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# Beaver ponds as habitat of amphibian communities in a central European highland

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**Abstract.** The Eurasian beaver *Castor fiber*, formerly occurred across the Palaearctic, but was nearly eradicated in the 19th century. Due to reintroductions in the 20th century, beaver populations are increasing and now extend into highland areas. Natural still waters are scarce in highlands of Central Europe. Therefore the question arises, "Are beaver ponds essential habitats for amphibians?", especially since fishes, predators of amphibian larval stages, also inhabit beaver ponds. We investigated the amphibian fauna of one typical valley in the Eifel, that was colonized by beavers in 1981, and compared areas with and without beaver ponds. All anuran species of the region occupied beaver ponds, including species that were absent (*Alytes obstetricans*, *Bufo bufo* and *Rana* kl. *esculenta*) or rare (*Rana temporaria*) in natural waters. *Alytes obstetricans* obviously benefited from pond construction and the removal of trees by beavers which leads to sunny plots along the slopes of the valley, crucial habitat for this species. The urodelans *Salamandra salamandra*, *Triturus alpestris* and *Triturus helveticus* were widely distributed in beaver ponds. Our results show clearly, that beaver altered landscapes offer high quality habitats for amphibians in our study area. Due to a considerable increase of habitat heterogeneity in impounded streams, the predator *Salmo trutta* was not able to extirpate the amphibian fauna. We conclude that the historic effects of beavers need to be considered for a proper understanding of patterns of amphibian distribution and habitat requirements in Central European Highlands. Furthermore, beaver-created landscapes will be of future relevance for conservation of endangered species, like *Alytes obstetricans*.

## Introduction

In Central Europe considerable differences in the composition of amphibian communities occur between types of landscapes i.e. lowland and highland areas, or forest and open agricultural landscapes. Today, numerous species prefer to reproduce in sunny, stagnant permanent waterbodies, or temporary wetlands of various types (Nöllert and Nöllert, 1992; Günther, 1996). In highland areas of Central Europe, small flowing streams are abundant, whereas natural still waters are scarce and known to be restricted to areas with special geological and geomorphological conditions or, if not destroyed, to the floodplains of large streams. Interestingly, although flowing waters dominate highland areas, the number, occurrence and abundance of amphibian species found in these waters is restricted. Only one species, *Salamandra salamandra*, clearly prefers flowing waters, predominantly cool and small headwaters without fish (Thiesmeier, 2004).

However, this view does not condsider the influence of Eurasian beaver *Castor fiber.* Like its New World sibling species *Castor canadensis*, Eurasian beaver act as an ecosystem engineer which is able to create and maintain special habitats to meet its own needs, leading to changes in biotic and abiotic conditions for other species as well.

The Eurasian beaver was formerly distributed throughout most of Europe and much of Asia (Durka et al., 2005). In the 17th Century overexploitation led to a dramatic decline and as a consequence the beaver disappeared from most of its range and survived only in small populations in the lowland parts of large rivers (Zahner, Schmidtbauer and Schwab, 2005). In these environments beavers usually do not create large ponds (Heidecke and Klenner-Fringes, 1992). As modern beaver populations expand,

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driven in part by reintroductions in many areas of its former range, it is increasingly clear that Eurasian beavers are very adaptable and able to colonise successfully even small waters like streams and ditches (Naumann, 1991; Heidecke and Klenner-Fringes, 1992). Today, beavers live not only in lowland areas, but also in highlands. Here beavers need to impound streams to create suitable habitat, including meadows and ponds that increase biotic, abiotic and structural heterogeneity on a landscape scale (Wright, Jones and Flecker, 2002; Rosell et al., 2005; Zahner, Schmidtbauer and Schwab, 2005). However, the exact role of beaver landscapes and ponds in providing habitat for amphibians in Europe is poorly understood (Elmeros, Madsen and Berthelsen, 2003). As predatory fishes, which eat amphibian larvae, often colonize ponds created by beavers (Keast and Fox, 1990; Hägglund and Sjöberg, 1999; Halley and Lamberg, 2001; Ray, Ray and Rebertus, 2004; Sigourney, Letcher and Cunjak, 2006) it is unclear if fish predation exclude amphibians from beaver altered waters.

One of the highland areas where beavers are expanding is the Eifel in Germany. In the "Hürtgenwald", a large forest, 12 Eurasian beavers from Poland were released between 1981 and 1989 (Naumann, 1991) in a tributary of the River Rur, part of the catchment area of the River Meuse. By 2004, these beavers had established a still increasing population of about 150 to 200 individuals (Schadewinkel, 2006). Soon after their reintroduction, these beavers began to impound streams and induced a remarkable change in the landscape that is still under way (Rolauffs, Hering and Lohse, 2001).

Based on a beaver census in 2004 (Schadewinkel, 2006), we started to study the suitability of beaver ponds as habitat for the amphibian fauna. In the present study we examine (1) if species richness of amphibian communities increases along with the increase in landscape heterogeneity due to the creation of lentic habitats and alteration of other environmental features caused by beaver activity, and (2) if the density of *S. salamandra*, a species typically reproducing in flowing water in the uplands declines due to loss of breeding habitat.

This study may serve as a basis for further investigations to determine the former role of beaver-dammed valleys as original habitat of amphibians and the possible role of beavers and the chances this species offers in future conservation of amphibian populations in Central Europe.

## Methods

### *Study area*

We chose one valley close to the reintroduction site situated in the "Hürtgenwald" (central coordinates: 50°42′30N, 6°22′30E), a large forest in the north of the Eifel, Germany (fig. 1). The Hürtgenwald is dominated by a forested plateau and small V-shaped valleys with steep slopes and narrow floodplains. The climate is sub-Atlantic i.e. temperate with cool summers and mild winters with an average temperature of ca. 8.5°C (MURL 1989). Elevation ranges from 250 m to 400 m above sea level. The central and lower parts of the valley that were surveyed stretch over ca. 2400 m and the stream flows into a drinking-water reservoir. The floodplain has a breadth of 30 m to 60 m. Most of the valley, including the rather steep slopes and the floodplain, is forested or was forested before beavers began to cut the trees and create ponds. The valley is inhabited by two beaver colonies. Beavers have created large ponds due to dams up to 50 m in length and up to 2.0 m high. All ponds are populated by *Salmo trutta*. As we wished to compare the amphibian fauna of the impounded parts of the stream with typical habitat in a valley that was not influenced by beaver activities, we divided the valley into three study areas (table 1, fig. 1):

*Old beaver ponds.* Within the last 15 years, beavers impounded a chain of 17 ponds in the middle reach of the valley on a stretch about 600 m in length. These ponds differ in size and depth depending on relief. Pond size increases from the upper to the lower end of this reach (fig. 1). Most of the dams stretch over the total breadth of the floodplain, therefore the bottom of the valley is largely flooded. As a consequence, the majority of trees in the floodplain died or were felled by beavers during the last 15 years. Only small groups of trees remain in the floodplain, mainly *Alnus glutinosa* and *Picea abies*. Beavers also felled many trees in up to 40 m distance from the ponds, therefore the ponds and surrounding slopes are more or less open and sunny. The shallow banks of the large ponds have a rich emergent vegetation, small inlets, dead trunks, piles of branches, high amounts of woody debris (imported from the surroundings by beavers), dams and burrows.

*Young beaver ponds.* A second beaver family occupies an area close to the reservoir (fig. 1). Here, beavers occurred sporradically for more than 10 years with activity increasing

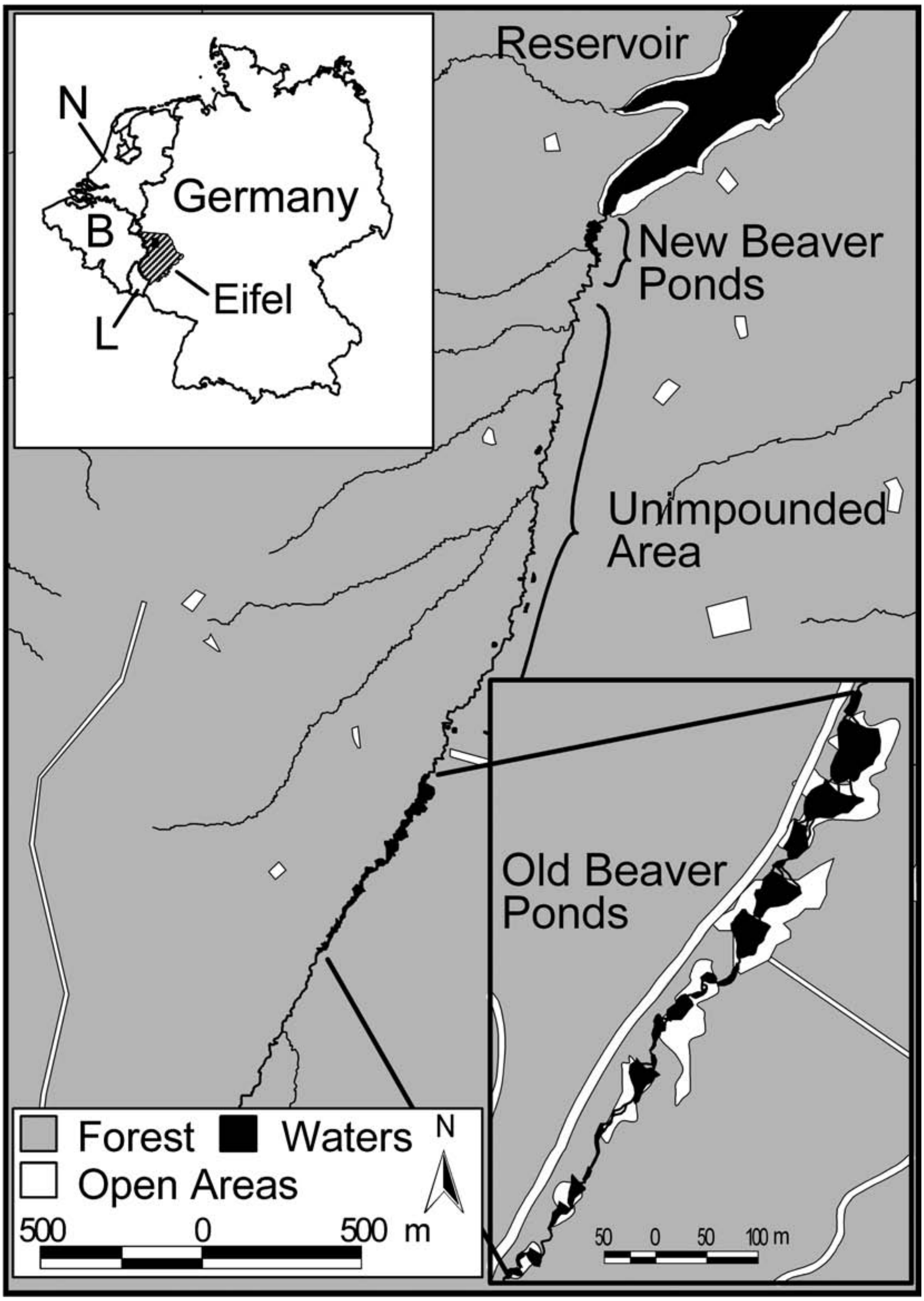


**Figure 1.** Map of the study area in the Hürtgenwald, Eifel (Germany).

**Table 1.** Types of waters in the study area. su: sunny (canopy cover <25%), sha: shady (canopy cover >75%), int: intermediate insolation (canopy cover 25-75%), [a]: artificial (bomb crater, waters caused by heavy vehicles) and [n]: natural (non artificial) waters of the floodplain.

| Type of water | *n* | Size | Structure | Insolation |
|---|---|---|---|---|
| old beaver ponds | 17 | 30-2000 $m^2$ | shallow-1.5 m deep, banks often with emergent vegetation | su-int |
| new beaver ponds | 3 | 400-2000 $m^2$ | shallow-1.0 m deep, banks with litter and some emergent vegetation | su-sha |
| springs [n] | 4 | 15-30 $m^2$ | shallow (<15 cm depth) with typical vegetation | sha |
| bomb crater [a] | 1 | 40 $m^2$ | silted up with debris | sha |
| dead waters [n] | 2 | 8 $m^2$/20 $m^2$ | shallow (<20 cm depth), no vegetation, intermittently connected to the brook | sha |
| pools on forest roads [a] | 2 | 15 $m^2$/20 $m^2$ | 30 cm depth, some vegetation | sha |
| uprooted root system [n] | 1 | 9 $m^2$ | shallow (<15 cm depth), no vegetation | sha |
| brook (breadth) [n] | 1 | 1.0-2.5 m | mainly natural, no vegetation | sha |

rapidly in 2004. As of spring 2005, the beavers had built three large dams, flooding a stretch ca. 125 m length and had felled many trees. Generally these ponds resemble those in the middle part of the valley, although vegetation is less developed and some of the ponds are shady, because large trees have not been cut or died. Besides *Salmo trutta*, we also observed cyprinids, mainly <10 cm in total length, in the ponds.

*Unaffected stream reaches and floodplain.* We investigated the valley between the two impounded areas, a stretch of about 1600 m. The stream is mainly unobstructed with a breadth of 1 m to 2.5 m and contains *Salmo trutta*. Due to old stands of floodplain forest or old spruce plantations, most of the unimpounded valley is rather shady. Only few standing waters exist in the floodplain and one third of them, the large ones, are artificial (table 1). Unlike other waterbodies in this survey, none of these waters including the two dead arms of the stream was populated by fishes.

*Data collection*

Between 21.03.2005 and 04.04.2006 all waters along the valley were surveyed five times. All observations started in the afternoon and continued into the night. During the first two surveys we counted egg masses of *Rana temporaria* and *Bufo bufo* and searched for newts of the Genus *Triturus* and larvae of *S. salamandra* at night with strong torches and hand nets. The aim of the latter surveys was to count calling individuals of the later breeding anuran species and to search for larvae. In April 2006 we conducted one night-survey on all waters to complete presence-absence data of urodelan species and fishes in the study area.

We did not use traps and mark-release-recapture methods, therefore quantitative or semi-quantitative data are available only for the following species: (1) *Rana temporaria*. It was possible to count the number of egg masses. However, this species might be underestimated in the beaver ponds, as large areas of these ponds were difficult to reach. (2) *Alytes obstetricans* and (3) *Rana* kl. *esculenta*: We counted calling males several times and therefore generated rough estimates of population sizes.

We used Mann-Whitney U-test to determine if the number of species and the number of clutches of *Rana temporaria*, differed between beaver ponds and waters not affected by beavers. As we have only presence-absence data for the two *Triturus* spp. and *S. salamandra,* it is only possible to estimate the importance of beaver ponds for caudates based on the number of sites occupied by these species.

## Results

### *Amphibian species richness in different types of aquatic habitats*

We identified 31 water bodies, the majority of them were beaver ponds (table 1). The seven amphibian species observed in the study area were not evenly distributed among the habitat types (table 2): Only three species were able to colonise the small and shady natural water bodies of the unimpounded part of the floodplain; a considerable number of these sites were not occupied at all, leading to low species richness (table 2). The artificial waterbodies on the floodplain were more attractive to amphibians, as all three of these shady and rather small ponds (table 1) contained amphibians representing four species (table 2). No amphibians were found in the stream.

The number of species per site was significantly higher in beaver ponds compared to all other aquatic habitats of the study area (Mann-Whitney-U-Test $P < 0.005$, $U = 14.00$, $n = 31$, fig. 2). All seven species encountered

**Table 2.** Number of sites of different habitat types occupied by amphibians in the study area. The artificial waters in the floodplain are described in table 1.

| Species | Beaver ponds | | Floodplain | | | Study area |
|---|---|---|---|---|---|---|
| | Old | New | Stream | Natural waters | Artificial waters | |
| Number of waters | 17 | 3 | 1 | 7 | 3 | 31 |
| Populated by amphibians (1 or more species) | 17 | 3 | 0 | 4 | 3 | 27 |
| Populated by fishes | 17 | 3 | 1 | 0 | 0 | 21 |
| *Salamandra salamandra* | 7 | – | – | 2 | 2 | 11 |
| *Triturus alpestris* | 15 | 2 | – | 1 | 3 | 21 |
| *Triturus helveticus* | 16 | 3 | – | – | 2 | 21 |
| *Rana temporaria* | 10 | 3 | – | 1 | 1 | 15 |
| *Rana* kl. *esculenta* | 2 | – | – | – | – | 2 |
| *Bufo bufo* | 7 | 2 | – | – | – | 9 |
| *Alytes obstetricans* | 7 | – | – | – | – | 7 |
| Average no. of species | 4.2 | 3.7 | 0.0 | 0.6 | 2.7 | 3.0 |

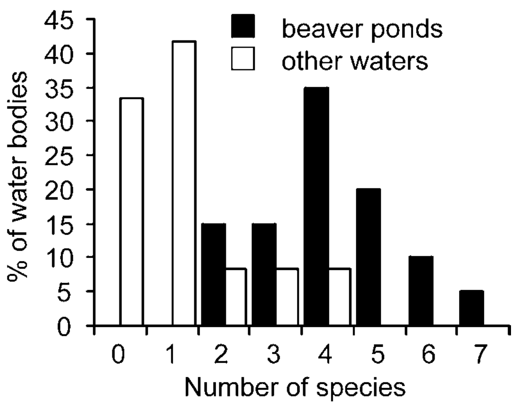


**Figure 2.** Relative frequency distribution of taxa richness of beaver ponds ($n = 20$, average number of species: 4.1) compared to all other waters ($n = 11$, average no of species: 1.2).

were observed in beaver ponds. One species, *Alytes obstetricans*, was exclusively found in old beaver ponds. Three species, *S. salamandra*, *Alytes obstetricans* and *Rana* kl. *esculenta*, were absent from young beaver ponds, and one species, *B. bufo*, was uncommon in young ponds and its reproductive status there was unclear.

### *Distribution of single species*

Newts were found mainly in beaver ponds; about 80% of all waters populated by *Triturus alpestris* and 90% by *Triturus helveticus* were created by beavers (table 2). The larvae of *S. salamandra* were equitably distributed in beaver ponds and other waterbodies on the floodplain but did not occur in the stream itself.

*Rana temporaria* significantly preferred beaver ponds for breeding (Mann-Whitney-U-Test $P < 0.005$, $U = 48.00$, $n = 31$): Most clutches (>96%) were deposited in beaver impoundments usually at one to three places per pond in sunny, shallow water (table 3). Other types of habitat, namely natural unimpounded waters (15 clutches = 0.6% of all clutches), played a minor role as breeding sites for this species.

*Rana* kl. *esculenta* was absent from new beaver ponds but we observed two calling males in two of the largest and fully insolated old beaver ponds app. 1700 m further up the valley. Among the old beaver ponds, *B. bufo* was fairly abundant in the larger, sunny ponds. It was much less common in new beaver ponds and we observed only a few males.

*Alytes obstetricans* was restricted to beaver ponds. While there were no observations of the species in new beaver ponds, we heard up to 20 calling males along slopes opened through tree-cutting by beavers around old ponds. In spring, at least two sunny ponds contained larvae that presumably had hibernated there.

## Discussion

Fifteen years of beaver activities have remarkably increased the habitat heterogeneity by in-

**Table 3.** Number of clutches of *Rana temporaria* in the waters of the study area. 1) 70 out of 85 clutches were found in a 2nd World War bomb crater, see table 1.

| Habitat type | *n* | Waters with clutches | Meter of the valley | *n* clutches | Average per pond | % Waters with clutches |
|---|---|---|---|---|---|---|
| Brook/Floodplain | 11 | 2 | 1600 m | 85 1) | 7.7 | 18.2% |
| Beaver Pond, old | 17 | 10 | 600 m | >1600 | >94.1 | 58.8% |
| Beaver Pond, new | 3 | 3 | 125 m | >800 | >268.0 | 100.0% |
| $\sum$ | 31 | 15 | 2325 m | ~2500 | ~81.0 | 46.9% |

creasing the absolute number of slow flowing or stagnant waters, the absolute area covered by water, and by creating sunny and shallow water stretches with submersed and emergent vegetation. Additionally beavers actively changed the character of the valley by creating clear-cuts in the proximity of their ponds leading to open, sunny plots especially along the steep slopes of the valley.

*Habitat diversification and species diversity of amphibians*

The natural waters of the floodplain in the study area are typical for highlands of Central European floodplains: small and very shallow springs, depressions caused by uprooted trees and small backwaters usually connected to the brook. Generally, in the Eifel and adjacent highlands, only *S. salamandra* and *Rana temporaria*, are known to build up stable populations in these shallow, shady, and cool waters. If some large and fishless waters exist, *Triturus alpestris* and *Triturus helveticus* occur (Dalbeck et al., 1997; Zehlius et al., 2001); newts rarely colonise flowing water (Thiesmeier, 2004). Therefore, the amphibian fauna of the unimpounded part of the study system is typical of extensive areas of the highlands of Germany. Natural waters of the unimpounded part of the valley were obviously not very attractive to amphibians: Half of them were not occupied by any species and three out of four anuran species were missing completely (table 2). No species was restricted to natural waters or exceptionally abundant there.

The increase in habitat heterogeneity caused by beaver damming and logging led to a remarkable increase in species in amphibian communities in the study area. While species living in the unimpounded part of the study area also successfully occupied beaver ponds, additional species were able to colonise the valley. Moreover, the number of species in the beaver ponds was considerably higher than in other water bodies in the study area (fig. 2). No negative effects were detected because of the loss of parts of the unimpounded floodplain.

Species found in beaver ponds, but absent from other sites on the floodplain, depend on beaver-created structures like sunny/warm reproductive sites with submersed vegetation (i.e. *Rana* kl. *esculenta*, see Günther, 1990), large, preferably sunny lentic or slow flowing waters (*B. bufo*, see Günther and Geiger, 1996) or a combination of suitable reproductive waters with adjacent open, fully insolated and ± steep slopes wich are crucial for *Alytes obstetricans* (Eislöffel, 2003; Sowig, Klemens and Laufer, 2003; Weber, 2003). *Rana temporaria* and the two newt species are also known to benefit from the structures mentioned.

*Alytes obstetricans* is of special interest, because in Central Europe the distribution of this species is limited mainly to highland and mountain areas. In our study area, it was the only species restricted to beaver ponds and obviously benefits from open terrestrial habitats created by beavers close to its reproduction sites.

As beavers are able to colonise brooks of less than 1.5 m breadth, beaver-altered landscapes may have been a common habitat for *Alytes obstetricans* in most of its Central European range and formerly enabled the species to colonise large parts of the highlands north of the Alps.

Note that species known from other beaver sites like *Bombina variegata* or *Hyla arborea* had no opportunity to colonise potentially suitable ponds created by beavers within the last 15 years because the remaining populations of these highly endangered species are >10 km away from the study area. Thus, the amphibian communities of valleys impounded by beavers in forested Central European highland areas may become even richer than observed in the study area.

### *Effect of beaver impoundment on stream-breeding amphibians*

In our study area, unimpounded free flowing streams obviously are not optimal habitat for the reproduction of *S. salamandra* which typically breeds in headwaters and springs in Central Europe. This may be due to predation by *Salmo trutta*, which generally prevents successful reproduction of *S. salamandra* (Blau, 2002; Thiesmeier, 2004). Beaver ponds obviously are a suitable substitute for stream habitat probably by providing shallow waters and numerous refuges for salamander larvae. Thus, in our study area, increased amphibian richness due to beaver damming is not at the expense of stream-dwelling amphibians, which appear to benefit from beaver activity as well.

In temperate North America considerable numbers of amphibians, namely salamanders, are more or less strictly associated with free flowing waters (Petranka, 1998), and may therefore not find favourable conditions in beaver ponds for reproduction. In contrast, in tempertate Central Europe, free flowing waters are of very low importance for amphibian reproduction and no species is restricted to flowing water, including *S. salamandra* (Dalbeck et al., 1997; Thiesmeier, 2004).

### *Effects of Salmo trutta on the amphibian community*

Salmonids have the potential to exclude amphibians due to predation of larvae or even adults (e.g. Kabisch and Weiss, 1968). In our study area *Salmo trutta* was present in all beaver ponds (table 2), but no specific data were collected on distributions or density of this species. Therefore the high species diversity and in case of *Rana temporaria* the high number of egg masses in beaver ponds compared to the remaining waters (table 3) is unexpected. The number of egg masses of *Rana temoraria* is clearly higher than known from many other parts of Germany (Schlüpmann and Günther, 1996). Moreover, Elmeros, Madsen and Berthelsen (2003) observed comparable high numbers of clutches of *Rana temporaria* in beaver impoundments in Denmark.

We observed high densities of larvae of *Rana temporaria* in old and new beaver ponds in edges with very shallow water (<5 cm) which are likely avoided by large fish, or in coarse woody debris accumulated in small inlets along the banks of beaver ponds where larvae could evade fish predation. Large areas of shallow water with submersed vegetation, woody debris, – and favourable conditions such as increased water temperature (Skelly and Freidenburg, 2000) and high productivity seem to make beaver impoundments attractive habitat for larval amphibians, as shown for in detail for *Rana sylvatica* in beaver ponds in Canada (Stevens, Paszkowski and Foote, 2006).

### *Woody debris*

A key factor for the suitability of beaver ponds for amphibians may be the large amount of coarse woody debris consisting of wood chips, pieces of bark and twigs actively imported by the beavers from the surroundings which is an unique feature of beaver ponds and dams in general (Rolauffs, Hering and Lohse, 2001). Woody debris in the waters as well as along the shoreline is generally expected to have positive effects on amphibians e.g. by reducing predation risk for larvae and adults, by increasing food availability for larvae due to an increase of surfaces for biofilm development, by providing structure for the attachment of eggs, or by providing potential terrestrial habitats e.g. for hibernation (Tockner et al., 2006).

*Comparison of old and new ponds*

A striking difference between old beaver ponds and the most recently created impoundments is the absence of nearly half of the amphibian species in the new ponds (table 2). We can speculate that the time available for the colonisation of the new ponds was too short for the establishment of populations. Interestingly, *Rana temporaria* was able to colonise the new beaver ponds very quickly. Other studies have reported large numbers of *Rana temporaria* moving to new ponds soon after their emergence (Gollmann et al., 2002).

*Conclusion*

In general, preliminary observations in several other valleys with beaver created wetlands in the vicinity of the study area indicate that caution must be exercised in generalising results from our surveys. For example, *Alytes obstetricans* is missing in valleys apparently looking suitable for this species, and densities of *Triturus* spp. and *Rana* kl. *esculenta* seem to vary considerably between different reaches occupied by beavers for yet unknown reasons. Thus further investigations are needed for a better understanding of the factors affecting the suitability of beaver ponds for individual amphibian species and communities in Central Europe.

However, it is clear that beaver ponds are an important primary habitat of Central European Amphibian species. The reintroduction of beavers has already led to a remarkable increase of suitable habitats for amphibians in highland areas north of the Alps. Furthermore, beaver-created wetlands and clearings have to be considered when assessing patterns of amphibian distribution and habitat requirements in Central Europe. Beavers may play a key role in successful conservation strategies for amphibians in the future.

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