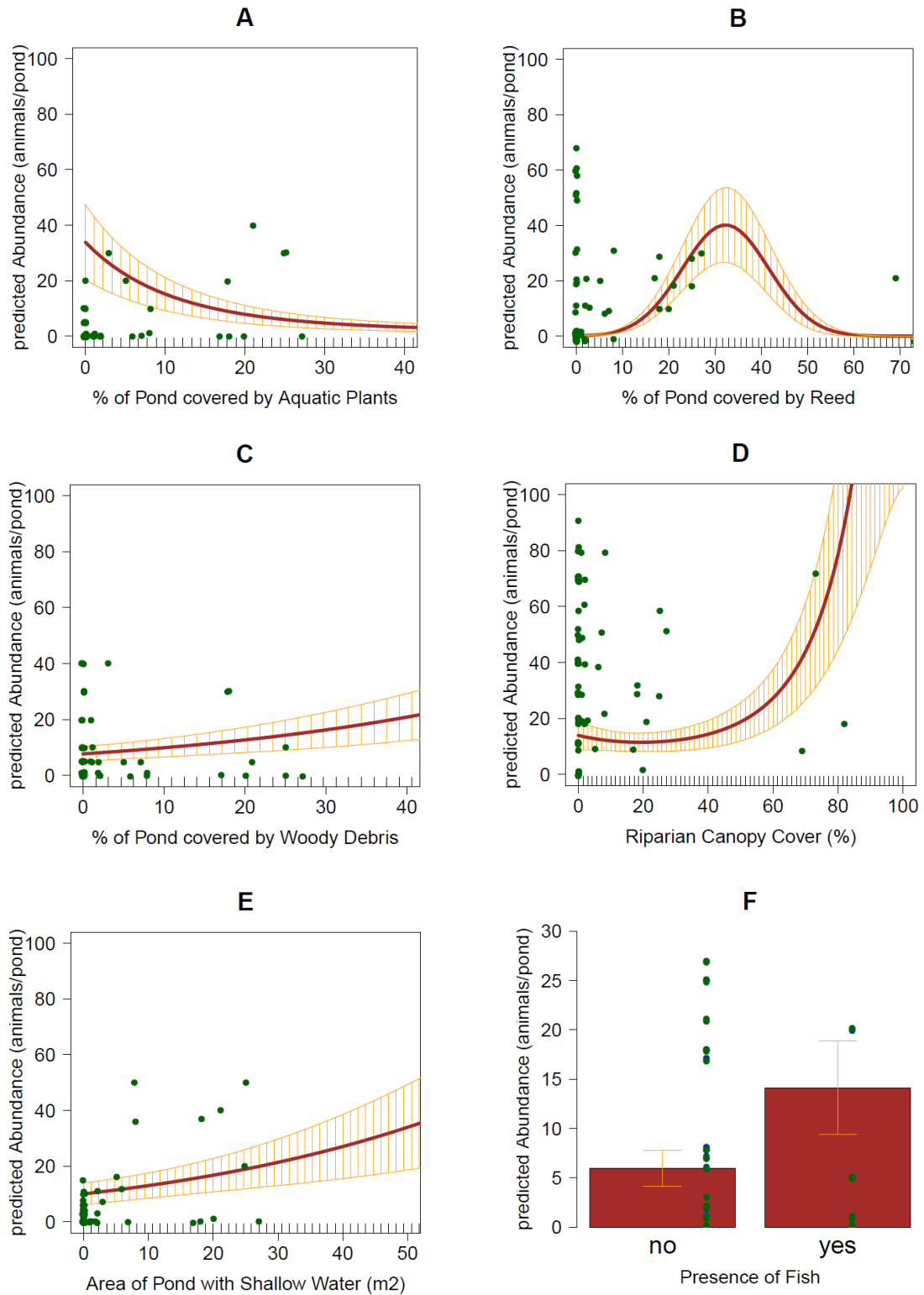


Figure 3: The effect of Aquatic Plant coverage (A), Reed coverage (B), Woody Debris coverage (C), Riparian Canopy Cover (D), Area of Shallow Water (E), and Fish (F) on the abundance of the Common Frog (*Rana temporaria*) predicted by the best abundance model (brown line/area). The orange-striped area represents the 95% confidence interval. The maximal value (out of 6 observations) of the abundance data for each pond is plotted as green dot. The values of the x-axis (=covariate) were not extrapolated, but represented to the maximum observed value. The y-axis (=predicted Abundance) are represented to a value of 100 for the covariates in the graphs A-E, whereas the y-axis in F ranges to a y-value of 30.

4. Discussion

This study aimed at finding habitat features determining the suitability of beaver ponds as habitat for the Common Frog and provides insight for discussions on the beaver-induced damage to agriculture. My results showed that the Common Frog indeed breed in beaver ponds both in the forest and in agricultural areas. Whether the pond was located in the forest or on agricultural land did not have a significant effect neither on occupancy nor on abundance of the Common Frog. Furthermore, I showed that also endangered amphibian species (Schmidt & Zumbach 2005) profit from the beaver-created habitat; *i.e.* we observed *Pelophylax esculentus*, *Pelophylax lessonae*, *Bufo bufo*, *Bufo calamita*, *Alytes obstetricians* and *Bombina variegata* at beaver ponds (Table 3). Conclusively, the present study highlights that beavers as an ecosystem engineers play a role in the conservation of the Common Frog and potentially other species by means of providing suitable habitat also in agricultural landscapes.

4.1 Factors affecting occupancy of the Common Frog (*Rana temporaria*) in beaver ponds

The null model was very poorly supported by the data of the Common Frog. Models with covariates were better supported by the data. The best model included the percentage of pond covered by reed as an explanatory variable. The relation of reed cover and probability of occurrence of the Common Frog was quadratic (Table 5) and showed highest occupancy at a reed cover of 30%. However, the effect was not significant because the confidence interval included zero (Table 5).

The Common Frog (*Rana temporaria*) is known to colonise new ponds very quickly (Gollmann *et. al* 2002), is widespread and has low habitat requirements compared to other amphibian species (Savage 1962). Thus, this might be the reason why it was the only species that occurred quite often.

4.2 Factors affecting abundance of the Common Frog (*Rana temporaria*) in beaver ponds

Reed cover was also incorporated in the best model for the abundance of the Common Frog. The best model for abundance of the Common Frog included the explanatory variables aquatic plant cover, reed cover, woody debris cover, riparian canopy cover, area of shallow water and fish. The abundance of the Common Frog increased at already low values of reed and woody debris cover. However, the coverage of aquatic plants had an opposite effect. I could observe during fieldwork that aquatic plants and reed barely appeared at the same pond, which might explain the slight opposite effect. The observation is supported by the negative correlation (-0.378) of these two variables. Riparian canopy cover, the area of shallow water and the presence of fish had a strong positive effect on the abundance of the Common Frog.

It has been shown previously that reed and other structures of aquatic vegetation at a pond are good indicators for predicting occupancy and abundance of the Common Frog (Reid *et al.* 2014) and other amphibians (Hartel *et al.* 2007, Sztatecsny *et al.* 2004). Dalbeck *et al.* (2007) proposed that the large amount of woody debris at beaver ponds may be a key factor for the suitability of the habitat for amphibians. Woody debris in the pond and along the shore might provide structures for spawn attachments for several amphibian species and the architectural modifications incorporated in the diversity of the habitat provide opportunities for predator avoidance and therefore might even better allow coexistence of fish and amphibians (Dalbeck & Weinberg 2009, Stott *et al.* 1998). Coexistence of fish and amphibians was also found in the present study. Moreover, woody debris enlarges the surface for biofilm development and therefore food availability for larvae is increased (Dalbeck *et al.* 2007). The present study rather supports the result of Sztatecsny *et al.* (2004), which found the highest abundance of amphibian embryos at ponds with intermediate cover of floating vegetation.

According to the literature, but also to the results of the present study, there are other important factors to mention. Shallow water is suggested to have an additional positive effect on high densities of larvae of the Common Frog (Dalbeck *et al.* 2007). The present study could confirm Dalbeck *et al.* (2007) in finding a significant positive effect of the area of shallow water on egg masses of the Common Frog. This is consistent with the

preferences of the Common Frog to lay their eggs in the shallow water at the edge of a pond (Savage 1962). I observed during fieldwork that the edges of flooded grassland on agricultural land had a very high number of egg masses and larvae of the Common Frog. Therefore, this combination of vegetation and very shallow water resulting of beaver damming might be highly attractive to Common Frogs as breeding sites. An additional factor here might be the warmer conditions due to the lack of shading by trees (reduced canopy cover) that is well documented (Savage 1962, Dalbeck *et al.* 2007, Stevens *et al.* 2006). However, the best model of the present study predicted higher abundance of the Common Frog for increasing riparian canopy cover. The different results might be due to climatic (mean annual temperatures) and topographic differences, *i.e.* the present study was conducted on midland ponds, whereas the study of Dalbeck *et al.* was conducted in a valley with steep slopes. Stevens *et al.* (2006) relate riparian canopy cover to the age of a beaver pond, whereas the canopy is reduced to a higher extent at older ponds due to foraging of beavers and dieback of less water-tolerant trees in flooded zones. They proposed larger breeding populations of wood frogs (*Rana sylvatica*) at older ponds primarily through selection by breeding adults for warmer conditions (Skelly & Kealoha 2000). The present study contradicts those results in parts, because here, the age of the pond was not contained in the best model and therefore did not play a role.

4.3 Conclusions and management implications

Whether the pond was located in the forest or on agricultural land did not have a significant effect, neither on occupancy nor on abundance of the Common Frog. Hence, the habitat constructed by beavers on agricultural land seems to be as suitable for Common Frogs as the habitat constructed by beavers in the forest. Due to the fast colonisation of new ponds by the Common Frog (Gollmann *et al.* 2002) and the only recent history of beavers migrating to agricultural land (personal communication with Christof Angst, CSSF), it might only be a matter of time until other amphibian species will follow in the beaver designed habitats.

The present study suggests that the beaver activity leads to valuable creation and modifications of the environment for amphibian species. As proposed by several other studies (Cunningham *et al.* 2007, Dalbeck *et al.* 2007, Stevens *et al.* 2006) beavers may play a

crucial role in successful conservation strategies for amphibians in the future. The decisive factors influencing abundance of the Common Frog did particularly concern vegetation heterogeneity, supplemented by canopy cover, area of shallow water and presence of fish. Vegetation heterogeneity also had a crucial impact for the occurrence of the Common Frog. The present study got similar results as previous studies (Sztatecsny *et al.* 2004, Dalbeck *et al.* 2007, Stevens *et al.* 2006); however, there are discrepancies discussed above which might be explained by geographic differences and therefore different requirements of amphibians.

The main question, whether amphibians do colonise the beaver ponds on agricultural land, can be verified at least for the Common Frog. The results of the present study confirm the hypotheses that habitat heterogeneity has a major impact on habitat suitability for the Common Frog. Additionally, the availability of areas with shallow water was hypothesised and confirmed by the results for the Common Frog. Unlike the results of other studies, connectivity was not contained in the best model and therefore not considered to be an important habitat feature in this study. However, the new wetlands created by beavers affect the fragmentation of habitats negatively and increase the necessary connectivity of wetlands in the landscape for numerous species (Cunningham *et al.* 2007, Hanski 1999, Tockner *et al.* 1999). Although there is high potential for conflict between beavers and farmers concerning land use, there are also beaver modifications that favour the land-owners in means of an increased biodiversity. Biodiversity performs a variety of ecological services; not at least in enhancing agricultural productivity (Bullock *et al.* 2001, Pimentel *et al.* 1992). Conclusively, beaver as ecosystem engineers are very valuable habitat constructors and their dams favour not only amphibian species.

The question whether conservationists and nature reserve managers should pay more attention to the role of ecosystem engineers is as old as the presentation of concept of ecosystem engineering (Jones *et al.* 1994). Crain & Bertness (2006) stress the importance of ecosystem engineers and propose them as primary target of conservation efforts due to their critical role in the structure and function of natural communities. The present, but also previous studies could show the significance of one ecosystem engineer, the beaver, for the conservation of other species and therefore supports the recommendation to include ecosystem engineers in conservation and management plans.

4.4 Further work

To provide deeper insight on amphibian population stability and dynamics at beaver ponds, it would be very interesting to put more effort in collecting abundance data for all amphibian species and conduct the study over several years. An additional interesting expansion of the study would be to include beaver dams located in other parts of Switzerland and get the opportunity to incorporate the two big beaver territories (that had to be partially excluded in this study) in the analysis as well. An additional question rises due to the impact on water chemistry and quality that beavers have. It would be interesting to investigate whether there is a relationship of amphibian pathogens and beaver dams, *i.e.* if amphibians at beaver ponds are less concerned by pathogens than their living relatives at non-beaver ponds in the same area. This could bring valuable information to moderate the threat of pathogens to amphibian populations (Woodhams *et al.* 2011)

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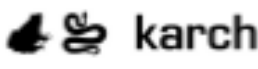
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6. Appendices

Appendix 1: Protocol provided by the CSCF.

Formular Amphibien in Biberteichen

Befinden sich mehrere Dämme im Biberrevier muss für jeden Biberteich ein Formular ausgefüllt werden. Kartierung immer bachabwärts vom ersten Biberteich zum letzten Biberteich in Fliessrichtung.

Datum:	Kartierer/in Name/Vorname:	
Adresse:	PLZ:	Tele:
e-mail:		

Gewässername:	Koordinaten Biberdamm (GPS Genauigkeit): x..... / y.....
Kanton:	Gemeinde: Flurname:

Angaben zum Gewässer und zum Biberteich

Grossräumige Umgebung

☐ Auengebiet / ☐ Moorgebiet / ☐ Waldgebiet / ☐ Siedlungsgebiet

☐ Landwirtschaftszone (vorwiegend Wiesen und Weiden) / ☐ Landwirtschaftszone (vorwiegend Ackerbau)

☐ Im Wald, Anteil Nadelbäume in %: Deckung Kronendach (%):

Lebensraumstruktur

☐ Graben / ☐ Bach / ☐ Wiesenbach / ☐ Bewässerungsgraben

Gefälle des Gewässers:

Durchschnittliches Gefälle des Gewässers: (wird durch Biberfachstelle/karch ausgefüllt)

Typ des Damms

☐ Hauptdamm¹ / ☐ « Nebendamm »² / gibt es mehrere Dämme im Revier? Anzahl Dämme³:

Biberdamm

Länge: m / Höhe: cm / Biberdamm wird unterhalten⁴: ja ☐ nein ☐

Dimensionen des Biberteiches (bitte Skizze auf Seite 3 erstellen)

Länge der gestauten Fläche: m / Breite maximal: m / Breite durchschnittlich: m

Flachwasserzonen (< 30 cm tiefe) am Ufer vorhanden: ☐ ja / ☐ nein Fläche: m²

Pflanzenbewuchs am Ufer/Länge des Uferbereichs mit Vegetation: m

Anteil des Ufers mit Vegetation:% Anteil der Teichfläche bedeckt mit Wasserpflanzen:%

Anteil der Teichfläche bedeckt mit holzigen Ablagerungen:%

Gibt es Teiche/Tümpel mit Grundwasseraufstoss⁵: ☐ ja / ☐ nein / Anzahl Teiche/Teiche:

Frische Biber Spuren vorhanden rund um den Biberteich: ja ☐ nein ☐ Fische vorhanden: ja ☐ nein ☐

Alter der Biberteiche⁶: Alter des Reviers:

¹ Der Hauptdamm schützt die Burg oder den Erdbau. Die Biber wohnen am Teich des Hauptdamms.

² «Nebendämme» werden bachauf- und abwärts vom Hauptdamm erstellt um neue Nahrungsgründe zu erschliessen. Diese können auch nur temporär sein.

³ Für jeden Damm ein Formular ausfüllen

⁴ Frisch abgenagte Äste im und auf dem Biberdamm.

⁵ Siehe Skizze Seite 3. Im Staubeereich des Biberteichs entstehen vom Fließgewässer losgelöst Tümpel.

⁶ Falls bekannt. Sonst bei Biberfachstelle nachfragen.

Amphibienarten

Art	1. Durchgang März am Tag (hauptsächlich Suche nach Grasfrosch & Erdkröte)	2. Durchgang März am Tag (hauptsächlich Suche nach Grasfrosch & Erdkröte)	3. Durchgang April (Nacht) (hauptsächlich Suche nach Molchen)	4. Durchgang Mai (Nacht) (hauptsächlich Suche nach Molchen und Salamander)	Bemerkungen
Datum & Uhrzeit					
Feuersalamander <i>Salamandra atra</i>					
Bergmolch <i>Ichthyosaura alpestris</i>					
Fadenmolch <i>Urospina helvetica</i>					
Erdkröte <i>Bufo bufo</i>					
Grasfrosch <i>Rana temporaria</i>					
Teichmolch <i>Urospina vulgaris</i>					
Kammolch <i>Triturus cristatus</i> & <i>Triturus cristatus</i>					
Geburtshelferkröte <i>Alytes obstetricans</i>					
Gelbbauchunke <i>Bombina orientalis</i>					
Kreuzkröte <i>Bufo calamita</i>					
Laubfrosch <i>Hyla arborea</i>					
Springfrosch <i>Rana dalmatina</i>					
Seefrosch <i>Pelodytes punctatus</i>					

ADU: Adulte LAI: Laichballen / Laich LAR: Larven JUV: Juvenile VOI: Stimmen

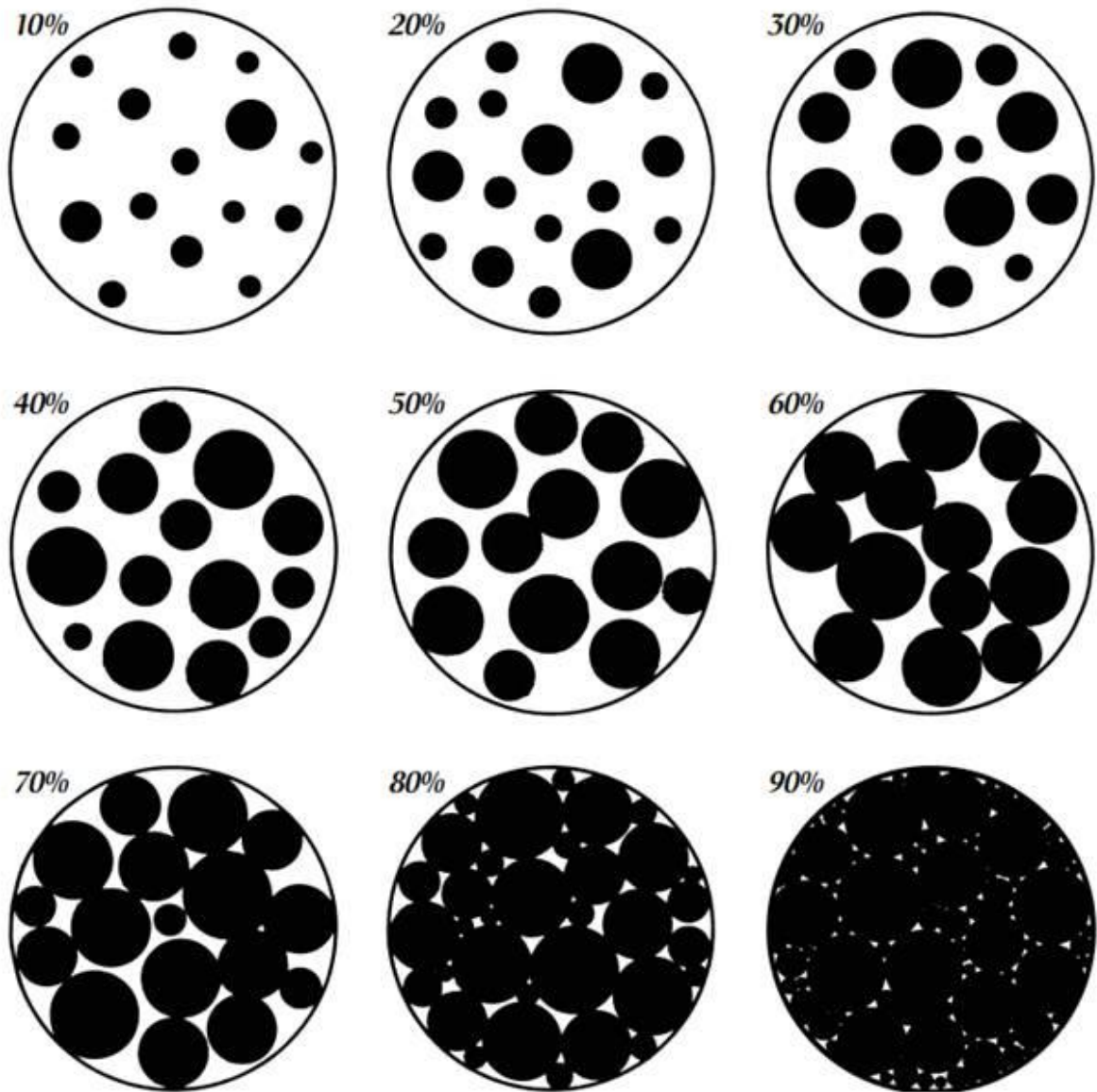
Anleitung zur Vermessung Biberzucht und zur Erstellung Skizze Seite 3

Richtung Fotoaufnahmen: →

Ufervegetation:



Appendix 2: Template to estimate riparian canopy cover.



Appendix 3: List of all applied candidate models with source.

Model- no.	Model Covariates	Source
00	No covariate	Simplest model
01	visit	Observation covariate
02	ADT	Pond independence
03	TER_NO	Pond independence
Univariate models		
1	LAND	Observations (own hypothesis)
2	AGEP	Stevens et al. 2006, Russel et al. 1999
3	AGEP + AGE2	
4	AGET	
5	AGET + AGET2	
6	CONNEC	
7	CONNEC + CONNEC2	Cunningham et al. 2007
8	AOSUR	Observation
9	ADT	Observation
10	BACT	Dalbeck & Weinberg 2009, Stevens et al. 2006, Cunningham et al. 2007
11	CANCOV	Sztatecsny et al. 2004, Stevens et al. 2006, Dalbeck et al. 2007
12	CANCOV + CANCOV2	Sztatecsny et al. 2004
13	SHAWAT	Savage 1962, Dalbeck et al. 2007
14	SHAWAT + SHAWAT2	
15	POSI	Sztatecsny et al. 2004
16	POSI + POSI2	
17	WAFLO	Dalbeck et al. 2007
18	FISH	Dalbeck et al. 2007, Dalbeck & Weinberg 2009, Cunningham et al. 2007
19	APCOV	Dalbeck et al. 2007, Sztatecsny et al. 2004
20	APCOV + APCOV2	
21	RCOV	
22	RCOV + RCOV2	
23	WDCOV	
24	WDCOV + WDCOV2	Observations
25	DAMW	
26	DAMW + DAMW2	
27	DAMH	
28	DAMH + DAMH2	
Landscape models		
29	LAND + AGE2 + AGET	Own hypothesis combined
30	LAND + AGE2 + AGE2 + AGET + AGET2	
31	LAND + CONNEC	
32	LAND + CONNEC + CONNEC2	
33	LAND + AGE2 + AGET + BACT	
34	LAND + AGE2 + AGE2+ AGET + AGET2 + BACT	
35	LAND + AGE2+ AGET + BACT + CANCOV + SHAWAT + FISH	

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36	LAND + AGEP + AGEP2 + AGET + AGET2 + BACT + CANCOV + CANCOV2 + SHAWAT + SHAWAT2 + FISH	
37	LAND + AOSUR + ADT	
<i>Pond age models</i>		
38	AGEP + AGET	Dalbeck et al. 2007
39	AGEP + AGEP2 + AGET + AGET2	
40	AGEP + AGET + CANCOV	Stevens et al. 2006
41	AGEP + AGEP2 + AGET + AGET2 + CANCOV + CANCOV2	
42	AGEP + AGET + AOSUR + ADT	Own combination
43	AGEP + AGEP2 + AGET + AGET2 + AOSUR + ADT	
<i>Vegetation structure models</i>		
44	APCOV + RCOV + WDCOV	Dalbeck et al. 2007
45	APCOV + APCOV2 + RCOV + RCOV2 + WDCOV + WDCOV2	Sztatecsny et al. 2004
46	APCOV + RCOV + WDCOV + SHAWAT	Savage 1962, Own combination
47	APCOV + APCOV2 + RCOV + RCOV2 + WDCOV + WDCOV2 + SHAWAT + SHAWAT2	
48	APCOV + SHAWAT	
49	APCOV + APCOV2 + SHAWAT + SHAWAT2	
50	RCOV + SHAWAT	
51	RCOV + RCOV2 + SHAWAT + SHAWAT2	
52	WDCOV + SHAWAT	
53	WDCOV + WDCOV2 + SHAWAT + SHAWAT2	
54	APCOV + RCOV + WDCOV + SHAWAT + WAFLO + FISH	Observation, Dalbeck et al. 2007
55	APCOV + APCOV2 + RCOV + RCOV2 + WDCOV + WDCOV2 + SHAWAT + SHAWAT2 + WAFLO + FISH	
56	APCOV + RCOV + WDCOV + CANCOV	Own combination
57	APCOV + APCOV2 + RCOV + RCOV2 + WDCOV + WDCOV2 + CANCOV + CANCOV2	
58	APCOV + RCOV + WDCOV + CANCOV + SHAWAT + FISH	Own combination
59	APCOV + APCOV2 + RCOV + RCOV2 + WDCOV + WDCOV2 + CANCOV + CANCOV2 + SHAWAT + SHAWAT2 + FISH	

Statement of Authorship

Name: Gabriela Patricia Gschwend

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Thesis supervisors: Dr. Benedikt R. Schmidt
Swiss Amphibian and Reptile Conservation Program (KARCH) &
Institute of Evolutionary Biology and Environmental Sciences,
University of Zurich

Prof. Dr. Arpat Ozgul
Institute of Evolutionary Biology and Environmental Sciences,
University of Zurich

Supported by: Christof Angst
Biberfachstelle (CSCF)

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Zurich, 27.02.2015

Gabriela Patricia Gschwend